



Contents lists available at ScienceDirect

Journal of Human Evolution

journal homepage: www.elsevier.com/locate/jhevol

Dental microwear and Pliocene paleocommunity ecology of bovids, primates, rodents, and suids at Kanapoi

Peter S. Ungar^{a, b, *}, Elicia F. Abella^a, Jenny H.E. Burgman^b, Ignacio A. Lazagabaster^c,
 Jessica R. Scott^d, Lucas K. Delezene^a, Fredrick K. Manthi^e, J. Michael Plavcan^a,
 Carol V. Ward^f

^a Department of Anthropology, University of Arkansas, Fayetteville, AR, USA^b Environmental Dynamics Program, University of Arkansas, Fayetteville, AR, USA^c Institute of Human Origins, Arizona State University, Tempe, AZ, USA^d Department of Sociology and Anthropology, University of Arkansas, Little Rock, AR, USA^e Department of Earth Sciences, National Museums of Kenya, P.O. Box 40658, Nairobi, Kenya^f Department of Pathology and Anatomical Sciences, University of Missouri, Columbia, MO, USA

ARTICLE INFO

Article history:

Received 13 September 2016

Accepted 3 March 2017

Available online xxx

Keywords:

Paleoenvironment

Tooth wear

Mammals

Hominin sites

ABSTRACT

Reconstructions of habitat at sites like Kanapoi are key to understanding the environmental circumstances in which hominins evolved during the early Pliocene. While *Australopithecus anamensis* shows evidence of terrestrial bipedality traditionally associated with a more open setting, its enamel has low $\delta^{13}\text{C}$ values consistent with consumption of C_3 foods, which predominate in wooded areas of tropical Africa. Habitat proxies, ranging from paleosols and their carbonates to associated herbivore fauna and their carbon isotope ratios, suggest a heterogeneous setting with both grass and woody plant components, though the proportions of each have been difficult to pin down. Here we bring dental microwear texture analysis of herbivorous fauna to bear on the issue. We present texture data for fossil bovids, primates, rodents, and suids ($n = 107$ individuals in total) from the hominin bearing deposits at Kanapoi, and interpret these in the light of closely related extant mammals with known differences in diet. The Kanapoi bovid results, for example, are similar to those for extant variable grazers or graze-browse intermediate taxa. The Kanapoi suid data vary by taxon, with one similar to the pattern of extant grazers and the other more closely resembling mixed feeders. The Kanapoi primates and rodents are more difficult to associate with a specific environment, though it seems that grass was likely a component in the diets of both. All taxa evince microwear texture patterns consistent with a mosaic of discrete microhabitats or a heterogeneous setting including both tree and grass components.

© 2017 Elsevier Ltd. All rights reserved.

1. Introduction

Reconstructions of habitat types in and around Kanapoi at the time of *Australopithecus anamensis* are important to help us understand the environmental circumstances surrounding hominin evolution during the early Pliocene. *Australopithecus anamensis* presents somewhat of a conundrum. It is the earliest hominin with clear evidence of committed terrestrial bipedality (Ward et al., 1999, 2001), which has long been assumed to relate to the spreading savannas. It is also the first hominin to display the beginnings of postcanine megadontia, with molars generally similar

in size to its putative descendent (Kimbel et al., 2006; Haile-Selassie et al., 2010) *Australopithecus afarensis* (Ward et al., 2001, 2013). Its molar microwear is similar to that of *A. afarensis* (Ungar et al., 2010b). However, its $\delta^{13}\text{C}$ values clearly indicate a preference for C_3 foods, as would have been found in more wooded settings (Sponheimer et al., 2013) than those in which later hominins likely lived. It is also the case that *A. anamensis* retains a more primitive canine-premolar complex and mandibular geometry than *A. afarensis* (Ward et al., 2001, 2010; Delezene and Kimbel, 2011; Manthi et al., 2012). Assessment of whether the apparent isotopic and morphological indicators of diet and dietary adaptation are a reflection of local habitat only, or if they signal a shifting adaptive strategy throughout the evolution of early *Australopithecus*, would benefit from a more detailed understanding of

* Corresponding author.

E-mail address: pungar@uark.edu (P.S. Ungar).

the paleoecology of Kanapoi, as it is the earliest site that has yielded *A. anamensis* fossils and holds the largest sample from this species.

1.1. Kanapoi paleoenvironments: paleosols and faunal composition

The fossil bearing deposits at Kanapoi are floodplain paleosols and deltaic sand bodies (Feibel, 2003). Hills or islands of volcanic basement rock provided topographic relief and variation in soil types, drainage, and overlying vegetation. The ancestral Kerio River and Lonyumun Lake (a precursor to Lake Turkana) complete the setting so that, as Feibel (2003:14) concluded, “the high degree of landscape heterogeneity and pronounced soil catenas of the Kanapoi setting provided some of the greatest habitat patchiness recorded from the Turkana Basin Plio-Pleistocene.” Indeed, Wynn (2000) suggested that paleosols from Kanapoi indicate a patchwork or mosaic of habitats similar to those seen today in the modern Omo River Delta at the north end of Lake Turkana. He found seven distinct types of paleosol consistent with settings ranging from sparsely vegetated, arid grasslands to gallery woodland. The proportion of soil carbonates from C_4 plants at the site runs between 25% and 40% (Harris and Leakey, 2003).

The faunal assemblage from the site has also been used to infer habitat. Herbivores collected during the Patterson expeditions in the 1960s and the Leakey excavations in the 1990s have been interpreted to suggest a relatively dry climate, with a mix of C_3 and C_4 plant types. Andrews and Humphrey (1999), for example, speculated that, given representation of both browsers and grazers, Kanapoi represented open woodland with abundant grass present. Based on fossil mammals, Harris and Leakey (2003) also inferred that there was a mixture of woodlands and grasslands at Kanapoi, but that there was predominantly woodland. Manthi's (2006) analysis of the rodents from Kanapoi further suggested a range of environments, from *Acacia* savanna and scrub to moist woodland. That said, the relative abundances of grass to woody plants has eluded consensus. Harris et al. (2003) note, for example, that mammals inferred to be grazers, based on taxonomic uniformitarianism, outnumber browsers two to one in terms of number of species and three to one in terms of individual specimens. Overall, the Kanapoi fauna seems to indicate a mixture of habitats, especially including drier and more open conditions (Bobe, 2011). However, ecological structure analysis, based on locomotor adaptation and trophic ecovariables (c.f., Reed, 1997), suggests a more closed, woodland habitat. Indeed, the apparent inconsistencies in interpretation led Harris and Leakey (2003:5) to speculate that faunal evidence may “be indicative that the habitats present in the region during the initial formation of the Turkana Basin may not be directly comparable with the modern habitats now characteristic of eastern Africa.”

1.2. Kanapoi paleoenvironments: foodprints

While analyses of paleosols and faunal composition provide important clues to the paleoenvironment at Kanapoi during hominin occupation, they do not provide direct evidence of resources exploited by the mammals that lived at these sites. Such evidence comes in the form of foodprints, traces of actual behavior like stable isotopes of elements in teeth and dental microwear. These provide insights into diet, free from both the assumptions that they ate what their own ancestors evolved to eat or what closely related forms eat today (e.g., see Sponheimer et al., 1999). We have a better chance of relating diet to habitat if freed from adaptationist assumptions and those of taxonomic uniformitarianism. There is, of course, no one-to-one correspondence between diet and habitat. Animals pick and choose from potential food items available,

especially in a patchy, mosaic habitat. Still, one cannot eat what is not present in a given place at a given time. If an individual is inferred to have eaten fruits or leaves, there must have been C_3 -type plants present. There are certainly clear tendencies for extant grazers, browsers, and mixed feeders to inhabit more open, closed, and mosaic or seasonal environments, respectively (Gagnon and Chew, 2000). Thus, inferred diet from foodprints can serve as a valuable proxy for paleohabitat, or at least some of the resources available within it.

Stable carbon isotope data for dental enamel of fauna from Kanapoi offer important clues about food choices. These provide dietary information on the scale of weeks or months during which those teeth formed. Results to date show that elephantoids, suids, and equids from Kanapoi had high $\delta^{13}C$ values indicative of a C_4 -plant diet dominated by tropical grasses or sedges, whereas deinotheres, sivatheres, impala, and ostriches had lower $\delta^{13}C$ values signifying consumption of more C_3 -plant foods. Further, the rhinocerotids from Kanapoi were largely browsers (Harris et al., 2003), and as already mentioned, *A. anamensis* too had a strong C_3 diet signal. These data are consistent with a patchwork of habitats in time or space in which both grass and bush/tree products were readily available. They also suggest varying habitat preferences and degrees of specificity for the taxa representing the herbivore guild at Kanapoi.

While this evidence is compelling, any additional insights on the diets of individuals found in the deposits could add valuable detail. Dental microwear is another line of evidence for diet and resource availability, independent of photosynthetic pathway. Microwear texture analysis has proven particularly useful for distinguishing extant ruminants on the basis of diet, separating taxa into at least six categories based on feeding preferences, with more graze reflected in high texture anisotropy and more browse in high complexity (Merceron et al., 2010, 2014; Schulz et al., 2010; Scott, 2012a; Ramdarshan et al., 2016). This approach has also been applied to fossil bovids, cervids, and tragulids to reconstruct diet and, by extension, paleohabitats (Ungar et al., 2007b, 2012, 2016; Merceron et al., 2016).

Microwear texture analysis has been shown to reflect aspects of diet in a broad variety of other mammals too. While the approach is still fairly new, it has already been applied to taxa ranging from rabbits (Schulz et al., 2013) to bats (Purnell et al., 2013), shrews (Withnell and Ungar, 2014), rodents (Burgman et al., 2016; Caporale and Ungar, 2016), bears (Donohue et al., 2013; Jones and DeSantis, 2016), dogs, hyenas, and cats (Schubert et al., 2010; Ungar et al., 2010a; DeSantis et al., 2012; Stynder et al., 2012), primates (Scott et al., 2006, 2009, 2012; Estalrich et al., 2015; Delezene et al., 2016; Shapiro et al., 2016), elephants (Zhang et al., 2016), pigs (Souron et al., 2015), horses (Merceron et al., 2016), marsupials (Prideaux et al., 2009), and even armadillos and sloths (Haupt et al., 2013). While specific attributes measured vary between studies, the trends are clear and consistent; those that consume hard, brittle foods tend to have higher microwear surface texture complexity compared to closely related taxa, whereas those that shear or slice tough items tend to have more surface anisotropy. This makes intuitive sense and is consistent with tough-food eaters having microwear surfaces dominated by uniform scratches running in the direction of shear and hard-object feeders having pits of varying sizes and shapes formed during crushing (see Ungar, 2015; Calandra and Merceron, 2016; DeSantis, 2016).

While dental microwear texture has been used as a paleoenvironmental proxy for a number of Neogene fossil sites, most studies have focused on a single higher-level taxon, usually ruminants (see above). Rodent microwear has also been used to infer paleohabitat, though most such studies have employed more conventional feature-based microwear characterizations (Lewis et al.,

2000; Rodrigues et al., 2009, 2012; Kaya and Kaymakci, 2013). Indeed, few if any studies to date have considered paleoenvironmental implications of mammalian microwear in multiple higher-level taxa from a single site. This is surprising given the broad applicability of the technique. Microwear study of whole mammalian herbivore guilds holds the potential to provide new insights not just into paleohabitats, but also into community-level paleoecological structure, and possibly even niche construction and partitioning in the past.

This study presents a first attempt to characterize microwear textures of several higher-level taxa from the site of Kanapoi, Kenya. We consider bovids, cercopithecids, rodents, and suids. Given that comparative baseline series are only well developed for bovids and primates, including cercopithecids, and very little is yet known about microwear textures of rodents and especially suids, any results from this study must be considered preliminary. Further, there are no published studies comparing microwear textures of whole communities of extant mammalian herbivores living in different habitats. Still, this represents a starting point, offers hints at the potential of this approach, and points to an important new direction for research in the future.

2. Materials and methods

All bovid, cercopithecid, rodent, and suid molars from Kanapoi available in the collections at the National Museums of Kenya up to the 2015 field season were examined for this study. A list of specimens used in this analysis is presented, along with taxonomic attributions as currently understood and raw data for each, in [Supplementary Online Material \(SOM\) Table S1](#). These include specimens collected during the Patterson expeditions in the 1960s, the Leakey excavations in the 1990s, and fieldwork by FKM from 2003 to 2008 and by the West Turkana Paleo Project led by FKM, CVW, and JMP from 2012 to 2015. First, occlusal surfaces were assessed visually using a binocular light microscope at the National Museums of Kenya, and those with obvious postmortem damage or with an obscuring, irremovable layer of matrix or preservative were excluded from molding. Individual rodent teeth mounted on pinheads with glyptol were also omitted, as removal of the glue encasing the occlusal surface would have risked damage to the original specimens.

Molars deemed suitable for microwear analysis were cleaned using alcohol-soaked cotton swabs, and high-resolution molds were produced using President's Jet regular body polyvinylsiloxane dental impression material (Coltène-Whaledent, Alstätten, Switzerland) by PSU, LKD, and JRS. High-resolution replicas of specimens were poured into these molds at the University of Arkansas using Epotek 301 epoxy resin and hardener (Epoxy Technologies, Billerica, MA, USA) and allowed to harden before analysis. All replicas were then further screened for antemortem microwear using confocal profilometry (see below) following the criteria of Teaford (1988) and King et al. (1999). Those surfaces lacking unobscured antemortem microwear at the micron scale were then excluded from further analysis. The final microwear sample included 43 bovids, 10 cercopithecids, 34 rodents, and 20 suids. Microwear texture data were collected for bovids by JRS, for cercopithecids by EFA, for rodents by JHEB, and for suids by IAL.

Replicas of the primate and bovid teeth were analyzed using methods described in Scott et al. (2006) and Scott (2012a), respectively. A Sensofar Plμ Standard confocal profiler (Solarius Corp., Sunnyvale, CA) was used with a 100× objective to collect data under white light. Four adjacent fields of 102 × 138 μm each were analyzed, for a total area of 204 × 276 μm. Elevations were sampled at a lateral (x, y) interval of 0.18 μm with a published vertical resolution of 5 μm. The resulting point clouds together sampled

elevations at approximately 1.74 million evenly spaced points on the replicas of each occlusal surface. For the bovids, facet 1 surfaces on the anterobuccal enamel band of the M¹ or M² paracone, or the posterobuccal enamel band on the M₁ or M₂ protoconid were targeted for analysis following convention (Ungar et al., 2007a; Merceron et al., 2010). For the cercopithecids, "Phase II" facet 9 was targeted, again following convention (Teaford and Walker, 1984; Krueger et al., 2008). These protocols were chosen to allow direct comparison with baseline data already published for these taxa.

The rodent study employed methods described in Burgman et al. (2016). Rodent molar enamel bands are often less than 100 μm thick and so present a much smaller potential work envelope than primate or bovid wear facets. They therefore required higher-resolution analysis to produce a sufficiently dense point cloud for texture analysis. A Sensofar Plμ Neox confocal profiler (Sensofar Corp., Barcelona, Spain) was used with a 150× objective to collect data under blue light. Blue light was employed because the objective is optimized for this light type. Three-dimensional point clouds were generated for each specimen with a field of view of 85 × 64 μm, a lateral spacing (x, y) of 0.13 μm, and a published vertical resolution <1 nm. The resulting cloud sampled elevations at approximately 322,000 equally spaced points. The enamel rim associated with the M₂ mesial loph was targeted, with preference given to the protoconid (following Silcox and Teaford, 2002; Hautier et al., 2009). The metaconid was analyzed when the protoconid lacked a sufficient surface for analysis. Propalinal chewing has been shown to produce continuous wear facets across the enamel surface (Lazzari et al., 2008) and negligible variation in scratch orientation among facets (Charles et al., 2007). This suggests no distinct buccal and lingual phases of mastication and provides justification for sampling the metaconid surface when necessary. For the suids, the buccal enamel band of the M₃ protoconid was sampled. As with the other taxa, the metaconid was analyzed when the protoconid lacked an appropriate surface for analysis. Again, this protocol was used as it was the same as that employed in previous studies.

We had no baseline data for the suids, so we used the newer Sensofar Plμ Neox confocal profiler in white-light mode with a 100× objective. This allowed us to take advantage of hardware resolution and software improvements (e.g., field-of-view stitching), but with the larger work envelope of the bovid and primate analyses. A stitched point cloud of 242 × 181 μm with a lateral spacing (x, y) of 0.17 μm and a published vertical resolution <1 nm was collected for each analyzed surface. This resulted in a cloud of approximately 1.52 million points representing each suid specimen. The M₃ was chosen because this is the most common tooth in the suid fossil record and the most taxonomically informative (Harris and White, 1979). Furthermore, because some suid taxa have elongated posterior molars, the M₃ mesial cusps are close to the center of the molar row, an area targeted when possible in most microwear studies. The adult individuals in some species, like the modern warthog, also end up losing cheek teeth with age, with the exception of the M₃.

Raw point clouds were processed using MountainsMap software (DigitalSurf, Besançon, France), the Solarmap Universal version (Solarius Corp., Sunnyvale, CA) for the bovid and primate samples, and the SensoMAP version (Sensofar Corp., Barcelona, Spain) for the rodent and suid samples. The different software versions used were those bundled with the instruments employed to collect the data. Surfaces were leveled and any data representing dust or other adherent particles on the original facet were deleted manually prior to analysis. Missing data points were not filled, but excluded from analysis.

Surfaces represented by the resulting point clouds were then analyzed using scale-sensitive fractal analysis software (ToothFrax

and SFrax, Surftract Corporation, Norwich, Vermont, USA). This has become a standard for the quantitative characterization of dental microwear surface texture over the past decade, and comparative baseline series of molars of extant taxa representing primates (Scott et al., 2012), bovids (Scott, 2012a), and rodents (Burgman et al., 2016) have all been produced on the same instruments using the same methods as those employed here for the analysis of the Kanapoi specimens. We include the results of a pilot study of 34 extant suids in the SOM (including SOM Tables S2 and S3) to provide some basis for an initial comparison and interpretation.

Detailed descriptions of the individual texture attributes generated from the point clouds are presented in Scott et al. (2006). Two variables were considered for the bovid, primate, and suid studies: area-scale fractal complexity (Asfc) and exact-proportion length-scale anisotropy (ePLsar), because these in combination have predictably separated related species by diet for a wide range of mammalian taxa (see Ungar, 2015; Calandra and Merceron, 2016; DeSantis, 2016 for review). Complexity measures change of roughness across scales of observation, with greater Asfc values typically reflecting a greater number of pits of varying size on the surface. Anisotropy values reflect variation in orientation of a wear surface texture, such that a surface dominated by aligned scratches would have a high ePLsar value. Median values for the four fields representing each bovid and primate individual are considered here, following convention (Scott et al., 2006).

For the rodents, heterogeneity of complexity (HASfc) was considered, because this is the only attribute that has consistently distinguished an admittedly limited extant baseline of taxa across habitats to date (Burgman et al., 2016). Results comparing extant baseline rodent taxa are presented in SOM Table S4. Heterogeneity measures variation in complexity across a surface subdivided into both 3×3 (HASfc₉) and 9×9 (HASfc₈₁) grids. Higher HASfc values indicate less uniformity of complexity across a surface.

Statistical comparisons of fossil data with those for extant baseline samples would require so many tests as to make analyses cumbersome, if not impractical and vulnerable to type I error. Nevertheless, means and ranges for fossil taxa could be compared with those for appropriate extant higher level baseline taxa to contextualize the Kanapoi specimens (see, for example, Teaford et al., 2008; Ungar et al., 2012). Both central tendencies and dispersions were considered, as these have been shown in past studies to be important for inferring food preferences and dietary specificity.

3. Results

Descriptive statistics are presented in Table 1 and comparisons between fossil taxa and extant samples with known diets are illustrated in Figures 1 (bovids), 2 (cercopithecids), 3 (rodents), and 4 (suids). Raw data for all Kanapoi specimens are presented in SOM Table S1.

3.1. Bovids

The bovid sample was the largest, including specimens originally analyzed by JRS (Scott, 2012b) and presented in Ungar et al. (2016) and individuals recovered during recent expeditions by FKM, CVW, and JMP. Complexity and anisotropy data for the Kanapoi bovids are plotted against those for the extant baseline series published by Scott (2012a). The extant taxa are divided into six diet categories following Gagnon and Chew (2000). These are: 1) obligate grazers (>90% monocotyledons), 2) variable grazers (60–90% monocots), 3) browser-grazer intermediates (30–70% monocots and dicots, including some fruit), 4) generalists (>20% of each of the three food types), 5) browsers (>70% dicots only part

fruit), and 6) frugivores (>70% fruits). For this study, the extant baseline was considered using a “taxon-free” approach, with extant specimens grouped by diet category. While there is overlap between individuals in each diet category, specimens do differ significantly by diet (see Scott, 2012a) and central tendencies separate the taxa along the graze-browse continuum as predicted. Grazers tend to have higher anisotropy and lower complexity values than browsers. Bovids with more flexible diets tend to have intermediate anisotropy and complexity values. This corresponds well with earlier studies suggesting that grazer microwear surfaces are dominated by long, parallel striations, whereas browsers have more pitted wear facets (e.g., Solounias et al., 1988).

The Kanapoi bovids as a group approximate the range of extant graze-browse intermediate taxa in complexity-anisotropy bivariate space (Table 1, Fig. 1). Most specimens fall outside the range of extant obligate grazers and do not extend to the frugivore extreme. While there is clearly no one-to-one correlation between habitat and diet, there is a practical association between grazing and grass availability and between browsing and the presence of woody cover (Estes, 1991; Kingdon, 1997; Sponheimer et al., 1999; Gagnon and Chew, 2000). These data therefore suggest a mixed setting or mosaic habitat at Kanapoi during deposition of these fossils, with both graze and browse dietary components available to and consumed by bovids at the site.

3.2. Cercopithecids

Complexity and anisotropy also often separate extant primates on the basis of food choice, though dietary versatility within species often yields disperse and overlapping distributions of microwear texture values (Scott et al., 2012). Hard object specialist primates, such as *Cercocebus atys* from Taï National Park in the Ivory Coast, tend to have microwear textures featuring high complexity and low anisotropy (Daegling et al., 2011). In contrast, species that more often consume tough leaves, such as *Alouatta palliata* and *Trachypithecus cristatus*, have lower complexity and higher anisotropy values on average (Ungar et al., 2007b). Soft fruit eaters, or those with mixed diets, tend to have intermediate complexity and anisotropy average values. These results correspond well with early studies indicating high ratios of pits to scratches for hard object feeders and low ratios for folivores (e.g., Teaford and Walker, 1984). Differences are mirrored in comparisons of baboons and geladas, wherein *Theropithecus* has significantly lower complexity and higher anisotropy averages than *Papio cynocephalus* (yellow baboon) or *Papio ursinus* (chacma baboon) (Scott et al., 2012). This makes sense in the light of the less variable diet of the gelada, typically composed of 90% grass, with a preference for leaf blades when available (Dunbar and Dunbar, 1974; Iwamoto, 1993).

The majority of cercopithecoid primates from Kanapoi evince postmortem damage and do not preserve unobscured antemortem microwear. This is common for Plio-Pleistocene primate specimens from open air eastern African sites. This greatly limits the interpretability of our primate results given variation inherent within extant species. Our Kanapoi sample includes only six individuals ascribed to *Parapapio*, three to Colobinae, and one identified only to family level. None of the specimens examined have the extreme complexity values expected of a hard object feeder (Table 1, Fig. 2). This mirrors previous results for fossil monkeys from East African fossil hominin sites (Lucas and Teaford, 1994; Leakey et al., 2003; Teaford et al., 2008). Further, while the colobines do not have the high anisotropy average expected of a tough-food specialist, the three still fall within extant colobine (*T. cristatus*) bivariate space. When the *Parapapio* specimens are compared with extant geladas and baboons, their texture complexity distribution falls intermediate between those of *Theropithecus* and *Papio*, both in terms of central tendency and

Table 1
Microwear texture summary statistics for Kanapoi.^a

	n	Asfc		epLsar	
		Mean	SD	Mean	SD
Bovidae					
Kanapoi^b	43	2.174	1.319	3.078×10^{-3}	1.401×10^{-3}
Frugivore	46	4.575	1.153	2.548×10^{-3}	1.029×10^{-3}
Browser	95	3.510	0.994	2.287×10^{-3}	6.654×10^{-4}
Generalist	70	2.211	0.646	3.977×10^{-3}	1.031×10^{-3}
Browse-Graze Int	128	2.192	0.665	3.674×10^{-3}	1.358×10^{-3}
Variable Grazer	133	1.516	0.491	5.186×10^{-3}	1.307×10^{-3}
Obligate Grazer	94	1.014	0.264	6.504×10^{-3}	1.103×10^{-3}
Primates					
Parapapio ado^b	6	1.457	1.135	4.549×10^{-3}	1.648×10^{-3}
<i>Papio cynocephalus</i>	27	3.375	3.235	3.167×10^{-3}	1.490×10^{-3}
<i>Papio ursinus</i>	12	2.353	1.343	3.017×10^{-3}	1.393×10^{-3}
<i>Theropithecus gelada</i>	12	0.727	0.210	5.729×10^{-3}	1.500×10^{-3}
Colobinae^b	3	0.884	0.506	3.539×10^{-3}	6.148×10^{-4}
Cercopithecidae^b	1	1.285		1.467×10^{-3}	
<i>Alouatta palliata</i>	11	0.360	0.183	6.060×10^{-3}	1.994×10^{-3}
<i>Trachypithecus cristatus</i>	12	0.734	0.660	4.788×10^{-3}	2.602×10^{-3}
<i>Lophocebus albigena</i>	15	1.769	1.740	4.104×10^{-3}	2.298×10^{-3}
<i>Cercocebus atys</i>	28	4.256	2.016	3.521×10^{-3}	1.438×10^{-3}
Suidae					
Notochoerus jaegeri^b	4	1.753	0.194	4.050×10^{-3}	7.853×10^{-4}
Nyanzachoerus pattersoni^b	15	2.613	0.818	2.073×10^{-3}	1.012×10^{-3}
Suidae^b	1	1.562		1.300×10^{-3}	
<i>Hylochoerus meinertzhageni</i>	3	1.399	0.235	6.433×10^{-3}	6.028×10^{-4}
<i>Phacochoerus</i> sp.	13	1.779	0.534	4.638×10^{-3}	1.457×10^{-3}
<i>Potamochoerus larvatus</i>	18	3.301	1.078	2.856×10^{-3}	1.137×10^{-3}
	n	HAsfc9		HAsfc81	
		Mean	SD	Mean	SD
Kanapoi Rodentia^b	34	0.463	0.366	0.740	0.378
<i>Rhabdomys pumilio</i>	56	0.541	0.241	0.887	0.298
<i>Michaelamys namaquensis</i>	45	0.983	0.858	1.331	0.796
<i>Mastomys coucha</i>	37	5.923	8.098	2.251	1.730

^a Asfc and epLsar defined in text. Data for extant samples from the previously published studies for bovids, primates, and rodents (Daegling et al., 2011; Scott, 2012a; Scott et al., 2012; Burgman et al., 2016). Data for extant pigs as described in SOM.

^b Fossils from Kanapoi in bold.

dispersion. This suggests a diet possibly intermediate between that of the gelada and those of chacma and yellow baboons. It could also reflect a habitat preference intermediate between the extremely arid Ethiopian highlands populated by geladas and the savannas, woodland, and forest fringe inhabited by baboons. We caution against over interpreting these results, however, given the small sample of Kanapoi *Parapapio* specimens and the range of variation in environments in which baboons are found today.

3.3. Rodents

Few rodent taxa have been studied for dental microwear texture analysis to date, and our interpretations are only as good as our baseline for comparison. Feature based molar microwear studies do however suggest patterns reflect diets of rodents, just as they do for bovids and primates. Rodrigues et al. (2009), for example, demonstrate that extant grass, fruit, and insect eaters have surfaces dominated by fine scratches, wide scratches, and pits respectively. They compare their baseline sample to fossil rodents from the Hadar to infer a grass eating diet and the presence of monotyledons at the site during the mid-Pliocene.

Our published molar microwear textures of extant rodents to date have been limited to three species, *Rhabdomys pumilio*, *Michaelamys namaquensis*, and *Mastomys coucha* (Burgman et al., 2016). All these species are opportunistic omnivores, though there are subtle differences in their food preferences. *Mastomys* is a generalist and includes a substantial amount of seeds in its diet

(Skinner and Chimimba, 2005; Avenant, 2011; Leirs, 2013). *Michaelamys* has been reported to include a high proportion of grass blades and lives in a narrower range of habitats than *Mastomys* (Perrin and Curtis, 1980; Kesner et al., 2013). *Rhabdomys* is also omnivorous (Skinner and Chimimba, 2005; Happold, 2013), but inconsistencies in reported diets in the literature make it difficult to better characterize their diets.

When the extant baseline sample of Burgman et al. (2016) is considered by species, taxa are best distinguished on the basis of heterogeneity of complexity (see SOM Table S4). *Mastomys* has the highest average values, driven by the highest dispersion. *Rhabdomys* has the lowest. The high dispersion in *Mastomys* might reflect variation in food choice or availability, with some individuals consuming mostly tough grass blades and others including more hard seeds in their diets. Burgman et al. (2016) further suggest that the lack of variation in microwear for *Rhabdomys* reflects a less opportunistic diet that remains constant despite variation in microhabitat, although more work is required to confirm this.

The distributions of microwear texture heterogeneity values for the Kanapoi rodents are most similar to those of *Michaelamys* and especially *Rhabdomys*, and most different from those of *Mastomys* (Table 1, Fig. 3). If Burgman et al. (2016) are correct in their interpretation, this implies a less variable diet for the Kanapoi rodents than for extant *Mastomys*. The lack of high HAsfc values for the Kanapoi sample may imply consumption of more grass blades and fewer seeds, though, again, more work with more extant taxa with better known and narrower diets is called for to confirm or refute

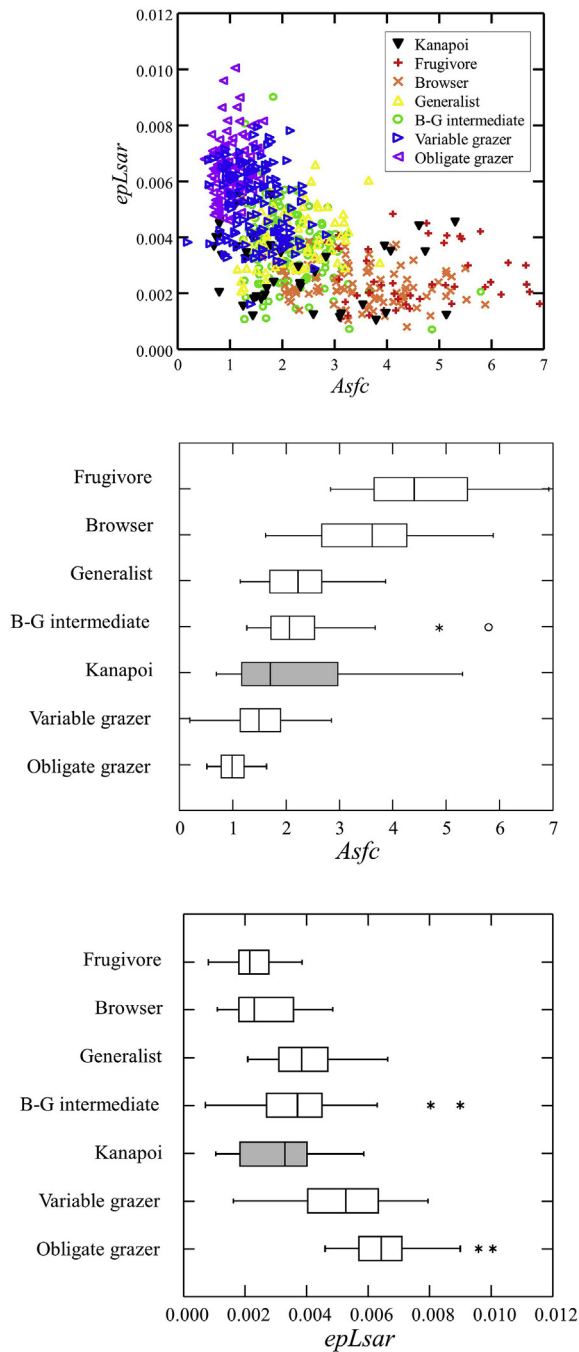


Figure 1. Dental microwear texture complexity and anisotropy data for extant bovids and specimens from Kanapoi. Extant bovids are partitioned following diet categories of Gagnon and Chew (2000), with data from Scott (2012a).

this assertion. Species specific comparisons of the fossil taxa would be valuable too, if sufficient numbers were identifiable to species level. Further, while we chose to study molars rather than incisors because they are taxonomically distinctive and identifiable, incisor microwear textures, which appear to be more sensitive to habitat variation (Caporale and Ungar, 2016), could also help.

3.4. Suids

This is the first study of which we are aware to employ dental microwear texture analysis to infer the diets of fossil suids. Souron

et al. (2015) recently demonstrated that extant suids differ significantly in microwear textures in a manner that makes sense in terms of diet differences. Notably, omnivores are distinguished from herbivores by texture complexity and generalists differ from specialists in terms of heterogeneity of complexity. Still, the instrument, software, and analytical procedures they used differ from those employed here, necessitating a new baseline sample for comparison with the fossil suids from Kanapoi (see Arman et al., 2016 for discussion). Comparative data for the extant suid taxa *Potamochoerus larvatus*, *Phacochoerus* sp., and *Hylochoerus meinertzhageni* are presented in SOM Tables S2 and S3. The *Hylochoerus* sample is too small to separate from *Phacochoerus*, though *Phacochoerus* is clearly distinguished from *Potamochoerus* (and *Hylochoerus* does not overlap with *Potamochoerus*). While the results for *Hylochoerus* are difficult to interpret given the extremely small sample ($n = 3$), the difference between the other two suids makes perfect sense in the light of diet differences (as with bovids, the grazer has lower average Asfc and higher epLsar than the mixed feeder), and the directions and magnitudes of differences are consistent with those obtained by Souron et al. (2015).

The Kanapoi suids are represented by two species of the subfamily Tetraconodontinae, the abundant *Nyanzachoerus pattersoni* and the less well represented *Notochoerus jaegeri* (Harris et al., 2003). *Nyanzachoerus pattersoni* is a generalized suid, showing typical tetraconodon molar morphology and very big premolars. *Notochoerus jaegeri* has more derived third molars and relatively reduced premolars suggesting a probable shift toward a grass-dominated diet (Harris and White, 1979; Harris et al., 2003). The dental microwear results correspond well with the diets as inferred from dental morphology of these suids. The values for complexity and anisotropy for *No. jaegeri* resemble those of the modern grazer, *Phacochoerus*, while those for *Ny. pattersoni* are more consistent with the range of variability of modern *Po. larvatus* (Table 1, Fig. 4). This is consistent with a mix of environmental settings at Kanapoi, with *Ny. pattersoni* inhabiting forested or semi-forested habitats and *No. jaegeri* occupying more open settings. It is important to note, though, that even *Phacochoerus*, the suid best adapted to open habitats in Africa, is also dependent on some non-grassy vegetation and water availability for its survival (Cumming, 1975, 2013).

4. Discussion and conclusions

The geology at Kanapoi hints at a strongly mosaic setting and, as Feibel (2003:14) notes, “some of the greatest habitat patchiness recorded from the Turkana Basin Plio-Pleistocene.” Indeed, there are at least seven distinct paleosols identified by Wynn (2000), evidently representing distinct microhabitats ranging from sparsely vegetated, arid grassland to gallery woodland. In addition, fossil herbivores recovered from the site over the past half century show taxa whose living representatives range from obligate grazers to dietary generalists to dedicated browsers. Further, carbon isotope ratios reported for fossil teeth of these fauna run the gamut of $\delta^{13}\text{C}$ values, from those specializing on C_3 resources, to those with mixed diets, to those that ate mostly C_4 foods. While the inferred proportion of bush/tree products to grass in the diet varies depending on the proxy considered—grazing taxa outnumber browsers three to one, whereas the proportion of soil carbonates from C_4 to C_3 plants runs as low as one to three (Harris and Leakey, 2003)—the evidence in aggregate points to a heterogeneous environment offering the hominins that lived there a broad range of resources from which to choose.

While much work remains to be done to establish a robust extant baseline to interpret microwear textures of the whole herbivore guild represented at Kanapoi, results presented here are consistent with a broad spectrum of foods and a mosaic of

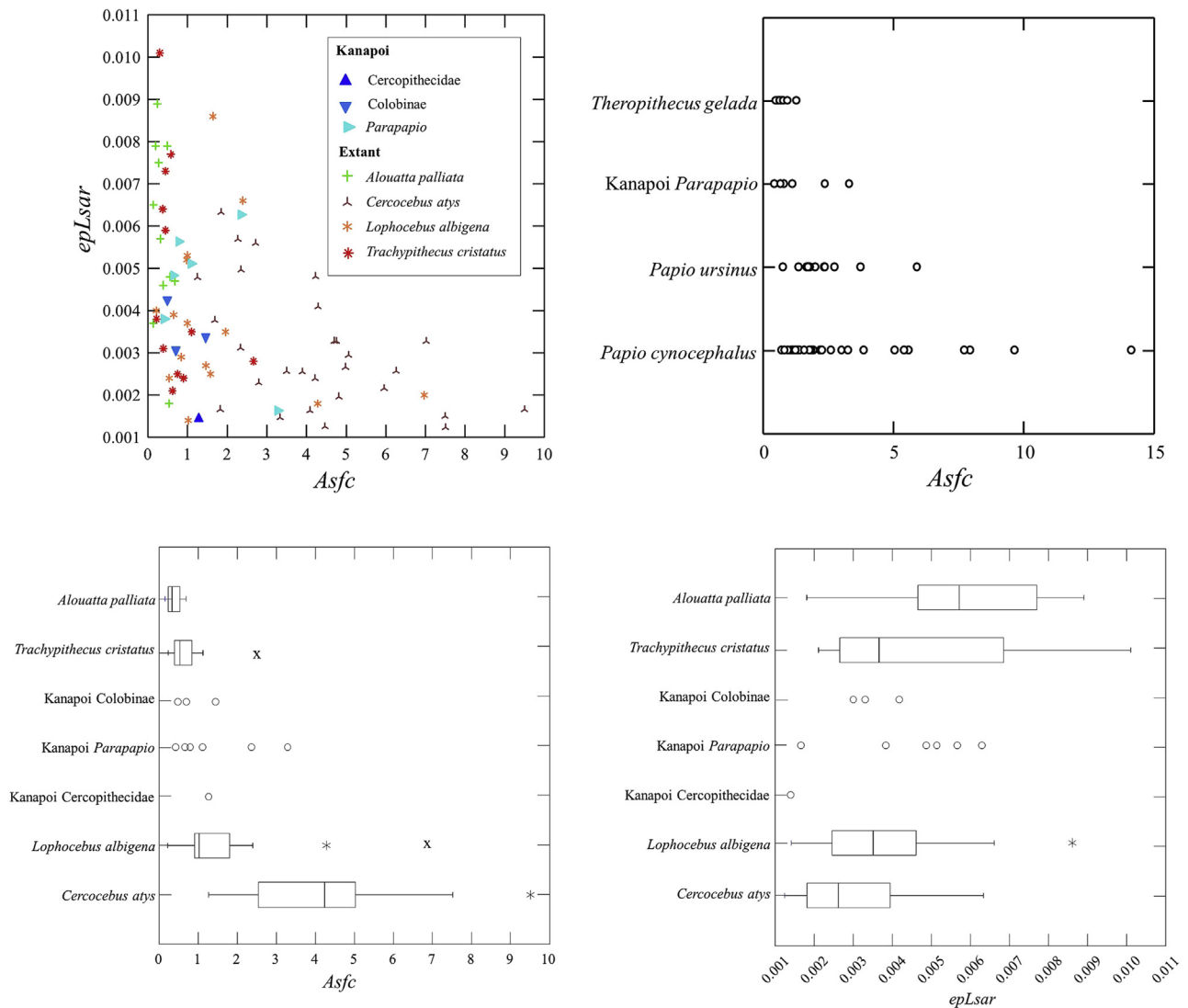


Figure 2. Dental microwear texture complexity and anisotropy data for extant primates and specimens from Kanapoi. The results in the upper right compare Kanapoi *Parapapio* with extant baboons and geladas, and those below compare data points for the Kanapoi cercopithecids with box-and-whiskers plots of extant primate folivores (*Alouatta*, *Trachypithecus*) and hard-object feeders (*Lophocebus*, *Cercocebus* from Tai National Park). Extant primate data are from Daegling et al. (2011) and Scott et al. (2012).

microhabitat types from which to draw them. We are on most solid ground with the bovids. The sample size of bovids from Kanapoi is excellent, the extant comparative baseline is well developed, and fossil ruminant microwear textures have proven to be a valuable paleoenvironmental proxy for a number of sites (Ungar et al., 2007b, 2012; Merceron et al., 2016). The bovids at Kanapoi lack the extreme high complexity values of frugivores and especially the high anisotropy values of obligate grazers. The distribution of texture values most closely resembles those of extant specimens categorized as variable grazers and browse-graze intermediates. This suggests that the ruminants at Kanapoi inhabited settings that included both grass and browse food items.

The cercopithecids from Kanapoi are more difficult to interpret, in part because of the small sample, and in part because monkeys in the eastern Rift Valley today tend to be catholic in their dietary proclivities and inhabit a broad range of environments. In other words, the relationship between diet and habitat may not be as clear for savanna/woodland-dwelling primates as it can be for bovids. The lack of high complexity values for any of the monkeys from Kanapoi suggest that hard items, such as nuts or seeds, were not commonly consumed. Further, *Parapapio* from Kanapoi has

microwear texture values intermediate between modern-day baboons and geladas. Modern geladas have lower average texture complexity and higher anisotropy than baboons. *Theropithecus* also has the narrowest range of texture complexity of any extant cercopithecoid studied to date (Scott et al., 2012; Shapiro et al., 2016), which is consistent with its narrow diet, focused on grass blades and seeds. Microwear textures of *Parapapio* specimens from Kanapoi likewise show low dispersions in complexity, with an average value consistent with grass as an important part of its diet, albeit probably not to the degree eaten by modern geladas.

The microwear textures of rodents and suids from Kanapoi are even more difficult to interpret, because of the lack of a sufficient comparative baseline series to facilitate interpretation of the patterns. Nevertheless, the low variability of heterogeneity values for the rodent microwear textures suggests these micromammals differed from extant *Mastomys*, which is reported to be a highly opportunistic omnivore, consuming foods ranging from seeds to insects to foliage. If interpretations of Burgman et al. (2016) hold, it may be that the Kanapoi rodents sampled for this study had narrower diets, perhaps including more grass blades than seeds or other hard objects. The fossil suid microwear texture anisotropy

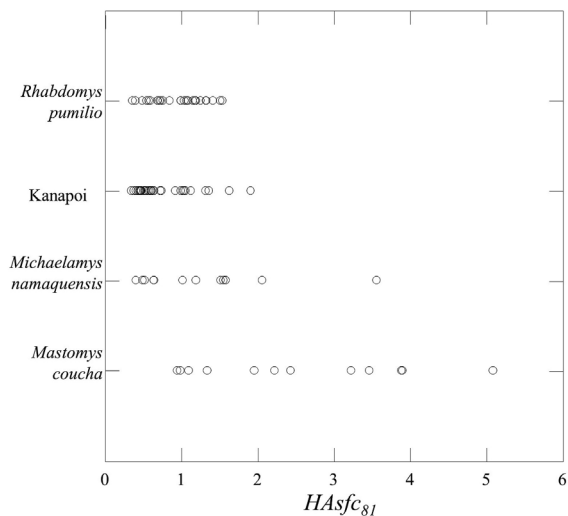
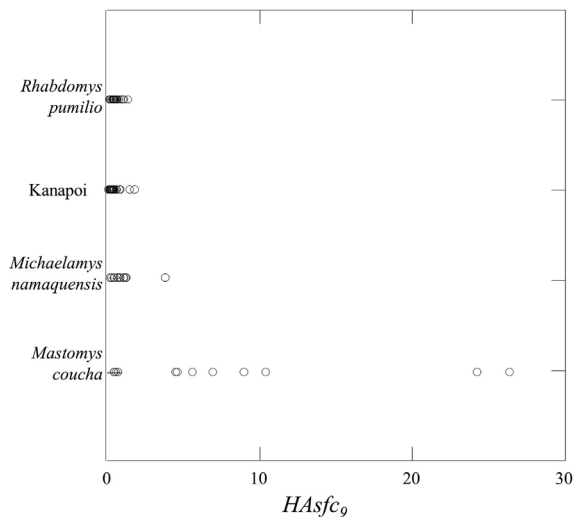


Figure 3. Dental microwear texture heterogeneity data for extant rodents and specimens from Kanapoi. $HASfc_9$ and $HASfc_{81}$ are based on dividing each surface into 3×3 and 9×9 grids respectively (see the text for details). Extant rodent data are from Burgman et al. (2016), with analyses of extant taxa in SOM Table S4.

and complexity distributions are, on the other hand, most consistent with a mixed setting, with the range of texture values overlapping those of the extant grazer *Phacochoerus* and the graze-browse mixed feeder *Potamochoerus*, but lacking the high-end anisotropy and complexity values of these species, respectively. This microwear texture evidence is consistent with a presence of grasses in combination with some woody plants.

As an aside, while samples of the other taxa from Kanapoi necessitated a taxon-free approach given small samples of individual taxa or uncertain species attributions, there does seem to be some separation between *Ny. pattersoni* and *No. jaegeri* indicative of a mixed feeding and a grazing niche, respectively, and consistent with interpretation based on dental morphology. This suggests not only a mosaic of environments, but also niche partitioning in which some taxa preferred specific microhabitats. That makes it difficult to distinguish between distinct microhabitats and heterogeneous settings with both grass and woody components. On the other hand, the geology certainly points to distinct microhabitats (Wynn,

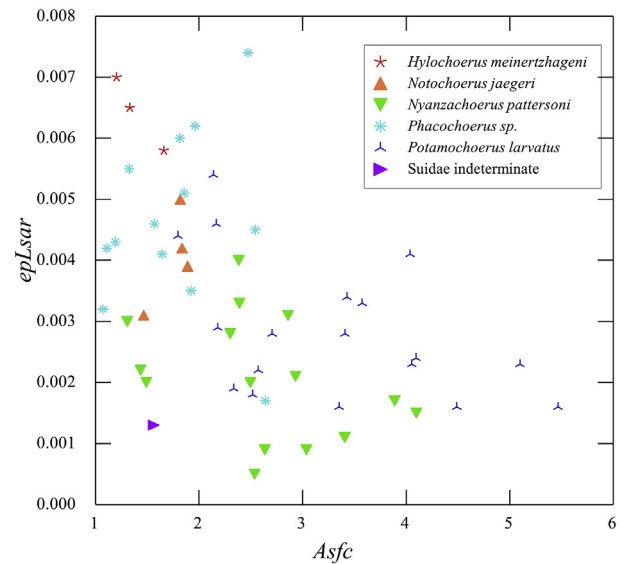


Figure 4. Dental microwear texture complexity and anisotropy data for extant suids and specimens from Kanapoi. The extant suid data are described in the SOM.

2000; Feibel, 2003), which is consistent with the faunal evidence, including the microwear.

4.1. Future directions

This study raises more questions than it answers. The microwear evidence is clearly consistent with a heterogeneous environment in and around Kanapoi during the early Pliocene. Nevertheless, it exposes current limitations of microwear texture analysis to determine the nuances of herbivore guild niche partitioning and paleocommunity dynamics. If microwear is to reach its potential as a tool to understand paleoecology, much more work is needed to establish baselines of textures for whole extant herbivore guilds from different environmental settings. We know that microwear textures of individual taxa can reveal food preferences in given environmental settings. Perhaps whole communities of mammals in different environments have distinctive patterns of microwear texture signatures because of differences in how they divvy up the resources available to them. If so, guild-wide studies of microwear might give us a better handle on paleocommunity ecology, both to help us understand the role of habitat in structuring life itself and to provide a better proxy for reconstructing environments of the past.

Acknowledgments

This study was funded by the US National Science Foundation grants BCS-1231749 (to CVW and FKM) and BCS-1231675 (to JMP and PSU). IAL was supported by a graduate student research grant from the School of Human Evolution and Social Change at Arizona State University. We thank curators in the departments of paleontology and mammalogy at the National Museums of Kenya for permission to study specimens in their care, Sarah Livengood for her assistance with data analysis for the suids, and Mark Teaford, Daniela Kalthoff, and an anonymous reviewer for their helpful comments on an earlier version of this manuscript.

Supplementary Online Material

Supplementary online material related to this article can be found at <http://dx.doi.org/10.1016/j.jhevol.2017.03.005>.

References

- Andrews, P.J., Humphrey, L., 1999. African Miocene environments and the transition to early hominines. In: Bromage, T.G., Schrenk, F. (Eds.), *African Biogeography, Climate Change, and Human Evolution*. Oxford University Press, Oxford, pp. 282–300.
- Arman, S.D., Ungar, P.S., Brown, C.A., DeSantis, L.R.G., Schmidt, C., Prideaux, G.J., 2016. Minimizing inter-microscope variability in dental microwear texture analysis. *Surf. Topogr. Metrol. Prop.* 4, 024007.
- Avenant, N., 2011. The potential utility of rodents and other small mammals as indicators of ecosystem 'integrity' of South African grasslands. *Wildl. Res.* 38, 626–639.
- Bobe, R., 2011. Fossil mammals and paleoenvironments in the Omo-Turkana Basin. *Evol. Anthropol.* 20, 254–263.
- Burgman, J.H.E., Leichliter, J., Avenant, N.L., Ungar, P.S., 2016. Dental microwear of sympatric rodent species sampled across habitats in southern Africa: implications for environmental influence. *Intl. Zool.* 11, 111–127.
- Calandra, I., Merceron, G., 2016. Dental microwear texture analysis in mammalian ecology. *Mammal Rev.* 46, 215–228.
- Caporale, S.S., Ungar, P.S., 2016. Rodent incisor microwear as a proxy for ecological reconstruction. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 446, 225–233.
- Charles, C., Jaeger, J.-J., Michaux, J., Viriot, L., 2007. Dental microwear in relation to changes in the direction of mastication during the evolution of Myodonta (Rodentia, Mammalia). *Naturwissenschaften* 94, 71–75.
- Cumming, D.H.M., 1975. A Field Study of the Ecology and Behaviour of the Warthog. Trustees of the National Museums and Monuments of Rhodesia, Salisbury.
- Cumming, D.H.M., 2013. *Phacochoerus africanus*. The Common Wart Hog. In: Kingdon, J., Happold, D., Butynski, T., Hoffman, M., Happold, M., Kalina, J.J. (Eds.), *Mammals of Africa, Volume 6*. Bloomsbury Publishing, London, pp. 54–60.
- 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.
- Delezene, L., Teaford, M.F., Ungar, P.S., 2016. Canine and incisor microwear in pitheciids and Ateles reflects documented patterns of tooth use. *Am. J. Phys. Anthropol.* 161, 6–25.
- Delezene, L.K., Kimbel, W.H., 2011. Evolution of the mandibular third premolar crown in early *Australopithecus*. *J. Hum. Evol.* 60, 711–730.
- DeSantis, L.R., Schubert, B.W., Scott, J.R., Ungar, P.S., 2012. Times not so tough at La Brea: Dental microwear texture analysis clarifies the feeding behavior of the saber-toothed cat, *Smilodon fatalis*, and American lion, *Panthera atrox*. *J. Vert. Paleontol.* 32, 86–87.
- DeSantis, L.R.G., 2016. Dental microwear textures: reconstructing diets of fossil mammals. *Surf. Topogr. Metrol. Prop.* 4, 023002.
- Donohue, S.L., DeSantis, L.R.G., Schubert, B.W., Ungar, P.S., 2013. Was the giant short-faced bear a hyper-scavenger? A new approach to the dietary study of ursids using dental microwear textures. *PLoS One* 8(10), e77531.
- Dunbar, R.I.M., Dunbar, E.P., 1974. Ecological relations and niche separation between sympatric terrestrial primates in Ethiopia. *Folia Primatol.* 21, 36–60.
- Estalrrich, A., Young, M.B., Teaford, M.F., Ungar, P.S., 2015. Environmental perturbations can be detected through microwear texture analysis in two platyrrhine species from Brazilian Amazonia. *Am. J. Primatol.* 77, 1230–1237.
- Estes, R.D., 1991. *The Behavior Guide to African Mammals: Including Hoofed Mammals, Carnivores and Primates*. University of California Press, Berkeley.
- Feibel, C.S., 2003. Stratigraphy and depositional setting of the Pliocene Kanapoi Formation, lower Kerio Valley, Kenya. In: Harris, J.M., Leakey, M.G. (Eds.), *Geology and Vertebrate Paleontology of the Early Pliocene Site of Kanapoi, Northern Kenya*. Natural History Museum of Los Angeles County, Los Angeles, pp. 9–20.
- Gagnon, M., Chew, A.E., 2000. Dietary preferences in extant African Bovidae. *J. Mammal.* 8, 490–511.
- Haile-Selassie, Y., Saylor, B.Z., Deino, A., Alene, M., Latimer, B.M., 2010. New hominid fossils from Woranso-Mille (Central Afar, Ethiopia) and taxonomy of early *Australopithecus*. *Am. J. Phys. Anthropol.* 141, 406–417.
- Happold, D.C.D., 2013. *Rhabdomys pumilio* four-striped grass mouse. In: Happold, D.C.D. (Ed.), *Mammals of Africa, Volume III*. Bloomsbury Publishing, London, pp. 544–547.
- Harris, J.M., Leakey, M.G., 2003. Introduction. In: Harris, J.M., Leakey, M.G. (Eds.), *Geology and Vertebrate Paleontology of the Early Pliocene Site of Kanapoi, Northern Kenya*. Natural History Museum of Los Angeles County, Los Angeles, pp. 1–8.
- Harris, J.M., White, T.D., 1979. Evolution of the Plio-Pleistocene African Suidae. *Trans. Am. Phil. Soc.* 69, 5–128.
- Harris, J.M., Leakey, M.G., Cerling, T.E., 2003. Early Pliocene tetrapod remains from Kanapoi, Lake Turkana Basin, Kenya. In: Harris, J.M., Leakey, M.G. (Eds.), *Geology and Vertebrate Paleontology of the Early Pliocene Site of Kanapoi, Northern Kenya*. Natural History Museum of Los Angeles County, Los Angeles, pp. 39–114.
- Haupt, R.J., DeSantis, L.R.G., Green, J.L., Ungar, P.S., 2013. Dental microwear texture as a proxy for diet in xenarthrans. *J. Mammal.* 94, 856–866.
- Hautier, L., Bover, P., Alcover, J.A., Michaux, J., 2009. Mandible morphometrics, dental microwear pattern, and palaeobiology of the extinct Balearic Dormouse *Hypnomys morpheus*. *Acta Palaeontol. Pol.* 54, 181–194.
- 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.
- Jones, D.B., DeSantis, L.R.G., 2016. Dietary ecology of the extinct cave bear: Evidence of omnivory as inferred from dental microwear textures. *Acta Palaeontol. Pol.* 61, 735–741.
- Kaya, F., Kaymakci, N., 2013. Systematics and dental microwear of the late Miocene Gliridae (Rodentia, Mammalia) from Hayranli, Anatolia: implications for paleoecology and paleobiodiversity. *Palaeontol. Electron.* 16(2), 22.
- Kesner, M.H., Linzey, A.V., Chimimba, C.T., 2013. *Aethomys namaquensis* Namaqua Veld Rat. In: Happold, D.C.D. (Ed.), *Mammals of Africa, Volume III*. Bloomsbury Publishing, London.
- Kimbel, W.H., Lockwood, C.A., Ward, C.V., Leakey, M.G., Rak, Y., Johanson, D.C., 2006. Was *Australopithecus anamensis* ancestral to *A. afarensis*? A case of anagenesis in the hominin fossil record. *J. Hum. Evol.* 51, 134–152.
- King, T., Andrews, P., Boz, B., 1999. Effect of taphonomic processes on dental microwear. *Am. J. Phys. Anthropol.* 108, 359–373.
- Kingdon, J., 1997. *The Kingdon Field Guide to African Mammals*. Academic Press, San Diego.
- Krueger, K.L., Scott, J.R., Ungar, P.S., 2008. Technical note: Dental microwear textures of "Phase I" and "Phase II" facets. *Am. J. Phys. Anthropol.* 137, 485–490.
- Lazzari, V., Charles, C., Tafforeau, P., Vianey-Liaud, M., Aguilar, J.P., Jaeger, J.J., Michaux, J., Viriot, L., 2008. Mosaic convergence of rodent dentitions. *PLoS One* 3(10), e3607.
- Leakey, M.G., Teaford, M.F., Ward, C.V., 2003. Cercopithecidae from Lothagam. In: Leakey, M.G., Harris, J.M. (Eds.), *Lothagam: The Dawn of Humanity in Eastern Africa*. Columbia University Press, New York, pp. 201–248.
- Leirs, H., 2013. *Mastomys coucha* Southern Africa Multimammate Mouse. In: Happold, D.C.D. (Ed.), *Mammals of Africa, Volume III*. Bloomsbury Publishing, London, p. 463.
- Lewis, P.J., Gutierrez, M., Johnson, E., 2000. *Ondatra zibethicus* (Arvicolinae, Rodentia) dental microwear patterns as a potential tool for palaeoenvironmental reconstruction. *J. Archaeol. Sci.* 27, 789–798.
- Lucas, P.W., Teaford, M.F., 1994. Functional morphology of colobine teeth. In: Davies, A.G., Oates, J.F. (Eds.), *Colobine Monkeys: Their Ecology, Behaviour and Evolution*. Cambridge University Press, Cambridge, pp. 173–203.
- Manthi, F.K., 2006. The Pliocene Micromammalian Fauna from Kanapoi, Northwestern Kenya, and its Contribution to Understanding the Environment of *Australopithecus anamensis*. University of Cape Town, Cape Town.
- Manthi, F.K., Plavcan, J.M., Ward, C.V., 2012. New hominin fossils from Kanapoi, Kenya, and the mosaic evolution of canine teeth in early hominins. *S. Afr. J. Sci.* 108, 35–43.
- Merceron, G., Escarguel, G., Angibault, J.M., Verheyden-Tixier, H., 2010. Can dental microwear textures record inter-individual dietary variations? *PLoS One* 5(3), e9542.
- Merceron, G., Hofman-Kaminska, E., Kowalczyk, R., 2014. 3D dental microwear texture analysis of feeding habits of sympatric ruminants in the Bialowieza Primeval Forest, Poland. *Forest Ecol. Manag.* 328, 262–269.
- Merceron, G., Novello, A., Scott, R.S., 2016. Paleoenvironments inferred from phytoliths and dental microwear texture analyses of meso-herbivores. *Geobios* 49, 135–146.
- Perrin, M.R., Curtis, B.A., 1980. Comparative morphology of the digestive system of 19 species of southern African myomorph rodents in relation to diet and evolution. *S. Afr. J. Zool.* 15, 22–33.
- Prideaux, G.J., Ayliffe, L.K., DeSantis, L.R.G., Schubert, B.W., Murray, P.F., Gagan, M.K., Cerling, T.E., 2009. Extinction implications of a chenopod browse diet for a giant Pliocene kangaroo. *Proc. Natl. Acad. Sci.* 106, 11646–11650.
- Purnell, M.A., Crumpton, N., Gill, P.G., Jones, G., Rayfield, E.J., 2013. Within-guild dietary discrimination from 3-D textural analysis of tooth microwear in insectivorous mammals. *J. Zool.* 291, 249–257.
- Ramdarshan, A., Blondel, C., Brunetiere, N., Francisco, A., Gautier, D., Surault, J., Merceron, G., 2016. Seeds, browse, and tooth wear: a sheep perspective. *Ecol. Evol.* 6, 1–11.
- Reed, K.E., 1997. Early hominid evolution and ecological change through the African Plio-Pleistocene. *J. Hum. Evol.* 32, 289–322.
- Rodrigues, H.G., Merceron, G., Viriot, L., 2009. Dental microwear patterns of extant and extinct Muridae (Rodentia, Mammalia): Ecological implications. *Naturwissenschaften* 96, 537–542.
- Rodrigues, H.G., Marivaux, L., Vianey-Liaud, M., 2012. Expansion of open landscapes in Northern China during the Oligocene induced by dramatic climate changes: paleoecological evidence. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 358, 62–71.
- Schubert, B.W., Ungar, P.S., DeSantis, L.R.G., 2010. Carnassial microwear and dietary behaviour in large carnivores. *J. Zool.* 280, 257–263.
- Schulz, E., Calandra, I., Kaiser, T.M., 2010. Applying tribology to teeth of hoofed mammals. *Scanning* 32, 162–182.
- Schulz, E., Piotrowski, V., Claus, 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.R., 2012a. Dental microwear texture analysis of extant African Bovidae. *Mammalia* 76, 157–174.
- Scott, J.R., 2012b. Dental Microwear Texture Analysis of Pliocene Bovids from Four Early Hominin Fossil Sites in Eastern Africa: Implications for Paleoenvironmental Dynamics and Human Evolution, Environmental Dynamics. University of Arkansas, Fayetteville.
- Scott, J.R., Godfrey, L.R., Jungers, W.L., Scott, R.S., Simons, E.L., Teaford, M.F., Ungar, P.S., Walker, A., 2009. Dental microwear texture analysis of two families of subfossil lemur from Madagascar. *J. Hum. Evol.* 56, 405–416.

- 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., Venkataraman, V.V., Nguyen, N., 2016. Dietary ecology of fossil *Theropithecus*: Inferences from dental microwear textures of extant geladas from ecologically diverse sites. *J. Hum. Evol.* 99, 1–9.
- Silcox, M.T., Teaford, M.F., 2002. The diet of worms: an analysis of mole dental microwear. *J. Mammal.* 83, 804–814.
- Skinner, J.D., Chimimba, C.T., 2005. *The Mammals of the Southern African Subregion*. Cambridge University Press, Cambridge.
- Solounias, N., Teaford, M., Walker, A., 1988. Interpreting the diet of extinct ruminants: The case of a non-browsing giraffid. *Paleobiology* 14, 287–300.
- Souron, A., Merceron, G., Blondel, C., Brunetiere, N., Colyn, M., Hofman-Kaminska, E., Boissarie, J.R., 2015. Three-dimensional dental microwear texture analysis and diet in extant Suidae (Mammalia: Cetartiodactyla). *Mammalia* 79, 279–291.
- Sponheimer, M., Reed, K.E., Lee-Thorp, J.A., 1999. Combining isotopic and ecomorphological data to refine bovid paleodietary reconstruction: a case study from the Makapansgat Limeworkshominin locality. *J. Hum. Evol.* 36, 705–718.
- Sponheimer, M., Alemseged, Z., Cerling, T.E., Grine, F.E., Kimbel, W.H., Leakey, M.G., Lee-Thorp, J.A., Manthi, F.K., Reed, K.E., Wood, B.A., Wynn, J.G., 2013. Isotopic evidence of early hominin diets. *Proc. Natl. Acad. Sci. USA* 110, 10513–10518.
- Stynder, D.D., Ungar, P.S., Scott, J.R., Schubert, B.W., 2012. A dental microwear texture analysis of the Mio-Pliocene hyaenids from Langebaanweg, South Africa. *Acta Palaeontol. Pol.* 57, 485–496.
- Teaford, M.F., 1988. Scanning electron microscope diagnosis of wear patterns versus artifacts on fossil teeth. *Scanning Microsc.* 2, 1167–1175.
- Teaford, M.F., Walker, A., 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.
- Teaford, M.F., Ungar, P.S., Kay, R.F., 2008. Molar shape and molar microwear in the Koobi Fora monkeys: ecomorphological implications. In: Jablonski, N.G., Leakey, M.G. (Eds.), *Koobi Fora Research Project, The Fossil Monkeys, Volume 6. Occasional Paper of the California Academy of Sciences, San Francisco*, pp. 337–358.
- Ungar, P.S., 2015. Mammalian dental function and wear: A review. *Biosurface Biotribol.* 1, 25–41.
- Ungar, P.S., Scott, R.S., Scott, J.R., Teaford, M.F., 2007a. Dental microwear analysis: historical perspectives and new approaches. In: Irish, J.D., Nelson, G.C. (Eds.), *Dental Anthropology*. Cambridge University Press, Cambridge, pp. 389–425.
- Ungar, P.S., Merceron, G., Scott, R.S., 2007b. Dental microwear texture analysis of Varswater bovids and early Pliocene paleoenvironments of Langebaanweg, Western Cape Province, South Africa. *J. Mammal. Evol.* 14, 163–181.
- Ungar, P.S., Scott, R.S., Grine, F.E., Teaford, M.F., 2010a. Molar microwear textures and the diets of *Australopithecus anamensis* and *Australopithecus afarensis*. *Philos. Trans. Roy. Soc. B Biol. Sci.* 365, 3345–3354.
- Ungar, P.S., Scott, J.R., Schubert, B.W., Stynder, D.D., 2010b. Carnivoran dental microwear textures: Comparability of carnassial facets and functional differentiation of postcanine teeth. *Mammalia* 74, 219–224.
- Ungar, P.S., Scott, J.R., Curran, S.C., Dunsforth, H.M., Harcourt-Smith, W.E.H., Lehmann, T., Manthi, F.K., McNulty, K.P., 2012. Early Neogene environments in East Africa: Evidence from dental microwear of tragulids. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 342, 84–96.
- Ungar, P.S., Scott, J.R., Steininger, C.M., 2016. Dental microwear and environments of Plio-Pleistocene bovids from southern and eastern Africa. *S. Afr. J. Sci.* 112, 134–138.
- Ward, C.V., Leakey, M., Walker, A., 1999. The new hominid species *Australopithecus anamensis*. *Evol. Anthropol.* 7, 197–205.
- Ward, C.V., Leakey, M.G., Walker, A., 2001. Morphology of *Australopithecus anamensis* from Kanapoi and Allia Bay, Kenya. *J. Hum. Evol.* 41, 255–368.
- Ward, C.V., Plavcan, J.M., Manthi, F.K., 2010. Anterior dental evolution in the *Australopithecus anamensis-afarensis* lineage. *Philos. Trans. Roy. Soc. B Biol. Sci.* 365, 3333–3344.
- Ward, C.V., Manthi, F.K., Plavcan, J.M., 2013. New fossils of *Australopithecus anamensis* from Kanapoi, West Turkana, Kenya (2003–2008). *J. Hum. Evol.* 65, 501–524.
- Withnell, C.B., Ungar, P.S., 2014. A preliminary analysis of dental microwear as a proxy for diet and habitat in shrews. *Mammalia* 78, 409–415.
- Wynn, J.G., 2000. Paleosols, stable carbon isotopes, and paleoenvironmental interpretation of Kanapoi, Northern Kenya. *J. Hum. Evol.* 39, 411–432.
- Zhang, H., Wang, Y., Janis, C.M., Goodall, R.H., Purnell, M.A., 2016. An examination of feeding ecology in Pleistocene proboscideans from southern China (*Sinomas-todon*, *Stegodon*, *Elephas*), by means of dental microwear texture analysis. *Quatern. Int.* <http://dx.doi.org/10.1016/j.quaint.2016.07.011>.