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Homoplasy and thick enamel in primates

James D. Pampush^{a,*}, Ana C. Duque^a, Brittany R. Burrows^a, David J. Daegling^a, William F. Kenney^b, W. Scott McGraw^c^a Department of Anthropology, University of Florida, Turlington Hall, Room 1112, P.O. Box 117305, Gainesville, FL, USA^b Land Use and Environmental Change Institute, University of Florida, Gainesville, FL, USA^c Department of Anthropology, The Ohio State University, Columbus, OH, USA

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ABSTRACT

Traditionally, thick enamel has often been used to infer durophagy (i.e., hard nut and seed consumption) in extinct hominins. These inferences are based on the hypothesis that thick enamel is primarily an adaptation to prevent tooth fracture or chipping resulting from high-stress loads produced during the mastication of large hard foods. An alternative view argues that thick enamel may aid in maintaining tooth function in the face of gradual dental wear from grit, phytoliths and acid, which may be found in foods of widely varying hardness. We use estimates of primate dietary abrasiveness and recorded lifespan to test the hypothesis that enamel thickness is selectively responsive to lifetime dental wear resistance. We use data from the literature to relate enamel thickness to measures of dietary abrasiveness, diet profiles, and longevity for 17 primate species and performed linear regression using several combinations of these variables. We found a positive association between lifetime dietary wear and enamel thickness, suggesting that thick molar enamel in primates may have evolved as a means to resist wear apart from selection to resist tooth fracture. Assuming our estimates of lifetime dietary wear are accurate, we caution against ascribing thick enamel solely to the presence of hard-object feeding in paleoanthropological contexts without also considering primate lifespan and other aspects of feeding ecology.

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Introduction

Teeth are of great interest to evolutionary primatologists because of their variable forms and correlated diverse functional capabilities, as well as their abundance in the fossil record (Kay, 1975; Strait, 1997; Ungar, 1998; Swindler, 2002). One dental feature that varies widely in primates is enamel thickness (Molnar and Gantt, 1977; Sperber, 1985; Beynon and Wood, 1986; Grine and Martin, 1988; Dumont, 1995; Teaford, 2007; Lucas et al., 2008a,b). Because enamel does not remodel or re-grow during a primate's lifespan (Hillson, 1986; Janis and Fortelius, 1988; Boyde, 1990; Arola et al., 2010), the initial enamel thickness of the permanent dentition is likely under considerable selective pressure. However, enamel thickness has also been demonstrated to be an evolutionarily plastic trait, capable of rapid adaptation in response to functional dietary requirements (Hlusko, 2004; Kelley and Swanson, 2008).

Enamel thickness has been hypothesized to be adaptively responsive to several different dietary characteristics. Some researchers have argued that enamel thickness is adaptively responsive to the mechanical properties of foods (Dumont, 1995; Lambert et al., 2004; Vogel et al., 2008; Lee et al., 2010; McGraw et al., 2012), with thicker enamel being associated with harder or stiffer diets. Research has also revealed correlations between enamel thickness, dietary guild, and food geometry (Yamashita, 1998; Kelley and Swanson, 2008; Vogel et al., 2008). In particular, thin enamel is associated with the consumption of leaves or sheet-like materials. Finally, dietary wear and abrasion (Molnar and Gantt, 1977; King et al., 2005) have also been linked to enamel thickness. Determining the covariates and adaptive significance of thick molar enamel in primates is worthy of further inquiry because enamel thickness is frequently invoked to reconstruct the diets and evolutionary history of primate species (e.g., Kay, 1985; Lucas et al., 2008a), and because thick molar enamel characterizes extinct hominins (Martin, 1985; Grine and Martin, 1988; White et al., 2009).

There are two competing arguments concerning the adaptive function of thick molar enamel: [1] thick enamel helps resist catastrophic tooth crown failure in durophagous species that could

* Corresponding author.

E-mail addresses: jpampush@ufl.edu (J.D. Pampush), anaduque@ufl.edu (A.C. Duque), brittanyburrows@ufl.edu (B.R. Burrows), daegling@ufl.edu (D.J. Daegling), kenney@ufl.edu (W.F. Kenney), mcgraw.43@osu.edu (W.S. McGraw).

result in sudden high volume tissue loss, with subsequent loss of whole teeth (Kay, 1981; Dumont, 1995; Lambert et al., 2004; Vogel et al., 2008; Lucas et al., 2008a,b; Constantino et al., 2011); and [2] thick enamel helps resist wear and abrasion (gradual low volume tissue loss) in order to maintain masticatory competence over the lifespan of the animal (Molnar and Gantt, 1977; King et al., 2005). These two hypotheses are not mutually exclusive. For example, hard-objects, which could fracture a tooth during mastication, may also contain adherent grit that could produce wear. In recent years, considerably more research has focused on the adaptive function of thick enamel in the context of hard-object feeding (e.g., Lambert et al., 2004; Vogel et al., 2008; Lucas et al., 2008a; Constantino et al., 2009), rather than alternative hypotheses. Still, wear and attrition resistance deserves more consideration in light of recent insights into the benefits of maintaining high dental function for primate longevity, reproduction, and health (DeGusta et al., 2003; King et al., 2005).

Hypsodonty (high-crowned teeth) and hypselodonty (ever-growing teeth) are common dental adaptations to wear and attrition resistance in many mammalian groups, yet no primate has evolved these characters (Janis and Fortelius, 1988) with the exception of the ever-growing incisors of aye-ayes (Fleagle, 1999). Given the general absence of hypsodonty or hypselodonty among primates, enamel thickness becomes fundamentally important to maintaining masticatory function in the face of dietary wear. Despite not developing more common mammalian dental wear adaptations, primate feeding niches are not devoid of dental wear agents, and these agents potentially impose selective pressures on primate enamel thickness (King et al., 2005; Cuzzo and Sauter, 2006). Specifically, Cuzzo and Sauter (2006) have noted that among some groups of ring-tailed lemurs, the amount of sustained wear is unusually high relative to other primates, such that dentally old individuals must resort to scavenging partially eaten or processed food items from troop mates. Noting the high costs of dealing with the extreme dental wear in these prosimians, and the relatively recent introduction of the abrasive yet desirable tamarind fruit to areas of Madagascar, Cuzzo and Sauter (2006) have concluded that these animals are maladapted to their current abrasive dietary regime because of their thin enamel (i.e., an 'ecological mismatch'). This circumstantially supports a hypothesis that primates, in general, avoid extreme dental wear with thicker enamel caps, and that enamel thickness may be generally tuned to dietary attrition.

Although researchers have long suspected that high dietary abrasion plays an important role in selection for increased enamel thickness among primates (e.g., Molnar and Gantt, 1977), it remains under-investigated using multi-species approaches. Such tests may provide insight into the general value of thick molar enamel in maintaining long-term competent masticatory function in primates, a clade known for long lifespans (Harvey et al., 1987; Ernest, 2003). Measuring lifetime dietary abrasion is a difficult task because of the varied nature of primate food abrasiveness, both due to intrinsic elements of the foods (Baker et al., 1959; Kay and Covert, 1983) and because of habitat differences in adherent grit (Ungar, 1998; Daegling and Grine, 1999). However, it can be theoretically disarticulated into two separate and potentially measurable components: rate and duration. Duration is estimated easily enough as the maximum recorded lifespan of a species. Recently, a paper published by Rabenold and Pearson (2011) described a method for estimating the wear rate of various primate diets. Their method involves quantifying the volume of phytoliths in primate foods by measuring the amount of feeding time primates dedicate to high phytolith content plants as a percentage of their total diet. Using these two variables, the rate variable (Rabenold and Pearson's, 2011: phytolith load) and the duration variable (maximum recorded lifespan), one can generate a 'wear years' index, which

estimates the expected lifetime dietary abrasion an individual is likely to encounter.

The purpose of this study is to investigate several factors associated with thick enamel in primates. We hypothesize that thick enamel in primates is a homoplastic trait that can arise as an adaptive solution to both durophagy and lifetime dietary wear. If supported, this hypothesis will have implications for interpreting enamel thickness in the primate fossil record.

Materials and methods

From the literature, we collected data for five variables on 17 primate species:

[1] Relative enamel thickness (RET, Table 1)

Relative enamel thickness is a dimensionless measure developed by Martin (1985) and is calculated by the following formula: $(AET/\sqrt{c}) \times 100$ where AET is average enamel thickness (cross-sectional area of the enamel crown divided by the length of the enamel dentine junction) and c is the area of the dentine under the enamel crown (Fig. 1). Martin's (1985) measure has the advantage of controlling for body size, making it an ideal variable to use in a cross-species comparison especially in light of Janis and Fortelius' (1988) theoretical demonstration that the amount of dental tissue lost due to wear during each chew stroke scales isometrically with body size. The number of species for which data on relative enamel thickness are available is modest. Consequently, the data used here are averages from any reported post-canine teeth. In some species, post-canine enamel thickness varies across teeth (e.g., M1 versus M2), particularly in humans and baboons (Schwartz, 2000a; Grine et al., 2005). However, it is not known if a consistent pattern exists. Therefore, we first averaged RET values by tooth and then used grand means in our analyses (Table 1).

[2] Maximum-recorded lifespan

Maximum-recorded lifespan was collected from published reports, including both wild and captive individuals (Table 2). Where separate reports document different maximum-recorded lifespan measures, we used the larger of the two values.

[3] Phytoload

Phytoload is measured as the percentage of high-phytolith content plants in a primate's total diet. Rabenold and Pearson (2011) designed this measure and reported it for 12 species (10 for which we have the additional variables are used in this study). In order to maximize statistical power, we expanded the phytoload sample to include an additional seven species, which Rabenold and Pearson (2011) did not use (Table 3). Using both the phytoload and maximum-recorded lifespan, we calculated a wear index as the product of the two variables (units are therefore years * % of phytoliths in diet). The availability of phytoload dietary data is another bottleneck for data collection, ultimately limiting our sample size to 17 species.

[4] Diet hardness

Diet hardness is treated as a binary factor in our analyses. Species were categorized as either durophagous or non-durophagous based on presence or absence of hard-object mastication reports from field studies.

[5] Folivory

Table 1
Enamel thickness data.

Species	Source	N-tooth type	Tooth RET ^a $\bar{X} \pm$ S.D.	RET species ^b weighted- \bar{X}
<i>Daubentonia madagascariensis</i>	Shellis et al., 1998	1–M ₂	21.70	21.70
<i>Lemur catta</i>	Shellis et al., 1998	1–M ₁	8.12	8.12
<i>Nycticebus coucang</i>	Shellis et al., 1998	2–M ¹	10.26	10.29
<i>Cacajao calvus</i>	Martin et al., 2003	1–M ₁	10.32	11.53
		1–M ₂	9.84	
		1–M ₃	12.83	
<i>Cebus apella</i>	Dumont, 1995	1–M ₁	19.68	19.45
	Martin et al., 2003	2–M ₁		
	Shellis et al., 1998	1–M ₂	19.21	
<i>Cebus capucinus</i>	Dumont, 1995	3–M ₁	15.13 \pm 1.58	15.13
<i>Chiropotes satanas</i>	Martin et al., 2003	1–M ²	7.92	9.13
		2–M ₂	10.35	
		2–P ₄	19.13	
<i>Cercocebus atys</i>	Daegling et al., 2011	3–M ₂	19.66 \pm 2.41	19.56
		4–M ₃	19.90 \pm 3.03	
		3–M ₁	12.89 \pm 1.65	
		1–M ₂	22.84	
<i>Cercocebus torquatus</i>	Dumont, 1995	3–M ₁	12.89 \pm 1.65	17.86
<i>Erythrocebus patas</i>	Shellis et al., 1998	1–M ₂	22.84	12.28
		2–M ₂	12.28	
<i>Lophocebus albigena</i>	Dumont, 1995	2–M ₁	16.85	18.32
		1–M ₂	19.79	
<i>Macaca mulatta</i>	Shellis et al., 1998	3–M ₂	13.15	13.58
		3–M ₃	14.01	
<i>Papio cynocephalus</i>	Shellis et al., 1998	1–M ₁	15.10	15.38
		1–M ₂	12.43	
		1–M ₃	18.62	
<i>Theropithecus gelada</i>	Shellis et al., 1998	1–M ₁	13.90	15.58
		3–M ₂	14.66	
		3–M ₃	18.19	
<i>Gorilla gorilla</i>	Shellis et al., 1998 Martin, 1983 Shellis et al., 1998 Martin, 1983 Shellis et al., 1998 Martin, 1983 Shellis et al., 1998 Martin, 1983	4–M ¹	8.10	10.08
		3–M ¹		
		3–M ₁	9.84	
		1–M ₁		
		3–M ²	9.61	
		3–M ²		
		1–M ₂	10.59	
		4–M ₂		
		1–M ³	9.88	
		1–M ₃	12.45	
		1–M ¹	10.59	
<i>Pan troglodytes</i>	Smith et al., 2005 Shellis et al., 1998 Smith et al., 2005 Shellis et al., 1998 Smith et al., 2005	3–M ₁	13.17	12.95
		17–M ₁		
		1–M ²	11.08	
		9–M ₂	13.40	
		1–M ₂		
		1–M ³	14.59	
		5–M ₃	14.89	
		2–M ₃		
		3–M ¹	13.73	
		8–M ¹		
<i>Pongo pygmaeus</i>	Shellis et al., 1998 Smith et al., 2005 Shellis et al., 1998 Smith et al., 2005 Shellis et al., 1998 Smith et al., 2005	1–M ₁	13.33	15.65
		9–M ₁		
		8–M ²	17.04	
		8–M ₂	16.33	
		4–M ³	17.22	
		2–M ₃	16.33	
		6–M ₃		
		Shellis et al., 1998		
		Smith et al., 2005		
		Smith et al., 2005		

^a Relative enamel thickness (RET) is calculated as the average thickness of the enamel cap divided by the square root of the area of the underlying dentine multiplied by 100. Standard deviations, when available from sources, are included.

^b Species weighted average is the grand mean for each measure as weighted by tooth type.

Folivory is the percentage of feeding time dedicated to eating leaves. Some researchers have proposed that primate molar enamel is 'designed to wear' (Ungar and Williamson, 2000; Ungar and M'Kirera, 2003). That is, in cases of folivorous specialization, it is hypothesized that enamel will be distributed unevenly throughout the enamel cap so as to induce beneficial shearing capabilities as the teeth wear (see also Rensberger, 1973; Walker and Murray, 1975; Kay, 1981; Schwartz, 2000b). In other words, selection for thin enamel may be important in some folivorous primates. If this hypothesis is valid, folivory (or selection for the

processing of tough foods in general), as well as other dietary guild specializations may be contributing factors that could negatively impact a more elegant modeling of enamel thickness selective pressures. Furthermore, RET, the summary measure employed here is an estimate of the thickness of enamel over the entire crown and is incapable of assessing homogeneity of enamel thickness across the crown. Thus, species with pockets of thin enamel over their tooth crowns may register smaller RET values even if their enamel is relatively thick throughout the rest of the crown.

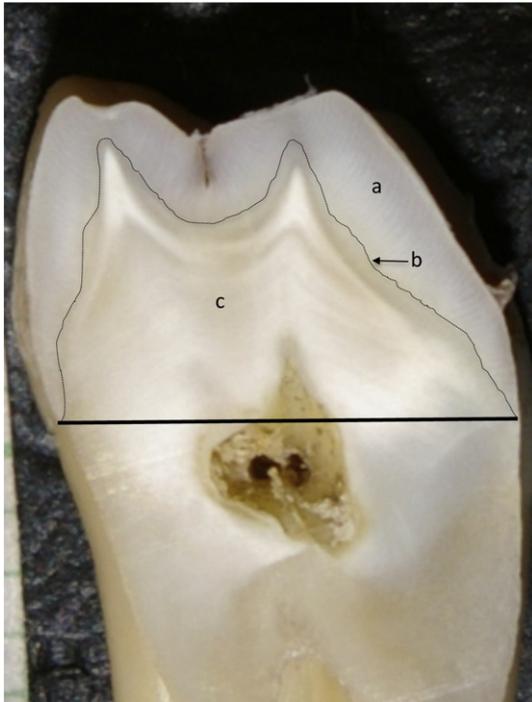


Figure 1. (a) Area of the enamel cap. (b) Thin line indicates enamel dentine junction (EDJ). (c) Dentine area under the enamel cap hemmed by both lines.

The analyses were performed in log-space and the described data and the following models were all tested for phylogenetic non-independence; analyses impacted by phylogenetic non-independence incorporated phylogenetic statistical controls. In this study, it is important to account for phylogeny because our hypothesis predicts that separate selective pressures are capable of producing thick enamel independent of phylogenetic covariation of the model variables. It is possible to have a homoplastic trait that shows phylogenetic covariation, if the covariation is manifested by the pairing of the dependent variable to particular independent variables. In other words, the phylogenetic covariation tests and corrections are aimed at detecting and eliminating phylogenetic artifacts in the relationships between our model variables, not the

Table 2
Longevity data.

Species	Maximum recorded age ^a	Source
<i>Daubentonia madagascariensis</i>	24.3	Hakeem et al., 1996
<i>Lemur catta</i>	37.3	de Magalhaes and Coasta, 2009
<i>Nycticebus coucang</i>	25.8	de Magalhaes and Coasta, 2009
<i>Cacajao calvus</i>	35.8	de Magalhaes and Coasta, 2009
<i>Cebus apella</i>	46	de Magalhaes and Coasta, 2009
<i>Cebus capucinus</i>	55	Ernest, 2003
<i>Chirotopes satanas</i>	19.6	de Magalhaes and Coasta (2009)
<i>Cercocebus atys</i>	26.8	Hakeem et al., 1996
<i>Cercocebus torquatus</i>	46	de Magalhaes and Coasta (2009)
<i>Erythrocebus patas</i>	28.3	de Magalhaes and Coasta (2009)
<i>Lophocebus albigena</i>	36	de Magalhaes and Coasta (2009)
<i>Macaca mulatta</i>	40	de Magalhaes and Coasta (2009)
<i>Papio cynocephalus</i>	35.1	Hakeem et al., 1996
<i>Theropithecus gelada</i>	36	de Magalhaes and Coasta (2009)
<i>Gorilla gorilla</i>	55.4	de Magalhaes and Coasta (2009)
<i>Pan troglodytes</i>	60.5	Ernest (2003)
<i>Pongo pygmaeus</i>	59	de Magalhaes and Coasta (2009)

^a Ages recorded in years. Where sources reported different ages, the larger of the two values was used.

model variables themselves. We ran three different analyses. First, we ran a generalized linear model (GLM) testing three variables (Wear Index, Folivory, and Durophagy) against RET. Because our hypothesis asserts that thick enamel may result from adaptations to dealing both with high lifetime dietary wear and durophagy, we also tested both variables independent of each other to deal with the potential confounding effect these variables may be having on one another. The durophagy measure is a binary factor, either a species is considered durophagous or not. Accurate testing of binary factors controlling for phylogeny is best performed using the BRUNCH algorithm developed by Purvis and Rambaut (1995) based on Felsenstein (1985). We performed a BRUNCH analysis on the data set to test if durophagy was significantly correlated with RET. Finally, while the proposed wear index and durophagy are not mutually exclusive in theory (i.e., a species may have both a high wear index and be durophagous), it is nevertheless predicted that if a species is durophagous it will have thick enamel (Kay, 1981, 1985; Dumont, 1995; Lucas et al., 2008b, 2009). We agree with this conclusion regardless of a species' potential lifetime dietary wear. Therefore, to avoid the potentially confounding effects of durophagy on our wear index variable, we dropped the seven durophagous taxa from the GLM analysis and re-performed it testing only wear index and folivory against RET. We used the open source R-platform (R Development Core Team [2011]) for all statistical analyses.

Results

Results of the GLM incorporating all three variables (Wear Index, Durophagy, and Folivory) are summarized in Table 4. An analysis for phylogenetic non-independence revealed a significant effect of phylogeny, and a Pagel's λ correction of 0.835 was incorporated into the model (Pagel, 1999; Freckleton et al., 2002). Similarly, we tested our model variables, including the decomposed elements of the wear index (i.e., longevity and Phytoload B) for collinearity and did not find any of them to be correlated. While the model overall showed significance (F -statistic = 4.464, $p = 0.017$, $r^2 = 0.507$), neither durophagy nor wear index showed a significant relationship to RET. Folivory did show a significant, although weak, negative relationship with RET. Results of the BRUNCH algorithm are summarized in Table 5, and are described in a non-phylogenetically corrected box plot in Fig. 2. Binary treatment of durophagy revealed a significant positive relationship with RET (T -value = 2.927, $p = 0.042$, $r^2 = 0.681$). Dropping the durophagous taxa from the analysis and re-performing the GLM with just wear index and folivory against RET (Table 6) revealed a significant positive correlation between our wear index and RET ($p = 0.018$), and a significant negative correlation between percentage of time spent on leaf consumption and RET ($p = 0.017$). Additionally, the GLM showed significant and strong predictive accuracy (F -statistic = 5.84, $p = 0.026$, $r^2 = 0.625$, Fig. 3). Testing for phylogenetic effect revealed no phylogenetic signature ($\lambda = 0.00$), and phylogenetic correction was therefore not necessary in the non-durophagous subset.

Discussion

Our results indicate both a positive relationship between our wear index and RET, as well as between durophagy and RET, thus supporting our hypothesis that thick enamel is a homoplastic trait that can arise as an adaptive response to either factor. Additionally, our results support the hypothesis that folivory, or the mastication of tough sheet-like materials, is negatively correlated with enamel thickness. While controlling for phylogenetic non-independence, these results suggest that thick enamel in primates may be a response to at least two different selective pressures.

Table 3
Dietary data.

Species	Phytoload B ^a	Leaves %	% Unknown phytoload ^b	Durophagous ^c	Sources
<i>Daubentonia madagascariensis</i>	49.13	0	0	No	Rabeno and Pearson, 2011
<i>Lemur catta</i>	24.73	34.03	34.91	No	Sussman, 1974
<i>Nycticebus coucang</i>	8.6	0	4.3	No	Wiens et al., 2006
<i>Cacajao calvus</i>	38.17	3.35	26.82	Yes	Ayres, 1989
<i>Cebus apella</i>	61.07	0	7.27	Yes	Bowler and Bodmer, 2011 Rabeno and Pearson, 2011
<i>Cebus capucinus</i>	39.38	1.97	19.41	No	Izawa and Mizuno, 1977 Rabeno and Pearson, 2011
<i>Chiropotes satanas</i>	32.05	1.72	47.68	Yes	Rabeno and Pearson, 2011 Kinzey and Norconk, 1990
<i>Cercocebus atys</i>	20.59	1.25	12.4	Yes	McGraw et al., 2011
<i>Cercocebus torquatus</i>	38.11	5.74	19.19	Yes	Rabeno and Pearson, 2011 McGraw et al., 2012
<i>Erythrocebus patas</i>	35.35	4.05	5.45	No	Isbell, 1998
<i>Lophocebus albigena</i>	36.7	3.9	19.46	Yes	Nakagawa, 1989 Rabeno and Pearson, 2011 McGraw et al., 2012
<i>Macaca mulatta</i>	31.26	78.37	17.23	No	Goldstein and Richard, 1989
<i>Papio cynocephalus</i>	77.02	2.4	13.47	No	Rabeno and Pearson, 2011
<i>Theropithecus gelada</i>	98.04	1.68	2.66	No	Dunbar, 1976
<i>Gorilla gorilla</i>	47.08	49.16	25.51	No	Rabeno and Pearson, 2011
<i>Pan troglodytes</i>	68.45	17.47	10.0	No	Rabeno and Pearson, 2011
<i>Pongo pygmaeus</i>	40.32	15.65	26.28	Yes	Rabeno and Pearson, 2011 Lee et al., 2010

^a Rabeno and Pearson (2011) also describe a 'Phytoload A' variable as the percentage of high phytolith containing plants among the plant-based portion of the primate's diet. We did not include this measure in our analyses.

^b Percentage of diet where the phytoload was unable to be assessed either because the plant species have not been examined for phytoliths, or the field data was unable to identify the food.

^c Species were classified as durophagous if they were known to orally process hard foods, regardless of which teeth were used in the processing (see discussion).

One interpretive limitation of our models is the low number of species sampled ($N = 17$), particularly in the non-durophagous subset ($N = 10$). These small samples are the result of several factors, including the number of species for which enamel thickness is available, and a general lack of reliable data on primate longevity. Primarily, however, the data set was limited by a dearth of reports on botanical lists for field feeding data. The biogenic silica content (e.g., diatoms, sponge spicules and phytoliths) of aquatic plants and sediments is routinely determined with basic dissolution (i.e., 1% NaCO₃) and colorimetric analysis (see Kenney et al., 2010). These methods are readily adaptable to the terrestrial plant materials contributing to primate diets. Using these techniques, we were able to expand our data set to include information on the sooty mangabey diet, directly determining their phytoload, but a lack of specimens for other species limited our ability to expand our data set further. Thus, while having additional species in our sample may increase the statistical certainty of our results, more data on the various factors in our models are simply unavailable at the present time, but hopefully will become available in the future. One additional problem with our approach is the proxy measures we used to calculate our wear index. Recall that the wear index is produced by multiplying the 'rate' variable (percentage of high phytolith containing plants in the diet, i.e., Rabeno and Pearson's, 2011: Phytolith load B) against the 'duration' variable (maximum recorded lifespan of each species). It should be noted, however, that Rabeno and Pearson's (2011) 'Phytolith load' measures do not

incorporate extrinsic wear agents. Adherent grit and other particles may well play a significant role in wearing teeth, and the amount of extrinsic wear agent consumption across species, whether because of dietary or habitat differences, may differ enough to confound our analyses. Therefore, the rate variable could be improved by incorporating information on extrinsic wear agents, some of which have been shown to cause dental wear among primates (e.g., Daegling and Grine, 1999). However, accounting for these extrinsic wear agents proved too difficult to address in our current study. Regardless of the issues outlined above, our analyses demonstrated enough statistical power to return significant associations between our wear index and enamel thickness, as well as between durophagy and enamel thickness.

Cacajao calvus and *Chiropotes satanas* represent an interesting case for understanding enamel thickness. There is a good deal of evidence suggesting that these species are durophagous (e.g., Ayres, 1989; Kinzey and Norconk, 1990) but these species are not durophagous in terms of mastication; they process the hardest portions of their foods, the seed husks, with their anterior dentition. The softer more pliable seeds are chewed with their post-canine teeth (Kinzey and Norconk, 1990; Martin et al., 2003). This is a different processing technique than that exhibited by *Cercocebus atys*, which crushes hard objects with its post-canine teeth (McGraw et al., 2011). Thus, the feeding behavior of *C. calvus* and *C. satanas* suggests that there may not have been a strong selective pressure for thick post-canine enamel in these species. Martin et al. (2003) specifically cite the feeding behavior data in explaining why these species have thinner than expected enamel given their durophagous diets. The analyses presented here focused on the post-

Table 4
Results of generalized linear model controlling for phylogeny.

Coefficients	Estimate	Standard error	T-value	p-value
Intercept	2.1188	0.2413	8.779	<0.001
Wear index	0.1281	0.0790	1.620	0.129
Durophagy	0.1825	0.1032	1.768	0.101
Folivory	-0.0278	0.0116	-2.394	0.033*

$\lambda = 0.835$, model F-statistic: 4.464 p-value = 0.0173, $r^2 = 0.507$.

Table 5
Results of 'BRUNCH' phylogenetically controlled test for durophagy effect.

Coefficients	Estimate	Standard error	T-value	p-value
Durophagy	0.6653	0.2273	2.927	0.042*

$r^2 = 0.6817$.

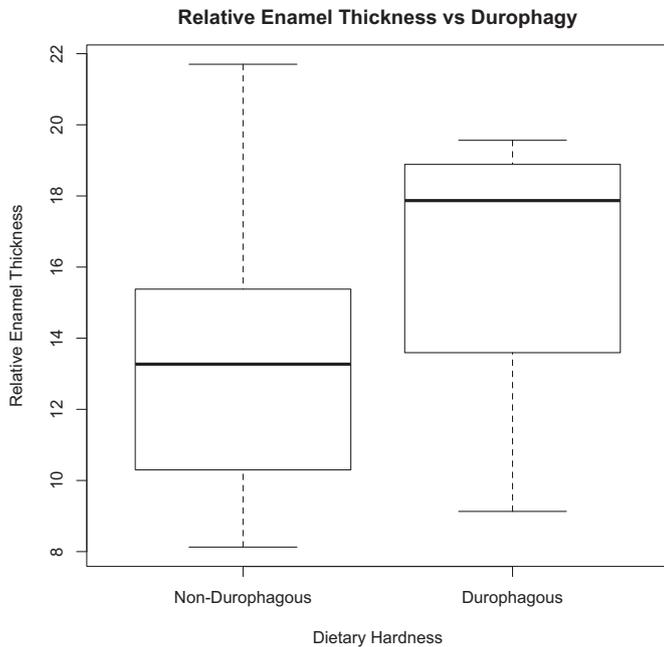


Figure 2. Box plot of RET values for durophagous and non-durophagous species. BRUNCH correction for phylogeny revealed a significant association between durophagy and RET.

canine dentition, and thus, a case could be made for treating the pitheciines as ‘non-durophagous.’ However, re-conducting our analyses with the pitheciines classified as non-durophagous did not alter the outcomes of our tests. In fact, this iteration strengthened the r^2 - and p -values in demonstrating associations between our wear index, and RET, as well as RET and durophagy ($p = 0.003$, $r^2 = 0.614$). Thus, while these species may not routinely crush hard foods with their post-canine teeth, classifying them as durophagous does not significantly impact our models; furthermore, their post-canine enamel thickness may be tuned to their relatively low amount of lifetime dental wear.

One other statistical result is worth briefly mentioning. Dropping the durophagous taxa from the data set, and testing for phylogenetic effect, showed that phylogeny did not have a significant impact on the covariation of wear-index and RET. It is tempting to argue then that the phylogenetic effect in the data set is contained within the durophagous taxa. However, it may also be a by-product of the small size of the non-durophagous subset. At any rate, in spite of the smaller sample size of the non-durophagous subset, the signal between our wear index and enamel thickness was large enough to manifest in a significant p -value ($p = 0.018$).

Adaptive value of thick enamel

Our results are consistent with the interpretation that thick enamel helps tooth crowns resist fracture during high loading,

Table 6
Results of generalized linear model without durophagous species.

Coefficients	Estimate	Standard error	T-value	p-value
Intercept	1.7771	0.2651	6.704	<0.001
Wear Index	0.2831	0.0932	3.038	0.018*
Leaves	-0.0414	0.0135	-3.080	0.017*

Tests for phylogenetic effect returned no significant phylogenetic constraint on the subset not including durophagous taxa. Model F -statistic: 5.84, p -value = 0.026, $r^2 = 0.625$.

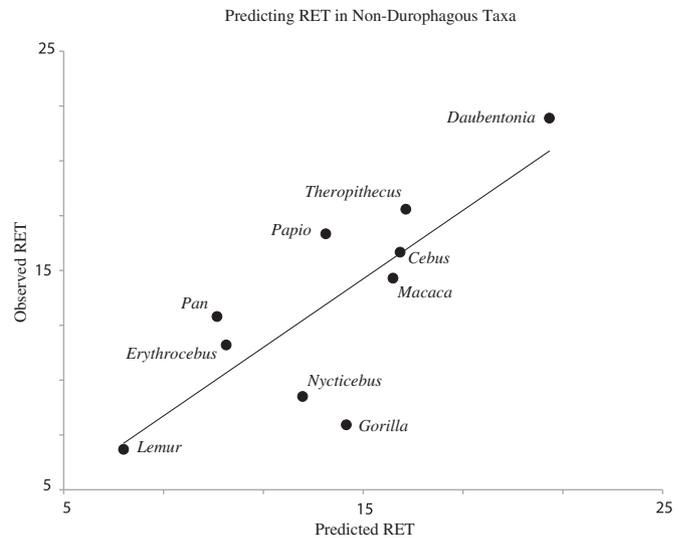


Figure 3. Plot shows predicted RET values (based on results presented in Table 6) against actual measures for RET among the non-durophagous species. $r^2 = 0.625$, $p = 0.026$.

a point particularly significant for durophagous primates (Table 5, Fig. 2). This is not a new conclusion; abundant evidence suggests that thick enamel is associated with the processing of hard foods (e.g., Kay, 1981; Dumont, 1995; Shellis et al., 1998; Lambert et al., 2004; Lucas et al., 2008a; Lee et al., 2010). However, our results also demonstrate an association between enamel thickness and dietary wear such that primates who have more abrasive diets, and live for a substantial period of time, have thicker enamel caps.

In a post hoc analysis of our data set, we took the five thickest-enameled durophagous primates and the five thickest-enameled non-durophagous primates and compared enamel thickness between them (Table 7). We performed a 10,000-iteration bootstrap, which pooled all 10 observations (species RET-values) sampling two sets of five with replacement. Means differences in RET were then calculated between the bootstrapped sets and the number of times they exceeded the original observed mean difference (durophagous RET mean minus non-durophagous RET mean) was recorded. The number of iterations exceeding the original mean difference was divided by 10,000 (the number of bootstrap iterations) to provide a p -value. This analysis of RET means showed no significant difference in the enamel thickness of these ten species ($p = 0.11$). This is consistent with the hypothesis that thick enamel may arise as an adaptation to two different sets of feeding demands. The close association between enamel thickness and the mechanical challenges of diet and food processing likely contributes to enamel thickness’ high degree of evolutionary plasticity, particularly among primates (Hlusko, 2004; Kelley and Swanson, 2008). Additionally, most mammal clades that have a large degree of dietary wear to cope with (e.g., Equidae, Castoridae), have evolved

Table 7
Species included in the post-hoc bootstrap analysis.

Durophagous species	RET	Non-durophagous species	RET
<i>Cercocebus atys</i>	19.565	<i>Daubentonia madagascariensis</i>	21.702
<i>Cebus apella</i>	19.450	<i>Theropithecus gelada</i>	15.585
<i>Lophocebus albigena</i>	18.325	<i>Papio cynocephalus</i>	15.380
<i>Cercocebus torquatus</i>	17.869	<i>Cebus capucinus</i>	15.130
<i>Pongo pygmaeus</i>	15.650	<i>Macaca mulatta</i>	13.585

Post-hoc 10,000 iteration bootstrap analysis revealed no significant differences between durophagous and non-durophagous RET values among the 10 thickest enameled species in the data set ($p = 0.11$).

hypsodonty and hypselodonty (Janis and Fortelius, 1988), but primates—for some reason—have been constrained from developing these adaptations in spite of their unusually long lifespans (Harvey et al., 1987). Perhaps the only available adaptive recourse for dealing with dental wear among primates is to thicken the enamel caps.

Enamel is a highly complex composite material constructed of long prisms of varying shapes, integrated via a variety of different patterns, and containing variable material properties; i.e., enamel is unlikely to be structurally identical across taxa (Maas and Dumont, 1999; Teaford, 2007). For this reason, several researchers have argued that the type and orientation of prism patterns expressed in enamel will impact not only the speed at which wear occurs (Maas and Dumont, 1999; Teaford, 2007), but also enamel's ability to halt fractures and prevent catastrophic tooth failure (von Koenigswald et al., 1987; Martin et al., 2003). Teaford (2007) argues that these are competing demands, either an enamel pattern is best suited to resist surface wear, in which case the enamel prisms are undecussated and radiate out towards the occlusal surface, or it is best suited to halt enamel crack propagation with a high degree of decussation, and enamel prisms oriented more horizontally with reference to the occlusal surface. In other words, there is no enamel pattern ideally suited to do both. This also means that enamel pattern may offer an alternative selective target for tuning teeth to particular dietary requirements (von Koenigswald et al., 1987; Rensberger, 1993). This complication in enamel tissue variation was not controlled for in our analyses and any attempt to include information on the degree of enamel decussation would have further limited our already small data set. However, we believe this to be a potentially fertile area for future research, particularly in reference to enamel's differing microstructure, and the ability of those various microstructural patterns to resist a lifetime of dietary wear.

Lastly, our analyses indicate that enamel thickness is negatively associated with degree of folivory. Ungar and colleagues' (Ungar and Williamson, 2000; Ungar and M'Kirera, 2003) investigations of enamel wear and surface crenulations have provided some evidence for a potential benefit to thin enamel, or at least an uneven thickness of the enamel cap, in folivorous species (see also, Rensberger, 1973; Kay, 1981). This suggests that enamel is 'designed to wear' so that exposed enamel dentine interfaces can act as sharp cutting surfaces during leaf mastication. Our multi-species comparison provides circumstantial support for this hypothesis.

Enamel thickness and the paleontological record

What implications do these results have for inferring the diets of fossil taxa? Ungar (1998) noted that in order for a dental trait to have value in interpreting the paleontological record, it must be uniquely linked to a specific diet, or usage pattern, or be a part of a unique suite of characteristics associated with a specific diet or usage pattern (see also Kay, 1984). While interpretations of thick enamel as part of a unique suite of characters used in durophagy are still valid, our models demonstrate that thick enamel also has adaptive value in resisting wear over the lifespan of an individual. Therefore, our analysis suggests that thick enamel by itself is not a diagnostic characteristic of durophagy. Modern humans are an example of a thick-enameled primate that does not appear to be adapted to hard or stiff diet (RET \approx 21.47 [Shellis et al., 1998]). Indeed, in terms of hardness or stiffness, the most challenging food items consumed by humans tend to be pre-orally processed with simple tools or cooking, and this cultural adaptation may have arisen as far back as 1.9 million years ago with the rise of *Homo ergaster* (Wrangham and Conklin-Brittain, 2003). In fact, only a small amount of roasting dramatically changes the mechanical properties of the most masticatorily demanding foods in the Hadza

diet, a group thought to exhibit a very primitive diet (Dominy et al., 2008). Chimpanzees also frequently use simple tools to process difficult to chew food items prior to ingestion (Boesch and Boesch, 1982). Therefore, it is conceivable that thick-enameled hominins, phylogenetically bracketed by tool-using chimps and humans, would have pre-orally processed hard food objects with simple tools rather than break them down with their post-canine teeth. The thick molar enamel observed in several species of *Australopithecus*, *Homo*, and *Paranthropus* could be related to an abrasive diet (Laden and Wrangham, 2005) or a mildly abrasive diet coupled with an ape-like lifespan (Teaford and Ungar, 2000).

The available evidence for the genus *Paranthropus* suggest a range in RET values for *Paranthropus robustus* of 23.82–29.61, and a range for *Paranthropus boisei* of 30.97–38.58 (Grine and Martin, 1988). Traditionally, these hyper-thick enamel measures have been used in support of durophagy in this genus (e.g., Kay, 1985; Constantino et al., 2009). However, recent isotopic insights suggest that the genus may have been more dietarily diverse than originally supposed. While *P. robustus* may well have been adapted to durophagy (Kay, 1985; Constantino et al., 2009), grains, sedges or other types of C₄ biomass appear to have made up a considerable portion of the diet of *P. boisei*, suggesting that at least this extinct taxon was not durophagous (Cerling et al., 2011). While it is possible that adherent grit and other wear agents were involved in the selection for thicker enamel in *P. boisei*, grasses and sedges, respectively, fall into the plant families Gramineae and Cyperaceae, both of which are known for high phytolith production (Piperno, 1988). Our model would predict that a species with a phytolith load similar to that of *Theropithecus* and with an ape-like lifespan of 50–60 years would have an RET higher than any taxa in our current data set. Indeed, if our model and hypothesis are correct, lifetime dietary wear could effectively explain the adaptive value of hyper-thick enamel seen in at least some members of *Paranthropus* and may be a useful tool for exploring the feeding ecology of other extinct primates generally. Perhaps some of the ideas on hominin origins and adaptations originally posited by Jolly (1970) and Du Brul (1977) should be revisited.

It is important to point out that recently Rabenold and Pearson (2011) have investigated the role of phytolith consumption in thickening enamel caps in primates. Indeed, their 'Phytolith Load B,' which is a measure of the percentage of the total diet composed of phytolith rich plants, was employed here in generating our wear index, enabling a more thorough investigation of the several selective pressures influencing enamel thickness. Rabenold and Pearson (2011) also report and use in their analyses 'Phytolith Load A,' which is the percentage of the plant-only portion of the diet rich in phytoliths. However, because only Phytolith Load B was incorporated into the present study (in addition to the way it was integrated to form our wear index), the conclusions reached here are slightly different from theirs and are worth outlining. Rabenold and Pearson's (2011:7) analyses and results cause them to argue that "in thick enameled primates, Phytolith Load B must be substantially lower than Phytolith Load A, a pattern that correlates with decreased percentage of plant foods in the diet." Under this interpretation, a hyper-thick enameled species like *P. boisei* should have a large portion of their diet composed of non-plant based materials, because Phytolith Load B is an assessment of the amount of phytoliths consumed as a percentage of the entire diet, and their analyses indicate that Phytolith Load B is negatively correlated with enamel thickness. Rabenold and Pearson's (2011) results therefore suggest that meat or some other type of food was an important part of *P. boisei*'s diet, although they explicitly argue that *P. boisei* was probably adapted to consuming the pith of sedges. Our finding of positive correlation between wear index and enamel thickness prompts us to posit the slightly different argument that the thick-

enameled *P. boisei* was a true C₄-plant specialist, using its large bunodont teeth as mill stones for grasses and sedges. More importantly, we argue that it is the interaction between longevity and abrasive diets that generated the thick enamel seen in *P. boisei* and that this interaction effect may well have played a role in thickening hominin enamel caps generally.

Conclusion

Results from comparative analyses of extant primates indicate that enamel thickness can be linked to lifetime dietary wear and that primates who have both long lifespans and high-wear diets tend to have thick enamel. The results presented here also demonstrate an association between enamel thickness and durophagy. We hypothesize that thickening of the enamel cap is an adaptation for both maintaining masticatory competence of the dentition in the face of lifetime dietary wear and a durophagous diet (i.e., is a homoplastic trait). Thus, enamel thickness, which seems to be an evolutionarily plastic trait, is influenced by an array of diet-related factors and by itself is an opaque indicator for the diets of extinct taxa.

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References

- Arola, D., Bajaj, D., Ivancik, J., Majd, H., Zhang, D., 2010. Fatigue of biomaterials: hard tissues. *Int. J. Fatigue* 32, 1400–1412.
- Ayres, J.M., 1989. Comparative feeding ecology of the uakari and bearded saki, *Cacajao* and *Chiropotes*. *J. Hum. Evol.* 18, 697–716.
- Baker, G., Jones, L.H.P., Wardrop, I.D., 1959. Causes of wear in sheeps' teeth. *Nature* 184 (4698), 1583–1584.
- Beynon, A.D., Wood, B.A., 1986. Variations in enamel thickness and structure in East African hominids. *Am. J. Phys. Anthropol.* 70, 177–193.
- Boesch, C., Boesch, H., 1982. Optimisation of nut-cracking with natural hammers by wild chimpanzees. *Behaviour* 83 (3/4), 265–286.
- Bowler, M., Bodmer, R.E., 2011. Diet and food choice in Peruvian red uakari (*Cacajao calvus ucayalii*): selective or opportunistic seed predation? *Int. J. Primatol.* 32, 1109–1122.
- Boydé, A., 1990. Developmental interpretations of dental microstructure. In: DeRousseau, C.J. (Ed.), *Primate Life History and Evolution*. Wiley-Liss, New York, pp. 229–267.
- Cerling, T.E., Mbua, E., Kiera, F.M., Manthi, F.K., Grine, F.E., Leakey, M.G., Sponheimer, M., Uno, K.T., 2011. Diet of *Paranthropus boisei* in the early Pleistocene of East Africa. *Proc. Natl. Acad. Sci.* 108 (23), 9337–9341.
- Constantino, P.J., Lucas, P.W., Lee, J.J.-W., Lawn, B.R., 2009. The influence of fallback foods on great ape tooth enamel. *Am. J. Phys. Anthropol.* 140, 653–660.
- Constantino, P.J., Lee, J.J.-W., Morris, D., Lucas, P.W., Hartstone-Rose, A., Lee, W.-K., Dominy, N.J., Cunningham, A., Wagner, M., Lawn, B.R., 2011. Adaptation to hard-object feeding in sea otters and hominins. *J. Hum. Evol.* 61, 89–96.
- Cuozzio, F.P., Sauther, M.L., 2006. Severe wear and tooth loss in wild ring-tailed lemurs (*Lemur catta*): a function of feeding ecology, dental structure, and individual life history. *J. Hum. Evol.* 51 (5), 490–505.
- Daegling, D.J., Grine, F.E., 1999. Terrestrial foraging and dental microwear in *Papio ursinus*. *Primates* 40 (4), 559–572.
- Daegling, D.J., McGraw, W.S., Ungar, P.S., Pampush, J.D., Vick, A.E., Bitty, E.A., 2011. Hard-object feeding in sooty mangabeys (*Cercocebus atys*) and interpretation of early hominin feeding ecology. *PLoS One* 6 (8), e23095. <http://dx.doi.org/10.1371/journal.pone.0023095>.
- de Magalhaes, J.P., Coasta, J., 2009. A database of vertebrate longevity records and their relation to other life-history traits. *J. Evol. Biol.* 22 (8), 1770–1774.
- DeGusta, D., Everett, M.A., Milton, K., 2003. Natural selection on molar size in a wild population of howler monkeys (*Alouatta palliata*). *Proc. R. Soc. Lond. B* 270 (Suppl.), S15–S17.
- Dominy, N.J., Vogel, E.R., Yeakel, J.D., Constantino, P.J., Lucas, P.W., 2008. Mechanical properties of plant underground storage organs and implications for dietary models of early hominins. *Evol. Biol.* 35, 159–175.
- Du Brul, E.L., 1977. Early hominid feeding mechanisms. *Am. J. Phys. Anthropol.* 47, 305–320.
- Dumont, E.R., 1995. Enamel thickness and dietary adaptation among extant primates and chiropterans. *J. Mammal.* 76 (4), 1127–1136.
- Dunbar, R.I.M., 1976. Australopithecine diet based on a baboon analogy. *J. Hum. Evol.* 5, 161–167.
- Ernest, S.K.M., 2003. Life history characteristics of placental nonvolant mammals: ecological archives E084-093. *Ecol.* 84 (12), 3402.
- Felsenstein, J., 1985. Phylogenies and the comparative method. *Am. Nat.* 125 (1), 1–15.
- Fleagle, J.G., 1999. *Primate Adaptation and Evolution*, second ed. Academic Press, New York.
- Freckleton, R.P., Harvey, P.H., Pagel, M., 2002. Phylogenetic analysis and comparative data: a test and review of the evidence. *Am. Nat.* 160 (6), 712–726.
- Goldstein, S.J., Richard, A.F., 1989. Ecology of rhesus macaques (*Macaca mulatta*) in northwest Pakistan. *Int. J. Primatol.* 10 (6), 531–567.
- Grine, F.E., Martin, L.B., 1988. Enamel thickness and development in *Australopithecus* and *Paranthropus*. In: Grine, F.E. (Ed.), *Evolutionary History of the "Robust" Australopithecines*. Aldine de Gruyter, New York, pp. 3–42.
- Grine, F.E., Spencer, M.A., Demes, B., Smith, H.F., Strait, D.S., Constant, D.A., 2005. Molar enamel thickness in the chacma baboon, *Papio ursinus* (Kerr 1792). *Am. J. Phys. Anthropol.* 128, 812–822.
- Hakeem, A., Sandoval, R., Jones, M., Allman, J., 1996. Brain and life span in primates. In: Birren, J. (Ed.), *Handbook of the Psychology of Aging*. Academic Press, Burlington, Massachusetts, pp. 78–104.
- Harvey, P.H., Martin, R.D., Clutton-Brock, T.H., 1987. Life histories in comparative perspective. In: Smuts, B.B., Cheney, D.L., Seyfarth, R.M., Wrangham, R.W., Struhsaker, T.T. (Eds.), *Primate Societies*. University of Chicago Press, Chicago, pp. 181–196.
- Hillson, S., 1986. *Teeth*. Cambridge University Press, Cambridge.
- Hlusko, L.J., 2004. Integrating the genotype and phenotype in hominid paleontology. *Proc. Natl. Acad. Sci.* 101 (9), 2653–2657.
- Isbell, L.A., 1998. Diet for a small primate: insectivory and gummivory in the (large) Patas monkey (*Erythrocebus patas pyrrhonotus*). *Am. J. Primatol.* 45, 381–398.
- Izawa, K., Mizuno, A., 1977. Palm-fruit cracking behavior of wild black-capped capuchin (*Cebus apella*). *Primates* 18 (4), 773–792.
- Janis, C.M., Fortelius, M., 1988. On the means whereby mammals achieve increased functional durability of their dentitions, with special reference to limiting factors. *Biol. Rev.* 63 (2), 197–230.
- Jolly, C.J., 1970. The seed-eaters: a new model of hominid differentiation based on a baboon analogy. *Man* 5 (1), 5–26.
- Kay, R.F., 1975. The functional adaptations of primate molar teeth. *Am. J. Phys. Anthropol.* 43, 195–216.
- Kay, R.F., 1981. The nut-crackers – a new theory of the adaptations of the Ramapithecinae. *Am. J. Phys. Anthropol.* 55 (2), 141–151.
- Kay, R.F., 1984. On the use of anatomical features to infer foraging behavior in extinct primates. In: Rodman, P.S., Cant, J.G.H. (Eds.), *Adaptations for Foraging in Nonhuman Primates: Contributions to an Organismic Biology of Prosimians, Monkeys, and Apes*. Columbia University Press, New York, pp. 21–53.
- Kay, R.F., 1985. Dental evidence for the diet of *Australopithecus*. *Ann. Rev. Anthropol.* 14, 315–341.
- Kay, R.F., Covert, H.H., 1983. True grit: a microwear experiment. *Am. J. Phys. Anthropol.* 61, 33–38.
- Kelley, J.L., Swanson, W.J., 2008. Dietary change and adaptive evolution of enamelin in humans and among primates. *Genetics* 178, 1595–1603.
- Kenney, W.F., Brenner, M., Curtis, J.H., Schelske, C.L., 2010. Identifying sources of organic matter in sediments of shallow lakes using multiple geochemical variables. *J. Paleolimnol.* 44 (4), 1039–1052.
- King, S.J., Arrigo-Nelson, S.J., Pochron, S.T., Semperebon, G.M., Godfrey, L.R., Wright, P.C., Jernvall, J., 2005. Dental senescence in a long-lived primate links infant survival to rainfall. *Proc. Natl. Acad. Sci.* 102 (46), 16579–16583.
- Kinzey, W.G., Norconk, M.A., 1990. Hardness as a basis of fruit choice in two sympatric primates. *Am. J. Phys. Anthropol.* 81, 5–15.
- Koenigswald, W., von Rensberger, J.M., Pfretzschner, H.U., 1987. Changes in the tooth enamel of early Paleocene mammals allowing increased dietary diversity. *Nature* 328, 150–151.
- Laden, G., Wrangham, R., 2005. The rise of the hominids as and adaptive shift in fallback foods: plant underground storage organs (USOs) and australopithecine origins. *J. Hum. Evol.* 49 (4), 482–498.
- Lambert, J.E., Chapman, C.A., Wrangham, R.W., Conklin-Brittain, N.L., 2004. Hardness of cercopithecine foods: implications for the critical function of enamel thickness in exploiting fallback foods. *Am. J. Phys. Anthropol.* 125 (4), 363–368.
- Lee, J.J.-W., Morris, D., Constantino, P.J., Lucas, P.W., Smith, T.M., Lawn, B.R., 2010. Properties of tooth enamel in great apes. *Acta Biomater.* 6, 4560–4565.
- Lucas, P.W., Constantino, P.J., Wood, B., Lawn, B.R., 2008a. Dental enamel as a dietary indicator in mammals. *BioEssays* 30, 374–385.
- Lucas, P.W., Constantino, P.J., Wood, B.A., 2008b. 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, P.W., Constantino, P.J., Chalk, J., Zisocovic, C., Wright, B.W., Fragaszy, D.M., Hill, D.A., Lee, J.J.-W., Chai, H., Darvell, B.W., Lee, P.K.D., Yuen, T.D.B., 2009. Indentation as a technique to assess the mechanical properties of fallback foods. *Am. J. Phys. Anthropol.* 140, 643–652.
- Maas, M.C., Dumont, E.R., 1999. Built to last: the structure, function and evolution of primate dental enamel. *Evol. Anthropol.* 8, 133–152.
- Martin, L.B., 1983. The relationships of the Later Miocene Hominoidea. Ph.D. Dissertation, University College London.
- Martin, L.B., 1985. Significance of enamel thickness in hominoid evolution. *Nature* 314, 260–263.
- Martin, L.B., Olejniczak, A.J., Maas, M.C., 2003. Enamel thickness and microstructure in pitheciine primates, with comments on dietary adaptations of the middle Miocene hominoid *Kenyapithecus*. *J. Hum. Evol.* 45, 351–367.
- McGraw, W.S., Vick, A.E., Daegling, D.J., 2011. Sex and age differences in the diet and ingestive behaviors of sooty mangabeys (*Cercocebus atys*) in the Tai Forest, Ivory Coast. *Am. J. Phys. Anthropol.* 144 (1), 140–153.
- McGraw, W.S., Pampush, J.D., Daegling, D.J., 2012. Brief communication: enamel thickness and durophagy in mangabeys revisited. *Am. J. Phys. Anthropol.* 147 (2), 326–333.
- Molnar, S., Gantt, D.G., 1977. Functional implications of primate enamel thickness. *Am. J. Phys. Anthropol.* 46, 447–454.
- Nakagawa, N., 1989. Activity budget and diet of Patas monkeys in Kala Maloue National Park, Cameroon: a preliminary report. *Primates* 30 (1), 27–34.
- Pagel, M.D., 1999. Inferring the historical patterns of biological evolution. *Nature* 401, 877–884.
- Piperno, D.R., 1988. *Phytolith Analysis: An Archaeological and Geological Perspective*. Academic Press, New York.
- Purvis, A., Rambaut, A., 1995. Comparative analysis by independent contrasts (CAIC): an apple macintosh application for analysing comparative data. *Comput. Appl. Biosci.* 11, 245–251.
- Rabenold, D., Pearson, O.M., 2011. Abrasive, silica phytoliths and the evolution of thick molar enamel in primates, with implications for the diet of *Paranthropus boisei*. *PLoS One* 6 (12), e28379. <http://dx.doi.org/10.1371/journal.pone.0028379>.
- Rensberger, J.M., 1973. Occlusion model for mastication and dental wear in herbivorous mammals. *J. Paleontol.* 47, 515–528.
- Rensberger, J.M., 1993. Adaptation of enamel microstructure to differences in stress intensity in the Eocene perissodactyl *Hyracotherium*. In: Kobayashi, I., Mutvei, H., Sahn, A. (Eds.), *Structure, Formation, and Evolution of Fossil Hard Tissues*. Tokai University Press, Tokyo, pp. 131–145.
- Schwartz, G.T., 2000a. Enamel thickness and the helicoidal wear plane in modern human mandibular molars. *Arch. Oral Biol.* 45, 401–409.
- Schwartz, G.T., 2000b. Taxonomic and functional aspects of the patterning of enamel thickness distribution in extant large-bodied hominoids. *Am. J. Phys. Anthropol.* 111, 221–224.
- Shellis, R.P., Beynon, A.D., Reid, D.J., Hiiemae, K.M., 1998. Variations in molar enamel thickness among primates. *J. Hum. Evol.* 35, 507–522.
- Smith, T.M., Olejniczak, A.J., Martin, L.B., Reid, D.J., 2005. Variation in hominoid molar enamel thickness. *J. Hum. Evol.* 48, 575–592.
- Sperber, G.H., 1974. Comparative primate dental enamel thickness: a radiodontological study. In: Tobias, P.V. (Ed.), *Hominid Evolution: Past, Present and Future Proceedings of the (Taung) Diamond Jubilee International Symposium*. Alan R. Liss, New York, pp. 443–454.
- Strait, S.C., 1997. Tooth use and the physical properties of food. *Evol. Anthropol.* 5 (6), 199–211.
- Sussman, R.W., 1974. Ecological distinctions of sympatric species of Lemur. In: Martin, R.D., Doyle, G.A., Walker, A.C. (Eds.), *Prosimian Biology*. University of Pittsburgh Press, Pittsburgh, pp. 75–108.
- Swindler, D.R., 2002. *Primate Dentition: An Introduction to the Teeth of Non-human Primates*. University Press, Cambridge.
- Teaford, M.F., 2007. What do we know and not know about diet and enamel structure? In: Ungar, P.S. (Ed.), *Evolution of the Human Diet: The Known, the Unknown, and the Unknowable*. Oxford University Press, New York, pp. 56–76.
- Teaford, M.F., Ungar, P.S., 2000. Diet and the evolution of the earliest human ancestors. *Proc. Natl. Acad. Sci.* 97 (25), 13506–13511.
- Ungar, P.S., 1998. Dental allometry, morphology, and wear as evidence for diet in fossil primates. *Evol. Anthropol.* 6 (6), 205–217.
- Ungar, P.S., Williamson, M., 2000. Exploring the effects of tooth wear on functional morphology: a preliminary study using dental topographic analysis. *Palaeontol. Electronica* 3 (1), 1–18.
- Ungar, P.S., M'Kirera, F., 2003. A solution to the worn tooth conundrum in primate functional anatomy. *Proc. Natl. Acad. Sci.* 100 (7), 3874–3877.
- Vogel, E.R., van Woerden, J.T., Lucas, P.W., Utami Atmoko, S.S., van Schaik, C.P., Dominy, N.J., 2008. Functional ecology and evolution of hominoid molar enamel thickness: *Pan troglodytes schweinfurthii* and *Pongo pygmaeus wurmbii*. *J. Hum. Evol.* 55, 60–74.
- Walker, P., Murray, P., 1975. An assessment of masticatory efficiency in a series of anthropoid primates with special reference to the Colobinae and Cercopitheciinae. In: Tuttle, R.H. (Ed.), *Primate Functional Morphology and Evolution*. Mouton and Co., Chicago, pp. 135–150.
- White, T.D., Asfaw, B., Beyene, Y., Haile-Selassie, Y., Lovejoy, C.O., Suwa, G., WoldeGabriel, G., 2009. *Ardipithecus ramidus* and the paleobiology of early hominids. *Science* 326, 76–86.
- Wiens, F., Zitzmann, A., Hussein, N.A., 2006. Fast food for slow lorises: is low metabolism related to secondary compounds in higher-energy plant diet? *J. Mammal.* 87 (4), 790–798.
- Wrangham, R., Conklin-Brittain, N.L., 2003. Cooking as a biological trait. *Comp. Biochem. Physiol. A* 136, 35–46.
- Yamashita, N., 1998. Functional dental correlates of food properties in five Malagasy lemur species. *Am. J. Phys. Anthropol.* 106, 169–188.