The Role of Extant Primate Models for Interpreting Premolar Crown Variation in Fossil Hominins

by Katherine Elizabeth "Kes" Schroer

B.A. in Anthropology, May 2008, Kenyon College
M.Phil. in Hominid Paleobiology, May 2011, The George Washington University

A Dissertation submitted to

The Faculty of
The Columbian College of Arts and Sciences
of The George Washington University
in partial fulfillment of the requirements
for the degree of Doctor of Philosophy

August 31, 2013

Dissertation directed by

Bernard Wood
University Professor of Human Origins

The Columbian College of Arts and Sciences of The George Washington University certifies that Katherine Elizabeth "Kes" Schroer has passed the Final Examination for the degree of Doctor of Philosophy as of May 23, 2013 . This is the final and approved form of the dissertation

The Role of Extant Primate Models for Interpreting
Premolar Crown Variation in Fossil Hominins

Katherine Elizabeth "Kes" Schroer

Dissertation Research Committee:

Bernard Wood, University Professor of Human Origins, Dissertation Director

L. Patricia Hernandez, Associate Professor of Biology, Committee Member

Mark Grabowski, Postdoctoral Scientist, Committee Member

© Copyright 2013 by Katherine Elizabeth “Kes” Schroer
All rights reserved

Dedication

The author wishes to dedicate this dissertation to

Rebecca Rose Schroer
and
Charles Edward Schroer

Acknowledgments

The author wishes to thank the members of the dissertation committee for their excellent advice and mentorship over the past five years of graduate school. She especially thanks Dr. Bernard Wood for making every resource available to his students and colleagues. The author also wishes to thank Dr. Paul Constantino, Marshall University, and Dr. Matthew Skinner, University College London, for their external reviews of this dissertation. The chapter on the inhibitory cascade was made possible through the guidance of Dr. Jukka Jernvall, University of Helsinki. Dr. Peter Ungar made possible a research visit to the cast collection of the University of Arkansas. Access to museum collections was provided by Linda Gordon, Darrin Lunde, Dr. Matt Tocheri, and Dr. Roberto Portela Miguez. Funding for this research was provided by the NSF-IGERT, NSF-GRF, Sigma Xi, Cosmos Club, and Lewis N. Cotlow Fund.

Abstract of Dissertation

The Role of Extant Primate Models for Interpreting
Premolar Crown Variation in Fossil Hominins

Paranthropus, a clade of extinct hominins closely related to the genus *Homo*, has distinctly molarized premolars. Molarized premolars are used to differentiate *Paranthropus* fossil remains from *Homo* remains, particularly at sites where the two genera are found in close temporal overlap. However, molarized premolars are a poorly defined morphological trait and their adaptive significance is not well understood. To address questions of the evolutionary origin and significance of premolar molarization, this dissertation uses three models to quantify the expression of molarization in extant primates and reevaluates the significance of the morphological differences between the premolars of *Paranthropus* and *Homo*. The results of the developmental, integration, and ecological models employed in this dissertation find that molarization is a trait prone to homoplasy and may not be a reliable synapomorphic character for the genus *Paranthropus*. Furthermore, the results of the ecological analyses suggest that the degree of the expression of molarization may relate to dietary divergence between species currently included in *Paranthropus* and sympatric *Homo*. Molarization is a morphological trait that should be used conservatively in phylogenetic analyses but its presence provides an additional line of evidence for reconstructing the paleoecology of fossil hominin communities.

Table of Contents

Dedication	iv
Acknowledgments	v
Abstract of Dissertation	vi
List of Figures	viii
List of Tables	ix
Chapter 1: Introduction	1
Chapter 2: Modeling the morphological relationship of primate postcanines through the inhibitory cascade	36
Chapter 3: Morphological integration of postcanine traits in extant primates and the influence of covariance on the evolution of hominin postcanine	73
Chapter 4: Assessing character displacement in hominin and primate premolar crown size	95
Chapter 5: Conclusion	123
References	132
Appendices	174

List of Figures

Figure 1.1	35
Figure 2.1	56
Figure 2.2	65
Figure 2.3	66
Figure 2.4	67
Figure 2.5	68
Figure 2.6	69
Figure 2.7	70
Figure 2.8	71
Figure 2.9	72
Figure 4.1	113
Figure 4.2	114
Figure 4.3	119
Figure 4.4	122

List of Tables

Table 1.1	19
Table 1.2	22
Table 1.3	24
Table 1.4	27
Table 1.5	30
Table 1.6	34
Table 2.1	57
Table 2.2	59
Table 2.3	60
Table 2.4	61
Table 2.5	61
Table 2.6	62
Table 3.1	91
Table 3.2	92
Table 3.3	93
Table 3.4	94
Table 4.1	120
Table 4.2	120
Table 4.3	121

Chapter 1: Introduction

1.1 Introduction

Molarized premolars are a diagnostic criterion for many mammalian taxa and are frequently invoked as a synapomorphic trait of mammalian clades. However, molarization is poorly defined and its developmental plasticity and adaptive significance are poorly understood. This dissertation examines the morphology of molarized premolars in living primates to determine whether it is a reliable trait for taxonomic assignment and phylogenetic reconstruction. The results of this study are then applied to the molarized premolars of a particular group of fossil primates, *Paranthropus*, a hominin and close relative of modern humans that lived in Africa c.2.5-1.5 million years ago.

1.2 What is a molarized premolar?

"Molarization" is a term that usually refers to the crown morphology of the distal mandibular premolar (P_4), although it is sometimes applied to other teeth within the jaw (e.g., Kantaputra and Gorlin, 1992; Ala-Mello and Peippo, 2004). Molarization has been used to describe the similarities of the crowns of the premolars to the crowns of the deciduous molars (Butler, 1952) and to denote a premolar that shares morphological characteristics with adult molars (Robinson, 1952, 1954, 1955). The latter definition has implications for integrated development between teeth, as it suggests that adult premolars and molars can come to share the same crown morphology despite their different developmental trajectories. Premolars, which develop beneath deciduous molars, are a transitional tooth class between the canine and molars. Molars develop *de novo* in the mandible with no deciduous precursors (Avery, 2001; Ash and Nelson, 2003). Using the term "molarization" to describe a premolar suggests that teeth of different types can

converge upon similar crown morphology during their development, perhaps to perform a common function. In this dissertation, unless otherwise specified, molarization refers to the phenomenon by which the P_4 morphology comes to resemble the morphology of an adult mandibular molar (Robinson, 1952, 1954, 1955; Lunt, 1976).

Molarized premolars are found in many mammalian taxa, including rhinoceroses (Groves, 1983; Tong and Wu, 2010), horses (MacFadden, 1976; Janis et al., 2010), pandas (du Brul, 1977; Schaller et al., 1985), sheep (Roussiakis, 2003), pigs (Pickford, 1984), and voles (Jernvall et al., 2000). Among primates, molarization is found in lemurs (Friant, 1950; Butler, 2000; Jernvall et al., 2008), galagos (Butler, 2000; Harrison, 2011), colobines (Swindler, 1976), sakis (Kinzey, 1992; Rosenberger, 1992), and several other groups. One of the most pronounced examples of molarization in primates occurs in the fossil hominin taxon *Paranthropus* (Bailey and Wood, 2007; Wood and Constantino, 2007). Most fossil hominins have premolars that are relatively larger than those of modern humans, but the premolars of *Paranthropus* are especially large and molarized. *Paranthropus boisei*, an East African variant of this genus, has an even more extreme form of this morphology and is sometimes described as a "hyper-robust" hominin (Wood and Chamberlain, 1987; Suwa et al., 2009; Lucas et al., 2008; Ungar and Sponheimer, 2011).

1.3 Theories on the origin of molarized premolars

Despite the ubiquity of molarized premolars, the developmental process by which a premolar comes to share the morphology of a molar is unknown. The earliest attempts to answer this question suggest that molarized premolars may retain morphological components of the deciduous molars they replace (Butler, 1952; Quinet and Verlinden,

1970). Robinson (1952, 1956) posits that molarization results from the development of additional cusp morphologies in the premolars, particularly the expansion of features of the talonid, the distal portion of the tooth. Additional cusps and cusp rearrangement are implicated in further studies of molarized premolar morphologies (Butler, 1997, 2000; Jernvall et al., 2008). Other researchers argue that allometric scaling (Gould, 1975), particularly an increase in the linear dimensions of the tooth crown (Butler, 1988), will generate a premolar that resembles a molar. Whatever the process of development, it appears that the formation of a molarized premolar may be highly integrated with other parts of the tooth, as the molarized crowns of *Paranthropus* premolars have been shown to also have molar-like roots (Wood, 1981).

1.4 Theories on the function of molarized premolars

Tooth morphology, and occlusal morphology in particular, is thought to correlate strongly with the mechanical and physical properties of foods consumed (Kay, 1975; Lucas and Luke, 1984; Lucas et al., 1985, 1986; Kay, 1975; Teaford and Ungar, 2000; Lucas, 2004). Premolars have similar functions to the molars and are responsible for the mastication of food particles (Lucas, 2004). In fact, the function of the premolars is often so similar to the molars that many researchers group premolars and molars together as simply "postcanine teeth" (e.g. Lucas et al., 1986; Wood et al., 1988; Wood and Engleman, 1988; Lucas and Peters, 2000; Bailey 2002).

Larger occlusal surfaces in the postcanine teeth, such as those found in molarized premolars, may aid in the processing of mechanically challenging foods (Jolly, 1970; Walker, 1981; Lucas et al., 1985). This hypothesis has been supported through the direct examination of diet in bamboo-eating golden lemurs (Jernvall et al., 2008) and indirect

evidence of dental microwear and chipping in *Paranthropus* (du Brul, 1977; Rak, 1983; Grine, 1986, 1987; Hylander, 1988; Teaford and Ungar, 2000; Scott et al., 2005, Constantino and Wood, 2007; Ungar et al., 2008). It has also been supported in finite element analysis of the premolars in the hominin genus *Australopithecus*, which demonstrated that the premolars of this genus would have withstood high mechanical loads during feedings (Strait et al., 2009). The plesiomorphic condition of hominins may therefore be teeth reflecting a diverse diet that includes mechanically challenging foods.

Mechanically challenging foods may be either hard or tough. Hard foods are difficult to deform (e.g., nuts), while tough foods are difficult to fracture (e.g., grass) (Lucas et al., 2008). The consumption of hard foods is particularly implicated in the dental morphology of *Paranthropus* (Kay, 1981; Lucas et al., 1986; Wood and Constantino, 2007). Dental enamel in *Paranthropus* is thick, which likely protects against deformation during hard-food consumption (Lucas et al., 2008), and premolar crowns are consistently larger in primates with diets that are especially hard (Lucas, 2009). The isotopic signature of *Paranthropus* indicates that C_4 resources, such as grasses, formed a substantial part of the diet of *Paranthropus* (Cerling et al., 2010, 2011), but these results are incongruent with the dental morphology of *Paranthropus*. Teeth reflecting tough diets are more likely to have thin enamel and pronounced cingula at the occlusal margins (Lucas et al., 2008). While *Paranthropus* may have consumed both tough and hard foods, it is more likely that a focus on the consumption of hard foods will inform interpretations of the molarization observed in *Paranthropus*.

1.5 Molarized premolars in Hominini

Determining the evolutionary significance of molarized premolars is especially critical to paleoanthropology, which seeks to reconstruct the evolution of the hominin clade. Modern humans have distinctly small and simple postcanine teeth, including non-molarized premolars (Carroll, 2003; Wood and Constantino, 2004; Organ et al., 2011). However, earlier hominins such as *Australopithecus* had larger premolars than modern humans and their genus, *Homo*. One of the other likely descendants of *Australopithecus*, the genus *Paranthropus*, had distinctly molarized premolars (Hillson, 1996; Wood and Strait, 2004; Bailey and Wood, 2007). Although *Homo* and *Paranthropus* may be sister-genera, their premolar morphologies are derived in opposite directions with respect to the inferred ancestral *Australopithecus*-like condition.

Many researchers argue that the significant dental reduction observed in *Homo* correlates with a change in diet (Robinson, 1954; Malone, 1987), perhaps with the advent of cooking (Wrangham and Conklin-Brittain, 2003; Wrangham, 2009). Stone tools are also frequently found in association with *Homo* remains (Leakey et al., 1964, Wood and Collard, 1999, Vekua et al., 2002, Foley and Lahr, 2003; Morwood et al., 2004), and such tools may have provided members of *Homo* the ability to process mechanically challenging foods without the use of teeth. The possible association of stone tools with *Australopithecus* (McPherron et al., 2010) is a challenge to this hypothesis, however, and more work on stone tool types, stone tool use, and the relationship between extra-oral processing and dental phenotypic change is needed.

The molarized premolars of *Paranthropus* may be the product of an adaptive divergence between this genus and the genus *Homo*. *Paranthropus* is currently

recognized as the closest relative of *Homo* on the basis of shared cranial base, mandibular, and canine morphologies (Strait et al., 1997), and some fossil specimens of *P. boisei* and early *Homo* have been found in the same fossil localities at sites in East Africa, thus it is possible that these genera lived sympatrically (Constantino and Wood, 2004; Wood and Strait, 2004; Fuentes et al., 2010; Leakey et al., 2012). The different postcanine tooth morphology of these hominin genera, with one genus forming molarized premolars and the other non-molarized ones may have been an adaptation to avoid resource competition in their shared environment (Schaffer, 1968; Laden and Wrangham, 2005).

The large postcanine teeth of *Paranthropus*, including its molarized premolars, are part of the supporting evidence for the hypothesis that *Paranthropus* was adapted to a dietary niche very different from that of *Homo*. Many authors have suggested that taxa included within *Paranthropus* likely consumed a more mechanically challenging diet than members of *Homo* (du Brul, 1974, 1977; Wood and Stack, 1980; Wood et al., 1983; Rak, 1983; McHenry, 1984; Grine, 1986, 1987; Kay and Grine, 1988; Hylander, 1988; Suwa et al., 1994; Teaford and Ungar, 2000; Scott et al., 2005; Constantino and Wood, 2007, Ungar et al., 2008). Indeed, *P. boisei* was colloquially known as the Nutcracker Man for decades, based on the idea that its large teeth were adapted to process hard foods (Tobias, 1967; Ungar et al., 2008; Lee-Thorp, 2011). New isotopic analysis suggests, however, that the staple items of the diet of this taxon were more likely to have been tough foods, such as grasses, rather than hard foods, such as nuts (Cerling et al., 2011).

However, the proposed dietary divergence between *Paranthropus* and early *Homo* simplifies a more complicated evolutionary story. The species included in *Paranthropus*

display considerable variation in their dental morphology, including their premolars (Ungar et al., 2008; Cerling et al., 2011; Ungar and Sponheimer, 2011). Although the definition of a genus is almost as intractable as the definition of a species (Mallet, 1995; de Queiroz, 2007), several authors have suggested that the component species of a genus must be of the same clade (i.e., they are each other's closest relatives) and grade (i.e., they share the same adaptive zone; Lemen and Freeman, 1984; Allmon, 1992; Wood and Collard, 1999). Phylogenetic and ecological similarity are therefore important characteristics of a genus. The differences in the masticatory morphology and inferred diet of the species within *Paranthropus* may exceed the variation expected in primate genera, and it is possible that the species of *Paranthropus* belong to different genera (Wood, 1988; Wood and Constantino, 2007). This possibility not only has implications for the reconstruction of evolutionary relationships among the species presently included within *Paranthropus* but also for assessing the possible influence of competition on the divergent evolution of *Paranthropus* and early *Homo*.

One of the controversies surrounding the suggested monophyly of *Paranthropus* concerns whether the molarized premolars of this clade represent a synapomorphy (Rak, 1983; Grine, 1985; Wood and Chamberlain, 1986, 1987). It is suggested that all *Paranthropus* species have molarized premolars. Combined with other aspects of craniodental morphology, the similarity of the dental morphology of *Paranthropus* taxa suggests that these species do indeed form a clade (Rak, 1983; Grine, 1985; Wood and Chamberlain 1986, 1987; Wood, 1988; Strait et al., 1997; Kimbel et al., 2004; Strait and Grine, 2004). However, many of the cranial and dental characters used in phylogenetic analysis relate to the masticatory complex, which has a high degree of functional

integration. The traits that make up the masticatory complex therefore may not evolve independently (Wood and Chamberlain, 1986; Skelton and McHenry, 1992; Begun, 2007; but see Collard and Wood, 2001). Additionally, similarities of the teeth on a macro-scale may mask more discrete sources of variation. This is particularly evident in the premolars of *P. boisei*, which appear more molarized than those of either *Paranthropus aethiopicus*, its likely predecessor in East Africa, or *Paranthropus robustus*, its proposed southern African relative (Robinson, 1965; Tobias, 1967; Wood, 1988; Wood and Richmond, 2000; Wood and Lonergan, 2008; Wood and Constantino, 2007). The premolars of *P. boisei* are so large and complex compared to any other hominin that they are sometimes referred to as "hyper-molarized" (Wood and Uytterschaut, 1987; Wood and Constantino, 2007).

These hyper-molarized premolars are likely not the result of a simple size difference overall between *P. boisei* and other *Paranthropus* species. Individual cusps apparently do not contribute in the same way to the expansion of the talonid in *P. robustus* and *P. boisei* (Suwa et al., 1994), premolar root morphology is not the same in the two taxa (Wood, 1981), and Skinner et al. (2011) have shown that the average *P. boisei* talonid is distinctly expanded compared with *P. robustus*, even when the shape of the talonid is size-corrected. These results suggest that molarization in the taxa of *Paranthropus* may not be equivalent, and that this trait cannot automatically be regarded as a synapomorphy uniting these taxa in *Paranthropus* (Wood, 1988; Constantino and Wood, 2007). In addition, the results of new isotopic analyses suggest the taxa of *Paranthropus* had distinctly different diets (Cerling et al., 2010) and may have occupied different ecological grades. Combined with morphological differences in the dentition of

Paranthropus taxa, this ecological difference further weakens the case for *Paranthropus* monophyly.

1.6 Outline of the dissertation

There are many unanswered questions concerning the developmental origin of molarized premolars, their adaptive significance, and their use in phylogenetic reconstructions. This dissertation quantifies the occlusal morphology of molarized premolars of *Paranthropus* taxa and uses extant primate comparisons to investigate 1) whether the range and pattern of variation in *Paranthropus* premolars is similar to the variation observed in living primate genera and 2) whether the range and pattern of variation in premolars differs significantly in the taxa of *Paranthropus*. By quantifying premolar variation and contextualizing this variation using living primate populations, this dissertation will test the hypotheses that premolar molarization is 1) a genuine synapomorphy of *Paranthropus*, and 2) evidence of adaptive divergence between *Paranthropus* and early *Homo*.

Specifically, this dissertation considers the following three hypotheses, each addressed in a separate chapter. These hypotheses are based on current mainstream phylogenetic reconstructions that include all *Paranthropus* species in the same genus and place this genus as a sister-taxon to early *Homo*. The hypotheses and the methods used to address them are:

1. The relative occlusal area of the P_4 to the molars follows the same proportions in all species within a genus. If similar proportions are observed within the species included in living primate genera, this provides support that the molarization observed in *Paranthropus* taxa may be a synapomorphy of this clade.

Conversely, if this pattern is not consistent within living primate genera, or if it is observed in living primate genera but not in the component species of *Paranthropus*, this result suggests that molarization is not a reliable synapomorphy of *Paranthropus*.

Testing this hypothesis uses the observation that postcanine teeth develop in series, and the empirical evidence that their occlusal areas correlate closely with one another. A developmental model, the inhibitory cascade (Kavanagh et al., 2007) is used to assess macroevolutionary trends in the relative occlusal areas of primate postcanines. This method uses reduced major axis regression to determine patterns of correlations in occlusal areas and what deviations from the regression prediction may indicate about phylogeny.

2. In molarized primates, there is a high degree of covariation in the occlusal morphology of the P_4 and its adjacent teeth. If this is observed in living primates, it suggests that there are constraints on the range of morphological variation of the P_4 and that molarization is not particularly evolvable (i.e., it is unlikely to evolve multiple times within a lineage). This result would support the idea that the molarization observed in *Paranthropus* taxa may be a synapomorphy of this clade. Conversely, if weak patterns of integration are observed in the P_4s of molarized primates, this finding suggests that the molarization observed in *Paranthropus* is relatively evolvable, and thus may not be a synapomorphy of this clade.

To test this hypothesis, this dissertation will use methods borrowed from the study of morphological integration. Teeth are highly integrated structures and

selection acts differently on species with different degrees and patterns of integration (Grabowski et al., 2011; Marroig et al., 2009; Porto et al., 2009). Residual covariance from MANOVAs of morphological traits and population descriptors (i.e., sex, geography) can estimate a phenotypic variance/covariance matrix. From this matrix, magnitudes of integration can be determined from certain statistics (i.e., evolvability, autonomy, flexibility) and results for each taxon plotted against one another can be used to determine how taxa differ in their trait-level patterns of integration.

3. Premolar morphology, as assessed through occlusal ratios and occlusal size, differs significantly in closely-related sympatric species. If this pattern is not observed in sympatric extant primates, it suggests that molarization is not a good criterion for supporting a sympatric relationship between *Paranthropus* and early *Homo*. Conversely, if this pattern is found in extant communities of sympatric populations, it supports the hypothesis that divergent premolar morphologies can reasonably predict geographic and temporal overlap in populations of fossil primates such as *Paranthropus* and early *Homo*.

Teeth and gnathic morphology may vary considerably in closely-related, sympatric populations, a phenomenon that some have proposed is the the result of ecological character displacement (Brown and Wilson, 1956; Slatkin, 1980; Schluter and McPhail, 1992). One method for assessing ecological character displacement is to quantify the observed values of morphological divergence in sympatric populations and then compare these to the expected values of divergence generated from the mean divergence of all possible pairs of solitary

populations in the sample. If the observed values exceed the expected values, it is likely that character displacement has occurred.

1.7 Modeling and the reconstruction of human evolution

Before commencing any program of paleontological analyses, it is prudent to examine some of the advantages and disadvantages of the different kinds of explanatory models to help determine the weight that should be given to certain models and their results. Like many studies of human evolution, this dissertation includes two categories of models: referential and conceptual (Tooby and Devore, 1987; Stanford and Allen, 1991). Referential models offer analogous interpretations while conceptual models provide theoretical frameworks for explaining phenomena. The limitations of both of the categories of modeling, and their implications for this dissertation, are discussed in below in sections 1.7.1 and 1.7.2. The specific conceptual models included in this dissertation were briefly outlined in the methods described above and will be discussed in more detail in the Introduction section of each of the following analytical chapters. Because the same referent sample is used in each the three analyses of this dissertation, an in-depth justification for the selection of comparative taxa is described in detail in section 1.8. The use of identical samples for each analysis allows for comparison between the results of the three studies. The results are discussed in detail immediately following the methods section of their respective chapters, with general trends in the results summarized in the Conclusion. Any modifications to the sample are described within the relevant chapter. 1.7.1 Referential modeling

Primates have been used as comparators for understanding human evolution since before the age of Darwin (Tyson, 1699). Although extant primates are close relatives of

fossil hominins, there are many other plausible models for human evolution, including modern hunter-gatherers (e.g., Hayden, 1972, 1981; King, 1976; Reynolds, 1978; Yesner et al., 1980; Hill, 1982; Harris and Ross, 1987; Belovsky, 1988), social carnivores (e.g., Schaller and Lowther, 1969; Thompson, 1976; King, 1980; Arcadi, 2006), cetaceans (e.g., Marino, 2002), and even birds (e.g., Snowdon, 1990). The primates used as referents in this dissertation are well-researched primates that are frequently used as models for human evolution. The most popular (Strier, 1994) are chimpanzees and their close-relatives, the bonobos (e.g., Wrangham and Pilbeam, 2001, Zihlman and Cramer, 1978; Wood, 1994; Sayers and Lovejoy, 2008; Sayers et al., 2012). Close seconds to chimpanzee models are models derived from studies of baboons (e.g., Zuckerman, 1932; Marais, 1969; DeVore, 1963; Washburn and DeVore, 1961; Hall and DeVore, 1965, Jolly, 1970) and macaques (e.g., DeVore, 1963; Enomoto, 1978; Huffman, 1984; Wolfe, 1986; Ruff, 1988; Westergaard, 1988). In more recent decades, gorillas and orangutans are also popular referents (e.g., Shea, 1985; Schwartz, 1987; Suarez and Gallup, 1981; Knott, 2001). The present dissertation adds to these comparatively well-known referential primate models by using tamarins.

Evoking any extant primate group, or taxon, as a straightforward analogue for the hominin lineage is problematic. On many occasions, descriptions of extant referents focus attention on a few similarities with hominins and ignore the many differences between them (Darwin, 1871; Tooby and Devore, 1987). The use of primates as referential models on the assumption that their phylogenetic closeness makes them uniquely suited as comparative models for fossil hominins helps enforce a false distinction between primates and other animals (Richard, 1981; Strier, 1994). Phylogeny

is thought by some authors to be a particularly poor rationale for referent choice, especially for traits that frequently evolve independently or that show a substantial range of variation (Losos, 2011). Molarization, which appears in one form or another in clades as diverse as horses and voles (MacFadden, 1976; Jernvall et al., 2008) may be such a trait, and comparative analyses with non-primate animals such as pandas and sea-otters have already demonstrated their utility (du Brul, 1977; Constantino et al., 2011).

This dissertation considers morphological diversity in a wide-range of species (e.g., Preuss, 2000; Nunn and Barton, 2001). Although the present may not be the time of greatest primate diversity, it is certainly the era in which the diversity of living and fossil primates is best known (Gingerich, 1984). Studies of variation among primates have provided researchers with insight into the potential forms that morphology and behavior may take in response to evolutionary pressures (Potts, 1987; Wrangham, 1987).

This dissertation also seeks to improve upon the use of extant primates in referential modeling of human evolution by investigating patterns of variation in taxonomic levels higher than the level of species. Species may not be independent points of comparison because of the "phylogenetic inertia" experienced in closely-related taxa (Pagel and Harvey, 1989; Blomberg and Garland, 2002; Hansen and Orzack, 2005). Phylogenetic inertia, which is the persistence of traits after the initial selection pressure has disappeared, is an influence that runs counter to the proposition that traits originate in response to selection (Darwin, 1859; Felsenstein, 1985; Harvey and Purvis, 1991). So instead of working at the level of the species, this study focuses on genus-level comparisons, which have the benefit of being less susceptible to sampling-bias than species-level. Unlike species-level comparisons, genus-level comparisons do not sample

single-occurrence taxa and are generally more stable over long periods of evolutionary time (Raup, 1979; Allmon, 1992; Sepkoski, 1997; Jablonski and Finarelli, 2009).

1.7.2 Conceptual models

Like referential models, conceptual models seek to explain correspondences between observations (Tooby and Cosmides, 1990). Conceptual models, which are more common than referential models, are used throughout the sciences, where they provide theoretical boundaries for the generation and testing of hypotheses (Tooby and Devore, 1987; Heemskerk et al., 2003; Nee, 2004).

Conceptual models of evolution require the assumption that present-day variation can explain past variation, an assumption that is also made in this dissertation. The assumption that the causes and patterns of past variation mimic those known from the present is a form of methodological uniformitarianism. This principle states that natural laws operate by the same processes at all times and in all places (Lyell, 1830; Gould, 1965; Shea, 1982). While uniformitarianism provides a useful means of extrapolating information obtained from modern observations to observations in the fossil record, it a theoretical concern for any model seeking to describe a potential adaptation, such as molarized premolars. Adaptation cannot be explained by present pressures because, by its nature, it is the product of past pressures (Symons, 1990; Tooby and Cosmides, 1990; Losos and Miles, 1994; Losos, 2011). To avoid this theoretical conflict, conceptual models of evolution are most informative when they focus on explaining evolutionary processes rather than specific scenarios. For example, an adaptation may be suggested when a trait appears frequently associated with certain ecological characteristics, but an

adaptation does not dictate the presence of identical environments in the past and the present (Nunn and Barton, 2001).

A second problem with conceptual models is that they often do not falsify, in the strict sense, alternative explanations of the same observations (Gingerich, 1984, Losos, 2011). The relative paucity of information in the fossil record suggests that conceptual models of evolution maybe best evaluated through Lakatosian standards of science rather than Popperian standards. Popperian standards emphasize the falsification of hypotheses (Popper, 1956, 1979), whereas Lakatosian standards emphasize the ability of hypotheses to explain a wide-range of observations (Lakatos, 1970, 1978; Ketelaar and Ellis, 2000). The two epistemologies could be summarized as one favoring the testing of hypotheses (Popperian) and the other the generation of hypotheses (Lakatosian). Under the paradigm of Lakatosian science, conceptual models of human evolution can be centered on agreed-upon, falsifiable principles and continually improved upon as they explain more aspects of phenomena. The models used in these analyses belong to this explanatory kind, in that they use statistics to demonstrate the strength of the fit between evolutionary hypotheses and morphological observations (Guisan et al., 2002), not whether or not these hypotheses can be rejected.

With these caveats in mind, conceptual models remain useful for evolutionary studies because evolution is best understood when past and present phenomena are considered together (Le Gros Clark, 1955; Latimer et al., 1981). Evolution in mammals is a long-term process and is notoriously difficult to observe in the course of a human lifetime (Slobodkin, 1961, Stanley, 1975; Butterfield, 2007; but see Thompson, 1998; Hairston et al., 2005). Fossils get around this by providing a wide-lens view of change

through time (Huxley, 1863; Darwin, 1871; Carroll, 1988; Erwin and Wing, 2000; Jackson and Erwin, 2006; Eldredge et al., 2008) and they are the "ultimate test" for reconstructing past stages of evolution (Gingerich, 1984:58). Modern organisms, although more limited in their temporal scope, have the benefit of offering knowable degrees and rates of variation within a lineage. In the absence of a full understanding of the diversity of the fossil record, conceptual models offer a critical link between past evidence and present outcomes of the same evolutionary processes.

1.8 Referent sample

In order to allow for comparison between the results of each of the three different studies included in this dissertation, a similar primate sample was used for each analysis. These primate referents were carefully chosen to provide close extant approximations for the proposed relationships among *Paranthropus* taxa and between *Paranthropus* and early *Homo*. Several groups of primate species were identified using relevant phylogenetic and ecological criteria to generate comparators for the fossil taxa, and the method used to choose these groups is described in detail below.

The construction of each group began by identifying a "target" primate species that shares relevant morphological similarities with *P. boisei*, the *Paranthropus* species thought to have lived sympatrically with early *Homo*. These taxa are marked with an asterisk in the tables in this section. Although no living analogue exists for the absolutely and relatively enormous premolars of *P. boisei*, several primates have been used as comparative models for *P. boisei* on account of their large teeth or because of aspects of their robust masticatory complex (see Wood and Schroer, 2012 for a review). After listing the target species, at least one congener of each species was chosen in order to

determine genus-level variation and to provide a context for evaluating the differences between *P. boisei* and *P. robustus*. These congeners were also determined on the basis of available sample sizes in research collections. The resulting pairs or triplets of extant primate species included in the same genus are relevant for addressing the first and second hypotheses proposed in this dissertation, which consider variations of premolar morphology within primate genera.

To address the third hypothesis, which considers the role of dietary competition on premolar morphology, the identification of additional comparative taxa was required for assessing morphological variation in overlapping primate populations. This additional sample was comprised of at least one population that lives in sympatry with the target species and one that lives allopatrically from the target species, or any of its congeners. Many primates share the same habitat or live in close proximity to one another (e.g., Ungar, 1995; Fleagle and Reed, 1996; Ramakrishnan and Coss, 2001; Wahungu, 2002), but the choice of this competitive taxon was further restricted to a species closely-related to the target species. This approximates the proposed sympatry between the close hominin relatives *Paranthropus* and early *Homo*. In cases where the sympatric taxa were of the same genus as the target species, or in cases where congeners of the competitive taxon had reasonable sample sizes, these taxa were also included in the consideration of variations of premolar morphology within primate genera.

Ideally, the competitive taxa included within each group would share a similar phylogenetic relationship as that observed between*Paranthropus* and *Homo*. However, few sympatric primate groups are separated by the exact evolutionary time proposed between *Paranthropus* and *Homo*. Therefore, intervals both longer and shorter than the

phylogenetic distance between *Paranthropus* and *Homo* were used in the following analyses. For some groups, the taxa were of different genera and therefore similar to a proposed *Paranthropus-Homo* dichotomy (i.e., Groups 1, 2, and 4). For other groups, however, the competitive taxon was of the same genus as the first few species chosen for the group (i.e., Groups 3 and 5). In these cases, the likelihood of finding morphological variation is decreased. This affects the likelihood of rejecting a true positive (i.e., increases Type II error) in the resulting analysis of sympatric versus allopatric variation. More details concerning the structuring of sympatric and allopatric groups are provided in Chapter 4.

An evaluation of primate diversity throughout the world yielded several groups that met these criteria and provided adequate comparators for the patterns of molarization in *Paranthropus* and early *Homo*. In order to restrict the sample further, preference was given first to groups with a close phylogenetic relationship to hominins or groups that had a high degree of sympatry. The rationale for selection and a brief description of the phylogenetic relationships within, and the ecology of, each comparative group is given below:

Group 1: African apes

Table 1.1 Ecological divisions of the taxa of African apes examined in the following analyses. An asterisk denotes the initial taxon chosen for analyses; the selection criteria for all of the taxa are described in the text.

Sympatric	Allopatric
*Gorilla gorilla**	*Gorilla beringei*
Pan troglodytes (population-level)	*Pan troglodytes* (population-level)

The African great apes are the closest non-human living relatives to the hominins (Patterson et al., 1993; Satta et al., 2000; Steiper and Young, 2006), with the genus *Pan*

sharing an especially close genetic relationship with modern humans (Ruvolo et al., 1991; Chen and Li, 2001; Kumar et al., 2005; Bradley, 2008). Two species are generally recognized in *Pan* (Bjarnason et al., 2011, von Cramon-Taubadel and Smith, 2012; Prufer et al., 2012), but specimens of the bonobo, *Pan paniscus*, are not well-represented in natural history collections. For this reason, *Gorilla* was chosen as the primary genus for this group. The large teeth and robust masticatory morphology of *Gorilla* (Constantino et al., 2012) also makes them a more suitable comparison with *Paranthropus* than *Pan*. Although *Gorilla* and *Pan* overlap extensively in their preferred diets (Ungar, 2007; Yamagiwa and Basabose, 2009), gorillas consume fewer fruits and animal foods than chimpanzees (Yamagiwa and Basabose, 2009) and lowland gorillas are known to consume much tougher foods than chimpanzees during times of food scarcity (Dominy, 2001; Elgart-Berry, 2004).

Current projections of molecular divergence in the hominines, the combined clade of African apes and hominins, suggests that the lineages leading to gorillans and the panin-hominin group split from a common ancestor c.10-8 million years ago (Scally et al., 2012), and panins and hominins split c.8-4 million years ago (Steiper and Young, 2006; Langergraber et al., 2012). New estimates of genetic divergence within *Gorilla* suggest that western and eastern populations split from one another c.1.75 million years ago (Scally et al., 2012).

Today, the two species of *Gorilla* occupy distinct, fragmented forest habitats in Central Africa. The western lowland gorillas (*Gorilla gorilla gorilla*, the common gorilla, and *Gorilla gorilla diehli*, the Cross-River gorilla) live in the tropical and subtropical forests of West Central Africa, and occupy a variety of habitats ranging from

montane to swamplike (Leigh, 2003; Groves, 2005). The subspecies of the eastern gorillas either occupy forests of the Virunga Mountains in Central Africa (*Gorilla beringei beringei*, the mountain gorilla) or a range of tropical habitats varying from woodland to peat bog (*Gorilla beringei graueri*, Grauer's gorilla) (Doran and McNeilage, 1998; Stanford, 2001; Leigh, 2003; Groves, 2005).

The two species of *Gorilla* do not overlap in their ranges, but gorillas and chimpanzees, (*Pan troglodytes*) are broadly sympatric. Although overlap has been observed between chimpanzees and both species of *Gorilla* (Hall et al., 1998; Stanford and Nkurunungi, 2003; Stanford, 2006), overlap with the western lowland gorillas occurs more frequently (Tutin and Fernandez, 1992, 1993; Tutin and Oslisly, 1995; Kuroda et al., 1996; M'kirera and Ungar, 2003; Matthews and Matthews, 2004; Morgan and Sanz, 2006; Sanz et al., 2007; Devos et al., 2008). *Pan troglodytes verus* (the West African or savanna chimpanzee is relegated to habitats in the far west of Africa (Sponheimer et al, 2006), *Pan troglodytes schweinfurthii* is found in East Central Africa, where it overlaps occasionally with *G. beringei* (Stanford and Nkurunungi, 2003), and *Pan troglodytes ellioti* (the Nigeria-Cameroon chimpanzee) is found only in small rainforest pockets of Central Africa. Most sympatry between *Gorilla* and *Pan* occurs in Central Africa, between *G. gorilla gorilla* and *Pan troglodytes troglodytes*, the central chimpanzee or tschego (Ungar, 2007). To reflect this sympatric relationship and to reduce the likelihood of conflicting signals of allopatry and sympatry from other *P. troglodytes* populations, only *P. troglodytes troglodytes* was included in the sympatric species sample for *Pan* (Table 1.1).

Group 2: Asian apes

Table 1.2 Ecological divisions of the taxa of Asian apes examined in the following analyses. An asterisk denotes the initial taxon chosen for analyses; the selection criteria for all of the taxa are described in the text.

Sympatric	Allopatric	Other
*Pongo pygmaeus**	*Pongo abelii*	-
Hylobates agilis	*Hylobates klossi*	*Hylobates lar*

After the African great apes, the Asian great ape, the orangutan, is the most closely-related living non-human primate to *Paranthropus*. Asian great apes diverged from African apes c.11 million years ago (Stauffer et al., 2001), with the two species of orangutan diverging c.3.6 million years ago (Arora et al., 2010). The Bornean species (*Pongo pygmaeus*) has been cited previously as a comparative model for understanding the dental and masticatory morphology of *P. boisei* due to its tougher and harder diet (Vogel et al., 2008). Although similar in their diets, *P. pygmaeus* and *Pongo abelii* (the Sumatran orangutan) have significantly different mandibular morphologies, likely due to the regular processing of harder foods in the diet of *P. pygmaeus* (Taylor, 2006). Although occupying similar, fragmented, tropical forests in Indonesia, the Bornean and Sumatran orangutans inhabit separate islands and have no contact with each other in the wild. They can, however, form hybrids in captivity, and some have suggested they may not be distinct species (Zhi et al., 1996; Zhang et al., 2001).

Pongo pygmaeus lives sympatrically with several primates, but its closest sympatric relative is *Hylobates agilis albibarbis* (the white-bearded gibbon; Vogel et al., 2009; Marshall et al., 2009). Estimates of the divergence of the great apes from the hylobatids (i.e., the lesser apes) differ widely. Some researchers place the divergence as

recently as c.17-11 million years ago (Raaum et al., 2005), with others favoring a much earlier divergence c.21 million years ago (Hasegawa et al., 2003, Chatterjee et al., 2009). Modern hylobatids began diverging from one another c.10-4 million years ago (Zehr et al., 1996; Porter et al., 1997; Goodman et al., 1998; Chatterjee, 2006, 2009; Matsudaira and Ishida, 2010; Thinh et al., 2010).

Within hylobatids, there is an unresolved polytomy between *Hylobates lar*, *Hylobates pileatus*, and a group formed by *Hylobates agilis*, *Hylobates moloch*, and *Hylobates klossii* (Chan et al., 2010). The divergence between *H. lar* and *H. pileatus* has been dated to 3.9 million years ago (Matsudaira and Ishida, 2010). There remains some debate as to whether *H. lar* is more closely-related to *H. pileatus* or the *H. agilis* group (Chan et al., 2010), but vocal and pelage data suggest a close relationship between *H. lar* and *H. agilis* (Haimoff et al., 1984).

Among the southern hylobatids, *H. agilis*, *H. moloch*, and *H. klossii* likely split from one another c.1.45 million years ago (Chan et al., 2010). *H. klossii* is allopatric from all other species of *Hylobates* as well as *Pongo*. It is a found on the Mentawai Islands west of Sumatra, and although more precise dates of genetic divergence are currently unknown, mitochondrial evidence suggests that *H. klossii* and *H. moloch* form a sister taxa to the *H. agilis* group (Takacs et al., 2005). Although *H. agilis* and *H. klossii* were designated as the sympatric and allopatric taxa, respectively, there sample sizes were relatively small. Additional species of *H. lar* were employed for the analysis of morphological variation in this genus.

The Bornean gibbons likely represent a more recent divergence, given the distance of Borneo from the southeastern Asian center of the gibbon range, and molecular

evidence suggests they diverged from other gibbons c.5-3 million years ago (Chatterjee, 2006; Matsudaira and Ishida, 2010). *Hylobates agilis albibarbis* is a controversial subspecies, having been considered a subspecies of *H. agilis* (Brandon-Jones et al., 2004), a vocalization variant of *H. agilis* (Marshall and Marshall, 1976), or a geographic variant of *Hylobates muelleri* (Groves, 1972). For the purposes of boosting sample size and the low degree of premolar variation between populations of *Hylobates albibarbis* and *H. agilis*, this dissertation uses the term *H. agilis albibarbis* to designate the Bornean gibbon.

Although overlap exists between sympatric gibbon and orangutan diets, *Pongo* eats much larger and harder fruits (MacKinnon, 1977; Lucas, 1980, 1989; Ungar, 1995). *Pongo* can also chew through stiff seeds and tough fruit flesh (Lucas et al, 1994; Vogel et al., 2008, 2009), and eats more bark and pith than gibbons (MacKinnon 1977; Chivers, 2001; Vogel et al., 2009; Cheyne, 2010; Harrison and Marshall, 2011). It is therefore likely that premolar morphology is significantly different in these genera, despite their dietary overlap. Table 1.2 provides a summary of the ecological and phylogenetic relationships described in this section.

Group 3: Macaques

Table 1.3 Ecological divisions of the taxa of macaques examined in the following analyses. An asterisk denotes the initial taxon chosen for analyses; the selection criteria for all of the taxa are described in the text.

Sympatric	Allopatric
*Macaca fascicularis**	*Macaca cyclopis*
Macaca nemestrina	*Macaca fuscata*

Macaques from laboratory colonies are frequently used to model mastication forces in comparative studies of extant primates and *Paranthropus* (Strait et al., 2007).

For this reason, *Macaca fascicularis* (the crab-eating macaque) is the target species in this group. It is broadly sympatric with *Macaca nemestrina* (the pig-tailed macaque; Rodman, 1991). Several isolated populations of macaques are known from different Asian islands, and *Macaca cyclopis* (the Taiwanese macaque) and *Macaca fuscata* (the Japanese macaque) were chosen for their larger available sample size (Table 1.3).

The macaques are a highly successful radiation of primates inhabiting many environments of eastern and southeastern Asia as well as parts of Africa. The diversity of the macaques has not lent itself to easily resolved phylogenies of this clade. It is known that macaques, like the closely-related baboon, are members of the primate tribe Papionini within the subfamily Cercopithecinae. The cercopithecines are a broad class of Old World monkeys that, together with colobines, form the family of Old World monkeys, Cercopithecidae, the extant sister taxa to all apes. Estimates of the divergence of cercopithecoids and hominoids are anywhere from c.47-20 million years ago (Easteal and Herbert, 1997; Arnason and Janke, 2002; Chatterjee, 2009), and macaques diverged from the rest of the papionin tribe c.18.6-10 million years ago (Steiper and Young, 2006; Raaum et al., 2005; Chatterjee, 2009).

The modern macaques likely diverged from a cercopithecoid ancestor c.7 million years ago (Li et al., 2012). Although temporal estimates are not available for species divergences within macaques, it is thought that the group including *M. nemestrina* diverged first from a common ancestor, followed sometime later by the *M. fascicularis* group, which includes crab-eating, Japanese, rhesus, and Taiwanese macaques (Hayasaki et al., 1996). *Macaca fascicularis* was the first species to diverge from the other

members of its group (Li et al., 2012), suggesting by extrapolation that *M. cyclopis* is the most recently emerged of the three macaque species considered in this study.

Comparative data on wild macaque diets is sparse. Macaques have quite "eclectic diets" with hundreds of food items (Wheatley, 1980; Berenstain, 1986; Lucas and Corlett, 1991; Yeager, 1996; Sussman et al., 2011) that include a large proportion of fruit (Gumert and Malaivijitnond, 2012) as well as vegetation, insects, eggs, and small animals (Son, 2003; Gumert and Malivijinond, 2012). *Macaca nemestrina* is known to consume seeds (Caldecott, 1986), and fiber is a larger portion of the diet in temperate macaques than in tropical ones (Hanya, 2004). Additionally, both *M. fuscata* and *Macaca sylvanus* are known to eat tougher foods than other macaques (Izawa and Nishida, 1963; Suzuki, 1965; Drunker, 1982; Constantino, 2007).

Ecological differences among macaques led some authors to use an alternative classification that divides macaques into "weed" (those which thrive in conditions of human disturbance) and "non-weed" (those which thrive away from human disturbance) macaques species (Richard et al., 1989; Thierry et al., 2001). *Macaca fascicularis* is the only weed macaque in this sample. *Macaca fascicularis* has an extensive range in Asia, from Bangladesh to the Philippine Islands, and it inhabits many different kinds of habitats throughout its range, including urban parks. It is rare in submontane primary forests but otherwise it is ubiquitous, favoring especially secondary forests near human settlements, rivers, and mangrove swamps (Richard et al., 1989). *Macaca cyclopis*, which is part of the broader *M. fascicularis* group, is known in modern times to have lived near human settlements, but it has retreated to subtropical and temperate hardwood forests and become elusive (Richard et al., 1989). Although broadly sympatric with *M. fascicularis*

(Rodman, 1991), *M. nemestrina* predominantly favors dense primary forests, either evergreen (as in Thailand, Fooden, 1971) or rain (Crockett and Wilson, 1980).

Group 4: Papionins

Table 1.4 Ecological divisions of the taxa of papionins examined in the following analyses. An asterisk denotes the initial taxon chosen for analyses; the selection criteria for all of the taxa are described in the text.

Sympatric	Allopatric	Other
*Papio cynocephalus**	*Papio ursinus*	*Papio anubis*
Cercocebus galeritus	*Cercocebus atys/torquatus*	

Papionins are a pan-African clade of cercopithecoids that split from macaques c.8-6 million years ago (Page et al., 1999; Steiper and Young, 2006; Perelman et al., 2011). Many authors have suggested that members of the papionin clade, especially baboons, may offer comparative models for understanding human evolution (Hall and DeVore, 1965; Dunbar, 1976, 1983; Jolly 1970, 2001; Delson, 1992; Lee-Thorp et al., 2003; Elton, 2006; Sponheimer et al., 2006). Savanna baboons likely diverged from other baboon populations during the time in which hominins began diverging into gracile and robust lineages (Codron et al., 2008). Among the living primates, papionins are one of few groups to consume a sizeable quantity of C_4 food items and signals of C_4 plants are indicated in several hominin diets (Lee-Thorpe, 2003; Peters and Vogel, 2005; Sponheimer, 2005, 2006; Codron et al., 2008). *Theropithecus gelada*, the last representative of its genus, may be the closest modern analogue to *P. boisei*, as the C_4 isotopic signatures of *P. boisei* closely match those of extinct species of *Theropithecus* (Codron et al., 2005; Cerling et al., 2011; Lee-Thorp, 2011; Cerling et al., 2013). The diets of *Theropithecus* and *Papio* suggest that C_4 signals detected in fossil hominin diets

may have originated from the consumption of grass, sedges, or insects that eat these items (Sponheimer et al., 2005, Codron et al., 2008).

Although this dissertation includes a sample of *T. gelada*, it is not a suitable comparison for understanding the potential effects of sympatric competition in the evolution of *Paranthropus* and *Homo* because there are no living congeners to *T. gelada* to represent an allopatric relationship. Instead, this dissertation focuses on its close relatives, the members of *Papio*, which form several species across Africa. Like hominins, the members of *Papio* diverged relatively recently and there are many questions concerning the processes of speciation and hybridization in this clade (Jolly et al., 1997, 2011; Jolly, 2001; Zinner et al., 2009; Keller et al., 2010). *Papio cynocephalus* was designated as the target species because it has extensive dietary overlap with a close relative, *Cercocebus galeritus*.

Theropithecus and *Papio* split from their common ancestor c.4 million years ago (Page et al., 1999) and the divergences within *Papio* are younger than 2 million years old (Zinner et al., 2009). On the basis of mitochondrial DNA, it is thought that a *Papio ursinus* clade emerged first, with *P. cynocephalus* diverging from this group around 0.74 million years ago (Zinner et al., 2013). This was followed by a clade including both *Papio anubis* and *Papio hamadryas*, which diverged from one another 0.39 million years ago (Zinner et al., 2013). The phylogenetic reconstruction of this clade is made much more complicated by species which have different divergent times indicated by their molecular phylogenies but similar pelages that hinder their identifications in the field and in museums (Keller et al., 2010; Zinner et al., 2011; Jolly et al., 2011).

It is possible that populations of *Papio* exert sympatric pressure on one another and that both sympatric and allopatric taxa of this genus could be considered in one group, as is the case with the proposed Groups 3 and 5 in this analysis. However, the confusion over the species within this genus and their relative potential to interbreed complicates any analysis of species-level sympatric competition. Instead, this dissertation examines the genus-level sympatric or allopatric relationships between *Papio* and *Cercocebus*. *Cercocebus* forms a sister-clade to *Mandrillus*, which for many years was thought to be more closely-related to *Papio* (Thorington and Groves, 1970; Szalay and Delson, 1979). The *Cercocebus-Mandrillus* clade split from the *Theropithecus-Papio* clade c. 5 million years ago (Page et al., 1999). Like other papionin clades, there are some unresolved aspects of the phylogeny of *Cercocebus*. *Cercocebus torquatus* is distinctly related to mandrills, but *C. galeritus* may belong to a different genus divergent from both *C. torquatus* and mandrills (Harris and Disotell, 1998). This clade may therefore be paraphyletic. *Cercocebus atys* is closely-related to *C. torquatus* and was thought for many years to be a subspecies of *C. torquatus* (Groves, 2005). However, divergence times between these two species are not well established.

The dietary differences between *Papio* and *Cercocebus* inform the potential sympatric competition of *Paranthropus* and *Homo*. Cercocebids are generally hard-object feeders, and *Cercocebus atys*, the sooty mangabey, has particularly molarized premolars that suggest it is a comparator for understanding the molarized premolars of *P. boisei* (Daegling et al., 2011). In contrasts to cercocebids, baboons tend to be more generalist and in some populations eat meat (Morris and Goodall, 1977; Hamilton and Busse, 1982; Rhine et al., 1986). Sympatric overlap occurs between *Papio* and

Cercocebus in the region of the Tana River of East Africa, where *P. cynocephalus* is sympatric with *C. galeritus*. The two taxa have a high degree of dietary overlap (Wahungu, 1998), with the largest proportions of both their diets being doum palm and wild date (Bentley-Condit, 2009). *Papio cynocephalus* also consumes fruit, seeds, some grasses, and corms, while *C. galeritus* also eats many fruits and seeds (Wieczkowski, 2009).

The target speices of this analysis was *P. cynocephalus*, a taxon with a high degree of dietary overlap with *C. galeritus*. *Papio ursinus*, which does not overlap with any cercoceboids, was therefore chosen as the allopatric taxon. The sample sizes of *P. cynocephalus* and *P. ursinus* were relatively small. Therefore, the two hypotheses concerning within-genus variation had sample sets supplemented by the inclusion of *P. anubis* (Table 1.4).

Group 5: Tamarins

Table 1.5 Ecological divisions of the taxa of tamarins examined in the following analyses. An asterisk denotes the initial taxon chosen for analyses; the selection criteria for all of the taxa are described in the text.

Sympatric	Allopatric
*Saguinus labiatus**	*Saguinus geoffroyi*
Saguinus fuscicollis	*Saguinus mystax*

Although not closely-related to hominoids, callitrichines are perhaps the most well-studied sympatric primate populations (Crandlemire-Sacco, 1988; Thorington, 1988; Rylands, 1989; Norconk, 1990; Bicca-Marques, 1999; Heymann et al., 2000; Porter, 2001; Rehg, 2010; Rylands et al., 2011). Callitrichines have a high degree of habitat and dietary overlap and sometimes travel in mixed-species troops (Heymann and Smith, 2000), yet they retain significant differences in aspects of their diet (Porter, 2001) and

morphology (Bicca-Marques, 1999). Additionally, the premolar morphologies of sympatric *Saguinus* species are known to differ significantly (Schroer and Wood, 2011), and the compositions of their diets are comparatively well known (Porter et al., 2001; Schroer et al., 2012). In light of the specific research questions of this dissertation, which address premolar morphological variation in closely-related primates and possible character divergence in sympatric populations of closely-related primates, the callitrichines are an appropriate model for comparison.

One of the longest field studies of sympatric callitrichines concerns the *Saguinus fuscicollis* (the brown-mantled or saddle-backed tamarin)*/Saguinus labiatus* (the white-lipped, red-bellied, or red-chested moustached tamarin) community of San Sebastian in Pando, northern Bolivia (Buchanan-Smith, 1990; Porter, 2001). This region of the Amazon is a sandy-clay, tropical forest. Analysis of the postcanines in this community demonstrates that larger P_4s characterize *S. labiatus* (Schroer and Wood, 2011) and that fungus, which forms a portion of the diet of *S. labiatus*, is quite tough (Porter et al., 2001; Schroer et al., 2012). *Saguinus labiatus* is therefore the target species in this group.

Saguinus geoffroyi (Geoffroy's tamarin), *Saguinus oedipus* (the cottontop tamarin), and several other species of tamarins live in isolated populations, and several species are widely available in museum collections. Among the large-bodied tamarins with similar ecologies to *S. labiatus, Saguinus mystax* (the moustached tamarin) and *S. geoffroyi* were chosen as the taxa for comparison due to their available sample sizex and comparatively better known diets (Madden et al., 2010) and behavioral ecologies (Garber, 1991).

All tamarins have similar ecological characteristics, with most species living in fragmented forests with a high diversity of food resources (Garber, 1988; Nickle and Heymann, 1996; Schnitzer and Carson, 2001; Madden et al., 2010). Among the Pando tamarins, *S. fuscicollis* and *S. labiatus* have a high degree of dietary overlap, although *S. labiatus* feeds more frequently on fruits and nectar and less on insects that *S. fuscicollis* (Porter, 2001). The extent of gummivory is approximately the same in both species. The dietary breadth of other tamarin species is similar to those of the Pando tamarins (Madden et al., 2010).

Tamarins belong to a large group of primates, the platyrrhines or New World Monkeys. Platyrrhines diverged from catarrhines, Old World monkeys and apes, c.25-20 million years ago (Goodman et al., 1998; Steiper and Young, 2006; Chatterjee et al., 2009). Although divergence times are not well-known for this clade, aspects of the morphology and genetics of tamarins suggests that *S. fuscicollis* is closely-related to a clade of large-bodied tamarins that includes both *S. labiatus* and *S. mystax* (Cropp et al., 1999). The phylogenetic relationship between *S. geoffroyi* and other tamarins is unresolved.

The tamarin group is summarized in Table 1.5. All taxa from all groups are summarized in Table 1.6 along with sample sizes for each taxon. A phylogeny of the taxa included in this study pictured in Figure 1.1 with divergence times (when available).

1.9 Conclusion

The selection of closely-related primates in sympatric and allopatric populations provides a comparative sample for increasing our understanding of the morphological differences in the dental morphology of the species of *Paranthropus* and the proposed

sympatric divergence between *Paranthropus* and early *Homo*. Comparison of fossil hominin morphologies with the diverse morphologies seen in several primate lineages will contextualize the variation observed in the fossil record and will aid in testing evolutionary hypotheses to explain that variation. Because of the significance of molarized premolars for reconstructing the relationships among *Paranthropus* taxa and its potential dietary divergence with early *Homo*, this dissertation will use this comparative sample to test three hypotheses concerning molarized premolars. The three studies included in this dissertation will address the patterning of relative occlusal area of molarized premolars and the molar row, the pattern of integration of occlusal structures in molarized premolars and adjacent teeth, and the divergence between these characters in the premolars of sympatric and allopatric populations. In doing so, this dissertation will shed light upon the evolutionary significance of molarized premolars and on the phylogenetic relationships of *Paranthropus* taxa and their ecological context.

Table 1.6 Fossil and extant primates considered in analysis.

Taxon	N	♀	♂
Fossil hominins		-	-
Australopithecus africanus	10	-	-
Australopithecus afarensis	10	-	-
Homo ergaster	10	-	-
Homo habilis	6	-	-
Homo rudolfensis	5	-	-
Paranthropus boisei	16	-	-
Paranthropus robustus	15	-	-
Group 1: African apes	62	22	40
Gorilla beringei	14	6	8
Gorilla gorilla	29	7	22
Pan (*Pan troglodytes*)	19	9	10
Group 2: Asian apes	90	50	40
Hylobates agilis	17	6	11
Hylobates klossii	8	5	3
Hylobates lar	18	11	7
Pongo abelii	9	5	4
Pongo pygmaeus	38	23	15
Group 3: Macaques	113	59	54
Macaca cyclopis	12	5	7
Macaca fascicularis	52	32	20
Macaca fuscata	11	8	3
Macaca nemestrina	38	14	24
Group 4: Papionins	116	31	85
Cercocebus atys	8	4	4
Cercocebus galeritus	8	4	4
Cercocebus torquatus	18	3	15
Papio anubis	55	12	43
Papio cynocephalus	9	4	5
Papio ursinus	19	6	13
Theropithecus gelada	9	2	6
Group 5: Tamarins	73	35	38
Saguinus fuscicollis	14	11	3
Saguinus geoffroyi	30	12	18
Saguinus labiatus	15	6	9
Saguinus mystax	14	6	8

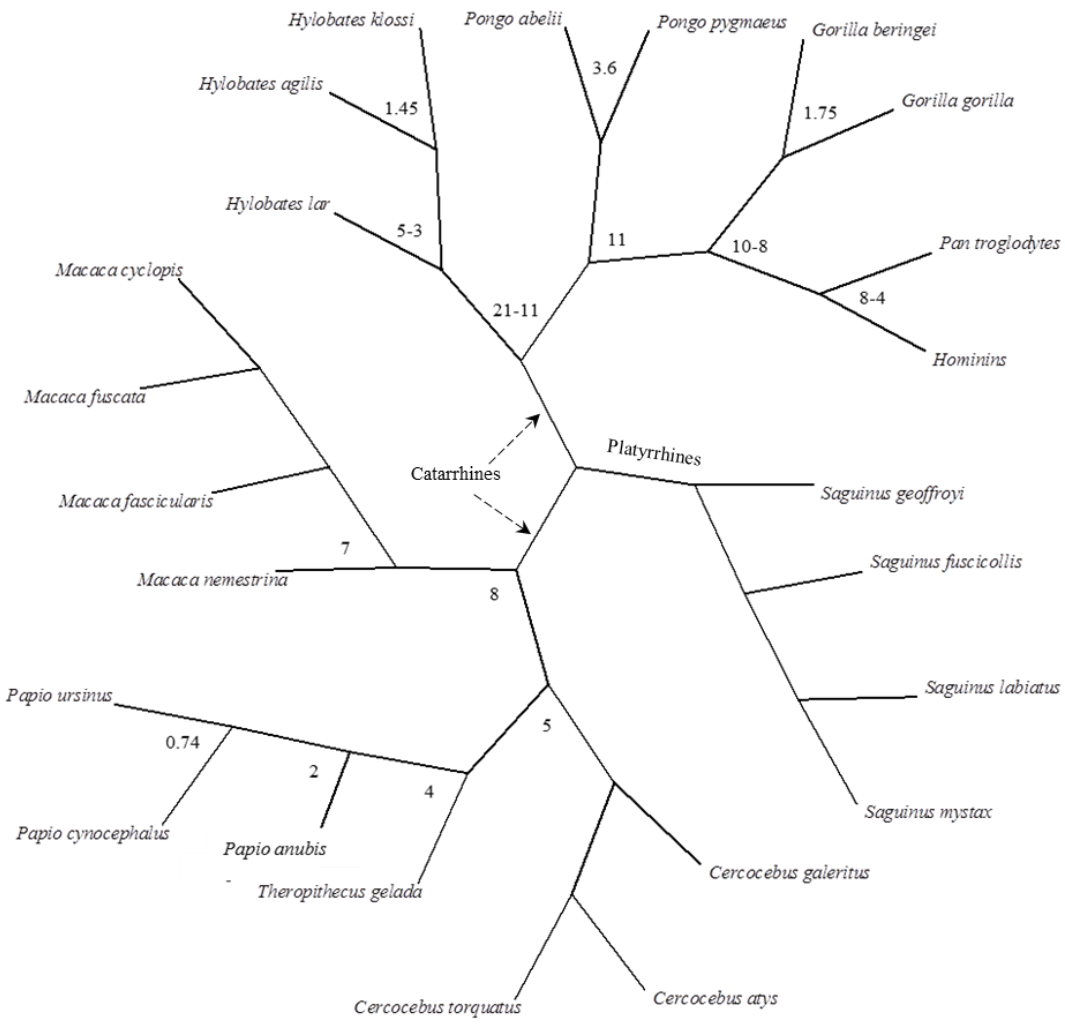


Figure 1.1 A radial phylogeny of primate taxa included in this study. Numbers indicate estimates of divergence times, when known. Estimates are in millions of years and drawn from morphological, molecular, and geological sources (see text for citations). Tree constructed in TreeView.

Chapter 2: Modeling the morphological relationship of primate postcanines through the inhibitory cascade

2.1 Introduction

Teeth are the most common elements preserved in mammalian fossil assemblages (Grine and Martin, 1988; Wilson et al., 2012), and their complex occlusal morphology is the source of many character traits used for taxonomy and phylogeny reconstruction. A prominent example of the importance of dental characters in phylogenetic analysis is *Paranthropus*, a fossil hominin clade, whose large teeth and molarized premolars have been argued to represent synapomorphies of the *Paranthropus* clade (Wood and Chamberlain, 1986; 1987; Wood, 1988; Strait et al., 1997; Wood and Richmond, 2000; Kimbel et al., 2004; Strait and Grine, 2004).

Evolutionary developmental biologists have begun to determine the regulatory pathways that govern the process of tooth formation including the details of occlusal morphology (e.g., numbers and types of cusps) that result from this process (Jernvall et al., 2000; Jernvall and Thesleff, 2000; Salazar-Ciudad and Jernvall, 2002, 2004, 2010; Tummers and Thesleff, 2003, 2009; Jarvinen et al., 2006; Munne et al., 2009; Renvoise et al., 2009). Such research has helped unravel the complicated relationship between genotype and phenotype (Arnold, 1992; Hall, 2003; Polly, 2008) and the influence of molecular processes on macroevolutionary trends (Peterson et al., 2007; Raff, 2007). In particular, understanding the mechanisms of tooth development aids in quantifying the sources of constraint on tooth evolvability and provides a critical link for understanding how adaptive modifications may be guided by existing regulatory pathways (Asahara, 2013; Halliday and Goswami, 2013).

Due to the lack of preserved genetic information, many fossils cannot be studied within a developmental context. However, a recent developmental model called the inhibitory cascade (IC model), proposed by Kavanagh and colleagues (2007), has been used to reconstruct macroevolutionary trends in mammalian teeth and may allow researchers to generate hypotheses about possible regulatory pathways in fossil mammals. By severing lab mouse (*Mus musculus*) lower molars from the mesenchyme in cell culture, Kavanagh and colleagues showed that the absence of anterior molars speeds the rate of initiation and subsequent size of posterior molars. They further hypothesized and experimentally validated their proposal that varying the levels of genetic activation and inhibition during dental development will result in molar rows with different phenotypes. Their simplified model to describe the genotype-phenotype relationship between tooth size and tooth position is:

$$y = 1 + [(a - i)/i](x - 1),$$

where y is the relative molar size estimated from occlusal area, x is the position of the molar in the tooth row, a is the strength of the genetic activators, and i is the strength of the genetic inhibitors.

Because teeth develop in sequence and because the size of anterior teeth affects the size of posterior teeth, this model can be expanded to test the "ratcheting" of the cascade through the entire molar row. The above equation gives, for the first three molars, the prediction that $M_1 = 1$, M_2=a/i, and M_3=2a/i-1. The IC model predicts a slope of 2.0 and an intercept of -1.0 to describe the relationship between the M_2:M_1 and M_3:M_1. Expressed another way, M_2 will consistently be 1/3rd the total area of the molar row ($M_2/(M_1 + M_2 + M_3) = (a/i)/[1 + a/i + (2a/i - 1)] = 1/3$; Kavanagh et al., 2007). A ratio

value that is greater than 1 suggests weak inhibition (i.e., a very high a/i) by M_1 on the posterior molars, which will result in a molar row increasing in size from front to back. Variability is expected to be higher for the M_3/M_1 ratio than the M_2/M_1 ratio, as the slope in the direction of M_3 is twice that of the other molars (Kavanagh et al., 2007; Renvoise et al., 2009). A schematic of the IC model is provided in Figure 1.1.

Application of this model to extant mammals and extinct mammal-like taxa indicates that the inhibitory cascade model describes the plesiomorphoic condition for all mammals (Halliday and Goswami, 2013). Deviations from this model indicate derived changes in the effects of the inhibitory mechanism, possibly allowing for decreased constraints upon variations in dental morphology. Deviations from this model are thus thought to relate to the evolution of specialized teeth, such as carnassials (Asahara, 2013; Halliday and Goswami, 2013). Few studies to date have included an examination of the IC model in primate postcanine teeth, although preliminary analyses of a few primate genera suggest that primates generally conform to the IC model (Polly, 2007; Halliday and Goswami, 2013).

This study applies the IC model to a much larger sample of primate specimens with greater genus-level diversity. It will test whether the IC model predicts the relative sizes of primate molars and it will determine if any phylogenetic signals are present in cascade patterning. Previous applications of the IC model in other mammalian orders have shown that molar size proportions are similar within clades (Wilson et al., 2012), and this study will specifically examine whether similarities in relative molar sizes describe primate genera. It is likely that most primates will have plesiomorphic molar proportions, in which case the M_2 will always be a third of the total molar area. This

study predicts that the few species which do derive from the plesiomorphic condition will share this derived pattern with their congeners.

Additionally, this study expands the application of the IC model by also considering premolar-molar proportions. Molarized premolars, such as those observed in *Paranthropus* and other primate clades, share phenotypic characteristics with the molars and have been hypothesized to share aspects of their development, such as the formation of more than two main cusps (Robinson, 1956; Butler, 1997, 2000; Jernvall et al., 2008). Although premolars are a different developmental class of teeth from molars (Avery, 2001; Ash and Nelson, 2003), they often share the same function as molars and lie just anterior to them in the jaw (Lucas, 2004). An examination of murine clades with and without the last premolar (P_4) found that the variability of the first molar (M_1) increased in the absence of the adjacent P_4, suggesting that the presence of a P_4 constrains the morphology of the M_1 and subsequently the morphology of the entire molar row (Labonne et al., 2012). It is therefore reasonable to expect that premolar morphology, and the relative size of molarized premolars in particular, can be predicted by the IC model.

To test whether the same pattern of enlargement describes species included in *Paranthropus*, the potential for phylogenetic signals will also be examined in this proposed premolar-molar cascade. As in the molar cascade, it is predicted that primates within the same genus will share the same premolar cascade pattern. Finding evidence of similar patterns in extant primate genera but not in *Paranthropus* would weaken the case for *Paranthropus* monophyly. In the case where one taxon of *Paranthropus* follows the plesiomorphic condition and a second taxon of *Paranthropus* follows a derived pattern,

this result would be especially indicative that the mechanisms underlying premolar enlargement are not the same in these two taxa (i.e., it is not the same character). Alternatively, the absence of genus-level similarities in extant primates would suggest that the IC model does not account for the ratio of premolar to molar size in extant primates and is not able to assess the premolar enlargement observed within the *Paranthropus* clade.

2.2 Materials and Methods

2.2.1 Sample

Lower jaws of extant primate genera were obtained from the collection of the National Museum of Natural History, Washington DC, and the Natural History Museum in London. Specimens were photographed using a Canon Digital Rebel XT camera fitted with a macro lens. For each photograph, specimens were oriented to maximize the occlusal area of each tooth. Levels on the camera and photography stand were employed to ensure the occlusal area was parallel to the lens of the camera. Teeth were positioned so as to occupy less than one third of the frame and therefore minimize distortion. A scale was set and leveled in the occlusal plane of the teeth. Maximum mesiodistal and buccolingual diameters for each postcanine tooth were obtained via scaled measurements in TPSDig (Rohlf, 2009), and estimates of occlusal areas were calculated by multiplying these diameters (Kavanagh et al., 2007; Polly, 2007; Wilson et al., 2012; Halliday and Goswami, 2013). Only specimens with complete postcanine rows were evaluated; data from the left sides were used unless teeth on that side were missing. All specimens were adult and from wild populations. Where possible the samples for each genus were sex-

balanced. Samples for each genus were a mix of species, except in the case of *Pan*, as no specimens of *Pan paniscus* were available for study.

To provide a suitable comparison for interpreting the extremely large premolars observed in the fossil hominin genus *Paranthropus*, the sample included several primate genera with morphological or phylogenetic similarity to *Paranthropus*. Species of *Cercocebus*, *Gorilla*, *Pongo*, *Macaca*, *Saguinus*, and *Theropithecus* have been previously used as morphological and ecological analogues for the postcanine megadontia and robust craniofacial morphology seen in *Paranthropus* (Strait et al., 2007; Vogel et al., 2008; Cerling et al., 2011; Daegling et al., 2011; Schroer and Wood, 2011; Wood and Schroer, 2012). Catarrhine primates compose the majority of the resulting sample, with *Saguinus* the only platyrrhine representative. The absence of the M_3 in this clade results in its inclusion only in the analysis of the proposed premolar-molar cascade. *Cercocebus*, *Macaca*, *Papio*, and *Theropithecus* are cercopithecoids; *Gorilla*, *Pan*, and *Pongo* are hominoids.

For both extant and fossil specimens, only individuals with complete M_1-M_3 or P_4-M_2 series were analyzed. Extensively worn specimens (i.e., occlusal wear great enough to mask the identification of individual cusps and interproximal wear that affected >20% of the occlusal margin) were not included in the extant sample. For teeth with moderately worn cusps, the location of the cusp was estimated from the center of the wear facet (Bailey, 2004; Gomez-Robles et al., 2008). For teeth with moderate interstitial wear the worn margin was reconstructed by approximating the curvature of the margin from overall crown shape (Wood and Uytterschaut, 1987; Bailey and Lynch, 2005).

Similar methods were employed for the fossil teeth, but fossil teeth were not included if <90% of the likely occlusal areas was preserved.

In addition to *Paranthropus*, two other fossil hominin genera were also included in the analysis: *Homo*, which includes modern humans, and *Australopithecus*, the likely ancestral clade of both *Paranthropus* and *Homo* (Strait et al., 1997). In this analysis, the *Homo erectus/ergaster* group includes the Dmanisi fossil hominins (Rosas et al., 1998; Gabunia et al., 2000; Vekua et al., 2002). For reasons of sample sizes, the East African species *Homo habilis* and *Homo rudolfensis* were pooled as an "early *Homo*" sample; results from analyses that assessed the two species separately did not reveal any significant differences. Measurements of fossil postcanines were obtained in the same manner as the extant sample from precision casts of fossil material in collections of The George Washington University and the University of Arkansas, or the data were taken from the literature. All specimens were from individuals with erupted M_3s, but sex was not controlled. Fossil specimen numbers and the sources of measurements are given in Table 2.1 and the individual measurements obtained from each fossil tooth are given in Table 2.2.

To calculate intra-observer error, a sample of 45 individuals representing all of the taxa in the extant primate sample was measured again at least two months after the initial measurements were taken. Technical error for linear measurements was ±0.1 mm for *Saguinus* and ±0.4 mm for all other taxa.

2.2.2 Analysis

In order to compare the results of this study to previous applications of the IC model, model II reduced major axis regression (RMA) was employed to examine the

correlations between relative occlusal areas in the postcanines. While there are reservations about the use of RMAs to assess any test other that the ratios of the standard deviations of y on x (Smith, 2009), the test is used in CI studies because a single line defines the ratio between x and y (i.e., the relationship of the data is symmetrical). Additionally, data considered to falsify the predictions of the IC model are those with regressions featuring a slope whose 95% confidence intervals do not include 2.00. Reduced major axis regression is prone to the tendency that small sample sizes have a correlation with a slope of 1; this drives the data away from the slope of 2 predicted by the IC model. Small sample sizes will also produce wide confidence intervals, suggesting that small samples that deviate from the IC model do so significantly.

All RMA regressions were conducted using RMA software developed in the C programming language with standard linear regression error estimates (Bohonak, 2004). Measures of statistical accuracy were bootstrapped 100 times. Even when the significance values for the r^2 variable were low, regressions with 95% confidence intervals that included the 2.0 slope and -1.0 intercept predicted by the IC model were determined "validated" as was the practice in previous applications of the IC model (Renvoise et al., 2009; Wilson et al., 2012; Halliday and Goswami, 2013). Prioritizing the relationship between 95% confidence intervals is standard for IC modeling, as it indicates whether the regression differs significantly from the regression predicated by the IC model (Kavanagh et al., 2007; Renvoise et al., 2009; Wilson et al., 2012; Halliday and Goswami, 2013). Two cascades were tested using the IC model: a standard M_1-M_3 cascade derived from the original IC model and a modified P_4-M_2 cascade that incorporates the occlusal area of the posterior premolar. In each case, the two ratios used

in the analysis are the occlusal areas of the intermediate tooth to the anterior tooth and the most posterior tooth to anterior tooth (i.e., M_2:M_1 and M_3:M_1 for the molar cascade and M_1:P_4 and M_2:P_4 for the proposed premolar-molar cascade).

To assess general variation in the postcanines of primate genera, means, standard deviations, and coefficients of variation were also calculated for the occlusal area of each postcanine tooth, P_4-M_3. These results are summarized in Table 2.3. Results of a MANOVA conducted in R indicated that all postcanine ratios for all taxa are statistically distinct from one another (Table 2.4). A Pillai trace, which estimates the amount of variance in dependence variables that can be explained by the greatest separation of independent variables, was applied to protect against Type I errors in small sample sizes. Small samples were of a particular concern in the comparative analyses of *P. boisei* and *P. robustus*, and Student's t-test was employed to determine the likelihood that the slopes of the regression lines for *P. boisei* and *P. robustus* were statistically different (Table 2.5).

2.3 Results

2.3.1 Molar cascade

RMA regressions of the molar ratios in extant primates consistently have 95% confidence intervals that include the predicted slope and intercept of the IC model, whether they are examined at the species or genus level (Table 2.6a). The single exception among extant primates is the genus *Papio*, which borders on a significant fit and whose component species each conform to the predictions of the IC model. Based on the results of this analysis, the IC model can be generally applied to extant primates. On the genus-level, the fossil hominin taxa *Australopithecus* and *Homo* also conform to the

predictions of the model, although at the species-level distinction, *Australopithecus africanus* does not. The molar proportions of *Australopithecus africanus* are described by the relationship $M_1<M_2>M_3$, a rare pattern among mammals that requires both low inhibition levels and a premature stop to M_3 development (Kavanagh et al., 2007; Polly, 2007; Labonne et al., 2012).

In this analysis, the only genus that does not conform to the IC model is *Paranthropus*. However, if *Paranthropus* is divided into its component species and RMA regression performed on separate *Paranthropus boisei* and *Paranthropus robustus* samples, it appears that the morphology of *P. boisei* is driving this divergence from the IC model. If *P. robustus* is considered alone, the 95% confidence intervals of its regressed molar ratios include the slope and intercept of the IC model. As in the case of *A. africanus*, *P. boisei* is best described by proportions in which the M_2 is larger than either the M_1 or M_3. When interpreting these results, however, it should be noted that a Student's t-test of the regression slopes of *P. boisei* and *P. robustus* showed that they did not significantly differ. The small size of the fossil samples may therefore be affecting the results of the RMA analysis of molar proportions.

2.3.2 Premolar-molar cascade

The macroevolutionary trend observed in the molar cascade is not observed in the proposed premolar-molar cascade in extant primate genera. With the exception of *Papio*, no extant or fossil genera appear to conform to the IC model (Table 2.6b). The morphology and the larger sample size of *Papio anubis* appears to drive this result, as at the species-level the IC model can predict the premolar-molar proportions of this taxon. Other species that also appear to conform to the IC model in their premolar-molar

portions are *A. africanus* and *P. boisei*. If the component species of *Australopithecus* and *Paranthropus* are regressed separately, the 95% confidence intervals of *A. africanus* and *P. boisei* include the predictions of the IC model. The 95% confidence intervals of *A. afarensis* and *P. robustus* indicate that they continue to follow the pattern of extant primates. All extant and fossil taxa, with the exception of *Saguinus* have a general increase in the relative size of the teeth from the $P_4<M_1<M_2$. In *Saguinus*, the M_1 is the largest tooth in this series.

2.3.3 Regression plots

The results of the RMA are summarized in linear regression plots of the molar cascade and the proposed premolar-molar cascade (Figure 2.2 and 2.3). The proportions of the molar occlusal areas of extant primates are highly correlated (Figure 2.2 and 2.3, $r^2 = 0.8$). When the data are divided into their superfamilies, it becomes apparent that cercopithecoids follow the trajectory of the IC model more closely than the hominoids (Figure 2.4). With the exception of *Pan*, a number of individual hominoids deviate from the model by having more similarly-sized M_2 and M_3s. *Pan* is distinct from the other genera in this study by having a number of individuals with consistently smaller M_2 occlusal area relative to both M_1 and M_3. Although hominoid individuals deviate more from the model than cercopithecoid individuals, the 95% confidence intervals of the slope and intercept of the regression lines of molar proportions in hominoids, with the exception of *Paranthropus*, still include the IC model. Indeed, some individuals of *P. boisei* appear to have a different relationship between their molar occlusal ratios than other taxa under examination, having a much narrower range of M_3:M_1 values than *P. robustus*, even when their M_2:M_1 values are similar (Figure 2.5).

In the proposed premolar-molar cascade, the premolar-molar ratios of extant primates are not highly correlated (Figure 2.6 and 2.7, $r^2 = 0.20$). Almost no primate genera and few primate species have premolar-molar ratios described by the predictions of an applied IC model. However, the premolar-molar ratios of catarrhine primates can be generally described by the relative size sequence $P_4<M_1<M_2$, which is similar to the pattern of relative size increase observed in the original molar cascade (i.e., $M_1<M_2<M_3$). When the data are divided by superfamily, catarrhines tend to have premolar-molar proportions above the trajectory of the proposed IC model and homionids tend to fall below it (Figure 2.8). This suggests that for equivalently sized P_4s, cercopithecoids tend to have larger M_2s compared to hominoids. *Saguinus* is distinct from other primate genera in this analysis, with a postcanine cascade described as $P_4<M_1>M_2$.

With respect to the proposed premolar-molar cascade, fossil hominins tend to follow the general hominoid pattern. However, some individuals, and notably several of both species of *Paranthropus*, are more similar to the pattern observed in cercopithecoids. Most specimens of
P. boisei are better described by the cercopithecoid pattern, and the M_1:P_4 ratio in *P. boisei* is smaller than the values for individuals of *P. robustus* with similar M_2:P_4 ratios (Figure 2.9).

2.4 Discussion

2.4.1 Molar cascade

This study found that the macroevolutionary trend predicted by the IC model describes the molar size ratios of extant primates. As suggested by previous studies of molar proportions in mammals generally, the IC model likely describes the plesiomorphic

condition for primates. As a group, catarrhines can generally be described by the molar ratio pattern $M_1<M_2<M_3$, with hominoids having more similarly-sized M_2s and M_3s than the cercopithecoids. As the IC model is derived from experimental data quantifying rates of activation and inhibition in murine teeth, these results suggest that hominoids have a derived developmental pathway in which either 1) there is less activation on the posterior molars or 2) there is more inhibition on these molars. Either of these two changes, or a combination, would result in constraints upon the size variation of the M_3, producing a pattern of $M_1<M_2\approx M_3$.

Heterochrony, especially changes in the timing of first molar development and subsequent initiation of the development of the posterior molars, may be a factor in the changing levels of activation and inhibition implicated in the hominoids. Evidence from dental microstructure suggests that the hominin lineage has undergone significant changes in the rate of postcanine development, including a much later emergence of the M_1 in *Homo ergaster/erectus* and later hominins (Dean et al., 2001). It is possible that the same developmental changes that cause later emergence of the M_1 in the hominoids relative to the cercopithecoids may be the precursor to the developmental changes that cause even later emergence in later *Homo*. The later emergence of the M_1 may also relate to the M_2s and M_3s being similar in size and it might be the first stage of a process that results in the reduced M_3s described in several hominoid lineages (Nanda, 1954; Garn, 1962, 1963; Garn et al., 1964; Frisch, 1967, 1973; Lavelle et al., 1970, 1973; Plavcan and Gomez, 1993).

The extant primates examined in this study included many of the closest relatives of fossil hominins. Because the IC model describes a plesiomorphic mammalian

condition and the likely plesiomorphic condition of primates, it is expected that the IC model can also describe morphological trends in the postcanines of fossil hominins. Indeed, application of the IC model to fossil hominin molars shows that fossil hominin taxa follow a similar pattern of molar proportions to extant primates, suggesting that they generally have not deviated from the plesiomorphic condition. However, two notable exceptions are *A. africanus* and *P. boisei*, which have larger second molars than predicted by the IC model. Current phylogenetic reconstructions suggest that it is unlikely *A. africanus* is ancestral to *P. boisei*; the similarity in the relative size of the M_2 may therefore be either evidence of a close phylogenetic relationship that is not supported by other morphological evidence or it is evidence of a homoplasy within the hominin lineage.

The unexpectantly large M2s of *A. africanus* and *P. boisei* may relate to an adaptation for increased omnivory compared to other species included in their genera. Bears, condylarths, and mesonychians also deviate in the same manner from the plesiomorphic condition and are true mammalian omnivores (Halliday and Goswami, 2013). Although this is comparison is incongruent with the signal from members of *Homo*, who are also likely to be omnivorous, signals of omnivory in *Homo* may be mitigated by the use of stones tools and fire (Wrangham, 2009). It must also be borne in mind that the departure from the hypothesized plesiomorphic condition in *A. africanus* and *P. boisei* may be an artifact of the small sample sizes of these taxa.

The deviation of *A. africanus* and *P. boisei* from the model is especially notable as species within primate genera generally have the same pattern of molar proportions. This study examined several pairs of species within six catarrhine genera, including some

close relatives of the hominins. In all of the extant primate genera, the species shared a common developmental pattern. The different developmental patterns of members of *Australopithecus* and *Paranthropus* are consistent with those who have expressed doubts about the monophyly of these taxa (Wood, 1988; Strait et al., 1997; Curnoe, 2002; Wood and Schroer, 2012; Foley, 2013).

2.4.2 Premolar-molar cascade

A premolar-molar cascade was not consistently observed in the primate genera or species examined here. However, when the data were considered at the level of superfamily, there is a general division between cercopithecoids and hominoids. Cercopithecoids tend to fall above the predictions of this model, whereas hominoids tend to fall below this prediction. That is to say, for similar P_4:M_1 occlusal area ratios, cercopithecoids tend to have larger M_2s than the hominoids. This is consistent with to the results of the molar cascade, which suggests that hominoids have reduced M_3s compared to cercopithecoids. A change in the regulatory pathway resulting in reduced activation or increased inhibition in the molars may therefore describe the relative occlusal areas of the entire postcanine tooth row.

Although only one ceboid genus, *Saguinus,* was used in this analysis, results suggest that this genus is influenced by a different regulatory pathway than either cercopithecoids or hominoids. In this genus, the P_4-M_2 row follows the pattern $P_4<M_1>M_2$, in which the M_1 is larger than predicted by the IC model. Likely, the unusual pattern in *Saguinus* is due to M_2 being the most posterior postcanine in the jaws of *Saguinus* and may thus be constrained by the size of the ramus (Kavanagh et al., 2007).

Further analysis of other ceboid primates is necessary to determine whether the $P_4<M_1>M_2$ pattern is plesiomorphic or derived within this clade.

There appears to be no correlation between molarized premolars and a premolar-molar cascade. Several species with molarized premolars predicted to conform to a premolar-molar cascade model do not have premolar-molar ratios similar to those observed in the molars (i.e., *Cercocebus atys*), and conversely several species with non-molarized P_4s have premolar-molar proportions similar to the molar proportions (i.e., *Hylobates klossii* and *Papio anubis*). It is unlikely that a premolar-molar cascade built on predictions from the IC model, which was only experimentally tested in molars, can describe relative premolar-molar sizes in primates beneath the level of superfamily. Further testing of this proposed cascade in experimental populations, such as those derived from mouse mutants with artificially induced premolars (Peterkova et al., 2005; Klein et al., 2006; D'Souza et al., 2007) is warranted. The determination of the balance between genetic activation and inhibition in developing premolars will aid in the determination of the factors resulting in molarized premolars.

Within the examination of fossil hominins, the two fossil taxa that deviate from the predicted trajectory of the IC model in their molar cascade follow the predictions of the proposed premolar-molar cascade. Both *A. africanus* and *P. boisei* have premolar-molar ratios described by the IC model. These results are suggestive, but not conclusive, of a frame shift in the development of the mandibular postcanines of fossil hominins. The frame shift hypothesis describes a general disassociation between morphological identity and developmental origin (Wagner and Gauthier, 1999). The hypothesis was first developed in the study of avian digits, which morphologically appear to be

vertebrate digits 1, 2, and 3, but according to developmental criteria they appear to be digits 2, 3, and 4. A frame shift is proposed to have occurred in which the initiation of the 2nd, 3rd, and 4th forming digits have the developmental pathways more typically associated with digits 1, 2, and 3 (Wagner and Gautheir, 1999; Wagner, 2005; Bever et al., 2011). Like digits, teeth are meristic structures composed of serial and similar parts and derived from alterations of a similar developmental theme (Tucker et al., 1998; Jernvall, 2005). It is therefore possible that a frame shift has occurred that pushes the developmental pathway of the M_1 anteriorly by one or more teeth. Additional lines of evidence, such as a consideration of cusp patterning and rates of cusp initiation, may indicate whether or not a frame shift has caused a tooth in the location of the P_4 to have the developmental characteristics of a molar.

While it is tempting to consider that the molar gradient has shifted forward in *A. africanus* and *P. boisei*, the occlusal morphology of the premolars of *A. africanus* and *P. boisei* is quite different. Some researchers have employed the term "hyper-molarized" to describe the close similarity between the P_4 and M_1 in *P. boisei* (Wood and Uytterschaut, 1987; Wood and Constantino, 2007), but the premolars of *A. africanus* do not share this occlusal morphology (Robinson, 1970). These results suggest that changes in relative occlusal area alone cannot account for molarization of the premolars.

The results of this study suggest that postcanine megadontia may not be a synapomorphy of the *Paranthropus* genus. Although both *P. boisei* and *P. robustus* have large postcanine teeth, the developmental processes underlying the formation of these teeth appear quite distinct. Whereas *P. robustus* follows the plesiomorphic pattern for mammals, *P. boisei* appears to have a derived regulatory pathway that results in different

premolar and molar proportions than predicted for mammals generally and for hominoids specifically. A Student's t-test of the regression slopes of *P. boisei* and *P. robustus* particularly implicates differences in the premolar-molar ratios of the two taxa, as the slopes are significantly different even with small sample sizes ($P<0.05$). The slopes of the molar cascade are not significantly different from one another ($P<0.50$), but the molar cascade of *P. boisei* differ from the cascade of *P. robustu* with respect to the IC model. Combined with indirect evidence that the developmental process of premolar molarization may be different in these two taxa (Wood, 1988; Suwa et al., 1994), the results of this study suggests there are critical differences in how postcanine megadontia might have evolved in two of the species presently subsumed within *Paranthropus*. Given these results, it may no longer be prudent to assume that postcanine megadontia is a synapomorphy of *Paranthropus*.

2.5 Conclusion

This study sought to determine whether the IC model predicts the observed relative molar proportions of primates. Additionally, it investigated whether the IC model could be applied to a proposed premolar-molar cascade, especially in primate dentitions that include molarized premolars. The results suggest there are consistent patterns of relative postcanine areas in both primate genera and superfamilies, but inconsistences in the patterns among species within the hominin clade.

The IC model describes relative molar proportions in extant primates generally, and all species within extant primate genera share the same relative molar proportions. Although the IC model could not differentiate among primate genera, it recovered macroevolutionary trends within the cercopithecoid and hominoid clades. In particular, it

demonstrated that hominoids have M_3s that are generally relatively smaller, and thus they are closer in size to the M_2, than those of cercopithecoids. This pattern may be part of the same developmental pathway that results in reduction of the M_3s in modern humans (Smith, 1994; Dean and Lucas, 2009) and chimpanzees (Mahler, 1980; Kinzey, 1984; Swindler, 1998).

Application of the IC model to a proposed premolar-molar cascade was not successful in describing relative postcanine areas in most primate species. A proposed premolar-molar cascade also did not consistently predict the presence of molarized premolars, and it is therefore unlikely that the IC model can account for the interaction of premolar and molar development. Although this proposed premolar-molar cascade does predict the relative postcanine size relationships in two of the fossil hominin taxa, only one of these taxa has molarized premolars. This suggests that P_4 molarization may be a more complex process developmentally than a simple increase in size of the posterior premolar.

Whereas all congeneric extant primates follow similar patterns, two fossil hominin species, one within *Australopithecus* and the other within *Paranthropus*, show different molar proportions. If the plesiomorphic condition for mammals and primates is the IC model, this suggests that species currently included in these two genera have a derived developmental pathway compared to their congeners. Such information should be included in future phylogenetic reconstructions of these genera, particularly since postcanine tooth size and its consequences play a large part in such analyses. If simple measures of tooth size are all that is considered, then this will not capture the type of nuance captured by the present study.

This study is an example of how models derived from the principles of evolutionary development can inform macroevolutionary trends in extant and fossil taxa. By determining how postcanine crown area may be influenced by an inhibitory cascade, it is possible to evaluate dependent relationships between dental morphologies that may otherwise appear as independent traits. The results of the analyses conducted here change our understanding of the evolutionary significance of premolar molarization and postcanine megadontia. As developmental biology continues to illuminate the details of the complex relationships between genotype and phenotype, we must use these new data to improve our attempts to assign taxonomy and reconstruct phylogeny within the hominin clade.

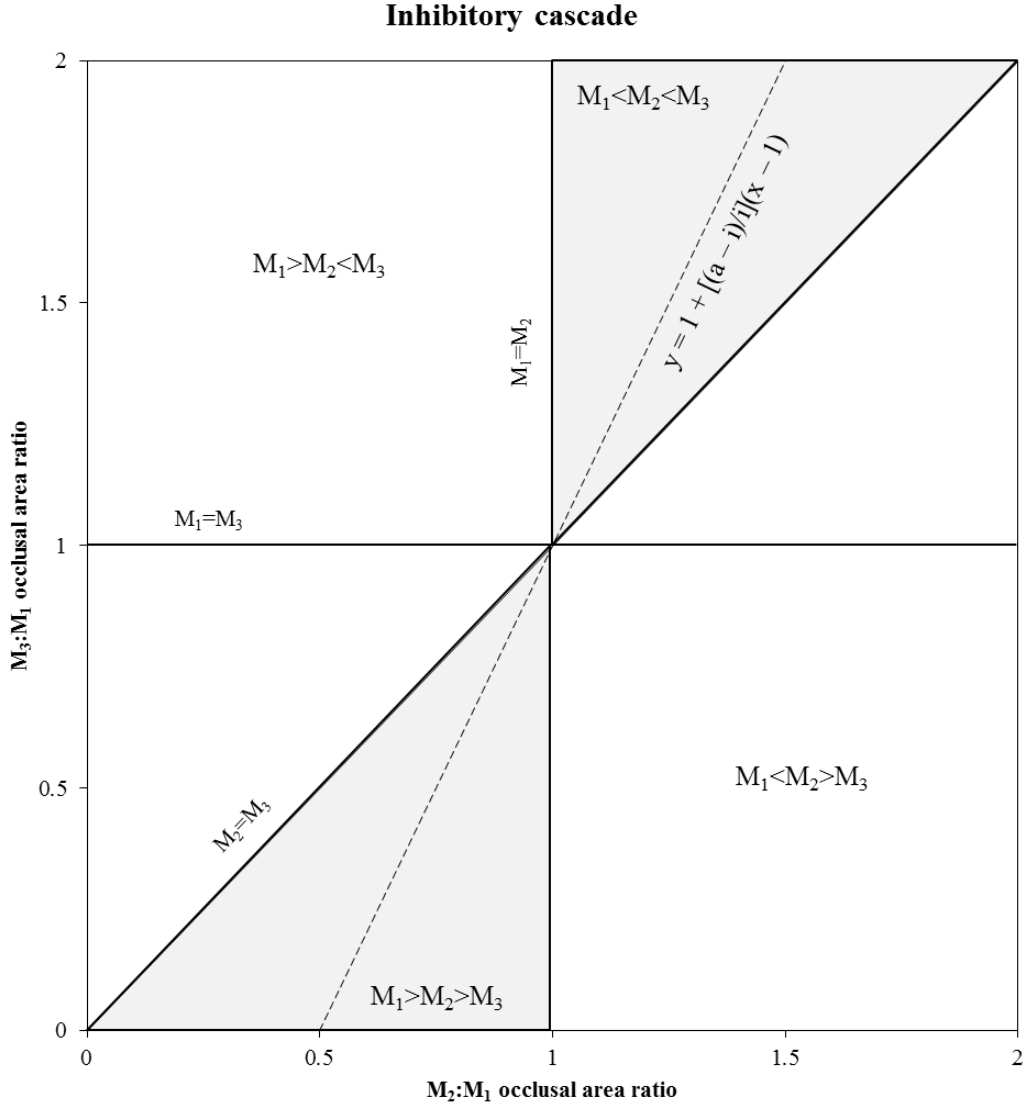


Figure 2.1 The inhibitory cascade (IC) model. This schematic shows the IC model as a dashed line plotting the function $y = 1 + [(a - i)/i](x - 1)$, which describes how the rates of activation and inhibition affect molars as they develop in sequence. M_2:M_1 and M_3:M_1 are ratios of relative molar size. As the ratio of M_2:M_1 ratio increases, the ratio of M_3:M_1 also increases, showing a high degree of gene activation acting along the molar row. The opposite, a decrease in molar ratios, denotes high rates of gene inhibition. Gray shading indicates areas of general size reduction or increase in the postcanine tooth row and is bounded by cases where M_1=M_2 and M_1=M_3.

Table 2.1 Fossil specimens used in the analyses.

Taxon	M_1-M_3 cascade	P_4-M_2 cascade	Source of the data
Australopithecus afarensis	-	AL 123-23	Ward et al., 2010
	AL 198-1	AL 198-1	Ward et al., 2010
	AL 225-8	-	Precision cast
	AL 266-1	AL 266-1	Ward et al., 2010
	-	AL 277-1	Ward et al., 2010
	-	AL 333w-60	Precision cast
	AL 400-1A	AL 400-1A	Precision cast
	LH 4	LH 4	Precision cast
	-	MAK-VP-1/12	Precision cast
Australopithecus africanus	MLD 18	MLD 18	Precision cast
	-	MLD 40	Dart, 1962
	STS 36	STS 36	Precision cast
	STS 52	STS 52	Precision cast
	STW 14	STW 14	Precision cast
	-	STW 327	Precision cast
	STW 384	STW 384	Precision cast
	STW 498	-	Precision cast
Homo ergaster	D211	D211	Martinon-Torres et al., 2008
	D2735	D2735	Martinon-Torres et al., 2008
	KGA-10	KGA-10	Suwa et al., 2007
	KNM-BK 67	KNM-BK 67	Wood, 1991
	KNM-ER 730	-	Wood, 1991
	KNM-ER 992	KNM-ER 992	Wood, 1991
	-	KNM-WT 15000	Wood, 1991
	-	OH 22	Wood, 1991
	SK 15	-	Wood, 1991

Table 2.1 Fossil specimens used in analysis, continued.

Taxon	M_1-M_3 cascade	P_4-M_2 cascade	Source of the data
Early *Homo* (*H. habilis* and *H. rudolfensis*)	-	KNM-ER 1482	Wood, 1991
	KNM-ER 1801	KNM-ER 1801	Wood, 1991
	-	KNM-ER 1802	Wood, 1991
	-	KNM-ER 3734	Wood, 1991
	KNM-ER 60000	KNM-ER 60000	Leakey et al., 2012
	OH 7	OH 7	Wood, 1991
	OH 13	OH 13	Wood, 1991
	OH 16	OH 16	Wood, 1991
	UR 501	UR 501	Bromage et al., 1995
Paranthropus boisei	-	KNM-ER 729	Wood, 1991
	KNM-ER 801	-	Precision cast
	KNM-ER 818	KNM-ER 818	Precision cast
	-	KNM-ER 1816	Wood, 1991
	KNM-ER 3230	KNM-ER 3230	Wood, 1991
	KNM-ER 15930	KNM-ER 15930	Wood, 1991
	-	Peninj	Precision cast
Paranthropus robustus	DNH 8	DNH 8	Keyser, 2000
	SK 6	SK 6	Precision cast
	SK 12	SK 12	Precision cast
	SK 23	SK 23	Wood, 1991
	SK 34	SK 34	Precision cast
	SK 843	-	Precision cast
	-	SK 1587	Wood, 1991
	-	SKW 5	Precision cast
	-	SKX 4446	Precision cast
	TM 1517	TM 1517	Precision cast

Table 2.2 Mesiodistal and buccolingual diameters measured in fossil hominin postcanine teeth.

		P_3		P_4		M_1		M_2		M_3	
Taxon	ID	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL
Australopithecus africanus	AL 123-23	7.0	7.2	7.3	8.6	9.9	9.3	10.8	10.7	NA	NA
	AL 198-1	7.3	7.9	7.4	8.4	8.0	8.9	9.9	10.5	12.0	12.4
	AL 225-8	NA	NA	NA	NA	8.8	10.4	10.2	12.7	10.3	12.6
	AL 266-1	7.7	8.3	7.7	8.1	10.1	9.5	11.3	10.8	13.4	11.3
	AL 277-1	7.6	10.2	8.7	9.4	9.7	10.1	12.6	12.3	NA	NA
	AL 333w-60	8.1	10.6	8.5	10.9	11.3	11.3	12.6	13.1	12.1	9.9
	AL 400-1A	9.5	11.1	9.4	11.3	12.8	12.6	14.8	14.2	15.6	13.5
	LH 4	9.0	8.3	9.0	9.5	11.1	11.3	13.2	11.8	14.6	12.7
	MAK-VP-1/12	8.8	9.2	9.5	8.8	12.3	12.8	13.6	14.6	13.9	15.0
Australopithecus africanus	MLD 18	NA	NA	8.9	11.8	12.6	13.1	14.2	14.7	14.2	13.9
	MLD 40	9.2	11.1	9.7	11.3	13.1	12.4	15.8	14.1	NA	NA
	STS 36	10.1	12.7	8.9	11.6	11.9	14.2	15.6	17.3	15.4	16.1
	STS 52	8.9	11.9	9.8	12.1	13.8	13.2	15.2	13.5	13.7	12.8
	STW 14	9.3	10.8	8.7	13.7	14.6	15.4	15.5	13.7	17.2	14.0
	STW 327	NA	NA	11.9	12.9	15.5	14.3	17.9	16.1	NA	NA
	STW 384	NA	NA	12.7	14.3	16.3	15.4	17.9	17.6	18.7	17.6
	STW 498	NA	NA	NA	NA	17.0	16.0	18.5	17.2	18.2	16.3
Homo ergaster	D211	9.7	8.0	8.3	9.5	12.5	11.7	11.7	10.7	11.7	10.4
	D2735	9.0	8.6	7.6	9.2	12.9	11.2	13.4	10.8	13.5	10.9
	KGA-10	NA	NA	7.8	9.4	11.8	11.6	12.8	11.4	11.9	10.5
	KNM-BK 67	NA	NA	9.4	7.9	11.7	10.8	10.8	11.2	12.9	11.4
	KNM-ER 730	NA	NA	NA	NA	12.6	11.5	13.0	11.6	13.7	11.5
	KNM-ER 992	10.3	9.7	8.8	10.9	11.4	10.9	13.0	12.2	13.4	12.3
	KNM-WT 15000	9.0	10.1	9.0	9.5	12.2	11.1	12.4	11.4	NA	NA
	OH 22	10.1	9.2	9.0	10.0	13.4	12.0	13.0	11.7	NA	NA
	SK 15	NA	NA	NA	NA	13.3	11.9	14.6	13.0	14.7	12.6
Homo habilis	KNM-ER 3734	8.9	8.0	9.1	8.1	13.6	10.6	14.1	11.7	NA	NA
	OH 7	9.5	9.7	10.4	10.7	14.1	12.6	15.7	13.7	12.1	10.7
	OH 13	9.0	8.4	9.0	9.8	13.0	11.6	14.2	12.0	14.8	12.4
	OH 16	10.6	11.1	10.1	11.0	14.6	12.8	15.4	15.1	15.9	14.4
Homo rudolfensis	KNM-ER 1482	NA	NA	9.7	12.2	13.2	13.3	15.0	14.0	NA	14.6
	KNM-ER 1801	NA	NA	9.8	11.5	13.9	13.2	12.7	13.2	17.0	14.6
	KNM-ER 1802	10.7	11.5	12.1	11.8	14.9	13.0	17.0	14.2	NA	NA
	KNM-ER 60000	8.9	9.5	8.8	9.8	12.8	11.4	14.0	12.8	15.7	12.9
	UR 501	NA	NA	9.7	10.1	11.1	10.4	15.5	12.6	16.4	14.0
Paranthropus boisei	KNM-ER 3230	11.4	13.9	13.7	16.5	17.0	15.4	20.2	18.6	20.5	16.5
	KNM-ER 729	NA	NA	15.0	14.6	16.4	16.0	20.5	18.0	22.2	19.0
	KNM-ER 801	NA	NA	NA	NA	12.7	13.8	17.8	15.9	17.9	15.5
	KNM-ER 818	NA	NA	14.3	16.7	16.7	13.4	20.1	18.2	19.0	17.6
	KNM-ER 1468	NA	NA	11.8	14.2	15.0	14.3	16.6	15.4	21.0	15.0
	KNM-ER 1816	10.8	11.7	14.9	14.5	16.5	13.7	17.3	16.1	NA	NA
	KNM-ER 15930	NA	NA	12.0	14.0	14.6	12.8	16.0	14.5	18.2	15.0
	Peninj	9.9	12.5	12.6	14.2	15.5	15.0	17.8	12.8	18.2	NA
Paranthropus robustus	DNH8	11.0	12.9	11.8	14.0	14.9	13.6	16.7	15.8	18.9	15.1
	SK 6	10.4	12.5	11.0	12.3	16.7	15.5	17.9	16.2	18.7	15.5
	SK 12	NA	NA	11.5	12.8	14.4	15.6	16.8	15.3	17.6	15.8
	SK 23	9.6	11.5	11.1	14.4	15.2	14.7	16.0	14.9	16.8	14.4
	SK 34	10.4	12.7	12.3	13.8	15.0	14.8	17.1	16.4	18.1	17.0
	SK 843	NA	NA	NA	NA	15.0	13.6	16.1	13.9	17.5	15.1
	SK 1587	NA	NA	10.8	11.7	15.1	13.1	15.5	13.2	NA	NA
	SKW 5	9.2	10.4	10.7	12.4	13.5	12.7	15.5	14.1	16.2	12.0
	SKX 4446	NA	NA	11.9	12.5	15.5	14.3	17.1	15.8	NA	NA
	TM 1517	10.8	13.8	10.8	13.3	14.8	13.2	17.1	15.9	16.4	14.3

Table 2.3 Population statistics for the postcanine crown areas of fossil hominin and extant primate taxa. SD is the standard deviation and CV is the coefficient of variation.

		P_4 area (mm^2)			M_1 area (mm^2)			M_2 area (mm^2)			M_3 area (mm^2)		
Taxon	N	Mean	SD	CV	Mean	SD	CV	Mean	SD	CV	Mean	SD	CV
Extant primates													
Cercocebus atys	8	32.0	4.8	6.7	44.7	5.9	7.5	59.8	8.0	7.4	66.8	9.6	6.9
Cercocebus torquatus	6	33.6	4.1	8.2	42.5	4.2	10.1	58.5	6.0	9.8	65.7	8.6	7.6
Gorilla beringei	12	152.7	21.4	7.1	217.7	32.1	6.8	269.9	39.9	6.8	269.6	37.0	7.3
Gorilla gorilla	27	127.7	15.0	8.5	182.6	18.2	10.0	228.6	27.4	8.3	231.2	37.2	6.2
Hylobates agilis	11	19.5	2.0	9.6	30.1	3.3	8.7	34.2	3.5	9.6	32.1	4.7	6.8
Hylobates klossii	8	15.5	1.8	8.8	25.0	2.9	8.6	27.8	3.8	7.2	22.8	3.8	6.0
Hylobates lar	14	18.9	2.4	7.9	25.9	2.0	12.7	29.2	3.0	9.9	28.5	3.8	7.4
Macaca cyclopis	10	24.1	1.8	13.4	32.4	1.9	17.2	46.3	3.1	15.0	66.3	7.2	9.2
Macaca fascicularis	49	22.1	4.4	5.0	30.5	5.0	6.1	41.5	8.6	4.8	50.1	12.2	4.1
Macaca fuscata	11	29.4	6.1	4.8	40.6	8.2	4.9	60.3	10.7	5.7	79.8	14.9	5.3
Macaca nemestrina	34	34.2	4.0	8.5	41.0	5.4	7.6	58.4	8.4	6.9	73.9	9.9	7.5
Pan troglodytes	16	63.3	7.6	8.3	95.1	8.4	11.3	110.8	12.8	8.7	100.7	15.9	6.3
Papio anubis	41	58.7	11.1	5.3	83.9	13.9	6.0	124.7	22.7	5.5	154.1	30.7	5.0
Papio ursinus	13	66.6	13.8	4.8	87.4	17.1	5.1	129.6	26.0	5.0	169.0	31.9	5.3
Pongo abelii	9	100.0	16.2	6.2	127.7	19.1	6.7	155.0	22.1	7.0	156.6	34.2	4.6
Pongo pygmaeus	32	115.7	17.0	6.8	147.4	22.3	6.6	166.1	28.2	5.9	161.4	30.8	5.2
Saguinus fuscicollis	13	3.3	0.3	9.9	4.4	0.6	7.3	3.3	0.5	7.3	NA	NA	NA
Saguinus geoffroyi	26	4.9	0.4	11.0	6.3	0.6	11.2	4.4	0.5	8.8	NA	NA	NA
Saguinus labiatus	14	4.0	0.4	10.8	5.0	0.3	16.5	4.0	0.4	11.4	NA	NA	NA
Saguinus mystax	13	4.4	0.3	12.8	5.8	0.6	10.6	5.0	0.6	8.2	NA	NA	NA
Theropithecus gelada	6	46.8	6.5	7.2	66.5	15.0	4.4	110.1	21.3	5.2	151.2	31.0	4.9
Fossil hominins													
Australopithecus afarensis	8	79.5	16.0	5.0	113.3	31.4	3.6	150.6	36.8	4.1	165.2	32.4	5.1
Australopithecus africanus	7	127.3	29.4	4.3	205.9	42.2	4.9	255.0	48.4	5.3	247.9	58.0	4.3
Homo ergaster	7	81.2	9.6	8.4	142.2	12.6	11.3	147.8	19.9	7.4	149.7	22.3	6.7
Homo habilis/rudolfensis	9	104.7	20.6	5.1	163.7	26.0	6.3	197.3	28.9	6.8	203.8	42.7	4.8
Paranthropus boisei	7	202.1	29.7	6.8	222.9	31.2	7.1	298.5	62.4	4.8	307.6	30.9	10.0
Paranthropus robustus	9	145.5	15.8	9.2	207.2	27.6	7.5	251.8	28.8	8.7	262.8	35.0	7.5

Table 2.4 Results of MANOVAs on the A) molar and B) premolar-molar cascade over all extant genera. DF is the degrees of freedom, Pillai is the result of Pillai's trace, and F and P are probability statistics.

A. M_2:M_1, M_3:M_1

	DF	Pillai	Approx. F	P
Factor (by taxon)	23	0.96	10.20	<2.2.e-16
Residuals	252			

B. M_1:P_4, M_2:P_4

	DF	Pillai	Approx. F	P
Factor (by taxon)	27	1.20	21.68	<2.2.e-16
Residuals	392			

Table 2.5 Results of Student's t-test on the slopes of the regressions of *P. boisei* and *P. robustus* for the molar and premolar-molar cascades. DF is the degrees of freedom, SS is the pooled residual sum of squares, SE is the standard error, T is the t value, and P is the probability.

Cascade	DF	SS	SE	T	P
M_1-M_3	12	0.05	0.09	2.81	<0.05
P_4-M_2	8	0.03	0.08	0.61	>0.5

Table 2.6 Reduced major axis regression results for lower A) molar and B) premolar-molar ratios in extant primates and fossil hominins. Values are compared to those predicted by the IC model applied to a murine sample (Kavanagh et al., 2007; Renvoise et al., 2009). *Saguinus* is not included in the molar results due to the absence of M_3s in this genus. C.I. = confidence interval.

A. M_1-M_3 cascade

Taxon	N	Slope	C.I. Min	C.I. Max	Intercept	C.I. Min	C.I. Max	r^2	Fits IC?
IC Prediction	-	2.00	-	-	-1.00	-	-	1.00	-
Murines	29	2.15	1.77	2.69	-1.22	-1.65	-0.93	0.55	YES
Extant primates									
Cercocebus	13	1.82	0.98	2.65	-0.92	-2.06	0.21	0.52	YES
C. atys	7	1.28	0.48	2.08	-0.18	-1.25	0.89	0.70	YES
C. torquatus	6	3.72	0.44	7.00	-3.57	-8.10	0.95	0.60	YES
Gorilla	39	1.63	1.20	2.07	-0.78	-1.33	-0.24	0.36	YES
G. beringei	12	1.60	0.51	2.69	-0.75	-2.10	0.61	0.07	YES
G. gorilla	27	1.64	1.13	2.15	-0.79	-1.43	-0.14	0.42	YES
Hylobates	4	1.64	1.14	2.14	-0.81	-1.38	-0.24	0.28	YES
H. agilis	12	1.42	0.84	2.00	-0.55	-1.23	0.12	0.66	YES
H. klossii	8	1.27	0.00	2.54	-0.50	-1.91	0.92	<0.00	YES
H. lar	14	1.68	0.74	2.62	-0.79	-1.85	0.27	0.20	YES
Macaca	65	1.99	1.64	2.33	-0.96	-1.44	-0.47	0.52	YES
M. cyclopis	9	3.83	0.41	7.25	-3.50	-8.46	1.45	<0.00	YES
M. fascicularis	35	1.58	1.13	2.03	-0.47	-1.07	0.13	0.37	YES
M. fuscata	8	1.27	0.40	2.13	0.15	-1.11	1.41	0.54	YES
M. nemestrina	13	1.81	1.25	2.37	-0.68	-1.49	0.14	0.78	YES
Pan (P. troglodytes)	16	1.67	0.97	2.37	-0.89	-1.71	-0.06	0.46	YES
Papio	27	1.62	1.32	1.93	-0.44	-0.89	0.02	0.79	NO
P. anubis	20	1.65	1.13	2.18	-0.48	-1.26	0.31	0.59	YES
P. ursinus	7	1.65	1.29	2.00	-0.48	-1.02	0.06	0.96	YES
Pongo	40	1.72	1.33	2.10	-0.86	-1.30	-0.42	0.54	YES
P. abelii	9	2.28	0.89	3.68	-1.56	-3.26	0.15	0.53	YES
P. pygmaeus	31	1.54	1.09	1.99	-0.66	-1.17	-0.14	0.40	YES
Theropithecus (T. gelada)	6	1.49	1.00	1.99	-0.18	-1.07	0.71	0.94	YES

Table 2.6 Reduced major axis regression results, continued.

A. M_1-M_3 cascade, continued

Taxon	N	Slope	C.I. Min	C.I. Max	Intercept	C.I. Min	C.I. Max	r^2	Fits IC?
Fossil hominins									
Australopithecus	11	1.78	0.78	2.88	-0.91	-2.20	0.38	0.44	YES
A. afarensis	5	3.07	-1.39	7.53	-2.53	-8.51	3.45	0.38	YES
A. africanus	6	0.85	0.24	1.46	0.14	-0.62	0.9	0.73	NO
Homo	13	1.46	0.78	2.14	-0.48	-1.26	0.31	0.51	YES
H. ergaster	7	1.16	0.30	2.03	-0.16	-1.08	0.77	0.58	YES
H. habilis/rudolfensis	6	1.58	-0.13	3.29	-0.64	-2.79	1.52	0.39	YES
Paranthropus	12	0.82	0.37	1.27	0.28	-0.31	0.87	0.39	NO
P. boisei	5	0.52	-0.40	1.43	0.72	-0.59	2.03	0.07	NO
P. robustus	7	1.05	-0.02	2.12	-0.01	-1.30	1.27	0.22	YES

B. P_4-M_2 cascade

Taxon	N	Slope	C.I. Min	C.I. Max	Intercept	C.I. Min	C.I. Max	r^2	Fits IC?
IC Prediction	-	2.00	-	-	-1.00	-	-	1.00	-
Extant hominins									
Cercocebus	14	1.03	0.56	1.49	0.44	-0.19	1.07	0.48	NO
C. atys	8	0.86	0.08	1.64	0.66	-0.43	1.76	0.18	NO
C. torquatus	6	1.61	0.27	2.96	-0.30	-2.00	1.40	0.64	YES
Gorilla	39	1.13	0.87	1.40	0.17	-0.22	0.55	0.51	NO
G. beringei	12	1.35	0.82	1.88	-0.16	-0.92	0.61	0.69	NO
G. gorilla	27	1.06	0.74	1.38	0.27	-0.20	0.73	0.46	NO
Hylobates	33	1.06	0.82	1.30	0.09	-0.27	0.46	0.62	NO
H. agilis	11	1.04	0.49	1.60	0.15	-0.73	1.02	0.50	NO
H. klossii	8	1.36	0.062	2.65	-0.40	-2.50	1.70	0.09	YES
H. lar	14	0.93	0.64	1.23	0.26	-0.15	0.68	0.74	NO
Macaca	104	1.5	1.26	1.74	-0.14	-0.46	0.18	0.34	NO
M. cyclopis	10	1.22	0.51	1.92	0.29	-0.67	1.24	0.49	NO
M. fascicularis	49	1.58	1.21	1.95	-0.32	-0.83	0.20	0.38	NO
M. fuscata	11	1.07	0.45	1.68	0.58	-0.29	1.45	0.42	NO
M. nemestrina	34	2.16	1.39	2.92	-0.87	-1.800	0.05	0.03	YES
Pan (P. troglodytes)	16	0.81	0.46	1.17	0.52	-0.02	1.06	0.42	NO

Table 2.6 Reduced major axis regression results, continued.

B. P_4-M_2 cascade, continued

Taxon	n	Slope	C.I. Min	C.I. Max	Intercept	C.I. Min	C.I. Max	r^2	Fits IC?
Papio	54	1.86	1.45	2.26	-0.52	-1.10	0.06	0.37	YES
P. anubis	41	1.84	1.42	2.26	-0.51	-1.11	0.10	0.51	YES
P. ursinus	13	-2.20	-3.65	-0.74	4.87	2.94	6.80	<0.00	NO
Pongo	41	1.29	0.99	1.59	-0.19	-0.57	0.20	0.49	NO
P. abelii	9	0.64	0.28	1.00	0.73	0.28	1.19	0.61	NO
P. pygmaeus	32	1.32	1.01	1.63	-0.25	-0.64	0.15	0.60	NO
Saguinus	66	1.15	0.90	1.41	-0.51	-0.85	-0.18	0.22	NO
S. fuscicollis	13	0.67	0.31	1.03	0.11	-0.38	0.60	0.36	NO
S. geoffroyi	26	1.05	0.66	1.44	-0.46	-0.96	0.05	0.23	NO
S. labiatus	14	0.88	0.39	1.38	-0.11	-0.73	0.52	0.21	NO
S. mystax	13	1.30	0.69	1.91	0.59	-1.39	0.21	0.50	NO
Theropithecus (T.gelada)	6	-1.31	-2.99	0.37	4.43	1.87	6.99	0.15	NO
Fossil hominins									
Australopithecus	15	1.23	0.59	1.88	0.09	-0.89	1.07	0.23	NO
A. afarensis	8	0.92	0.44	1.39	0.59	-0.10	1.29	0.73	NO
A. africanus	7	1.84	-0.26	3.93	-0.91	-4.19	2.38	0.02	YES
Homo	16	0.93	0.43	1.44	0.30	-0.55	1.15	0.10	NO
H. ergaster	7	0.81	0.08	1.54	0.35	-0.93	1.63	0.39	NO
H. habilis/rudolfensis	9	1.01	0.19	1.83	0.31	-1.01	1.62	0.17	NO
Paranthropus	16	0.95	0.57	1.34	0.37	-0.15	0.88	0.50	NO
P. boisei	7	1.29	-0.19	2.78	0.00	-1.72	1.71	<0.00	YES
P. robustus	9	0.95	0.36	1.54	0.35	-0.51	1.22	0.52	NO

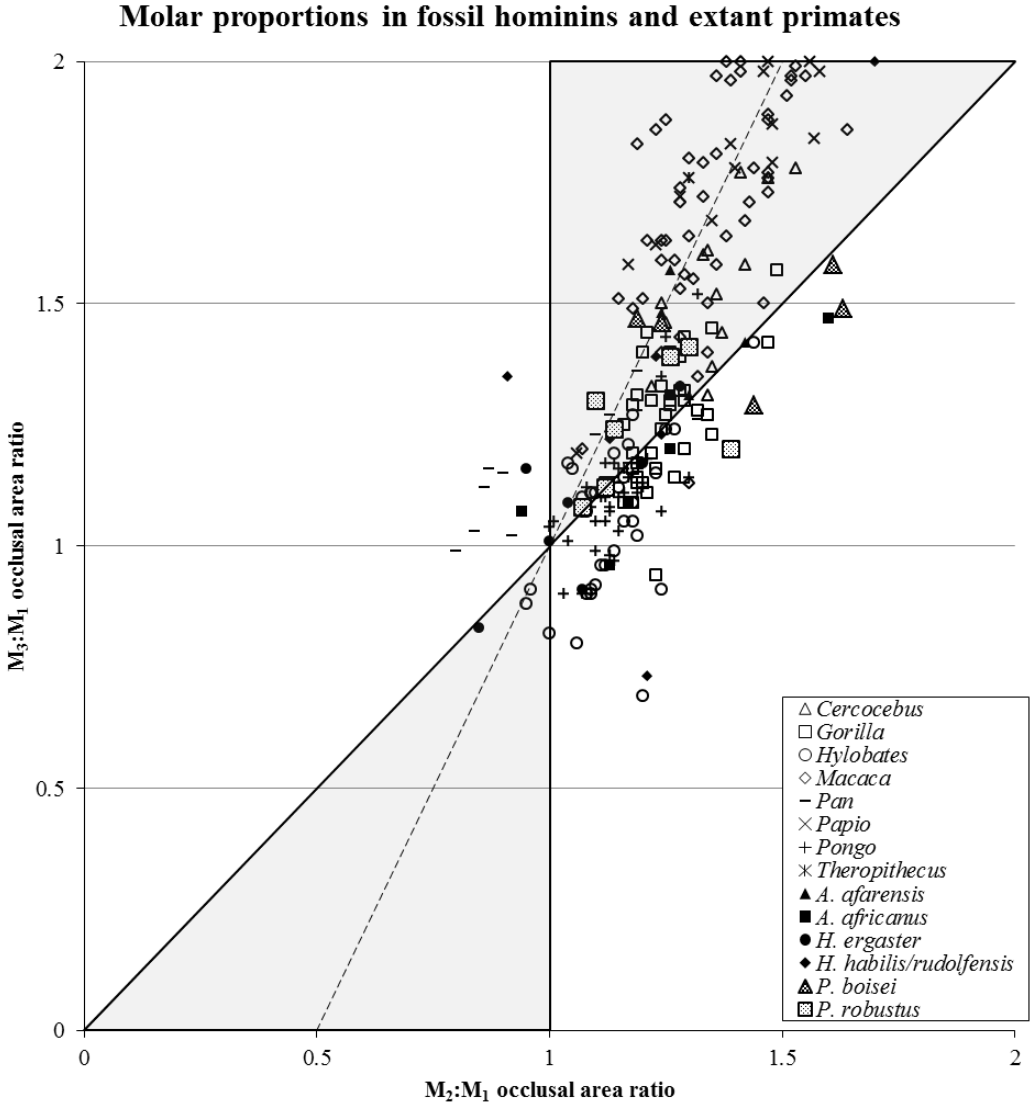


Figure 2.2 Results of linear regressions between occlusal area ratios for the molar cascade. Ratios are calculated from area measurements derived from maximum mesiodistal and buccolingual diameters for M_1-M_3. The dashed line represents the IC function and gray shading represents areas of general decrease and increase along the molar row. Open symbols and line symbols represent extant primates, black symbols represent non-robust fossil hominins, and patterned symbols represent species of *Paranthropus*.

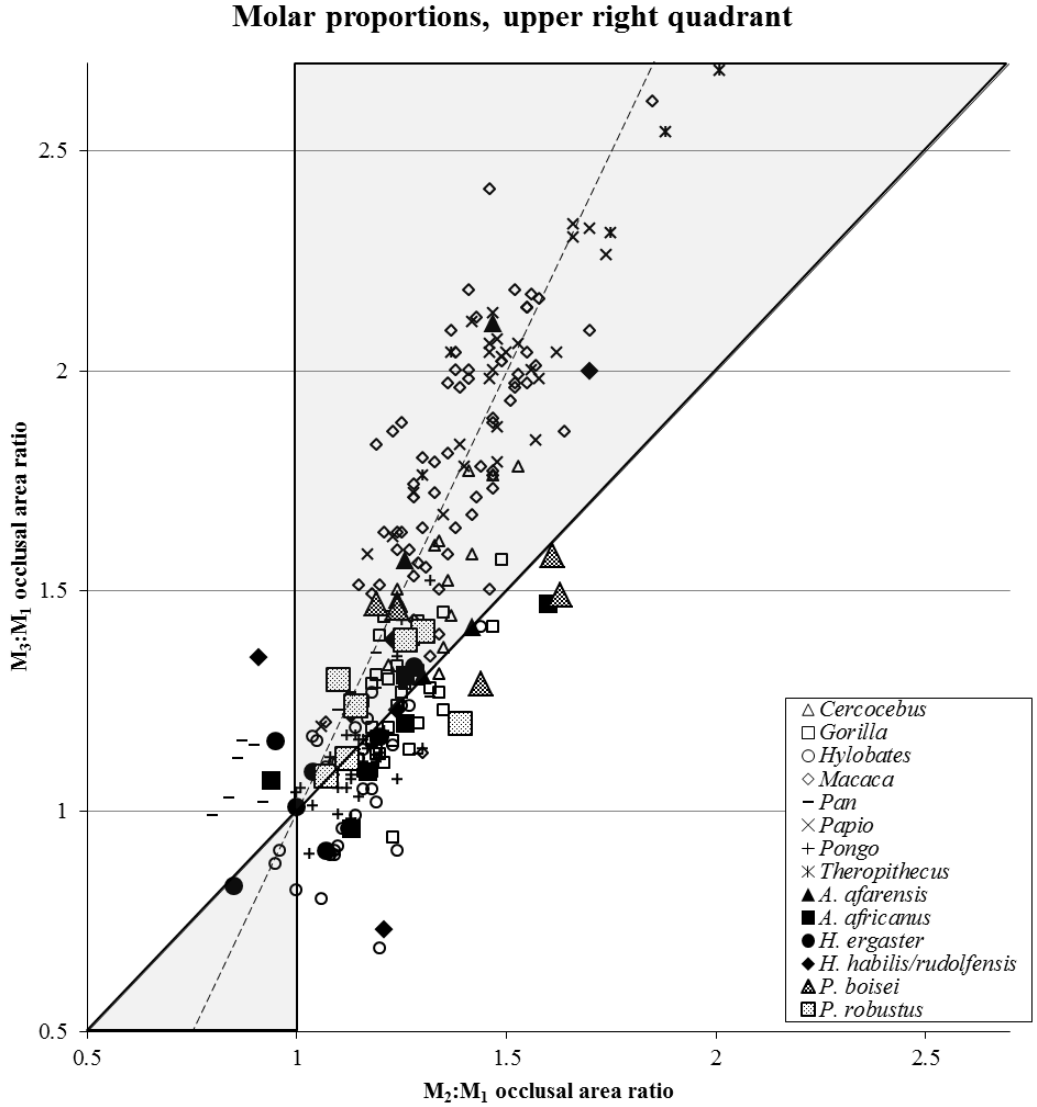


Figure 2.3 Close-up of the upper right quadrant of Figure 2.2, the molar cascade regression. Ratios are calculated from area measurements derived from maximum and buccolingual diameters for M_1-M_3. The dashed line represents the IC function and gray shading represents areas of general decrease and increase along the molar row. Open symbols and line symbols represent extant primates, black symbols represent non-robust fossil hominins, and patterned symbols represent species of *Paranthropus*.

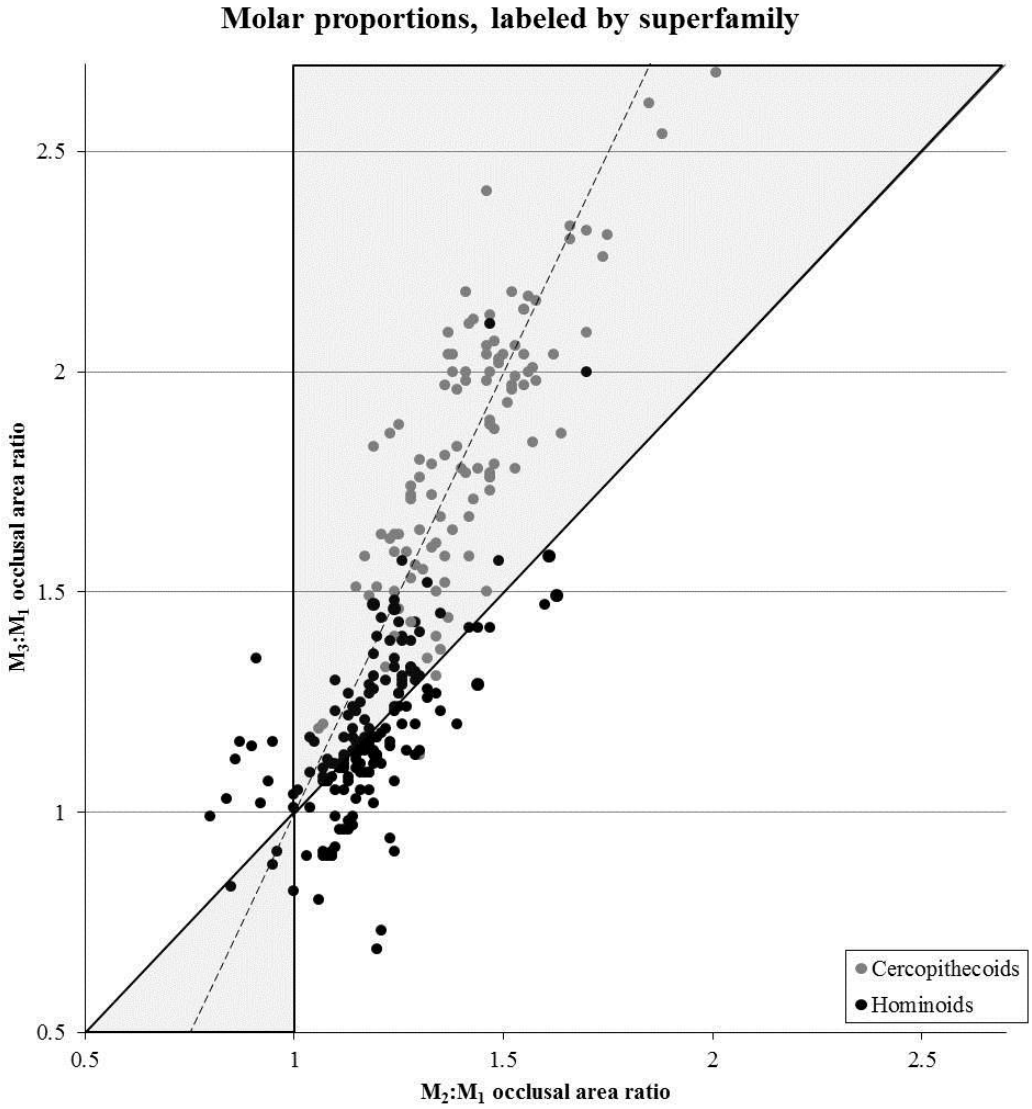


Figure 2.4 Results of the molar cascade regression, presented by primate superfamily. Gray circles represent cercopithecoids, and black circles represent hominoids.

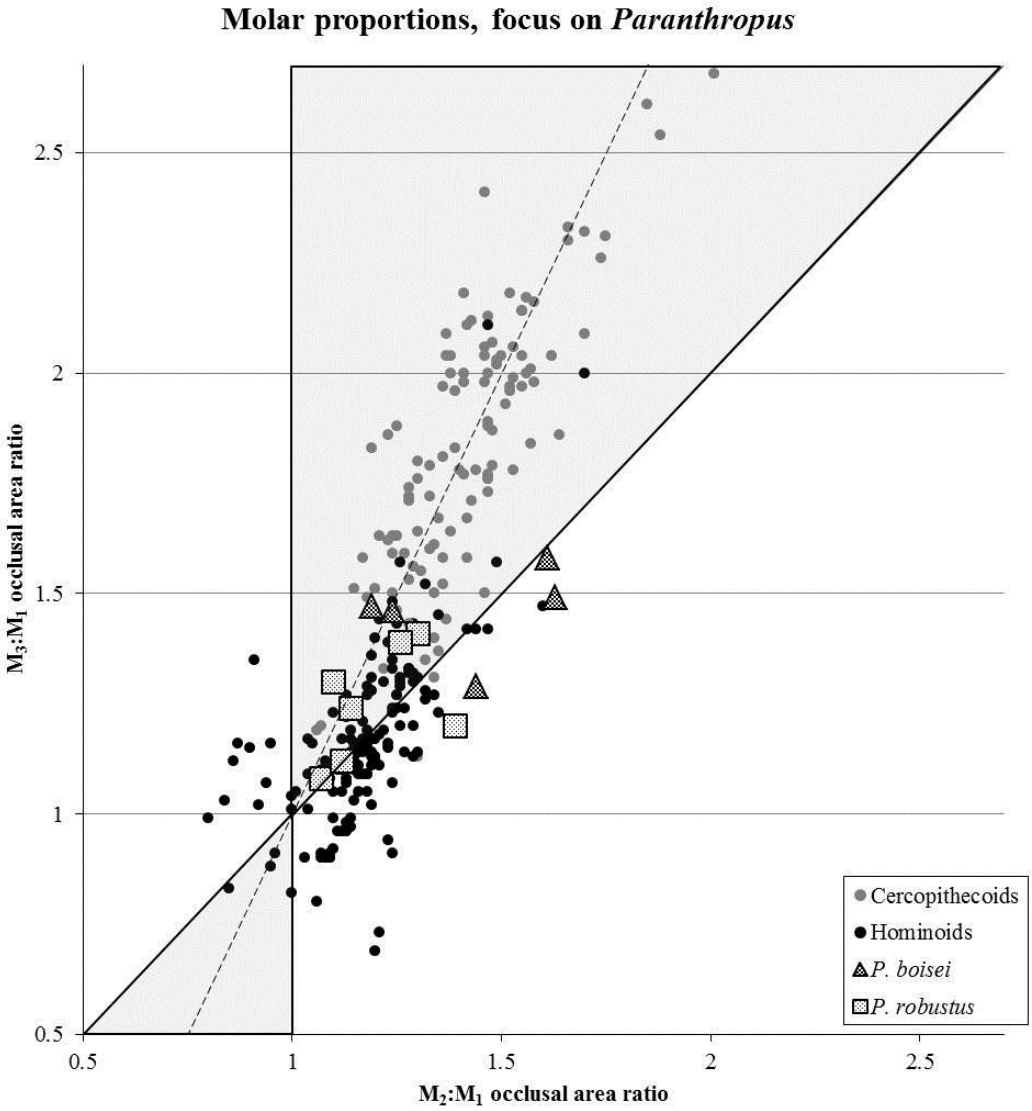


Figure 2.5 Results of the molar cascade regression, presented by primate superfamily, plus *Paranthropus*. Gray circles represent cercopithecoids, and black circles represent hominoids. Patterned symbols represent species of *Paranthropus*; the patterned triangles represent *P. boisei* and the patterned squares *P. robustus*.

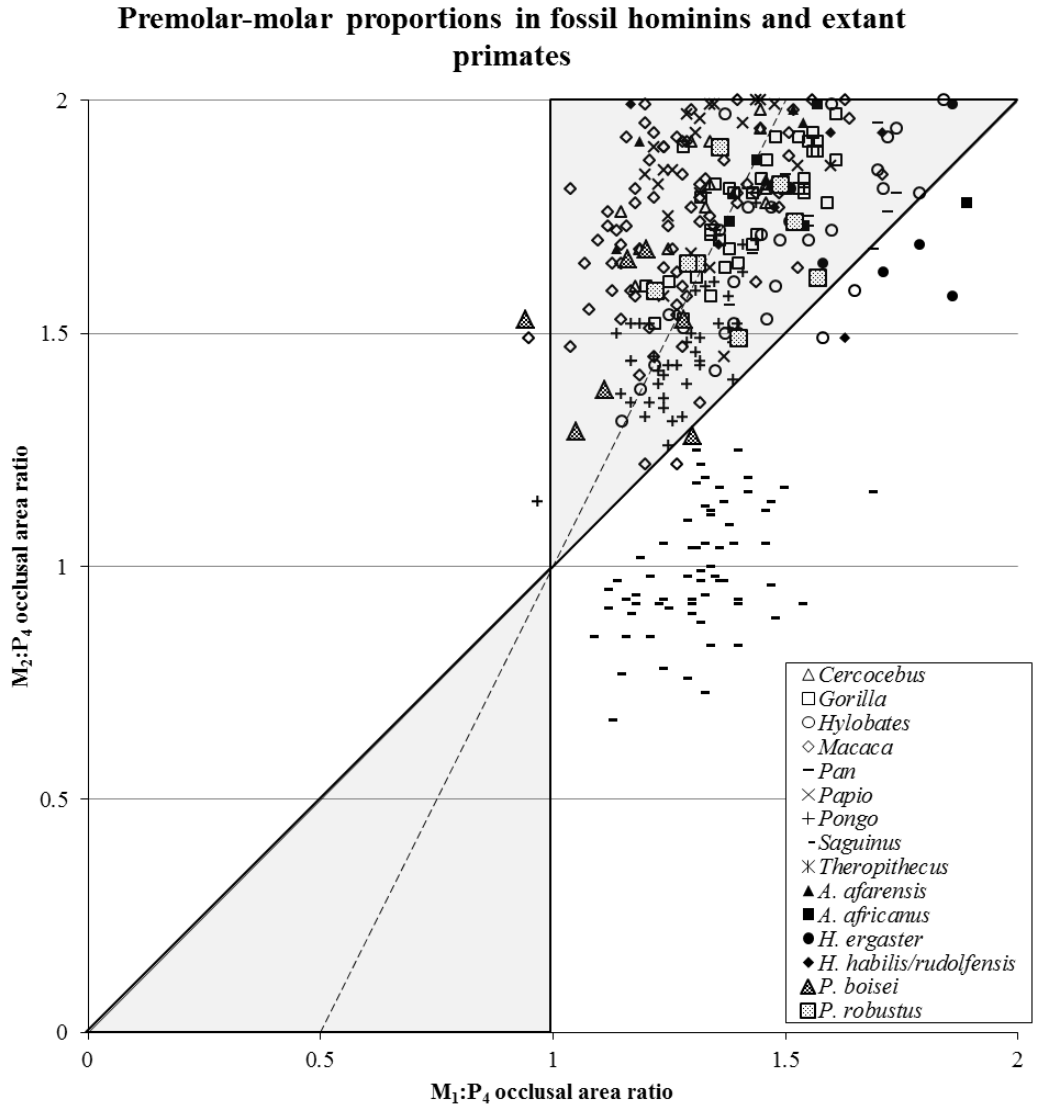


Figure 2.6 Results of linear regressions between occlusal area ratios for the proposed premolar-molar cascade. Ratios are calculated from area measurements derived from maximum mesiodistal and buccolingual diameters for P_4-M_2. The dashed line represents the IC function and gray shading represents areas of general decrease and increase along the molar row. Open symbols and line symbols represent extant primates, black symbols represent non-robust fossil hominins, and patterned symbols represent species of *Paranthropus*.

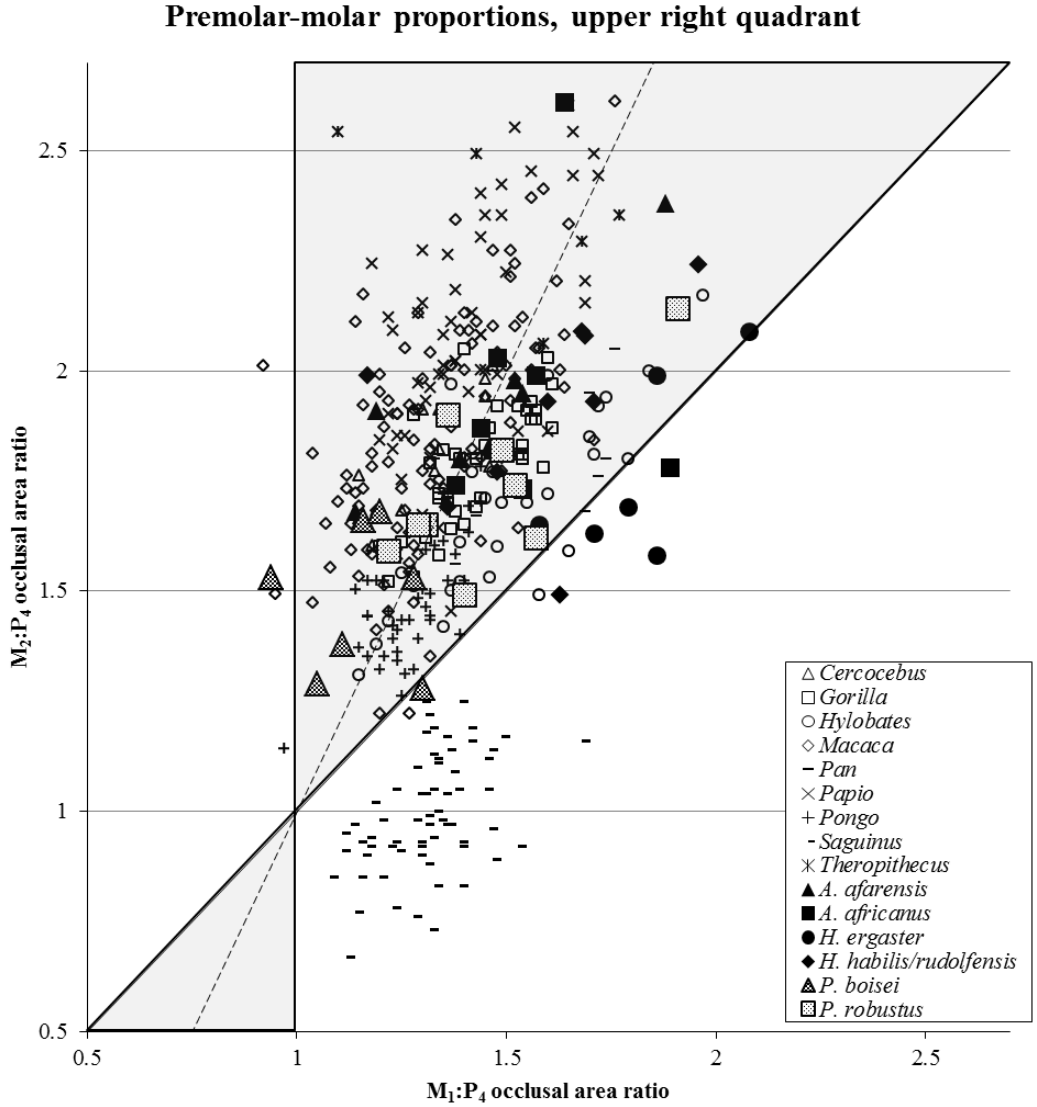


Figure 2.7 Close-up of the upper right quadrant of Figure 2.6, the proposed premolar-molar cascade regression. Ratios are calculated from area measurements derived from maximum and buccolingual diameters for P_4-M_2. The dashed line represents the IC function and gray shading represents areas of general decrease and increase along the molar row. Open symbols and line symbols represent extant primates, black symbols represent non-robust fossil hominins, and patterned symbols represent species of *Paranthropus*.

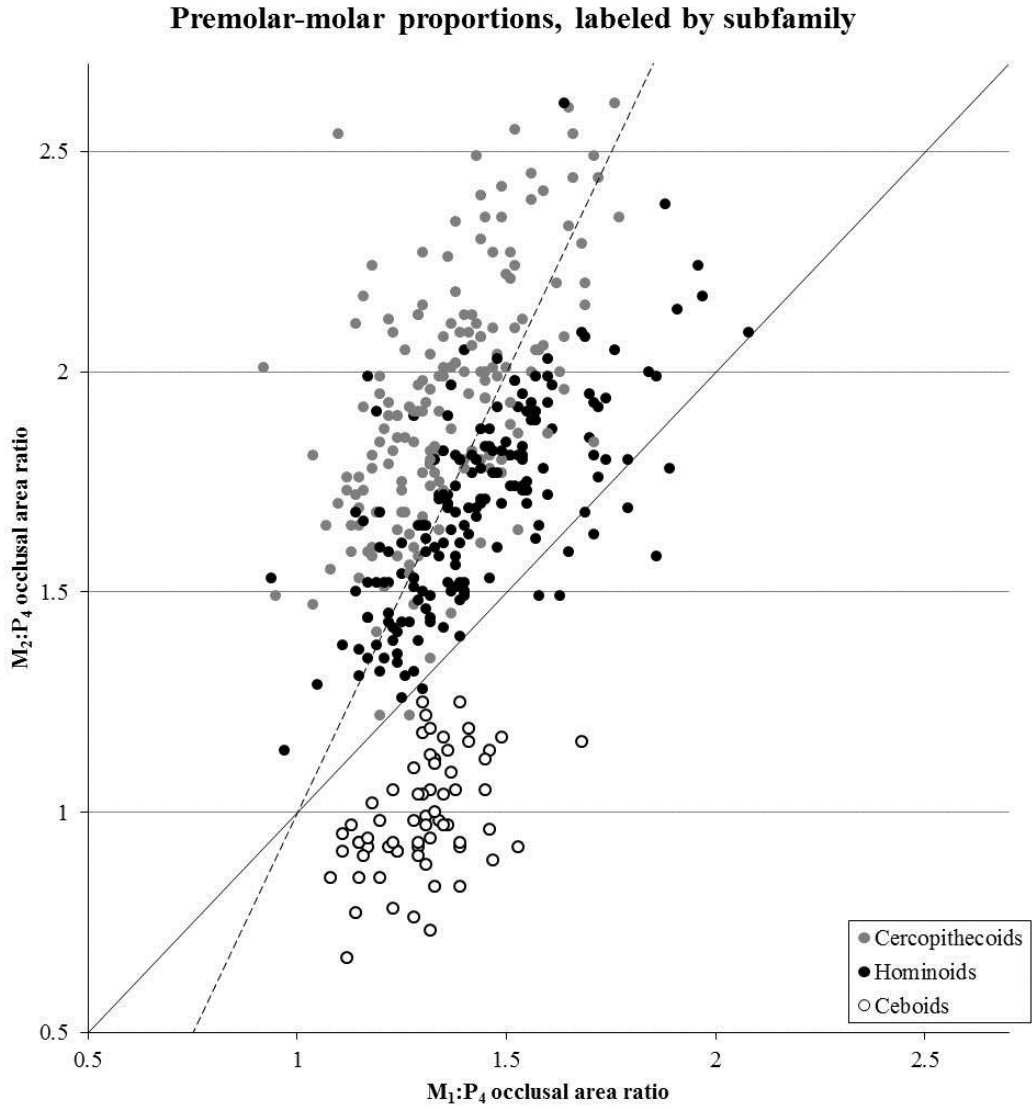


Figure 2.8 Results of the proposed premolar-molar cascade regression, presented by primate superfamily. Gray circles represent cercopithecoids, black circles represent hominoids, and open circles represent ceboids.

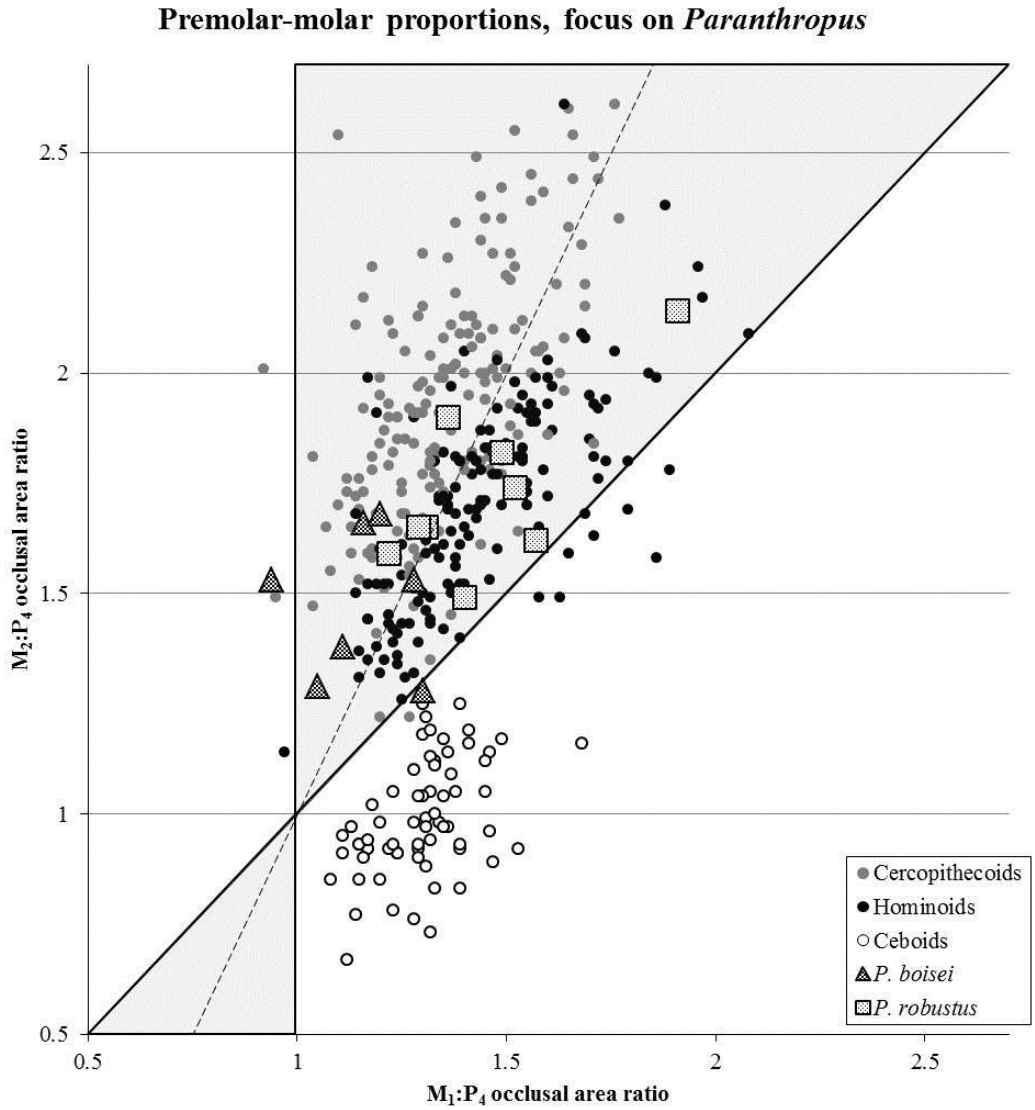


Figure 2.9 Results of the proposed premolar-molar cascade regression, presented by primate superfamily, plus *Paranthropus*. Gray circles represent cercopithecoids, black circles represent hominoids, and open circles represent ceboids. Patterned symbols represent species of *Paranthropus*, with patterned triangles representing *P. boisei* and patterned squares represent *P. robustus*.

Chapter 3: Morphological integration of postcanine traits in extant primates and the influence of covariance on the evolution of hominin postcanine teeth

3.1 Introduction

The mammalian dentition is a complex and highly integrated organismal system. Each tooth within the dentition develops as a separate organ from an individual tooth bud, and by the time of dental emergence, each tooth aligns in a coordinated fashion with other teeth in the jaws. The integration of dental morphology is of particular relevance to the study of fossil hominins, because differences in dental morphology form the majority of characters that are used to identify and diagnose taxa (Wood and Abbott, 1983; Wood et al., 1983; Wood and Uytterschaut, 1987; Wood and Engleman, 1988; Suwa et al., 1994; Wood and Richmond, 2000; Martinon-Torres et al., 2006; Moggi-Cecchi et al., 2006; Gomez-Robles et al., 2007, 2008; Skinner et al., 2008; Bailey et al., 2009; Quam et al., 2009) and reconstruct phylogeny (Read, 1975; Strait et al.,1997; Wood and Collard, 1999; Gomez-Robles and Polly, 2012). This study assesses the presence and strength of integration within and among extant primate postcanine teeth in order to provide a comparative context for any patterns of morphological covariation observed in fossil hominins.

Morphological integration refers to the relationships among morphological traits and can be broken into hierarchical levels of developmental, functional, genetic, and evolutionary integration (Cheverud, 1996). Jaws and teeth are familiar examples of functional integration, as the proper alignment between teeth influences the feeding performance of an individual (Butler, 1983; Cheverud, 1984, 1996; Hall, 1992; Dayan et al., 2009). Functional and developmental integration are likely closely connected

(Cheverud, 1996, 1997; Mezey et al., 2000; Klingenberg et al., 2004; Rolian and Willmore, 2009; but see Klingenberg 2003, 2005), and many studies of the murine dentition have provided evidence for this connection (McCollum and Sharpe, 2001; Thesleff and Mikkola, 2002; Mitsiadis and Smith, 2006; Bei et al., 2009). Determining morphological integration patterns in the jaw can inform hypotheses about how the function and development of teeth covary and how changes in either function or development may influence resulting phenotypes.

Molarization is one source of variation in postcanines with particular relevance to taxonomy and phylogeny. Molarization describes premolars that are similar to the molars in their shape and size. Most often, molarization describes morphological variations of the P_4, the lower fourth premolar (Butler, 1941). All fossil hominins have relatively more molarized premolars than modern humans, but molarization takes an extreme form in the megadont hominin genus *Paranthropus*. Describing a premolar as "molarized" is not trivial, as this implies that teeth of different developmental trajectories have converged upon similar phenotypes. Premolars replace deciduous molars whereas molars originate *de novo* in the adult jaw (Scott, 1892; Butler, 1941, 1967, 1995; Posen, 1965). Functionally molars and premolars often act together as a grinding surface to break down food particles and several authors have argued that molarized premolars provide an adaptation for mechanically challenging diets, specifically hard diets (Robinson, 1963; Maier, 1984; Leonard and Hegmon, 1987; Butler, 1995; Lucas, 2009). Examining premolar size through the lens of morphological integration can tease apart the relationship between premolar function and development and subsequently improve our understanding of the evolutionary origins of morphological variation in premolars.

The field of quantitative genetics provides models for approximating morphological integration. One common method evaluates the covariances of morphological traits to determine whether the traits that are statistically dependent (Klingenberg, 2008). Quantitative trait loci (QTL) may act on multiple phenotypic traits, and covariance can detect the dependent patterns of morphological variation (Lande, 1979; Cheverud, 1984; Schluter, 1996; Klingenberg, 2005). The structuring of this covariance, called the genetic architecture, can indicate sources of developmental constraint upon, or facilitation of, new morphological variations (Cheverud, 1984; Arnold, 1992; Schluter, 1996; Zeng et al., 1999; Mackay, 2001; Mackay et al., 2009). Determining covariation between morphological traits therefore has the potential to provide insight into how morphological responses to selection may arise and the form they might take. Additionally, the combination of covariation and mean change in traits can reveal traits that which have changed in response to selection versus those that have changed in response to selection acting on a different, but integrated, trait (Lande, 1979; Lande and Arnold, 1983).

Studies of covariance have recovered patterns of integration governing variation in primate crania (Cheverud, 1982, 1995; Lieberman et al., 2000; Strait, 2001; Ackermann, 2005; Mitteroecker and Bookstein, 2008; Singh et al., 2012), limbs (Hallgrimsson et al., 2002; Rolian, 2009; Williams, 2010; Villmoare et al., 2011), and pelves (Grabowski et al., 2011; Lewton, 2012), with critical implications for evaluating the adaptive independence of traits observed in the hominin lineage (Lieberman et al., 2000; Roseman et al., 2009; Williams, 2010; Grabowski et al., 2012, Singh et al., 2012). Relatively few studies have yet considered the patterns of integration in primate

dentitions (Ackermann, 2009), although Hlusko and colleagues have provided several studies of variation in baboons (Hlusko et al., 2004; Hlusko and Mahaney, 2009) and a study by Gomez-Robles and Polly (2012) in fossil hominins suggests there may not be integrated premolar and molar classes within this lineage.

Fossil hominins are generally too few in number to provide reasonable assessments of integration (Ackermann, 2009; Roseman et al., 2011), although at least one study of integration has bolstered sample size by using measurements from isolated teeth (Gomez-Robles and Polly, 2012). Extant primate samples are more abundant than fossil samples and provide comparative contexts in which to assess morphological variation and resulting patterns of integration. Additionally, extant primate samples can be restricted to individuals with complete dentitions, which provide more accurate assessments of the patterns of covariation. Studies of integration in the crania and pelves of several primate taxa indicate that some patterns that are shared broadly among primates may also describe morphological variation in fossil hominins (Cheverud, 1996; Ackermann and Cheverud, 2000, 2004; Marroig and Cheverud, 2001; Marroig et al., 2004; Mitteroecker and Bookstein, 2008). This analysis seeks to determine the patterns of covariance in primate postcanine teeth by testing a series of hypothetical integration matrices against the observed morphological variation in several primate genera. Determining the pattern of covariation of dental variation in primates improves our understanding of hominin evolution by 1) identifying potentially independent traits for phylogeny (Cheverud, 1984; Roseman et al., 2011; Lovejoy et al., 1999), 2) evaluating the relationship between functional and developmental integration (Cheverud, 1996, 1997; Mezey et al., 2000; Klingenberg et al. 2004; Rolian and Willmore, 2009), and 3)

predicting paths of morphological change in response to selection (Cheverud 1982; Lande and Arnold, 1983; Cheverud, 1984; Schluter, 1996).

3.2 Methods

3.2.1 Materials

Lower jaws of extant primate genera were obtained from the collection of the National Museum of Natural History, Washington DC, and the Natural History Museum in London. Only specimens with complete postcanine rows were evaluated; data from the left sides were used unless that side was missing. All specimens were adult from wild populations. Where possible, the samples for each genus were sex-balanced; sex distribution of the samples is given in Table 3.1.

Specimens were photographed using a Canon Digital Rebel XT camera fitted with a macro lens. The maximum linear dimensions of each postcanine tooth were obtained via scaled measurements in TPSDig (Rohlf, 2009). For each photograph, specimens were oriented to maximize the occlusal area of each tooth. Levels on the camera and photography stand were employed to ensure the occlusal plane was parallel to the lens of the camera. Teeth were positioned so as to occupy less than one third of the frame and therefore minimize distortion. A scale was set and leveled in the occlusal plane of the teeth.

For both extant and fossil specimens, only individuals with complete M_1-M_3 or P_4-M_2 series were analyzed. Extensively worn specimens were also not included in the extant sample. Excessive wear on the occlusal surface was defined as wear great enough to mask the identification of individual cusps. Excessive interproximal wear was defined as wear that affected greater than 20% of the occlusal margin. For teeth with moderately

worn cusps, the location of the cusp was estimated from the center of the wear facet (Bailey, 2004; Gomez-Robles et al., 2008). For teeth with moderately worn margins, the margin was reconstructed by approximating the curvature of the margin from overall crown shape (Wood and Uytterschaut, 1987; Bailey and Lynch, 2005). For fossil teeth, similar methods were employed, but teeth with <90% of their likely occlusal areas preserved were not considered.

This study assessed variation in linear measurements of the postcanine teeth, M_3s excepted. The M_3 was excluded in this analysis because, as the most posterior tooth in the jaw, it is more likely to come under the influence of space constraints in the jaw (Dermaut et al., 1986; Kajii et al., 2004; Kavanagh et al., 2007) and is known to be highly variable as a result of a ratchet effect of activation and inhibition in the molars (Kavanagh et al., 2007; Laffont et al., 2009; Wilson et al., 2012). Morphological variation was limited to linear measures to restrict the number of QTLs acting on traits (Klingenberg et al., 2001, 2004). Linear measurements of the postcanines included standard measures of mesiodistal and buccolingual diameters and the length between the most mesial cusps, the protoconid and metaconid. Not all cusps lengths in the molars were considered because only the protoconid and metaconid are consistently observed in the premolars of all primate taxa and for this investigation homologous lengths were required from each tooth. In some taxa, the P_3 can appear unicuspid. In these cases, the intercusp distance was measured from the prominent cusp to a distal cuspsule on the occlusal margin in a similar place as the second cusp on the P_4. If no prominent distal cuspsule was present, the specimen was excluded from analysis. Lengths for each specimen are given in Appendix 1.

To calculate intra-observer error, a sample of 45 individuals representing all taxa in the extant primate sample was measured again two months after initial measurements. Technical error for linear measurements was ±0.1 mm for *Saguinus* and ±0.4 mm for all other taxa.

Samples for each genus were a mix of species, except in the case of *Pan* for no specimens of *Pan paniscus* were available for study. Subspecies and species were pooled in this analysis, as the taxa are closely-related. It should be noted that the environment can be a source of variance in morphological features, thus complicating the estimation of covariance resulting from the effect of genes and development. Pooling subspecies and species conflates covariation from the genetic architecture with effects of variance that may arise from population structuring in particular environments. Such conflation is of particular concern to studies of dental morphological variation, which are closely connected to changes in diet (Kay, 1975; Maier, 1984; Lucas et al., 1986). Ideally, a study of covariation of the postcanine teeth would have large samples from subpopulations of each species and would correct for any signals of environmental variance within a species. Unfortunately, subspecies and locality are not well known for most primate specimens in museums, and little is known about intraspecific variation in dental morphology outside of great ape populations (Uchida, 1996, 1998a, 1998b; Pilbrow, 2003, 2006). Thus, the sample used in this study remains uncorrected for environmental influences.

3.2.2 Analysis

3.2.2.1 Preparing the phenotypic matrix

Ideally, the study of integration between QTLs would consider the covariance between morphological traits of individuals whose pedigrees are well established. However, in primate studies, pedigrees are often unobtainable. Since the matrix of genotypic covariance (**G**) has been shown to be proportional to **P**, the matrix of phenotypic covariance (Lande, 1979; Cheverud, 1988, 1995; Roff, 1995, 1996; Roseman and Weaver, 2004; Porto et al., 2009; Rolian, 2009; Young et al., 2010; but see Willis et al., 1991; Kruuk et al., 2008; Morrissey et al., 2010), we substitute **P** for **G** in this analysis. **P** is a symmetric matrix with the morphological variance of each trait on the diagonal and the covariance with other traits on the off-diagonals.

Among the many factors that confound attempts to estimate the covariance of morphological traits are the effects of sexual dimorphism (Marroig and Cheverud, 2004; Marroig et al., 2009; Grabowski et al., 2011; Grabowski, 2013). However, those effects can be ameliorated by using the residual covariances from a MANOVA that sets sex as the independent variable and by pooling the residual covariances from both sexes (Ackermann and Cheverud, 2000; Marroig et al., 2009; Porto et al., 2009; Grabowski et al., 2011; Grabowski, 2013). In cases where no sex was assigned to museum specimens, a discriminant function analysis was used to classify specimens by probable sex. This analysis is available in R (R Core Development Team, 2010) as part of the fit function in the MASS package (Venables and Ripley, 2002).

3.2.2.2 Preparing the hypothetical matrices

Observed morphological variation was tested against hypothetical matrices of morphological integration (Cheverud, 1989; Olson and Miller, 1999; Hallgrimsson et al., 2004; Monteiro et al., 2005). Several of these hypothetical matrices describe functional or developmental modules within the dentition. A module denotes a system whose components are highly integrated within themselves and which is relatively independent from other highly integrated systems (Klingenberg, 2008). Modules can be summarized as "nested integrations" (Willmore et al., 2007). Models describing integration in multiple modules should be designed and interpreted with care, as modularity does not always account for the disproportionality of pleiotropic effects in different modules (Klingenberg, et al., 2001, 2004) or the synchronous interactions of several developmental and functional processes (Cheverud 1982, 1995, 1996; Hallgrimsson and Lieberman, 2008; Roseman et al., 2009). With these caveats in mind, the hypothetical matrices and their justifications are described below.

H1: "Tooth bud" hypothesis: Each tooth is formed from a primordial tooth bud, which has the developmental capacity to form an entire tooth even in ectopic tissues (Sharpe, 2000; Song et al., 2008). The construction of this hypothetical matrix assumes that the dentition is best described by an integrated module for each tooth, to the exclusion of the effects of variations observed in all other teeth.

H2: "Tooth class" hypothesis: Premolars replace deciduous teeth whereas molars have no precursors (Scott, 1892; Butler, 1941, 1967, 1995; Posen, 1965). Some authors have proposed that each postcanine tooth class represents a developmental module (Dahlberg, 1945; Jernvall and Jung, 2000). Two modules were therefore set in this analysis, one describing the premolar class and one describing the molar class.

H3: “Measurement” hypothesis: Analyses of the regulatory pathways of tooth development in mice have shown that the same regulatory pathways are shared among teeth within the same jaw (Tucker and Sharpe, 2004; Tummers and Thesleff, 2009). That is, when a genetic change affects one regulatory pathway, this difference is likely to affect all dental structures that develop using the same pathway. Changes in initiation and development of enamel knots of the tooth bud are known to affect resulting cusp morphologies (Vaahtokari et al., 1996; Thesleff et al., 2001; Kassai et al., 2005; Jernvall et al., 2008), and changes in overall crown size may be the product of an inhibitory cascade acting on the serial development of teeth (Kavanagh et al., 2007). The “measurement” hypothesis therefore tests whether integration is present among the same measurements taken on different teeth.

H4: “Simple molarization” hypotheses: In some primates, including fossil hominins, the P_4 is described as molarized, which denotes a general similarity between the P_4 and M_1 (Butler, 1941; Robinson, 1956). The frequent appearance of molarization in primate lineages suggests that, at least in some clades, integration may describe covariation of the P_4 and M_1. In this hypothesis, one module assumes integration between morphological variations of the P_4 and M_1, to the exclusion of the integrative effects of the P_3 and M_2 upon these teeth.

H5: “Nested molarization” hypothesis: In this hypothesis, it is assumed that tooth class is an important factor in determining the morphologies of the P_4 and M_1, even in cases where molarized P_4s are observed. In this analysis, a P_4 and M_1 module is considered in addition to a modules describing integration within premolars and molars. There are three modules present in this analysis, with the premolar and molar modules

independent from one another, and the P_4 and M_1 module interacting with both of these modules. This hypothesis suggests that molarization is a cumulative effect of integrative changes in tooth class and integrative changes between the P_4 and M_1.

3.2.2.3 Testing matrix similarity

Each hypothetical matrix was tested against the observed linear measurements in order to determine which matrix (if any) best fit the pattern of dental covariation observed in extant primate postcanines. Pattern similarities in matrices are evaluated by comparisons of matrix indices. Although there are several methods for determining matrix indices, the method typically used in studies of morphological integration is the matrix correlation index (Sneath and Sokal, 1972; Cheverud et al., 1989). This uses the cross-product of individual entries to generate an observed correlation coefficient between two matrices on a scale from -1 to 1. The statistical significance of this correlation is evaluated by Mantel's test (Mantel, 1967), which randomly permutes the rows and columns of one matrix to generate a distribution of all possible correlation values.

3.3 Results

The magnitude of integration in each primate genus is reported in Table 3.2. While these results can suggest integration patterns between primate genera, there are confounding effects of species and subspecies variation that are not included in this analysis and which directly affect the reported values of magnitude of integration. Genera with high degrees of morphological variation between component species (i.e., *Gorilla*) may have artificially low magnitudes of integration. With this limitation in mind, the magnitude of integration in the primate genera included in this analysis ranges

from r^2=0.115 in *Pan* to r^2=0.370 in *Macaca*. That is to say, across all measures of postcanine covariation included in this study, the postcanine dentition of *Macaca* is relatively more integrated than is the dentition of *Pan*. Overall, measurements of the teeth in primates are more integrated than measures of the cranium and pelvis (Porto et al., 2009; Grabowski et al., 2010).

Correlation coefficients and their significance are listed in Table 3.3. The significance of the correlation between the observed and hypothetical matrices in each primate genus is not predicted by the overall magnitude of integration within that genus. For example, although the relative magnitude of integration is similar between *Cercocebus* and *Hylobates*, these two genera have significant fits to different hypothetical matrices.

Across primates broadly, the best hypothetical fit to the data is H3, the measurement hypothesis. In this hypothesis, each linear dimension of a tooth is integrated with the homologous dimension in other postcanine teeth. Length, width, and intercuspal distances appear to each be highly integrated among teeth, even in cases where the teeth belong to different developmental classes. In the great apes, *Saguinus*, and *Cercocebus*, this pattern is highly significant ($P<0.01$) and in *Macaca* it is significant ($P<0.05$).

Hylobates and *Papio* do not show significant correlations to the measurement hypothesis. Rather, these two primate genera are better described by the tooth bud hypothesis (H1), in which each tooth acts as its own module. In this hypothesis, each linear trait of a tooth covaries with other linear traits within its own tooth organ, to the exclusion of the influences of other teeth. The morphological covariation present in

Macaca also shows a significant fit to the tooth bud hypothesis, suggesting that both homologous structures between teeth and structures within a tooth are integrated in this genus.

Few primates show significant fits to the tooth class hypothesis (H2), which expected premolars and molars to form distinct modules due to their different developmental trajectories. *Hylobates* and *Macaca*, however, are exceptions to this pattern and in *Hylobates*, the fit between the predicted matrix and observed values is especially significant.

No primate genus conformed to the predicted fit of the simple molarization hypothesis (H4). However, when the influences of tooth type and tooth class are considered in the nested molarization hypothesis (H5), *Hylobates*, *Papio*, and *Macaca* share a similar pattern of covariance that suggests highly significantly integration within each tooth, between teeth of the same class, and between the P_4 and M_1.

3.4 Discussion

Overall, the fit of most of the primate genera considered here to the measurement hypothesis suggests that even though teeth develop from individual tooth buds, their resulting phenotype covaries closely with changes in homologous linear measurements of crown size and intercuspal distance. Length, width, and intercuspal distances may each form a different morphological module affecting the final morphology of primate postcanine dentitions. The results of this study are consistent with previous studies of morphological variation in the teeth of fossil hominins that found no evidence of premolar and molar modules (Gomez-Robles and Polly, 2012). These results support the field model proposed by Butler (1939), which argued that all postcanines shared similar

sources of morphological influence, regardless of their presence or absence in the deciduous dentition. It also supports the results of the work of Harris (2003), who found that tooth diameters are closely linked by their functional type and account for the majority of size variances between teeth. The integration of basic size dimensions between the postcanines suggests that the functional integration between the teeth and space in the jaw may be an important determinant of dental morphological variation.

Some primate genera deviate from the measurement hypothesis. Covariance in the dental traits of *Hylobates*, *Papio*, and *Macaca* better fits the hypothesis that consider each tooth as a module (H2) or the hypothesis of nested molarization (H5) that includes individual tooth, tooth class, and P_4-M_1 modules. Significant covariation between premolar and molar measurements has previously been described in *Papio* (Hlusko and Mahaney, 2009). Although *Hylobates* is more closely-related to the hominoids, many aspects of its dentition are comparatively primitive and are similar to other cercopithecines, including *Papio* and *Macaca* (Schroer and Wood, 2013; Swindler, 2002). On example is prominent canines in both sexes that form a honing complex with the P_3s (Frisch, 1963, 1973; Kelley, 1995; Vogel et al., 2009). Although other hominoids also have honing complexes, they are less developed than those found in *Hylobates* and non-hominoid cercopithecoids (Greenfield and Washburn, 1992). If the effects of a honing complex are removed from the analysis by eliminating dimensions of the P_3, *Hylobates* alone remains consistent with the tooth bud hypothesis (Table 3.4). This suggests that the integration observed in the individual tooth modules of *Macaca* and *Papio* may relate to variations in P_3 morphology. It is possible that a general catarrhine pattern describes the integration of morphological variation in the postcanines in these

genera, with *Hylobates* having a derived form of this pattern; this would eliminate the influence of the P_3 on morphological variation.

Along with *Macaca* and *Papio*, *Cercocebus* belongs to the cercopithecoid lineage and is hypothesized to share its integration patterns with closely-related primate genera. However, *Cercocebus* follows the pattern of *Saguinus* and the hominoids and is best described by the measurement hypothesis. This discrepancy may relate to the molarization of the P_4 in this clade. Molarization, in terms of a general increase in the crown size of the premolars, is seen in the morphology of the premolars of *Cercocebus* (Daegling et al., 2011; McGraw and Daegling, 2012), the great apes (Leonard and Hegmon, 1987; de Castro and Nicolas et al., 1996) and tamarins (Kleiman, 1981; Schroer and Wood, 2011), The genera that best fit the nested molarization hypothesis are those with the least degree of molarization, suggesting that molarization may be the phenotypic result of the loss of integration *within* the P_4 and M_1, respectively, rather than the development of a derived module *between* the P_4 and M_1. The lack of integration between and within the P_4 and M_1 may explain why the pattern of integration in *Cercocebus* is different from other cercopithecoids.

The results of this analysis confirm the results of other studies that suggest that dental traits may not be discrete characters (Kangas et al., 2004). There appears to be great dependence of a linear measurement in one postcanine tooth upon how those measures vary in other postcanine teeth. Integration among dental measurements may affect how characters are used in phylogenetic reconstructions of primate and hominin evolution, particularly in cases where traits of several postcanine teeth are used. For

example, the inclusion of size dimensions of both the M_1 and M_2 might inflate the degree of difference among taxa as the sizes of these teeth are highly dependent.

In addition to its implications for phylogeny, the results of this study suggest several avenues by which selection may have acted on fossil primate dentitions, including the dentitions of fossil hominins. Integration may act as a source of stabilizing selection, keeping integrated traits near their fitness optima during episodes of directional selection (Hansen and Houle, 2004, 2008). This coordination reduces the rate of morphological change and constrains how morphology can adapt to selection pressures (Marroig et al., 2009; Porto et al., 2009). In morphospace, which denotes the theoretical range of all morphological possibilities (Raup, 1966; Raup and Michelson, 1965; Foot 1997; Eble, 2000, 2003), the dental variation observed in primates may occupy relatively small regions.

In living primates, it is apparent that the dentitions of certain primate taxa, such as *Pan*, are less integrated and have particularly large areas of morphospace in which morphology may respond to selection. The dentitions of other genera, such as *Macaca*, appear more constrained. Future analyses that include dental variation in modern humans may indicate whether or not the comparatively low degree of integration *Pan* is a plesiomorphic trait of the human-chimpanzee lineage. Future analyses should also include large sample sizes of each species included within a genus in order to determine the extent to which patterns of integration may be linked to phylogeny.

Such analyses may indicate whether or not hominins are described by a P_4 and M_1 module. In this analysis, great apes and other relatively molarized taxa do not show evidence of P_4 and M_1 module. This suggests the P_4 may have occupied a wide range of

regions in morphospace during hominoid evolution and hominin evolution more specifically. The high degree of molarization found in certain members of this clade, especially *Paranthropus* (Hillson, 1996; Wood and Strait, 2004; Bailey and Wood, 2007) may be the result of a further breakdown in the integration of dental traits. This breakdown may have allowed taxa to occupy morphospace that was previously off-limits, resulting in more ways the hominin dentition could respond to selective pressures.

3.5 Conclusion

The results of this analysis do not indicate a pattern of integration in postcanine teeth that is easily described by developmental class. Postcanine teeth in most primate genera are best described by a hypothetical matrix in which each type of measurement taken on the postcanine teeth (i.e., overall length and width, and intercuspal distance) is highly integrated above the level of individual tooth or tooth class. Some primate genera are better described by a hypothetical matrix in which each tooth is an independent module, again to the exclusion of the influences of tooth class. The results of this study suggest that premolars and molars are integrated in patterns that are not predicted by whether or not they have deciduous precursors.

In primate genera with relatively molarized premolars, no indication of a P_4-M_1 module is recovered in this analysis. Rather, it is primates with relatively non-molarized premolars that are best described by this hypothetical module. This result suggests that molarization may represent a loss of integration between these teeth, rather than an additional source of integration. The presence of molarization in several primate lineages, including representatives of ceboids, cercopithecoids, and hominoids, suggests that such a loss may be common in primates. However, whether or not molarization

represents a plesiomorphic character or instances of convergence remains to be determined. Future studies are needed to determine the relative independence of molarization and other the dental traits frequently cited in phylogenetic reconstructions of primates and hominins.

"Mismatches," such as the mismatches found in this study between the observed data and the proposed developmental and functional modules, are important sources of information concerning how modules form (Klingenberg, 2008). Although modules have been proposed for developmental fields, specific regulatory pathways, and other recognizable anatomic and developmental units (Schlosser and Wagner, 2004; Klingenberg, 2008), sources of mismatch can illuminate the complex relationships among such units. Integration may occur simultaneously at many levels of hierarchy (e.g, functional, developmental, genetic, and evolutionary) thus making such mismatches critical for interpreting the possible response of a population to selection pressures. Reconstructing the patterns of evolution in fossil lineages, such as the hominins, necessitates a more sophisticated understanding of the process by which that evolution occurs.

Table 3.1 Extant primates examined in this analysis.

Taxon	N	♀	♂
Cercocebus	34	11	23
Cercocebus atys	8	4	4
Cercocebus galeritus	8	4	4
Cercocebus torquatus	18	3	15
Gorilla	43	13	30
Gorilla beringei	14	6	8
Gorilla gorilla	29	7	22
Hylobates	43	22	21
Hylobates agilis	17	6	11
Hylobates klossii	8	5	3
Hylobates lar	18	11	7
Macaca	113	59	54
Macaca cyclopis	12	5	7
Macaca fascicularis	52	32	20
Macaca fuscata	11	8	3
Macaca nemestrina	38	14	24
Pan (*Pan troglodytes*)	19	9	10
Papio	74	18	56
Papio anubis	55	12	43
Papio ursinus	19	6	13
Pongo	47	28	19
Pongo abelii	9	5	4
Pongo pygmaeus	38	23	15
Saguinus	73	35	38
Saguinus fuscicollis	14	11	3
Saguinus geoffroyi	30	12	18
Saguinus labiatus	15	6	9
Saguinus mystax	14	6	8

Table 3.2 Magnitude of integration in extant primate postcanine teeth, P_4-M_2.

Taxon	r^2
Cercocebus	0.247
Gorilla	0.285
Hylobates	0.222
Macaca	0.370
Pan	0.115
Papio	0.149
Pongo	0.286
Saguinus	0.325

Table 3.3 Results of Mantel's test of correlation between morphological and hypothetical matrices, where R is the regression coefficient and P is the probability. H1= tooth bud hypothesis; H2 = tooth class hypothesis; H3 = homologous measurement hypothesis; H4 = simple molarization hypothesis, and H5 = nested molarization hypothesis.

	H1		H2		H3	
Taxon	R	P	R	P	R	P
Cercocebus	0.024	0.408	0.119	0.123	0.355	0.003
Gorilla	-0.041	0.680	0.056	0.174	0.365	0.004
Hylobates	0.358	0.001	0.252	0.006	0.040	0.328
Macaca	0.203	0.011	0.164	0.038	0.159	0.034
Pan	-0.072	0.767	-0.106	0.879	0.321	0.003
Papio	0.227	0.009	0.141	0.063	0.100	0.127
Pongo	-0.047	0.724	0.042	0.238	0.373	0.001
Saguinus	-0.028	0.573	0.151	0.091	0.341	0.002

	H4		H5	
Cercocebus	0.022	0.416	0.071	0.237
Gorilla	0.040	0.406	-0.006	0.458
Hylobates	-0.242	0.918	0.245	0.034
Macaca	0.187	0.171	0.309	0.018
Pan	0.154	0.183	-0.191	0.933
Papio	0.200	0.139	0.239	0.036
Pongo	0.252	0.135	0.059	0.298
Saguinus	0.113	0.243	0.186	0.094

Table 3.4 Results of Mantel's test of correlation between the morphological matrix and the tooth bud hypothesis (H2), tested with and without the inclusion of P_3 variation. R is the regression coefficient and P is the probability.

	H2		H2 (no P_3)	
Taxon	R	P	R	P
Cercocebus	0.119	0.123	-0.111	0.772
Gorilla	0.056	0.174	-0.091	0.723
Hylobates	0.252	0.006	0.342	0.005
Macaca	0.164	0.038	0.042	0.301
Pan	-0.106	0.879	-0.044	0.620
Papio	0.141	0.063	0.203	0.077
Pongo	0.042	0.238	-0.162	0.846
Saguinus	0.151	0.091	0.018	0.434

Chapter 4: Assessing character displacement in hominin and primate premolar crown size

4.1 Introduction

Two fossil hominin genera, *Paranthropus* and *Homo*, are found synchronically in many of the same Plio-Pleistocene fossil localities in East and southern Africa. Though separated from their proposed *Australopithecus*-like ancestor by less than a million years (Strait et al., 1997; Strait and Grine, 2004), these two genera have remarkably different dental morphologies. The postcanines of *Paranthropus* are absolutely and relatively large compared to other hominin taxa, especially compared to the reduced dentition of early *Homo* (Constantino and Wood, 2004; Wood and Constantino, 2007). Researchers have suggested that competition over shared resources may have resulted in these divergent dental morphologies (Schaffer, 1968; Laden and Wrangham, 2005). Competition may also have led *Paranthropus* and early *Homo* in East Africa to adapt to different dietary niches, with *P. boisei* eventually consuming more C_4 resources than any other hominin known to date (Cerling et al., 2011).

The influence of competition on adaptation is a common theme in the ecological literature (Burger et al., 2006) and the effects have been formalized by the competitive exclusion principle (Gause, 1934). This principle, derived from observations made on the relatively simple system of 'competing' bacterial cultures on agar plates, states that two taxa in competition for the same resources cannot coexist. Rather, either one competitor will evolve some advantage over the other and drive it to extinction in their shared habitat, or the two taxa will instead evolve non-competing ecological niches and maintain coexistence. The competitive exclusion principle may be extrapolated to

describe divergence in two closely-related mammalian taxa sharing the same complex habitat, such as may be the case between *Paranthropus* and *Homo*. This type of divergence has been called character displacement (Brown and Wilson, 1956). The large teeth of *Paranthropus* and small teeth of *Homo*, which diverge in different directions from the hypothesized generalized archaic hominin dentition, may offer an example of character displacement at work in the hominin fossil record (Schaffer, 1968).

Character displacement can be quantified as the displacement statistic D_S-D_A, where D_S denotes the divergence between sympatric (i.e., shared location) populations of two taxa and D_A denotes the divergence between allopatric (i.e., different locations) populations of the same two taxa (Schluter and McPhail, 1992). D_S quantifies the variation of two taxa in areas where they may be in competition, while D_A quantifies the variation of the two taxa in the absence of competition, when the two taxa are isolated from one another. When the value of D_S exceeds the value of D_A, this indicates that selection has favored distinction between the two taxa and that character displacement has occurred (Figure 4.1). Character divergence may involve several kinds of variation, including behavioral and reproductive (Waage, 1979; Armbruster, 1985; Levin, 1985; Marshall and Cooley, 2000; Geyer and Palumbi, 2003; Adams, 2004), but in general the term has been applied to morphological divergence (Slatkin, 1980; Schluter and McPhail, 1992; Adams and Rohlf, 2000; Losos, 2000). Although the displacement statistic has been shown to explain morphological variation in many sympatric vertebrate species (Dayan et al., 1989, 1990, 1992; Losos, 1990; Dayan and Simberloff, 1994; Simberloff et al., 2000), it has rarely been applied to fossil hominins (but see Schaffer, 1968).

This study applies the displacement statistic D_S-D_A to the morphological differences between *Paranthropus* and early *Homo* teeth. Previous studies of character displacement in a variety of mammals have found that changes in dental morphology may be the result from character displacement (Dayan et al., 1989, 1990, 1992; Yom-Tov, 1991; Reig, 1992; Dayan and Simberloff, 1994; Werdelin, 1996). In particular, this study focuses on aspects of the lower fourth premolar (P_4), a tooth that is distinctly molarized in *Paranthropus* and non-molarized in *Homo* (Hillson, 1996; Wood and Strait, 2004; Bailey and Wood, 2007).

One method of applying the character displacement statistic to observed morphological differences is to use a generalized linear model (GLM) that can approximate the relationship between observed P_4 morphologies and the ecological relationship between two taxa. GLMs are widely used in studies of species distribution (Guisan and Zimmermann, 2000; Scott et al., 2002) because they can be used to interpret the strength of the fit between response (i.e., morphological) variables and explanatory (i.e., ecological) variables (Austin, 1987; Yee and Mitchell, 1991; Guisan et al., 2002). The use of general linear models is especially common in character displacement studies (Bolnick, 2004; Bolnick and Fitzpatrick, 2007; Collyer and Adams, 2007; Russo et al., 2007). This is partly due to the theoretical origins of character displacement, for there are relatively few natural experiments in which to observe character displacement (Bonick and Fitzpatrick, 2007). Some researchers even argue that random mating and genetic similarity prohibits sympatric groups from forming (Mayr, 1963; but see Doebeli, 1996). The derived nature of the *Paranthropus* dentition, however, suggests that a relatively strong selection pressure was at work during its evolution, and the proximity in time and

location of *Paranthropus* and early *Homo* suggests character displacement is one potential source of selection pressure that should be considered.

The model proposed in this study builds on one for multivariate phenotypic change proposed by Collyer and Adams (2007). The Collyer and Adams model is especially suitable for this study as it does not presume a specific taxonomic level. While early character displacement studies only considered sympatric and allopatric populations of the same species (i.e., Schluter and McPhail, 1992), this model and others have shown that character displacement can account for morphological divergence of sympatric and allopatric species (Dayan et al., 1990; Dayan and Simberloff, 1994), family (Monroe, 2012) and higher taxa, such as would be used for an ecological guild (Schluter, 1986). So long as the taxonomic unit is standard, the Collyer and Adams model does not require that the sample is limited to populations of the same species.

The Collyer and Adams model was tested in salamanders and pupfish, but it has not been applied to living or extinct primates. There are many primate populations that live in sympatry, including species of strepsirrhines (Tan, 1999), platyrrhines (Puertas and Bodmer, 1993; Agostini, 2008), and catarrhines (Fleagle, 1977; Sterk and Steenbeek, 1997; Lambert, 2004). If the Collyer and Adams model describes dental variation primate populations of known sympatry, it may provide one means of assessing the likelihood that extinct primates, such as fossil hominins, lived in sympatry. This study applies the Collyer and Adams model to premolar size variation in sympatric populations of living primates, focusing on those primates that have previously been proposed as comparative models for understanding the ecology of *Paranthropus* and *Homo* (Wood and Schroer, 2012). Once we determined the model could be applied to variation in

premolar crown size among sympatric primates, we then applied it to the premolars of fossil hominins to assess the likelihood of character displacement as a factor in the divergence of the postcanine teeth of *Paranthropus* and early *Homo*.

4.2 Materials and Methods

4.2.1 Sample

The living primate groups chosen for examination in this study were African apes, Asian apes, macaques, and papionins. Members of each of these groups have been previously proposed as comparators for the unusual morphology of *Paranthropus* (Jolly, 1970; Vogel et al., 2009; Wood and Schroer, 2012); the comparisons were either species-level (*Macaca, Saguinus*) or genus-level (*Gorilla-Pan*, *Hylobates-Pongo*, *Cercocebus-Papio*). Genus-level distinctions are the appropriate comparisons for the ecological context of *Paranthropus* and *Homo* (Strait et al., 1997; Wood and Richmond, 2000), but there is controversy surrounding the definition of a genus (Wood and Collard, 1999) and questions concerning the monophyly of both *Paranthropus* and *Homo* (Wood, 1988).

The same groups are also suitable comparators to test the hypothesis of dietary divergence between *Paranthropus* and *Homo*. Dietary differentiation is one common in which competitive taxa diverge (Ackerly et al., 2006) and several lines of evidence suggest that *Paranthropus* adapted to eat a more mechanically challenging diet than *Homo* (du Brul, 1974, 1977; Rak, 1983; Grine, 1986, 1987; Kay and Grine, 1988; Hylander, 1988; Teaford and Ungar, 2000; Scott et al., 2005, Constantino and Wood, 2007; Ungar et al., 2008). Each of the sympatric extant primate taxa included in this study are known to differ in the mechanical properties of their diets. *Gorilla* consume more tough foods than sympatric *Pan* (M'Kirera and Ungar, 2003), and *Saguinus*

labiatus has recently been shown to consume more tough foods than its sympatric congener, *Saguinus fuscicollis* (Schroer et al., 2012). Both *Pongo* and *Cercocebus* eat harder food than sympatric primates in their regions (Vogel et al., 2009; Daegling et al., 2011), *Macaca nemestrina* is also durophagous, and the molarized premolars of *Cercocebus* have been cited as an adaptation to the mechanical challenges of their diet (Daegling et al., 2011).

Lower jaws of the extant primate taxa were photographed from the collections of the National Museum of Natural History in Washington, DC, and the Natural History Museum in London. Photographs were taken with a Canon Digital Rebel XT camera fitted with a macro lens, and they were digitized in TPSDig (Rohlf, 2009). For each photograph, specimens were oriented to maximize the occlusal plane of each tooth. Levels on the camera and photography stand were employed to ensure the occlusal area was parallel to the lens of the camera. To minimize distortion, teeth were positioned so as to occupy less than one third of the frame and a scale was set and leveled in the occlusal plane of the teeth. Standard measures of the P_4 included maximum mesiodistal and buccolingual diameters and overall occlusal area was calculated from a curve fitted around the occlusal margin in TPSDig. The latter was resampled to 20 semilandmarks of equal distance around the curve before calculating the area. Although mesiodistal (MD) and buccolingual (BL) length are most likely correlated with occlusal area, these three measurements represent the three most common measures used to describe the size of premolar crowns in fossil studies. The extant primate sample featured only wild adults of mixed-sex, and left sides of the mandibles were used unless that side was missing. Maps

showing the relative ranges of overlap for the extant primate taxa are shown in Figure 4.2.

Ideally, the phylogenetic distance between the members of each group would be the same as the phylogenetic distance separating *Paranthropus* and *Homo*, but few sympatric primate genera are separated by such a comparatively short evolutionary time since their divergence from a common ancestor. Therefore, intervals of divergence times both longer and shorter than the estimate time of divergence between *Paranthropus* and *Homo* were used in the following analyses. For the majority of groups, the taxa were of different genera and therefore similar to the structuring of a proposed *Paranthropus-Homo* dichotomy (i.e., Groups 1, 2, and 4). For some groups, however, the competitive taxon was of the same genus as the first few species chosen for the group (i.e., Groups 3 and 5). In these cases, the likelihood of finding morphological variation is decreased, since the group has a relatively shorter divergence time from their common ancestor. This inflates the D_A value and decreases the theoretical distance between D_S and D_A. Subsequently, this will increase the likelihood of rejecting a true positive (i.e., increases Type II error) in the resulting analysis of sympatric versus allopatric variation. Increases in Type II error can be permitted in character displacement analysis, as such increases make it *less* likely that a signal of character displacement will be detected.

The fossil hominin sample is composed of representatives of the genera *Paranthropus* and *Homo.* The sympatric populations of these two genera are composed of East African representatives of both genera. In the case of East African *Paranthropus*, two species are recognized, *P. boisei* and *Paranthropus aethiopicus*. *Paranthropus boisei* is generally considered a close relative of *P. aethiopicus* (Strait et al., 1997; Wood

and Richmond, 2000; Wood and Constantino, 2007; Wood and Lonergan, 2008), and some authors have argued that these two taxa represent a chronospecies in East Africa (Foley, 1991; Bobe et al., 2007; Constantino, 2013; Wood and Schroer, 2013). The taxa are grouped together as *P. boisei* in this analysis. The allopatric population of *Paranthropus* is the southern African representative of that genus, *Paranthropus robustus*.

The East African sample of *Homo* includes remains reliably associated with members of *Homo habilis*, *Homo rudolfensis*, or *Homo ergaster*. The allopatric sample of *Homo* includes remains of *Homo* found outside of East Africa that date to more than 0.5 million years ago and includes representatives of several later *Homo* taxa. The *Homo* specimens found at the site of Dmanisi in Georgia have been linked with *H. ergaster*, or to a closely-related taxon (Rosas and Bermudez de Castro, 1998; Gabunia et al., 2000; Vekua et al., 2002). The *Homo* found at Rabat has also been assigned to *H. ergaster* (Martinon-Torres et al., 2007; Gomez-Robles et al., 2008; or its close relative and possible descendant *Homo erectus* (Groves, 1999). Sangiran and Zhoukoudian are assigned to *H. erectus*. The inclusion of later *Homo*, such as those specimens found at Rabat and Ternifine, increases the morphological and geographic variation in the allopatric sample and will thus likely inflate the value of D_A and increase the likelihood of Type II error.

Some fossil finds in southern Africa also have affinities to *Homo*, but these specimens are not included in this analysis due to questions concerning their taxonomy and stratigraphy. Specimens that have been assigned to early *Homo* include STW 53, SK 847, and SK 1587 (Hughes and Tobias, 1977; Howell, 1978; Tobias, 1978, 1991;

Corruccini et al., 1980; Chamberlain and Wood, 1987; Grine et al., 1993, 1996; Clarke, 1990, 1994), but these specimens also have traits in common with later *Homo* (Robinson, 1960, 1967; Clarke, 1977; Tobias, 1978; Groves and Mazak, 1975; Walker, 1981; Dean and Wood, 1982; Spoor et al., 1994) and have occasionally been referred to non-*Homo* taxa (Mann, 1970; Wolpoff, 1970, 1971; Krantz, 1977; Wood and Abbott, 1983; Wood and Uytterschaut, 1987; Kuman and Clarke, 2000; Berger et al., 2010). Southern African specimens of *Homo* that can be reliably referred to *Homo*, such as SK 15, are found in late deposits of southern African sites and do not indicate sympatry with other fossil hominins (Broom and Robinson, 1949; Robinson, 1953; Clarke, 1977; Rightmire, 1990). Some have suggested that one southern African *Homo* specimen, STW 53, may be evidence of sympatry between *Homo* and *Paranthropus* in southern Africa (Curnoe and Tobias, 2006), but a recent analysis suggests that STW 53 comes from a hanging remnant of Sterkfontein Member 4 (Clarke, 1994, 2008) and therefore provides no indication of sympatry with other hominins. For the purposes of this analysis, which examines the influence of competition on East African hominin populations, no southern African fossil with close affinities to *Homo* was included. The allopatric population of *Homo* was restricted to individuals in areas with no known overlap with any non-*Homo* hominin.

Measurements for most fossil hominin premolars were obtained in the same manner as the extant primates from photographs of precision casts of fossil material in the collections of The George Washington University and the University of Arkansas, or they were taken from high-resolution photos of fossil specimens. In cases where photographs and casts were unavailable, measurements were taken from the literature. These sources are given in Table 4.1, along with fossil specimen numbers. In the case of

these fossil specimens, occlusal areas could not be directly measured and an approximation (MD x BL) was used instead. This method will usually overestimate occlusal area; specimens whose occlusal area was computed and not measured are marked with an asterisk in Table 4.1. All fossil specimens represent adult dentitions, but sex was not controlled. The relative geographic locations of the fossil specimens are given in Figure 4.3.

For both extant and fossil specimens, only individuals with complete M_1-M_3 or P_4-M_2 series were analyzed. Extensively worn specimens (i.e., occlusal wear great enough to mask the identification of individual cusps and interproximal wear that affected >20% of the occlusal margin) were not included in the extant sample. For teeth with moderately worn cusps, the location of the cusp was estimated to be the center of the wear facet (Bailey, 2004; Gomez-Robles et al., 2008). For teeth with moderately worn margins, the margin was reconstructed by approximating the curvature of the margin from overall crown shape (Wood and Uytterschaut, 1987; Bailey and Lynch, 2005). For fossil teeth, similar methods were employed, but teeth with <90% of their likely occlusal areas preserved were not considered.

To calculate intra-observer error, a sample of 45 individuals representing all taxa in the extant primate sample was measured again two months after initial measurements. Technical error for linear measurements was $\pm$0.1 mm for *Saguinus* and ±0.4 mm for all other taxa. Technical error for areal measurements was $\pm$0.1 mm^2 for *Saguinus* and $\pm$6.10 mm^2 for all other taxa.

4.2.2 Analysis

Measurements of premolar crown size were log-transformed to normalize variance among primate and hominin taxa. Individuals were analyzed separately in the following comparative groups: African apes, Asian apes, macaques, papionins, tamarins, and fossil hominins. Each group comprised four sample populations, a sympatric pair and an allopatric pair. The observed variation in each primate or fossil group was fitted to a general linear model of:

$$Y = BX + U$$

where Y is the morphological matrix, X is the design matrix, B is the estimate of the parameters, and U is the residual error.

The design matrix encodes each individual by taxon and either sympatric or allopatric location. A taxon was assigned either 1 or -1, which are arbitrary designations as any set of two numbers could be used to denote the two different taxa. Location was also described by two numbers, 1 for sympatric taxa and -1 for allopatric taxa. The design matrix also includes a third variable, which is the interaction variable of taxon and location. This is obtained by multiplying the values of taxon and location. Thus, the sympatric population of the first taxon is (1 x 1 = 1), the allopatric population of the first taxon is (1 x -1 = -1), the sympatric population of the second taxon is (-1 x 1 = -1), and the allopatric population of the second taxon is
(-1 x -1 =1). A sample design matrix is described in Appendix 2 and the actual design matrices used for each of the five primate groups are given in Appendix 3.

The Y-matrix is constructed from the observed morphological values of the three premolar size traits considered for each individual. This matrix is given in Appendix 3.

The model parameters, B, are the regression coefficients that describe the relationship between the design matrix and the observed morphological values for each individual. After the application of a least-squares regression, U is minimized so that B describes theoretically all of the relationships between the design and observed matrices (Guisan et al., 2002). After determining B, the vectors for sympatric morphological difference and allopatric morphological difference were subtracted to obtain the D_S-D_A statistic.

To evaluate the significance of the D_S-D_A value obtained from this model, a distribution list was generated from randomized values for each primate group. To generate a randomized list of D_S'-D_A' values, the interaction variable (taxon x location) was stripped from the design matrix so that individuals were no longer encoded by their taxon and location information. From this randomized design matrix and holding the Y-matrix constant, a new set of parameters were generated. The vectors of sympatric and allopatric morphological difference were subtracted to obtain the randomized D_S-D_A statistic and this process was reiterated 999 times to generate the distribution list. Probability was obtained through encoding each D_S-D_A result as either 1 (greater than or equal to the observed D_S-D_A) or 0 (less than the observed D_S-D_A). The results were summed and divided by the number of iterations to generate the likelihood that the observed D_S-D_A was significant. Significance was assumed at the $P<0.05$ level. This analysis was performed using R (R Development Core Team, 2010) through a script modified from Collyer and Adams (2007) and provided in Appendix 2.

4.3 Results

The divergence of premolar dimensions in sympatric populations is consistently greater than the divergence of premolar dimensions in allopatric populations of the same

taxon group ($D_S > D_A$). The probability of observing a higher divergence in sympatric populations compared to allopatric populations is nonrandom ($P<0.50$) in all groups observed in this study and it is significant ($P<0.05$) in the African ape, Asian ape, macaque, tamarin, and fossil hominin groups (Table 4.2).

Although sympatric and allopatric divergence vectors differ, the means of the three traits of premolar crown size are similar in populations of the same taxon group, regardless of hierarchical level (Table 4.3). This appears especially true for the MD and BL measurements. For example, in the case of the sympatric (i.e., East African) and allopatric (i.e., southern African) populations of *Paranthropus* and early *Homo*, the two early *Homo* taxa are morphologically more similar to one another than either is to a *Paranthropus* taxon. However, there is greater divergence between the sympatric group (i.e., *P. boisei* and early *Homo*) than the allopatric group (i.e., *P. robustus* and early *Homo*). The difference between these fossil hominin populations, tested against randomized distributions of morphological variation, is significant ($P=0.014$). That is to say, within the 999 randomly generated D_S-D_A values from a *Paranthropus/Homo* matrix, less than 2% of the random values were greater than the D_S-D_A value obtained when sympatric and allopatric populations are encoded in the design matrix. The results of this model suggest that shared location has an effect on premolar size differences among East African hominins and support previous hypotheses that the extremely large teeth of *P. boisei* may relate to increased competitive pressures from geographic overlap with members of *Homo* (Schaffer, 1968; Wood and Strait, 2004; Laden and Wrangham, 2005).

4.4 Discussion

In the five primate and fossil hominin groups studied here, D_S-D_A is consistently positive and nonrandom, indicating a greater divergence in the size of premolar crowns between sympatric populations than between allopatric populations. This suggests that character divergence is a factor driving the size of premolar crowns in populations of primates and fossil hominins that share the same habitat. This trend occurs regardless of whether species- or genus-level differences are examined.

Although all D_S-D_A values in the extant primate groups were nonrandom, not all were significant. Papionins, the group found to be nonrandom but not significantly different in the size of their premolar crowns, have the smallest amount of geographic overlap of any of the sympatric populations examined in this study. Additionally, some of the papionin sample sizes were small. This group had only 17 individuals from the two taxa with sympatric overlap. The small sample size of this group should be of concern, since it likely underestimates the variation present in the actual populations of sympatric taxa. Future analysis of character displacement would benefit greatly from larger sample sizes. Examining additional groups of sympatric and allopatric primates will also help define the role of character displacement in influencing primate and hominin dental morphologies.

The phylogenetic proximity of two taxa does not necessarily predict how well the model will perform in each group. Papionins are separated by only c.5 million years (Page et al., 1999) and could be predicted to have a high degree of divergence in order to maintain their coexistence in East Africa. However, African apes, which are separated by c.10-8 million years (Scally et al., 2012), are more divergent between their sympatric and

allopatric populations (i.e., a D_S-D_A of 0.34 compared to 0.05) than papionins, but whereas the divergence value is only nonrandom in the papionins, there is a significant difference between the sympatric and allopatric populations of African apes (P=0.001). African apes have a much greater range of overlap than the papionins, and it may be that geographic overlap may be a better indicator of sympatric divergence than phylogenetic similarity.

The results of the African ape group are particularly informative for assessing the role sympatry may play in determining premolar size and morphology. With P=0.001, the sympatric divergence in this clade compared to its allopatric divergence is the most significant of any primate group examined in this study. This is an especially intriguing result, as the allopatric group includes a very large bodied primate, *Gorilla beringei*. On the basis of its large body size, *G. beringei* would likely have large premolars and therefore show a great divergence from the comparative allopatric group, the much smaller-bodied *Pan troglodytes verus/schweinfurthi*. Instead, this analysis detects greater divergence in premolar size between the sympatric and more similar-sized *Gorilla gorilla* and *Pan troglodytes troglodytes*. This provides strong evidence that shared location has contributed to the evolution of premolar size in this clade.

Specifically, overlapping diets within a shared location may cause competition between *G. gorilla* and *P. troglodytes troglodytes*. A study of one sympatric *G. gorilla* and *P. troglodytes troglodytes* group in Lope Reserve of Gabon found that gorillas shared 73% of the chimpanzee food items and the chimpanzees shared 57% of the gorilla food items, but the diets of the two taxa also differ, with gorillas eating larger quantities of vegetative foods, especially in times of fruit scarcity (Tutin and Fernandez, 1993), and

different kinds of insects (Tutin and Fernandez 1992). Further study of sympatric *G. gorilla* and *P. troglodytes troglodytes* in Kahuzi-Biega National Park, Zaire also showed that although gorillas consumed 50% of the fruit species also eaten by chimpanzees, they ate less fruit overall (Yamagiwa et al., 1996).

In the case of fossil hominins, the D_S-D_A difference in this group may be indicative of competition pressures occurring on the East African landscape of c.2 million years ago. Divergence in synchronous East African populations is greater than between allopatric, non-overlapping hominin populations, despite the separation of these populations by greater geographic and phylogenetic distances. One explanation of this phenomenon would be a rapid divergence between the two closely-related taxa, perhaps as a result of high levels of competition. Another explanation may involve the multiple early *Homo* taxa proposed to have existed contemporaneously in East African at this time (Wood, 1992; Lieberman et al., 1996; Spoor et al., 2007; Leakey et al., 2012). Although this is a rare situation among mammals, the presence of more than two closely-related taxa in the same habitat would likely have generated high levels of competition among the taxa.

The results of this study suggest that changes in premolar crown size may relate to dietary divergence between competitive taxa. Dietary differences are implicated in the earliest statistical studies of the character displacement of gnathic and dental morphologies (Schluter and McPhail, 1992) and dietary divergence is a common response to competitive pressures (Ackerly et al., 2006). Although premolars have not been specifically examined in most studies of character displacement, the close relationship between dental morphology and diet (Kay, 1975; Lucas and Luke, 1984;

Lucas et al., 1985, 1986; Teaford and Ungar, 2000; Lucas, 2004) suggests that increases in premolar crown size reflect an enlarged grinding surfaces for mechanically challenging foods (Jolly, 1970; Walker, 1981; Lucas et al., 1985, Kay and Grine, 1988). In the sympatric extant primate groups examined here, the species with the larger premolars does indeed consume the more mechanically challenging diet. The results of this study are therefore highly suggestive that the large premolars of *Paranthropus* reflect dietary divergence via the consumption of more mechanically challenging foods.

4.5 Conclusion

In hominins premolar crown size is known to differ markedly between the megadont and hypermegadont dentition of the genus *Paranthropus* and the reduced dentition of the genus *Homo*. This study applied a modified Collyer and Adams model of character displacement to the premolar crown size of fossil hominins in order to test the probability that sympatric competition may have influenced the divergence of *Paranthropus* and *Homo* postcanine teeth (Figure 4.4). The model was first applied to living primate populations whose sympatry and allopatry are well-established in order to determine the relative success of this model for detecting signals of character displacement in primate populations.

In all groups examined, the difference between the premolar crown size of sympatric populations exceeds the difference between the premolar crown size of allopatric taxa at a nonrandom probability ($P<0.50$ of occurrences). In some taxa, including fossil hominins, this difference was significant at $P<0.05$. Fossil hominins showed both the largest distance between the premolar crown sizes of sympatric and allopatric taxa as well as the greatest degree of significance in this difference. The results

of this study failed to falsify the hypothesis that character divergence occurred during the evolution of *Paranthropus* and *Homo* and that competition played a role in forming hominin dental morphologies.

The results of this study indicate that ecological modeling can provide insights into reconstructing the evolution of our hominin relatives. Most studies of character displacement consider only contemporary populations in a relatively restricted geographic area, and many only examine variation in populations of the same species. This study expands the application of character displacement both hierarchically and geographically, and demonstrates that the same theoretical frameworks that account for variation in living taxa can also be applied to variation observed in the fossil record. By considering the importance of species and location interactions in the evolution of morphological adaptations, studies such as this one move us closer to understanding the processes behind our evolution in addition to their observed morphological patterns.

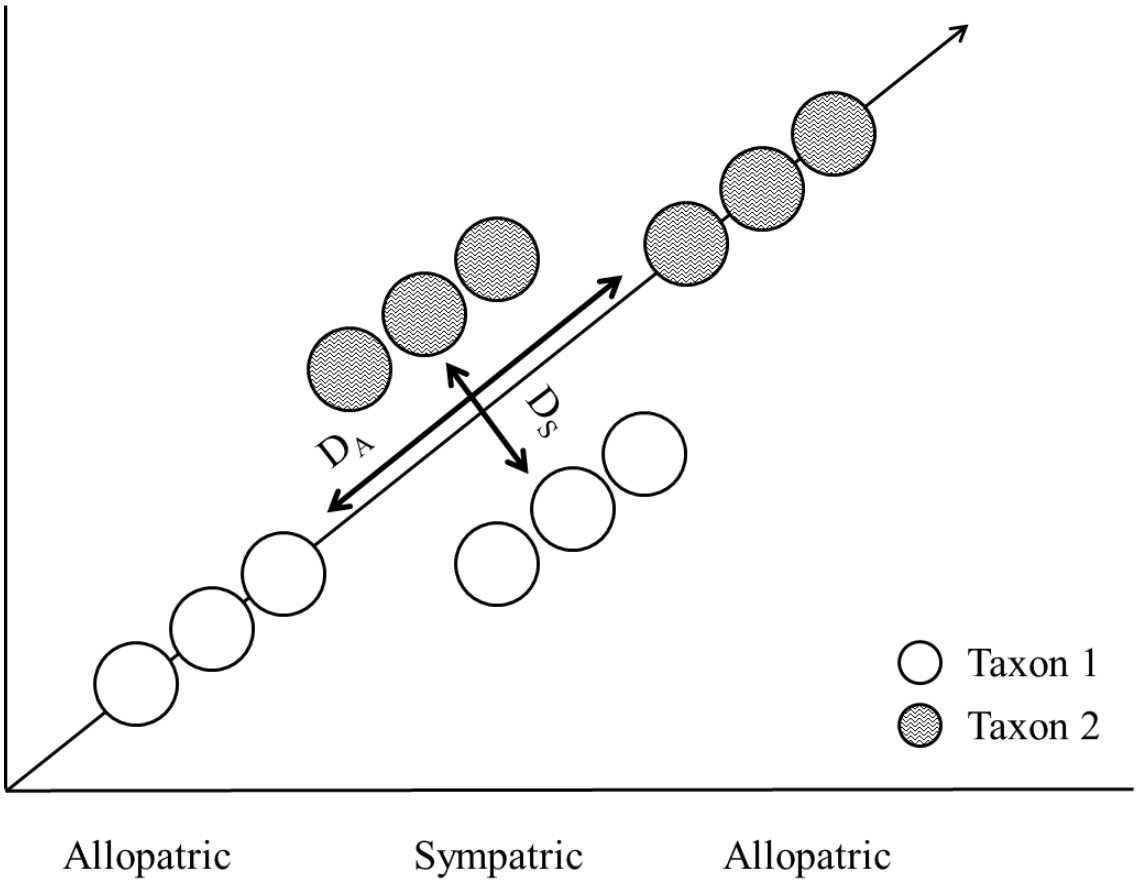
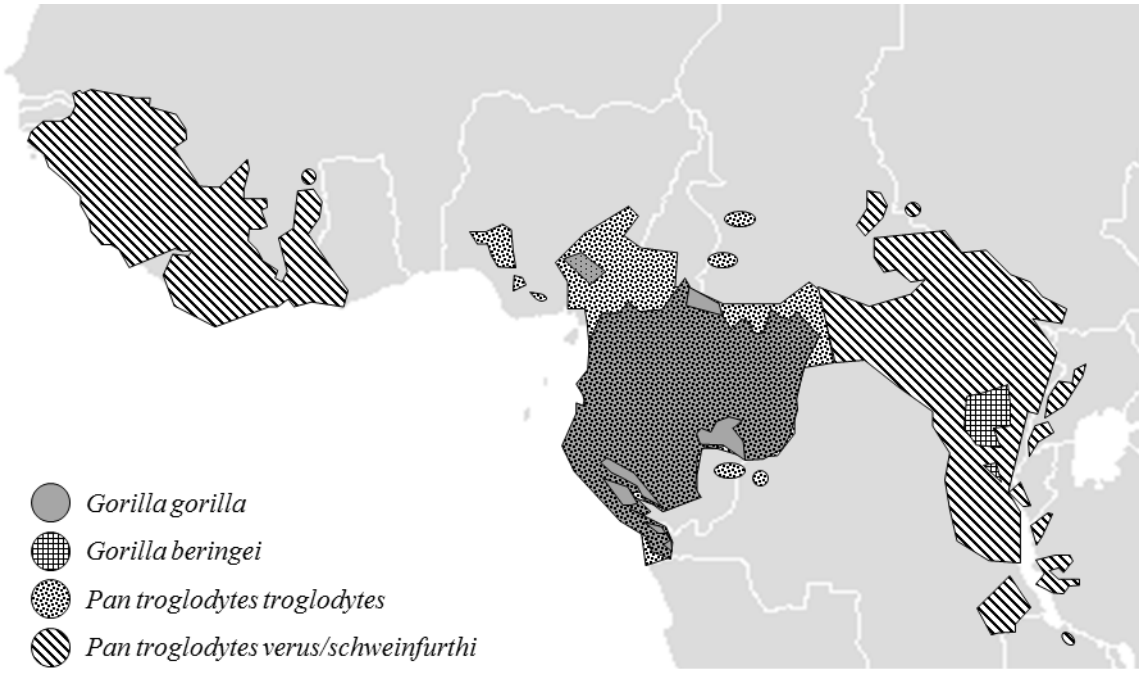


Figure 4.1 Schematic of character displacement, measured through the D_S-D_A statistic. D_S denotes the difference between two taxa that overlap in geographic location while D_A denotes the difference between the same two taxa in non-overlapping populations. When $D_S > D_A$, character displacement is indicated. The straight line indicates a function of similarity between two taxa, and in this analysis this similarity is assumed to be morphological.

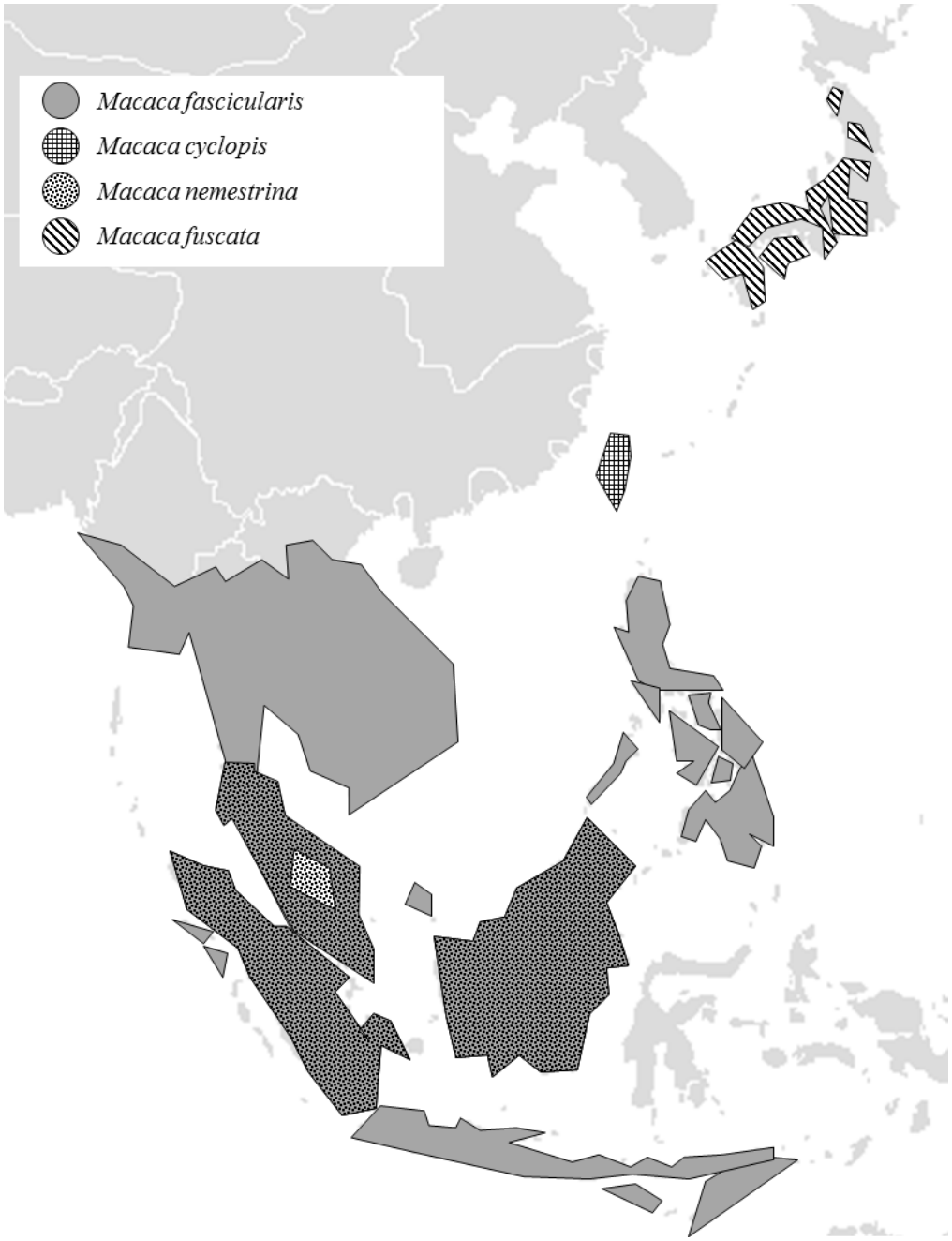


A) African apes

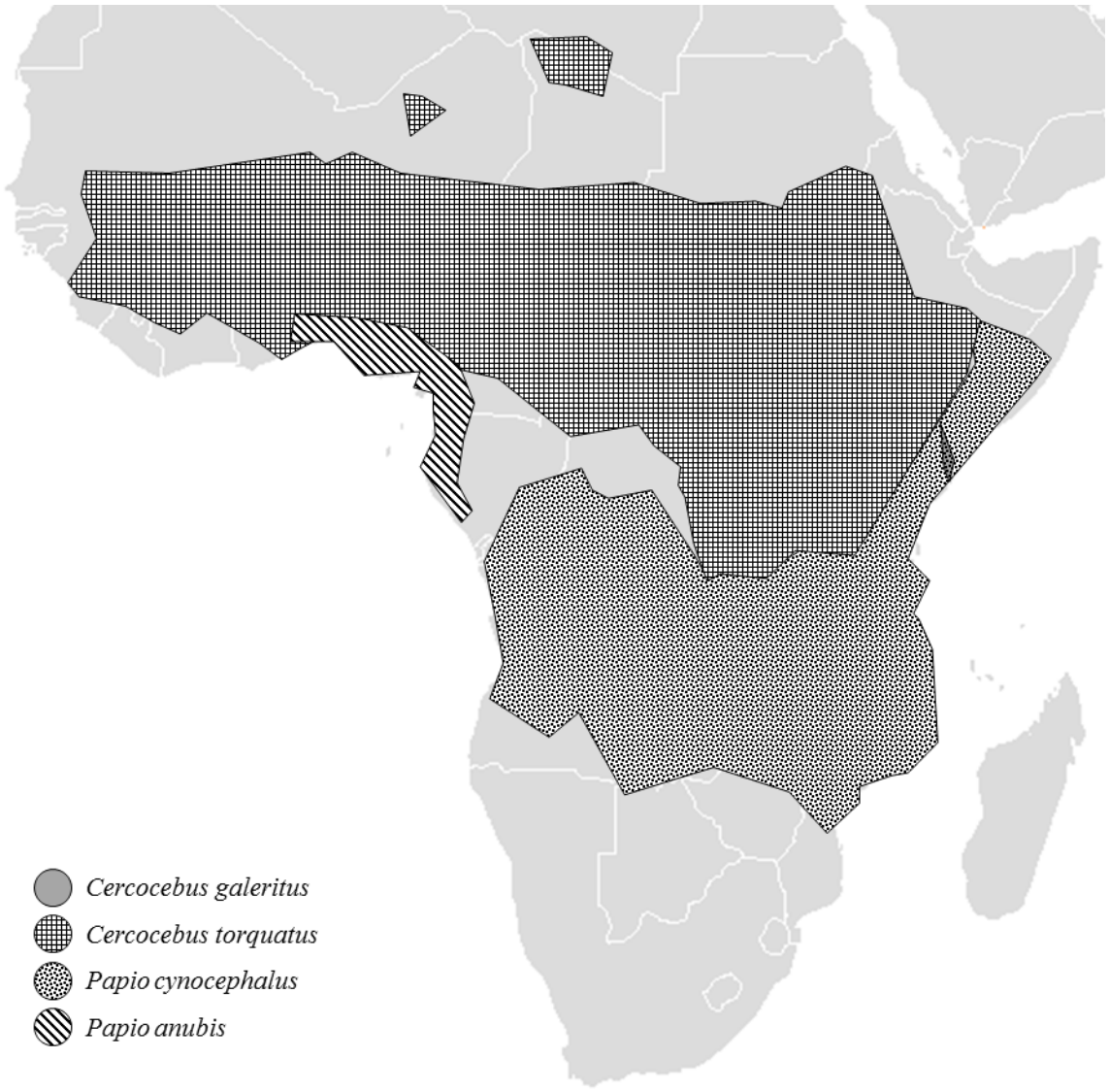
Figure 4.2 Maps showing the ranges of living primates used as comparative models for fossil hominins in this study. Shaded areas with dots mark the locations of overlap between two sympatric taxa, one of which is marked by shaded areas and one of which is marked by dotted areas. Maps are divided into the following groups: A) African apes, B) Asian apes, C) macaques, D) papionins, and E) tamarins.

Hylobates agilis
Hylobates klossii
Pongo pygmaeus
Pongo abelii)

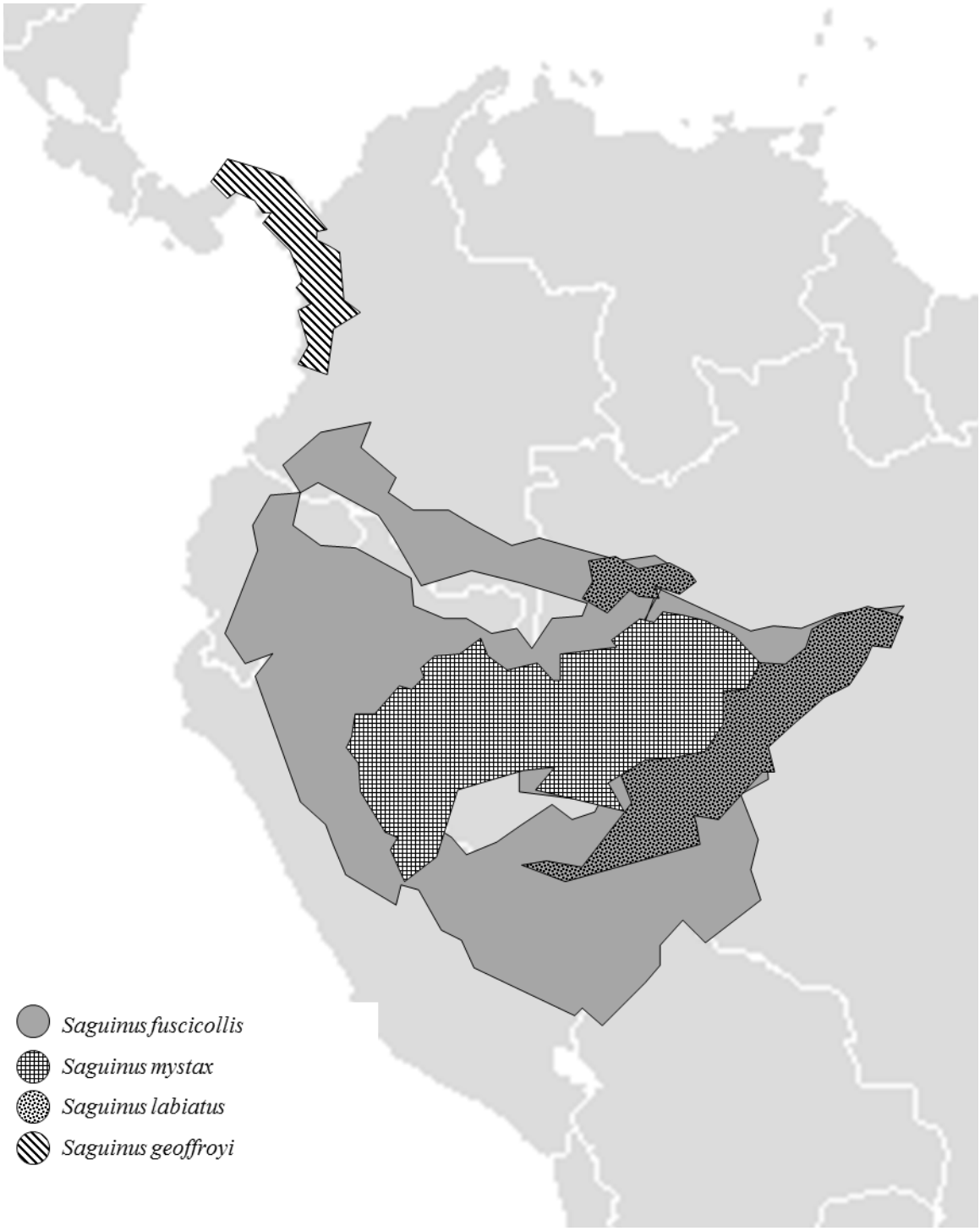
B) Asian apes


Macaca fascicularis
Macaca cyclopis
Macaca nemestrina
Macaca fuscata

C) Macaques


Cercocebus galeritus
Cercocebus torquatus
Papio cynocephalus
Papio anubis

D) Papionins


Saguinus fuscicollis
Saguinus mystax
Saguinus labiatus
Saguinus geoffroyi

E) Tamarins

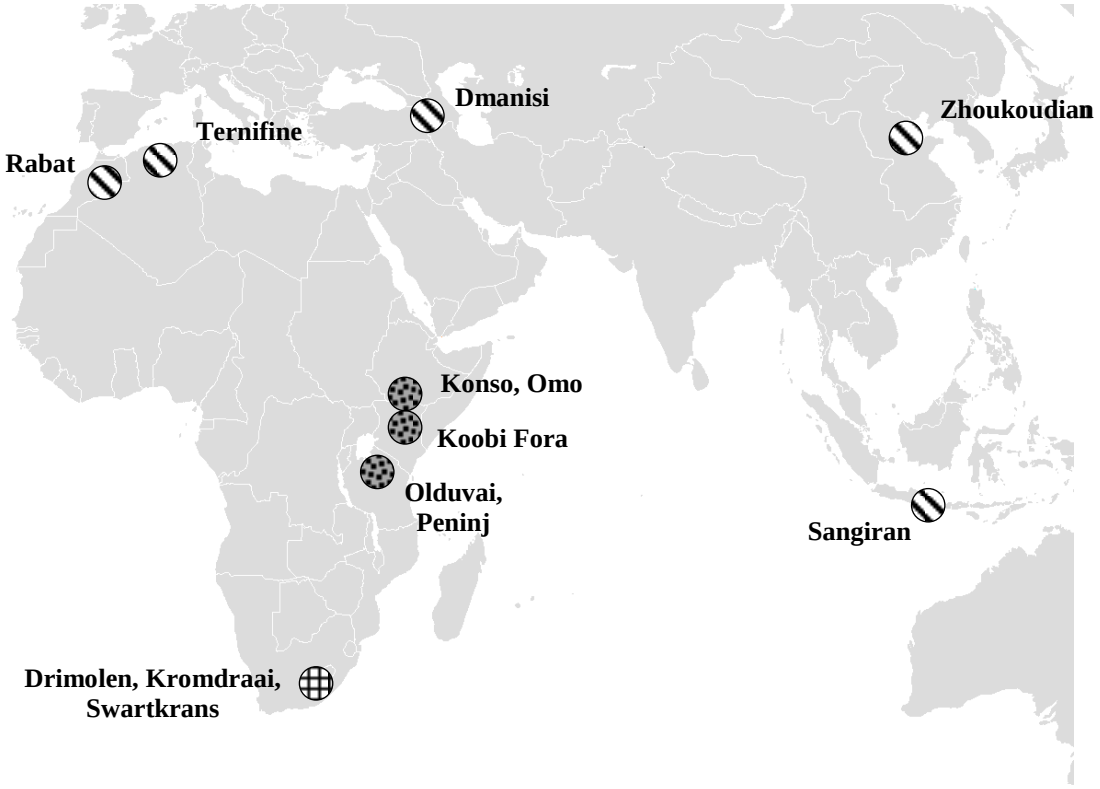


Figure 4.3 Map indicating the sites of fossil specimens examined in this analysis. Shaded areas with dots mark the locations of overlap between two sympatric taxa, one of which is marked by shaded areas and one of which is marked by dotted areas.

Table 4.1 Fossil hominin P_4 sample. Asterisks denote specimens with estimated occlusal areas. The binary labels used in the X-matrix are marked in each population as 1 or -1. These labels separate the two taxa from one another and also separate sympatric and allopatric populations.

Taxon 1 (1)		Taxon 2 (-1)	
Sympatric (1)	Allopatric (-1)	Sympatric (1)	Allopatric (-1)
Paranthropus boisei	*Paranthropus robustus*	*Homo* (East Africa)	*Homo* (not East Africa)
KNM-ER 729	DNH 8*	KGA 10-1*	Dmanisi 211*
KNM-ER 802	SK 6	KNM-ER 992	Dmanisi 2735*
KNM-ER 818*	SK 7	KNM-ER 1482*	Rabat*
KNM-ER 1171	SK 9	KNM-ER 1801*	Sangiran 1b
KNM-ER 15930*	SK 12*	KNM-ER 3734	Sangiran 6
KNM-ER 1816	SK 23	KNM-WT 15000*	Sangiran 9*
KNM-ER 3229	SK 34	OH 7	Sangiran 22*
KNM-ER 3230	SK 57*	OH 13	Sangiran Sb 8103*
KNM-ER 3885	SK 74	OH 16	Ternifine 1*
KNM-ER 15930	SK 827	OH 22	Ternifine 2*
KNM-ER 802	SK 88		Ternifine 3*
KNM-ER 818*	SKW 5		ZKD B1-3
OMO 74A-21*	SKX 4446		ZKD B5-77
OMO 75-14*	TM 1517b		ZKD C3-46
OMO L33-508	TM 1601		ZKD F3-37
OMO L51-79			
OMO L55-33			
OMO L628-4			
Peninj			

Table 4.2 Results of the character displacement model on a dataset of primate P_4s.

Group	D_S	D_A	$D_S - D_A$	P
African apes	0.38	0.04	0.34	0.001
Asian apes	0.99	0.87	0.12	0.011
Macaques	0.24	0.08	0.15	0.006
Papionins	0.29	0.24	0.05	0.346
Tamarins	0.10	0.05	0.04	0.036
Fossil hominins	0.34	0.20	0.14	0.014

Table 4.3 Means and standard deviations of three premolar measurements in extant primates and fossil hominins. Note that there is a wide distribution about the mean in all fossil taxa.

			P_4 area (mm^2)		P_4 MD (mm)		P_4 BL (mm)	
Group	Taxon	N	Mean	SD	Mean	SD	Mean	SD
African apes	*Gorilla gorilla* (sympatric)	19	109	12.9	11	0.7	12	1.1
	Gorilla beringei (allopatric)	14	121	15.7	12	1.4	12	1.0
	Pan t. troglodytes (sympatric)	17	53	6.0	8	0.6	8	0.6
	Pan t. verus/schweinfurthi (allopatric)	5	55	5.3	8	0.7	8	0.7
Asian apes	*Hylobates albibarbis* (sympatric)	17	15	2.3	5	0.4	4	0.3
	Hylobates klossii (allopatric)	8	18	2.2	5	0.3	4	0.23
	Pongo pygmaeus (sympatric)	36	98	16	11	0.9	11	1.0
	Pongo abelii (allopatric)	9	86	8.4	10	0.9	10	0.9
Macaques	*Macaca fascicularis* (sympatric)	35	17	3.9	5	0.5	4	0.6
	Macaca fuscata (allopatric)	11	25	5.5	6	0.6	5	0.6
	Macaca nemestrina (sympatric)	34	27	5	6	0.8	5	0.5
	Macaca cyclopis (allopatric)	12	21	2.1	6	0.5	5	0.2
Papionins	*Cercocebus galeritus* (sympatric)	8	25	5.6	6	0.6	5	0.7
	Cercocebus torquatus (allopatric)	19	31	3.7	6	0.6	6	0.6
	Papio cynocephalus (sympatric)	9	41	8.9	8	1.1	6	0.7
	Papio anubis (allopatric)	47	47	10.4	8	0.8	7	0.6
Tamarins	*Saguinus fuscicollis* (sympatric)	14	2.5	0.3	1.9	0.1	1.8	0.2
	Saguinus mystax (allopatric)	14	3.5	0.2	2.2	0.2	2.0	0.1
	Saguinus labiatus (sympatric)	15	3.0	0.3	2.1	0.1	1.9	0.1
	Saguinus geoffroyi (allopatric)	30	3.8	0.3	2.3	0.2	2.2	0.1
Fossil hominins	*Paranthropus boisei* (sympatric)	17	156	37.3	13	1.9	20	23.8
	Paranthropus robustus (allopatric)	16	122	19.0	11	1.1	13	0.9
	Homo (sympatric)	10	86	20.6	9	0.6	10	1.2
	Homo (allopatric)	15	90	12.4	9	0.7	10	1.0

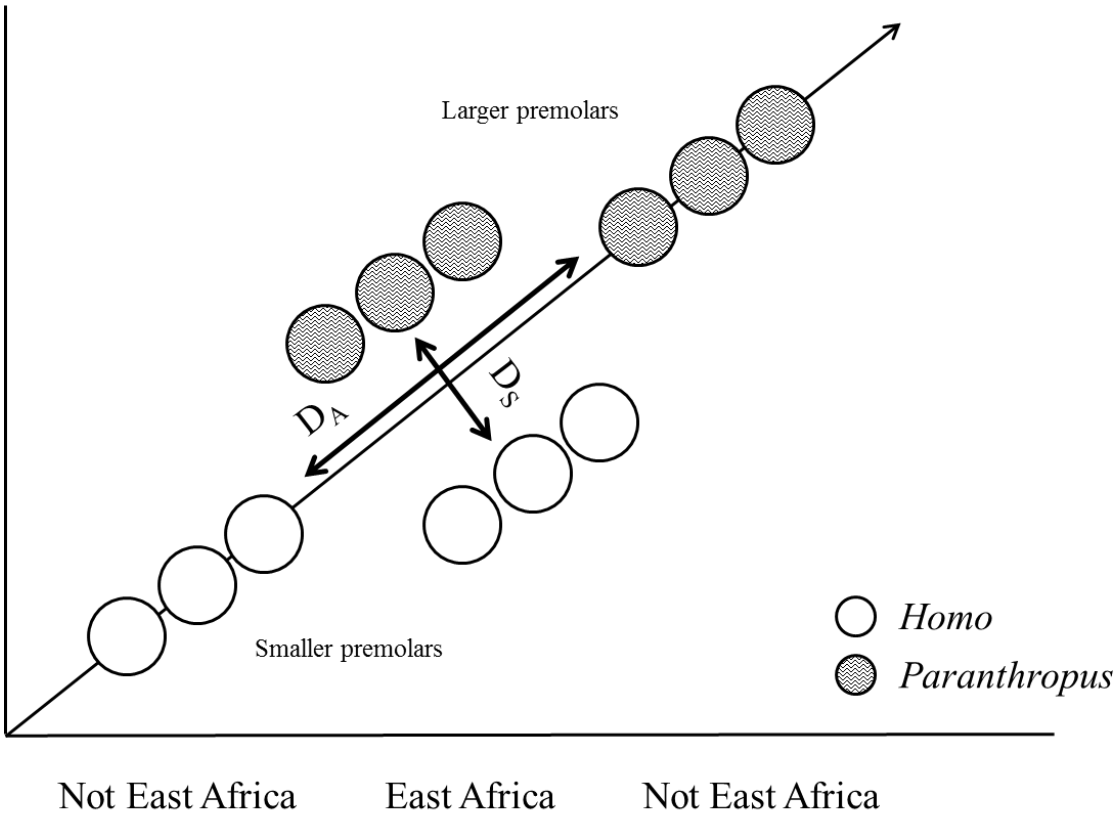


Figure 4.4 Schematic of character displacement acting on premolar size in fossil hominins. Recall that D_S denotes the difference between two taxa that overlap in geographic location while D_A denotes the difference between the same two taxa in non-overlapping populations. In East African hominins, populations of *Homo* and *Paranthropus* diverge further from the trajectory of premolar size than in allopatric populations of *Homo* and *Paranthropus*. Specimens of *Homo* in East Africa have smaller premolars than expected by this trajectory, while specimens of *Paranthropus boisei* in East Africa have larger premolars.

Chapter 5: Conclusion

5.1 Summary of Chapter 1, Introduction

Tooth morphology is generally highly conserved (Slavkin et al., 1997), and therefore any changes in tooth morphology in fossil hominins are likely to be the result of strong evolutionary pressures. Within the hominin clade, the lower fourth premolar (P_4) is one of most morphologically distinctive teeth. Later members of the genus *Homo* such as modern humans are characterized by reduced premolars (Carroll, 2003; Wood and Constantino, 2004; Organ et al., 2011), while members of the genus *Paranthropus* have distinctly molarized premolars (Robinson, 1956; Hillson, 1996; Wood and Strait, 2004; Bailey and Wood, 2007). The difference between the occlusal morphology of the crowns of the P_4s of these two genera suggests that different selection pressures influenced their evolution.

As set out in the first chapter this dissertation considers three hypotheses concerning the evolution of molarization in *Paranthropus*. They are:

1. The relative occlusal area of the P_4 to the molars (i.e., the extent of any molarization) follows the same proportions in all species within a genus. If similar proportions are observed within the species included in living primate genera, this provides support that the molarization observed in *Paranthropus* taxa may be a synapomorphy of this clade. Conversely, if this pattern is not consistent within living primate genera, or if it is observed in living primate genera but not in the component species of *Paranthropus*, this result suggests that molarization is not a reliable synapomorphy of *Paranthropus*.

2. In molarized primates, there is a high degree of covariation in the occlusal morphology of the P_4 and its adjacent teeth. If this is observed in living primates, it suggests that there are constraints on the range of morphological variation of the P_4 and that molarization is not particularly evolvable (i.e., it is unlikely to evolve multiple times within a lineage). This result would support the idea that the molarization observed in *Paranthropus* taxa may be a synapomorphy of this clade. Conversely, if weak patterns of integration are observed in the P_4s of molarized primates, this finding suggests that the molarization observed in *Paranthropus* is relatively evolvable, and thus may not be a synapomorphy of this clade.
3. Premolar morphology, as assessed through occlusal ratios and occlusal size, differs significantly in closely-related sympatric species. If this pattern is not observed in sympatric extant primates, it suggests that molarization is not a good criterion for supporting a sympatric relationship between *Paranthropus* and early *Homo*. Conversely, if this pattern is found in extant communities of sympatric populations, it supports the hypothesis that divergent premolar morphologies can reasonably predict geographic and temporal overlap in fossil primates such as *Paranthropus* and early *Homo*.

Models borrowed from the fields of development biology, quantitative genetics, and ecology were employed to address these hypotheses and help explain differences in the P_4 crown morphology in fossil hominins. These models were originally developed from observations made in several non-hominin vertebrates, including mice (Kavanagh et al., 2007), salamanders and pupfish (Collyer and Adams, 2007), sticklebacks (Schluter

and McPhail, 1992), and some primates (Cheverud, 1995). To demonstrate the utility of these models for assessing variation in fossil hominins, the models were first validated by application to samples of extant primates. The latter were selected because they provide appropriate referential models for understanding the adaptations and behavior of extinct primates such as the hominins (Wood and Schroer, 2012). The results of the applications of these models to extant primates and fossil hominins are discussed below.

5.2 Summary of Chapter 2, Inhibitory cascade

The first of the analytical chapters, Chapter 2, considered variation in postcanine crown size within the framework of the inhibitory cascade, which is a developmental model. The inhibitory cascade model suggests that molar size ratios are integrated during development by the cumulative genetic effects of gene activation and inhibition; in this model it is proposed that the development of the anterior molar affects the subsequent development of the posterior molars. A proposed premolar-molar cascade was also considered in this analysis, and in this cascade model the gradient was shifted forward to include the possible effects of the size of the P_4 on the more posterior teeth in the postcanine tooth row. An examination of the molar and premolar-molar cascade patterns suggested that while most primates exhibit the plesiomorphic mammalian pattern of molar size proportions, they did not conform to the predictions of a premolar-molar cascade. Premolar crown size appears to be unrelated to the size ratios present in the molars, and this suggests that the molarized premolars found in some primates do not follow the same developmental pattern as the molars.

An examination of the inhibitory cascade in fossil hominins found that while most hominins followed the plesiomorphic mammalian pattern seen in other primates, there

were key differences in the postcanine proportions of two of the taxa within the genus *Paranthropus*. *Paranthropus boisei,* the extremely molarized East African species, did not conform to the predictions of the inhibitory cascade model (e.g., its second molar (M_2) was unusually large). It did, however, conform, to a premolar-molar cascade that shifted the cascade effect anteriorly by one tooth. In contrast, the southern African *Paranthropus robustus,* the congener of *P. boisei,* followed the pattern of most extant primates and fossil hominins. If the patterns of variation found in extant primate genera are an appropriate model for fossil hominin genera, then this would suggest that the genus *Paranthropus* has an unusual degree of inter-generic variation with respect to the patterning of postcanine tooth proportions.

5.3 Summary of Chapter 3, Morphological integration

Chapter 3, which considered premolar crown size variation in the context of an integration model, tested whether postcanine teeth size dimensions exhibited strong patterns of covariation. This study tested a number of hypothetical modules based on developmental and functional theories concerning the integration of postcanine teeth and found that two modules described the pattern of integration in all of the primates considered. The trend of postcanine integration in most primates fitted a module describing integration between measurements of the same type on different teeth. Primates that did not conform to this module were instead best described by a module that emphasized integration among linear measures within each tooth. These results suggest that the separation of postcanine teeth into premolar and molar classes does not reflect their observed integration patterns. Rather, the predominant "measurement module" suggests that postcanine teeth, as a whole, are integrated in extant primates. A

second result of this integration analysis was that in primates with non-molarized premolars there appear to be more modules that describe integration between the postcanine teeth, whereas in primates with large or molarized premolars there are fewer modules, and thus perhaps less constraint on the morphology of their premolars. The sample of fossil hominins was not large enough to be included in the analyses of postcanine integration, but the lack of any evidence of additional modularity in primates with molarized premolars suggests that molarization may be due to a breakdown in morphological constraints between the P_4 and the M_1.

5.4 Summary of Chapter 4, Character displacement

The final analytic chapter examined premolar crown size in overlapping (i.e., sympatric) and non-overlapping (i.e., allopatric) populations of closely-related taxa. A character displacement model was used to assess whether the degree of divergence in the P_4 size of two closely-related taxa increased when the two taxa were sympatric. Although character displacement has been used as one explanation for divergence in many vertebrate populations, it has only rarely been explored in the primates (Gingerich, 1984; Schaffer, 1968). The model detected significantly more divergence in the sympatric pair of populations than in the allopatric pair in four out of five groups of extant primates. The results of this analysis demonstrate that overlapping populations and subsequent competitive pressures may influence variation in P_4 crown size in primates.

When applied to fossil hominins, the character displacement model found a greater degree of divergence between *Paranthropus* and *Homo* in East Africa than between the same taxa in samples that are allopatric. This difference was significant in spite of a wide range of geographic and temporal diversity in the allopatric population.

This result, in combination with the relative success of the model for detecting patterns of divergence in known primate populations, is consistent with hypotheses that have suggested that the greatly enlarged premolars of *P. boisei* may be the result of competitive pressures between sympatric populations of *Paranthropus* and *Homo* in East Africa around 2 million years ago (Schaffer, 1968; Wood and Strait, 2004; Laden and Wrangham, 2005).

5.5 How do these results bear on the three initial hypotheses?

The completion of these studies permits some response to the questions raised by the three hypotheses set out in the introduction of this dissertation. For hypothesis 1, which questioned whether the relationship between the occlusal area of the P_4 to that of the molars follows the same pattern in all species within a genus, the answer is no. Not all primate or hominin species within a genera exhibit the same premolar-molar proportions. For hypothesis 2, which questioned whether there is a high degree of integration in the occlusal morphology of the P_4 and its adjacent teeth in molarized primates, the answer is also no. While there are several modules describing the integration of postcanine teeth in primates with small and unmolarized premolars, there are relatively few such modules in primates with large or molarized teeth. In most primates, the integration of postcanine teeth is best described by a high degree of covariance between homologous structures found throughout the postcanine row. For hypothesis 3, which questioned whether premolar morphology differs significantly in closely-related sympatric species, the answer is yes. Closely-related sympatric species consistently showed higher degrees of divergence in premolar size than similar species in allopatric populations.

5.6 Implications of these results for reconstructing human evolution

Taken overall, the results of these studies suggest that molarization is a complicated phenomenon. Straightforward size-similarity between the P_4 and M_1 (i.e., relatively large P_4s) is not enough to account for molarization, for some primates with similarly-sized P_4s and M_1s do not exhibit molarization (Chapters 2 and 3). It is therefore unlikely that molarization is the result of 'simple' allometric scaling or of an increase in linear dimensions of the crown, as some authors have proposed (Gould, 1975; Butler, 1988).

It is also unlikely that molarization among hominin taxa is homologous in the species currently subsumed in the genus *Paranthropus*. *Paranthropus boisei* and *P. robustus* exhibit different developmental cascades in their postcanine teeth. Whereas the molar proportions of *P. robustus* exhibit the same pattern as other primates, *P. boisei* does not conform to this pattern. Instead, *P. boisei* exhibits a derived cascade in which the P_4-M_2 series has the same proportional patterns as M_1-M_3 of *P. robustus* and other primates (Chapter 2). This result suggests that molarization is not the same in these two taxa. Additionally, there is a relative lack of morphological constraint in primates with enlarged or molarized premolars; this suggests that molarization is relatively evolvable and thus it may be prone to homoplasy (Chapter 3). Future phylogenetic analyses of the hominin genus might benefit from the removal of molarization as a synapomorphic character for *Paranthropus*.

The frequent appearance of molarized premolars in many different primate clades, including *Paranthropus*, may relate to ecological pressures resulting from competition. The results of the sympatric study (Chapter 4) suggest that a general increase in premolar

crown size, but not necessarily molarization, is the result of character displacement between closely-related and geographically overlapping species. While this does not directly support the hypothesis that molarization is an adaptation for mechanically challenging diets (Kay, 1975; Lucas and Luke, 1984; Lucas et al., 1985, 1986; Teaford and Ungar, 2000; Lucas, 2004), dietary competition is one of the reasons why the morphology of closely-related species may differ (Ackerly et al., 2006).

Applying these results to fossil hominins, the extreme increase in premolar crown size observed in *P. boisei* was likely the result of competitive pressures with other hominins leading to character displacement. This size increase may have been facilitated by a breakdown in integration between the postcanines and by an alteration to the typical inhibitory cascade of the molars. The removal of two constraints may have opened up a previously-unoccupied part of hominin morphospace that the extreme P_4 morphology of *P. boisei* then occupied. The lack of a similar change observed in the developmental cascade of *P. robustus*, and the possibility of different selection pressures acting on *Paranthropus* in East Africa, suggest that molarization of the P_4 should not be considered a synapomorphy of the *Paranthropus* clade. Investigations of the monophyly of *Paranthropus* might benefit from reassessing the character states of postcanine megadontia and robust cranial morphologies through similar morphological models.

5.7 The role of modeling in studies of human evolution

Referential and conceptual models provide two frameworks for evaluating morphological diversity in fossil hominins, and they are especially informative when used in combination. The current study provides three examples of how these two types of models may be combined to provide more powerful interpretations of morphological

variation in fossil hominins. More specifically, the analytical chapters in this dissertation proposed three conceptual models for understanding the various influences on premolar crown variation. The models then used observations from several referent primate populations to test how well the models can explain observed variation in the fossil record.

This dissertation restricted its scope to one morphological phenomenon, molarization, but the models used in this dissertation can be broadened to incorporate many aspects of morphological diversity, especially the morphological diversity of the dentition. While not all of the specific characters or conditions of extant analogues can be applied directly to fossils (Harvey and Purvis, 1991; Strier, 1994), a well-validated model that uses a diverse sampling of analogues can detect general evolutionary trends. The knowledge of these trends can influence reconstructions of the taxonomy, phylogeny, and ecology of fossil hominins. In the case of this study, models helped determine that molarization is most likely not a taxonomically informative trait for hominins, but that evidence of molarization may be helpful in reconstructing the ecological communities of hominins. As this study has demonstrated, the use of well-validated models can help in reconstructing the most likely scenario for the origin and evolution of humankind.

References

Ackerly DD, Schwilk DW, and Webb CO. 2006. Niche evolution and adaptive radiation: testing the order of trait divergence. Ecol. S87: 50-61.

Ackermann RR, and Cheverud JM. 2000. Phenotypic covariance structure in tamarins (Genus *Saguinus*): a comparison of variation patterns using matrix correlation and common principal component analysis. Am. J. Phys. Anthropol. 111: 489-501.

Ackermann RR, and Cheverud JM. 2004. Detecting genetic drift versus selection in human evolution. P. Natl. Acad. Sci. USA 101: 17946-51.

Ackermann RR. 2005. Ontogenetic integration of the hominoid face. J. Hum. Evol. 48: 175-97.

Ackermann RR. 2009. Morphological integration and the interpretation of fossil hominin diversity. Evol. Biol. 36: 149-56.

Adams DC. 2004. Character displacement via aggressive interference in Appalachian salamanders. Ecol. 85: 2664-70.

Adams DC, and Rohlf FJ. 2000. Ecological character displacement in *Plethodon*: biomechanical differences found from a geometric morphometric study. P. Natl. Acad. Sci. USA 97:4106-11.

Agostini I, Holzmann I, and Di Bitetti MS. 2008. Infant hybrids in a newly formed mixed-species group of howler monkeys (*Alouatta guariba clamitans* and *Alouatta caraya*) in northeastern Argentina. Primates 49(4): 304-7.

Ala-Mello S, and Peippo M. 2004. The first Finnish patient with the Floating-Harbor syndrome: the follow-up of eight years. Am. J. Med. Genet. A. 130: 317-19.

Alimon WD. 1992. Role of temperature and nutrients in extinctions of turritelline gastropods: Cenozoic of the northwestern Atlantic and Northeastern Pacific. Palaeogeogr. Palaeocl. 92: 41-54.

Arcadi AC. 2006. Species resilience in Pleistocene hominids that traveled far and ate widely: an analogy to the wolf-like canids. J. Hum. Evol. 51: 383-94.

Arora N, Nater A, van Schaik CP, Willems EP, van Noordwijk M, et al. 2010. Effects of Pleistocene glaciations and rivers on the population structure of Bornean orangutans (*Pongo pygmaeus*). P. Natl. Acad. Sci. USA 107: 21376-81.

Armbruster WS. 1985. Patterns of character divergence and the evolution of reproductive ecotypes of *Dalechampia scandens* (Euphorbiaceae). Evolution 39: 733-52.

Arnason U, and Janke A. 2002. Mitogenomic analyses of eutherian relationships. Cytogenet. Genome Res. 96: 20-32.

Arnold SJ. 1992. Constrains of phenotypic evolution. Am. Nat. 130: 85-107.

Asahara M. 2013. Unique inhibitory cascade pattern of molars in canids contributing to their potential to evolutionary plasticity of diet. Ecol. Evol. 3: 278-85.

Ash M, and Nelson SJ. 2003. The primary (deciduous) teeth. In: Nelson SJ (Ed.), *Wheeler's Dental Anatomy, Physiology and Occlusion*. Elsevier, St. Louis.

Austin MP. 1987. Models for the analysis of species' response to environmental gradients. Vegetatio 69(1-3): 35-45.

Avery DM. 2001. The Plio-Pleistocene vegetation and climate of Sterkfontein and Swartkrans, South Africa, based on micromammals. J. Hum. Evol. 41: 113-32.

Bailey SE. 2002. A closer look at Neanderthal postcanine morphology: the mandibular dentition. Anat. Rec. 269: 148-56.

Bailey SE. 2004. A morphometric analysis of maxillary molar crowns of Middle-Late Pleistocene hominins. J. Hum. Evol. 47(3): 183-98.

Bailey SE, and Lynch JM. 2005. Diagnostic differences in mandibular P4 shape between Neandertals and anatomically modern humans. Am. J. Phys. Anthropol. 126(3): 268-77.

Bailey SE, and Wood B. 2007. Trends in postcanine occlusal morphology within the hominid clade: the case of *Paranthropus*. In: Bailey SE, and Hublin J-J (Eds.), *Dental Perspectives on Human Evolution*. Springer, New York, pp. 33-52.

Bailey SE, Weaver TD, and Hublin J-J. 2009. Who made the Aurignacian and other early Upper Paleolithic industries? J. Hum. Evol. 57: 11-26.

Bei M. 2009. Molecular genetics of tooth development. Curr. Opin. Genet. Dev. 19: 504-510.

Begun DR. 2007. How to identify (as opposed to define) a homoplasy: examples from fossil and living great apes. J. Hum. Evol. 52:559-72.

Belovsky GE. 1988. An optimal foraging-based model of hunter-gatherer population dynamics. J. Anthropol. Archaeol. 7(4): 329-72.

Bentley-Condit VK. 2009. Food choices and habitat use by the Tana River yellow baboons (*Papio cynocephalus*): a preliminary report on five years of data. Am. J. Primatol. 71: 432-6.

Berenstain L. 1986. Responses of long-tailed macaques to drought and fire in eastern Borneo: a preliminary report. Biotropica 18: 257-62.

Berger LR, de Ruiter DJ, Churchill SE, Schmid P, Carlson KJ, et al. 2010. *Australopithecus sediba*: a new species of *Homo*-like australopiths from South Africa. Science 328: 195-204.

Bermudez de Castro JM, and Nicolas ME. 1996. Changes in the lower premolar-size sequence during hominid evolution. Phylogenetic implication. J. Hum. Evol. 11: 205-15.

Bever GS, Gauthier JA, and Wagner GP. 2011. Finding the frame shift: digit loss, developmental variability, and the origin of the avian hand. Evol. Dev. 13(3): 269-79.

Bicca-Marques JC. 1999. Hand specialization, sympatry, and mixed-species associations in callitrichines. J. Hum. Evol. 36: 349-78.

Bjarnason A, Chamberlain AT, and Lockwood CA. 2011. A methodological investigation of hominoid craniodental morphology and phylogenetics. J. Hum. Evol. 60(1): 47-57.

Blomberg SP, and Garland T. 2002. Tempo and mode in evolution: phylogenetic inertia, adaptation and comparative methods. J. Evolution. Biol. 15: 899-910.

Bobe R, Behrensmeyer AK, Eck GG, and Harris JM. 2007. Patterns of abundance and diversity in late Cenozoic bovids from the Turkana and Hadar Basins, Kenya and Ethiopia. In: Bobe R, Alemseged Z, and Behrensmeyer AK (Eds.), *Hominin Environments in the East African* Pliocene. Springer, New York.

Bohonak AJ, and van der Linde K. 2004. RMA: software for reduced major axis regression, Java version. www.kimvdlinde.com/professional/rma.html.

Bolnick DI. 2004. Can intraspecific competition drive disruptive selection? An experimental test in natural populations of sticklebacks. Evolution 58: 608-18.

Bolnick DI, and Fitzpatrick BM. 2007. Sympatric speciation: models and empirical evidence. Annu. Rev. Ecol. Evol. S. 38: 459-87.

Bradley BJ. 2008. Reconstructing phylogenies and phenotypes: a molecular view of human evolution. J. Anat. 212: 337-53.

Brandon-Jones D, Eudey AA, Geissman T, Groves CP, Melnick DJ, et al. 2004. Asian primate classification. Int. J. Primatol. 25: 97-164.

Bromage TG, Schrenk F, and Zonneveld, FW. 1995. Paleoanthropology of the Malawi Rift: an early hominid mandible from the Chiwondo Beds, northern Malawi. J. Hum. Evol. 28: 71-108.

Broom R, and Robinson JT. 1949. Sterkfontein ape-man: *Plesianthropous*. Transvaal Museum Memoir 4: 1-117.

Brown WL, and Wilson EO. 1956. Character displacement. Syst. Zool. 5: 49-64.
Buchanan-Smith H. 1990. Polyspecific association of two tamarin species, *Saguinus labiatus* and *Saguinus fuscicollis* in Bolivia. Am. J. Primatol. 22: 205-14.

Burger R, Schneider KA, and Willensdorfer M. 2006. The conditions for speciation through intraspecific competition. Evolution 60: 2185-206.

Butler PM. 1939. Studies of the mammalian dentition – differentiation of the postcanine dentition. P. Zool. Soc. Lond. B: 1-36.

Butler PM. 1941. A theory of the evolution of mammalian molar teeth. Am. J. Science 239: 421-50.

Butler PM. 1952. Molarization of the premolars in the Perissodactyla. P. Zool. Soc. Lond. 121: 819-43.

Butler PM. 1967. The prenatal development of the human first upper permanent molar. Arch. Oral Biol. 12: 551-63.

Butler PM. 1983. Evolution and mammalian dental morphology. J. Biol. Buccale 11: 285-302.

Butler PM. 1988. Molarization of the first upper deciduous molar. J. Dent. Assoc. S. Afr. 43: 503-5.

Butler PM. 1995. Ontogenetic aspects of dental evolution. Int. J. Dev. Biol. 39: 25-34.

Butler PM. 1997. An alternative hypothesis on the origin of docodont molar teeth. J. Vert. Paleontol. 17: 435-9.

Butler PM. 2000. The evolution of tooth shape and tooth function in primates. In: Teaford MF, Smith MM, and Ferguson MWJ (Eds.), *Development, Function and Evolution of Teeth*. Cambridge University Press, Cambridge, pp. 201-11.

Butterfield NJ. 2007. Macroevolution and macroecology through deep time. Palaeontol. 50: 41-55.

Caldecott JO. 1986. *An Ecological and Behavioural Study of the Pig-tailed Macaque*. Basel, Karger.

Carroll RL. 1988. *Vertebrate Paleontology and Evolution*. Freeman, New York.

Carroll SB. 2003. Genetics and the making of *Homo sapiens*. Nature 422: 849-57.

Cerling TE, Harris JM, Leakey MG, Passey BH, and Levin NE. 2010. Stable carbon and oxygen isotopes in East African mammals: modern and fossil. In: Werdelin L, and Sanders WJ (Eds.), *Cenozoic Mammals of Africa*. Berkeley, University of California Press, pp. 941-52.

Cerling TE, Mbua E, Kirera FM, Manthi FK, Grine FE, et al. 2011. Diet of *Paranthropus boisei* in the early Pleistocene of East Africa. P. Natl. Acad. Sci. USA 108:9337-41.

Cerling TE, Chritz KL, Jablonski NG, Leakey MG, and Manthi FK. 2013. Diet of *Theropithecus* from 4 to 1 Ma in Kenya. P. Natl. Acad. Sci. USA 110(26): 10507-12.

Chamberlain A, and Wood B. 1987. Early hominid phylogeny. J. Hum. Evol. 16:118-33.

Chan Y-C, Roos C, Inoue-Murayama M, Inoue E, Shih C-C, et al. 2010. A comparative analysis of y chromosome and mtDNA phylogenies of the *Hylobates* gibbons. BMC Evol. Biol. 12: 150.

Chatterjee HJ. 2006. Phylogeny and biogeography of gibbons: a dispersal-vicariance analysis. Int. J. Primatol. 27: 699-712.

Chatterjee HJ. 2009. Evolutionary relationships among the gibbons: a biogeographic perspective. In: Lappan S, and Whittaker DJ (Eds.), *The Gibbons*. Springer, New York.

Chatterjee HJ, Ho SYW, Barnes I, and Groves C. 2009. Estimating the phylogeny and divergence times of primates using a supermatrix approach. BMC Evol. Biol. 9: 259.

Chen F-C, and Li W-H. 2001. Genomic divergences between humans and other hominoids and the effective population size of the common ancestor of humans and chimpanzees. Am. J. Hum. Genet. 68: 444-58.

Cheyne SM. 2010. Behavioural ecology and sociobiology of gibbons (*Hylobates albibarbis*) in a degraded peat-swamp forest. In: Supriatna J, and Gursky SL (Eds.), *Indonesian Primates*. Springer, New York, pp. 121-56.

Cheverud JM. 1982. Phenotypic, genetic, and environmental morphological integration in the cranium. Evolution 36: 499-516.

Cheverud JM. 1984. Quantitative genetics and developmental constraints on evolution by selection. J. Theor. Biol. 110: 155-71.

Cheverud JM. 1988. The evolution of genetic correlation and developmental constraints. In: de Jong G (Ed.), *Population Genetics and Evolution*. Springer-Verlag, Berlin.

Cheverud JM. 1989. A comparative analysis of morphological variation patterns in the papionins. Evolution 43: 1737-47.

Cheverud JM. 1995. Morphological integration in the saddle-back tamarin (*Saguinus fuscicollis*) cranium. Am. Nat. 145: 63-89.

Cheverud JM. 1996. Developmental integration and the evolution of pleiotropy. Am. Zool. 36: 44-50.

Cheverud JM, Wagner GP, and Dow MM. 1989. Methods for the comparative analysis of variation patterns. Syst. Zool. 38: 201-13.

Cheverud JM, Routman EJ, and Irschick DJ. 1997. Pleiotropic effects of individual gene loci on mandibular morphology. Evolution 51: 2006-16.

Clarke RJ. 1990. The Ndutu cranium and the origin of *Homo sapiens*. J. Hum. Evol. 19: 699-736.

Clarke RJ. 1994. On some new interpretations of Sterkfontein stratigraphy. Suid-Afrikaanse Tydskrif vir Wetenskap 90: 211-14.

Clarke RJ. 2008. Latest information on Sterkfontein's *Australopithecus* skeleton and a new look at *Australopithecus*. S. Afr. J. Sci. 104.

Codron D, Luyt J, Lee-Thorp JA, Sponheimer M, de Ruiter D, et al. 2005. Utilization of savanna-based resources by Plio-Pleistocene baboons. S. Afr. J. Sci. 101(5): 245-9.

Codron D, Lee-Thorp J, Sponheimer M, de Ruiter D, and Codron J. 2008. Insights into early hominin differentiation from a comparison with baboon feeding ecology. Int. J. Primatol. 29: 757-72.

Collard M and Wood B. 2001. Homoplasy and the early hominid masticatory system: inferences from analyses of extant hominoids and papionins. J. Hum. Evol. 41: 167-94.

Collyer ML, and Adams DC. 2007. Analysis of two-state multivariate phenotypic change in ecological studies. Ecol. 88: 683-92.

Constantino PJ. 2007. Primate masticatory adaptations to fracture-resistant foods. Ph.D. Dissertation, George Washington University.

Constantino PJ. 2013. The “robust” australopiths. Nature Education Knowledge 4: 1.

Constantino PJ, and Wood B. 2007. The evolution of *Zinjanthropus boisei*. Evol. Anthropol. 16:49–62.

Constantino PJ, Lee JJ-W, Morris D, Lucas PW, Hartstone-Rose A, et al. 2011. Adaptation to hard-object feeding in sea otters and hominins. J. Hum. Evol. 61:89-96.

Constantino PJ, Markham K, and Lucas PW. 2012. Tooth chipping as a tool to reconstruct diets of great apes (*Pongo*, *Gorilla*, *Pan*). Int. J. Primatol. 33: 661-72.

Corruccini RS, Baba M, Goodman M, Ciochon RL, and Cronin JE. 1980. Non-linear macromolecular evolution and the molecular clock. Evolution 34: 1216-19.

Crandlemire-Sacco J. 1988. An ecological comparison of two sympatric primates: *Saguinus fuscicollis* and *Callicebus moloch* of Amazonian Peru. Primates 29: 465-75.

Crockett C, and Wilson WL. 1980. Ecological separation of Sumatran macaques. In: Lindburg DG (Ed.), *The Macaques: Studies in Ecology, Behavior and Evolution*. Van Nostrand-Reinhold, New York.

Cropp SJ, Larson A, and Cheverud JM. 1999. Historical biogeography of tamarins, genus *Saguinus*: the molecular phylogenetic evidence. Am. J. Phys. Anthropol. 108: 65-89.

Curnoe D. 2002. Testing human taxonomic hypotheses with topology-dependent permutation tail probability tests: research letter. S. Afr. J. Sci. 98: 310-2.

Curnoe D, and Tobias PV. 2006. Description, new reconstruction, comparative anatomy, and classification of the Sterkfontein Stw 53 cranium, with discussions about the taxonomy of other southern African early *Homo* remains. J. Hum. Evol. 50: 36–77.

D’Souza RN, and Klein OD. 2007. Unraveling the molecular mechanisms that lead to supernumerary teeth in mice and men: current concepts and novel approaches. Cells, Tissues, Organs 186: 60-9.

Daegling DJ, McGraw WS, Ungar PS, Pampush JD, Vick AE, et al. 2011. Hard-object feeding in sooty mangabeys (*Cercocebus atys*) and interpretation of early hominin feeding ecology. PloS One 6: e23095.

Dahlberg AA. 1945. The paramolar tubercle. Am. J. Phys. Anthropol. 3(1): 97-103.

Dart RA. 1962. A cleft adult mandible and the nine other lower jaw fragments from Makapansgat. Am. J. Phys. Anthropol. 20: 267-86.

Darwin C. 1859. *On the Origins of Species by Means of Natural Selection*. John Murray, London.

Darwin C. 1871. *The Descent of Man and Selection in Relation in Sex*. John Murray, London.

Dayan T, and Simberloff D. 1994. Character displacement, sexual dimorphism, and morphological variation among British and Irish mustelids. Ecol. 75: 1063-73.

Dayan T, Simberloff D, Tchernov E, and Yom-Tov Y. 1989. Inter- and intraspecific character displacement in mustelids. Ecol. 70: 1526-39.

Dayan T, Simberloff D, Tchernov E, and Yom-Tov Y. 1990. Feline canines: community-wide character displacement among the small cats of Israel. Am. Nat. 136: 39-60.

Dayan T, Simberloff D, Tchernov E, and Yom-Tov Y. 1992. Canine carnassials: character displacement in the wolves, jackals and foxes of Israel. Biol. J. Linn. Soc. 45: 315-31.

De Queiroz K. 2007. Species concepts and species delimitation. Syst. Biol. 56(6): 879-86.

Dean MC, and Lucas VS. 2009. Dental and skeletal growth in early fossil hominins. Ann. Hum. Biol. 36: 545-61.

Dean MC, and Wood B. 1982. Basicranial anatomy of Plio-Pleistocene hominids from East and South Africa. Am. J. Phys. Anthropol. 59:157–74.

Dean C, Leakey MG, Reid D, Schrenk F, Schwartz GT, et al. 2001. Growth processes in teeth distinguish modern humans from *Homo erectus* and earlier hominins. Nature 414(6864): 628-31.

Delson E. 1992. Evolution of Old World monkeys. In: Jones S, Martin R, and Pilbeam D (Eds.), *The Cambridge Encyclopedia of Human Evolution*. Cambridge University Press, Cambridge, pp. 217-22.

Dermaut LR, Goeffers KR, and De Smit AA. 1986. Prevalence of tooth agenesis correlated with jaw relationship and dental crowding. Am. J. Orthod. Dentofac. 90: 204-10.

DeVore I. 1963. A comparison of the ecology and behavior of monkeys and apes. In: Washburn SL (Ed.), *Classification and Human Evolution*. Aldine Publishing Company, Chicago, pp. 301-19.

Devos C, Sanz C, Morgan D, Onononga J-R, Laporte N, et al. 2008. Comparing ape densities and habitats in northern Congo: surveys of sympatric gorillas and chimpanzees in the Odzala and Ndoki regions. Am. J. Primatol. 70: 1-13.

Doebeli M. 1996. A quantitative genetic competition model for sympatric speciation. J. Evolution. Biol. 9: 893-909.

Dominy N. 2001. Trichromacy and the ecology of food selection in four African primates. Ph.D. Dissertation, University of Hong Kong.

Doran DM, and McNeilage A. 1998. Gorilla ecology and behavior. Evol. Anthropol. 6: 120-31.

Drucker GR. 1984. The feeding ecology of the Barbary macaque and cedar forest conservation in the Moroccan moyen atlas. In: Fa JE (Ed.), *The Barbary Macaque: A Case Study in Conservation*. Plenum Press, London.

Du Brul EL. 1977. Early hominid feeding mechanisms. Am. J. Phys. Anthropol. 47(2): 305.

Dunbar R. 1976. Australopithecine diet based on a baboon analogy. J. Hum. Evol. 5: 161-7.

Dunbar R. 1983. Theropithecines and hominids: contrasting solutions to the same ecological problem. J. Hum. Evol. 12: 647-58.

Easteal S, and Herbert G. 1997. Molecular evidence from the nuclear genome for the time frame of human evolution. J. Mol. Evol. 44: 121-32.

Eble GJ. 2000. Theoretical morphology: state of the art. Paleobiology 26(3): 520-8.

Eble GJ. 2003. Developmental morphospaces and evolution. In: Crutchfield JP, and Schuster P (Eds.), *Evolutionary Dynamics: Exploring the Interplay of Selection, Accident, Neutrality, and Function*. Oxford University Press, Oxford, pp. 33-63.

Eldredge N, Thompson JN, Brakefield PM, Gavrilets S, Jablonski D, et al. 2005. The dynamics of evolutionary stasis. Paleobiology 31: 133-45.

Elgart-Berry A. 2004. Fracture toughness of mountain gorilla (*Gorilla gorilla beringei*) food plants. Am. J. Primatol. 62: 275-85.

Ellis BJ, and Ketelaar T. 2000. On the natural selection of alternative models: evaluation of explanations in evolutionary psychology. Psychol. Inq. 11: 56-68.

Elton S. 2006. Forty years on and still going strong: the use of hominin-cercopithecid comparisons in paleoanthropology. J. Roy. Antropol. Inst. 12: 19-38.

Enomoto T. 1978. On social preference in sexual behavior of Japanese monkeys (*Macaca fuscata*). J. Hum. Evol. 7: 283-93.

Erwin DH, and Wing SL. 2000. Deep time: paleobiology's perspective: a special volume commemorating the 25th anniversary of the journal *Paleobiology*. Paleontol. Soc. 26(4): 1-371.

Felsenstein J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. Evolution 39: 783-91.

Fleagle JG. 1977. Locomotor behavior and muscular anatomy of sympatric Malaysian leaf-monkeys (*Presbytis obscura* and *Presbytis melalophos*). Am. J. Phys. Anthropol. 46(2): 297-307.

Fleagle JG, and Reed KE. 1996. Comparing primate communities: a multivariate approach. J. Hum. Evol. 30(6): 489-510.

Foley RA. 1991. How many species of hominid should there be? J. Hum. Evol. 20: 413-27.

Foley RA. 2013. Comparative evolutionary models and the "australopiths radiations." In: Reed KE, Fleagle JG, and Leakey RE (Eds.), *The Paleobiology of* Australopithecus. Springer, New York, pp. 163-74.

Foley RA, and Lahr MM. 2003. On stony ground: lithic technology, human evolution, and the emergence of culture. Evol. Anthropol. 12(3): 109-22.

Fooden J. 1971. Report on primates collected in western Thailand January-April, 1967. Fieldiana 59: 1-62.

Friant M. 2009. On the evolution of the teeth in Erinaceidae. P. Zool. Soc. Lond. 199: 821.

Frisch JE. 1963. Dental variability in a population of gibbons (*Hylobates lar*). In: Brothwell DR (Ed.), *Dental Anthropology Volume 5*. Macmillan Co., New York, pp. 15-28.

Frisch JE. 1967. The gibbons of the Malay peninsula and of Sumatra. Primates 8: 297-310.

Frisch JE. 1973. The society and life of Japanese monkeys. Am. Anthropol. 75: 2009-10.

Fuentes A, Wyczalkowski MA, and MacKinnon KC. 2010. Niche construction through cooperation: a nonlinear dynamics contribution to modeling facets of the evolutionary history in the genus *Homo*. Curr. Anthropol. 51: 435-44.

Gabunia L, Vekua A, and Lordkipanidze D. 2000. The environmental contexts of early human occupation of Georgia (Transcaucasia). J. Hum. Evol. 38: 785-802.

Garber PA. 1988. Diet, foraging patterns, and resource defense in a mixed species troop of *Saguinus mystax* and *Saguinus fuscicollis* in Amazonian Peru. Behavior 105: 18-34.

Garber PA. 1991. A comparative study of positional behavior in three species of tamarin monkeys. Primates 32: 219-30.

Garn SM. 1962. The newer physical anthropology. Am. Anthropol. 64: 917-8.

Garn SM. 1963. Physical anthropology today. Am. J. Phys. Anthropol. 21: 225-6.

Garn SM, Lewis AB, and Kerewsky RS. 1964. Third molar agenesis and variation in size of the remaining teeth. Nature 201: 839.

Gause GF. 1934. Experimental analysis of Vito Volterra's mathematical theory of the struggle for existence. Science 79: 16-7.

Geyer LB, and Palumbi SR. 2003. Reproductive character displacement and the genetics of gamete recognition in tropical sea urchins. Evolution 57: 1049-60.

Gingerich PD. 1974. Size variability of the teeth in living mammals and the diagnosis of closely related sympatric fossil species. J. Paleontol. 48: 895-903.

Gingerich PD. 1984. Primate evolution: evidence from the fossil record, comparative morphology, and molecular biology. Am. J. Phys. Anthropol. 27(S5): 57-72.

Gómez-Robles A, and Polly PD. 2012. Morphological integration in the hominin dentition: evolutionary, developmental, and functional factors. Evolution 66: 1024-43.

Gómez-Robles A, Martinón-Torres M, Bermúdez de Castro JM, Prado L, Sarmiento S, et al. 2008. Geometric morphometric analysis of the crown morphology of the lower first premolar of hominins, with special attention to Pleistocene *Homo*. J. Hum. Evol. 55: 627 38.

Goodman M, Porter CV, Czelusniak J, Page SL, Schneider H, et al. 1998. Toward a phylogenetic classification of primates based on DNA evidence complemented by fossil evidence. Mol. Phylogenet. Evolution 9: 585-98.

Gould SJ. 1965. Is uniformitarianism necessary? Am. J. Sci. 263: 223-8.

Gould SJ. 1975. Allometry in primates, with emphasis on scaling and the evolution of the brain. Contrib. to Primatol. 5: 244-92.

Grabowski MW. 2013. Hominin obstetrics and the evolution of constraints. J. Evolution. Biol. 40: 57-75.

Grabowski MW, and Roseman CC. 2013. Complex patterns of selection and constraint explain the evolution of the hominin hip bone. Am. J. Phys. Anthropol. 150(S56): 64-301.

Grabowski MW, Polk JD, and Roseman CC. 2011. Divergent patterns of integration and reduce constraint in the human hip and the origins of bipedalism. Evolution 65: 1336-56.

Greenfield LO, and Washburn A. 1992. Polymorphic aspects of male anthropoid honin premolars. Am J. Phys. Anthropol. 87: 173-86.

Grine FE. 1985. Australopithecine evolution: the deciduous dental evidence. In: Delson E (Ed.), *Ancestors: The Hard Evidence*. Wiley and Sons, New York.

Grine FE. 1986. Dental evidence for dietary differences in *Australopithecus* and *Paranthropus*: a quantitative analysis of permanent molar microwear. J. Hum. Evol. 15:783-822.

Grine FE. 1987. Quantitative analysis of occlusal microwear in *Australopithecus* and *Paranthropus*. Scanning Microscopy 1: 647-56.

Grine FE, and Martin LB. 1988. Enamel thickness and development in *Australopithecus* and *Paranthropus*. In: Grine FE (Ed.), *Evolutionary History of the Robust Australopithecines*. Aldine de Gruyter, New York.

Grine FE, Demes B, Jungers WL, and Cole TM. 1993. Taxonomic affinity of the early *Homo* cranium from Swartkrans, South Africa. Am. J. Phys. Anthropol. 92: 411-26.

Grine FE, Jungers WL, and Schlutz J. 1996. Phenetic affinities among early *Homo* crania from East and South Africa. J. Hum. Evol. 30: 189-225.

Groves CP. 1972. Systematics and phylogeny of gibbons. Gibbon and Siamang 1: 1-89.

Groves CP. 1983. Phylogeny of the living species of rhinoceros. Sonderdruck aus Z. f. zool. Systematik u. Evolutionsforschung Bd 21: 293-313.

Groves CP. 1999. Nomenclature of African Plio-Pleistocene hominins. J. Hum. Evol. 37: 869-72.

Groves CP, and Mazák V. 1975. An approach to the taxonomy of the Hominidae: gracile Villafranchian hominids of Africa. Casopis pro mineralogii a geologii 20(3): 225-47.

Guisan A, and Zimmermann NE. 2000. Predictive habitat distribution models in ecology. Ecol. Model. 135: 147-86.

Guisan A, Edwards TC, and Hastie T. 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. Ecol. Model. 157: 89-100.

Gumert MD, and Malaivijitnond S. 2012. Marine prey processed with stone tools by Burmese long-tailed macaques (*Macaca fascicularis aurea*) in intertidal habitats. Am. J. Phys. Anthropol. 149: 447-57.

Haimoff EH. 1984. The organization of song in the Hainan black gibbon (*Hylobates concolor hainanus*). Primates 25: 235-55.

Hairston NG, Ellner SP, Geber M, Yoshida T, and Fox JA. 2005. Rapid evolution and the convergence of ecological and evolutionary time. Ecol. Lett. 8(10): 1114-27.

Hall BK. 2003. Evo-devo: evolutionary developmental mechanisms. Int. J. Developmental Biol. 47(7/8): 491-6.

Hall KRL, and Devore I. 1965. Baboon social behavior. In: Devore I (Ed.), *Primate Behavior: Field Studies of Monkeys and Apes*. Holt, Rhinehart, and Winston, New York.

Hall JS, White LJ, Inogwabini BI, Omari I, Morland HS, et al. 1998. Survey of Grauer's gorillas (*Gorilla gorilla graueri*) and eastern chimpanzees (*Pan troglodytes schweinfurthi*) in the Kahuzi-Biega National Park lowland sector and adjacent forest in eastern Democratic Republic of Congo. Int. J. Primatol. 19(2): 207-35.

Hallgrímsson B, and Lieberman DE. 2008. Mouse models and the evolutionary developmental biology of the skull. Integr. Comp. Biol. 48(3): 373-84.

Hallgrimsson B, Willmore K, and Hall BK. 2002. Canalization, developmental stability, and morphological integration in primate limbs. Am. J. Phys. Anthropol. 119:131-58.

Hallgrimsson B, Willmore K, Dorval C, and Cooper DM. 2004. Craniofacial variability and modularity in macaques and mice. J. Exp. Zool. Part B 302(3): 207-25.

Halliday TJD, and Goswami A. 2013. Testing the inhibitory cascade model in Mesozoic and Cenozoic mammaliforms. BMC Evol. Biol. 13: 79.

Hamilton WJ, and Busse C. 1982. Social dominance and predator behavior of chacma baboons. J. Hum. Evol. 11: 567-73.

Hansen TF, and Houle D. 2004. Evolvability, stabilizing selection, and the problem of stasis. In: Pigliucci M, and Preston K (Eds.), *Phenotypic Integration*. Oxford University Press, Oxford.

Hansen TF, and Houle D. 2008. Measuring and comparing evolvability and constraint in multivariate characters. J. Evolution. Biol. 21: 1201-19.

Hansen TF, and Orzack SH. 2005. Assessing current adaptation and phylogenetic inertia as explanations of trait evolution: the need for controlled comparisons. Evolution 59(10): 2063-72.

Hanya G. 2004. Seasonal variations in the activity budget of Japanese macaques in the coniferous forest of Yakushima: effects of food and temperature. Am. J. Primatol. 63(3): 165-77.

Harris EF. *2003*. Where's the variance? Variance components in *tooth sizes* of the permanent dentition. *Dent. Anthropol.* 16: 84-94.

Harris EE, and Disotell TD. 1998. Nuclear gene trees and the phylogenetic relationships of the mangabeys (primates: Papionini). Mol. Biol. Evol. 15: 892-900.

Harris M, and Ross EB. 1987. *Food and Evolution: Toward a Theory of Human Food Habits*. Temple University Press, Philadelphia.

Harrison T. 2011. Galagidae (Lorisoidea, Primates). In: Harrison T (Ed.), *Paleontology and Geology of Laetoli: Human Evolution in Context*. Springer, New York, pp. 75-81.

Harrison ME, and Marshall AJ. 2011. Strategies for the use of fallback foods in apes. Int. J. Primatol. 32(3): 531-65.

Harvey PH, and Purvis A. 1991. Comparative methods for explaining adaptations. Nature 351(6328): 619-24.

Hasegawa M, Thorne JL, and Kishino H. 2003. Time scale of eutherian evolution estimated without assuming a constant rate of molecular evolution. Genes Genet. Syst. 78(4): 267-83.

Hayasaka K, Fujii K, and Horai S. 1996. Molecular phylogeny of macaques: implications of nucleotide sequences from an 896-base pair region of mitochondrial DNA. Mol. Biol. Evol. 13(7): 1044-53.

Hayden B. 1972. Population control among hunter/gatherers. World Archaeol. 4(2): 205-21.

Hayden B. 1981. Subsistence and ecological adaptations of modern hunter/gatherers. In: Harding RSO, and Teleki G (Eds.), *Omnivorous Primates: Gathering and Hunting in Human Evolution*. Columbia University Press, New York, pp. 344-421.

Heemsker M, Wilson K, and Pavao-Zuckerman M. 2003. Conceptual models as tools for communication across disciplines. Conserv. Ecol. 7(3): 8.

Heymann EW. 2000. Spatial patterns of scent marking in wild moustached tamarins, *Saguinus mystax*: no evidence for a territorial function. Anim. Behav. 60: 723-30.

Heymann EW, and Buchanan-Smith HM. 2000. The behavioural ecology of mixed-species troops of callitrichine primates. Biol. Rev. 75: 169-90.

Hill K. 1982. Hunting and human evolution. J. Hum. Evol. 11(6): 521-44.

Hillson S. 1996. Variation in size and shape of teeth. In: Hillson S (Ed.), *Dental Anthropology*. Cambridge University Press, Cambridge, pp. 68-84.

Hlusko LJ, and Mahaney MC. 2009. Quantitative genetics, pleiotropy, and morphological integration in the dentition of *Papio hamadryas*. J. Evolution. Biol. 36: 5–18.

Hlusko LJ, Maas M-L, and Mahaney MC. 2004. Statistical genetics of molar cusp patterning in pedigreed baboons: implications for primate dental development and evolution. J. Exp. Zool. B 302: 268-83.

Howell FC, Washburn SL, and Ciochon RL. 1978. Relationship of *Australopithecus* and *Homo*. J. Hum. Evol. 7(2): 127-31.

Huffman MA. 1984. Stone-play of *Macaca fuscata* in Arashiyama B troop: transmission of a non-adaptive behavior. J. Hum. Evol. 13(8): 725-35.

Hughes AR, and Tobias PV. 1977. A fossil skull probably of the genus *Homo* from Sterkfontein, Transvaal. Nature 265(5592): 310-12.

Hylander WL. 1988. Interpreting the functional significance of "robust" australopithecine jaw. In: Grine FE (Ed.), *Evolutionary History of the Robust Australopithecines*. Aldine de Gruyter, New York.

Izawa K, and Nishida T. 1963. Monkeys living in the northern limits of their distribution. Primates 4(2): 67-88.

Jablonski D, and Finarelli JA. 2009. Congruence of morphologically-defined genera with molecular phylogenies. P. Natl. Acad. Sci. USA 106: 8262-6.

Jackson JBC, and Erwin DH. 2006. What can we learn about ecology and evolution from the fossil record? Trends Ecol. Evol. 21: 322-8.

Janis CM, Constable EC, Houpt KA, Streich WJ, and Clauss M. 2010. Comparative ingestive mastication in domestic horses and cattle: a pilot investigation. J. Anim. Physiol. An. N. 94(6): 402-9.

Jernvall J, and Jung HS. 2000. Genotype, phenotype, and developmental biology of molar tooth characters. Am. J. Phys. Anthropol. 31:171-90.

Jernvall J, and Thesleff I. 2000. Reiterative signaling and patterning during mammalian tooth morphogenesis. Mech. Develop. 92: 19-29.

Jernvall J, Keränen SV, and Thesleff I. 2000. Evolutionary modification of development in mammalian teeth: quantifying gene expression patterns and topography. P. Natl. Acad. Sci. USA 97: 14444-8.

Jernvall J, Gilbert CC, and Wright PC. 2008. Peculiar tooth homologies of the greater bamboo lemur (Prolemur=*Hapalemur simus*). In: Fleagle J, and Gilbert C (Eds.), *Elwyn Simons: A Search for Origins*. Springer, New York, pp. 335-42.

Järvinen E, Salazar-Ciudad I, Birchmeier W, Taketo MM, Jernvall J, et al. 2006. Continuous tooth generation in mouse is induced by activated epithelial Wnt/beta-catenin signaling. P. Natl. Acad. Sci. USA 103: 18627-32.

Jernvall J. 2005. Graduality and innovation in the evolution of complex phenotypes: insights from development. J. Exp. Zool. B 304(6): 619-31.

Jolly CJ. 1970. The seed-eaters: a new model of hominid differentiation based on a baboon analogy. Man 5(1): 5-26.

Jolly CJ. 2001. A proper study of mankind: analogies from the papionin monkeys and their implications for human evolution. Am. J. Phys. Anthropol. 116: 177-204.

Jolly CJ, Woolley-Barker T, Beyene S, Distoll TR, and Phillips-Conroy JEP. 1997. Intergeneric hybrid baboons. Int. J. Primatol. 18: 597-627.

Jolly CJ, Burrell AS, Phillips-Conroy JE, Bergey C, and Rogers J. 2011. Kinda baboons (*Papio kindae*) and grayfoot chacma baboons (*P. ursinus griseipes*) hybridize in the Kafue river valley, Zambia. Am. J. Primatol. 73: 291-303.

Kajii TS, Sato Y, Kajii S, Sugawara Y, and Iida J. 2004. Agenesis of third molar germs depends on sagittal maxillary jaw dimensions in orthodontic patients in Japan. Angle Orthod. 74: 337-42.

Kangas AT, Evans AR, Thesleff I, and Jernvall J. 2004. Nonindependence of mammalian dental characters. Nature 432: 211-4.

Kantaputra PN, Gorlin RJ, and Langer LO. 1992. Dominant mesomelic dysplasia, ankle, carpal, and tarsal synostosis type: a new autosomal dominant bone disorder. Am. J. Med. Genet. 44(6): 730-7.

Kassai Y, Munne P, Hotta Y, Penttila E, Kavanagh K, et al. 2005. Regulation of mammalian tooth cusp patterning by ectodin. Science 309: 2067-70.

Kavanagh KD, Evans AR, and Jernvall J. 2007. Predicting evolutionary patterns of mammalian teeth from development. Nature 449: 427–32.

Kay RF. 1975. The functional adaptations of primate molar teeth. Am. J. Phys. Anthropol. 43(2): 195-215.

Kay RF. 1981. The nut-crackers–a new theory of the adaptations of the Ramapithecinae. Am. J. Phys. Anthropol. 55(2): 141-51.

Kay RF, and Grine FE. 1988. Tooth morphology, wear and diet in Australopithecus and Paranthropus from Southern Africa. In: Grine FE (Ed.), *Evolutionary History of the Robust Australopithecines*. Aldine de Gruyter, New York, pp. 427-47.

Keller C, Roos C, Groeneveld LF, Fischer J, and Zinner D. 2010. Introgressive hybridization in southern African baboons shapes patterns of mtDNA variation. Am. J. Phys. Anthropol. 142(1): 125-36.

Kelley J. 1995. Sexual dimorphism in canine shape among extant great apes. Am. J. Phys. Anthropol. 96(4): 365-89.

Ketelaar T, and Ellis BJ. 2000. Are evolutionary explanations unfalsifiable? Evolutionary psychology and the Lakatosian philosophy of science. Psychol. Inq. 11(1): 1-21.

Keyser A. 2000. The Drimolen skull: the most complete australopithecine cranium and mandible to date. S. Afr. J. Sci. 96: 189–97.

Kimbel WH, Rak Y, Johanson DC, Holloway RL, and Yuan MS. 2004. The skull of *Australopithecus afarensis*. Oxford University Press, Oxford.

King GE. 1976. Society and territory in human evolution. J. Hum. Evol. 5(4): 323-31.

King GE. 1980. Alternative uses of primates and carnivores in the reconstruction of early hominid behavior. Ethol. Sociobiol. 1(2): 99-109.

Kinzey WG. 1984. The dentition of the pygmy chimpanzee, *Pan paniscus*. In: Susman RL (Ed.), *The Pygmy Chimpanzee*. Springer, New York, pp. 65-88.

Kinzey WG. 1992. Dietary and dental adaptations in the Pitheciinae. Am. J. Phys. Anthropol. 88(4): 499-514.

Kleiman DG. 1981. *Leontopithecus rosalia*. Mammalian Species 148: 1-7.

Klein OD, Minowada G, Peterkova R, Kangas A, Yu BD, et al. 2006. Sprouty genes control diastema tooth development via bidirectional antagonism of epithelial-mesenchymal FGF signaling. Dev. Cell 11(2): 181-90.

Klingenberg CP. 2003. A developmental perspective on developmental instability: theory, models and mechanisms. In: Polak M (Ed.), *Developmental Instability: Causes and Consequences*. Oxford University Press, Oxford, pp. 14-34.

Klingenberg CP. 2005. Developmental constraints, modules and evolvability. In: Hallgrimsson B and Hall BK (Eds.), *Variation: A central Concept in Biology*. Academic Press, New York, pp. 219-247.

Klingenberg CP. 2008. Morphological integration and developmental modularity. Annu. Rev. Ecol. Evol. S. 39: 115-32.

Klingenberg CP, Leamy LJ, Routman EJ, and Cheverud JM. 2001. Genetic architecture of mandible shape in mice: effects of quantitative trait loci analyzed by geometric morphometrics. Genetics 157: 785-802.

Klingenberg CP, Mebus K, and Auffray J-C. 2003. Developmental integration in a complex morphological structure: how distinct are the modules in the mouse mandible? Evol. Dev. 5: 522-31.

Klingenberg CP, Leamy LJ, and Cheverud JM. 2004. Integration and modularity of quantitative trait locus effects on geometric shape in the mouse mandible. Genetics 166: 1909-21.

Kruuk LE, Slate J, and Wilson AJ. 2008. New answers for old questions: the evolutionary quantitative genetics of wild animal populations. Annu. Rev. Ecol. Evol. S. 39: 525-48.

Knott CD. 2001. Female reproductive ecology of the apes: implications for human evolution. In: Ellison P (Ed.), *Reproductive Ecology and Human Evolution*. Aldine de Gruyter, New York, pp. 429-63.

Krantz GS. 1977. A revision of australopithecine body sizes. Evol. Theor. 2(2): 65-94.

Kuman K, and Clarke RJ. 2000. Stratigraphy, artifact industries and hominid associations for Sterkfontein, Member 5. J. Hum. Evol. 38: 827-47.

Kumar S, Filipski A, Swarna V, Walker A, and Hedges SB. 2005. Placing confidence limits on the molecular age of the human-chimpanzee divergence. P. Natl. Acad. Sci. USA 102(52): 18842-7.

Kuroda S, Nishihara T, Suzuki S, and Oko RA. 1996. Sympatric chimpanzees and gorillas in the Ndoki Forest, Congo. In: Marchant LF, and Isihida T (Eds.), *Great Ape Societies*. Cambridge University Press, Cambridge, pp. 71-81.

Labonne G, Laffont R, Renvoise E, Jebrane A, Labruere C, et al. 2012. When less means more: evolutionary and developmental hypotheses in rodent molars. J. Evolution. Biol. 25: 2102-11.

Laden G, and Wrangham R. 2005. The rise of the hominids as an adaptive shift in fallback foods: plant underground storage organs (USOs) and australopiths origins. J. Hum. Evol. 49: 482-98.

Laffont R, Renvoise E, Navaroo N, Alibert P, and Montuire S. 2009. Morphological modularity and assessment of developmental processes within the vole dental row (*Microtus arvalis*, Arvicolinae, Rodentia). Evol. Dev. 11: 302-11.

Lakatos I. 1970. *Wetenschapsfilosofie en wetenschapsgeschiedenis : de controverse tussen Popper en Kuhn*. Boom, Meppel.

Lakatos I. 1978. *The Methodology of Scientific Research Programs*. Cambridge University Press, Cambridge.

Lambert JE, Chapman C, Wrangham RW, and Conklin-Brittain NL. 2004. Hardness of cercopithecine foods: implications for the critical function of enamel thickness in exploiting fallback foods. Am. J. Phys. Anthropol. 125: 363-8.

Lande R. 1979. Quantitative genetic analysis of multivariate evolution, applied to brain: body size allometry. Evolution 33: 402-16.

Lande R, and Arnold SJ. 1983. The measurement of selection on correlated characters. Evolution 37: 1210-26.

Langergraber KE, Prüfer K, Rowney C, Boesch C, Crockford C, et al. 2012. Generation times in wild chimpanzees and gorillas suggest earlier divergence times in great ape and human evolution. P. Natl. Acad. Sci. USA 109(39): 15716-21.

Lavelle CLB. 1970. Analysis of attrition in adult human molars. J. Dent. Res. 49: 822-8.

Lavelle CLB, and Moore WJ. 1973. The incidence of agenesis and polygenesis in the primate dentition. Am. J. Phys. Anthropol. 38(3): 671-9.

Leakey LS, Tobias PV, and Napier JR. 1964. A new species of the genus *Homo* from Olduvai Gorge. Nature 202(4927): 7-9.

Leakey MG, Spoor F, Dean MC, Feibel CS, Anton SC, et al. 2012. New fossils from Koobi Fora in northern Kenya confirm taxonomic diversity in early *Homo*. Nature 488: 201-4.

Lee-Thorp J. 2011. The demise of "Nutcracker Man." P. Natl. Acad. Sci. USA 108: 9319-20.

Lee-Thorp J, Sponheimer M, and van der Merwe NJ. 2003. What do stable isotopes tell us about hominid dietary and ecological niches in the Pliocene? Int. J. Osteoarchaeol. 13(1-2): 104-13.

Lehtonen S, Sääksjärvi IE, Ruokolainen K, and Tuomisto H. 2011. Who is the closest extant cousin of humans? Total-evidence approach to hominid phylogenetics via simultaneous optimization. J. Biogeogr. 38: 805-8.

Leigh SR, Relethford JH, Park PB, and Konigsberg LW. 2003. Morphological differentiation of *Gorilla* subspecies. In: Taylor AB, and Goldsmith ML (Eds.) *Gorilla Biology: A Multidisciplinary Perspective*. Cambridge University Press, Cambridge, pp. 104-31.

Lemen CA, and Freeman PW. 1984. The genus: a macroevolutionary problem. Evolution 38: 1219-37.

Leonard WR, and Hegmon M. 1987. Evolution of P3 morphology in *Australopithecus afarensis*. Am. J. Phys. Anthropol. 73(1): 41-63.

Levin DA. 1985. Reproductive character displacement in *Phlox*. Evolution 39: 1275-1281.

Lewton KL. 2012. Complexity in biological anthropology in 2011: species, reproduction, and sociality. Am. Anthropol. 114: 196-202.

Li J, Han K, Xing J, Kim HS, Rogers J, et al. 2009. Phylogeny of the macaques (Cercopithecidae: *Macaca*) based on *Alu* elements. Gene 448(2): 242-9.

Lieberman DE, Wood BA, and Pilbeam DR. 1996. Homoplasy and early *Homo* : an analysis of the evolutionary relationships of *H* . *habilis sensu stricto* and *H. rudolfensis*. J. Hum. Evol. 30: 97-120.

Lieberman DE, Pearson OM, and Mowbray KM. 2000. Basicranial influences on overall cranial shape. J. Hum. Evol. 38: 291-315.

Losos JB. 1990. A phylogenetic analysis of character displacement in Caribbean Anolis lizards. Evolution 44: 558-69.

Losos J. 2000. Ecological character displacement and the study of adaptation. P. Natl. Acad. Sci. USA 97: 5693-5.

Losos J. 2011. Seeing the forest for the trees: the limitations of phylogenies in comparative biology. Am. Nat. 177: 709-27.

Losos JB, and Miles DB. 1994. Adaptation, constraint, and the comparative method: phylogenetic issues and methods. In: Wainwright PC, and Reilly S (Eds.), *Ecological Morphology: Integrative Organismal Biology*. University of Chicago, Chicago, pp. 60-98.

Lovejoy CO, Cohn MJ, and White TD. 1999. Morphological analysis of the mammalian postcranium: a developmental perspective. P. Natl. Acad. Sci. USA 96(23): 13247-52.

Lucas P. 1980. Adaptation and form of the mammalian dentition with special reference to primates and the evolution of man. Ph.D. Dissertation, University College London.

Lucas PW. 1989. A new theory relating seed processing by primates to their relative tooth sizes. In: Schmitt LH, Freedman L, and Bruce NW (Eds.), *The Growing Scope of Human Biology*. University of Western Australia, Perth, pp. 37-49.

Lucas P. 2004. *Dental Functional Morphology: How Teeth Work*. Cambridge University Press, Cambridge.

Lucas P, and Luke DA. 1984. Optimum mouthful for food comminution in human mastication. Arch. Oral Biol. 29: 205-10.

Lucas P, and Corlett RT. 1991. Relationship between the diet of *Macaca fascicularis* and forest phenology. Folia Primatol. 57(4): 201-15.

Lucas P, and Peters CR. 2000. Function of postcanine tooth shape in mammals. In: Teaford MF, Smith MM, and Ferguson MWJ (Eds.), *Development, Function and Evolution of Teeth*. Cambridge University Press, Cambridge, pp. 282-9.

Lucas P, Corlett RT, and Luke DA. 1985. Plio-Pleistocene hominid diets: an approach combining masticatory and ecological analysis. J. Hum. Evol. 14(2): 187-202.

Lucas P, Corlett R, and Luke D. 1986. Postcanine tooth size and diet in anthropoid primates. Z. Morphol. Anthropol. 76: 253-76.

Lucas P, Ow RKK, Ritchie GM, Chew CL, and Keng SB. 1986. Relationship between jaw movement and food breakdown in human mastication. J. Dent. Res. 65(3): 400-4.

Lucas P, Peters CR, and Arrandale SR. 1994. Seed-breaking forces exerted by orangutans with their teeth in captivity and a new technique for estimating forces produced in the wild. Am. J. Phys. Anthropol. 94(3): 365-78.

Lucas P, Constantino PJ, and Wood B. 2008. Inferences regarding the diet of extinct hominins: structural and functional trends in dental and mandibular morphology within the hominin clade. J. Anat. 212: 486-500.

Lucas L, Schwartz GT, and Spencer MA. 2009. Molarization in extant primates. Am. J. Phys. Anthropol. 140(4): 771-87.

Lunt DA. 1976. Molarization of the mandibular second premolars. J. Dent. 4(2): 83-6.

Lyell C. 1830. *Principles of geology: being an attempt to explain the former changes of the earth's surface, by reference to causes now in operation*. John Murray, London.

M'kirera F, and Ungar PS. 2003. Occlusal relief changes with molar wear in *Pan troglodytes troglodytes* and *Gorilla gorilla gorilla*. Am. J. Primatol. 60: 31-41.

MacFadden BJ. 1976. Cladistic analysis of primitive equids, with notes on other Perissodactyls. Syst. Biol. 25: 1-14.

Mackay TF, Stone EA, and Ayroles JF. 2009. The genetics of quantitative traits: challenges and prospects. Nat. Rev. Genet. 10(8): 565-77.

Mackay TF. 2001. The genetic architecture of quantitative traits. Annu. Rev. Genet. 35(1): 303-39.

MacKinnon J. 1977. A comparative ecology of Asian apes. Primates 18: 747-72.

Madden D, Garber PA, Madden SL, and Snyder CA. 2010. Rain-forest canopy-connectivity and habitat selection by a small neotropical primate, Geoffroy's tamarin (*Saguinus geoffroyi*). J. Trop. Ecol. 26: 637.

Mahler P. 1973. Metric variation in the pongid dentition. Ph.D. Dissertation, University Of Michigan.

Maier W. 1984. Tooth morphology and dietary specialization. In: Chivers DJ (Ed.), *Food Acquisition and Processing in Primates*. Springer, New York, pp. 303-30.

Mallet J. 1995. A species definition for the modern synthesis. Trends Ecol. Evol. 10(7): 294-9.

Malone D. 1987. Mechanisms of hominoid dispersal in Miocene East Africa. J. Hum. Evol. 16(6): 469-81.

Mann A. 1970. "*Telanthropus*" and the single species hypothesis: a further comment. Am. Anthropol. 72(3): 607-9.

Mantel N. 1967. Ranking procedures for arbitrarily restricted observation. Biometrics 23: 65-78.

Marais EN. 1969. *The Soul of the Ape*. Atheneum, Little Rock.

Marino L. 2002. Convergence of complex cognitive abilities in cetaceans and primates. Brain, Behav. Evolut. 59(1-2): 21-32.

Marroig G, and Cheverud JM. 2001. A comparison of phenotypic variation and covariation patterns and the role of phylogeny, ecology and ontogeny during cranial evolution of New World monkeys. Evolution 55: 2576-600.

Marroig G, and Cheverud JM. 2004. Did natural selection or genetic drift produce the cranial diversification of neotropical monkeys? Am. Nat. 163: 417-28.

Marroig G, de Vivo M, and Cheverud JM. 2004. Cranial evolution in sakis (*Pithecia*, Platyrrhini) II: evolutionary processes and morphological integration. J. Evolution. Biol. 17: 144-55.

Marroig G, Shirai LT, Porto A, de Oliveira FB, and De Conto, V. 2009. The evolution of modularity in the mammalian skull II: evolutionary consequences. J. Evolution. Biol. 36: 136-48.

Marshall DC, and Cooley JR. 2000. Reproductive character displacement and speciation in periodical cicadas, with description of a new species, 13-year *Magicicada neotredecim.* Evolution 54(4): 1313-25.

Marshall JT, and Marshall ER. 1976. Gibbons and their territorial songs. Science 193(4249): 235-7.

Marshall AJ, Cannon CH, and Leighton M. 2009. Competition and niche overlap between gibbons (*Hylobates albibarbis*) and other frugivorous vertebrates in Gunung

Palung National Park, West Kalimantan, Indonesia. In: Marshall AJ, Cannon CH, and Leighton M (Eds.), *The Gibbons*. Springer, New York, pp. 161-88.

Martinon-Torres M, Bermudez de Castro JM, Gomez-Robles A, Arsuaga JL, Carbonell E, et al. 2007. Dental evidence on the hominin dispersals during the Pleistocene. P. Natl. Acad. Sci. USA 104: 13279-82.

Martinón-Torres M, Bermúdez de Castro JM, Gómez-Robles A, Margvelashvili A, Prado L, et al. 2008. Dental remains from Dmanisi (Republic of Georgia): morphological analysis and comparative study. J. Hum. Evol. 55: 249-73.

Matsudaira K, and Ishida T. 2010. Phylogenetic relationships and divergence dates of the whole mitochondrial genome sequences among three gibbon genera. Mol. Phylogenet. Evol. 55: 454-9.

Matthews A, and Matthews A. 2004. Survey of gorillas (*Gorilla gorilla gorilla*) and chimpanzees (*Pan troglodytes troglodytes*) in southwestern Cameroon. Primates 45: 15-24.

Mayr E. 1963. *Animal Species and Evolution*. Belknap Press, Cambridge.

McCollum M, and Sharpe PT. 2001. Evolution and development of teeth. J. Anat. 199: 153-9.

McGraw WS, and Daegling DJ. 2012. Primate feeding and foraging: integrating studies of behavior and morphology. Annu. Rev. Anthropol. 41: 203-19.

McHenry HM. 1984. Relative cheek-tooth size in *Australopithecus*. Am. J. Phys. Anthropol. 64-297-306.

McPherron SP, Alemseged Z, Marean CW, Wynn JG, Reed D, et al. 2010. Evidence for stone-tool-assisted consumption of animal tissues before 3.39 million years ago at Dikika, Ethiopia. Nature 466(7308): 857-60.

Mezey JG, Cheverud JM, and Wagner GP. 2000. Is the genotype-phenotype map modular? A statistical approach using mouse quantitative trait loci data. Genetics 156(1): 305-11.

Mitsiadis TA, and Smith MM. 2006. How do genes make teeth to order through development? J. Exp. Zool. B 306: 177-82.

Mitteroecker P, and Bookstein F. 2011. Linear discrimination, ordination, and the visualization of selection gradients in modern morphometrics. J. Evolution. Biol. 38: 100–14.

Moggi-Cecchi J, Grine FE, and Tobias PV. 2006. Early hominid dental remains from Members 4 and 5 of the Sterkfontein Formation (1966–1996 excavations): catalogue, individual associations, morphological descriptions and initial metrical analysis. J. Hum. Evol. 50(3): 239-328.

Monroe MJ. 2012. Does competition drive character differences between species on a macroevolutionary scale? J. Evolution. Biol. 25: 1-7.

Monteiro LR, Bonato V, and Dos Reis SF. 2005. Evolutionary integration and morphological diversification in complex morphological structures: mandible shape divergence in spiny rats (Rodentia, Echimyidae). Evol. Dev. 7(5): 429-39.

Morgan D, and Sanz C. 2006. Chimpanzee feeding ecology and comparisons with sympatric gorillas in the Goualougo Triangle, Republic of Congo. In: Hohmann G, Robbins MM, and Boesch C (Eds.), *Feeding Ecology in Apes and Other Primates*. Cambridge University Press, Cambridge.

Morris K, and Goodall J. 1977. Competition for meat between chimpanzees and baboons of the Gombe National Park. Folia Primatol. 28(2): 109-21.

Morrissey MB, Kruuk LEB, and Wilson AJ. 2010. The danger of applying the breeder's equation in observational studies of natural populations. J. Evolution. Biol. 23(11): 2277-88.

Morwood MJ, Soejono RP, Roberts RG, Sutikna T, Turney CS, et al. 2004. Archaeology and age of a new hominin from Flores in eastern Indonesia. Nature 431(7012): 1087-91.

Munne PM, Tummers M, Järvinen E, Thesleff I, and Jernvall J. 2009. Tinkering with the inductive mesenchyme: Sostdc1 uncovers the role of dental mesenchyme in limiting tooth induction. Development 136: 393-402.

Nanda RS. 1954. Agenesis of the third molar in man. Amer. J. Orthodont. 40: 698-706.

Nunn C, and Barton R. 2001. Comparative methods for studying primate adaptation and allometry. Evol. Anthropol. 10: 81-98.

Nickle DA, and Heymann EW. 1996. Predation on Orthoptera and other orders in insects by tamarin monkeys, *Saguinus mystax mystax* and *Saguinus fuscicollis nigrifrons* (Primates: Callitrichidae) in north-eastern Peru. J. Zool. 239(4): 799-819.

Norconk MA. 1990. Mechanisms promoting stability in mixed *Saguinus mystax* and *S. fuscicollis* troops. Am. J. Primatol. 21(2): 159-170.

Olson EC, and Miller RL. 1999. *Morphological Integration*. University of Chicago Press, Chicago.

Organ C, Nunn CL, Machanda Z, and Wrangham RW. 2011. Phylogenetic rate shifts in feeding time during the evolution of *Homo*. P. Natl. Acad. Sci. USA 108(35): 14555-59.

Page SL, Chiu C, and Goodman M. 1999. Molecular phylogeny of Old World monkeys (Cercopithecidae) as inferred from y-globin DNA sequences. Mol. Phylogenet. Evol. 13: 348-59.

Pagel MD, and Harvey PH. 1989. Comparative methods for examining adaptation depend on evolutionary models. Folia Primatol. 53(1-4): 203-20.

Patterson C, Williams DM, and Humpries CJ. 1993. Congruence between molecular and morphological phylogenies. Annu. Rev. Ecol. Syst. 24: 153-88.

Perelman P, Johnson WE, Roos C, Seuánez HN, Horvath JE, et al. 2011. A molecular phylogeny of living primates. PLoS Genetics 7(3): e1001342.

Peterkova R, Lesot H, Viriot L, and Peterka M. 2005. The supernumerary cheek tooth in tabby/EDA mice-a reminiscence of the premolar in mouse ancestors. Arch. Oral Biol. 50: 219-25.

Peters CR, and Vogel JC. 2005. Africa's wild C_4 plant foods and possible early hominid diets. J. Hum. Evol. 48(3): 219-36.

Peterson KJ, Summons RE, and Donoghue PC. 2007. Molecular palaeobiology. Palaeontol. 50(4): 775-809.

Pickford M. 1984. A revision of the sanitheriidae, a new family of suiformes (Mammalia). Geobios 17: 133-54.

Pilbrow V. 2003. Dental variation in African apes with implications for understanding Patterns of variation in species of fossil apes. Ph.D. Dissertation, New York University.

Pilbrow V. 2006. Population systematics of chimpanzees using molar morphometrics. J. Hum. Evol. 51: 646-62.

Plavcan JM, and Gomez AM. 1993. Dental scaling in the Callitrichinae. Int. J. Primatol. 14(1): 177-92.

Polly PD. 2007. Evolutionary biology: development with a bite. Nature 449(7161): 413-15.

Polly PD. 2008. Developmental dynamics and G-Matrices: Can morphometric spaces be used to model phenotypic evolution? J. Evolution. Biol. 35(2): 83-96.

Popper K. 1956. Three views concerning human knowledge. In: Lewis HD (Ed.), *Contemporary British Philosophy*. Allen and Unwin, London, pp. 355-88.

Popper KR. 1979. *Truth, Rationality and the Growth of Scientific Knowledge*. Vittorio Klostermann, Frankfurt.

Porter CA, Page SL, Czelusniak J, Schneider H, Schneider MPC, et al. 1997. Phylogeny and evolution of selected primates as determined by sequences of the ε-globin locus and 5′ flanking regions. Int. J. Primatol. 18(2): 261-95.

Porter LM. 2001. Dietary differences among sympatric callitrichinae in northern Bolivia: *Callimico goeldii* , *Saguinus fuscicollis* and *S* . *labiatus*. Int. J. Primatol. 22: 961-92.

Porter LM, Garber PA, and Nacimento E. 2009. Exudates as a fallback food for *Callimico goeldii*. Am. J. Primatol. 71:120-9.

Porto A, de Oliveira FB, Shirai LT, De Conto V, and Marroig G. 2009. The evolution of modularity in the mammalian skull I: morphological integration patterns and magnitudes. J. Evolution. Biol. 36(1): 118-35.

Posen AL. 1965. The effect of premature loss of deciduous molars on premolar eruption. Angle Orthod.35(3): 249-52.

Potts R. 1987. Reconstructions of early hominid socioecology: A critique of primate models. In: Kinzey W (Ed.), *The Evolution of Human Behavior: Primate Models*. State University of New York Press, Albany, pp. 28-47.

Preuss TM. 2000. Taking the measure of diversity: comparative alternatives to the model-animal paradigm in cortical neuroscience. Brain Behav. Evolut. 55: 287-99.

Prüfer K, Munch K, Hellmann I, Akagi K, Miller JR, et al. 2012. The bonobo genome compared with the chimpanzee and human genomes. Nature 486: 527.

Puertas P, and Bodmer RE. 1993. Conservation of a high diversity primate assemblage. Biodiversity & Conservation 2(6): 586-93.

Quam R, Bailey S, and Wood B. 2009. Evolution of M1 crown size and cusp proportions in the genus *Homo*. J. Anat. 214(5): 655-70.

Quinet GE, and Verlinden W. 1970. Molarization of Pd4 and Pd3; premolarization of P4 and P3 in man and animals; molarization of P4 and P3 in animals. Rev. Belge Med. Dent. 25(3): 451.

R Development Core Team. 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna. http://www.R-project.org.

Raaum RL, Sterner KN, Noviello CM, Stewart CB, and Disotell TR. 2005. Catarrhine primate divergence dates estimated from complete mitochondrial genomes: concordance with fossil and nuclear DNA evidence. J. Hum. Evol. 48(3): 237-57.

Raff R. 2007. Written in stone: fossils, genes and evo-devo. Nature 8: 911-20.

Rak Y. 1983. *The Australopithecine Face*. Academic Press, New York.

Ramakrishnan U, and Coss RG. 2001. A comparison of the sleeping behavior of three sympatric primates. Folia Primatol. 72(1): 51-3.

Raup DM. 1966. Geometric analysis of shell coiling: general problems. J. Paleontol. 40: 1178-90.

Raup DM. 1979. Biases in the fossil record of species and genera. B. Carnegie Mus. Nat. Hist. 13: 85-91.

Raup DM, and Michelson A. 1965. Theoretical morphology of the coiled shell. Science 147(3663): 1294-5.

Read DW. 1975. Hominid teeth and their relationship to hominid phylogeny. Am. J. Phys. Anthropol. 42(1): 105-25.

Rehg JA. 2010. Plant feeding patches: patterns of use by associating *Callimico goeldii*, *Saguinus labiatus*, and *S. fuscicollis*. Neotrop. Primates 17(1): 18-21.

Reig S. 1992. Geographic variation in pine marten (*Martes martes*) and beech marten (*M. foina*) in Europe. J. Mammal. 73: 744-69.

Renvoisé E, Evans AR, Jebrane A, Labruère C, Laffont R, et al. 2009. Evolution of mammal tooth patterns: new insights from a developmental prediction model. Evolution 63: 1327-40.

Reynolds RG. 1978. On modeling the evolution of hunter-gatherer decision-making systems. Geogr. Anal. 10(1): 31-46.

Rhine RJ, Norton GW, Wynn GM, Wynn RD, and Rhine HB. 1986. Insect and meat eating among infant and adult baboons (*Papio cynocephalus*) of Mikumi National Park, Tanzania. Am. J. Phys. Anthropol. 70(1): 105-18.

Richard AF. 1981. Changing assumptions in primate ecology. Am. Anthropol. 83(3): 517-33.

Richard AF, Goldstein SJ, and Dewar RE. 1989. Weed macaques: the evolutionary implications of macaque feeding ecology. Int. J. Primatol. 10(6): 569-94.

Rightmire GP. 1990. *The Evolution of* Homo erectus. Cambridge University Press, Cambridge.

Robinson JT. 1952. The australopithecines and their evolutionary significance. Proc. Linn. Soc. Lond. 163: 196-204.

Robinson JT. 1953. *Meganthropus*, australopithecines and hominids. Am. J. Phys. Anthropol. 11: 1-38.

Robinson JT. 1954. The genera and species of the Australopithecinae. Am. J. Phys. Anthropol. 12: 181-200.

Robinson JT. 1955. Further remarks on the relationship between "*Meganthropus*" and australopithecines. Am. J. Phys. Anthropol. 13(3): 429-45.

Robinson JT. 1956. The dentition of the Australopithecinae. Transvaal Museum Memoir 9: 1-179.

Robinson JT. 1960. The affinities of the new Olduvai australopithecine. Nature 186(4723): 456-8.

Robinson JT. 1963. Adaptive radiation in the australopithecines and the origin of man. African Ecology and Human Evolution 36: 385-416.

Robinson JT. 1965. *Homo habilis* and the australopithecines. Nature 205: 121-4.

Robinson JT. 1967. Variation and the taxonomy of the early hominids. J. Evolution. Biol. 1: 69-100.

Robinson JT. 1970. New finds at the Swartkrans australopithecine site: two new early hominid vertebrae from Swartkrans. Nature 225: 1217-19.

Rodman PS. 1991. Structural differentiation of microhabitats of sympatric *Macaca fascicularis* and *M. nemestrina* in East Kalimantan, Indonesia. Int. J. Primatol. 12(4): 357-75.

Roff DA. 1995. The estimation of genetic correlations from phenotypic correlations: a test of Cheverud's conjecture. Heredity 74(5): 481-90.

Roff DA. 1996. The evolution of genetic correlations: an analysis of patterns. Evolution 50: 1392-1403.

Rohlf FJ. 2009. tpsDig. Version 2.14. Department of Ecology and Evolution, State University of New York.

Rolian C, and Willmore KE. 2009. Morphological integration at 50: patterns and processes of integration in biological anthropology. J. Evolution. Biol. 36(1): 1-4.

Rolian C. 2009. Integration and evolvability in primate hands and feet. J. Evolution. Biol. 36(1): 100-17.

Rosas A, and Bermudez De Castro JM. 1998. On the taxonomic affinities of the Dmanisi mandible (Georgia). Am. J. Phys. Anthropol. 107(2): 145-62.

Roseman CC, and Weaver TD. 2004. Multivariate apportionment of global human craniometric diversity. Am. J. Phys. Anthropol. 125(3): 257-63.

Roseman CC, Kenny-Hunt JP, and Cheverud JM. 2009. Phenotypic integration without modularity: testing hypotheses about the distribution of pleiotropic quantitative trait loci in a continuous space. J. Evolution. Biol. 36: 282-91.

Roseman CC, Weaver TD, and Stringer CB. 2011. Do modern humans and Neandertals have different patterns of cranial integration? J. Hum. Evol. 60(6): 684-93.

Rosenberger AL. 1992. Evolution of feeding niches in New World monkeys. Am. J. Phys. Anthropol. 88(4): 525-62.

Roussiakis SJ. 2003. *Oioceros rothii* (Wagner, 1857) from the late Miocene of Pikermi (Greece): cranial and dental morphology, comparison with related forms. Geodiversitas 25(4): 717-35.

Ruff C. 1988. Hindlimb articular surface allometry in Hominoidea and *Macaca*, with comparisons to diaphyseal scaling. J. Hum. Evol. 17(7): 687-714.

Russo D, Mucedda M, Bello M, Biscardi S, Pidinchedda E, et al. 2007. Divergent echolocation call frequencies in insular rhinolophids (Chiroptera): a case of character displacement? J. Biogeogr. 34(12): 2129-38.

Ruvolo M, Disotell TR, Allard MW, Brown WM, and Honeycutt RL. 1991. Resolution of the African hominoid trichotomy by use of a mitochondrial gene sequence. P. Natl. Acad. Sci. USA 88(4): 1570-4.

Rylands AB. 1989. Sympatric Brazilian callitrichids: the black tufted-ear marmoset, *Callithrix kuhli*, and the golden-headed lion tamarin, *Leontopithecus chrysomelas*. J. Hum. Evol. 18(7): 679-95.

Rylands AB, Matauschek C, Aquino R, Encarnación F, Heymann EW, et al. 2011. The range of the golden-mantle tamarin, *Saguinus tripartitus* (Milne Edwards, 1878): distributions and sympatry of four tamarins in Colombia, Ecuador, and northern Peru. Primates 52: 25-39.

Salazar-Ciudad I, and Jernvall J. 2002. A gene network model accounting for development and evolution of mammalian teeth. P. Natl. Acad. Sci. USA 99: 8116-20.

Salazar-Ciudad I, and Jernvall J. 2004. How different types of pattern formation mechanisms affect the evolution of form and development. Evol. Dev. 6: 6-16.

Salazar-Ciudad I, and Jernvall J. 2010. A computational model of teeth and the developmental origins of morphological variation. Nature 464: 583-6.

Sanz C, Morgan D, Strindberg S, and Onononga JR. 2007. Distinguishing between the nests of sympatric chimpanzees and gorillas. J. Appl. Ecol. 44(2): 263-72.

Satta Y, Klein J, and Takahata N. 2000. DNA archives and our nearest relative: the trichotomy problem revisited. Mol. Phylogenet. Evol.14(2): 259-75.

Sayers K, and Lovejoy CO. 2008. The chimpanzee has no clothes: a critical examination of Pa*n troglodyte*s in models of human evolution. Curr. Anthropol. 49: 87-114.

Sayers K, Raghanti MA, and Lovejoy CO. 2012. Human evolution and the chimpanzee referential doctrine. Annu. Rev. Anthropol. 41: 119-38.

Schaller GB, and Lowther GR. 1969. The relevance of carnivore behavior to the study of early hominids. Southwest. J. Anthrop. 25: 307-41.

Schaller GB, Hu J, Pan W, and Zhu J. 1985. *Wolong's Giant Panda*. University of Chicago Press, Chicago.

Scally A, Dutheil JY, Hillier LW, Jordan GE, Goodhead I, et al. 2012. Insights into hominid evolution from the gorilla genome sequence. Nature 483(7388): 169-75.

Schaffer WM. 1968. Character displacement and the evolution of the Hominidae. Am. Nat. 102: 559-71.

Schlosser G, and Wagner GP. 2004. *Modularity in Development and Evolution*. University of Chicago Press, Chicago.

Schluter D. 1986. Tests for similarity and convergence of finch communities. Ecology 67: 1073-1085.

Schluter D. 1996. Adaptive radiation along genetic lines of least resistance. Evolution 50: 1766-1774.

Schluter D, and McPhail JD. 1992. Ecological character displacement and speciation in sticklebacks. Am. Nat.140: 85-108.

Schnitzer SA, and Carson WP. 2001. Treefall gaps and the maintenance of species diversity in a tropical forest. Ecology 82(4): 913-9.

Schroer K, and Wood B. 2011. Mandibular premolar molarization: a platyrrhine comparative model. Am. J. Phys. Anthropol. 147(1): 150-62.

Schroer K, and Wood B. 2013. Evolution of hominin postcanine macromorphology: a comparative meta-analysis. In: Irish J and Scott GR (Eds.), *Anthropological Perspectives on Tooth Morphology*. Cambridge University Press, Cambridge.

Schroer K, Porter L, Garber P, and Wood B. 2012. Mandibular premolar morphology is correlated with dietary toughness in sympatric callitrichids. Am. J. Phys. Anthropol. 149(4): 642-53.

Schwartz JH. 1987. *The Red Ape: Orang-utans and Human Origins*. Houghton Mifflin, Boston.

Scott RS, Ungar PS, Bergstrom TS, Brown C, Grine FE, et al. 2005. Dental microwear texture analysis shows within-species diet variability in fossil hominins. Nature 436: 6935.

Scott JM, Heglund P, and Morrison ML (Eds.). 2002. *Predicting Species Occurrences: Issues of Accuracy and Scale*. Island Press, Washington DC.

Scott WB. 1892. The evolution of the premolar teeth in the mammals. P. Acad. Nat. Sci. Phila. 44: 405-44.

Sepkoski JJ. 1997. Biodiversity: past, present, and future. J. Paleontol. 71(4): 533-9.

Shea BT. 1985. On aspects of skull form in African apes and orangutans, with implications for hominoid evolution. Am. J. Phys. Anthropol. 68(3): 329-42.

Shea JH. 1982. Twelve fallacies of uniformitarianism. Geology 10(9): 455-60.

Simberloff D, Dayan T, Jones C, and Ogura G. 2000. Character displacement and release in the small Indian mongoose, *Herpestes javanicus*. Ecology 81(8): 2086-99.

Singh N, Harvati K, Hublin J-J, and Klingenberg CP. 2012. Morphological evolution through integration: a quantitative study of cranial integration in *Homo*, *Pan*, *Gorilla* and *Pongo*. J. Hum. Evol. 62(1): 155-64.

Sharpe PT. 2000. Homeobox genes in initiation and shape of teeth during development in mammalian embryos. In: Teaford MF, Smith MM, and Ferguson MWJ (Eds.), *Development, Function and Evolution of Teeth*. Cambridge University Press, Cambridge, pp. 3-12.

Skelton R, and McHenry H. 1992. Evolutionary relationships among early hominids. J. Hum. Evol. 23: 309–49.

Skinner MM, Wood BA, Boesch C, Olejniczak AJ, Rosas A, et al. 2008. Dental trait expression at the enamel-dentine junction of lower molars in extant and fossil hominoids. J. Hum. Evol. 54(2): 173-86.

Slatkin M. 1980. Ecological character displacement. Ecology 61: 163-77.

Slavkin HC, and Diekwisch TG. 1997. Molecular strategies of tooth enamel formation are highly conserved during vertebrate evolution. Dent. Enamel 205: 73-84.

Slobodkin LB. 1961. Preliminary ideas for a predictive theory of ecology. Am. Nat. 95(882): 147-153.

Smith BH. 1994. Patterns of dental development in *Homo, Australopithecus, Pan,* and *Gorilla*. Am. J. Phys. Anthropol. 94(3): 307-25.

Smith RJ. 2009. Use and misuse of the reduced major axis for line-fitting. Am. J. Phys. Anthropol. 140(3): 476-86.

Snowdon CT. 1990. Language capacities of nonhuman animals. Am. J. Phys. Anthropol. 33(S11): 215-43.

Sponheimer M, Lee-Thorp J, de Ruiter D, Codron D, Codron J, et al. 2005. Hominins, sedges, and termites: new carbon isotope data from the Sterkfontein valley and Kruger National Park. J. Hum. Evol. 48(3): 301-12.

Sponheimer M, Loudon JE, Codron D, Howells ME, Pruetz JD, et al. 2006. Do "savanna" chimpanzees consume C_4 resources? J. Hum. Evol. 51(2): 128-33.

Spoor F, Wood B, and Zonneveld F. 1994. Implications of early hominid labyrinthine morphology for evolution of human bipedal locomotion. Nature 369(6482): 645-8.

Spoor F, Leakey MG, Gathogo PN, Brown FH, Antón S, et al. 2007. Implications of new early *Homo* fossils from Ileret, east of Lake Turkana, Kenya. Nature 448(7154): 688-91.

Springer MS, Meredith RW, Gatesy J, Emerling CA, Park J, et al. 2012. Macroevolutionary dynamics and historical biogeography of primate diversification inferred from a species supermatrix. PloS One 7(11): e49521.

Sneath PH, and Sokal RR. 1973. *Numerical Taxonomy*. WH Freeman, San Francisco.

Stanford CB. 2001. *Significant Others: The Ape-Human Continuum and the Quest for Human Nature*. Basic Books, New York.

Stanford CB. 2006. The behavioral ecology of sympatric African apes: implications for understanding fossil hominoid ecology. Primates 47(1): 91-101.

Stanford CB, and Allen JS. 1991. On strategic storytelling: current models of human behavioral evolution. Curr. Anthropol. 32: 58-61.

Stanford CB, and Nkurunungi JB. 2003. Behavioral ecology of sympatric chimpanzees and gorillas in Bwindi Impenetrable National Park, Uganda: Diet. Int. J. Primatol. 24(4): 901-18.

Stanley SM. 1975. A theory of evolution above the species level. P. Natl. Acad. Sci. USA 72(2): 646-50.

Stauffer RL, Walker A, Ryder OA, Lyons-Weiler M, and Hedges SB. 2001. Human and ape molecular clocks and constraints on paleontological hypotheses. J. Hered. 92(6): 469-74.

Steiper ME, and Young NM. 2006. Primate molecular divergence dates. Mol. Phylogenet. Evol. 41(2): 384-94.

Strait DS. 2001. Integration, phylogeny, and the hominid cranial base. Am. J. Phys. Anthropol. 114(4): 273-97.

Strait DS, Grine FE, and Moniz M. 1997. A reappraisal of early hominid phylogeny. J. Hum. Evol. 32: 17-82.

Strait DS, Richmond BG, Spencer MA, Ross CF, Dechow PC, et al. 2007. Masticatory biomechanics and its relevance to early hominid phylogeny: an examination of palatal thickness using finite-element analysis. J. Hum. Evol. 52(5): 585-99.

Strait DS, Weber GW, Neubauer S, Chalk J, Richmond BG, et al. 2009. The feeding biomechanics and dietary ecology of *Australopithecus africanus*. P. Natl. Acad. Sci. USA 106(7): 2124-9.

Strier KB. 1994. Myth of the typical primate. Yearb. Phys. Anthropol. 37: 233-71.

Suárez SD, and Gallup GG. 1981. Self-recognition in chimpanzees and orangutans, but not gorillas. J. Hum. Evol. 10(2): 175-88.

Sussman RW, Shaffer CA, and Guidi L. 2011. *Macaca fascicularis* in Mauritius: implications for macaque-human interactions and for future research on long-tailed macaques. In: Fuentes A, Gumert MD, and Jones-Engel L (Eds.), *Monkeys on the Edge*. Cambridge University Press, Cambridge, pp. 207-35.

Suwa G, Wood B, and White TD. 1994. Further analysis of mandibular molar crown and cusp areas in Pliocene and early Pleistocene hominids. Am. J. Phys. Anthropol. 93:407-26.

Suwa G, Kono RT, Katoh S, Asfaw B, and Beyene Y. 2007. A new species of great ape from the late Miocene epoch in Ethiopia. Nature 448: 921-4.

Suwa G, Kono RT, Simpson SW, Asfaw B, Lovejoy CO, et al. 2009. Paleobiological implications of the *Ardipithecus ramidus* dentition. Science 326(5949): 69-99.

Suzuki A. 1965. An ecological study of wild Japanese monkeys in snowy areas, focused on their food habits. Primates 7: 481-7.

Swindler DR. 1976. *Dentition of Living Primates*. Academic Press, London.

Swindler DR. 1998. *Introduction to the Primates*. University of Washington Press, Seattle.

Swindler DR. 2002. *Primate Dentition*. Cambridge University Press, Cambridge.

Symons D. 1990. Adaptiveness and adaptation. Ethol. Sociobiol. 11(4): 427-44.

Szalay FS, and Delson E. 1979. *Evolutionary History of the Primates*. Academic Press, New York.

Takacs Z, Morales JC, Geissman T, and Melnick DJ. 2005. A complete species-level phylogeny of the Hylobatidae based on mitochondrial ND3-ND4 gene sequences. Mol. Phylogenet. Evol. 36: 456-67.

Tan Y, and Li WH. 1999. Vision: trichromatic vision in prosimians. Nature 402(6757): 36.

Taylor AB. 2006. Feeding behavior, diet, and the functional consequences of jaw form in orangutans, with implications for the evolution of *Pongo*. J. Hum. Evol. 50(4): 377-93.

Teaford MF, and Ungar PS. 2000. Diet and the evolution of the earliest human ancestors. P. Natl. Acad. Sci. USA 97(25): 13506-11.

Thesleff I, and Mikkola, M. 2002. The role of growth factors in tooth development. Int. Rev. Cytol. 217: 93-135.

Thierry B, Singh M, and Kaumanns V (Eds.). 2001. *Macaque Societies: A Model for the Study of Social Organization.* Cambridge University Press, Cambridge.

Thinh VN, Rawson B, Hallam C, Kenyon M, Nadler T, et al. 2010. Phylogeny and distribution of crested gibbons (genus *Nomascus*) based on mitochondrial cytochrome b gene sequence data. Am. J. Phys. Anthropol. 72(12): 1047-54.

Thompson PR. 1976. A behavior model for *Australopithecus africanus*. J. Hum. Evol. 5(6): 547-58.

Thompson JN. 1998. Rapid evolution as an ecological process. Trends Ecol. Evol. 13(8): 329-32.

Thorington RW, and Groves CP. 1970. An annotated classification of the Cercopithecoidea. In: Napier J (Ed.), *Old World Monkeys: Evolution, Systematics, and Behavior*. Academic Press, New York, pp. 629-48.

Tobias PV. 1967. *Olduvai Gorge: The Cranium and Maxillary Dentition of* Australopithecus (Zinjanthropus) boisei. Cambridge University Press, Cambridge.

Tobias PV. 1978. The earliest Transvaal members of the genus *Homo* with another look at some problems of hominid taxonomy and systematics. Z. Morphol. Anthropol. 225-65.

Tobias PV. 1991. The environmental background of hominid emergence and the appearance of the genus *Homo*. J. Hum. Evol. 6(2): 129-42.

Tooby J, and Cosmides L.1990. The past explains the present: Emotional adaptations and the structure of ancestral environments. Ethol. Sociobiol. 11(4): 375-424.

Tooby J, and Devore I. 1987. The reconstruction of hominid behavioral evolution through strategic modeling. In: Kinzey W (Ed.), *The Evolution of Human Behavior: Primate Models*. State University of New York Press, Albany, pp. 183-237.

Tong H, and Wu X. 2010. *Stephanorhinus kirchbergensis* (Rhinocerotidae, Mammalia) from the Rhino Cave in Shennongjia, Hubei. Chinese Sci. Bull. 55(12): 1157-68.

TreeView. 1996. TreeView: An application to display phylogenetic trees on personal computers. *Comput. Appl. Biosci.* 12 (4): 357-8.

Tucker A, and Sharpe, P. 2004. The cutting-edge of mammalian development; how the embryo makes teeth. Nat. Rev. Genet. 5(7): 499-508.

Tucker AS, Matthews KL, and Sharpe PT. 1998. Transformation of tooth type induced by inhibition of BMP signaling. Science 282(5391): 1136-8

Tummers M, and Thesleff I. 2003. Root or crown: a developmental choice orchestrated by the differential regulation of the epithelial stem cell niche in the tooth of two rodent species. Development 130(6): 1049-57.

Tummers M, and Thesleff I. 2009. The importance of signal pathway modulation in all aspects of tooth development. J. Exp. Zool. B 312(4): 309-19.

Tutin CE, and Fernandez M. 1992. Insect-eating by sympatric Lowland gorillas (*Gorilla g. gorilla*) and chimpanzees (*Pan t. troglodytes*) in the Lopé Reserve, Gabon. Am. J. Primatol. 28(1): 29-40.

Tutin CE, and Fernandez, M. 1993. Composition of the diet of chimpanzees and comparisons with that of sympatric lowland gorillas in the Lopé Reserve, Gabon. Am. J. Primatol. 30(3): 195-211.

Tutin CE, and Oslisly R. 1995. *Homo, Pan* and *Gorilla*: co-existence over 60 000 years at Lopé in central Gabon. J. Hum. Evol. 28(6): 597-602.

Tyson E. 1699. *Orang-utan, sive Homo sylvestris: or, the anatomy of a pygmie compared with that of a monkey, an ape and a man. To which is added, a philological essay concerning the pygmies, the cynocephali, the satyrs, and sphinges of the ancients. Wherein it will appear that they are all either apes or monkeys, and not men, as formerly pretended.* Bennet, London.

Uchida A. 1996. What we don't know about great ape variation. Trends Ecol. Evol. 11(4): 163-8.

Uchida A. 1998. Variation in tooth morphology of *Gorilla gorilla*. J. Hum. Evol. 34(1): 55-70.

Uchida A. 1998. Variation in tooth morphology of *Pongo pygmaeus*. J. Hum. Evol. 34(1): 71-9.

Ungar PS. 1995. Fruit preferences of four sympatric primate species at Ketambe, Northern Sumatra, Indonesia. Int. J. Primatol. 16(3): 221-45.

Ungar PS. 2007. *Evolution of the Human Diet*. Oxford University Press, Oxford.

Ungar PS, and Sponheimer M. 2011. The diets of early hominins. Science 334(6053): 190-3.

Ungar PS, Grine FE, and Teaford MF. 2008. Dental microwear and diet of the Plio Pleistocene hominin *Paranthropus boisei*. PloS One 3:e2044.

Vaahtokari A, Åberg T, Jernvall J, Keränen S, and Thesleff I. 1996. The enamel knot as a signaling center in the developing mouse tooth. Mech. Develop. 54(1): 39-43.

Vekua A, Lordkipanidze D, Rightmire GP, Agusti J, Ferring R, et al. 2002. A new skull of early *Homo* from Dmanisi, Georgia. Science 297(5578): 85-9.

Venables WN, and Ripley BD. 2002. *Modern Applied Statistics with S, Fourth Edition*. Springer, New York.

Villmoare B, Fish J, and Jungers W. 2011. Selection, morphological integration, and strepsirrhine locomotor adaptations. J. Evolution. Biol. 38(1): 88-99.

Vogel ER, van Woerden JT, Lucas PW, Utami Atmoko SS, van Schaik CP, et al. 2008. Functional ecology and evolution of hominoid molar enamel thickness: *Pan troglodytes schweinfurthii* and *Pongo pygmaeus wurmbii*. J. Hum. Evol. 55(1): 60-74.

Vogel ER, Haag L, Mitra-Setia T, van Schaik CP, and Dominy NJ. 2009. Foraging and ranging behavior during a fallback episode: *Hylobates albibarbis* and *Pongo pygmaeus wurmbii* compared. Am. J. Phys. Anthropol. 140(4): 716-26.

von Cramon-Taubadel N, and Smith HF. 2012. The relative congruence of cranial and genetic estimates of hominoid taxon relationships: implications for the reconstruction of hominin phylogeny. J. Hum. Evol. 62(5): 640-53.

Waage JK. 1979. Reproductive character displacement in *Calopteryx* (Odonata: Calopterygidae). Evolution 33: 104-16.

Wagner GP. 2005. The developmental evolution of avian digit homology: an update. Theor. Biosci. 124(2): 165-83.

Wagner GP, and Gauthier JA. 1999. 1, 2, 3= 2, 3, 4: a solution to the problem of the homology of the digits in the avian hand. P. Natl. Acad. Sci. USA 96(9): 5111-6.

Wahungu G. 1998. Diet and habitat overlap in two sympatric primate species, the Tana crested mangabey *Cercocebus galeritus* and yellow baboon *Papio cynocephalus*. Afr. J. Ecol. 36(2): 159-73.

Wahungu G, Catterall CP, and Olsen MF. 2002. Seedling predation and growth at a rainforest–pasture ecotone, and the value of shoots as seedling analogues. Forest Ecol. Manag. 162(2): 251-60.

Walker A. 1981. Dietary hypotheses and human evolution. Philos. T. R. Soc. Lon. B 292: 57-64.

Ward CV, Plavcan JM, and Manthi FK. 2010. Anterior dental evolution in the *Australopithecus anamensis-afarensis* lineage. Philos. T. R. Soc. B 365: 3333-44.

Washburn SL, and DeVore I. 1961. The social life of baboons. Sci. Am. 204: 62-71.

Werdelin L. 1996. Carnivoran ecomorphology: a phylogenetic perspective. Carnivore Behavior, Ecology, and Evolution 2: 582-624.

Westergaard GC. 1988. Lion-tailed macaques (*Macaca silenus*) manufacture and use tools. J. Comp. Psychol. 102(2): 152.

Wheatley BP. 1980. Feeding and ranging of East Bornean *Macaca fascicularis*. In: Lindburg D (Ed.), *The Macaques: Studies in Ecology, Behavior and Evolution*. Van Nostrand Reinhold Company, New York, pp. 215-46.

Wieczkowski J. 2009. Puncture and crushing resistance scores of Tana River mangabey (*Cercocebus galeritus*) diet items. Am. J. Phys. Anthropol. 140(3): 572-77.

Williams SA. 2010. Morphological integration and the evolution of knuckle-walking. J. Hum. Evol. 58(5): 432-40.

Willis JH, Coyne JA, and Kirkpatrick M. 1991. Can one predict the evolution of quantitative characters without genetics? Evolution 45(2): 441-4.

Willmore KE, Young NM, and Richtsmeier JT. 2007. Phenotypic variability: Its components, measurement and underlying developmental processes. J. Evolution. Biol. 34(3-4): 99-120.

Wilson GP, Evans AR, Corfe IJ, Smits PD, Fortelius M, et al. 2012. Adaptive radiation of multituberculate mammals before the extinction of dinosaurs. Nature 483(7390): 457-60.

Wolfe LD. 1986. Reproductive biology of rhesus and Japanese macaques. Primates 27(1): 95-101.

Wolpoff MH. 1970. The evidence for multiple hominid taxa at Swartkrans. Am. Anthropol. 72(3): 576-607.

Wolpoff MH. 1971. *Metric Trends in Hominid Dental Evolution*. Case Western Reserve University Press, Cleveland.

Wood BA. 1981. Human origins: fossil evidence and current problems of analysis and interpretation. In: Harrison RJ, and Holmes RL (Eds.), *Progress in Anatomy*. Cambridge University Press, Cambridge, pp. 229-45.

Wood B. 1988. Are "'robust'" australopithecines a monophyletic group? In: Grine FE (Ed.), *Evolutionary History of the Robust Australopithecines*. Aldine de Gruyter, New York, pp. 269-84.

Wood B. 1991. *Koobi Fora Research Project, Vol. 4 Hominid Cranial Remains*. Oxford University Press, Oxford.

Wood B. 1992. Early hominid species and speciation. J. Hum. Evol. 22(4): 351-65.

Wood B, and Abbott S. 1983. Analysis of the dental morphology of Plio-Pleistocene hominids. I. Mandibular molars: crown area measurements and morphological traits. J. Anat.136: 197-219.

Wood B, and Chamberlain AT. 1986. *Australopithecus*: grade or clade. In: Wood B, Martin L, and Andrews P (Eds.), *Major Topics in Primate and Human Evolution*. Cambridge University Press, Cambridge, pp. 220-48.

Wood B, and Chamberlain A. 1987. The nature of affinities of the robust australopithecines. J. Hum. Evol. 16: 625-41.

Wood B, and Collard M. 1999. The changing face of the genus *Homo*. Evol. Anthropol. 8: 195-207.

Wood B, and Constantino P. 2004. Human origins: life at the top of the tree. In: Cracraft J, and Donoghue MJ (Eds.), *Assembling the Tree of Lif*e. Oxford University Press, Oxford, pp. 517-35.

Wood B, and Constantino P. 2007. *Paranthropus boisei*: fifty years of evidence and analysis. Am. J. Phys. Anthropol. S45: 106-32.

Wood B, and Engleman CA. 1988. Analysis of the dental morphology of Plio-Pleistocene hominids. V. Maxillary postcanine tooth morphology. J. Anat. 161: 1.

Wood B, and Lonergan N. 2008. The hominin fossil record: taxa, grades and clades. J. Anat. 212(4): 354-76.

Wood B, and Richmond B. 2000. Human evolution : taxonomy and paleobiology. J. Anat. 196: 19-60.

Wood B, and Schroer K. 2012. Reconstructing the diet of an extinct hominin taxon: the Role of extant primate models. Int. J. Primatol. 33: 716-42.

Wood B, and Schroer K. 2013. Paranthropus. In: Begun DR (Ed.), *A Companion to Paleoanthropology*. Wiley, New York, pp. 457-78.

Wood B, and Stack CG. 1980. Does allometry explain the differences between “gracile” And “robust” australopithecines? Am. J. Phys. Anthropol. 52: 55-62.

Wood B, and Strait D. 2004. Patterns of resource use in early *Homo* and *Paranthropus*. J. Hum. Evol. 46: 119-62.

Wood B, and Uytterschaut H. 1987. Analysis of the dental morphology of Plio-Pleistocene hominids. III. Mandibular premolar crowns. J. Anat. 154: 121.

Wood B, Abbott S, and Graham S. 1983. Analysis of the dental morphology of Plio Pleistocene hominids. II. Mandibular molars-study of cusp areas, fissure pattern and cross sectional shape of the crown. J. Anat. 137: 287-314.

Wood B, Abbott S, and Uytterschaut H. 1988. Analysis of the dental morphology of Plio Pleistocene hominids. IV. Mandibular postcanine root morphology. J. Anat. 156:107-39.

Wood C. 1994. The correspondence between diet and masticatory morphology in a range of extant primates. Z. Morphol. Anthropol. 80: 19-50.

Wrangham RW. 1987. The significance of African apes for reconstructing human social evolution. In: Kinzey W (Ed.), *The Evolution of Human Behavior: Primate Models*. State University of New York Press, Albany, pp. 51-71.

Wrangham RW. 2009. *Catching Fire: How Cooking Made Us Human*. Basic Books, New York.

Wrangham R, and Conklin-Brittain N. 2003. Cooking as a biological trait. Comp. Biochem. Phys. A 136(1): 35-46.

Wrangham R, and Pilbeam D. 2001. African apes as time machines. In: Galdikas BMF, Briggs N, Sheeran LK, Shapiro GL, and Goodall J (Eds.), *All Apes Great and Small*. Plenum/Kluwer, New York, pp. 5-18.

Yamagiwa J, and Basabose AK. 2009. Fallback foods and dietary partitioning among *Pan* and *Gorilla*. Am. J. Phys. Anthropol. 140(4): 739-50.

Yamagiwa J, Maruhashi T, Yumoto T, and Mwanza N. 1996. Dietary and ranging overlap in sympatric gorillas and chimpanzees in Kahuzi-Biega National Park, Zaire. In: McGrew WC, Marchant LF, Nishida T, Itani J, and Goodall J (Eds.), *Great Ape Societies*. Cambridge University Press, Cambridge, pp. 82-98.

Yeager CP. 1996. Feeding ecology of the long-tailed macaque (*Macaca fascicularis*) in Kalimantan Tengah, Indonesia. Int. J. Primatol. 17(1): 51-62.
.
Yee TW, and Mitchell ND. 1991. Generalized additive models in plant ecology. J. Veg. Sci. 2(5): 587-602.

Yesner DR, Ayres WS, Carlson DL, Davis RS, Dewar R, et al. 1980. Maritime hunter-gatherers: ecology and prehistory. Curr. Anthropol. 21: 727-50.

Yom-Tov Y. 1991. Character displacement in the psammophile Gerbillidae of Israel. Oikos 60: 173-9.

Young NM, Wagner GP, and Hallgrímsson B. 2010. Development and the evolvability of human limbs. P. Natl. Acad. Sci. USA 107(8): 3400-5.

Zehr S, Ruvolo M, Heider J, and Mootnick A. 1996. Gibbon phylogeny inferred from mitochondrial DNA sequences. Am. J. Phys. Anthropol. (22): 251.

Zeng ZB, Kao CH, and Basten CJ. 1999. Estimating the genetic architecture of quantitative traits. Genet. Res. 74(3): 279-89.

Zhang YW, Ryder OA, and Zhang YP. 2001. Genetic divergence of orangutan subspecies (*Pongo pygmaeus*). J. Mol. Evol. 52(6): 516-26.

Zhi L, Karesh WB, Janczewski DN, Frazier-Taylor H, Sajuthi D, et al. 1996. Genomic differentiation among natural populations of orang-utan (*Pongo pygmaeus*). Curr. Biol. 6(10): 1326-36.

Zihlman AL, and Cramer DL. 1978. Skeletal differences between pygmy (*Pan paniscus*) and common chimpanzees (*Pan troglodytes*). Folia Primatol. 29(2): 86-94.

Zinner D, Groeneveld LF, Keller C, and Roos C. 2009. Mitochondrial phylogeography of baboons (*Papio spp.*): indication for introgressive hybridization. BMC Evol. Biol. 9: 83.

Zinner D, Wertheimer J, Liedigk R, Groeneveld LF, and Roos C. 2013. Baboon phylogeny as inferred from complete mitochondrial genomes. Am. J. Phys. Anthropol. 150(1): 133-140.

Zuckerman S. 1932. *The Social Behavior of Monkeys and Apes*. Harcourt, New York.

Appendices

Appendix 1 Postcanine measurements in extant primate sample.

			Mesiodistal length (mm)				Buccolingual length (mm)				Intercusp distance (mm)			
ID	Taxon	Sex	P_3	P_4	M_1	M_2	P_3	P_4	M_1	M_2	P_3	P_4	M_1	M_2
1946.848	*Cercocebus atys*	F	8.2	6.1	8.0	9.0	4.5	5.7	6.3	7.7	2.5	3.1	3.9	4.4
1954.931	*Cercocebus atys*	M	5.7	5.6	7.2	7.8	3.7	5.1	5.6	7.0	2.8	4.0	3.7	4.0
63305	*Cercocebus atys*	M	11.3	6.4	7.6	8.7	5.3	5.3	6.1	7.6	3.2	3.5	3.7	4.4
270954	*Cercocebus atys*	M	6.2	5.2	6.9	7.8	3.7	4.9	5.4	6.6	2.6	2.9	3.3	3.8
481745	*Cercocebus atys*	M	6.6	6.5	7.5	8.5	5.4	5.7	5.7	7.8	NA	NA	NA	NA
481746	*Cercocebus atys*	F	5.7	5.1	6.5	7.1	4.5	5.0	5.7	6.5	NA	NA	NA	NA
481747	*Cercocebus atys*	F	5.9	6.9	7.7	8.3	4.2	5.1	6.6	7.5	2.1	3.2	4.0	4.8
481748	*Cercocebus atys*	F	10.6	6.3	7.3	7.7	5.5	5.6	7.0	8.3	2.9	3.9	NA	4.9
14.7.23.1	*Cercocebus galeritus*	M	6.6	6.0	6.3	7.5	4.1	5.1	5.9	6.6	2.8	2.2	2.7	3.1
14.7.23.2	*Cercocebus galeritus*	F	5.6	5.6	6.2	6.9	4.4	5.1	5.5	6.5	2.3	2.6	2.7	3.1
14.7.23.3	*Cercocebus galeritus*	M	9.3	5.5	6.9	7.7	4.7	4.7	5.8	7.1	2.6	2.3	3.1	3.6
23.10.15.3	*Cercocebus galeritus*	F	4.5	4.7	6.1	7.0	3.3	4.2	4.9	NA	1.7	2.0	2.3	2.4
30.11.11.45	*Cercocebus galeritus*	M	5.6	5.3	6.6	7.1	3.6	4.8	5.4	6.6	2.0	2.2	2.2	3.1
30.11.11.48	*Cercocebus galeritus*	F	4.7	5.3	5.7	6.6	3.7	5.1	4.9	6.5	2.1	2.1	2.3	3.3
30.11.11.49	*Cercocebus galeritus*	F	5.5	5.8	6.6	7.8	4.2	4.9	5.5	6.7	2.2	2.1	3.4	4.2
5.5.23.2	*Cercocebus galeritus*	M	8.9	6.0	6.7	7.7	5.1	NA	5.7	7.0	3.2	2.7	3.7	4.2
1939.1068	*Cercocebus torquatus*	M	11.2	7.4	8.4	NA	5.2	7.2	7.1	9.1	2.7	3.5	3.7	4.3
1948.45	*Cercocebus torquatus*	M	9.3	7.5	NA	NA	4.7	6.3	7.1	8.5	2.7	4.0	3.9	4.0
1957.313	*Cercocebus torquatus*	M	8.3	6.4	8.0	9.1	4.8	6.3	6.8	7.8	3.2	3.1	4.2	4.7
1967.1712	*Cercocebus torquatus*	F	7.9	6.3	7.4	8.3	4.6	5.7	6.3	7.8	3.7	3.1	4.3	4.3
1971.2314	*Cercocebus torquatus*	M	5.4	5.2	NA	NA	4.2	NA	NA	NA	2.7	3.5	3.8	4.4
218844	*Cercocebus torquatus*	M	7.0	6.0	7.1	8.1	4.2	5.3	5.9	7.1	2.5	3.3	3.7	3.7
220088	*Cercocebus torquatus*	M	9.0	6.6	7.2	8.3	4.9	5.9	6.4	7.5	3.7	3.6	4.1	4.4
220090	*Cercocebus torquatus*	M	9.5	6.8	7.3	8.5	4.9	5.5	6.1	7.4	2.5	3.3	3.6	4.0
220092	*Cercocebus torquatus*	F	8.1	6.0	7.2	8.2	4.8	5.9	6.6	7.6	3.2	3.0	3.8	4.4
220354	*Cercocebus torquatus*	M	7.3	6.1	7.0	8.5	4.7	5.1	5.8	7.0	2.8	2.9	3.8	4.4
220366	*Cercocebus torquatus*	M	5.7	5.7	6.7	7.8	4.3	4.9	5.3	6.1	2.7	3.2	3.6	4.1
1855.12.6.21	*Cercocebus torquatus*	M	8.9	6.4	7.1	8.4	4.8	6.1	6.6	8.1	2.5	3.7	4.5	NA
1902.11.2.1	*Cercocebus torquatus*	M	7.5	6.2	7.6	8.6	4.8	5.9	6.5	8.7	2.9	3.3	4.4	4.2
1903.2.4.1	*Cercocebus torquatus*	M	7.8	6.6	7.7	8.6	4.8	6.2	7.1	8.6	3.6	3.9	5.0	4.8
1903.2.4.2	*Cercocebus torquatus*	M	9.5	NA	6.6	8.0	4.9	6.0	7.3	9.5	2.5	3.9	3.7	4.4
1930.12.16.5	*Cercocebus torquatus*	M	7.6	6.2	7.6	8.1	4.3	5.6	6.2	7.3	2.5	3.2	2.9	3.7
1938.7.7.3	*Cercocebus torquatus*	M	8.5	6.4	7.8	9.0	5.2	5.8	6.7	8.0	NA	NA	NA	NA
1938.7.7.5	*Cercocebus torquatus*	F	6.2	5.5	6.9	7.9	4.4	4.9	5.6	7.5	NA	NA	NA	NA
395636	*Gorilla beringei*	M	14.2	11.9	16.4	17.4	12.4	11.9	13.4	15.5	10.5	8.1	8.9	10.8
396934	*Gorilla beringei*	M	16.3	12.1	15.9	17.2	11.9	11.5	13.0	15.5	7.9	7.8	7.2	9.0
396935	*Gorilla beringei*	F	13.3	12.2	16.0	17.0	10.2	12.1	12.7	14.6	6.2	6.2	7.1	8.0
396936	*Gorilla beringei*	F	16.1	15.5	16.2	16.8	10.7	11.4	14.0	16.1	7.3	8.4	7.6	8.6
396942	*Gorilla beringei*	M	15.5	13.2	16.4	18.1	12.2	13.6	14.3	16.0	6.6	7.1	7.0	7.8
397356	*Gorilla beringei*	F	13.4	11.4	14.7	15.3	10.0	11.4	12.3	14.0	7.6	7.0	8.6	9.1
545027	*Gorilla beringei*	F	15.1	13.4	16.7	17.4	10.5	11.8	13.6	15.6	8.5	7.2	7.5	7.6
545028	*Gorilla beringei*	M	18.2	13.3	18.1	19.3	12.6	13.0	14.9	17.1	6.6	7.2	7.4	9.8
545030	*Gorilla beringei*	M	14.0	11.0	14.1	16.1	11.5	11.9	12.3	14.6	7.4	8.4	9.4	8.7
545031	*Gorilla beringei*	F	13.6	10.9	14.6	14.9	10.3	11.0	12.5	13.5	6.0	7.5	8.2	7.8

Postcanine measurements in extant primate sample, continued.

			Mesiodistal length (mm)				Buccolingual length (mm)				Intercusp distance (mm)			
ID	Taxon	Sex	P_3	P_4	M_1	M_2	P_3	P_4	M_1	M_2	P_3	P_4	M_1	M_2
545032	*Gorilla beringei*	M	18.5	12.7	18.2	19.2	13.2	13.6	14.6	17.3	9.2	8.3	7.4	9.3
545034	*Gorilla beringei*	M	17.0	12.8	16.1	18.8	12.2	13.0	14.3	16.1	9.0	8.8	9.1	9.3
545036	*Gorilla beringei*	M	17.3	13.8	18.8	19.4	14.9	14.2	14.8	18.6	8.0	8.0	8.6	10.6
1922.2.10.2	*Gorilla beringei*	F	13.4	10.3	14.4	15.8	9.9	11.3	12.0	13.3	6.8	7.3	8.3	8.4
1939.914	*Gorilla gorilla*	F	12.6	11.2	15.1	15.9	9.7	10.2	12.0	12.7	8.7	7.1	6.7	6.6
1939.919	*Gorilla gorilla*	M	14.5	11.5	16.2	17.7	11.8	12.2	13.6	15.4	8.0	7.2	6.1	8.3
1939.92	*Gorilla gorilla*	M	14.5	11.5	15.3	16.9	12.4	12.8	12.9	14.9	10.7	7.6	6.6	9.0
1939.923	*Gorilla gorilla*	M	14.2	11.6	16.1	17.3	13.2	12.5	13.9	15.3	8.7	8.3	8.2	9.3
1939.927	*Gorilla gorilla*	F	13.6	10.3	15.4	17.0	12.0	12.3	13.2	15.1	6.5	6.8	6.7	7.9
1939.933	*Gorilla gorilla*	F	11.3	9.5	13.2	14.8	9.8	10.3	10.9	12.4	6.5	6.3	7.7	8.0
1939.934	*Gorilla gorilla*	F	12.4	10.8	13.6	14.7	12.7	12.1	12.0	14.3	8.0	6.2	5.5	6.9
1939.936	*Gorilla gorilla*	F	12.1	10.7	14.7	15.3	10.7	12.1	11.9	13.4	6.8	7.0	6.6	7.8
1948.435	*Gorilla gorilla*	M	12.9	10.5	14.7	16.0	10.1	12.1	12.5	14.5	6.3	7.5	7.7	9.0
1949.603	*Gorilla gorilla*	M	15.0	11.4	15.2	16.9	9.6	11.9	12.7	14.4	8.4	7.4	8.4	8.7
1986.534	*Gorilla gorilla*	M	13.1	10.8	14.7	16.2	11.1	10.8	12.2	13.1	6.9	6.4	7.3	8.5
1986.535	*Gorilla gorilla*	M	15.7	10.6	14.9	17.3	11.4	12.6	12.6	15.8	9.5	7.3	7.7	9.4
1986.54	*Gorilla gorilla*	M	12.6	9.5	NA	14.4	9.0	9.7	NA	12.1	7.6	6.0	6.6	7.5
174712	*Gorilla gorilla*	M	13.8	10.3	14.9	16.0	12.5	11.0	12.4	13.4	8.9	5.8	6.3	7.9
174715	*Gorilla gorilla*	M	13.9	10.2	14.1	15.7	11.0	12.0	11.7	13.5	6.6	6.9	6.7	7.1
174720	*Gorilla gorilla*	M	13.3	10.2	13.9	15.3	12.9	12.0	12.3	14.4	9.2	6.9	6.6	8.8
176207	*Gorilla gorilla*	M	13.4	9.9	14.3	15.1	10.3	11.5	12.3	13.6	7.0	8.0	6.6	7.5
176208	*Gorilla gorilla*	M	14.7	11.8	14.9	16.8	11.8	11.0	11.7	14.1	8.0	6.7	7.1	7.8
176209	*Gorilla gorilla*	M	17.2	11.2	14.7	16.2	13.1	12.3	12.6	14.4	7.2	6.4	5.9	8.9
176211	*Gorilla gorilla*	M	15.9	11.6	15.0	18.1	13.5	12.9	12.8	15.8	9.3	8.7	9.3	9.6
176216	*Gorilla gorilla*	M	13.4	11.0	15.9	17.2	10.5	12.0	12.9	14.5	9.6	8.0	7.8	9.4
197037	*Gorilla gorilla*	M	12.3	10.3	13.0	13.3	10.4	9.9	11.2	12.9	7.9	6.4	7.1	8.1
220324	*Gorilla gorilla*	M	16.9	11.2	15.2	15.3	9.8	12.1	12.1	14.5	6.6	5.9	6.6	6.9
252577	*Gorilla gorilla*	F	11.8	10.4	14.1	15.6	9.8	10.2	12.1	13.4	6.4	5.4	6.3	6.9
1923.11.29.4	*Gorilla gorilla*	M	12.4	12.8	14.2	15.4	13.1	11.3	12.2	15.0	9.0	8.4	7.2	9.0
1923.11.29.6	*Gorilla gorilla*	M	14.8	11.0	14.8	16.3	10.6	11.0	12.6	13.5	6.8	5.8	7.3	8.4
1925.1.4.3	*Gorilla gorilla*	M	15.4	12.4	NA	17.2	14.4	13.1	NA	15.7	8.7	8.5	7.8	8.3
1936.7.14.1	*Gorilla gorilla*	M	16.6	11.4	15.0	16.1	11.2	14.0	12.9	15.0	8.8	7.9	7.0	9.1
1948.3.31.2	*Gorilla gorilla*	F	13.8	10.5	14.4	15.4	12.0	10.9	12.5	14.1	7.8	6.6	7.0	8.0
1955.1484	*Hylobates agilis*	F	7.0	4.7	7.1	6.2	4.8	5.0	NA	6.2	2.5	2.8	3.9	4.1
1955.1485	*Hylobates agilis*	M	6.0	5.1	6.4	NA	4.4	4.5	5.3	4.5	2.7	2.9	3.6	4.0
1955.1486	*Hylobates agilis*	F	6.7	4.7	5.9	5.9	3.7	4.1	4.6	5.3	2.7	2.4	2.3	3.5
1955.1487	*Hylobates agilis*	M	6.1	3.9	5.8	5.9	3.7	3.9	4.8	5.2	2.1	2.3	2.8	2.8
113177	*Hylobates agilis*	M	6.2	4.4	5.8	6.0	4.4	4.4	4.9	5.1	2.6	2.7	3.3	3.7
123151	*Hylobates agilis*	M	6.2	4.2	5.3	6.3	3.7	4.3	4.2	5.6	2.2	2.3	2.8	4.0
123154	*Hylobates agilis*	M	6.0	4.6	5.9	6.4	3.7	4.6	4.8	5.6	2.3	2.2	3.2	3.4
123155	*Hylobates agilis*	M	6.4	4.5	6.3	6.2	4.5	4.1	5.7	6.4	2.7	2.3	3.6	3.8
143576	*Hylobates agilis*	F	5.8	4.5	6.0	6.3	3.7	4.0	5.2	5.5	2.6	2.0	3.3	3.5
144089	*Hylobates agilis*	M	5.4	5.0	6.4	6.1	4.1	4.1	5.3	5.4	2.7	2.3	2.9	3.5
144090	*Hylobates agilis*	F	6.1	4.4	5.7	6.1	4.9	4.3	4.5	6.0	2.9	2.3	2.7	3.0
144091	*Hylobates agilis*	M	5.8	4.0	5.6	NA	3.7	4.4	4.8	4.8	2.3	2.3	2.3	3.1
145326	*Hylobates agilis*	M	7.0	5.6	6.7	6.8	4.1	4.1	5.1	5.8	2.7	NA	4.0	4.7

Postcanine measurements in extant primate sample, continued.

			Mesiodistal length (mm)				Buccolingual length (mm)				Intercusp distance (mm)			
ID	Taxon	Sex	P_3	P_4	M_1	M_2	P_3	P_4	M_1	M_2	P_3	P_4	M_1	M_2
145329	*Hylobates agilis*	M	5.5	4.1	5.4	6.0	3.6	NA	4.8	5.1	2.1	2.5	2.8	3.5
1860.5.4.47	*Hylobates agilis*	F	5.9	4.8	5.9	6.0	3.7	4.5	4.9	5.1	2.0	2.5	2.9	3.4
1879.9.15.1	*Hylobates agilis*	M	6.6	5.0	6.0	6.5	4.0	4.1	5.0	5.4	2.8	2.5	3.2	4.0
A49657	*Hylobates agilis*	F	5.6	4.0	5.7	NA	3.2	3.8	4.7	NA	1.7	2.5	2.4	2.9
121675	*Hylobates klossii*	F	6.4	4.3	5.9	6.0	4.3	3.9	5.1	5.0	2.9	2.4	3.0	3.1
121680	*Hylobates klossii*	F	5.7	3.8	5.3	5.1	3.8	3.9	4.3	4.2	2.5	2.0	2.7	2.7
122176	*Hylobates klossii*	M	6.1	4.4	5.7	5.9	3.8	3.8	4.3	5.0	2.8	2.4	2.3	3.2
252307	*Hylobates klossii*	F	5.9	4.0	5.7	6.3	4.0	4.1	4.7	5.3	2.7	2.2	2.8	3.1
252309	*Hylobates klossii*	M	6.2	4.0	5.6	5.9	4.0	4.2	4.6	4.9	2.2	2.0	2.7	2.8
252310	*Hylobates klossii*	F	6.0	4.0	5.3	5.8	3.8	4.0	4.5	5.0	2.4	2.2	2.6	3.3
12.2.2.1	*Hylobates klossii*	F	6.0	4.1	5.7	5.9	3.7	3.7	4.5	4.8	2.3	2.1	2.4	2.8
A49656	*Hylobates klossii*	M	5.6	3.4	5.0	5.3	NA	3.4	4.1	4.3	2.1	1.7	2.2	2.5
1955.1494	*Hylobates lar*	M	6.1	5.0	5.7	6.2	4.3	4.4	4.8	5.4	2.6	2.7	3.1	3.8
1986.1823	*Hylobates lar*	M	6.9	5.4	6.4	6.4	4.6	4.7	NA	5.9	2.7	2.3	3.4	3.7
271047	*Hylobates lar*	F	5.7	4.3	5.1	5.3	4.1	3.9	4.6	4.7	2.4	2.4	2.6	3.2
296922	*Hylobates lar*	M	6.0	4.8	6.2	6.6	4.8	4.4	NA	5.7	3.0	2.7	3.5	4.2
300024	*Hylobates lar*	M	NA	4.9	NA	7.0	NA	4.3	NA	6.0	2.9	2.4	3.0	4.1
307763	*Hylobates lar*	F	5.7	4.4	5.6	5.5	3.6	3.6	4.7	5.2	2.3	2.0	2.8	3.5
1856.5.6.9	*Hylobates lar*	F	6.0	4.3	4.9	5.4	3.8	3.9	NA	4.7	1.9	2.1	2.4	3.4
1910.10.1.7	*Hylobates lar*	F	6.3	4.3	5.1	5.4	3.7	4.2	4.5	5.0	2.8	2.7	3.0	3.5
1914.12.8.3	*Hylobates lar*	F	6.1	5.1	5.3	5.7	4.0	4.0	4.5	4.7	2.5	2.0	2.8	3.2
1914.12.8.5	*Hylobates lar*	M	6.4	4.4	5.6	5.4	3.8	4.0	4.6	5.0	2.7	1.9	2.7	3.0
1914.12.8.6	*Hylobates lar*	F	6.3	4.7	5.7	6.1	3.7	3.8	4.7	5.0	2.5	2.3	2.7	3.1
1914.12.8.7	*Hylobates lar*	F	6.1	5.1	5.3	5.7	3.3	3.8	4.4	4.8	1.8	2.4	2.6	3.2
1914.8.22.1	*Hylobates lar*	F	6.3	4.7	5.4	5.8	3.5	3.8	4.6	4.7	2.5	2.4	2.4	3.2
1924.9.2.2	*Hylobates lar*	M	6.5	5.1	5.9	5.9	4.3	4.0	4.8	5.2	2.6	2.4	3.4	3.3
1924.9.2.3	*Hylobates lar*	F	5.9	4.4	5.9	5.8	3.4	3.7	4.5	4.8	2.2	1.9	2.8	3.3
1924.9.2.4	*Hylobates lar*	M	NA	5.4	5.8	6.1	4.1	4.6	5.2	5.7	2.5	2.3	2.8	3.8
1924.9.2.6	*Hylobates lar*	F	6.0	4.7	5.6	6.2	3.9	3.9	4.7	5.3	2.4	2.4	2.8	3.5
1936.9.10.1	*Hylobates lar*	F	6.2	5.2	5.9	5.8	3.7	3.8	4.6	5.1	2.0	2.2	2.9	3.3
296795	*Macaca cyclopis*	M	8.3	5.7	6.6	8.0	5.2	4.7	5.0	6.0	3.3	2.6	2.9	3.4
308718	*Macaca cyclopis*	F	8.2	5.0	6.5	7.3	4.5	4.2	4.9	5.6	2.6	2.0	2.5	NA
358613	*Macaca cyclopis*	M	8.0	5.8	6.9	7.6	4.6	4.4	4.9	6.1	2.9	2.9	2.9	3.6
358615	*Macaca cyclopis*	F	6.4	5.7	6.6	7.8	4.5	4.6	5.1	6.2	3.0	2.6	3.1	4.0
358616	*Macaca cyclopis*	F	5.6	5.1	6.2	7.4	4.1	4.3	4.8	5.9	2.3	2.5	2.9	3.7
358617	*Macaca cyclopis*	M	5.6	5.2	6.6	7.8	4.5	4.7	4.7	5.9	2.8	2.5	2.8	3.6
397645	*Macaca cyclopis*	F	6.0	5.1	6.6	7.5	4.8	4.7	4.9	5.9	NA	2.5	2.7	3.1
397646	*Macaca cyclopis*	F	6.2	5.6	6.3	7.6	4.2	4.2	4.7	6.0	2.2	2.4	2.9	3.4
397647	*Macaca cyclopis*	F	4.9	NA	6.1	7.6	5.2	4.9	5.5	6.6	2.7	2.8	3.1	3.9
397707	*Macaca cyclopis*	F	6.0	5.1	6.5	7.7	3.8	4.7	5.3	6.5	2.0	2.3	3.2	3.3
399110	*Macaca cyclopis*	M	7.0	5.4	7.0	8.0	4.6	4.5	5.1	6.3	2.9	3.0	2.9	3.3
399112	*Macaca cyclopis*	M	9.0	5.7	7.3	8.1	4.9	4.4	NA	6.9	2.6	2.6	3.3	3.2
1939.18	*Macaca fascicularis*	M	8.4	5.2	6.3	6.9	4.4	4.1	4.3	5.8	2.8	2.8	1.9	3.5
1939.181	*Macaca fascicularis*	F	7.0	5.4	6.0	7.6	3.8	4.3	4.5	5.9	2.2	3.0	2.7	3.5
1939.891	*Macaca fascicularis*	M	7.2	4.9	6.3	7.5	4.2	4.4	5.1	6.4	1.6	2.1	2.6	3.0
1939.893	*Macaca fascicularis*	F	7.5	5.1	6.8	8.2	4.3	4.1	5.4	6.6	2.3	2.9	3.0	3.9

Postcanine measurements in extant primate sample, continued.

			Mesiodistal length (mm)				Buccolingual length (mm)				Intercusp distance (mm)			
ID	Taxon	Sex	P_3	P_4	M_1	M_2	P_3	P_4	M_1	M_2	P_3	P_4	M_1	M_2
1955.1509	*Macaca fascicularis*	M	NA	5.5	6.9	7.7	NA	4.4	5.1	6.4	NA	3.3	2.8	3.0
1955.1511	*Macaca fascicularis*	M	7.4	5.1	6.5	6.6	4.7	4.7	5.2	5.7	2.0	2.4	2.7	3.1
1955.1512	*Macaca fascicularis*	M	7.7	4.3	5.7	7.3	3.9	3.5	4.2	5.0	2.3	2.3	2.5	2.8
1955.1515	*Macaca fascicularis*	F	6.4	4.7	6.3	6.9	3.7	3.9	4.7	5.8	1.8	2.1	2.3	2.9
1955.1519	*Macaca fascicularis*	M	8.1	5.5	6.0	7.4	4.7	4.3	4.8	6.0	3.0	3.0	3.2	4.1
1955.1520	*Macaca fascicularis*	M	7.1	4.5	6.0	7.2	5.0	4.0	4.5	5.5	2.7	2.5	2.4	2.9
1955.1521	*Macaca fascicularis*	M	5.5	5.2	5.9	6.6	4.8	3.8	4.9	5.3	2.4	2.5	2.5	2.9
1955.1528	*Macaca fascicularis*	F	6.1	5.4	7.1	7.9	4.3	4.6	5.7	6.3	2.5	3.0	2.9	3.6
83273	*Macaca fascicularis*	M	8.1	6.1	7.2	8.6	5.6	5.7	5.9	6.9	3.5	2.7	2.3	2.7
101666	*Macaca fascicularis*	F	6.1	4.5	5.8	6.4	3.6	3.7	4.4	5.1	1.9	2.1	2.6	3.0
101711	*Macaca fascicularis*	M	8.1	4.9	6.0	6.8	4.7	4.2	4.6	5.5	3.0	2.7	3.0	3.8
114162	*Macaca fascicularis*	F	6.3	5.2	6.2	7.1	4.2	5.1	4.4	5.4	2.6	2.8	3.1	3.6
114165	*Macaca fascicularis*	F	5.9	4.6	6.0	6.6	3.8	4.2	4.6	5.4	2.4	2.5	3.0	3.2
114166	*Macaca fascicularis*	F	6.1	5.0	6.0	7.2	4.3	5.1	5.0	6.0	2.5	2.7	2.8	3.1
114411	*Macaca fascicularis*	M	7.6	5.1	6.1	6.8	4.8	4.9	4.8	5.1	3.1	2.3	2.5	3.1
114643	*Macaca fascicularis*	M	7.1	5.6	5.8	7.2	4.6	4.5	5.3	5.3	2.6	2.3	2.4	3.1
121513	*Macaca fascicularis*	F	6.1	4.8	5.7	6.4	4.1	4.5	4.5	5.4	2.4	2.3	2.9	2.7
121802	*Macaca fascicularis*	F	6.2	4.4	5.8	6.3	4.2	4.7	4.6	4.9	2.8	3.0	2.6	3.1
121803	*Macaca fascicularis*	M	6.6	4.9	6.2	7.0	4.8	4.4	4.6	5.4	2.6	2.3	2.7	3.1
121869	*Macaca fascicularis*	F	4.5	4.3	5.8	6.1	3.2	3.6	4.2	5.1	NA	2.3	NA	2.8
121871	*Macaca fascicularis*	M	9.3	4.4	6.0	6.3	4.5	4.5	5.0	5.1	2.6	2.6	2.6	3.1
123147	*Macaca fascicularis*	M	6.6	4.3	5.5	6.0	4.7	4.0	4.0	4.5	3.0	1.6	2.3	2.5
123992	*Macaca fascicularis*	F	6.5	5.4	6.1	7.4	3.7	4.2	5.3	6.4	2.2	2.7	3.0	3.0
143583	*Macaca fascicularis*	M	7.6	4.4	6.3	7.2	5.0	4.8	5.1	5.5	2.6	2.1	2.2	2.4
156456	*Macaca fascicularis*	F	5.4	5.2	6.1	7.1	4.3	5.1	5.7	6.5	2.2	2.3	2.1	2.2
271018	*Macaca fascicularis*	F	5.4	5.3	6.2	6.9	4.1	5.1	5.3	5.6	2.5	2.7	2.4	2.9
271168	*Macaca fascicularis*	M	7.9	4.9	7.0	7.0	5.2	4.2	5.0	5.4	2.6	2.3	2.7	2.6
344990	*Macaca fascicularis*	M	9.2	5.0	6.2	7.3	5.0	4.9	4.7	6.0	3.3	2.4	2.6	3.5
14.12.8.12	*Macaca fascicularis*	F	7.0	5.9	6.9	8.5	4.8	4.8	5.4	6.8	2.8	2.5	3.3	3.3
14.12.8.14	*Macaca fascicularis*	F	5.5	5.7	7.3	8.0	3.9	4.9	5.4	6.3	2.3	2.8	2.6	3.3
1909.11.1.1	*Macaca fascicularis*	M	8.0	4.9	5.9	7.0	4.1	4.9	5.0	6.5	2.5	2.5	3.2	3.2
1909.4.1.24	*Macaca fascicularis*	F	4.6	4.1	5.6	6.2	3.2	3.5	4.3	4.9	1.8	2.6	2.5	2.4
1909.4.1.25	*Macaca fascicularis*	F	4.2	4.2	5.4	5.7	3.1	3.3	4.2	4.7	2.0	2.2	2.2	2.8
1909.4.1.29	*Macaca fascicularis*	F	4.6	4.9	5.8	6.9	2.7	3.8	4.7	5.3	NA	NA	NA	NA
1909.4.1.31	*Macaca fascicularis*	M	7.1	4.4	5.4	6.6	3.7	3.7	4.6	5.5	2.4	2.2	2.8	2.8
1909.4.1.37	*Macaca fascicularis*	M	4.3	3.6	NA	NA	2.9	3.4	3.7	4.5	1.7	1.8	2.2	2.2
1914.12.8.15	*Macaca fascicularis*	F	6.5	5.3	6.2	7.7	4.5	5.0	5.6	7.3	2.2	3.0	3.4	3.6
1914.12.8.17	*Macaca fascicularis*	F	4.7	4.9	6.2	6.9	3.8	4.5	5.3	5.7	2.3	2.3	2.9	3.4
1914.8.22.3	*Macaca fascicularis*	F	6.7	5.1	6.4	8.3	4.4	5.1	5.6	7.4	2.0	3.5	3.5	NA
1914.8.22.4	*Macaca fascicularis*	F	5.0	4.9	6.3	7.1	3.7	4.6	5.2	5.7	2.2	2.5	2.8	3.1
1924.9.2.8	*Macaca fascicularis*	F	6.0	4.8	6.6	7.4	3.6	4.4	5.0	5.8	2.9	3.0	2.7	3.4
1934.7.18.2	*Macaca fascicularis*	F	4.9	4.3	5.4	6.2	3.2	3.6	4.1	5.2	1.9	1.9	2.4	2.8
1934.7.18.5	*Macaca fascicularis*	F	5.1	4.3	6.0	6.7	3.2	4.1	4.7	5.5	2.0	2.2	2.5	2.2
1936.9.10.11	*Macaca fascicularis*	F	5.9	5.4	NA	7.5	3.6	5.2	5.5	6.1	1.9	3.6	2.2	3.3
1936.9.10.4	*Macaca fascicularis*	M	8.2	5.2	6.8	7.3	5.6	5.3	5.2	6.1	3.1	2.9	3.6	3.5
1936.9.10.5	*Macaca fascicularis*	M	8.0	6.2	6.6	8.1	5.0	4.5	5.1	6.7	2.2	3.4	2.9	3.4

Postcanine measurements in extant primate sample, continued.

			Mesiodistal length (mm)				Buccolingual length (mm)				Intercusp distance (mm)			
ID	Taxon	Sex	P_3	P_4	M_1	M_2	P_3	P_4	M_1	M_2	P_3	P_4	M_1	M_2
1936.9.10.6	*Macaca fascicularis*	F	6.6	5.4	NA	8.2	4.3	5.7	6.3	6.7	1.9	3.2	3.2	3.3
25.7.2.1	*Macaca fascicularis*	M	9.3	5.9	7.0	8.1	4.9	5.0	5.7	7.2	3.1	3.6	NA	NA
1939.105	*Macaca fuscata*	M	8.9	6.2	8.4	9.1	4.9	5.5	6.1	7.6	2.9	3.5	3.8	4.1
174730	*Macaca fuscata*	F	6.5	5.0	6.4	7.4	3.8	4.0	4.8	5.7	2.9	2.5	2.9	3.3
344996	*Macaca fuscata*	F	7.3	6.5	7.6	9.6	4.9	5.4	5.7	7.1	3.3	3.1	3.4	4.0
1905.11.3.1	*Macaca fuscata*	F	6.4	5.4	6.7	7.6	4.0	4.1	5.1	6.2	NA	NA	NA	NA
1905.11.3.2	*Macaca fuscata*	M	7.6	6.2	7.1	9.1	4.6	4.6	6.0	7.2	3.1	3.2	3.3	4.1
1905.11.3.3	*Macaca fuscata*	F	7.2	5.5	7.8	9.1	4.9	5.0	5.8	7.0	3.0	3.5	3.4	3.6
1905.11.3.4	*Macaca fuscata*	F	4.7	5.1	6.5	8.2	4.6	5.3	5.8	7.0	3.1	3.4	3.6	4.2
1905.11.3.5	*Macaca fuscata*	F	NA	5.4	6.8	7.9	NA	5.4	4.0	7.4	NA	2.8	2.9	3.8
1906.1.4.2	*Macaca fuscata*	F	5.8	6.4	7.9	9.4	4.8	5.0	6.4	8.2	2.8	3.2	4.0	4.5
1906.1.4.3	*Macaca fuscata*	M	6.4	6.6	7.6	8.7	5.2	6.3	6.4	7.5	3.1	3.8	4.4	4.3
42.1.19.45	*Macaca fuscata*	F	6.6	5.1	6.7	7.3	5.1	5.1	5.4	6.7	3.2	3.0	3.1	3.6
84.1733	*Macaca nemestrina*	F	9.9	6.7	8.3	9.3	5.4	5.9	5.7	7.9	3.5	3.0	3.0	4.1
1947.448	*Macaca nemestrina*	M	10.3	6.5	7.6	8.1	6.2	5.9	6.4	7.3	3.6	3.7	2.9	3.5
1955.1502	*Macaca nemestrina*	F	8.8	NA	8.5	8.9	5.4	6.1	6.8	6.7	3.5	3.3	2.9	3.1
1955.1504	*Macaca nemestrina*	M	8.2	7.0	7.7	7.4	5.2	5.8	6.3	6.7	2.5	4.2	3.0	3.1
1955.1505	*Macaca nemestrina*	F	6.8	6.4	7.4	7.4	4.5	5.3	6.0	6.2	2.0	3.4	2.8	2.6
1955.707	*Macaca nemestrina*	M	11.2	5.8	6.9	8.5	5.6	5.6	5.7	7.7	3.1	3.2	3.2	3.8
1955.708	*Macaca nemestrina*	F	5.8	7.3	7.6	8.9	5.3	5.4	5.6	6.9	3.4	3.4	3.0	3.4
1955.709	*Macaca nemestrina*	F	7.0	6.3	7.7	8.9	5.4	5.2	5.9	7.3	3.2	3.0	3.2	3.0
1972.1337	*Macaca nemestrina*	M	NA	6.8	7.7	9.4	NA	4.9	5.7	7.0	NA	3.4	3.0	3.4
49691	*Macaca nemestrina*	M	9.0	6.6	7.7	7.3	5.5	5.4	5.9	6.0	3.2	3.3	2.5	2.7
49696	*Macaca nemestrina*	M	7.1	NA	NA	5.9	4.1	NA	NA	NA	2.3	2.6	NA	2.4
49874	*Macaca nemestrina*	M	11.3	7.0	7.5	8.9	6.4	5.1	5.5	6.9	3.2	3.2	2.9	3.0
114502	*Macaca nemestrina*	F	7.4	6.7	7.6	8.2	4.1	5.0	5.6	6.3	2.6	2.9	2.9	3.1
123143	*Macaca nemestrina*	M	12.9	6.6	7.7	8.3	7.3	5.6	5.6	6.8	NA	3.1	3.4	3.5
123144	*Macaca nemestrina*	M	13.1	6.7	7.6	8.3	7.6	5.3	5.4	7.0	3.0	2.7	2.7	3.0
123145	*Macaca nemestrina*	M	11.5	7.1	7.1	7.6	5.8	4.6	5.2	6.9	3.4	2.5	2.8	3.3
142227	*Macaca nemestrina*	M	11.3	7.2	7.3	8.6	6.1	5.2	5.8	7.7	4.2	3.2	3.3	3.6
142228	*Macaca nemestrina*	M	10.3	6.2	7.0	9.2	7.1	5.1	5.1	7.1	3.1	2.7	2.8	3.1
143585	*Macaca nemestrina*	M	11.0	6.8	7.1	8.7	5.0	5.1	5.5	6.9	2.4	3.2	3.3	3.7
144093	*Macaca nemestrina*	M	12.2	6.4	7.0	7.7	5.5	5.3	4.7	6.7	3.3	2.6	2.7	3.1
144094	*Macaca nemestrina*	M	12.1	6.3	7.4	8.4	5.8	5.5	5.9	6.8	2.9	3.2	3.4	4.0
153804	*Macaca nemestrina*	M	10.2	6.8	6.6	7.9	5.6	5.0	5.4	7.0	2.9	2.5	3.0	3.7
154367	*Macaca nemestrina*	M	13.6	6.6	7.1	9.7	6.4	4.7	5.1	6.9	3.7	2.6	3.0	3.0
199165	*Macaca nemestrina*	F	6.7	6.7	7.3	9.0	5.4	4.8	5.2	6.5	2.3	2.6	3.0	3.0
241022	*Macaca nemestrina*	M	11.8	5.5	6.7	7.9	5.2	5.2	5.5	6.4	3.3	2.8	2.9	3.0
258230	*Macaca nemestrina*	F	6.6	5.4	6.8	7.2	4.3	5.2	5.8	7.0	2.3	2.7	2.6	2.6
399506	*Macaca nemestrina*	F	7.2	6.3	7.4	8.6	5.0	5.6	5.4	6.8	2.9	3.0	3.3	3.1
1842.3.14.4	*Macaca nemestrina*	M	9.1	7.1	7.8	8.6	6.7	5.6	6.4	7.6	3.8	4.2	3.5	3.2
1850.11.22.19	*Macaca nemestrina*	F	6.3	7.2	7.4	9.0	4.8	5.4	6.0	7.5	2.5	3.4	3.1	4.4
1855.12.26.33	*Macaca nemestrina*	M	11.2	7.5	8.4	9.1	7.0	5.3	6.4	7.5	3.7	3.3	3.3	4.5
1855.12.26.42	*Macaca nemestrina*	M	11.3	6.5	7.1	8.0	4.9	4.8	5.2	6.8	2.7	3.0	3.3	3.1
1858.5.4.202	*Macaca nemestrina*	F	5.4	5.6	5.8	7.0	4.4	4.7	5.0	6.4	2.6	3.4	2.8	2.8
1858.5.4.215	*Macaca nemestrina*	M	5.9	NA	NA	6.4	3.8	NA	4.2	NA	2.2	2.5	2.2	2.5

Postcanine measurements in extant primate sample, continued.

			Mesiodistal length (mm)				Buccolingual length (mm)				Intercusp distance (mm)			
ID	Taxon	Sex	P_3	P_4	M_1	M_2	P_3	P_4	M_1	M_2	P_3	P_4	M_1	M_2
1915.11.4.11	*Macaca nemestrina*	F	5.8	5.7	6.6	7.5	3.9	4.7	5.2	5.8	2.2	3.3	2.6	2.6
1923.1.6.77	*Macaca nemestrina*	M	8.4	5.6	6.6	8.1	4.4	4.6	5.5	6.7	2.9	3.2	3.7	2.7
1938.11.30.6	*Macaca nemestrina*	F	11.3	6.5	7.8	8.8	5.8	NA	6.1	7.9	3.1	3.9	2.9	4.2
28.5.2.3	*Macaca nemestrina*	M	11.4	7.0	6.7	8.7	6.0	5.0	5.5	7.4	3.5	3.2	3.2	3.6
43.4.29.1	*Macaca nemestrina*	F	8.8	7.0	7.7	9.8	5.3	5.4	6.1	7.9	3.6	3.5	NA	3.7
1939.3363	*Pan troglodytes*	M	9.0	8.2	10.0	11.4	8.9	8.7	9.5	11.2	4.8	5.1	5.4	6.5
1939.3364	*Pan troglodytes*	M	9.7	7.8	9.9	10.9	8.3	8.3	9.4	10.0	4.1	5.0	5.1	5.7
1939.3365	*Pan troglodytes*	M	8.8	7.4	9.5	10.1	8.6	8.4	9.1	9.6	4.3	4.2	5.5	NA
1939.3369	*Pan troglodytes*	M	9.8	8.1	11.4	11.2	9.2	8.1	NA	9.9	5.1	4.7	5.6	NA
1939.3383	*Pan troglodytes*	F	8.9	7.2	10.0	11.3	8.0	9.0	9.2	10.4	4.9	5.4	5.9	6.7
174701	*Pan troglodytes*	M	8.6	6.5	9.6	10.6	5.8	7.6	NA	9.2	4.4	4.4	5.6	6.2
174703	*Pan troglodytes*	F	9.2	8.5	11.3	11.9	10.4	8.9	9.0	10.8	4.7	5.0	5.4	7.0
174704	*Pan troglodytes*	M	10.2	7.3	9.7	10.5	7.0	8.0	9.2	9.7	4.6	4.4	5.0	6.1
174707	*Pan troglodytes*	M	NA	7.0	10.0	10.4	6.9	7.5	9.2	9.1	3.6	4.9	5.4	5.8
176226	*Pan troglodytes*	F	9.3	7.0	10.2	10.0	6.3	7.8	9.1	9.5	4.1	4.8	5.3	6.4
176243	*Pan troglodytes*	F	9.8	8.3	11.2	11.3	7.9	8.1	9.3	10.3	5.0	4.9	4.9	6.0
220062	*Pan troglodytes*	F	9.7	7.4	10.7	11.0	7.9	7.6	9.2	10.4	4.9	4.1	4.8	6.0
220064	*Pan troglodytes*	F	9.2	8.0	9.1	10.0	7.1	8.9	9.1	10.3	3.9	4.6	5.5	5.9
220327	*Pan troglodytes*	F	8.5	7.4	10.2	11.3	8.8	8.8	9.0	10.3	5.2	5.3	5.3	6.0
1864.12.1.7	*Pan troglodytes*	M	9.6	8.4	10.7	11.3	6.9	7.3	8.9	9.6	4.8	4.5	5.6	6.3
1924.8.6.1	*Pan troglodytes*	M	9.5	7.7	10.2	10.5	8.2	8.0	NA	10.1	5.1	4.5	4.8	6.2
1936.7.7.2	*Pan troglodytes*	F	9.8	8.1	NA	11.9	8.6	9.2	9.2	11.5	4.5	4.5	6.2	NA
1950.1863	*Pan troglodytes*	M	10.3	7.8	10.7	10.6	8.3	9.3	9.9	10.7	4.4	4.4	5.7	6.4
481804	*Pan troglodytes*	F	8.5	7.5	11.7	10.7	8.8	8.0	9.3	9.9	4.3	4.6	4.9	5.1
12.127	*Papio anubis*	M	11.4	9.0	10.9	13.8	7.7	7.8	9.0	11.8	5.3	5.3	5.4	6.0
71.2353	*Papio anubis*	M	12.8	8.0	10.7	12.9	6.6	7.7	8.8	12.2	3.1	5.1	4.9	6.5
1939.1021	*Papio anubis*	M	14.7	8.2	9.8	12.6	7.0	7.0	8.7	11.0	3.9	4.1	5.4	7.3
1962.25	*Papio anubis*	F	6.8	7.3	10.3	11.3	4.6	6.4	7.7	9.0	2.6	3.5	4.0	4.6
1976.13	*Papio anubis*	M	11.0	8.9	11.3	13.4	6.0	6.5	8.7	9.6	2.6	4.8	3.6	4.7
1990.0535	*Papio anubis*	M	13.9	8.8	11.0	12.2	6.3	6.8	7.9	9.8	3.1	4.4	3.8	4.3
144059	*Papio anubis*	M	16.0	8.7	10.8	13.6	7.0	7.5	8.2	11.4	3.8	4.5	4.8	6.5
164518	*Papio anubis*	M	14.4	8.2	10.3	12.3	6.1	7.3	7.9	9.7	3.2	5.2	5.2	6.4
182148	*Papio anubis*	F	8.2	7.1	8.4	10.4	4.8	5.8	6.3	8.4	2.6	3.9	4.1	4.9
216605	*Papio anubis*	M	12.9	8.8	10.8	12.7	6.5	6.7	7.9	10.8	3.7	4.4	4.7	5.1
236976	*Papio anubis*	M	17.0	9.5	12.0	13.6	8.5	8.5	9.6	12.7	5.1	4.4	5.6	7.2
293174	*Papio anubis*	M	14.6	7.8	9.9	12.5	7.8	6.5	7.1	9.7	2.7	4.1	4.0	5.0
354986	*Papio anubis*	M	13.0	8.2	11.3	11.9	6.3	6.7	8.3	9.3	3.7	3.7	5.7	5.8
354987	*Papio anubis*	M	13.7	9.0	10.6	13.4	5.9	6.9	8.8	10.9	NA	4.3	NA	5.8
354988	*Papio anubis*	M	17.0	8.5	9.8	12.4	6.6	6.6	7.0	9.4	3.2	3.9	4.7	4.8
354989	*Papio anubis*	M	15.8	7.6	10.4	11.9	7.1	6.7	8.4	10.3	3.8	3.9	3.7	5.0
354992	*Papio anubis*	F	8.2	7.4	8.8	10.8	5.5	6.3	7.1	8.6	3.5	5.0	4.2	5.4
354993	*Papio anubis*	M	12.4	9.4	10.9	11.9	5.8	7.0	7.9	9.2	4.1	3.7	4.2	5.5
384219	*Papio anubis*	F	7.2	7.0	9.4	10.0	5.0	6.1	7.2	8.1	3.3	4.1	3.5	5.0
384220	*Papio anubis*	M	16.3	7.7	9.2	10.7	6.2	6.2	7.2	9.0	3.2	3.8	3.8	4.6
384222	*Papio anubis*	F	7.5	6.8	9.1	10.6	4.4	5.5	7.0	8.8	2.7	3.3	4.2	5.0
384223	*Papio anubis*	M	15.5	7.7	10.4	12.6	6.7	6.7	8.2	9.9	3.8	4.7	4.5	5.6

Postcanine measurements in extant primate sample, continued.

			Mesiodistal length (mm)				Buccolingual length (mm)				Intercusp distance (mm)			
ID	Taxon	Sex	P_3	P_4	M_1	M_2	P_3	P_4	M_1	M_2	P_3	P_4	M_1	M_2
384224	*Papio anubis*	F	8.1	7.8	9.4	10.2	5.1	6.4	7.2	8.1	3.7	4.3	4.4	4.9
384227	*Papio anubis*	F	9.8	7.1	9.4	11.3	5.5	6.0	7.5	9.6	3.6	3.4	4.9	5.8
384228	*Papio anubis*	F	10.2	7.4	9.8	12.9	6.1	6.6	7.4	10.4	NA	4.1	5.4	6.2
384230	*Papio anubis*	M	12.2	7.5	9.6	12.7	7.3	6.6	7.2	10.6	4.3	4.1	4.5	6.2
384234	*Papio anubis*	M	13.8	7.6	10.9	12.5	7.2	NA	8.0	10.1	4.3	4.5	4.5	5.6
384235	*Papio anubis*	F	8.9	7.7	9.3	10.5	5.5	6.7	6.9	8.5	4.6	4.1	4.4	5.1
384236	*Papio anubis*	F	13.7	8.1	9.7	13.5	6.2	6.5	7.2	10.2	3.8	4.3	4.8	5.7
395433	*Papio anubis*	M	14.0	8.0	9.9	12.8	7.4	6.8	7.5	10.4	4.3	4.5	4.9	6.1
395434	*Papio anubis*	M	15.5	9.8	12.2	14.5	8.2	8.5	9.4	NA	4.7	4.7	5.4	6.8
395436	*Papio anubis*	M	11.4	6.5	NA	10.1	5.8	5.6	6.6	8.8	NA	NA	3.7	4.5
395437	*Papio anubis*	M	14.1	8.7	9.9	11.9	7.2	7.2	8.2	10.1	3.6	4.2	4.3	5.3
395441	*Papio anubis*	F	7.7	7.6	10.2	11.4	5.5	6.2	6.9	9.2	3.2	4.1	3.8	4.4
1899.6.10.2	*Papio anubis*	M	11.8	8.3	10.6	12.2	6.6	7.2	7.8	9.9	3.4	4.3	4.3	5.6
1899.7.8.1	*Papio anubis*	M	13.0	6.9	9.3	11.2	5.9	6.6	7.1	9.8	3.2	4.0	5.1	5.1
1900.3.18.1	*Papio anubis*	M	15.4	9.0	11.5	13.0	6.3	7.4	8.6	10.2	4.6	5.1	4.3	5.7
1901.8.9.21	*Papio anubis*	M	10.2	8.5	10.4	12.3	6.2	7.2	8.0	10.8	4.1	4.7	4.4	6.2
1902.9.2.1	*Papio anubis*	M	14.4	9.9	11.8	13.9	8.5	8.3	9.5	12.4	4.4	5.0	5.2	6.1
1904.11.5.2	*Papio anubis*	M	14.2	8.0	9.9	12.6	6.7	6.4	8.5	10.5	3.6	4.0	4.6	6.3
1905.5.10.1	*Papio anubis*	M	15.4	10.1	11.2	13.1	7.5	7.7	8.4	10.9	3.6	5.2	4.7	6.0
1906.11.1.6	*Papio anubis*	M	13.9	9.1	10.8	12.9	6.5	7.3	8.3	10.7	2.7	4.3	4.6	5.6
1907.7.8.11	*Papio anubis*	M	14.3	8.1	10.9	12.7	7.1	7.0	8.0	10.8	3.4	5.1	4.4	5.5
1911.12.1.1	*Papio anubis*	M	10.8	8.0	10.4	12.8	7.2	7.1	8.0	10.9	3.8	4.3	4.3	5.7
1924.8.6.15	*Papio anubis*	M	15.4	9.8	11.7	13.4	8.1	7.7	8.6	11.2	3.9	4.6	5.0	5.2
1924.8.6.16	*Papio anubis*	F	9.1	7.7	9.6	11.3	5.3	6.5	7.6	9.3	2.5	4.7	3.8	4.5
1925.5.12.1	*Papio anubis*	M	13.4	9.1	9.8	12.1	6.0	7.4	8.6	10.3	2.8	4.7	4.6	5.7
1930.12.1.1	*Papio anubis*	M	12.7	8.8	11.2	14.1	6.1	7.2	9.1	12.3	2.6	4.5	4.6	5.4
1931.4.1.1	*Papio anubis*	M	16.4	10.3	11.2	13.5	7.0	8.2	9.2	11.4	3.0	4.4	4.9	5.5
1935.2.14.1	*Papio anubis*	M	10.9	9.0	11.3	11.9	6.3	7.6	9.3	10.7	3.5	5.1	4.9	5.2
1936.12.28.1	*Papio anubis*	M	15.9	8.3	10.2	12.7	6.8	7.3	7.7	10.8	2.6	5.1	5.0	6.0
1936.12.28.2	*Papio anubis*	M	13.4	8.3	10.6	12.1	5.9	7.0	7.8	9.9	2.3	5.5	4.6	5.1
37.19.19.77	*Papio anubis*	M	11.5	8.7	10.5	12.3	6.9	7.3	8.8	10.5	4.2	4.7	5.0	5.2
55.12.24.17	*Papio anubis*	M	12.6	10.1	11.7	12.6	8.1	NA	9.0	11.1	4.2	4.9	4.7	6.1
95.5.4.1	*Papio anubis*	M	12.3	8.8	9.9	11.3	5.7	6.6	7.7	9.3	3.5	4.5	4.2	5.1
1973.129	*Papio ursinus*	M	15.3	10.9	7.4	11.7	7.0	NA	8.2	10.1	4.8	4.4	3.7	5.8
1973.181	*Papio ursinus*	M	13.5	10.8	11.2	13.0	6.2	7.8	9.2	10.2	4.1	4.6	5.1	7.0
1973.1957	*Papio ursinus*	M	16.5	10.0	10.7	15.4	5.9	7.1	7.9	10.4	2.5	3.8	4.6	5.2
197162	*Papio ursinus*	M	16.1	9.7	11.3	13.4	6.3	7.5	8.3	10.6	3.7	4.1	5.0	5.8
197164	*Papio ursinus*	F	10.0	7.9	9.8	13.4	6.2	6.1	7.6	10.6	4.4	4.2	4.9	5.9
197171	*Papio ursinus*	M	16.5	9.8	11.3	11.4	6.5	7.7	9.0	9.5	3.2	5.3	4.3	5.3
197172	*Papio ursinus*	M	18.8	9.0	10.0	13.5	8.0	6.6	7.6	10.7	2.8	3.7	4.7	5.8
237320	*Papio ursinus*	M	16.7	10.3	11.2	13.3	7.3	7.3	9.5	11.1	3.1	NA	6.4	5.7
301518	*Papio ursinus*	F	8.6	8.1	10.1	12.7	5.5	6.6	7.3	9.6	3.6	4.1	3.4	5.1
337249	*Papio ursinus*	F	9.6	6.9	7.8	9.8	5.0	5.6	6.4	8.3	3.1	NA	3.6	5.4
337253	*Papio ursinus*	F	10.1	7.9	9.7	10.6	6.1	6.5	8.5	9.1	4.3	4.2	5.3	5.9
365737	*Papio ursinus*	M	18.5	8.8	9.8	12.9	7.8	7.2	7.9	10.5	3.2	4.4	5.6	5.1
367879	*Papio ursinus*	F	9.0	7.4	9.7	9.9	5.4	6.3	7.3	NA	3.4	3.9	3.9	4.1

Postcanine measurements in extant primate sample, continued.

			Mesiodistal length (mm)				Buccolingual length (mm)				Intercusp distance (mm)			
ID	Taxon	Sex	P_3	P_4	M_1	M_2	P_3	P_4	M_1	M_2	P_3	P_4	M_1	M_2
367883	*Papio ursinus*	M	19.4	9.9	9.6	13.1	7.6	6.1	7.8	10.6	NA	4.2	5.6	6.9
425420	*Papio ursinus*	M	12.9	10.6	11.6	13.3	7.8	7.2	8.0	10.9	NA	4.8	4.6	5.0
469923	*Papio ursinus*	M	18.7	11.2	11.2	13.4	7.7	7.3	9.1	11.4	4.3	5.1	5.1	6.1
586506	*Papio ursinus*	M	15.7	8.9	10.5	11.7	7.2	7.3	8.1	10.3	4.2	4.1	4.6	5.4
47.3.5.6	*Papio ursinus*	M	11.5	10.1	12.1	14.2	6.8	7.0	8.4	11.5	4.2	4.0	5.5	6.6
65.12.8.27	*Papio ursinus*	F	NA	7.8	9.1	10.7	NA	6.5	7.3	9.3	NA	3.2	3.6	5.0
143587	*Pongo abelii*	M	13.1	10.6	12.9	14.3	9.9	11.1	10.8	12.4	5.3	6.8	6.7	7.9
143588	*Pongo abelii*	M	14.7	10.6	11.5	13.2	10.2	10.4	10.9	12.5	5.9	5.8	5.9	6.2
143593	*Pongo abelii*	M	13.4	10.1	12.7	13.6	10.6	11.3	11.0	12.7	6.0	5.7	6.8	7.5
143594	*Pongo abelii*	M	11.2	10.4	12.9	13.8	9.7	10.8	11.8	12.4	6.4	7.8	7.0	8.0
143596	*Pongo abelii*	F	11.3	9.6	12.3	13.2	8.4	10.1	11.4	12.5	5.1	6.6	6.4	8.4
143597	*Pongo abelii*	F	11.6	8.1	10.6	11.2	8.0	9.0	9.8	10.7	6.3	6.1	7.6	7.4
143598	*Pongo abelii*	F	11.8	11.1	12.7	13.0	9.0	9.7	11.1	12.5	6.2	6.5	7.2	8.3
143600	*Pongo abelii*	F	11.5	9.2	11.3	12.3	7.6	9.5	9.1	10.8	4.7	5.5	6.4	7.0
143601	*Pongo abelii*	F	11.7	9.3	10.9	11.8	7.4	8.6	9.7	10.8	5.5	5.3	6.1	6.8
1939.1007	*Pongo pygmaeus*	F	12.6	11.4	13.5	14.4	11.6	11.0	11.9	12.8	5.6	6.5	6.9	7.5
1939.1008	*Pongo pygmaeus*	F	11.8	11.2	13.7	14.0	13.6	12.5	12.8	13.4	6.4	7.3	8.0	7.8
1976.1415	*Pongo pygmaeus*	F	12.2	10.7	12.6	13.7	10.3	10.7	11.2	11.6	5.3	5.3	6.1	6.1
1976.1416	*Pongo pygmaeus*	F	11.4	9.8	11.8	12.0	10.9	9.8	10.4	10.5	5.4	5.5	5.1	6.2
1976.1417	*Pongo pygmaeus*	F	11.4	8.4	10.6	11.3	9.5	9.3	10.2	10.3	5.5	5.2	5.1	6.0
1976.1419	*Pongo pygmaeus*	F	10.5	9.9	11.7	12.2	10.7	9.9	10.5	10.5	6.2	5.4	4.9	5.4
1976.142	*Pongo pygmaeus*	F	9.0	9.0	11.5	11.8	10.4	9.6	10.4	10.8	4.8	6.4	6.4	6.3
1976.1421	*Pongo pygmaeus*	F	11.6	9.3	11.8	12.2	10.8	10.7	11.1	11.8	5.0	6.4	6.0	6.6
1976.1424	*Pongo pygmaeus*	M	15.0	12.1	13.6	14.4	12.4	12.3	11.9	14.9	7.3	7.1	7.2	8.3
1976.1425	*Pongo pygmaeus*	M	13.0	10.5	13.4	14.6	12.4	11.6	12.3	13.5	6.7	6.5	6.3	7.2
1976.1428	*Pongo pygmaeus*	M	13.5	11.3	14.0	14.4	12.4	12.1	12.8	13.9	6.4	6.3	5.7	7.4
1976.1429	*Pongo pygmaeus*	M	13.3	10.3	12.4	13.4	10.4	10.9	11.0	11.4	7.2	6.4	6.1	6.8
1976.143	*Pongo pygmaeus*	F	11.8	9.7	12.4	13.3	10.3	10.7	11.5	12.4	5.6	6.6	7.1	7.2
1976.1434	*Pongo pygmaeus*	M	10.8	9.6	12.3	12.3	10.9	10.0	10.8	11.7	5.3	5.3	5.7	7.6
1976.1437	*Pongo pygmaeus*	M	11.8	11.3	12.9	14.7	10.9	11.3	11.7	12.7	6.3	6.1	5.8	7.0
1976.1439	*Pongo pygmaeus*	M	11.3	10.2	12.3	12.9	10.1	10.2	10.8	11.5	5.5	5.6	5.6	6.2
1976.1442	*Pongo pygmaeus*	M	11.5	10.5	13.6	15.2	11.9	11.0	12.2	13.5	6.7	7.0	7.2	8.0
1976.1443	*Pongo pygmaeus*	M	13.2	11.3	13.6	13.9	11.8	11.1	12.9	12.6	5.8	6.3	6.5	7.4
1986.1101	*Pongo pygmaeus*	F	11.1	9.7	12.1	11.4	9.0	9.4	11.0	10.5	4.7	4.7	5.8	5.9
1986.1112	*Pongo pygmaeus*	M	NA	NA	NA	NA	NA	NA	NA	NA	5.5	5.9	6.9	5.8
1986.1113	*Pongo pygmaeus*	F	13.7	10.4	12.1	12.8	10.6	10.0	11.0	11.2	6.5	5.9	6.8	7.1
1986.1118	*Pongo pygmaeus*	M	11.5	10.3	12.6	13.5	11.4	10.5	11.3	12.8	5.7	6.3	6.9	8.0
142169	*Pongo pygmaeus*	F	12.1	11.3	13.1	13.5	12.6	12.1	12.1	13.6	6.7	6.9	8.0	9.3
142188	*Pongo pygmaeus*	M	13.1	11.6	13.1	14.7	11.6	11.9	12.2	13.5	7.9	6.1	7.4	8.4
142195	*Pongo pygmaeus*	M	14.1	10.8	13.3	13.6	11.5	12.2	11.8	12.9	4.7	6.4	6.4	7.6
142196	*Pongo pygmaeus*	M	13.5	11.2	12.7	13.5	12.5	12.4	13.6	12.9	5.7	6.2	7.3	8.0
142200	*Pongo pygmaeus*	M	13.8	10.7	13.4	13.7	11.4	12.1	12.0	13.3	5.6	5.9	6.0	6.4
142202	*Pongo pygmaeus*	F	11.5	9.4	11.6	13.1	10.9	11.0	11.7	11.3	5.2	6.4	5.7	7.2
145309	*Pongo pygmaeus*	F	12.9	10.8	12.2	12.9	9.3	10.1	10.3	11.6	6.0	6.5	6.5	7.3
153806	*Pongo pygmaeus*	M	11.3	10.9	12.3	14.2	11.6	10.6	11.5	11.6	6.9	7.9	7.8	8.6
153810	*Pongo pygmaeus*	M	14.5	11.3	14.5	15.8	13.5	13.7	NA	14.1	5.7	7.5	8.4	9.4

Postcanine measurements in extant primate sample, continued.

			Mesiodistal length (mm)				Buccolingual length (mm)				Intercusp distance (mm)			
ID	Taxon	Sex	P_3	P_4	M_1	M_2	P_3	P_4	M_1	M_2	P_3	P_4	M_1	M_2
153832	*Pongo pygmaeus*	F	10.3	9.8	10.5	11.3	9.7	10.4	9.4	10.2	5.9	5.5	5.7	6.9
153833	*Pongo pygmaeus*	M	12.4	10.5	12.9	13.4	10.1	10.5	11.4	12.3	5.2	6.0	6.3	7.1
521078	*Pongo pygmaeus*	M	15.2	11.5	13.6	14.8	10.9	10.8	12.7	14.7	7.9	7.3	7.0	8.8
1844.3.30.18	*Pongo pygmaeus*	M	13.6	11.5	13.4	14.3	13.3	11.6	12.1	13.6	6.4	6.7	7.9	8.8
1856.11.8.2	*Pongo pygmaeus*	M	14.4	12.2	15.0	16.2	11.3	11.6	13.3	14.8	6.4	7.0	7.7	9.1
1868.4.16.2	*Pongo pygmaeus*	M	13.0	10.7	13.3	14.5	9.6	11.8	11.9	12.4	6.6	7.2	5.9	7.9
1879.11.21.213	*Pongo pygmaeus*	M	11.9	11.1	13.4	13.2	11.0	11.4	11.7	13.0	6.1	6.8	7.3	7.4
194331	*Saguinus fuscicollis*	F	1.9	1.9	2.5	2.2	2.0	1.9	2.0	1.8	1.0	1.0	1.3	NA
336299	*Saguinus fuscicollis*	F	1.8	1.9	2.3	2.1	1.8	1.9	2.0	1.7	0.9	1.2	1.0	0.9
336300	*Saguinus fuscicollis*	F	1.7	1.8	2.1	1.8	1.5	1.7	1.7	1.4	1.0	1.0	1.2	1.0
337331	*Saguinus fuscicollis*	F	1.7	1.8	2.1	2.0	1.7	1.8	1.7	1.5	1.2	1.2	0.9	1.0
397281	*Saguinus fuscicollis*	F	1.7	1.8	2.5	2.1	1.7	1.8	2.1	1.7	1.1	0.9	1.1	1.0
397284	*Saguinus fuscicollis*	F	2.0	2.1	2.5	2.3	1.9	1.8	2.1	1.9	1.1	1.2	1.0	0.9
397285	*Saguinus fuscicollis*	F	1.9	1.9	2.4	2.3	2.1	NA	2.4	1.8	1.2	1.4	1.1	1.0
397302	*Saguinus fuscicollis*	F	1.5	1.7	2.1	1.9	1.6	1.6	1.8	1.7	1.0	1.0	1.1	1.0
397659	*Saguinus fuscicollis*	M	2.0	2.0	2.3	2.2	1.7	1.7	2.1	1.6	0.9	0.8	0.9	1.0
398735	*Saguinus fuscicollis*	F	1.7	1.8	2.2	1.9	1.6	1.7	1.8	1.6	1.0	0.9	1.1	1.0
518576	*Saguinus fuscicollis*	F	1.9	1.8	2.3	1.9	1.9	1.8	2.1	1.6	0.9	0.9	1.1	1.0
518577	*Saguinus fuscicollis*	M	2.0	1.9	2.4	2.2	1.8	1.9	2.0	1.8	1.2	1.2	1.1	1.1
534806	*Saguinus fuscicollis*	F	NA	1.7	2.2	1.9	1.5	1.7	1.9	1.7	0.8	1.0	1.1	1.0
536709	*Saguinus fuscicollis*	M	1.9	2.0	2.2	1.9	1.8	1.7	1.8	1.6	1.0	1.0	1.0	0.9
170913	*Saguinus geoffroyi*	M	2.5	2.5	3.1	2.7	2.2	2.4	2.3	2.0	1.1	1.2	1.1	1.2
170914	*Saguinus geoffroyi*	F	2.2	2.3	2.9	2.2	2.1	2.4	2.1	1.7	1.2	1.3	1.3	1.0
170915	*Saguinus geoffroyi*	M	2.2	2.3	3.0	2.6	2.1	2.3	2.4	2.1	1.4	1.4	1.5	1.2
170916	*Saguinus geoffroyi*	F	2.2	2.2	2.6	2.3	2.0	2.3	2.6	1.8	1.4	1.5	1.4	1.2
200290	*Saguinus geoffroyi*	M	2.2	2.3	2.8	2.3	1.7	2.0	2.1	1.8	1.2	1.2	1.4	1.1
291244	*Saguinus geoffroyi*	F	2.2	2.4	3.0	2.5	2.1	2.3	NA	2.0	1.3	1.5	1.3	1.1
291245	*Saguinus geoffroyi*	F	NA	NA	3.0	2.6	2.3	2.4	2.3	1.9	1.4	1.4	1.6	1.2
296290	*Saguinus geoffroyi*	F	2.3	2.4	2.8	2.4	2.0	2.0	2.1	1.9	1.2	1.1	1.4	1.3
301398	*Saguinus geoffroyi*	F	2.1	2.0	2.7	2.6	2.0	2.2	2.1	1.9	1.1	1.3	1.2	1.3
301656	*Saguinus geoffroyi*	F	2.3	2.3	2.9	2.3	1.9	2.2	2.3	1.9	1.1	1.3	1.5	1.2
301657	*Saguinus geoffroyi*	F	2.1	2.0	2.8	2.5	2.2	2.4	2.5	1.9	1.3	1.3	1.0	1.2
302474	*Saguinus geoffroyi*	F	2.3	2.2	2.7	2.5	2.1	2.1	2.0	1.7	1.2	1.4	1.5	1.1
306836	*Saguinus geoffroyi*	M	2.2	2.2	2.9	2.3	2.0	2.3	2.6	2.0	1.2	1.2	1.4	1.2
306838	*Saguinus geoffroyi*	M	2.0	2.1	2.6	2.3	1.8	2.2	2.3	1.8	1.4	1.3	1.3	1.1
306840	*Saguinus geoffroyi*	M	2.3	2.3	2.9	2.3	2.2	2.2	2.1	1.7	1.2	1.2	1.2	1.1
306841	*Saguinus geoffroyi*	M	2.1	2.1	2.7	2.3	2.0	2.0	2.0	1.8	1.4	1.4	1.4	1.1
306843	*Saguinus geoffroyi*	M	2.3	2.4	NA	2.5	2.4	2.4	2.5	2.1	1.2	1.4	1.4	1.0
306844	*Saguinus geoffroyi*	M	1.9	2.3	2.8	2.3	2.2	2.1	2.2	1.9	1.2	1.2	1.2	1.1
306845	*Saguinus geoffroyi*	M	1.9	2.3	2.8	2.3	2.2	2.1	2.2	1.9	1.3	1.4	1.4	1.3
310344	*Saguinus geoffroyi*	M	1.9	2.2	2.6	NA	2.0	2.1	2.2	NA	1.4	1.2	1.0	NA
310345	*Saguinus geoffroyi*	F	2.4	2.3	2.8	2.2	2.1	2.2	2.3	1.8	1.4	1.5	1.4	1.0
310346	*Saguinus geoffroyi*	M	2.2	2.3	2.8	2.3	2.1	2.1	2.4	1.9	1.4	1.4	1.1	1.1
310347	*Saguinus geoffroyi*	M	2.4	2.5	3.0	2.6	2.2	2.3	2.4	2.0	1.5	1.2	1.1	1.2
310348	*Saguinus geoffroyi*	M	2.3	2.2	2.7	2.5	1.9	2.2	2.4	2.0	1.2	1.3	1.2	1.1
310349	*Saguinus geoffroyi*	F	2.2	2.2	2.7	2.3	2.0	2.0	2.2	1.9	1.4	1.4	1.2	1.2

Postcanine measurements in extant primate sample, continued.

			Mesiodistal length (mm)				Buccolingual length (mm)				Intercusp distance (mm)			
ID	Taxon	Sex	P_3	P_4	M_1	M_2	P_3	P_4	M_1	M_2	P_3	P_4	M_1	M_2
335456	*Saguinus geoffroyi*	F	2.4	2.3	2.9	2.4	2.0	2.3	2.2	1.7	1.4	1.2	1.2	1.1
335457	*Saguinus geoffroyi*	M	2.3	2.2	2.8	2.1	1.9	2.2	2.3	1.7	1.5	1.3	1.2	1.1
335462	*Saguinus geoffroyi*	M	2.4	2.3	2.9	2.7	2.2	2.3	2.4	2.0	1.6	1.6	1.7	NA
363152	*Saguinus geoffroyi*	M	2.2	2.2	2.8	2.4	2.1	2.0	2.2	1.7	1.3	1.4	1.2	1.1
397249	*Saguinus geoffroyi*	M	2.3	2.1	2.8	2.4	2.5	2.3	2.2	1.8	1.4	1.3	1.0	NA
398815	*Saguinus labiatus*	F	1.8	2.0	2.2	NA	1.8	1.9	NA	1.6	1.1	0.8	1.0	0.9
398816	*Saguinus labiatus*	M	2.0	2.0	2.4	2.4	2.1	2.1	2.1	1.8	NA	NA	NA	NA
398817	*Saguinus labiatus*	M	2.2	2.2	2.4	2.3	1.9	2.0	2.1	1.8	1.1	1.0	1.1	1.0
398818	*Saguinus labiatus*	M	1.9	2.1	2.6	2.2	2.0	1.9	2.0	1.7	NA	NA	NA	NA
398819	*Saguinus labiatus*	F	2.1	2.2	2.2	2.2	1.9	1.9	2.1	1.8	0.9	1.1	1.2	1.1
398820	*Saguinus labiatus*	F	2.0	2.0	2.3	2.2	1.9	1.9	1.9	1.7	NA	NA	NA	NA
398821	*Saguinus labiatus*	F	2.2	2.3	2.5	2.4	2.1	2.1	2.2	1.9	1.2	1.3	1.2	NA
398822	*Saguinus labiatus*	M	2.0	2.0	2.5	2.2	1.7	1.8	1.9	1.7	1.1	1.0	1.3	1.0
398823	*Saguinus labiatus*	M	2.1	1.9	2.3	2.3	1.9	2.0	2.1	1.9	NA	NA	NA	NA
398824	*Saguinus labiatus*	M	2.0	2.0	2.5	2.0	1.8	1.9	2.1	1.6	1.0	1.1	0.9	1.0
398825	*Saguinus labiatus*	M	2.1	2.2	2.5	2.3	1.9	1.9	2.0	1.8	1.2	1.2	1.0	1.0
398826	*Saguinus labiatus*	M	1.9	2.1	2.5	2.3	1.8	1.8	2.1	1.8	1.0	1.0	1.2	1.0
464971	*Saguinus labiatus*	F	1.9	2.0	2.5	2.2	1.8	1.7	2.1	1.8	1.1	1.1	NA	NA
522949	*Saguinus labiatus*	F	2.1	2.3	2.6	2.4	1.9	1.9	2.1	1.7	1.1	1.2	1.2	1.0
522950	*Saguinus labiatus*	M	1.7	2.2	2.3	2.3	2.0	1.8	2.2	2.0	0.9	NA	1.1	NA
397242	*Saguinus mystax*	M	2.2	2.2	2.6	2.4	2.0	1.9	2.4	2.0	1.4	1.3	1.3	1.0
397870	*Saguinus mystax*	F	2.4	2.5	2.7	2.6	2.2	2.0	2.4	2.3	1.1	1.2	1.3	1.2
397871	*Saguinus mystax*	F	2.5	NA	2.7	2.5	2.0	2.1	2.3	2.3	1.1	1.1	1.3	1.0
397873	*Saguinus mystax*	M	2.3	2.1	2.4	2.2	2.2	2.4	2.2	1.9	0.9	1.1	1.2	0.9
397876	*Saguinus mystax*	M	2.2	2.3	2.7	2.5	2.0	2.1	2.3	2.3	0.8	1.0	1.1	0.8
397877	*Saguinus mystax*	M	2.3	2.2	2.5	2.3	1.7	1.9	2.3	1.9	0.9	1.0	NA	1.0
397880	*Saguinus mystax*	F	2.2	2.0	2.6	2.6	1.9	2.2	2.3	2.0	1.1	1.1	1.2	1.0
397930	*Saguinus mystax*	F	2.1	2.3	2.7	2.3	1.8	2.1	2.3	2.1	1.0	1.1	1.4	1.1
399077	*Saguinus mystax*	F	2.2	2.1	2.5	2.4	1.9	1.9	2.1	2.1	0.9	1.0	1.1	1.2
399078	*Saguinus mystax*	M	2.0	2.2	2.6	2.5	1.8	1.9	2.1	2.0	1.0	1.2	1.1	NA
399079	*Saguinus mystax*	M	2.2	2.2	2.6	2.5	1.8	1.9	2.1	1.9	1.1	1.1	1.2	1.2
518582	*Saguinus mystax*	M	2.2	2.2	2.7	2.7	2.0	2.0	2.3	2.1	1.2	1.1	1.2	1.2
518584	*Saguinus mystax*	M	NA	2.1	2.4	2.3	1.7	2.0	2.1	1.8	1.1	1.1	1.1	1.1
543489	*Saguinus mystax*	F	2.4	2.4	2.8	2.7	1.9	2.0	2.3	2.1	1.3	1.2	1.3	1.3

Appendix 2 Character displacement model.

The following R script can determine the probability that sympatry contributes to the observed shape divergence between two taxa. It is modified from codes by Collyer and Adams, (2007) and details of its application can be found within the associated chapter. Output (i.e., y variables) should be comprised of three highly informative morphological traits or principal components. Input (i.e., x variables) should be coded as 1 and -1 in the taxon column, which denotes the two different taxa, and 1 and -1 in the location column, which denotes sympatry or allopatry, respectively. This codes for the four different groups (1,1; 1,-1; -1,1; -1,-1). The X -matrix should include an intercept of 1 for all values in the first column and an interaction variable (taxon x location) in the fourth column. From an example dataset, Y- and X- matrices would look like:

	Y-matrix			X-matrix			
Specimen	Trait1	Trait2	Trait3	Intercept	Species	Location	Interaction
Species A, sympatric	4.5	5.5	6.2	1	1	1	1
Species A, sympatric	5.3	5.7	6.0	1	1	1	1
Species A, allopatric	5.1	5.5	5.9	1	1	-1	-1
Species B, sympatric	4.2	4.7	6.0	1	-1	1	-1
…	…	…	…	…	…	…	…

After setting up the data matrices, the script is:

#Read in matrices, replacing ### with the appropriate file names and row dimensions.

```
y.mat<-read.csv("###.csv",header=T)
x.mat<-read.csv("###.csv",header=T)
y.mat<-as.matrix(y.mat)
dim(y.mat)<-c(###,3)
x.mat<-as.matrix(x.mat)
dim(x.mat)<-c(###,4)
```

#Remove the interaction variable to free taxon and location in the resampling analysis. All variables for this analysis will be denoted by “res.”

```
x.mat.res<-x.mat[,-4]

#Estimate parameters (i.e., matrix coefficients).  Note that y variables are held constant in
both the observed and resampled analyses.

b.mat<-solve((t(x.mat)%*%x.mat))%*%(t(x.mat)%*%y.mat)
b.mat.res<-solve((t(x.mat.res)%*%x.mat.res))%*%(t(x.mat.res)%*%y.mat)


#Project least-squares means for groups.  The first species is noted by "a," the second
species by "b", the sympatric location by "1", and both allopatric locations by "2."

a1b1<-cbind(1,1,1,1)
a1b2<-cbind(1,1,-1,-1)
a2b1<-cbind(1,-1,1,-1)
a2b2<-cbind(1,-1,-1,1)
x.ls<-rbind(a1b1,a1b2,a2b1,a2b2)

obs.ls<-x.ls%*%b.mat

#Repeat in preparation for resampling.
x.ls.res<-x.ls[,-4]
obs.ls.res<-x.ls.res%*%b.mat.res

#Contrast the means of the sympatric taxa with the allopatric taxa.

obs.b1.vector<-obs.ls[1,]-obs.ls[3,]
obs.b2.vector<-obs.ls[2,]-obs.ls[4,]
obs.b1.length<-sqrt(t(obs.b1.vector)%*%obs.b1.vector)
obs.b2.length<-sqrt(t(obs.b2.vector)%*%obs.b2.vector)
obs.contrast<-abs(obs.b1.length-obs.b2.length)

#Set-up resampling procedure.  Note that "y.hat" denotes the predicted values from the
reduced model, while y.mat is held constant from the observed values.  "y.mat.resid"
therefore denotes the residuals of these matrices.  It is the residuals that will be randomly
assigned in the following permutations.  The prefix "p" denotes that the value will be
used in probability assessment.

y.hat<-x.mat.res%*%b.mat.res
y.mat.resid<-y.mat-y.hat

permute<-999

dist.b1.length<-NULL
```

```
dist.b1.length<-rbind(dist.b1.length,obs.b1.length)
dist.b2.length<-NULL
dist.b2.length<-rbind(dist.b2.length,obs.b2.length)
dist.contrast<-NULL
dist.contrast<-rbind(dist.contrast,obs.contrast)
pdist.contrast<-NULL
pdist.contrast<-rbind(pdist.contrast,1)

line<-array(1:(length(x.mat[,1])),dim=c(length(x.mat[,1])))
for(i in 1:permute){
#Randomize the residuals.

line.rand<-sample(line,replace=FALSE)
y.res.temp<-cbind(line.rand,y.mat.resid)
z<-(order(line.rand))
y.res.temp2<-as.matrix(y.res.temp[z,])
y.res.rand<-y.res.temp2[,-1]

#Generate resampled values and calculate means.

y.rand<-y.hat+y.res.rand
b.mat.rand<-solve((t(x.mat)%*%x.mat))%*%(t(x.mat)%*%y.rand)
random.ls<-x.ls%*%b.mat.rand

#Repeat produce for contrasting means for the resampled values.

resample.b1.vector<-random.ls[1,]-random.ls[3,]
resample.b2.vector<-random.ls[2,]-random.ls[4,]
resample.b1.length<-sqrt(t(resample.b1.vector)%*%resample.b1.vector)
resample.b2.length<-sqrt(t(resample.b2.vector)%*%resample.b2.vector)
resample.contrast<-abs(resample.b1.length-resample.b2.length)

#Attach the distributions.

dist.b1.length<-rbind(dist.b1.length,resample.b1.length)
dist.b2.length<-rbind(dist.b2.length,resample.b2.length)
dist.contrast<-rbind(dist.contrast,resample.contrast)

#Determine whether the resampled contrasts are equal to, less than, or greater than the
observed contrast.

code<-ifelse(resample.contrast>=obs.contrast,1,0)
pdist.contrast<-rbind(pdist.contrast,code)}
```

```
#Determine the empirical probability of finding the observed value or greater from these data.

p.contrast<-sum(pdist.contrast)/(permute+1)

#Report and save the observed and resampled contrasts.  Be sure to indicate a destination file.

out.head<-cbind("iteration","b1","b2","abs_diff")
iter<-array(1:permute)
iter.lab<-"observed"
iter.lab<-append(iter.lab,iter)
#Character displacement model, continued.

out.mat<-cbind(iter.lab,dist.b1.length,dist.b2.length,dist.contrast)
out.mat<-rbind(out.head,out.mat)
write.csv(out.mat,file="###.csv",row.names=FALSE)

#Generate a text summary of analysis (optional).  Be sure to indicate a destination file.

result1<-"The length of vector b1, which approximates the difference between a
sympatric population of two taxa, is "
result1<-append(result1,obs.b1.length)
result2<-"The length of vector b2, which approximates the difference between allopatric
populations of two taxa, is "
result2<-append(result2,obs.b2.length)
result3<-"The absolute difference between these lengths is |b1 - b2|= "
result3<-append(result3,obs.contrast)
result4<-"The residuals produced by these populations were resampled this many times: "
result4<-append(result4, permute)
result5<-"Based on this resampling, the probability of randomly observing this difference
or a greater difference is P= "
result5<-append(result5,p.contrast)
result<-rbind(result1,result2,result3,result4,result5)
write.table(result,file="###.txt",row.names=FALSE,col.names=FALSE,quote=FALSE)
```

Appendix 3 Matrices for assessment of character displacement.

Listed here are the Y- and X-matrices for the extant primates and fossil hominins used in the analysis. The Y-matrix is listed first and includes log-transformed measures of P_4 area, mesiodistal length and buccolingual length. These columns are followed by the x-matrix (i.e., design matrix) of ecological variables. I is a standard intercept, T is the code for taxon (1 or -1, see text), L is the code for sympatric or allopatric location (1 or -1, see text), and IV is the interaction variable (see text).

A) African apes

		Y-matrix			X-matrix			
ID	Taxon	logarea	logmd	logbl	I	T	L	IV
176207	*Gorilla gorilla*	2.04	1.00	1.06	1	1	1	1
176208	*Gorilla gorilla*	2.05	1.07	1.04	1	1	1	1
176209	*Gorilla gorilla*	2.06	1.05	1.09	1	1	1	1
176211	*Gorilla gorilla*	2.14	1.07	1.11	1	1	1	1
176216	*Gorilla gorilla*	2.02	1.04	1.08	1	1	1	1
1936.7.14.1	*Gorilla gorilla*	2.14	1.06	1.14	1	1	1	1
1939.914	*Gorilla gorilla*	2.02	1.05	1.01	1	1	1	1
1948.435	*Gorilla gorilla*	2.02	1.02	1.08	1	1	1	1
174712	*Gorilla gorilla*	1.98	1.01	1.04	1	1	1	1
174715	*Gorilla gorilla*	1.99	1.01	1.08	1	1	1	1
174720	*Gorilla gorilla*	2.07	1.01	1.08	1	1	1	1
197037	*Gorilla gorilla*	2.00	1.01	1.00	1	1	1	1
220324	*Gorilla gorilla*	2.07	1.05	1.08	1	1	1	1
1939.919	*Gorilla gorilla*	2.11	1.06	1.08	1	1	1	1
1939.920	*Gorilla gorilla*	2.02	1.06	1.11	1	1	1	1
1939.927	*Gorilla gorilla*	2.02	1.01	1.09	1	1	1	1
1939.933	*Gorilla gorilla*	1.96	0.98	1.01	1	1	1	1
1939.934	*Gorilla gorilla*	2.06	1.04	1.08	1	1	1	1
1939.936	*Gorilla gorilla*	2.00	1.03	1.08	1	1	1	1
1986.534	*Gorilla gorilla*	2.04	1.03	1.03	1	1	1	1
1986.535	*Gorilla gorilla*	2.06	1.03	1.10	1	1	1	1
1986.540	*Gorilla gorilla*	1.95	0.98	0.99	1	1	1	1
252577	*Gorilla gorilla*	1.96	1.02	1.01	1	1	1	1
1923.11.29.4	*Gorilla gorilla*	2.04	1.11	1.05	1	1	1	1
395636	*Gorilla beringei*	1.71	0.89	0.91	1	1	-1	-1
396934	*Gorilla beringei*	1.71	0.89	0.91	1	1	-1	-1
396935	*Gorilla beringei*	1.71	0.89	0.91	1	1	-1	-1
396936	*Gorilla beringei*	1.71	0.89	0.91	1	1	-1	-1

A) African apes, continued.

		Y-matrix			X-matrix			
ID	Taxon	logarea	logmd	logbl	I	T	L	IV
396942	*Gorilla beringei*	1.71	0.89	0.91	1	1	-1	-1
397356	*Gorilla beringei*	1.71	0.89	0.91	1	1	-1	-1
545027	*Gorilla beringei*	1.71	0.89	0.91	1	1	-1	-1
545028	*Gorilla beringei*	1.71	0.89	0.91	1	1	-1	-1
545030	*Gorilla beringei*	1.71	0.89	0.91	1	1	-1	-1
545031	*Gorilla beringei*	1.71	0.89	0.91	1	1	-1	-1
545032	*Gorilla beringei*	1.71	0.89	0.91	1	1	-1	-1
545034	*Gorilla beringei*	1.71	0.89	0.91	1	1	-1	-1
545036	*Gorilla beringei*	1.71	0.89	0.91	1	1	-1	-1
1922.2.10.2	*Gorilla beringei*	1.71	0.89	0.91	1	1	-1	-1
1939.3369	*Pan t. troglodytes*	1.76	0.91	0.91	1	-1	1	-1
1939.3383	*Pan t. troglodytes*	1.74	0.86	0.96	1	-1	1	-1
176226	*Pan t. troglodytes*	1.67	0.84	0.89	1	-1	1	-1
176243	*Pan t. troglodytes*	1.74	0.92	0.91	1	-1	1	-1
1924.8.6.1	*Pan t. troglodytes*	1.75	0.89	0.90	1	-1	1	-1
1936.7.7.2	*Pan t. troglodytes*	1.80	0.91	0.96	1	-1	1	-1
1939.3363	*Pan t. troglodytes*	1.76	0.92	0.94	1	-1	1	-1
1939.3364	*Pan t. troglodytes*	1.73	0.89	0.92	1	-1	1	-1
1939.3365	*Pan t. troglodytes*	1.72	0.87	0.93	1	-1	1	-1
174701	*Pan t. troglodytes*	1.59	0.81	0.88	1	-1	1	-1
174703	*Pan t. troglodytes*	1.76	0.93	0.95	1	-1	1	-1
174704	*Pan t. troglodytes*	1.68	0.86	0.90	1	-1	1	-1
174707	*Pan t. troglodytes*	1.63	0.84	0.88	1	-1	1	-1
220062	*Pan t. troglodytes*	1.68	0.87	0.88	1	-1	1	-1
220064	*Pan t. troglodytes*	1.73	0.90	0.95	1	-1	1	-1
220327	*Pan t. troglodytes*	1.73	0.87	0.94	1	-1	1	-1
1864.12.1.7	*Pan t. troglodytes*	1.72	0.92	0.87	1	-1	1	-1
481804	*Pan t. verus*	1.69	0.87	0.90	1	-1	-1	1
1950.1863	*Pan t. verus*	1.77	0.89	0.97	1	-1	-1	1
20.4.13.2	*Pan t. schweinfurthi*	1.72	0.89	0.93	1	-1	-1	1
22.12.19.1	*Pan t. schweinfurthi*	1.80	0.97	0.94	1	-1	-1	1
22.12.19.2	*Pan t. schweinfurthi*	1.71	0.89	0.91	1	-1	-1	1

B) Asian apes

		Y-matrix			X-matrix			
ID	Taxon	logarea	logmd	logbl	I	T	L	IV
113177	*Hylobates agilis*	1.18	0.64	0.64	1	1	1	1
123151	*Hylobates agilis*	1.12	0.63	0.63	1	1	1	1
123154	*Hylobates agilis*	1.14	0.66	0.66	1	1	1	1
123155	*Hylobates agilis*	1.18	0.65	0.61	1	1	1	1
143576	*Hylobates agilis*	1.10	0.65	0.60	1	1	1	1
144089	*Hylobates agilis*	1.19	0.70	0.61	1	1	1	1
144090	*Hylobates agilis*	1.18	0.64	0.63	1	1	1	1
144091	*Hylobates agilis*	1.13	0.60	0.65	1	1	1	1
1955.148	*Hylobates agilis*	1.26	0.67	0.70	1	1	1	1
1955.149	*Hylobates agilis*	1.28	0.71	0.66	1	1	1	1
1955.149	*Hylobates agilis*	1.23	0.68	0.61	1	1	1	1
1955.149	*Hylobates agilis*	1.08	0.59	0.59	1	1	1	1
1860.5.4.47	*Hylobates agilis*	1.24	0.68	0.65	1	1	1	1
1879.9.15.1	*Hylobates agilis*	1.17	0.70	0.61	1	1	1	1
145326	*Hylobates agilis*	1.25	0.68	0.57	1	1	1	1
145329	*Hylobates agilis*	1.09	0.63	0.60	1	1	1	1
A49657	*Hylobates agilis*	1.05	0.60	0.58	1	1	1	1
12.2.2.1	*Hylobates klossii*	1.20	0.64	0.56	1	1	-1	-1
121675	*Hylobates klossii*	1.17	0.62	0.54	1	1	-1	-1
121680	*Hylobates klossii*	1.26	0.66	0.60	1	1	-1	-1
122176	*Hylobates klossii*	1.28	0.68	0.60	1	1	-1	-1
252307	*Hylobates klossii*	1.23	0.66	0.56	1	1	-1	-1
252309	*Hylobates klossii*	1.24	0.68	0.56	1	1	-1	-1
252310	*Hylobates klossii*	1.34	0.72	0.62	1	1	-1	-1
A49656	*Hylobates klossii*	1.23	0.66	0.57	1	1	-1	-1
1939.101	*Pongo pygmaeus*	2.07	1.05	1.10	1	-1	1	-1
1939.101	*Pongo pygmaeus*	1.98	1.03	1.03	1	-1	1	-1
1976.142	*Pongo pygmaeus*	1.90	0.99	0.99	1	-1	1	-1
1976.142	*Pongo pygmaeus*	1.81	0.92	0.97	1	-1	1	-1
1976.142	*Pongo pygmaeus*	1.89	1.00	0.99	1	-1	1	-1
1976.142	*Pongo pygmaeus*	1.85	0.95	0.98	1	-1	1	-1
1976.1420	*Pongo pygmaeus*	1.92	0.97	1.03	1	-1	1	-1
1976.142	*Pongo pygmaeus*	2.09	1.08	1.09	1	-1	1	-1
1976.142	*Pongo pygmaeus*	2.03	1.02	1.07	1	-1	1	-1
1976.143	*Pongo pygmaeus*	2.05	1.05	1.08	1	-1	1	-1
1976.143	*Pongo pygmaeus*	1.98	1.01	1.04	1	-1	1	-1

B) Asian apes, continued.

		Y-matrix			X-matrix			
ID	Taxon	logarea	logmd	logbl	I	T	L	IV
1976.143	*Pongo pygmaeus*	1.95	0.99	1.03	1	-1	1	-1
1976.1430	*Pongo pygmaeus*	1.91	0.98	1.00	1	-1	1	-1
1976.143	*Pongo pygmaeus*	2.01	1.05	1.05	1	-1	1	-1
1976.144	*Pongo pygmaeus*	1.95	1.01	1.01	1	-1	1	-1
1976.144	*Pongo pygmaeus*	2.01	1.02	1.04	1	-1	1	-1
1976.144	*Pongo pygmaeus*	2.04	1.05	1.04	1	-1	1	-1
1976.144	*Pongo pygmaeus*	1.88	0.99	0.97	1	-1	1	-1
1986.11	*Pongo pygmaeus*	1.94	1.02	1.00	1	-1	1	-1
1986.111	*Pongo pygmaeus*	1.98	1.01	1.02	1	-1	1	-1
1986.112	*Pongo pygmaeus*	2.08	1.05	1.08	1	-1	1	-1
142169	*Pongo pygmaeus*	2.05	1.06	1.07	1	-1	1	-1
142188	*Pongo pygmaeus*	2.04	1.03	1.08	1	-1	1	-1
142195	*Pongo pygmaeus*	2.08	1.05	1.09	1	-1	1	-1
142196	*Pongo pygmaeus*	2.01	1.03	1.08	1	-1	1	-1
142200	*Pongo pygmaeus*	1.91	0.97	1.04	1	-1	1	-1
142202	*Pongo pygmaeus*	1.95	1.03	1.01	1	-1	1	-1
145309	*Pongo pygmaeus*	2.00	1.04	1.02	1	-1	1	-1
153806	*Pongo pygmaeus*	2.05	1.05	1.14	1	-1	1	-1
153810	*Pongo pygmaeus*	1.91	0.99	1.02	1	-1	1	-1
153832	*Pongo pygmaeus*	1.96	1.02	1.02	1	-1	1	-1
153833	*Pongo pygmaeus*	2.09	1.06	1.03	1	-1	1	-1
521078	*Pongo pygmaeus*	2.03	1.06	1.06	1	-1	1	-1
1844.3.30.18	*Pongo pygmaeus*	2.08	1.09	1.06	1	-1	1	-1
1856.11.8.2	*Pongo pygmaeus*	2.02	1.03	1.07	1	-1	1	-1
1868.4.16.2	*Pongo pygmaeus*	2.00	1.05	1.06	1	-1	1	-1
1879.11.21.213	*Pongo abelii*	1.96	1.03	1.04	1	-1	-1	1
143588	*Pongo abelii*	1.98	1.02	1.02	1	-1	-1	1
143593	*Pongo abelii*	1.97	1.01	1.05	1	-1	-1	1
143594	*Pongo abelii*	1.96	1.02	1.03	1	-1	-1	1
143596	*Pongo abelii*	1.91	0.98	1.01	1	-1	-1	1
143597	*Pongo abelii*	1.89	0.91	0.96	1	-1	-1	1
143598	*Pongo abelii*	1.94	1.05	0.99	1	-1	-1	1
143600	*Pongo abelii*	1.95	0.96	0.98	1	-1	-1	1
143601	*Pongo abelii*	1.84	0.97	0.93	1	-1	-1	1

C) Macaques

		Y-matrix			X-matrix			
ID	Taxon	logarea	logmd	logbl	I	T	L	IV
101666	*Macaca fascicularis*	1.14	0.66	0.56	1	1	1	1
101711	*Macaca fascicularis*	1.25	0.69	0.62	1	1	1	1
114411	*Macaca fascicularis*	1.22	0.71	0.69	1	1	1	1
114643	*Macaca fascicularis*	1.25	0.75	0.65	1	1	1	1
121802	*Macaca fascicularis*	1.12	0.64	0.67	1	1	1	1
121803	*Macaca fascicularis*	1.24	0.69	0.64	1	1	1	1
121869	*Macaca fascicularis*	1.12	0.63	0.56	1	1	1	1
121871	*Macaca fascicularis*	1.11	0.64	0.65	1	1	1	1
143583	*Macaca fascicularis*	1.15	0.64	0.68	1	1	1	1
156456	*Macaca fascicularis*	1.24	0.72	0.70	1	1	1	1
1909.4.1.24	*Macaca fascicularis*	1.08	0.64	0.52	1	1	1	1
1909.4.1.25	*Macaca fascicularis*	1.11	0.65	0.53	1	1	1	1
1909.4.1.29	*Macaca fascicularis*	1.16	0.68	0.58	1	1	1	1
1909.4.1.31	*Macaca fascicularis*	1.10	0.63	0.55	1	1	1	1
1909.4.1.37	*Macaca fascicularis*	1.06	0.63	0.52	1	1	1	1
1939.893	*Macaca fascicularis*	1.23	0.70	0.61	1	1	1	1
1955.1509	*Macaca fascicularis*	1.32	0.74	0.64	1	1	1	1
1955.1511	*Macaca fascicularis*	1.24	0.70	0.67	1	1	1	1
1955.1528	*Macaca fascicularis*	1.28	0.74	0.66	1	1	1	1
83273	*Macaca fascicularis*	1.33	0.78	0.75	1	1	1	1
123992	*Macaca fascicularis*	1.29	0.73	0.62	1	1	1	1
1914.8.22.3	*Macaca fascicularis*	1.35	0.72	0.69	1	1	1	1
1914.8.22.4	*Macaca fascicularis*	1.24	0.69	0.62	1	1	1	1
1924.9.2.8	*Macaca fascicularis*	1.19	0.68	0.62	1	1	1	1
1939.180	*Macaca fascicularis*	1.26	0.71	0.61	1	1	1	1
1939.181	*Macaca fascicularis*	1.26	0.73	0.63	1	1	1	1
1955.1512	*Macaca fascicularis*	1.04	0.63	0.55	1	1	1	1
1955.1515	*Macaca fascicularis*	1.15	0.67	0.59	1	1	1	1
1955.1519	*Macaca fascicularis*	1.30	0.74	0.63	1	1	1	1
1955.1520	*Macaca fascicularis*	1.24	0.65	0.61	1	1	1	1
1955.1521	*Macaca fascicularis*	1.15	0.71	0.58	1	1	1	1
1909.11.1.1	*Macaca fascicularis*	1.30	0.71	0.69	1	1	1	1
1914.12.8.15	*Macaca fascicularis*	1.38	0.77	0.70	1	1	1	1
1914.12.8.17	*Macaca fascicularis*	1.29	0.72	0.65	1	1	1	1
1934.7.18.2	*Macaca fascicularis*	1.14	0.65	0.57	1	1	1	1
1934.7.18.5	*Macaca fascicularis*	1.23	0.73	0.64	1	1	1	1

C) Macaques, continued.

		Y-matrix			X-matrix			
ID	Taxon	logarea	logmd	logbl	I	T	L	IV
1936.9.10.11	*Macaca fascicularis*	1.36	0.73	0.72	1	1	1	1
1936.9.10.4	*Macaca fascicularis*	1.36	0.78	0.66	1	1	1	1
1936.9.10.5	*Macaca fascicularis*	1.38	0.79	0.66	1	1	1	1
1936.9.10.6	*Macaca fascicularis*	1.42	0.73	0.75	1	1	1	1
1939.1050	*Macaca fuscata*	1.51	0.79	0.74	1	1	-1	-1
174730	*Macaca fuscata*	1.24	0.69	0.60	1	1	-1	-1
344996	*Macaca fuscata*	1.46	0.81	0.73	1	1	-1	-1
1905.11.3.1	*Macaca fuscata*	1.29	0.74	0.61	1	1	-1	-1
1905.11.3.2	*Macaca fuscata*	1.40	0.79	0.67	1	1	-1	-1
1905.11.3.3	*Macaca fuscata*	1.40	0.74	0.70	1	1	-1	-1
1905.11.3.4	*Macaca fuscata*	1.35	0.71	0.72	1	1	-1	-1
1905.11.3.5	*Macaca fuscata*	1.23	0.73	0.73	1	1	-1	-1
1906.1.4.2	*Macaca fuscata*	1.44	0.81	0.70	1	1	-1	-1
1906.1.4.3	*Macaca fuscata*	1.52	0.82	0.80	1	1	-1	-1
42.1.19.45	*Macaca fuscata*	1.35	0.71	0.71	1	1	-1	-1
49691	*Macaca nemestrina*	1.46	0.82	0.73	1	-1	1	-1
49696	*Macaca nemestrina*	1.11	0.63	0.59	1	-1	1	-1
49874	*Macaca nemestrina*	1.47	0.84	0.71	1	-1	1	-1
114502	*Macaca nemestrina*	1.47	0.82	0.70	1	-1	1	-1
123143	*Macaca nemestrina*	1.48	0.82	0.75	1	-1	1	-1
123144	*Macaca nemestrina*	1.40	0.83	0.72	1	-1	1	-1
123145	*Macaca nemestrina*	1.37	0.85	0.66	1	-1	1	-1
142227	*Macaca nemestrina*	1.47	0.86	0.72	1	-1	1	-1
142228	*Macaca nemestrina*	1.40	0.79	0.70	1	-1	1	-1
144093	*Macaca nemestrina*	1.44	0.81	0.73	1	-1	1	-1
144094	*Macaca nemestrina*	1.45	0.80	0.74	1	-1	1	-1
153804	*Macaca nemestrina*	1.41	0.83	0.69	1	-1	1	-1
154367	*Macaca nemestrina*	1.49	0.82	0.67	1	-1	1	-1
199165	*Macaca nemestrina*	1.43	0.82	0.68	1	-1	1	-1
399506	*Macaca nemestrina*	1.44	0.77	0.70	1	-1	1	-1
1923.1.6.77	*Macaca nemestrina*	1.34	0.75	0.66	1	-1	1	-1
1938.11.30.6	*Macaca nemestrina*	1.56	0.81	0.82	1	-1	1	-1
1955.1504	*Macaca nemestrina*	1.27	0.84	0.77	1	-1	1	-1
1955.1505	*Macaca nemestrina*	1.37	0.80	0.72	1	-1	1	-1
241022	*Macaca nemestrina*	1.40	0.74	0.72	1	-1	1	-1
258230	*Macaca nemestrina*	1.38	0.73	0.72	1	-1	1	-1

C) Macaques, continued.

		Y-matrix			X-matrix			
ID	Taxon	logarea	logmd	logbl	I	T	L	IV
241022	*Macaca nemestrina*	1.40	0.74	0.72	1	-1	1	-1
258230	*Macaca nemestrina*	1.38	0.73	0.72	1	-1	1	-1
1915.11.4.11	*Macaca nemestrina*	1.35	0.76	0.67	1	-1	1	-1
1947.448	*Macaca nemestrina*	1.52	0.81	0.77	1	-1	1	-1
1955.1502	*Macaca nemestrina*	1.57	0.91	0.78	1	-1	1	-1
1955.707	*Macaca nemestrina*	1.50	0.77	0.75	1	-1	1	-1
1955.708	*Macaca nemestrina*	1.48	0.86	0.73	1	-1	1	-1
1955.709	*Macaca nemestrina*	1.46	0.80	0.71	1	-1	1	-1
296795	*Macaca cyclopis*	1.36	0.76	0.67	1	-1	-1	1
308718	*Macaca cyclopis*	1.24	0.70	0.63	1	-1	-1	1
358613	*Macaca cyclopis*	1.33	0.77	0.64	1	-1	-1	1
358615	*Macaca cyclopis*	1.33	0.76	0.66	1	-1	-1	1
358616	*Macaca cyclopis*	1.28	0.70	0.63	1	-1	-1	1
358617	*Macaca cyclopis*	1.28	0.71	0.67	1	-1	-1	1
397645	*Macaca cyclopis*	1.30	0.71	0.67	1	-1	-1	1
397646	*Macaca cyclopis*	1.31	0.75	0.63	1	-1	-1	1
397647	*Macaca cyclopis*	1.41	0.82	0.69	1	-1	-1	1
397707	*Macaca cyclopis*	1.30	0.71	0.67	1	-1	-1	1
399110	*Macaca cyclopis*	1.33	0.73	0.65	1	-1	-1	1
399112	*Macaca cyclopis*	1.33	0.76	0.65	1	-1	-1	1

D) Papionins

		Y-matrix			X-matrix			
ID	Taxon	logarea	logmd	logbl	I	T	L	IV
14.7.23.1	*Cercocebus galeritus*	1.52	0.82	0.75	1	1	1	1
14.7.23.2	*Cercocebus galeritus*	1.38	0.75	0.71	1	1	1	1
14.7.23.3	*Cercocebus galeritus*	1.38	0.74	0.67	1	1	1	1
23.10.15.3	*Cercocebus galeritus*	1.23	0.67	0.63	1	1	1	1
30.11.11.45	*Cercocebus galeritus*	1.31	0.72	0.68	1	1	1	1
30.11.11.48	*Cercocebus galeritus*	1.36	0.73	0.71	1	1	1	1
30.11.11.49	*Cercocebus galeritus*	1.37	0.76	0.69	1	1	1	1
5.5.23.2	*Cercocebus galeritus*	1.51	0.78	0.81	1	1	1	1
1971.2314	*Cercocebus torquatus*	1.44	0.72	0.58	1	1	-1	-1
218844	*Cercocebus torquatus*	1.38	0.78	0.72	1	1	-1	-1
220088	*Cercocebus torquatus*	1.49	0.82	0.77	1	1	-1	-1
220090	*Cercocebus torquatus*	1.51	0.83	0.74	1	1	-1	-1
220092	*Cercocebus torquatus*	1.52	0.78	0.77	1	1	-1	-1
220354	*Cercocebus torquatus*	1.41	0.79	0.71	1	1	-1	-1
220366	*Cercocebus torquatus*	1.44	0.76	0.69	1	1	-1	-1
1948.450	*Cercocebus torquatus*	1.60	0.88	0.80	1	1	-1	-1
1957.313	*Cercocebus torquatus*	1.53	0.81	0.80	1	1	-1	-1
1967.1712	*Cercocebus torquatus*	1.39	0.80	0.75	1	1	-1	-1
1902.11.2.1	*Cercocebus torquatus*	1.52	0.79	0.77	1	1	-1	-1
1903.2.4.1	*Cercocebus torquatus*	1.50	0.82	0.79	1	1	-1	-1
1903.2.4.2	*Cercocebus torquatus*	1.48	0.68	0.78	1	1	-1	-1
1930.12.16.5	*Cercocebus torquatus*	1.48	0.79	0.75	1	1	-1	-1
1938.7.7.3	*Cercocebus torquatus*	1.49	0.81	0.77	1	1	-1	-1
1938.7.7.5	*Cercocebus torquatus*	1.48	0.74	0.69	1	1	-1	-1
267862	*Papio cynocephalus*	1.45	0.81	0.74	1	-1	1	-1
384210	*Papio cynocephalus*	1.53	0.84	0.79	1	-1	1	-1
384211	*Papio cynocephalus*	1.69	0.94	0.85	1	-1	1	-1
384216	*Papio cynocephalus*	1.63	0.91	0.81	1	-1	1	-1
384217	*Papio cynocephalus*	1.57	0.87	0.76	1	-1	1	-1
384239	*Papio cynocephalus*	1.50	0.82	0.75	1	-1	1	-1
396185	*Papio cynocephalus*	1.68	0.93	0.86	1	-1	1	-1
396188	*Papio cynocephalus*	1.72	0.96	0.87	1	-1	1	-1
452509	*Papio cynocephalus*	1.68	0.96	0.83	1	-1	1	-1
1939.1021	*Papio anubis*	1.72	0.92	0.84	1	-1	-1	1
1905.5.10.1	*Papio anubis*	1.79	0.96	0.86	1	-1	-1	1
1906.11.1.6	*Papio anubis*	1.76	0.91	0.84	1	-1	-1	1

D) Papionins, continued.

		Y-matrix			X-matrix			
ID	Taxon	logarea	logmd	logbl	I	T	L	IV
1907.7.8.11	*Papio anubis*	1.66	0.91	0.85	1	-1	-1	1
1924.8.6.15	*Papio anubis*	1.77	0.89	0.81	1	-1	-1	1
1924.8.6.16	*Papio anubis*	1.62	0.96	0.87	1	-1	-1	1
1925.5.12.1	*Papio anubis*	1.69	0.94	0.86	1	-1	-1	1
1911.12.1.1	*Papio anubis*	1.66	0.99	0.88	1	-1	-1	1
1962.25	*Papio anubis*	1.56	0.86	0.81	1	-1	-1	1
1976.13	*Papio anubis*	1.69	0.95	0.81	1	-1	-1	1
1990.0535	*Papio anubis*	1.67	0.94	0.84	1	-1	-1	1
164518	*Papio anubis*	1.77	0.91	0.86	1	-1	-1	1
182148	*Papio anubis*	1.58	0.85	0.76	1	-1	-1	1
216605	*Papio anubis*	1.74	0.94	0.82	1	-1	-1	1
236976	*Papio anubis*	1.79	0.98	0.93	1	-1	-1	1
354986	*Papio anubis*	1.64	0.92	0.83	1	-1	-1	1
354987	*Papio anubis*	1.71	0.96	0.84	1	-1	-1	1
354988	*Papio anubis*	1.64	0.93	0.82	1	-1	-1	1
354989	*Papio anubis*	1.55	0.88	0.82	1	-1	-1	1
354992	*Papio anubis*	1.59	0.87	0.80	1	-1	-1	1
354993	*Papio anubis*	1.66	0.97	0.85	1	-1	-1	1
384219	*Papio anubis*	1.55	0.84	0.79	1	-1	-1	1
384220	*Papio anubis*	1.64	0.88	0.79	1	-1	-1	1
384222	*Papio anubis*	1.47	0.83	0.74	1	-1	-1	1
384223	*Papio anubis*	1.66	0.89	0.82	1	-1	-1	1
384224	*Papio anubis*	1.63	0.89	0.81	1	-1	-1	1
384227	*Papio anubis*	1.55	0.85	0.78	1	-1	-1	1
384228	*Papio anubis*	1.61	0.87	0.82	1	-1	-1	1
384230	*Papio anubis*	1.70	0.88	0.82	1	-1	-1	1
384234	*Papio anubis*	1.75	0.88	0.82	1	-1	-1	1
384235	*Papio anubis*	1.63	0.91	0.81	1	-1	-1	1
384236	*Papio anubis*	1.63	0.90	0.83	1	-1	-1	1
395433	*Papio anubis*	1.21	0.99	0.93	1	-1	-1	1
395434	*Papio anubis*	1.72	0.94	0.85	1	-1	-1	1
395437	*Papio anubis*	1.69	0.88	0.79	1	-1	-1	1
395441	*Papio anubis*	1.55	0.92	0.86	1	-1	-1	1
1899.6.10.2	*Papio anubis*	1.62	0.84	0.82	1	-1	-1	1
1899.7.8.1	*Papio anubis*	1.53	0.95	0.87	1	-1	-1	1
1900.3.18.1	*Papio anubis*	1.73	0.93	0.85	1	-1	-1	1

D) Papionins, continued.

		Y-matrix			X-matrix			
ID	Taxon	logarea	logmd	logbl	I	T	L	IV
1901.8.9.21	*Papio anubis*	1.71	1.00	0.92	1	-1	-1	1
1902.9.2.1	*Papio anubis*	1.83	0.90	0.80	1	-1	-1	1
1904.11.5.2	*Papio anubis*	1.61	1.00	0.89	1	-1	-1	1
1930.12.1.1	*Papio anubis*	1.71	0.95	0.88	1	-1	-1	1
1931.4.1.1	*Papio anubis*	1.87	0.92	0.86	1	-1	-1	1
1935.2.14.1	*Papio anubis*	1.74	0.92	0.84	1	-1	-1	1
1936.12.28.1	*Papio anubis*	1.68	0.94	0.86	1	-1	-1	1
1936.12.28.2	*Papio anubis*	1.77	0.95	0.82	1	-1	-1	1

E) Tamarins

		Y-matrix			X-matrix			
ID	Taxon	logarea	logmd	logbl	I	T	L	IV
194331	*Saguinus fuscicollis*	0.46	0.28	0.29	1	1	1	1
336299	*Saguinus fuscicollis*	0.43	0.28	0.27	1	1	1	1
336300	*Saguinus fuscicollis*	0.39	0.25	0.22	1	1	1	1
337331	*Saguinus fuscicollis*	0.37	0.24	0.26	1	1	1	1
397281	*Saguinus fuscicollis*	0.37	0.25	0.24	1	1	1	1
397284	*Saguinus fuscicollis*	0.42	0.32	0.25	1	1	1	1
397285	*Saguinus fuscicollis*	0.50	0.27	0.35	1	1	1	1
397302	*Saguinus fuscicollis*	0.35	0.24	0.19	1	1	1	1
397659	*Saguinus fuscicollis*	0.34	0.30	0.24	1	1	1	1
398735	*Saguinus fuscicollis*	0.38	0.24	0.23	1	1	1	1
518576	*Saguinus fuscicollis*	0.38	0.26	0.25	1	1	1	1
518577	*Saguinus fuscicollis*	0.45	0.28	0.28	1	1	1	1
534806	*Saguinus fuscicollis*	0.39	0.23	0.23	1	1	1	1
536709	*Saguinus fuscicollis*	0.39	0.29	0.24	1	1	1	1
397242	*Saguinus mystax*	0.55	0.35	0.29	1	1	-1	-1
397870	*Saguinus mystax*	0.54	0.39	0.31	1	1	-1	-1
397871	*Saguinus mystax*	0.61	0.41	0.33	1	1	-1	-1
397873	*Saguinus mystax*	0.52	0.31	0.37	1	1	-1	-1
397876	*Saguinus mystax*	0.50	0.35	0.32	1	1	-1	-1
397877	*Saguinus mystax*	0.52	0.34	0.28	1	1	-1	-1
397880	*Saguinus mystax*	0.54	0.31	0.34	1	1	-1	-1
397930	*Saguinus mystax*	0.57	0.36	0.33	1	1	-1	-1
399077	*Saguinus mystax*	0.54	0.32	0.28	1	1	-1	-1
399078	*Saguinus mystax*	0.53	0.33	0.28	1	1	-1	-1
399079	*Saguinus mystax*	0.53	0.34	0.27	1	1	-1	-1
518582	*Saguinus mystax*	0.52	0.35	0.30	1	1	-1	-1
518584	*Saguinus mystax*	0.54	0.32	0.30	1	1	-1	-1
543489	*Saguinus mystax*	0.55	0.38	0.29	1	1	-1	-1
398815	*Saguinus labiatus*	0.45	0.30	0.27	1	-1	1	-1
398816	*Saguinus labiatus*	0.55	0.30	0.32	1	-1	1	-1
398817	*Saguinus labiatus*	0.52	0.33	0.31	1	-1	1	-1
398818	*Saguinus labiatus*	0.53	0.32	0.27	1	-1	1	-1
398819	*Saguinus labiatus*	0.47	0.34	0.28	1	-1	1	-1
398820	*Saguinus labiatus*	0.52	0.30	0.27	1	-1	1	-1
398821	*Saguinus labiatus*	0.49	0.37	0.32	1	-1	1	-1
398822	*Saguinus labiatus*	0.43	0.30	0.26	1	-1	1	-1

E) Tamarins, continued.

		Y-matrix			X-matrix			
ID	Taxon	logarea	logmd	logbl	I	T	L	IV
398823	*Saguinus labiatus*	0.44	0.28	0.30	1	-1	1	-1
398824	*Saguinus labiatus*	0.41	0.29	0.28	1	-1	1	-1
398825	*Saguinus labiatus*	0.50	0.34	0.29	1	-1	1	-1
398826	*Saguinus labiatus*	0.48	0.32	0.25	1	-1	1	-1
464971	*Saguinus labiatus*	0.47	0.30	0.24	1	-1	1	-1
522949	*Saguinus labiatus*	0.49	0.36	0.28	1	-1	1	-1
522950	*Saguinus labiatus*	0.45	0.33	0.26	1	-1	1	-1
170913	*Saguinus geoffroyi*	0.61	0.40	0.38	1	-1	-1	1
170914	*Saguinus geoffroyi*	0.54	0.37	0.37	1	-1	-1	1
170915	*Saguinus geoffroyi*	0.62	0.35	0.35	1	-1	-1	1
170916	*Saguinus geoffroyi*	0.56	0.33	0.36	1	-1	-1	1
200290	*Saguinus geoffroyi*	0.56	0.36	0.30	1	-1	-1	1
291244	*Saguinus geoffroyi*	0.59	0.38	0.36	1	-1	-1	1
291245	*Saguinus geoffroyi*	0.62	0.44	0.38	1	-1	-1	1
296290	*Saguinus geoffroyi*	0.57	0.39	0.31	1	-1	-1	1
301398	*Saguinus geoffroyi*	0.59	0.30	0.34	1	-1	-1	1
301656	*Saguinus geoffroyi*	0.61	0.36	0.34	1	-1	-1	1
301657	*Saguinus geoffroyi*	0.58	0.30	0.38	1	-1	-1	1
302474	*Saguinus geoffroyi*	0.53	0.34	0.32	1	-1	-1	1
306836	*Saguinus geoffroyi*	0.57	0.34	0.37	1	-1	-1	1
306838	*Saguinus geoffroyi*	0.58	0.31	0.34	1	-1	-1	1
306840	*Saguinus geoffroyi*	0.61	0.37	0.35	1	-1	-1	1
306841	*Saguinus geoffroyi*	0.60	0.32	0.29	1	-1	-1	1
306843	*Saguinus geoffroyi*	0.65	0.38	0.37	1	-1	-1	1
306844	*Saguinus geoffroyi*	0.48	0.37	0.32	1	-1	-1	1
306845	*Saguinus geoffroyi*	0.63	0.37	0.32	1	-1	-1	1
310344	*Saguinus geoffroyi*	0.53	0.34	0.33	1	-1	-1	1
310345	*Saguinus geoffroyi*	0.56	0.36	0.35	1	-1	-1	1
310346	*Saguinus geoffroyi*	0.57	0.36	0.32	1	-1	-1	1
310347	*Saguinus geoffroyi*	0.59	0.39	0.37	1	-1	-1	1
310348	*Saguinus geoffroyi*	0.59	0.34	0.35	1	-1	-1	1
310349	*Saguinus geoffroyi*	0.55	0.35	0.30	1	-1	-1	1
335456	*Saguinus geoffroyi*	0.56	0.36	0.36	1	-1	-1	1
335457	*Saguinus geoffroyi*	0.59	0.34	0.33	1	-1	-1	1
335462	*Saguinus geoffroyi*	0.64	0.36	0.36	1	-1	-1	1

E) Tamarins, continued.

		Y-matrix			X-matrix			
ID	Taxon	logarea	logmd	logbl	I	T	L	IV
363152	*Saguinus geoffroyi*	0.55	0.34	0.31	1	-1	-1	1
397249	*Saguinus geoffroyi*	0.56	0.32	0.36	1	-1	-1	1

F) Fossil hominins

		Y-matrix			X-matrix			
ID	Taxon	logarea	logmd	logbl	I	T	L	IV
KNM-ER 729	*Paranthropus boisei*	2.24	1.18	1.16	1	1	1	1
KNM-ER 802	*Paranthropus boisei*	2.19	1.14	1.16	1	1	1	1
KNM-ER 818	*Paranthropus boisei*	2.38	1.18	1.20	1	1	1	1
KNM-ER 1171	*Paranthropus boisei*	2.26	1.20	1.18	1	1	1	1
KNM-ER 1816	*Paranthropus boisei*	2.20	1.17	1.16	1	1	1	1
KNM-ER 3229	*Paranthropus boisei*	2.10	1.11	1.12	1	1	1	1
KNM-ER 3230	*Paranthropus boisei*	2.28	1.16	1.22	1	1	1	1
KNM-ER 3885	*Paranthropus boisei*	2.09	1.09	1.15	1	1	1	1
KNM-ER 15930	*Paranthropus boisei*	2.23	1.08	1.15	1	1	1	1
OMO 74A-21	*Paranthropus boisei*	2.23	1.13	1.10	1	1	1	1
OMO 75-14	*Paranthropus boisei*	2.16	1.06	1.10	1	1	1	1
OMO L33-508	*Paranthropus boisei*	2.01	0.99	1.11	1	1	1	1
OMO L51-79	*Paranthropus boisei*	2.02	0.99	1.02	1	1	1	1
OMO L55-33	*Paranthropus boisei*	2.08	1.10	2.05	1	1	1	1
OMO L628-4	*Paranthropus boisei*	2.07	1.01	1.06	1	1	1	1
Peninj	*Paranthropus boisei*	2.26	1.16	1.18	1	1	1	1
DNH 8	*Paranthropus robustus*	2.11	1.00	1.11	1	1	-1	-1
SK 6	*Paranthropus robustus*	2.01	1.04	1.09	1	1	-1	-1
SK 7	*Paranthropus robustus*	2.04	1.04	1.13	1	1	-1	-1
SK 9	*Paranthropus robustus*	2.03	1.03	1.11	1	1	-1	-1
SK 12	*Paranthropus robustus*	2.23	1.10	1.14	1	1	-1	-1
SK 23	*Paranthropus robustus*	2.10	1.05	1.15	1	1	-1	-1
SK 34	*Paranthropus robustus*	2.13	1.09	1.14	1	1	-1	-1
SK 57	*Paranthropus robustus*	2.11	0.98	1.13	1	1	-1	-1
SK 74	*Paranthropus robustus*	2.03	1.04	1.08	1	1	-1	-1
SK 88	*Paranthropus robustus*	2.13	1.08	1.17	1	1	-1	-1
SK 827	*Paranthropus robustus*	1.99	1.04	1.06	1	1	-1	-1
SKW 5	*Paranthropus robustus*	2.10	1.07	1.13	1	1	-1	-1
SKX 4446	*Paranthropus robustus*	2.12	1.12	1.13	1	1	-1	-1
TM 1517b	*Paranthropus robustus*	2.14	1.08	1.15	1	1	-1	-1

F) Fossil hominins, continued.

		Y-matrix			X-matrix			
ID	Taxon	logarea	logmd	logbl	I	T	L	IV
TM 1601	*Paranthropus robustus*	1.99	1.04	1.08	1	1	-1	-1
KGA 10-1	*Homo sp.*	2.00	0.99	1.01	1	-1	1	-1
KNM-ER 992	*Homo ergaster*	1.86	0.94	1.04	1	-1	1	-1
KNM-ER 1482	*Homo habilis*	2.07	0.99	1.09	1	-1	1	-1
KNM-ER 1801	*Homo habilis*	2.06	0.99	1.07	1	-1	1	-1
KNM-ER 3734	*Homo sp.*	1.74	0.96	0.91	1	-1	1	-1
KNM-WT 15000	*Homo ergaster*	1.93	0.95	0.98	1	-1	1	-1
OH 7	*Homo habilis*	1.93	1.02	1.03	1	-1	1	-1
OH 13	*Homo habilis*	1.83	0.95	0.99	1	-1	1	-1
OH 16	*Homo habilis*	1.95	1.00	1.04	1	-1	1	-1
OH 22	*Homo ergaster*	1.85	0.95	1.00	1	-1	1	-1
Dmanisi 211	*Homo ergaster*	1.89	0.90	0.99	1	-1	-1	1
Dmanisi 2735	*Homo ergaster*	1.85	0.88	0.97	1	-1	-1	1
Rabat	*Homo erectus*	1.93	0.95	0.98	1	-1	-1	1
Sangiran 1b	*Homo erectus*	2.00	0.97	1.00	1	-1	-1	1
Sangiran 6	*Homo erectus*	2.08	0.98	1.10	1	-1	-1	1
Sangiran 9	*Homo erectus*	1.98	0.95	1.03	1	-1	-1	1
Sangiran 22	*Homo erectus*	1.99	0.96	1.03	1	-1	-1	1
Sangiran Sb 8103	*Homo erectus*	1.94	0.92	1.02	1	-1	-1	1
Ternifine 1	*Homo erectus*	1.90	0.90	1.00	1	-1	-1	1
Ternifine 2	*Homo erectus*	2.00	0.98	1.02	1	-1	-1	1
Ternifine 3	*Homo erectus*	1.91	0.91	1.00	1	-1	-1	1
ZKD B1-3	*Homo erectus*	1.90	1.00	0.90	1	-1	-1	1
ZKD B5-77	*Homo erectus*	1.94	0.95	0.99	1	-1	-1	1
ZKD C3-46	*Homo erectus*	2.01	0.96	1.05	1	-1	-1	1
ZKD F3-37	*Homo erectus*	1.92	0.94	0.98	1	-1	-1	1