



# Dietary ecology of fossil *Theropithecus*: Inferences from dental microwear textures of extant geladas from ecologically diverse sites



Amy E. Shapiro <sup>a, \*</sup>, Vivek V. Venkataraman <sup>b</sup>, Nga Nguyen <sup>c, d, e</sup>, Peter J. Fashing <sup>c, d, e</sup>

<sup>a</sup> School of Human Evolution and Social Change, Arizona State University, Tempe, AZ 85287, USA

<sup>b</sup> Department of Biological Sciences, Dartmouth College, Hanover, NH 03755, USA

<sup>c</sup> Department of Anthropology, California State University Fullerton, Fullerton, CA 92834, USA

<sup>d</sup> Environmental Studies Program, California State University Fullerton, Fullerton, CA 92834, USA

<sup>e</sup> Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biosciences, University of Oslo, Oslo, Norway

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## ABSTRACT

As the only extant graminivorous primate, gelada monkeys (*Theropithecus gelada*) offer unique insights into how hominins and other extinct primates with strong C<sub>4</sub> isotopic signatures may have subsisted on graminoid-rich diets. Fossil *Theropithecus* species sharing a strong C<sub>4</sub> signal (i.e., *Theropithecus brumpti*, *Theropithecus darti*, and *Theropithecus oswaldi*) have been reconstructed as predominantly graminivorous and potentially in ecological competition with contemporaneous hominins. However, inferring the breadth and variation of diet in these species (and therefore hominins) has proven problematic. Understanding how ecological variation within extant geladas impacts microwear and isotopic signatures may contribute to reconstructions of diet in fossil *Theropithecus*. Here, we build on a recent study at an ecologically intact tall grass ecosystem (Guassa, Ethiopia) that expanded the known diversity of gelada diets by demonstrating lower reliance on graminoids, greater consumption of forbs, and greater dietary species richness than previously described at disturbed sites. We used dental microwear texture analysis to explore how dietary variation among extant geladas may inform our understanding of the diets of fossil *Theropithecus*. First, we compared the dental microwear textures of geladas at Guassa to those of geladas from other sites. The microwear textures of geladas at Guassa exhibited more complexity, less anisotropy, and more variance in anisotropy and heterogeneity, reflecting the greater dietary diversity of Guassa geladas. Comparing microwear texture variables among this expanded gelada sample to those for *T. brumpti*, *T. oswaldi*, and *T. darti* yielded no significant differences. These results raise the intriguing possibility that data on how ecological variation and diet impact dental microwear and (possibly) isotopic signatures in extant geladas can be used to reconstruct the diets of extinct theropithecids and, more broadly, hominins with strong C<sub>4</sub> isotopic signatures. We conclude that extant gelada populations offer a powerful analog for inferring dietary variation among predominantly graminivorous fossil primates.

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## 1. Introduction

The influence of open environments on the dietary ecology and evolution of hominins is a topic of long-standing interest to paleoanthropologists (Dart, 1925; Robinson, 1963; Jolly, 1970; Vrba, 1988; Aiello and Wheeler, 1995; Reed, 1997; Cerling et al., 2011). In the past decade, studies based on stable carbon isotopes have concluded that several hominin species (e.g., *Paranthropus boisei*

[Cerling et al., 2011, 2013], *Australopithecus bahrelghazali* [Lee-Thorp et al., 2012], and *Australopithecus afarensis* [Wynn et al., 2013]) consumed diets consisting of up to ~80% C<sub>4</sub> foods.<sup>1</sup> The focus on C<sub>4</sub> foods poses a stark contrast to chimpanzees, which

<sup>1</sup> C<sub>4</sub> and C<sub>3</sub> refer to different carbon fixation pathways used by plants. From hard tissues, stable carbon isotope analyses can estimate the contributions of C<sub>4</sub> plants (mostly tropical grasses and sedges) and C<sub>3</sub> plants (most other plants such as trees, shrubs, and non-tropical grasses and sedges), or the animals that consumed these plants, in the diet of fossil species. Tissues high in C<sub>4</sub> indicate a substantial open environment component to the diet since C<sub>4</sub> plants are found almost exclusively in open environments.

\* Corresponding author.

E-mail address: [aeshapiro@asu.edu](mailto:aeshapiro@asu.edu) (A.E. Shapiro).

exhibit C<sub>3</sub> isotopic signatures even in open environments where edible C<sub>4</sub> foods are abundant (Schoeninger et al., 1999; Carter, 2001; Sponheimer et al., 2006). In concert with these isotopic findings, dental microwear studies of East African hominins (Ungar et al., 2008, 2010; Grine et al., 2012) have called into question the long-standing assumption that the derived suite of dentognathic features of the robust australopiths was adapted for cracking hard objects (Kay, 1981; Lee-Thorp et al., 2012; Strait et al., 2013). The finding that *P. boisei* bears a strong C<sub>4</sub> signature similar to that of the coeval Pliocene grazing monkey *Theropithecus oswaldi* in East Africa has led to the suggestion that hominins regularly consumed grasses and/or sedges (i.e., graminoids<sup>2</sup>; van der Merwe et al., 2008; Cerling et al., 2011, 2013; Ungar and Sponheimer, 2011). This interpretation emphasizes the repetitive mastication of tough foods in the evolution of robust masticatory morphology and suggests that some hominins, like *P. boisei*, were essentially grazers in competition with graminivorous theropiths (Cerling et al., 2011, 2013; Scott et al., 2014). These studies have generated a renewed interest in the *Theropithecus* clade as a referential model for hominins (Wood and Schroer, 2012; Fashing et al., 2014). Yet as Cerling et al. (2013:10507) noted with respect to the diet of *T. oswaldi* and its relative *T. brumpti*, “many questions remain about their respective dietary specializations.”

For decades, researchers have attempted to distinguish diet among three of the most abundant fossil theropiths recovered from Plio-Pleistocene deposits (Jablonski and Frost, 2010): *T. brumpti* (3.4–2.0 Ma; East Africa), *T. darti* (3.5–2.4 Ma; East and South Africa), and *T. oswaldi* (2.5–0.25 Ma; East and South Africa). In addition to postcranial features related to manual terrestrial foraging (Jolly, 1970; Guthrie, 2011), all members of the *Theropithecus* genus exhibit expanded high-crowned molars with rugged topography and increased cusp relief (Jablonski, 1993a, b), suggesting that graminivory was primitive for the genus. In addition to morphological analysis, evidence for subsequent dietary evolution in the clade has been informed by dental microwear and stable isotope analyses.

Dental microwear directly preserves evidence of the physical properties of consumed foods on the molar surface (Teaford and Walker, 1984; Teaford, 1988; Teaford and Oyen, 1989; Scott et al., 2005; Schulz et al., 2013). Studies using scanning electron microscopy (SEM) on molar teeth suggested that primates eating tough foods, such as leaves or graminoids, would have thinner scratches and higher scratch frequencies, while primates eating hard foods, such as hard fruits and seeds, as well as grittier items, would have larger pits and higher pit frequencies (Teaford and Walker, 1984; Teaford, 1988, 1993; Teaford and Robinson, 1989; Teaford and Glander, 1996; Daegling and Grine, 1999). Using SEM on East African specimens, Teaford (1993) found more pitting and higher frequencies of wear in *T. brumpti* than in *T. oswaldi* and *Theropithecus gelada*, which he interpreted as indicating a diet containing more fruit or grit for *T. brumpti*. He also found similar frequencies and sizes of pits and scratches in *T. oswaldi* and *T. gelada*, suggesting that diets in the two species were similar. Also using SEM, El-Zaatari et al. (2005) found that *T. oswaldi* from South African sites did not differ from *T. gelada* in microwear features; additionally, these researchers examined two specimens of *T. darti* from South African sites, which were similar to the *T. gelada* and *T. oswaldi* samples (El-Zaatari et al., 2005), suggesting a similar diet in *T. darti*. Taken together, these previous analyses have suggested that the diets of *T. oswaldi* and *T. darti* were similar to that of extant *T. gelada*, while

the diet of *T. brumpti* was different, containing more wear-causing particles, either from hard fruits or grittier items.

Recent research on the isotopic ecology of fossil *Theropithecus* has painted a somewhat different picture. Cerling et al. (2013) estimated *T. brumpti* C<sub>4</sub> plant consumption at 55–75%, while *T. oswaldi* averaged ~80% and effectively 100% C<sub>4</sub> plant consumption towards the end of its temporal range. Results for *T. darti* also indicate frequent consumption of C<sub>4</sub> tissues (Lee-Thorp et al., 1989; Cerling et al., 2013). These results are in the range of modern C<sub>4</sub> grazers, indicating high amounts of C<sub>4</sub> graminoid consumption in all fossil species of *Theropithecus* (Cerling et al., 2013). Cerling et al.'s (2013) results, along with those of the Guthrie's (2011) study of the *T. brumpti* postcrania, have shifted our understanding of *T. brumpti* as a semi-arboreal frugivore (Eck and Jablonski, 1987; Benefit and McCrossin, 1990; Bobe and Behrensmeyer, 2004) to that of a terrestrially adapted open-habitat grazer.

Cerling et al.'s (2013) results invite re-interpretation of the dental microwear analyses by Teaford (1993) and El-Zaatari et al. (2005) described above. In particular, Teaford's (1993) results are compatible with those of Cerling et al. (2013) if we consider that substantial dietary variation can exist within a graminoid-eating niche. According to this framework, higher pitting and wear frequencies in *T. brumpti* could result from exogenous grit on vegetation or quartz particles adhering to underground storage organs (USOs; Lucas et al., 2013), the physical properties of graminoids (see Venkataraman et al., 2014), or some other dietary component within the larger pattern of graminivory. Addressing this question requires revisiting the dental microwear of *Theropithecus*, and particularly that of the gelada, the only extant primate graminivore, for which substantial variation in diet among populations has recently been described (Fashing et al., 2014). Furthermore, despite recent advances in microwear analysis methodology such as three-dimensional texture analysis, which is less prone to data loss and inter-observer error (Scott et al., 2005, 2006), the microwear of fossil *Theropithecus* has not been revisited since the studies of Teaford (1993) and El-Zaatari et al. (2005). Accordingly, the goal of the present study is to use three-dimensional texture analysis to explore how dietary variation among extant gelada populations may be used to reconstruct variation in the diets of fossil *Theropithecus*.

The strength of inference for inferring diet in fossil taxa depends heavily on our understanding of the feeding ecology of extant species. As the only extant grazing primate, the ecology of the gelada (*T. gelada*) is therefore fundamental to understanding broader patterns of dietary evolution in the *Theropithecus* clade. Until recently, surprisingly little was known about the dietary diversity of geladas, which has in turn complicated interpretations of fossil *Theropithecus* (Fashing et al., 2014). Geladas have traditionally been characterized as obligate graminivores (Dunbar and Bose, 1991; Jablonski, 1994; Swedell, 2011; Cerling et al., 2013), though this characterization has been based on only a few short studies in disturbed ecosystems where livestock grazing and other anthropogenic impacts are common (e.g., Bole Valley, Ethiopia: Dunbar and Dunbar, 1974; Simien Mountains National Park, Ethiopia: Dunbar, 1977; Iwamoto, 1979; Hunter, 2001).

A recent multi-year study (Fashing et al., 2014) at Guassa, a more ecologically intact site in the Menz Highlands of north-central Ethiopia, has expanded the documented diversity of gelada diets. Geladas at Guassa fed less heavily on graminoids and more heavily on forbs and invertebrates, while consuming a more species-rich diet than geladas at more disturbed sites (Fashing et al., 2014: Table 4). Further, while geladas at all sites increased consumption of USOs in the dry season, geladas at Guassa relied much less intensively on USOs than conspecifics at disturbed sites (Fashing et al., 2014).

<sup>2</sup> 'Graminoids' worldwide include the grasses, sedges, and rushes. Because extant geladas are not known to consume rushes, however, the term 'graminoids' as used in this manuscript implies only grasses and sedges.

The present study addresses how heterogeneity of the diet documented at Guassa influences dental microwear signals. Our study examined whether microwear from geladas at Guassa (a) resembled that of previously examined individuals from more degraded sites and (b) reflected the more heterogeneous diet consumed by geladas at this site. Microwear of geladas from populations living in ecologically disturbed areas tends to exhibit thin scratches and strongly directional wear or anisotropic textures (Teaford, 1993; Scott et al., 2012). The frequent dry season consumption of USOs in these geladas (Hunter, 2001), which would be expected to produce pitted features (Daegling and Grine, 1999; Lucas et al., 2013) or complex surfaces (Scott et al., 2012), is not strongly reflected in the microwear of these specimens (Teaford, 1993; Scott et al., 2012). Additionally, gelada occlusal surfaces appear homogeneous (Scott et al., 2012), potentially reflecting low variation in diet during the time microwear was accumulating in these individuals. By expanding our comparative sample to include Guassa geladas, we hope to refine our understanding of the dietary breadth of extinct *Theropithecus*.

We employed microwear texture analyses using scale-sensitive fractal analysis variables to characterize the dental surface in three dimensions at different scales; three parameters that relate to primate diets are area-scale fractal complexity ( $Asfc$ , or complexity), exact proportion length-scale anisotropy of relief ( $epLsar$ , or anisotropy), and heterogeneity of area-scale fractal complexity ( $HAsfc$ , or heterogeneity; Scott et al., 2005, 2006, 2012). Complexity measures changes in relative surface area with scale; as the scale at which area is calculated decreases, more complex surfaces have a greater increase in surface area than less complex surfaces (Scott et al., 2006). Anisotropy measures the directionality of surface roughness, such that more features in a single direction increase anisotropy while more features in many directions decrease anisotropy (Scott et al., 2006). Complexity has been shown to be greater on molars of primates that eat more hard, brittle foods, such as hard fruits, while anisotropy has been shown to be greater on molars of primates that eat tough foods, such as leaves (Scott et al., 2005, 2006, 2012; Calandra et al., 2012). Heterogeneity measures the variation in textures across the tooth's surface when it is broken down into equal size quadrants; it is related to both the size and variability in wear-causing particles and, thus, has been suggested to be greater in species with more diverse or varying diets (Scott et al., 2006, 2012).

Our predictions for microwear texture variables are based on the documented diet of Guassa geladas and previous reconstructions of fossil *Theropithecus* diets. Less frequent consumption of graminoids and greater dietary variability at Guassa suggest that Guassa geladas should have 1) greater complexity and lower anisotropy, 2) greater intra-site variance in complexity and anisotropy, and 3) greater heterogeneity than specimens from more degraded sites. For fossil analyses, we expected *T. brumpti* to have more complex microwear textures than other species of *Theropithecus* typically reconstructed as more specialized graminivores. Based on previous research, we expected no differences in microwear textures among the species *T. darti*, *T. oswaldi*, and *T. gelada*.

## 2. Materials and methods

Our extant sample included first or second molars from 24 specimens of geladas, 15 from museum collections, and nine new specimens from Guassa (see [Supplementary Online Material \[SOM\]](#)). Data from eight of the museum specimens were previously published by Scott et al. (2012). While using data collected by other individuals may introduce interobserver error, paired *t*-tests on microwear textures from five specimens analyzed by both Scott et al. (2012) and this study showed no significant differences

between collectors in any microwear variables (see [SOM](#)).<sup>3</sup> Twelve of the 15 museum specimens have known provenience and date of collection, although ecological conditions at the collection sites were not recorded. Because the specimens from Guassa were from individuals who died naturally and were generally found (opportunistically) much later on the landscape, season of death is unknown for all but one individual. This individual (MCA 601) died and was collected during the dry season (April), when thick layers of grit usually cover the vegetation at Guassa (Fashing et al., 2014; Venkataraman et al., 2014). We expected this individual to display greater complexity as grit consumption has been implicated in surface pitting (Teaford, 1993; Daegling and Grine, 1999). Five of the specimens from Guassa were also used in a recent study of gelada chewing efficiency (Venkataraman et al., 2014). For more details about ecological conditions at Guassa and the Guassa Gelada Research Project, see Fashing et al. (2014) and Nguyen et al. (2015).

Our fossil sample included 16 first or second molars of *Theropithecus* from East African Pliocene deposits, including specimens of *T. brumpti*, *T. darti*, and *T. oswaldi* (see [SOM](#)). The *T. brumpti* specimens are from Koobi Fora (Lokochot Area 117), with a time estimate of ~3.4 Ma (Jablonski et al., 2008). The *T. darti* specimens are from the Sidi Hakoma and Denen Dora Members of Hadar and have estimated ages of ~3.42–3.20 Ma (Campisano and Feibel, 2008). The *T. oswaldi* specimens are from Koobi Fora (~2–1.5 Ma), Ologesailie (~1 Ma), Olduvai (~1.98–1.86 Ma), and Omo (Shungura Formation, Member G, 2.12–2.10 Ma; Feibel et al., 1989), representing a wide range of localities and dates.

Specimens were cleaned with alcohol-soaked cotton swabs, and vinyl impressions were made using President's Jet Regular Body Dental Impression Material (Coltene-Whaledent). Specimens were molded in the field at Guassa or at the museums housing the specimens (see [SOM](#)). Molds of fossil specimens were obtained from B. Benefit or collected directly in the National Museum of Ethiopia in 2011. Casts were made using Epotek 301 epoxy resin and hardener (Epoxy Technologies) and then scanned on Phase II occlusal facets (Kay, 1977) using a Sensofar Plμ white-light scanning confocal profiler (Solaris, Sunnyvale, CA) with a 100× objective following previous studies (Scott et al., 2005, 2006, 2012). The resulting point clouds had a lateral sampling interval of 0.18 μm and a vertical resolution of 0.005 μm, and four adjoining fields were collected for a total area of 276 μm × 204 μm. Scans were leveled using Solarmap Universal software, and artifacts, such as dust particles, were excluded by thresholding and erase operators. Complexity, anisotropy, and heterogeneity were calculated through the scale-sensitive fractal analysis program Toothfrax (Surfract), and medians of the four scans were used as in previous studies (Scott et al., 2005, 2006, 2012).

We made four main comparisons in microwear textures among the *Theropithecus* groups: 1) Guassa geladas versus all other geladas, 2) gelada individuals collected in the wet season versus those collected in the dry season, 3) all *Theropithecus* individuals by species, and 4) all *Theropithecus* individuals with known collection location by site. Because microwear may be heavily impacted by foods eaten around the time of death (i.e., the 'last meal(s) eaten,' Grine, 1986), we undertook the second comparison to evaluate the impact of season of death on microwear patterns. Since time of death was known for only one Guassa specimen, only one of nine specimens in this analysis was from Guassa. Additionally, small sample size allowed only qualitative analyses for this comparison.

<sup>3</sup> It is important to note that microwear values are not expected to be equivalent for different scans of the same specimen, such as scans collected by different researchers, since each scan will differ in its topography due to differing locations on the tooth.

The fourth comparison was only conducted among sites that had three or more individuals ( $n = 7$  sites). We compared the means of microwear texture variables using Mann–Whitney  $U$  tests for the two-way comparison since the data were not normally distributed. For the multiple comparisons, we used multiple analysis of variance (MANOVA) on the natural log-transformed variables; if this was significant, we then conducted single analysis of variance (ANOVA) and post hoc Tukey's honestly significant difference (HSD) tests to identify significant differences, following previous studies (Ungar et al., 2010; Scott et al., 2012). To compare variances, we used Levene's test, which is an ANOVA on the residuals and is robust to deviances from normality, making it appropriate for testing non-normal microwear data (Donnelly and Kramer, 1999; Plavcan and Cope, 2001; Ungar et al., 2010). Using the calculated residuals rather than the log-transformed data and the default Levene's test allows for post hoc comparisons (e.g., Ungar et al., 2010). All analyses were conducted in RStudio (v. 0.98.978).

### 3. Results

#### 3.1. Guassa geladas vs. other geladas

We first compared the means and variances of microwear texture variables from Guassa to those of other geladas (Tables 1 and 2). Compared to other geladas, geladas from Guassa had 1) higher mean complexity (Mann–Whitney  $U$  test:  $U = 113$ ,  $p < 0.01$ ), 2) lower mean and variance in anisotropy (Mean, Mann–Whitney  $U$  test:  $U = 32$ ,  $p < 0.05$ ; Variance, Levene's test:  $F(1,22) = 5.31$ ,  $p < 0.05$ ), and 3) higher variance in heterogeneity (Levene's test:  $F(1,22) = 15.82$ ,  $p < 0.001$ ; Table 2, Fig. 1). Because one specimen (GUA 202) was an outlier with high complexity and heterogeneity, these tests were rerun with this specimen removed; however, all test results remained unchanged. We present photosimulations of selected enamel surfaces of geladas in Figure 2a–c.

#### 3.2. Effects of season of death on microwear textures

We then compared gelada specimens collected in the dry season (February, March, and April) to those collected at the end of the wet season (October). Because sample sizes were small (dry:  $n = 7$ , wet:  $n = 2$ ), we only compared these groups qualitatively. Specimens collected in the dry season had higher heterogeneity and marginally higher complexity than those collected in the wet season (Fig. 3), but anisotropy did not appear to differ between the seasons. The sole specimen included in this analysis from Guassa, MCA 601, belonged to an adult female that died in the dry season (April) but did not have high complexity, contrary to our expectations.

**Table 1**  
Summary statistics.<sup>a</sup>

Species	n	Asfc		epLsar		HASfc	
		Mean	SD	Mean	SD	Mean	SD
<i>T. gelada</i>	24	1.02	0.55	0.00413	0.0016	0.629	0.19
Guassa	9	1.32	0.74	0.0032	0.00093	0.745	0.28
Other Sites	15	0.835	0.31	0.00469	0.0016	0.559	0.056
Wet	2	0.717	0.13	0.00501	0.0038	0.491	0.028
Dry	7	0.991	0.41	0.00444	0.0015	0.585	0.051
<i>T. brumpti</i>	3	0.756	0.37	0.003	0.00093	0.695	0.062
<i>T. darti</i>	3	0.506	0.048	0.00428	0.0018	0.671	0.19
<i>T. oswaldi</i>	10	0.75	0.22	0.00474	0.0021	0.665	0.17

<sup>a</sup> Mean and standard deviation (SD) of complexity (Asfc), anisotropy (epLsar), and heterogeneity (HASfc) for each *Theropithecus* species and intraspecific group.

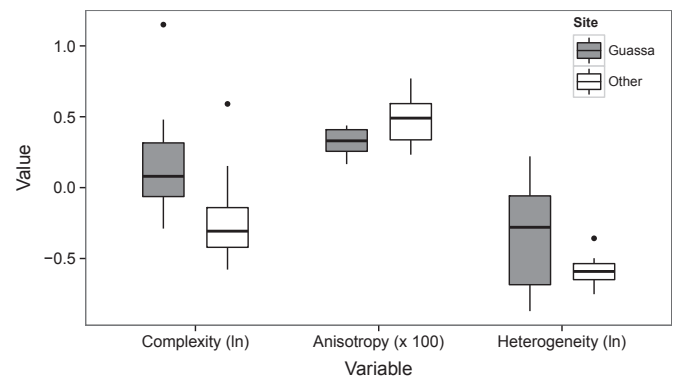
**Table 2**  
Mann–Whitney and Levene's test results.<sup>a</sup>

Variable	Mean (Mann–Whitney)		Variance (Levene's)	
	U	p	F(1, 22)	p
Asfc	113	<0.01 <sup>c</sup>	3.81	ns
epLsar	32	<0.05 <sup>b</sup>	5.31	<0.05 <sup>b</sup>
HASfc	90	ns	15.82	<0.001 <sup>c</sup>

<sup>a</sup> Tests for differences in mean and variance in complexity (Asfc), anisotropy (epLsar), and heterogeneity (HASfc) between Guassa geladas and geladas from other sites.

<sup>b</sup> Guassa geladas lower than geladas from other sites.

<sup>c</sup> Guassa geladas greater than geladas from other sites.



**Figure 1.** Distribution of gelada microwear. Box plots showing the distribution of values for complexity (ln-transformed), anisotropy ( $\times 100$ ), and heterogeneity (ln-transformed) for geladas from Guassa ( $n = 9$ ) and other sites ( $n = 15$ ). Guassa geladas had greater complexity (Mann–Whitney  $U$  test:  $U = 113$ ,  $p < 0.01$ ), lower anisotropy (Mann–Whitney  $U$  test:  $U = 32$ ,  $p < 0.05$ ), lower variance in anisotropy (Levene's test:  $F(1,22) = 5.31$ ,  $p < 0.05$ ), and higher variance in heterogeneity (Levene's test:  $F(1,22) = 15.82$ ,  $p < 0.001$ ).

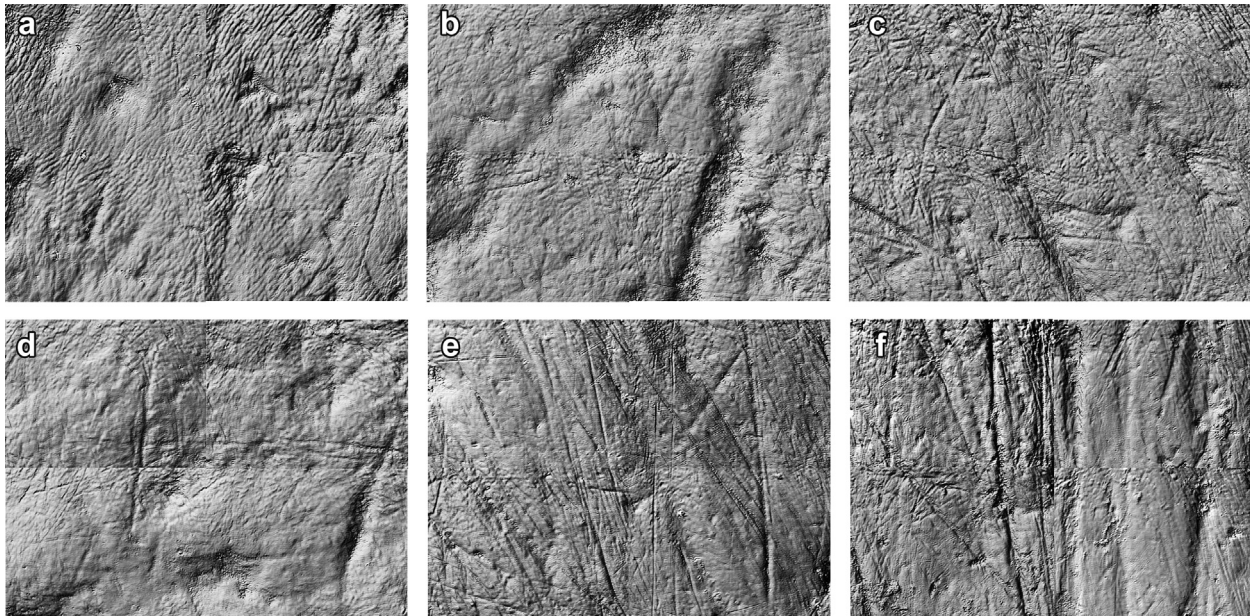
#### 3.3. Comparisons of microwear textures in extant and fossil *Theropithecus*

Next, we compared our entire *Theropithecus* sample by species. Our sample showed no differences among species of *Theropithecus* in means or variances (Means, MANOVA: Pillai's trace = 0.35,  $F(3,36) = 1.58$ ,  $p > 0.05$ ; Variances, MANOVA: Pillai's trace = 0.28,  $F(3,36) = 1.25$ ,  $p > 0.05$ ; Table 3, Fig. 4). When we ran the same tests by taxon and site, however, we found differences among the groups in means (MANOVA: Pillai's trace = 1.08,  $F(6,24) = 2.05$ ,  $p < 0.05$ ), but not in variances (MANOVA: Pillai's trace = 0.86,  $F(6,24) = 1.61$ ,  $p > 0.05$ ); individual ANOVAs showed that groups varied in mean complexity (ANOVA:  $F(6,24) = 5.08$ ,  $p < 0.01$ ; Fig. 5) but not in mean anisotropy or heterogeneity (Table 3). A post hoc Tukey's HSD test showed that Guassa *T. gelada* had higher mean complexity than *T. gelada* from the area of Debre Birhan, *T. darti* from Hadar, and *T. oswaldi* from Olduvai, but no other differences were found. These results held when the Guassa outlier (GUA 202) was removed, which is not surprising since the lowest complexity value found in the Guassa sample is still higher than any found in *T. darti* from Hadar or *T. oswaldi* from Olduvai. We present photosimulations of selected fossil *Theropithecus* microwear scans in Figure 2d–f.

### 4. Discussion

Recent research has indicated that all known fossil theropithecids were probably strongly graminivorous, but detecting dietary variation within the clade has proven difficult in part because there is





**Figure 2.** a–f. Photosimulations of *Theropithecus* microwear scans. Each montage derives from 3D point clouds representing four scans and a total occlusal area of  $276 \mu\text{m} \times 204 \mu\text{m}$ . Specimens are (a) *Theropithecus gelada* (MCA 601) from Guassa, (b) *T. gelada* (GUA 202) from Guassa, (c) *T. gelada* (FMNH 27186) from Gich, (d) *T. darti* (A.L. 412-1) from Hadar, (e) *T. oswaldi* (Old 63DK1-105) from Olduvai, and (f) *T. brumpti* (KNMER 3738) from Koobi Fora.

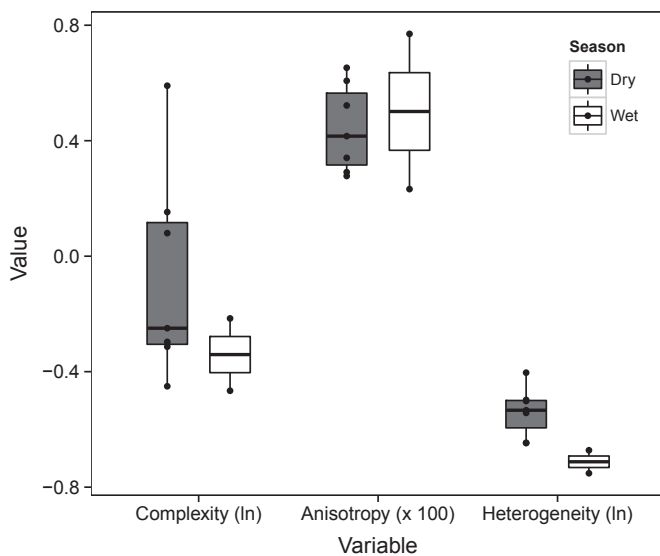
only one extant graminivorous primate, *T. gelada*. We explored whether dental microwear textures from an expanded sample of gelada specimens from ecologically diverse sites could enable fine-grained dietary distinctions among fossil *Theropithecus* diets. Our results demonstrate that dietary variation among gelada populations is reflected in microwear textures, a finding which holds important implications for reconstructing the diets of fossil *Theropithecus*.

#### 4.1. Variation among extant geladas

Microwear textures of geladas from Guassa were more complex and less anisotropic than those of geladas from other sites. Guassa

geladas also exhibited lower variation in anisotropy and greater variation in heterogeneity. Our microwear results are consistent with ecological data demonstrating that Guassa geladas have a more diverse diet compared with geladas at other sites (Fashing et al., 2014) and support a connection between variation in texture variables and variation in diet, as other researchers have suggested (Merceron et al., 2004, 2010; Scott et al., 2006, 2012; Ungar et al., 2010; Shapiro, 2015).

The lower proportion of graminoids and higher proportion of forbs in the Guassa gelada diet may be responsible for the observed differences from other gelada populations, since forbs and graminoids vary in silica content (forbs contain less silica than graminoids: e.g., Epstein, 1999; Richmond and Sussman, 2003; Hodson et al., 2005). Experimental work in rabbits indicates that higher levels of silica consumption lead to lower variance in the number of pits and length of microwear scratches, potentially because abrasive, silica-heavy diets quickly and consistently overwrite microwear features (Schulz et al., 2013). In contrast, diets higher in dicotyledonous plants, such as forbs, provide less overwriting and allow for greater variance in these microwear

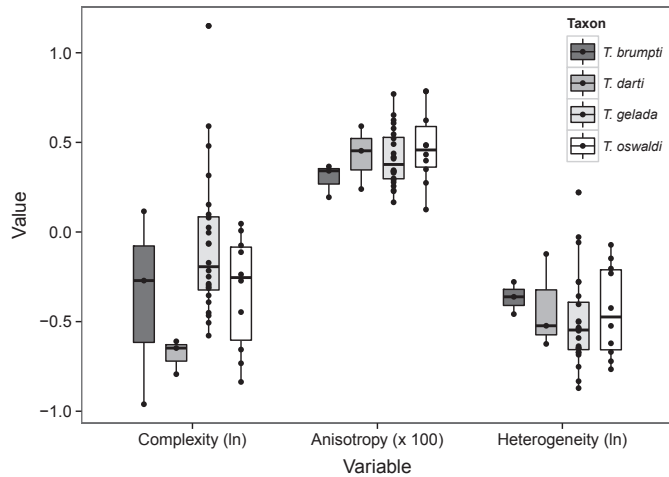


**Figure 3.** Distribution of gelada microwear by season. Box plots and distribution points of complexity (ln-transformed), anisotropy ( $\times 100$ ), and heterogeneity (ln-transformed) for gelada specimens collected from the dry ( $n = 7$ ) and wet ( $n = 2$ ) seasons.

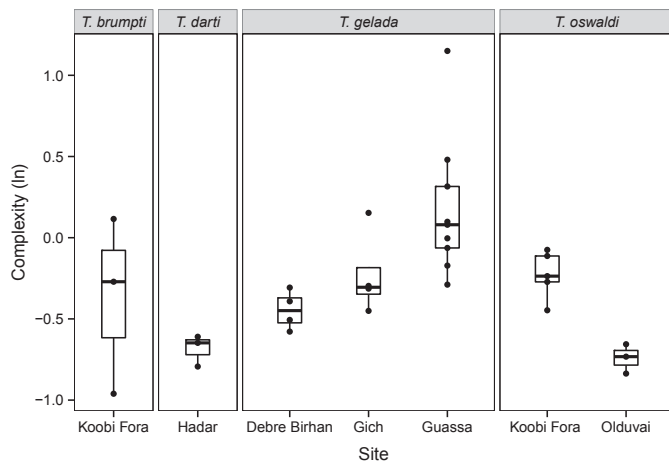
**Table 3**  
MANOVA and ANOVA results.<sup>a</sup>

	Mean (MANOVA)				Variance (MANOVA)			
	Pillai's Trace	df	F	p	Pillai's Trace	df	F	p
Taxon	0.23	(3, 36)	1.00	ns	0.202	(3, 36)	0.87	ns
Taxon & Site	0.88	(6, 24)	1.90	<0.05	0.88	(6, 24)	1.66	ns
Mean (ANOVA)								
Taxon & Site	F (6, 24)	p						
<i>Asfc</i>	5.05	<0.001						
<i>epLsar</i>	1.07	ns						
<i>HAsfc</i>	1.28	ns						

<sup>a</sup> Test results for differences among *Theropithecus* species for mean and variance in the microwear variables of complexity (*Asfc*), anisotropy (*epLsar*), and heterogeneity (*HAsfc*). Analyses were run by taxon and by sites with at least three specimens.



**Figure 4.** Distribution of *Theropithecus* microwear by species. Box plots and distribution points of complexity (ln-transformed), anisotropy ( $\times 100$ ), and heterogeneity (ln-transformed) for each *Theropithecus* species. The species did not differ in microwear texture means (MANOVA: Pillai's trace = 0.35,  $F(3,36) = 1.58$ ,  $p > 0.05$ ) or variances (MANOVA: Pillai's trace = 0.28,  $F(3,36) = 1.25$ ,  $p > 0.05$ ).



**Figure 5.** Distribution of complexity by site. Box plots and distribution points of complexity (ln-transformed) for *Theropithecus* species for each site with at least three specimens. Guassa *T. gelada* had higher complexity than *T. darti* from Hadar, *T. gelada* from Debre Birhan, and *T. oswaldi* from Olduvai (ANOVA:  $F(6,24) = 5.08$ ,  $p < 0.01$ ; Tukey's HSD test).

parameters (Schulz et al., 2013). These experimental results are consistent with our findings that geladas at Guassa exhibit lower anisotropy and higher complexity with a diet of comparatively less graminoid tissue and more forb tissue compared to other gelada populations.

Overall, results from extant geladas illustrate a range of microwear textures despite highly specialized anatomical adaptations for graminivory. We should note here, however, that although our results indicate an expanded range of variance in dental microwear textures for geladas, this species remains the least variant cercopithecoid species in its dental microwear textures (Scott et al., 2012; Shapiro, 2015; Fig. 6), reflecting the specialized nature and high abrasiveness of their diets. Geladas may have more variable diets and microwear than previously thought, but they still exhibit low variation in multiple microwear texture variables and an overall texture pattern clearly discernable from other cercopithecoids (Scott et al., 2012; Shapiro, 2015).

#### 4.2. Role of USO consumption in creating microwear textures

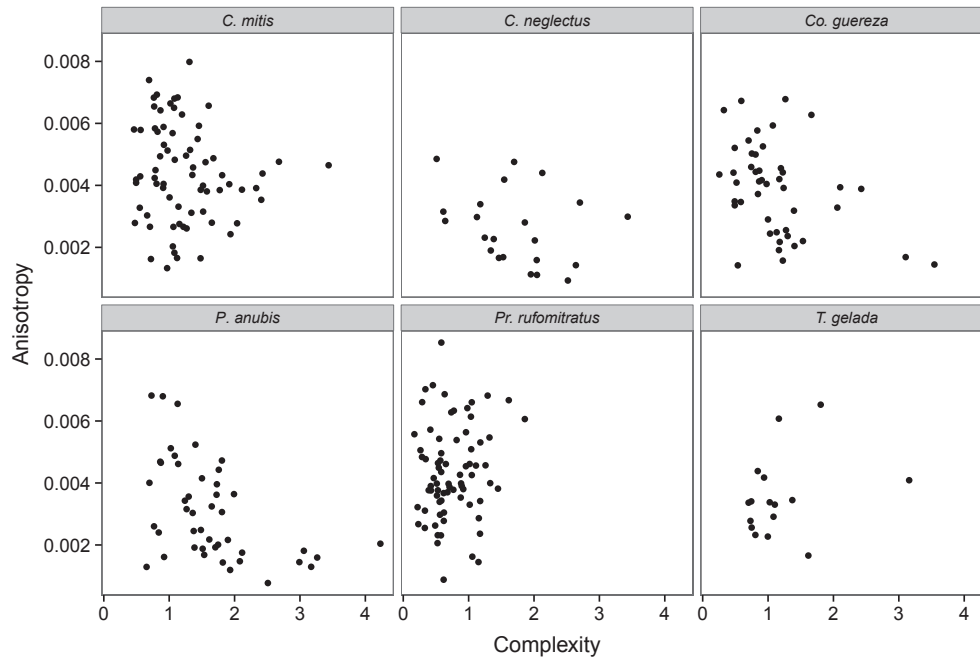
As studies of gelada feeding ecology and food mechanical properties have recently highlighted (Fashing et al., 2014; Venkataraman et al., 2014), having an accurate referential model of primate graminivory and USO consumption that includes seasonal variation may continue to change our understanding of graminivorous microwear signatures and refine our ability to infer graminivorous behavior in the primate fossil record. Gelada diets can vary widely over time (Dunbar and Dunbar, 1974; Dunbar, 1977; Iwamoto, 1979; Hunter, 2001; Fashing et al., 2014). Comparing specimens collected at different times of the year provides the opportunity to refine concepts of how diet and exogenous material impact microwear patterns. We expected to observe higher complexity and lower anisotropy in geladas that died during the dry season due to the high frequency of USO consumption (>50% of diet, versus > 90% short graminoids during the wet season) reported from disturbed sites during this time (Dunbar, 1977; Iwamoto, 1993; Hunter, 2001). Although complexity appeared marginally higher in dry season specimens, anisotropy did not differ between seasons, and only heterogeneity was clearly greater during the dry season. It is surprising that a seasonal dietary switch to USOs coated in exogenous grit was generally not discernable in microwear textures. Geladas do, however, manually clean USOs prior to consumption and expel corm tunics (Fashing et al., 2014), potentially reducing the abrasive effect of grit. Our results suggest it may not be possible to detect an unambiguous USO signal in gelada microwear. More broadly, our findings suggest that systematic ecological and dietary differences among gelada populations have a greater impact on microwear patterns than seasonal shifts in diet. This result implies that seasonal shifts in diet in fossil species, such as shifts to hard objects or USOs, may be difficult to detect in graminivores with present analytical techniques. However, this conclusion is provisional given the small sample size of this comparison.

#### 4.3. Extant and fossil *Theropithecus*

Our results provide a novel comparative context for revisiting the microwear textures of fossil *Theropithecus*. Contrary to our expectations and previous findings (e.g., Teaford, 1993), we found no differences among geladas and any fossil *Theropithecus* species in either the means or variances of any microwear variables. The microwear data presented here corroborate Cerling et al.'s (2013) recent finding based on stable isotopes that all known fossil *Theropithecus* were likely highly graminivorous.

By examining the microwear textures of geladas inhabiting different environments, we have provided a framework for discerning dietary variability and its hard-tissue correlates within a predominantly graminoid-eating niche. Intriguingly, intraspecific differences in microwear textures among gelada populations were greater than the differences among *Theropithecus* species. Given that gelada populations consume varying proportions of graminoids, forbs, USOs, and invertebrates (Fashing et al., 2014), this result is not surprising, but it does complicate traditional notions of the simplicity of gelada diets based on early studies (Dunbar, 1977; Swedell, 2011) that continue to pervade the paleoanthropological literature (e.g., Cerling et al., 2013).

We suggest that modern gelada populations represent a powerful analog for inferring dietary variation among fossil *Theropithecus*, and potentially hominins, although sample sizes are too small for fossil *Theropithecus* in the present study to do so. For example, consider the analog between Guassa geladas and *T. brumpti*, which appear to have consumed similar amounts of



**Figure 6.** Complexity vs. anisotropy for six species of Cercopithecidae. Scatter plots of complexity versus anisotropy for *T. gelada* and five other species of Cercopithecidae (adapted from Shapiro, 2015; other species are *Cercopithecus mitis*, *C. neglectus*, *Colobus guereza*, *Papio anubis*, and *Procolobus rufomitratus*).

graminoids. Compared to other fossil theropiths such as *T. oswaldi*, *T. brumpti* consumed less (55–75%)  $C_4$  plant material, and the  $C_3$  material it consumed appears to have derived from non-forest sources (Cerling et al., 2013). Guassa geladas consumed an annual diet that included 56% graminoids and consumed no more than 74% graminoids during any month of the year (Fashing et al., 2014). Consumption of non-graminoids came mostly, though not entirely, in the form of forbs, which were consistently present in the diet in substantial amounts (19–61% of the monthly diet and 38% of the annual diet; Fashing et al., 2014). From this perspective, the feeding ecology of Guassa geladas strikingly resembles that of *T. brumpti*. Consistent with this notion, Guassa geladas evince the highest microwear complexity values of any theropith, followed by one specimen of *T. brumpti*, then the other theropiths (Fig. 4). If analyses involving larger sample sizes confirm this trend of *T. brumpti* having more complex microwear than other fossil theropiths, such a signal might be consistent with terrestrial forb consumption from non-forest environments. While coarse, this example demonstrates how matching hard-tissue data with dietary variation in a modern analog can provide insight into finer aspects of diet in fossil *Theropithecus*. Carrying out this research agenda would necessitate obtaining larger sample sizes for microwear analyses of fossil specimens (especially *T. brumpti*) and characterizing gelada feeding ecology and its hard-tissue correlates (dental microwear and isotopic chemistry) at the individual level.

#### 4.4. Implications for hominin evolution

Since the discovery that several hominins bear strong  $C_4$  isotopic signals and likely consumed grasses and/or sedges intensively, research devoted to inferring dietary ecology in these species has increased (Sponheimer et al., 2006; Ungar et al., 2010; Cerling et al., 2011; Grine et al., 2012; Lee-Thorp et al., 2012; Wynn et al., 2013). Several recent reviews cover this topic thoroughly (e.g., Ungar and Sponheimer, 2011; Grine et al., 2012).

Here, we update the arguments presented in Fashing et al.'s (2014) study on variation in the ecology of geladas and its implications for understanding theropith and hominin dietary evolution. Relevant to the present study, two arguments were advanced using modern geladas as referential models for extinct graminoid-eating primates. First, Fashing et al. (2014) argued that extinct graminoid-eating primates could have consumed a wide variety of food items and plant species. In the present study, dietary differences between gelada populations were clearly manifested in their molar microwear, indicating that variation in food items within graminoid-eating primates is associated with a hard-tissue signal. This result appears to derive from variation in the amount of graminoids and forbs consumed across populations. We conclude that detecting variation in graminoid consumption by fossil species, including hominins, is achievable.

Second, Fashing et al. (2014) also argued that extinct graminoid-eating primates may have relied seasonally on underground foods. Detecting the extent and nature of underground food consumption by hominins is currently a major goal of research in paleoanthropology (e.g., Yeakel et al., 2007, 2014; Dominy et al., 2008; Macho, 2014). USOs represent plausible candidate foods for hominins because they use the  $C_4$  photosynthetic pathway and are mechanically resistant (hard and tough), qualities consistent with the isotopic signals and robust morphological features of hominins such as *P. boisei* (Dominy et al., 2008). Unfortunately, differentiating the consumption of aboveground versus belowground plant tissues is not resolvable using current stable isotope analyses (Cerling et al., 2011). Our results on gelada microwear contribute to ongoing discussions about the extent to which theropiths and hominins exploited aboveground versus belowground graminoids.

Gelada microwear textures differed little across seasons, and dry season specimens were unremarkable in microwear textures. Major shifts to underground foods observed among geladas on a seasonal basis were not reflected in microwear signals. Graminoid-eating primates can, therefore, consume a wide variety of foods and exhibit microwear variation within the graminoid-eating niche. Geladas could never be mistaken for hard-object feeders, however,



no matter the season of death. These results suggest a minimal confounding impact of exogenous grit on dietary signals of graminivory, supporting the fidelity of microwear to diet (Scott et al., 2012). However, the disconcerting fact that the mechanisms of microwear formation remain poorly understood (see Lucas et al., 2013) render this conclusion provisional. At any rate, our study could somewhat minimize concern, at least in graminoid-eating primates, about a misleading 'Last Supper Effect,' whereby a dietary shift in the last week of an animal's life records an unfaithful dietary signal (Grine, 1986; Gogarten and Grine, 2013). Despite increased complexity seen in Guassa geladas in comparison to geladas from other sites, the overall microwear pattern remains consistent with a graminivorous diet.

The preceding discussion is relevant to the interpretation of microwear in several hominins (*Australopithecus anamensis*, *A. afarensis*, and *P. boisei*), which, contrary to expectations based on masticatory morphology, show little evidence of hard-object consumption (Grine et al., 2006a, b; Ungar et al., 2008, 2010, 2012). Unfortunately, our results suggest there is little hope of using microwear alone to distinguish between aboveground and belowground plant consumption in fossil taxa, since both aboveground and belowground dietary items can lead to similar microwear patterns, and gelada individuals that likely consumed USOs do not exhibit complex microwear. The isotopic and microwear signals of several hominins and theropithecids seem to be consistent with substantial consumption of both USOs and aboveground graminoids, and higher complexity in any new specimens of these species would still be consistent with an overall signal of graminivory. Further studies on how wild primates exploit aboveground and belowground foods, and how such behaviors are reflected and absorbed in hard-tissue, are needed to shed further light on hominin dietary adaptations to C<sub>4</sub> plants.

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## Appendix A. Supplementary Online Material

Supplementary online material related to this article can be found at <http://dx.doi.org/10.1016/j.jhevol.2016.05.010>.

## References

Aiello, L.C., Wheeler, P., 1995. The expensive-tissue hypothesis: the brain and the digestive system in human and primate evolution. *Curr. Anthropol.* 36, 199–221.

- Benefit, B.R., McCrossin, M.L., 1990. Diet, species diversity and distribution of African fossil baboons. *Kroeber Anthropol. Soc. Pap.* 71, 79–93.
- Bobe, R., Behrensmeyer, A.K., 2004. The expansion of grassland ecosystems in Africa in relation to mammalian evolution and the origin of the genus *Homo*. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 207, 399–420.
- Calandra, I., Schulz, E., Pinnow, M., Krohn, S., Kaiser, T.M., 2012. Teasing apart the contributions of hard dietary items on 3D dental microtextures in primates. *J. Hum. Evol.* 63, 85–98.
- Campisano, C.J., Feibel, C.S., 2008. Depositional environments and stratigraphic summary of the Pliocene Hadar formation at Hadar, Afar depression, Ethiopia. *Geol. S. Am. S.* 446, 179–201.
- Carter, M.L., 2001. Sensitivity of stable isotopes (<sup>13</sup>C, <sup>15</sup>N, and <sup>18</sup>O) in bone to dietary specialization and niche separation among sympatric primates in Kibale National Park, Uganda. Ph.D. Dissertation, University of Chicago.
- Cerling, T.E., Mbua, E., Kirera, F.M., Manthi, F.K., Grine, F.E., Leakey, M.G., Sponheimer, M., Uno, K.T., 2011. Diet of *Paranthropus boisei* in the early Pleistocene of East Africa. *Proc. Natl. Acad. Sci.* 108, 9337–9341.
- Cerling, T.E., Chritz, K.L., Jablonski, N.G., Leakey, M.G., Manthi, F.K., 2013. Diet of *Theropithecus* from 4 to 1 Ma in Kenya. *Proc. Natl. Acad. Sci.* 110, 10507–10512.
- Daegling, D.J., Grine, F.E., 1999. Terrestrial foraging and dental microwear in *Papio ursinus*. *Primates* 40, 559–572.
- Dart, R.A., 1925. *Australopithecus africanus*: The man-ape of South Africa. *Nature* 115, 195–199.
- Dominy, N.J., Vogel, E.R., Yeakel, J.D., Constantino, P., Lucas, P.W., 2008. Mechanical properties of plant underground storage organs and implications for dietary models of early hominins. *Evol. Biol.* 35, 159–175.
- Donnelly, S.M., Kramer, A., 1999. Testing for multiple species in fossil samples: an evaluation and comparison of tests for equal relative variation. *Am. J. Phys. Anthropol.* 108, 507–529.
- Dunbar, R.I.M., 1977. Feeding ecology of gelada baboons: a preliminary report. In: Clutton-Brock, T.H. (Ed.), *Primate Ecology*. Academic Press, London, pp. 250–273.
- Dunbar, R.I.M., Bose, U., 1991. Adaptation to grass-eating in gelada baboons. *Primates* 32, 1–7.
- Dunbar, R.I.M., Dunbar, E.P., 1974. Ecological relations and niche separation between sympatric terrestrial primates in Ethiopia. *Folia Primatol.* 21, 36–60.
- Eck, G.G., Jablonski, N.G., 1987. The skull of *Theropithecus brumpti* compared with those of other species of the genus *Theropithecus*. In: Coppens, Y., Howell, F.C. (Eds.), *Les Faunes Plio-Pleistocenes de la Basse Vallée de L'Omo (Ethiopie): Cercopithecidae de la Formation de Shungura, Cahiers de Palaeontologies, Travaux de Palaeontologie East-Africaine*. Centre National de la Recherche Scientifique, Paris, pp. 11–122.
- El-Zaatar, S., Grine, F.E., Teaford, M.F., Smith, H.F., 2005. Molar microwear and dietary reconstructions of fossil Cercopithecoidea from the Plio-Pleistocene deposits of South Africa. *J. Hum. Evol.* 49, 1–26.
- Epstein, E., 1999. Silicon. *Annu. Rev. Plant Phys.* 50, 641–664.
- Fashing, P.J., Nguyen, N., Venkataraman, V.V., Kerby, J.T., 2014. Gelada feeding ecology in an intact ecosystem at Guassa, Ethiopia: variability over time and implications for theropithecid and hominin dietary evolution. *Am. J. Phys. Anthropol.* 155, 1–16.
- Feibel, C.S., Brown, F.H., McDougall, I., 1989. Stratigraphic context of fossil hominids from the Omo Group deposits: northern Turkana Basin, Kenya and Ethiopia. *Am. J. Phys. Anthropol.* 78, 595–622.
- Gogarten, J.F., Grine, F.E., 2013. Seasonal mortality patterns in primates: implications for the interpretation of dental microwear. *Evol. Anthropol.* 22, 9–19.
- Grine, F.E., 1986. Dental evidence for dietary differences in *Australopithecus* and *Paranthropus*: a quantitative analysis of permanent molar microwear. *J. Hum. Evol.* 15, 783–822.
- Grine, F.E., Ungar, P.S., Teaford, M.F., El-Zaatar, S., 2006a. Molar microwear in *Praeanthropus afarensis*: evidence for dietary stasis through time and under diverse paleoecological conditions. *J. Hum. Evol.* 51, 297–319.
- Grine, F.E., Ungar, P.S., Teaford, M.F., 2006b. Was the Early Pliocene hominin "*Australopithecus*" *anamensis* a hard object feeder? *S. Afr. J. Sci.* 102, 301–310.
- Grine, F.E., Sponheimer, M., Ungar, P.S., Lee-Thorp, J., Teaford, M.F., 2012. Dental microwear and stable isotopes inform the paleoecology of extinct hominins. *Am. J. Phys. Anthropol.* 148, 285–317.
- Guthrie, E.H., 2011. Functional morphology of the postcranium of *Theropithecus brumpti* (Primates: Cercopithecidae). Ph.D. Dissertation, University of Oregon.
- Hodson, M.J., White, P.J., Mead, A., Broadley, M.R., 2005. Phylogenetic variation in the Silicon composition of plants. *Ann. Bot.* 96, 1027–1046.
- Hunter, C.P., 2001. Ecological determinants of gelada ranging patterns (*Theropithecus gelada*). Ph.D. Dissertation, University of Liverpool.
- Iwamoto, T., 1979. Feeding ecology. In: Kawai, M. (Ed.), *Ecological and Sociological Studies of Gelada Baboons*. Springer, Basel, pp. 279–330.
- Iwamoto, T., 1993. The ecology of *Theropithecus gelada*. In: Jablonski, N.G. (Ed.), *Theropithecus: The Rise and Fall of a Primate Genus*. Cambridge University Press, Cambridge, pp. 441–452.
- Jablonski, N.G., 1993a. Evolution of the masticatory apparatus in *Theropithecus*. In: Jablonski, N.G. (Ed.), *Theropithecus: The Rise and Fall of a Primate Genus*. Cambridge University Press, Cambridge, pp. 299–319.
- Jablonski, N.G. (Ed.), 1993b. *Theropithecus: The Rise and Fall of a Primate Genus*. Cambridge University Press, Cambridge, p. 556.



- Jablonski, N.G., 1994. Convergent evolution in the dentitions of grazing macropodine marsupials and the grass-eating cercopithecine primate *Theropithecus gelada*. *J.R. Soc. West. Aust.* 77, 37–43.
- Jablonski, N.G., Frost, S., 2010. Cercopithecoidea. In: Werdelin, L., Sanders, W. (Eds.), *Cenozoic Mammals of Africa*. University of California Press, Berkeley, pp. 393–428.
- Jablonski, N.G., Leakey, M.G., Antón, M., 2008. Systematic paleontology of the cercopithecines. In: Jablonski, N.G., Leakey, M.G. (Eds.), *Koobi Fora Research Project, Volume 6: The Fossil Monkeys*. California Academy of Sciences, San Francisco, pp. 103–300.
- Jolly, C.J., 1970. The seed eaters: a new model of hominid differentiation based on a baboon analogy. *Man* 5, 5–26.
- Kay, R.F., 1977. The evolution of molar occlusion in the Cercopithecidae and early catarrhines. *Am. J. Phys. Anthropol.* 46, 327–352.
- Kay, R.F., 1981. The nut-crackers: a new theory of the adaptations of the Ramapithecinae. *Am. J. Phys. Anthropol.* 55, 141–151.
- Lee-Thorp, J., van der Merwe, N.J., Brain, C.K., 1989. Isotopic evidence for dietary differences between two extinct baboon species from Swartkrans. *J. Hum. Evol.* 18, 183–190.
- Lee-Thorp, J., Likius, A., Mackaye, H.T., Vignaud, P., Sponheimer, M., Brunet, M., 2012. Isotopic evidence for an early shift to C<sub>4</sub> resources by Pliocene hominins in Chad. *Proc. Natl. Acad. Sci.* 109, 20369–20372.
- Lucas, P.W., Omar, R., Al-Fadhalah, K., Almusallam, A.S., Henry, A.G., Michael, S., Thai, L.A., Watzke, J., Atkins, A.G., 2013. Mechanisms and causes of wear in tooth enamel: implications for hominin diets. *J.R. Soc. Interface* 10, 20120923.
- Macho, G.A., 2014. Baboon feeding ecology informs the dietary niche of *Paranthropus boisei*. *PLoS One* 9, e84942.
- Merceron, G., Viriot, L., Blondel, C., 2004. Tooth microwear pattern in roe deer (*Capreolus capreolus*) from Chizé (Western France) and relation to food composition. *Small Ruminant Res* 53, 125–132.
- Merceron, G., Escarguel, G., Angibault, J.M., Verheyden-Tixier, H., 2010. Can dental microwear textures record inter-individual dietary variations? *PLoS One* 5, e9542.
- Nguyen, N., Fashing, P.J., Boyd, D.A., Barry, T.S., Burke, R.J., Goodale, C.B., Jones, S.C.Z., Kerby, J.T., Kellogg, B.S., Lee, L.M., Miller, C.M., Nurmi, N.O., Ramsay, M.S., Reynolds, J.D., Stewart, K.M., Turner, T.J., Venkataraman, V.V., Knauf, Y., Roos, C., Knauf, S., 2015. Fitness impacts of tapeworm parasitism on wild gelada monkeys at Guassa, Ethiopia. *Am. J. Primatol.* 77, 579–594.
- Plavcan, J.M., Cope, D.A., 2001. Metric variation and species recognition in the fossil record. *Evol. Anthropol.* 10, 204–222.
- Reed, K.E., 1997. Early hominid evolution and ecological change through the African Plio-Pleistocene. *J. Hum. Evol.* 32, 289–322.
- Richmond, K.E., Sussman, M., 2003. Got silicon? The non-essential beneficial plant nutrient. *Curr. Opin. Plant Biol.* 6, 268–272.
- Robinson, J.T., 1963. Adaptive radiation in the australopithecines and the origin of man. In: Howell, F.C., Bourliere, F. (Eds.), *African Ecology and Human Evolution*. Aldine, Chicago, pp. 385–416.
- Schoeninger, M.J., Moore, J., Sept, J.M., 1999. Subsistence strategies of two “savanna” chimpanzee populations: the stable isotope evidence. *Am. J. Primatol.* 49, 297–314.
- Schulz, E., Piotrowski, V., Clauss, M., Mau, M., Merceron, G., Kaiser, T.M., 2013. Dietary abrasiveness is associated with variability of microwear and dental surface texture in rabbits. *PLoS ONE* 8, e56167.
- Scott, J.E., McAbee, K.R., Eastman, M.M., Ravosa, M.J., 2014. Experimental perspective on fallback foods and dietary adaptations in early hominins. *Biol. Letters* 10, 20130789.
- Scott, R.S., Ungar, P.S., Bergstrom, T.S., Brown, C.A., Grine, F.E., Teaford, M.F., Walker, A., 2005. Dental microwear texture analysis shows within-species diet variability in fossil hominins. *Nature* 436, 693–695.
- Scott, R.S., Ungar, P.S., Bergstrom, T.S., Brown, C.A., Childs, B.E., Teaford, M.F., Walker, A., 2006. Dental microwear texture analysis: technical considerations. *J. Hum. Evol.* 51, 339–349.
- Scott, R.S., Teaford, M.F., Ungar, P.S., 2012. Dental microwear texture and anthropoid diets. *Am. J. Phys. Anthropol.* 147, 551–579.
- Shapiro, A.E., 2015. Variation in dental microwear textures and dietary variation in African Old World monkeys (Cercopithecidae). Ph.D. Dissertation, Arizona State University.
- Sponheimer, M., Passey, B., de Ruiter, D., Guatelli-Sternberg, D., Cerling, T., Lee-Thorp, J., 2006. Isotopic evidence for dietary flexibility in the early hominin *Paranthropus robustus*. *Science* 314, 980–982.
- Straat, D.S., Constantino, P., Lucas, P.W., Richmond, B.G., Spencer, M.A., Dechow, P.C., Ross, C.F., Grosse, I.R., Wright, B.W., Wood, B.A., Weber, G.W., Wang, Q., Byron, C., Slice, D.E., Chalk, J., Smith, A.L., Smith, L.C., Wood, S., Berthaume, M., Benazzi, S., Dzialo, S., Tamvada, K., Ledogar, J.A., 2013. Diet and dietary adaptations in early hominins: The hard food perspective. *Am. J. Phys. Anthropol.* 151, 339–355.
- Swedell, L., 2011. African papionins: diversity of social organization and ecological flexibility. In: Campbell, C.J., Fuentes, A., MacKinnon, K.C., Bearder, S.K., Stumpf, R.M. (Eds.), *Primates in Perspective*. Oxford University Press, New York, pp. 241–277.
- Teaford, M.F., 1988. A review of dental microwear and diet in modern mammals. *Scanning Microscopy* 2, 1149–1166.
- Teaford, M.F., 1993. Dental microwear and diet in extant and extinct *Theropithecus*: preliminary analyses. In: Jablonski, N.G. (Ed.), *Theropithecus: The Life and Death of a Primate Genus*. Cambridge University Press, Cambridge, pp. 331–349.
- Teaford, M.F., Glander, K.E., 1996. Dental microwear and diet in a wild population of mantled howlers (*Alouatta palliata*). In: Norconk, M., Rosenberger, A., Garber, P. (Eds.), *Adaptive Radiations of Neotropical Primates*. Plenum Press, New York, pp. 433–449.
- Teaford, M.F., Oyen, O.J., 1989. *In vivo* and *in vitro* turnover in dental microwear. *Am. J. Phys. Anthropol.* 80, 447–460.
- Teaford, M.F., Robinson, J.G., 1989. Seasonal or ecological zone differences in diet and molar microwear in *Cebus nigrivittatus*. *Am. J. Phys. Anthropol.* 80, 391–401.
- Teaford, M.F., Walker, A.C., 1984. Quantitative differences in dental microwear between primate species with different diets and a comment on the presumed diet of *Sivapithecus*. *Am. J. Phys. Anthropol.* 64, 191–200.
- Ungar, P.S., Sponheimer, M., 2011. The diets of early hominins. *Science* 334, 190–193.
- Ungar, P.S., Grine, F.E., Teaford, M.F., 2008. Dental microwear indicates that *Paranthropus boisei* was not a hard-object feeder. *PLoS ONE* 3, 1–6.
- Ungar, P.S., Scott, R.S., Grine, F.E., Teaford, M.F., 2010. Molar microwear textures and the diets of *Australopithecus anamensis* and *Australopithecus afarensis*. *Phil. Trans. R. Soc. B* 365, 3345–3354.
- Ungar, P.S., Krueger, K.L., Blumenshine, R.J., Njau, J., Scott, R.S., 2012. Dental microwear texture analysis of hominins recovered by the Olduvai Landscape Paleanthropology Project, 1995–2007. *J. Hum. Evol.* 63, 429–437.
- van der Merwe, N.J., Masao, F.T., Bamford, M.K., 2008. Isotopic evidence for contrasting diets of early hominins *Homo habilis* and *Australopithecus boisei* of Tanzania. *S. Afr. J. Sci.* 104, 153–155.
- Venkataraman, V.V., Glowacka, H., Fritz, J., Clauss, M., Seyoum, C., Nguyen, N., Fashing, P.J., 2014. Effects of dietary fracture toughness and dental wear on chewing efficiency in geladas (*Theropithecus gelada*). *Am. J. Phys. Anthropol.* 155, 17–32.
- Vrba, E.S., 1988. Late Pliocene climatic events and hominid evolution. In: Grine, F.E. (Ed.), *Evolutionary History of the “Robust” Australopithecines*. Aldine de Gruyter, New York, pp. 405–426.
- Wood, B., Schroer, K., 2012. Reconstructing the diet of an extinct hominin taxon: the role of extant primate models. *Int. J. Primatol.* 33, 716–742.
- Wynn, J.G., Sponheimer, M., Kimbel, W.H., Alemseged, Z., Reed, K., Bedaso, Z.K., Wilson, J.N., 2013. Diet of *Australopithecus afarensis* from the Pliocene Hadar Formation, Ethiopia. *Proc. Natl. Acad. Sci.* 110, 10495–10500.
- Yeakel, J.D., Bennett, N.C., Koch, P.L., Dominy, N.J., 2007. The isotopic ecology of African mole rats informs hypotheses on the evolution of human diet. *P. Roy. Soc. B-Biol. Sci.* 274, 1723–1730.
- Yeakel, J.D., Dominy, N.J., Koch, P.L., Mangel, M., 2014. Functional morphology, stable isotopes, and human evolution: a model of consilience. *Evolution* 68, 190–203.