



2016

Dietary Adaptations and Intra- and Interspecific Variation in Dental Occlusal Shape in Hominin and Non-hominin Primates

Kelsey O'Neill

Virginia Commonwealth University

Follow this and additional works at: <https://scholarscompass.vcu.edu/etd>

 Part of the [Biological and Physical Anthropology Commons](#), and the [Biology Commons](#)

© The Author

Downloaded from

<https://scholarscompass.vcu.edu/etd/4626>

This Thesis is brought to you for free and open access by the Graduate School at VCU Scholars Compass. It has been accepted for inclusion in Theses and Dissertations by an authorized administrator of VCU Scholars Compass. For more information, please contact libcompass@vcu.edu.

Dietary Adaptations and Intra- and Interspecific Variation in Dental Occlusal
Shape in Hominin and Non-hominin Primates

A thesis submitted in partial fulfillment of the requirements for the degree of
Master of Science at Virginia Commonwealth University.

by

Kelsey D. O'Neill

Bachelor of Science, Virginia Commonwealth University, 2012

Bachelor of Art, Virginia Commonwealth University, 2012

Bachelor of Art, Virginia Commonwealth University, 2012

Directors:

Amy Rector Verrelli, Ph.D.

Assistant Professor, School of World Studies

AND

Brian Verrelli, Ph.D.

Associate Professor, Department of Biology & VCU Life Sciences

Virginia Commonwealth University

Richmond, Virginia

December, 2016

Acknowledgment

I would like to thank my advisors, Amy Rector Verrelli and Brian Verrelli, for their unwavering support, patience, advice, and help. Without the numerous opportunities Amy provided me and showing me how adventurous it is to be a woman in science, I most certainly would not be completing this Master's in Science. To my committee members, Clint Turbeville and Chris Stevenson, thank you for your guidance and help with edits. I would like to thank Marie Vergamini from the Verrelli Paleoecology Lab for helping me collect data at various museums in South Africa, check my analyses in PAST, and survive the writing process. I am eternally grateful to Lucas Delezene for sharing photos of primate teeth, the Ditsong National museum, and the University of the Witwatersrand for access to their collections.

A very large thank you goes to Dr. Enrique Gerszten for giving me my first lab experience and being a valued mentor. I would also like to thank the patrons of Rosie Connolly's pub for letting me teach them about teeth and hominin evolution, and practicing my presentation skills on them. I would like to thank Mom, without you I literally would not be here writing this, and without you as a role model I would not have such a successful academic career. To my family and friends, thank you for supporting me through the process of graduate school and being a stress venting system. Finally, to my partner, Scott Banning, thanks for supporting and pushing me, challenging my research with though provoking questions, editing proposals and drafts, and listening to the seemingly never ending research stream of consciousness.

TABLE OF CONTENTS

List of Tables	iv
List of Figures	iv
Abstract	v
1. Introduction	1
1.1 <i>Paranthropus robustus</i> and Southern African non-hominin primates of the Plio-Pleistocene	3
1.2 Dental anatomy and characteristics of primate teeth	5
1.3 Teeth as an indicator for paleoecology and adaptations for the mosaic habitats of the Plio-Pleistocene era southern Africa	6
2. Materials and Methods	8
2.1 Primate and hominin sample	8
2.2 Data acquisition	9
2.3 Elliptical Fourier functional analysis	11
2.4 Multivariate analyses	12
3. Results	14
3.1 Variability in all apes: first molars	14
3.2 Variability in all taxa: first molars	16
3.3 Variability in all taxa: third premolars and first molars	19
3.4 Variability in all taxa: anterior and post-canine teeth	22
4. Discussion	25
5. Conclusion	27
6. References cited	28

LIST OF TABLES

1. Dental Specimens Analyzed in this Study	9
2. Abbreviations for Specimen Samples	13
3. <i>P</i> -values for Pairwise Comparisons on Ape Molars	15
4. <i>F</i> -values for Pairwise Comparisons on Ape Molars	15
5. <i>P</i> -values for Pairwise Comparisons of First Molars	17
6. <i>F</i> -values For Pairwise Comparisons of First Molars	17
7. <i>P</i> -values for Pairwise Comparisons of Third Premolars and First Molars	20
8. <i>F</i> -values for Pairwise Comparisons of Third Premolars and First Molars	20
9. <i>P</i> -values for Pairwise Comparisons of All Species and All Teeth	23
10. <i>F</i> -values for Pairwise Comparisons of All Species and All Teeth	24

LIST OF FIGURES

1. <i>Paranthropus robustus</i>	4
2. Occlusal outline	11
3. Principal Component Analysis of molars	16
4. Principal Component Analysis of first molars	19
5. Principal Component Analysis of third premolar and first molar	21

Abstract

DIETARY ADAPTATIONS AND INTRA- AND INTERSPECIFIC VARIATION IN DENTAL OCCLUSAL SHAPE IN HOMININ AND NON-HOMININ PRIMATES

Dental morphology and tooth shape have been used to recreate the dietary adaptations for extinct species, and thus dental variation can provide information on the relationship between fossil species and their paleoenvironments. Variation in living species with known behaviors can provide a baseline for interpreting morphology, and behavior, in the fossil record. Tooth occlusal surface outlines in hominins and non-hominin primates, and other mammals, have been used for assessments of taxonomic significance, with variability often considered as being primarily phylogenetic. Few studies have attempted to assess how diet might influence the pattern of variability in closely related species. Here the occlusal surface shape variability in anterior and post-canine maxillary dentition in primates is measured to assess whether the relationship between diet and variability is consistent.

Data were collected from five non-hominin primates in a range of dietary categories, as well as two hominin species, including the derived *Paranthropus robustus* and a gracile australopith. Mapping a series of 50 sliding semi-landmarks based on 2-D photographs using tpsDig software, occlusal surfaces were outlined. Thereafter, outline shapes were quantified using Elliptical Fourier Functional Analysis, and principle components and multivariate analyses were performed to explore the pattern of intra and interspecific variability in occlusal outlines.

These results suggest that there is not a clear relationship between dietary feeding adaptations for all categories examined and selection for larger premolars and molars, as well as smaller incisors, led to less variation in both anterior and post-canine teeth of the fossil hominin *Paranthropus robustus*.

By Kelsey D. O'Neill, B.A., B.S.

A thesis submitted in partial fulfillment of the requirement for the degree of Master of Science at Virginia Commonwealth University.

Virginia Commonwealth University, 2016.

Directors:

Amy Rector Verrelli, Ph.D.

Assistant Professor, School of World Studies

AND

Brian Verrelli, Ph.D.

Associate Professor, Department of Biology & VCU Life Sciences

1. Introduction

Dental morphology has often been used to understand paleoecology and dietary habits of extinct and living species. Tooth shape, specifically, has been used to recreate the dietary habits of extinct species (Bailey and Lynch, 2005; Bailey, 2004; Brophy, et al., 2014). A lack of abundant fossil specimens creates a difficult problem when reconstructing adaptations and dietary habits in extinct species. However, by placing variation in fossil taxa within the context of known variation and behavior of modern species using a comparative approach (Jolly, 1970), a baseline is provided for interpretation of the paleobiology of extinct species.

When discussing dietary adaptations in the hominin clade, or humans and their ancestors, *Paranthropus* is possibly the single most confusing taxon. Characteristics such as megadontia, chewing musculature, and sagittal crests combine to provide evidence for a highly specialized diet (the composition of which is unclear) (Cerling et al., 2011; Rabenold and Pearson, 2011; Ungar and Sponheimer, 2011). For *Paranthropus robustus*, it is generally accepted that these characteristics, especially increase in post-canine dentition size, were selected for as part of a suite of features related to a specialized diet unique to the *Paranthropus* clade (e.g., Daegling et al., 2011; Strait et al., 2013), but it is unknown how selection affected intraspecific variability in dental size and shape. More broadly, the relationship between diet in primates and variability in dental size and shape has not been fully explored. The overall goal of this research

project will be to explore the influence of selective pressures for dietary adaptations on tooth occlusal surface shape, focusing especially on the selective pressures on *Paranthropus robustus*. From these unknowns, four hypotheses can be derived to explore the influence of diet on variability in dental shape in a sample of primates and fossil hominins, including *Paranthropus robustus*:

Hypothesis 1: There is more variation in anterior teeth compared to post-canine teeth in species with folivorous adaptations, because the anterior teeth do not play a critical role in the mastication process of leafy diets.

Hypothesis 2: There is more variation in post-canine teeth compared to anterior teeth in species with frugivorous adaptations, because the anterior teeth have a critical role in the mastication process of diets composed primarily of ripe fruits.

Hypothesis 3: There is no discernable pattern of variation between anterior and post-canine dentition in omnivorous feeders, because anterior and post-canine teeth both have critical roles in the mastication process of diets that are not clearly associated with one specific food source; therefore selection would not be stronger for one tooth type or another.

Hypothesis 4: *P. robustus* is characterized by statistically significantly more intra-specific variability within anterior dentition compared to posterior dentition, reflecting the influence of selective pressures on post-canine teeth.

1.1. *Paranthropus robustus* and southern African non-hominin primates of the Plio-Pleistocene

During the Plio-Pleistocene there were multiple hominin species that were living across the African continent at the same time. Between 3.0 million years ago (mya) and 1.6 mya there was a minimum of four known sympatric hominin taxa living in eastern and southern Africa. There is evidence to suggest that in eastern Africa at ~3.0 mya *Australopithecus afarensis* and *Keyanthropus platyops* overlapped in time and space; at ~2.5 mya *Paranthropus aethiopicus* and *Australopithecus garhi* lived only kilometers from one another; between ~1.9 and 1.5 mya *Paranthropus boisei* and *Homo erectus* species were both recovered from Olduvai Gorge (Leakey 1959, 1966; Asfaw et al., 1999; Johanson and White, 1979; Leakey et al., 2001; Stanford, 2006). In southern Africa at ~2.5 mya *Paranthropus robustus*, *Australopithecus africanus*, and *Homo habilis* were sympatric and synchronic, and between ~1.9 and 1.0 mya multiple hominin species were likely sympatric, including *Paranthropus robustus*, *Homo erectus*, *Homo habilis*, and *Australopithecus sediba* (Grine et al., 1993; Fuentes et al., 2010; Balter et al., 2012).

Paranthropus robustus lived approximately 1.8 – 1.2 million years ago in southern Africa. This species is likely a descendant of the eastern African species, *Paranthropus aethiopicus*, *P. robustus* is generally characterized with physical features such as wide and flaring zygomatics that extend forward in front of the nasal opening, an orthognathic face, low and receding frontal bone, a frontal trigon on the frontal bone, a sagittal crest in males, post-canine

megadontia, small incisors, and small canines (Figure 1) (Daegling et al., 2011; Strait et al., 2013). This suite of cranial and dental features, shared by all members of the *Paranthropus* clade, is interpreted as an adaptation for hard and/or tough foods, and isotopic evidence suggests a general Paranthropith diet heavy in C₄ grasses/sedges or CAM foods (Lee-Thorp et al., 1994; Sponheimer et al., 2005, 2013; Cerling et al., 2011). In *P. robustus*, details of enamel thickness and microwear (Cerling et al., 2011; Rabenold and Pearson, 2011; Ungar and Sponheimer, 2011) suggest that this southern African member of the clade might be associated with increasing specialization for a dietary resource that required extensive chewing or grinding (Macho and Shimizu, 2009; Sponheimer et al., 2013)

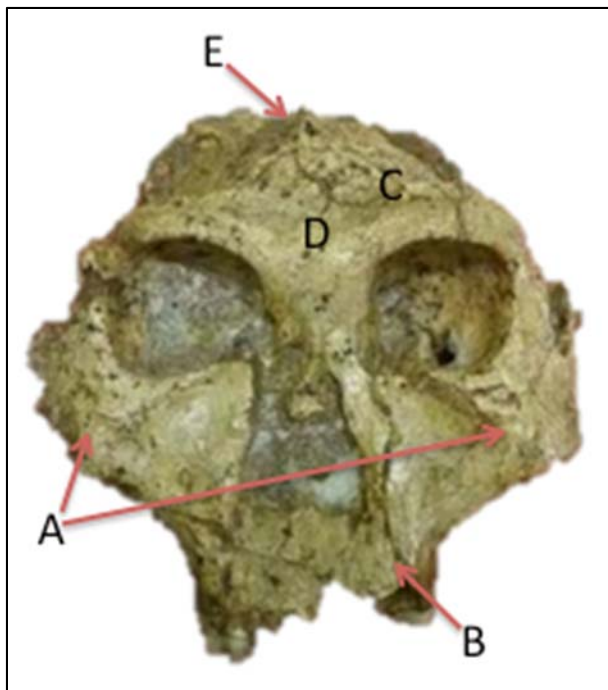


Figure 1: Figure 1: *Paranthropus robustus* (SK-48) characterized by A) wide and flaring zygomatics B) orthognathic face C) low frontal bone D) frontal trigon E) sagittal crest.

1.2 Dental anatomy and characteristics of primate teeth

Fossil and living Old World Monkeys (cercopithecoids) and apes, including humans and their ancestors, all have a generalized dental layout (Fleagle, 2013). Every mouth is divided into four quadrants: upper left, upper right, lower left, lower right. The left and right quadrants are separated along the midline, while the upper and lower quadrants refer to the maxillary and mandibular dentition, respectively. Within each quadrant there are four types of teeth: incisors, canines, premolars, and molars. The incisors and canines grouped together are generally referred to as the anterior teeth; the premolars and molars together have a variety of names such as posterior, post-canine, or cheek teeth; how each tooth type functions during mastication differs depending on the diet (Fleagle, 2013). For adult cercopithecoids and apes the dental formula is 2.1.2.3, reflecting that each species has two incisors (one central and one lateral), one canine, two premolars, and three molars. In primates, including humans, the two permanent premolars in each quadrant are anthropologically defined and named as the third and fourth premolars, due to loss of the ancestral first and second premolars over evolutionary history (White et al., 2011).

There are two main anatomical designations for a tooth, a crown and a root. The crown is the part of the tooth that is visible in the mouth, while the root is embedded in bone under the gum line. The crown is covered in enamel, and under that lies the dentine, which surrounds a pulp cavity. Because enamel contains almost no organic component, tooth crowns preserve well in the fossil record and are often studied in terms of size and shape (Hillson, 2005).

1.3 Teeth as an indicator for paleoecology and adaptations for the mosaic habitats of the Plio-Pleistocene era southern Africa

Variations in dental shape have been interpreted as indicators of primate species adapting to changing food sources as environments and habitats change over time. Food properties that have been associated with specific dental morphologies because of processing requirements include toughness and brittleness (Teaford and Ungar, 2000). Tough foods are those that are difficult to fracture, like insect exoskeletons and leaves (e.g., Fleagle, 2013). These foods are generally sheared between edges of sharp crests on the occlusal surfaces of teeth. On the contrary, brittle foods are those that are easy to fracture but difficult to penetrate to get the internal structure. In order to get the food source, the object is crushed between planar surfaces on the teeth. Planar surfaces tend to have round and flat cusps on teeth and are most often associated with a frugivorous diet (Fleagle, 2013). Though there are some folivorous hominoids, all apes, including hominins, share relatively low-cusped teeth that are efficient at grinding (Kay, 1975; Bailey et al., 2004; Fleagle, 2013).

Tooth size, in both the anterior and post-canine regions of the mouth, is correlated with primate dietary habits. Large incisors are found in species, such as frugivores, that choose foods that are larger in size that need to be processed in bite-sized pieces for efficient mastication (Strait et al., 2009). Smaller incisors are useful in primates that will choose foods that are already bite-sized, such as leaves and insects (Hylander, 1975; Wood and Strait, 2004). Teaford and Ungar (2000) hypothesized that smaller incisors are actually the result of absence of

selection for larger size, suggesting that sizes and shapes of teeth are going to be influenced most by selection when they are integral to the mastication of food resources.

A discussion of biomechanical forces must accompany a discussion of post-canine tooth size. As a generality, the force of a bite should increase as the bite point moves posteriorly during mastication (Wood and Strait, 2004). Following this rule, the premolars should always have a lower bite force than the molars, meaning that there is not biomechanical advantage to chewing with the premolars, unless, as seen in *Paranthropus*, the cranial morphology reflects the enlargement and more anterior placement of the temporalis and masseter muscles, which increases the efficiency of these muscles and incorporates the premolars into the biting/grinding area of the tooth row (Daegling et al., 2011; Strait et al., 2013). The premolars of *Paranthropus* have thus been described as “molarized,” meaning that that they are enlarged in size and *act* like molars in terms of their bite force and grinding efficiency (Strait et al., 2008). Given that premolars and molars in *Paranthropus* are together described as “megadont” or “hypermegadont” due to their large sizes relative to anterior teeth, and together with the derived robust craniofacial morphology result in extreme bite force and grinding efficiency, it is expected that selection on these teeth has resulted in less variability in tooth shape compared to the dentition of other primates relying on diets that do not need such modification of the masticatory apparatus for efficient food processing (Daegling et al., 2011).

2. Materials and methods

2.1 Hominin and non-hominin primate sample

Extant primates species included in this study as a comparative sample include *Gorilla gorilla*, *Pan troglodytes*, and *Papio ursinus*. *Gorilla* and *Pan* are modern apes with primarily folivorous and frugivorous diets, respectively (M'Kirera and Ungar, 2003; Stanford, 2006). *Papio ursinus* is the chacma baboon, and is considered a terrestrial omnivore eating fruits, leaves, underground storage organs, and insects (Williams and Geissler, 2014). These three species provide modern examples of folivores, frugivores, and omnivores that are closely related to the fossil taxa included in this study, and will together provide a baseline for exploring the relationship between diet and dental shape variability in primates. The *Gorilla* and *Pan* specimens are housed at the Powell-Cotton Museum in, Kent, United Kingdom, while the *Papio* specimens are housed at the mammal store collections at the University of the Witwatersrand, Johannesburg, South Africa.

Fossil species included in this study are *Paranthropus robustus*, *Parapapio broomi*, and *Australopithecus afarensis*. *Parapapio* is an extinct baboon genus similar to modern mangabeys distributed in Plio-Pleistocene southern and eastern Africa, with *Pp. broomi* found only in South Africa (Thackeray and Myer, 2004). Exploration of *Pp. broomi* microwear suggests that this species relied on an omnivorous diet similar to modern *Papio* species (Williams and Geissler, 2014). *Australopithecus afarensis* was an east African member of the gracile australopith lineage, which is considered the sister group

to the paranthropith clade (Wood and Lonergan, 2008). Unlike the *Paranthropus* species, this hominin was likely a frugivore with a more flexible diet, and was not characterized by the derived chewing adaptations of *Paranthropus* (Wynn et al., 2016).

Specimens of *Paranthropus robustus*, and *Parapapio broomi* are housed at the Ditsong Museum, Pretoria, South Africa and *Australopithecus afarensis* specimens are housed at the Ethiopia National Museum in Addis Ababa, Ethiopia. All specimens are listed in Table 1, and abbreviations for tooth names are listed in Table 2.

Table 1: Dental samples from hominin and non-hominin specimens analyzed in this study.

Species sampled	Dietary Category	1 st Incisor	3 rd Premolar	1 st Molar	2 nd Molar	3 rd Molar
Non-Hominins						
<i>Pan troglodytes</i>	Frugivore	23	17	17	17	17
<i>Gorilla gorilla</i>	Folivore	24	19	27	29	29
<i>Papio ursinus</i>	Omnivore	4	5	3	0	0
<i>Parapapio broomi</i>	Omnivore	2	3	6	0	0
Hominins						
<i>Paranthropus robustus</i>	Hard- object	2	7	9	4	4
<i>Australopithecus afarensis</i>	Frugivore	0	3	3	0	0

2.2 Data acquisition

Data were collected from photographs of the occlusal surface of each tooth in the analysis. It was preferred to use a right tooth for photographs, however if a left tooth was used, the image was later flipped horizontally in

Adobe Photoshop® to artificially make the tooth a right (Bailey and Lynch, 2005; Brophy et al., 2014; Nova Delgado et al., 2016). Photographs were taken with a digital SLR on macro setting that was leveled and with a tripod and the camera placed directly centered above the tooth, with the occlusal surface visible through the eyepiece. Teeth were arranged and held in place with beanbags, props, and/or modeling clay. A scale bar was placed to the side of each tooth photographed for accuracy. All available teeth for each species were photographed, regardless of their level of attrition, as long as at least 80% of the enamel was visible on the occlusal surface of the tooth. When photographing a tooth, if a tooth was near the 80% mark, it was noted in the study.

The occlusal outlines for this study were drawn and prepared on the digital images using tpsDIG (Rohlf, 2001). There are several ways of designating the occlusal outline of a tooth (Bailey and Lynch, 2005; Delezene and Kimbel, 2011; Clement and Hillson, 2013; Brophy et al., 2014), and in this study occlusal outlines were based on the actual outline of the tooth involved in occlusion instead of the crown outline. This standardized definition of occlusal outline allows for the comparison of individual occlusal surface outlines to each other. There are other methods that compare the outlines to a predetermined shape (typically a circle or oval) in order to record the amount of variation between the shapes (Daegling and Jungers, 2000; Brophy et al., 2014), but in this study the tooth shapes are compared directly to each other. All occlusal outlines began at the most buccomesial point on the tooth, and proceed in a counterclockwise manner. Fifty sliding semi-landmarks were used to complete the occlusal outline

(Figure 2.) creating coordinate data that was imported into PAST v. 3.07 (Hammer et al., 2001) where elliptical Fourier coefficients were obtained for analyses.

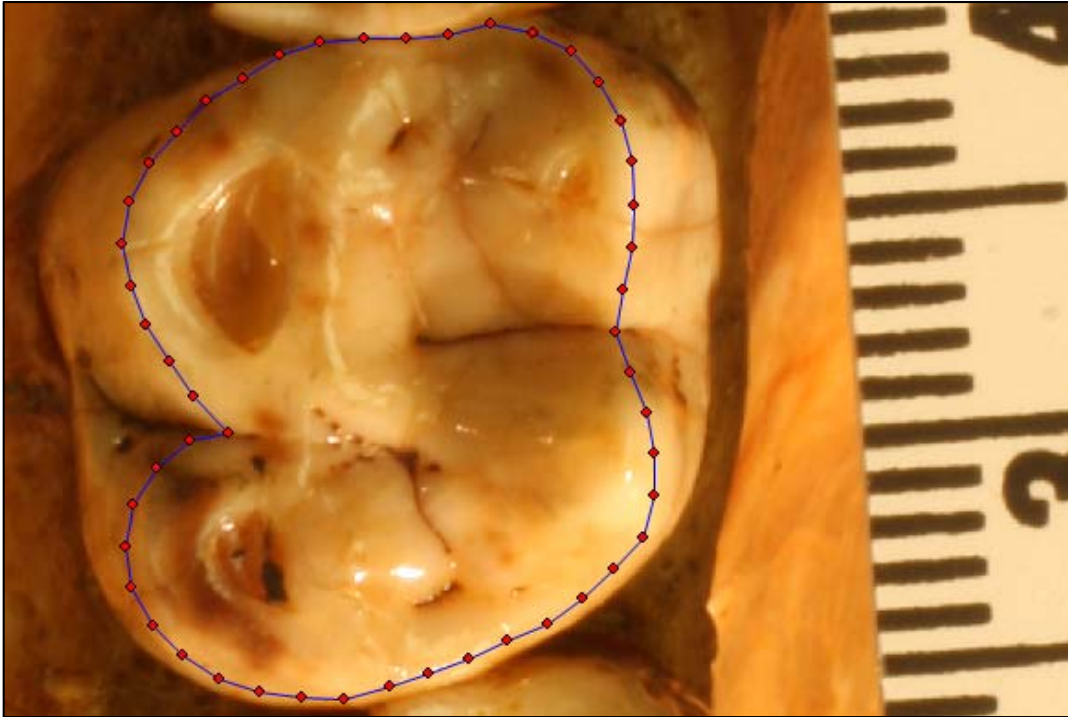


Figure 2: Occlusal outline of 2nd molar with 50 sliding semi-landmarks.

2.3 Elliptical Fourier functional analysis

Elliptical Fourier function analysis (EFFA) is different from traditional Fourier analysis since it does not require points on an outline to be evenly spaced. EFFA uses the landmarks to tightly fit a curved area of irregular morphologies in a two-dimensional coordinate plane (Lestrel, 1974,1989). The curved area is a closed outline that is created by fitting elliptical Fourier function harmonics, which are defined by four elliptic Fourier coefficients. The coefficients derive from x- and y- coordinates that define a shape, acting as a function of distance from the outline. Because each tooth outline was created using 50

points, Fourier analyses were calculated using the recommended $n/2$ harmonics, or 25. Each harmonic uses 4 coefficients, resulting in 200 coefficients used in each multivariate analysis to compare the shapes of teeth. Outlines from each tooth was analyzed separately, and subsequently merged for multivariate analyses to examine the differences in occlusal shape between and among species. In PAST, the EFA simultaneously will run a generalized Procrustes analysis in which the size of the shape is removed from the calculation (Rohlf and Slice, 1990; Rohlf, 1999; Adams et al., 2004).

2.4 Multivariate analyses

Two sets of multivariate analyses were used to assess the variability in tooth shape between and among the species in the analysis. Each analysis was based on the first 200 of elliptical Fourier coefficients for each specimen (which are associated with the first 25 harmonics calculated for each tooth). The differences in inter- and intraspecies tooth shape were first assessed using a one-way non-parametric permutational multivariate analysis of variance (PERMANOVA) in PAST v. 3.07 (Hammer et al. 2001), which tests the homogeneity of multivariate dispersions within groups on the basis of similarity and the significance of a p -value for between group comparisons. A non-parametric analysis of variance is appropriate in this study because it is unlikely that the data are normally distributed. A bootstrapping procedure of 9999 iterations was done simultaneously with the PERMANOVA in PAST. A pairwise comparison is considered statistically significant when $p < 0.05$, and F -values are

reported to describe the relative differences between the groups. A pairwise comparison that showed greater interspecific occlusal shape variation would have higher *F*-values. Once the PERMANOVA data were calculated, a principal component analysis (PCA) was performed on the total sample of teeth from all species to demonstrate the interspecific and intraspecific variation in the occlusal outline shapes.

The PCA described the significant amount of inter- and intraspecific variation within and between the tooth shapes. A PCA is a way to visualize the tooth-shape variation among and within the species and samples to one another (Johnson and Wichern, 2007). The first two principal components constructed by the PCA were plotted to visualize how the variation within the relevant samples are distributed. The multivariate analyses were calculated with four different samples: 1) the first, second, and third molars of all apes to explore the baseline variability within apes with different diets and *Paranthropus*, 2) the first molars of all taxa to compare the variability within the baseline ape sample to the fossil and living baboon as well as *Australopithecus afarensis*, 3) the third premolars and first molars of all taxa to explore the effects of molarization and function on premolars in the various taxa, and 4) the anterior teeth of all taxa, as represented by incisors, and the post-canine teeth included third premolars and molars to directly compare the variability in anterior compared to posterior teeth.

Table 2: Abbreviations for specimen samples.

Abbreviation:	Specimen:
GI ¹	<i>Gorilla gorilla</i> first incisor
PI ¹	<i>Pan troglodytes</i> first incisor
UI ¹	<i>Papio ursinus</i> first incisor

RI ¹	<i>Paranthropus robustus</i> first incisor
AI ¹	<i>Australopithecus afarensis</i> first incisor
BI ¹	<i>Parapapio broomi</i> first incisor
GP ³	<i>Gorilla gorilla</i> third premolar
PP ³	<i>Pan troglodytes</i> third premolar
UP ³	<i>Papio ursinus</i> third premolar
RP ³	<i>Paranthropus robustus</i> third premolar
AP ³	<i>Australopithecus afarensis</i> third premolar
BP ³	<i>Parapapio broomi</i> third premolar
GM ¹	<i>Gorilla gorilla</i> first molar
PM ¹	<i>Pan troglodytes</i> first molar
UM ¹	<i>Papio ursinus</i> first molar
RM ¹	<i>Paranthropus robustus</i> first molar
AM ¹	<i>Australopithecus afarensis</i> first molar
BM ¹	<i>Parapapio ursinus</i> first molar
GM ²	<i>Gorilla gorilla</i> second molar
PM ²	<i>Pan troglodytes</i> second molar
UM ²	<i>Papio ursinus</i> second molar
RM ²	<i>Paranthropus robustus</i> second molar
AM ²	<i>Australopithecus afarensis</i> second molar
BM ²	<i>Parapapio broomi</i> second molar
GM ³	<i>Gorilla gorilla</i> third molar
PM ³	<i>Pan troglodytes</i> third molar
UM ³	<i>Papio ursinus</i> third molar
RM ³	<i>Paranthropus robustus</i> third molar
AM ³	<i>Australopithecus afarensis</i> third molar
BM ³	<i>Parapapio broomi</i> third molar

3. Results

3.1 Variability in all apes: first molars

The PERMANOVA comparing the variation in ape molars with *Paranthropus* resulted in an overall p -value of 0.0001 and a F -value of 11.61. Results of pairwise comparisons are reported in Table 3. Pairwise F -values are reported in Table 4, and show that there is greater interspecific variability between the RM³ and the PM³ ($F = 37.54$, $p = 0.0001$), and least interspecific

variability between GM¹ and PM¹ ($F = 1.35$, $p = 0.2132$). For all taxa, at least one intraspecific pairwise comparison was found to be significantly different except for within *Paranthropus*.

Table 3: P-values for pairwise comparisons on ape molars.

	RM ¹	RM ²	RM ³	GM ¹	GM ²	GM ³	PM ¹	PM ²	PM ³
RM ¹		0.9105	0.5107	0.0005	0.0001	0.0001	0.0017	0.0001	0.0001
RM ²	0.9105		0.8038	0.0041	0.0014	0.0002	0.0092	0.0003	0.0001
RM ³	0.5107	0.8038		0.0004	0.0003	0.0001	0.0027	0.0002	0.0001
GM ¹	0.0005	0.0041	0.0004		0.0061	0.0002	0.2132	0.0001	0.0001
GM ²	0.0001	0.0014	0.0003	0.0061		0.2296	0.0795	0.0304	0.0027
GM ³	0.0001	0.0002	0.0001	0.0002	0.2296		0.0074	0.0473	0.0015
PM ¹	0.0017	0.0092	0.0027	0.2132	0.0795	0.0074		0.0119	0.0025
PM ²	0.0001	0.0003	0.0002	0.0001	0.0304	0.0473	0.0119		0.2327
PM ³	0.0001	0.0001	0.0001	0.0001	0.0027	0.0015	0.0025	0.2327	

Table 4: F-values for pairwise comparisons on ape molars.

	RM1	RM2	RM3	GM1	GM2	GM3	PM1	PM2	PM3
RM1		0.19	0.66	11.83	20.29	34.03	10.67	31.34	35.16
RM2	0.19		0.37	7.27	12.08	22.12	6.85	21.93	26.36
RM3	0.66	0.37		11.16	16.50	30.20	10.33	30.42	37.54
GM1	11.83	7.27	11.16		6.77	13.73	1.48	14.64	18.60
GM2	20.29	12.08	16.50	6.77		1.35	2.71	3.73	6.49
GM3	34.03	22.12	30.20	13.73	1.35		5.52	2.87	6.19
PM1	10.67	6.851	10.33	1.48	2.71	5.52		5.39	6.77
PM2	31.34	21.93	30.42	14.64	3.73	2.87	5.39		1.31
PM3	35.16	26.36	37.54	18.60	6.49	6.19	6.77	1.31	

The M¹, M², and M³ PCA of the entire ape collection including *Paranthropus* result in the first two PCs that explain 86.3% of the total variance in the sample (PC1: 69.6%, PC2: 16.7%), as shown in Figure 3. The *Paranthropus robustus* first, second, and third molars are all distributed on the negative scores of the PC1 axis, closest in morphospace to the majority of the three *Gorilla gorilla* molars. The *P. robustus* M¹s are all located along the positive scores of PC2, while the M² and M³ samples are distributed between both positive and negative

scores of PC2. The M² and M³ samples are in close proximity to all three *Gorilla* molars and the M¹ of *Pan*.

The *G. gorilla* first, second, and third molars are distributed widely along the negative and positive axes of both PC1 and PC2. The positive PC1 and PC2 scores overlap widely with the all three *Pan* molars, while the *Gorilla* negative PC1 and positive PC2 scores are in close proximity to the *P. robustus* samples and slightly overlap with the *Pan* samples. While there is some overlap between the shape space described by *Gorilla* and *Pan* molars, *Paranthropus* molars occupy a unique area of the figure with less variability between them.

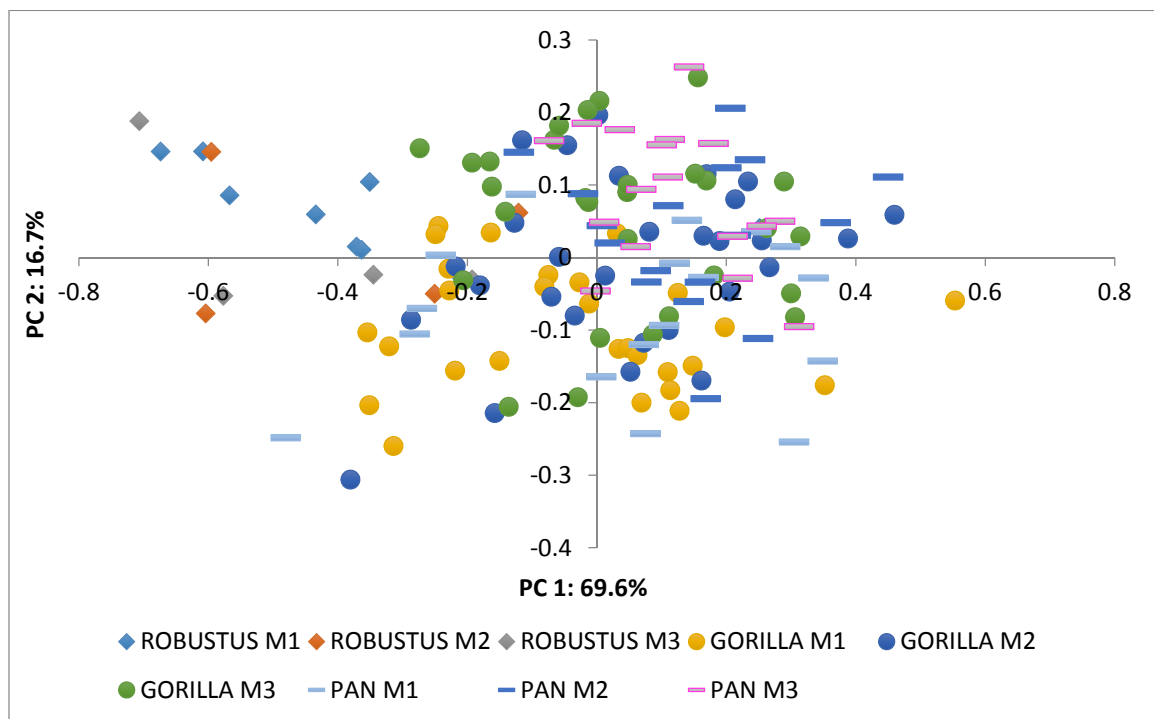


Figure 3: Principal component analysis of modern ape and *Paranthropus* M¹, M², and M³ shape variability.

3.2 Variability in all taxa: first molars

The PERMANOVA test resulted in an overall *p*-value of 0.0021 and a *F*-value of 3.46. Both values support evidence for significant differences within the

groups in the sample. Since only M¹ is considered in this sample, only interspecific variation is examined. The *p*-values and *F*-values for the pairwise results are recorded in Tables 5 and 6, showing that samples with most interspecific variability are between RM¹ and GM¹ ($F = 11.83$, $p = 0.0003$). The samples with the least interspecific variability are UM¹ and BM¹ ($F = 0.19$, $p = 0.9164$). The variation within RM¹ is significantly different from the first molars of the other ape taxa, but not when compared to *Australopithecus* or the living and fossil baboons. The latter three taxa are also not significantly different from each other in terms of the variation in tooth shape.

Table 5: *P*-values for pairwise comparisons of first molars.

	RM ¹	GM ¹	PM ¹	AM ¹	UM ¹	BM ¹
RM ¹		0.0003	0.0014	0.8062	0.0605	0.1344
GM ¹	0.0003		0.2111	0.0248	0.3720	0.2944
PM ¹	0.0014	0.2111		0.0237	0.3070	0.2082
AM ¹	0.8062	0.0248	0.0237		0.2013	0.3250
UM ¹	0.0605	0.3720	0.3070	0.2013		0.9164
BM ¹	0.1344	0.2944	0.2082	0.3250	0.9164	

Table 6: *F*-values for pairwise comparisons of first molars.

	RM1	GM1	PM1	AM1	UM1	BM1
RM1		11.83	10.67	0.28	3.08	2.21
GM1	11.83		1.48	4.99	0.82	1.06
PM1	10.67	1.48		4.89	1.09	1.54
AM1	0.28	4.99	4.89		2.22	1.07
UM1	3.08	0.82	1.09	2.22		0.19
BM1	2.21	1.06	1.54	1.07	0.19	

In Figure 4, the PCA analyzing M¹s from all taxa in the sample results in the first two PCs that together explain 86.99% of the total variance in the sample (PC1: 76.72%, PC2: 10.27%). The RM¹ is distributed primarily on the negative PC1 axis, with only one specimen with a positive score. For PC2, the RM¹

specimens are all distributed on the positive axis, in close proximity to the GM¹, AM¹, and PM¹ specimens.

The GM¹ samples are distributed across the entire figure, and overlap considerably with the PM¹ and UM¹. The BM¹ sample is also distributed widely across the axes. The PM¹ samples are distributed across the positive and negative PC1 and PC2 axes, overlapping with the GM¹, though most of the PM¹ specimens are located on the positive PC1 and split between the positive and negative PC2 scores. There are only three UM¹ specimens, and they are widely distributed. The AM¹ samples are solely on the negative PC1 axis, and on both the positive and negative PC2 axes. AM¹ is in closest proximity to the RM¹ and the GM¹ samples. While there is significant overlap between *Gorilla* and *Pan* specimens, again *Paranthropus* occupies mostly unique morphospace. The *Australopithecus* specimens are also distributed in this area of the figure, suggesting shape similarities between the two hominin species to the exclusion of the other taxa.

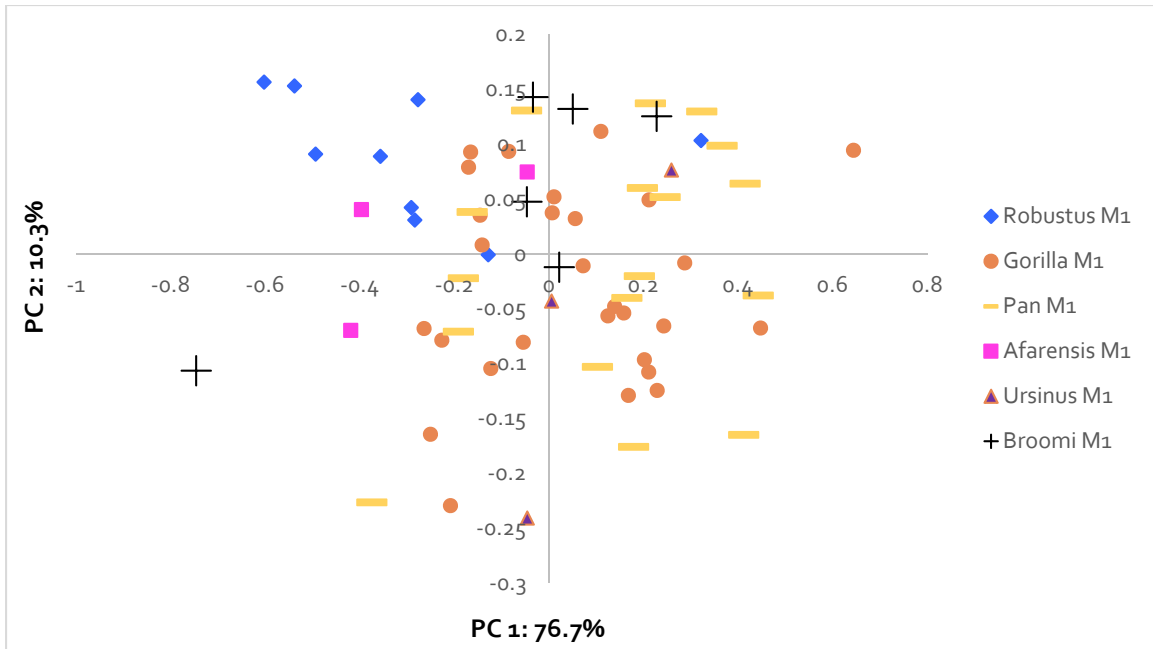


Figure 4: Principal component analysis of all specimen first molar variability.

3.3 Variability in all taxa: third premolars and first molars

Overall significant variability between P³ and M¹ is reported by the PERMANOVA by a p -value of 0.0001 and a F -value of 7.45. The pairwise comparison p -values are reported in Table 7. The table shows that overall the amount of variation sampled by RP³ is significantly different from all other samples. Aside from the RP³ samples, the most intraspecific variable sample is the GP³ to GM¹ comparison ($p = 0.0001$), and the most interspecific variable samples are the PP³, GM¹ and GP³, PM¹ comparisons ($p = 0.0001$). The p -values also report that the least significantly variable samples are UM¹ and BM¹ ($p = 0.9119$). Another large p -value reported is that for RM¹ and AM¹ ($p = 0.8066$). The pair-wise F -values report that the greatest intraspecific variation is in GP³, GM¹ ($F = 47.38$) and interspecific variation is GP³, PM¹ ($F = 37.86$). The lowest intraspecific variation is AP³, AM¹ ($F = 1.20$). The lowest interspecific

variation is reported BM¹, UM¹ ($F = 0.19$), with the next lowest being BP³, UP³ ($F = 0.23$).

Table 7: P-values for pairwise comparisons of third premolars and first molars.

	RM ¹	GM ¹	PM ¹	AM ¹	UM ¹	BM ¹	AP ³	GP ³	BP ³	UP ³	PP ³	RP ³
RM ¹		0.0003	0.0016	0.8066	0.0694	0.1350	0.3062	0.0319	0.3594	0.7255	0.2718	0.0021
GM ¹	0.0003		0.2077	0.0232	0.3732	0.3020	0.0009	0.0001	0.0003	0.0009	0.0001	0.0001
PM ¹	0.0016	0.2077		0.0262	0.3139	0.2059	0.0039	0.0001	0.0028	0.0036	0.0018	0.0034
AM ¹	0.8066	0.0232	0.0262		0.2027	0.3288	0.4952	0.1591	0.2990	0.5835	0.5914	0.0258
UM ¹	0.0694	0.3732	0.3139	0.2027		0.9119	0.0987	0.0067	0.0967	0.1245	0.1050	0.024
BM ¹	0.1350	0.302	0.2059	0.3288	0.9119		0.1508	0.0034	0.1556	0.1788	0.1198	0.011
AP ³	0.3062	0.0009	0.0039	0.4952	0.0987	0.1508		0.7107	0.7004	0.7823	0.2129	0.0173
GP ³	0.0319	0.0001	0.0001	0.1591	0.0067	0.0034	0.7107		0.6233	0.3007	0.0037	0.0001
BP ³	0.3594	0.0003	0.0028	0.299	0.0967	0.1556	0.7004	0.6233		0.7689	0.2068	0.0077
UP ³	0.7255	0.0009	0.0036	0.5835	0.1245	0.1788	0.7823	0.3007	0.7689		0.3151	0.0137
PP ³	0.2718	0.0001	0.0018	0.5914	0.1050	0.1198	0.2129	0.0037	0.2068	0.3151		0.0039
RP ³	0.0021	0.0001	0.0034	0.0258	0.024	0.011	0.0173	0.0001	0.0077	0.0137	0.0039	

Table 8: F-values for pairwise comparisons of third premolars and first molars.

	RM ¹	GM ¹	PM ¹	AM ¹	UM ¹	BM ¹	AP ³	GP ³	BP ³	UP ³	PP ³	RP ³
RM ¹		11.83	10.67	0.28	3.08	2.21	1.17	4.18	0.94	0.33	1.24	12.37
GM ¹	11.83		1.48	4.99	0.82	1.06	12.11	47.38	11.40	9.91	10.68	14.44
PM ¹	10.67	1.48		4.89	1.09	1.54	10.50	37.86	10.53	8.64	8.83	7.02
AM ¹	0.28	4.99	4.89		2.22	1.07	1.20	1.95	1.27	0.38	0.41	7.87
UM ¹	3.08	0.82	1.09	2.22		0.19	4.63	8.39	5.58	2.39	2.36	4.96
BM ¹	2.21	1.063	1.54	1.07	0.19		2.60	9.48	2.31	1.84	2.28	4.44
AP ³	1.17	12.11	10.50	1.20	4.63	2.60		0.28	0.54	0.23	1.59	10.15
GP ³	4.18	47.38	37.86	1.95	8.39	9.48	0.28		0.38	1.11	8.36	27.76
BP ³	0.94	11.40	10.53	1.27	5.58	2.31	0.54	0.38		0.23	1.54	13.06
UP ³	0.33	9.91	8.64	0.38	2.39	1.84	0.23	1.11	0.23		1.02	8.07
PP ³	1.24	10.68	8.83	0.41	2.36	2.28	1.59	8.36	1.54	1.02		8.96
RP ³	12.37	14.44	7.02	7.87	4.96	4.44	10.15	27.76	13.06	8.07	8.96	

The P³ and M¹ PCA of the entire sample results in the first two PCs that explain 87.65% of the total variance (PC1: 71.42%, PC2: 16.23%), as shown in Figure 5. There is significant overlap of taxonomic samples found across the PC1 and PC2 axes. When the shapes of both third premolars and first molars are considered together on these axes, the *Paranthropus robustus* P³ primarily are located on the positive PC1 axis again in a morphospace that is mostly separate

from the other taxa. There is little to no overlap with the RM¹, which are primarily located on the negative PC1 axis and only one with a positive PC2 score.

Considering results of the PERMANOVA and PCA together, it can be interpreted that the least amount of variability in the sample is found within the *Paranthropus* P³s.

Generally, the shapes of the P³s and M¹s of all the taxa, including the hominins, do not overlap with each other, suggesting that there are shape differences between these teeth.

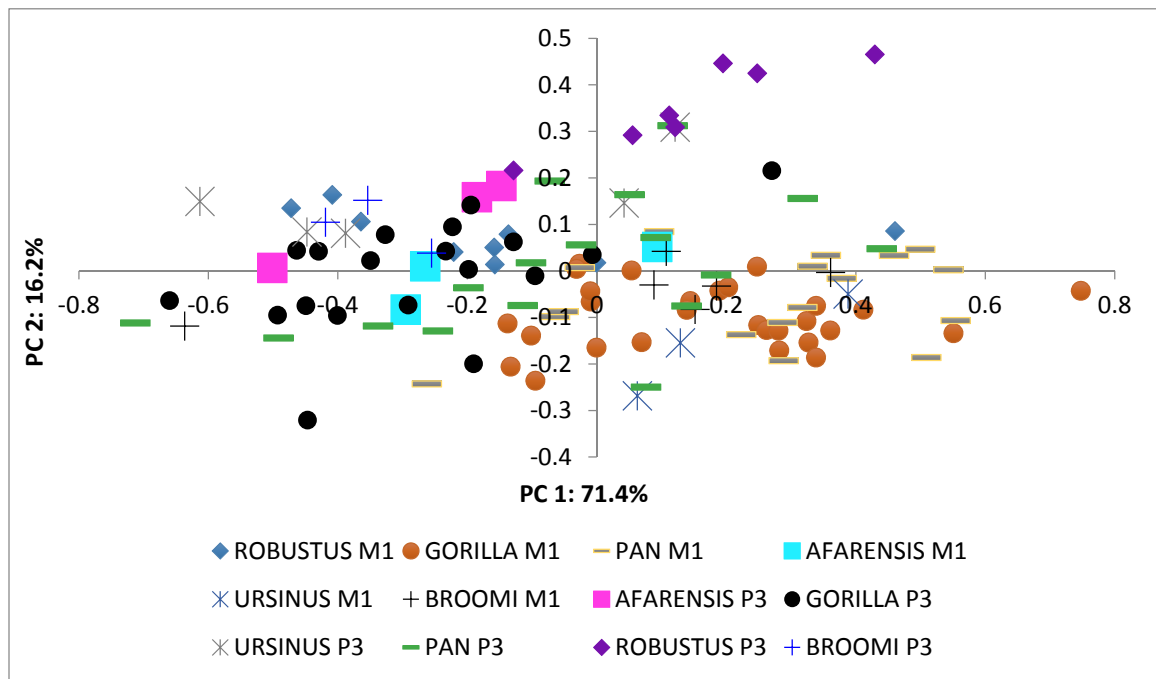


Figure 5: Principal component analysis of all specimen third premolar and first molar variability.

3.4 Variability in all taxa: anterior and post-canine teeth

When the variability within incisors is compared to the post-canine teeth, the overall p -value is 0.0001. Pairwise comparison p -values and F -values are reported in Tables 9 and 10, and these values suggest that the most variability in

the entire sample is found in the incisors of *Pan* and *Gorilla*. When the variation within these incisors is compared to the post-canine teeth, they are also found to be significantly different. *Paranthropus* incisors are less variable than either of the living ape taxa.

Table 9: P-values for pairwise comparisons of all species and all teeth

	RM ¹	GM ¹	PM ¹	AM ¹	UM ¹	BM ¹	GI ¹	BI ¹	RI ¹	UI ¹	PI ¹	AP ³	GP ³	BP ³	UP ³	PP ³	RP ³
RM ¹		0.0002	0.0017	0.8092	0.0624	0.1324	0.0001	0.0164	0.0181	0.0015	0.0001	0.3104	0.0287	0.3609	0.7257	0.2653	0.0032
GM ¹	0.0002		0.2052	0.023	0.3748	0.3033	0.0001	0.0022	0.003	0.0001	0.0001	0.001	0.0001	0.0004	0.0018	0.0003	0.0002
PM ¹	0.0017	0.2052		0.0254	0.3101	0.2071	0.0001	0.006	0.005	0.0001	0.0001	0.0045	0.0001	0.0022	0.0045	0.0016	0.0021
AM ¹	0.8092	0.023	0.0254		0.2035	0.3228	0.0001	0.0977	0.1009	0.0286	0.0004	0.5085	0.158	0.3	0.5874	0.6028	0.023
UM ¹	0.0624	0.3748	0.3101	0.2035		0.9175	0.0003	0.0993	0.1013	0.0306	0.0002	0.1039	0.0063	0.101	0.1224	0.1066	0.0266
BM ¹	0.1324	0.3033	0.2071	0.3228	0.9175		0.0001	0.0356	0.033	0.0043	0.0001	0.1574	0.0019	0.1596	0.1746	0.118	0.0119
GI ¹	0.0001	0.0001	0.0001	0.0001	0.0003	0.0001		0.3239	0.0038	0.0481	0.0036	0.0022	0.0001	0.0003	0.0003	0.0001	0.0001
BI ¹	0.0164	0.0022	0.006	0.0977	0.0993	0.0356	0.3239		0.3376	0.2067	0.2461	0.1043	0.0045	0.0993	0.0462	0.0062	0.0259
RI ¹	0.0181	0.003	0.005	0.1009	0.1013	0.033	0.0038	0.3376		0.1366	0.0032	0.0938	0.0042	0.0912	0.0473	0.0077	0.0255
UI ¹	0.0015	0.0001	0.0001	0.0286	0.0306	0.0043	0.0481	0.2067	0.1366		0.0142	0.0308	0.0002	0.027	0.0074	0.0004	0.0036
PI ¹	0.0001	0.0001	0.0001	0.0004	0.0002	0.0001	0.0036	0.2461	0.0032	0.0142		0.0002	0.0001	0.0007	0.0001	0.0001	0.0001
AP ³	0.3104	0.001	0.0045	0.5085	0.1039	0.1574	0.0022	0.1043	0.0938	0.0308	0.0002		0.7118	0.6931	0.7887	0.2032	0.0152
GP ³	0.0287	0.0001	0.0001	0.158	0.0063	0.0019	0.0001	0.0045	0.0042	0.0002	0.0001	0.7118		0.6158	0.2994	0.0034	0.0001
BP ³	0.3609	0.0004	0.0022	0.3	0.101	0.1596	0.0003	0.0993	0.0912	0.027	0.0007	0.6931	0.6158		0.7628	0.2169	0.0091
UP ³	0.7257	0.0018	0.0045	0.5874	0.1224	0.1746	0.0003	0.0462	0.0473	0.0074	0.0001	0.7887	0.2994	0.7628		0.3276	0.0147
PP ³	0.2653	0.0003	0.0016	0.6028	0.1066	0.118	0.0001	0.0062	0.0077	0.0004	0.0001	0.2032	0.0034	0.2169	0.3276		0.0039
RP ³	0.0032	0.0002	0.0021	0.023	0.0266	0.0119	0.0001	0.0259	0.0255	0.0036	0.0001	0.0152	0.0001	0.0091	0.0147	0.0039	

Table 10: F-values for pairwise comparisons of all species and all teeth.

	RM ¹	GM ¹	PM ¹	AM ¹	UM ¹	BM ¹	GI ¹	BI ¹	RI ¹	UI ¹	PI ¹	AP ³	GP ³	BP ³	UP ³	PP ³	RP ³
RM ¹		11.83	10.67	0.28	3.08	2.21	18.35	17.02	20.18	24.48	64.92	1.17	4.18	0.94	0.33	1.24	12.37
GM ¹	11.83		1.48	4.99	0.82	1.06	69.36	36.41	30.18	52.87	198.10	12.11	47.38	11.40	9.91	10.68	14.44
PM ¹	10.67	1.48		4.89	1.09	1.54	44.67	27.18	21.50	35.49	131.20	10.50	37.86	10.53	8.64	8.83	7.02
AM ¹	0.28	4.99	4.89		2.22	1.07	6.92	15.41	24.84	13.53	29.21	1.20	1.95	1.27	0.38	0.41	7.87
UM ¹	3.08	0.82	1.09	2.22		0.19	7.72	14.31	16.87	11.88	31.99	4.63	8.39	5.58	2.39	2.36	4.96
BM ¹	2.21	1.063	1.54	1.07	0.19		13.57	9.02	8.53	12.32	45.05	2.60	9.48	2.31	1.84	2.28	4.44
GI ¹	18.35	69.36	44.67	6.92	7.72	13.57		1.17	3.75	3.60	7.77	5.16	31.16	5.96	8.90	34.50	17.18
BI ¹	17.02	36.41	27.18	15.41	14.31	9.02	1.17		7.27	2.21	1.31	9.56	14.99	21.02	7.74	12.73	15.67
RI ¹	20.18	30.18	21.50	24.84	16.87	8.53	3.75	7.27		4.61	11.25	19.10	20.61	61.18	10.32	12.42	12.53
UI ¹	24.48	52.87	35.49	13.53	11.88	12.32	3.60	2.21	4.61		4.68	11.05	33.61	15.03	12.24	23.52	12.95
PI ¹	64.92	198.10	131.20	29.21	31.99	45.05	7.77	1.31	11.25	4.68		21.18	94.57	27.39	32.11	87.39	49.06
AP ³	1.173	12.11	10.50	1.20	4.626	2.60	5.16	9.56	19.10	11.05	21.18		0.28	0.54	0.23	1.59	10.15
GP ³	4.18	47.38	37.86	1.95	8.39	9.48	31.16	14.99	20.61	33.61	94.57	0.28		0.38	1.11	8.36	27.76
BP ³	0.94	11.40	10.53	1.27	5.58	2.31	5.96	21.02	61.18	15.03	27.39	0.54	0.38		0.23	1.54	13.06
UP ³	0.33	9.91	8.64	0.38	2.39	1.84	8.90	7.74	10.32	12.24	32.11	0.23	1.11	0.23		1.02	8.07
PP ³	1.24	10.68	8.83	0.41	2.36	2.28	34.50	12.73	12.42	23.52	87.39	1.59	8.36	1.54	1.02		8.96
RP ³	12.4	14.44	7.02	7.87	4.96	4.44	17.18	15.67	12.53	12.95	49.06	10.15	27.76	13.06	8.07	8.96	

4. Discussion

Results of the analyses did not support the first hypothesis stating that the anterior teeth of folivorous species are expected to be more variable than posterior teeth. The folivorous representative (*Gorilla gorilla*) showed the same degree of variation in anterior dentition and first molars as that of the *Pan* sample. The only tooth that resulted in a statistically significant comparison was the third premolar, for which the *Gorilla* sample has more variation compared with other species, including *Pan*.

Results also did not support the second hypothesis that the frugivorous species would be characterized by more variation in the post-canine teeth. Tutin and Fernandez (1992) found the diets of sympatric *G. gorilla* and *P. troglodytes* in a reserve in Gabon overlapped in terms of food items with gorillas choosing foods usually associated with chimps 73% of the time, and chimpanzees choosing gorilla food items 57% of the time. This dietary overlap and flexibility is most likely to happen in times of primary food resource scarcity, thus making species choose their 'fallback' foods for survival (Tutin and Fernandez, 1992). Reliance on fallback foods and dietary flexibility might limit the amount of selection on tooth shape variability, resulting in similar variation in *Gorilla* and *Pan* anterior and posterior teeth.

The data did support the third hypothesis that omnivorous feeders would have no discernable pattern of variation between anterior and post-canine teeth. The variability in *Pp. broomi* and *P. ursinus* first molars were not significantly different compared to any other first molars or each other. This is unsurprising

considering how closely related these two baboon taxa are, and that the molar occlusal surface morphology of papionins is the derived bilophodonty, which is well adapted for a folivorous diet (Fleagle, 2013). This morphological adaptation does not prevent cercopithecoids, especially the papionins, from having a wide ranging (i.e. omnivorous) diet (Wood and Strait, 2004), but does evidently result in very similar and predictable molar shapes between the species. The *Pp. broomi* first incisors were not significantly different compared to first incisors of any other taxa, while those of *P. ursinus* were only significantly variable when compared with the *P. troglodytes* first incisors; this significance was a result of high variability in *Pan* incisors.

The analyses of extant primates provides a baseline of variability with which to compare the variability in *Paranthropus* dentition. In all analyses, including anterior and posterior teeth, *Paranthropus* was found to be significantly different in terms of tooth shape variability compared with many other taxa. In terms of shape and variability, *Paranthropus* is most similar to *Australopithecus afarensis*, but the variation in incisors and third premolars of *Paranthropus* was significantly different compared with all other teeth from all other taxa because the variation within *Paranthropus* teeth was very small, just as the variability within *Paranthropus* molars was also very low. This pattern can be interpreted for both anterior and posterior teeth of *Paranthropus* as suggesting that these teeth underwent more selective pressures than those of the other taxa in the analyses, especially *Gorilla* and *Pan*, and that the fourth hypothesis in this study is partly supported. While it was expected to find low variability in *Paranthropus* molars

and premolars as they became molarized, it also was unexpected to also find that anterior teeth of *Paranthropus* are also among the least variable in the sample. The molarization of the *Paranthropus* premolars to include them as functional molars for chewing and grinding, along with the inflation of the molars themselves, was associated with reduction in anterior teeth as well.

5. Conclusion

Variation in the occlusal shape of anterior and posterior teeth in primate dentition has been interpreted as under the influence of selective pressures for dietary adaptations (Teaford and Ungar, 2000), and the molarized premolars and megadont molars of *Paranthropus robustus*, along with other derived craniofacial morphology associated with hard object chewing or grinding, have been hypothesized as the most extreme example of this. Results of the current study indicate that *Paranthropus robustus* does not show high levels of inter- and intraspecific variation in the shape of anterior and posterior teeth compared with living apes, and that selection for larger premolars and molars, as well as smaller incisors, led to less variation in both incisors and post-canine teeth. When considering the extinction of the *Paranthropus* clade, what is most often invoked is hyperspecialization to a hard object diet that must have disappeared as paleohabitats changed (Wood and Strait, 2004). The results of this study support the uniquely specialized way in which *Paranthropus* dentition was derived and linked them to their paleoecological contexts.

6. References cited

- Adams, D.C., Rohlf, F.J., Slice, D.E., 2004. Geometric morphometric: Ten years of progress following the 'revolution'. *Italian Journal of Zoology*. 71, 5–16.
- Anderson, M. J., 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology*. 26, 32–46.
- Asfaw, B., White, T., Lovejoy, O., Latimer, B., Simpson, S., Suwa, G. 1999. *Australopithecus garhi*: A new species of early hominin from Ethiopia. *Science*. 284, 629–635.
- Bailey, S.E., 2004. A morphometric analysis of maxillary molar crowns of Middle-Late Pleistocene hominins. *Journal of Human Evolution*. 47, 183–98.
- Bailey, S.E., Pilbrow, V.C., Wood, B.A. 2004. Interobserver error involved in independent attempts to measure cusp base areas of *Pan* M¹s. *Journal of Anatomy*. 205, 323–331.
- Bailey, S.E., Lynch, J.M., 2005. Diagnostic differences in mandibular p4 shape between Neanderthals and anatomically modern humans. *American Journal of Physical Anthropology*. 126, 268 – 277.
- Balter, V., Braga, J., Télouk, P., Thackeray, J.F. 2012. Evidence for dietary change but not landscape use in South African early hominins. *Nature*. 489, 558–560.
- Brophy, J.K., de Ruiter, D.J., Athreya, S., DeWitt, T.J., 2014. Quantitative morphological analysis of bovid teeth and implications for paleoenvironmental reconstruction of Plovers Lake, Gauteng Province, South Africa. *Journal of Archaeological Science*. 41, 376–388.
- Cerling, T.E., Mbuya, E., M'Kirera, F.M., Manthi, F.K., Grine, F.E., Leakey, M.G., Sponheimer, M., Uno, K.T., 2011. Diet of *Paranthropus boisei* in the early Pleistocene of East Africa. *Proceedings of the National Academy of Sciences*. 108, 9337–9341.
- Clement, A.F., Hillson, S.W., 2012. Intrapopulation variation in macro tooth wear patterns—a case study from Igloodik, Canada. *American Journal of Physical Anthropology*. 149, 517–524.
- Daegling, D.J., Jungers, W.L., 2000. Elliptical Fourier analysis of symphyseal shape in great ape mandibles. *Academic Press Journal of Human Evolution*. 39, 107–122.
- Daegling, D.J. McGraw, W.S., Ungar, P.S., Pampush, J.D., Vick, A.E., Bitty, E.A.,

2011. Hard-object feeding in Sooty Mangabeys (*Cercocebus atys*) and interpretation of early hominin feeding ecology. PLoS ONE. 6, 8.
- Delezene, L.K., Kimbel, W.H., 2011. Evolution of the mandibular third premolar crown in early *Australopithecus*. Journal of Human Evolution. 60, 711–730.
- Fleagle, J.G., 2013. Primate Adaptation and Evolution, Third ed. Elsevier, San Diego, CA.
- Fuentes, A., Wyczalkowski, M.A., MacKinnon, K.C., 2010. Niche construction through cooperation: A nonlinear dynamics contribution to modeling facets of the evolutionary history in the genus *Homo*. Current Anthropology. 51, 435–444.
- Grine, F.E., Demes, B., Jungers, W.L., Cole III, T.M., 1993. Taxonomic affinity of the early *Homo* cranium from Swartkrans, South Africa. American Journal of Physical Anthropology. 92, 411–426.
- Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. PAST: Paleontological statistics software package for education and data analysis. Palaeontologia Electronica 4(1): 9pp.
- Hillson, S., 2005. Teeth, Second ed. Cambridge University Press, New York.
- Hylander, W. L., 1975. Incisor size and diet in anthropoids with special reference to Cercopithecidae. Science (New York, N.Y.). 189, 1095-1098;
- Johanson, D.C., White, T.D., 1979. A Systematic Assessment of Early African Hominids. Source: Science, New Series. 203, 321–330.
- Johnson, R.A., Wichern, D.W., 2007. Applied Multivariate Statistical Analysis, Sixth ed. Prentice-Hall, Upper Saddle River, NJ.
- Jolly, C.J., 1970. The Seed-Eaters: A New Model of Hominid Differentiation Based on a Baboon Analogy DIFFERENTIATION BASED ON A BABOON ANALOGY. Source: Man, New Series. 5172351, 5–26.
- Kay, R.F., 1975. The functional adaptations of primate molar teeth. American Journal of Physical Anthropology. 43, 195–216.
- Leakey, L.S.B., 1959. A New Fossil Skull from Olduvai. Nature. 184, 491.
- Leakey, M.G., Spoor, F., Brown, F.H., Gathogo, P.N., Kiarie, C., Leakey, L.N., Mcdougall, I., 2001. New hominin genus from eastern Africa shows diverse middle Pliocene lineages. Nature. 410, 433–440.

- Lee-Thorp, J.A., van der Merwe, N.J., Brain, C.K., 1994. Diet of *Australopithecus robustus* at Swartkrans from stable carbon isotopic analysis. *Journal of Human Evolution*. 27, 361–372.
- Lestrel P.E., 1974. Some problems in the assessment of morphological shape differences. *Yearbook of Physical Anthropology*. 18, 140–162.
- Lestrel, P.E., 1989. Method for analyzing complex two-dimensional forms: elliptical Fourier functions. *American Journal of Human Biology*. 1, 149–164.
- M'Kirera, F.M., Ungar, P.S., 2003. Occlusal relief with molar wear in *Pan troglodytes troglodytes* and *Gorilla gorilla gorilla*. *American Journal of Primatology*. 60, 31–41.
- Macho, G.A., Shimizu, D., 2010. Kinematic parameters inferred from enamel microstructure: New insights into the diet of *Australopithecus anamensis*. *Journal of Human Evolution*. 58, 23–32.
- Nova Delgado, M., Galbany, J., Pérez-Pérez, A., 2016. Molar Shape variability in platyrrhine primates. *Journal of Human Evolution*. 99, 79–92.
- Rabenold, D., Pearson, O.M. 2011. Abrasive, silica phytoliths and the evolution of thick molar enamel in primates, with implications for the diet of *Paranthropus boisei*. *PLoS ONE*. 6,12.
- Rohlf, F.J., Slice, D.E., 1990. Extensions of the Procrustes method for the optimal superimposition of landmarks. *Systematic Biology*. 39, 40–59.
- Rohlf, F.J., 1999. Shape statistics: Procrustes superimpositions and tangent spaces. *Journal of Classification*. 16, 197–223.
- Rohlf F.J., 2001. *TPSDig*. Stony Brook, NY: Department of Ecology and Evolution, State University of New York at Stony Brook.
- Sponheimer, M., de Ruiter, D., Lee-Thorp, J. A., Späth, A., 2005. Sr/Ca and early hominin diets revisited: New data from modern and fossil tooth enamel. *Journal of human Evolution*. 48, 147–156.
- Sponheimer, M., Alemseged, Z., Cerling, T.E., Grine, F.E., Kimbel, W.H., Leakey, M.G., et al., 2013. Isotopic evidence of early hominin diets. *Proceedings of the National Academy of Sciences*. 110, 10513–10518.
- Strait, D.S., Wright, B.W., Richmond, B.G., Ross, C.F., Dechow, P.C., Spencer, M.A., et al., 2008. Craniofacial trait patterns during premolar loading: Implications for human evolution. In C. Vinyard et al., (Eds.), *Primate Craniofacial Function and Biology* (173–195). New York, NY: Springer.

- Strait, D.S., Weber, G.W., Neubauer, S., Chalk, J., Richmond, B.G., Lucas, P.W., et al., 2009. The feeding biomechanics and dietary ecology of *Australopithecus africanus*. *Proceedings of the National Academy of Sciences*. 106, 2124–2129.
- Strait, D.S., Constantino, P., Lucas, P.W., Richmond, B.G., Spencer, M.A., Dechow, P.C., et al., 2013. Viewpoints: Diets and dietary adaptations in early hominins: The hard food perspective. *American Journal of Physical Anthropology*. 151, 339–355.
- Standford, C.B., 2006. The behavioral ecology of sympatric African apes: implications for understanding fossil hominin ecology. *Primates*. 47, 91–101.
- Teaford, M.F., Ungar, P.S., 2000. Diet and the evolution of the earliest human ancestors. *Proceedings of the National Academy of Sciences*. 97, 13506–13511.
- Thackeray, J.F., Myer, S., 2004. *Parapapio broomi* and *Parapapio jonesi* from Sterkfontein: Males and females of one species?. *Annals of the Transvaal museum*. 41, 79–82.
- Tutin, C.E.G., Fernandez, M., 1992. Insect-eating by sympatric Lowland gorillas (*Gorilla g. gorilla*) and chimpanzees (*Pan t. troglodytes*) in the Lopé Reserve, Gabon. *American Journal of Primatology*. 28, 29–40.
- Ungar, P.S., Sponheimer, M., 2011. The diets of early hominins. *Science*. 334, 190–193.
- White, T.D., Black, M.T., Folkens, P.A., 2011. *Human Osteology*. Third ed. Elsevier, San Diego, CA.
- Williams, F.L., Geissler, E., 2014. Reconstructing the diet and paleoecology of Plio-Pleistocene *Cercopithecoides Williamsi* from Sterkfontein, South Africa. *PALAIOS*. 48, 483–494.
- Wood, B., Lonergan, N., 2008. The hominin fossil record: taxa, grades and clades. *Journal of Anatomy*. 212, 354–376.
- Wood, B., Strait, D., 2004. Patterns of resource use in early *Homo* and *Paranthropus*. *Journal of Human Evolution*. 46, 119–62.
- Wynn, J.G., Reed, K.E., Sponheimer, M., Kimbel, W.H., Alemseged, Z., Bedaso, Z.K., et al., 2016. Dietary flexibility of *Australopithecus afarensis* in the face of paleoecological change during the middle Pliocene: Faunal evidence from Hadar, Ethiopia. *Journal of Human Evolution*. 99, 93–106.