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Dental Microwear Texture Analysis of Pliocene Bovids from Four Early Hominin Fossil Sites in Eastern Africa: Implications for Paleoenvironmental Dynamics and Human Evolution

Dental Microwear Texture Analysis of Pliocene Bovids from Four Early Hominin Fossil Sites in Eastern Africa: Implications for Paleoenvironmental Dynamics and Human Evolution

A dissertation submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy in Environmental Dynamics

By

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ABSTRACT

Many researchers have suggested that Pliocene climate change was a motive force for human evolution. The basic idea is that a shift toward drier, more open settings, led to adaptations for bipedality and the consumption of savanna resources, including large grazing mammals. However, more recent paleoenvironmental reconstructions suggest that Pliocene hominins occupied variable or mosaic habitats, including both open and closed settings. Many techniques have been used to refine our understanding of the paleoenvironments of eastern Africa; however these have not led to consensus reconstructions. At Kanapoi, ecological diversity analysis indicates that at least part of the site was composed of closed woodland forest; however, taxonomic uniformitarianism of bovid taxa suggests a dry, arid habitat. Similarly contradictory reconstructions exist for Allia Bay, with paleosol analysis and palynology suggesting a mosaic habitat dominated by savanna, and taxonomic uniformitarianism of faunal assemblages suggesting an environment composed of gallery forest, open woodland, floodplains and edaphic grasses. The Laetoli faunal assemblages have also led to varying reconstructions, with some suggesting habitats as disparate as open grassland and closed woodland. Hadar has been reconstructed as a shifting mosaic environment, with various proxies supporting different levels of habitat fluctuation. This dissertation aims to test these opposing hypotheses by bringing a new, independent dataset for the inference of diet, and by extension habitats of actual individuals in the days before death. I use dental microwear texture analysis to reconstruct ratios of graze to browse in the diet and therefore ecological contexts of fossil bovids from Kanapoi, Allia Bay, Laetoli and Hadar. This dissertation tests competing hypotheses concerning early hominin habitats at Kanapoi, Allia Bay, Laetoli and Hadar and how ecological settings may have

changed over the temporal span of *Australopithecus anamensis* and *A. afarensis*. It also serves as an important test of the principle of taxonomic uniformitarianism, often applied to fossil fauna.

High resolution casts of 220 fossil bovids from the four sites and 575 extant African bovids were scanned for dental microwear textures using a white-light confocal profiler. Four adjacent scans were collected from each specimen, resulting in a total work envelope of 204 x 276 µm. The scans were then analyzed using Toothfrax and Sfrax software packages and compared to a database of extant bovids with known diets. The extant bovids collected for use in this study include 25 extant African taxa, representing the full obligate grazer-browser-frugivore continuum.

The extant bovids showed significant variation that separated the taxa predictably by known dietary category, with the exception of generalists and browser-grazer intermediates. Some variation was also noted within the dietary categories, suggesting seasonal and/or geographic variation. In general, browsing taxa had significantly higher values for complexity, heterogeneity and fill volume than grazing taxa, which evince higher values for anisotropy.

The microwear textures of the fossil taxa were compared to the extant database and classified by diet. The Kanapoi and Allia Bay samples indicated that the bovids were primarily browsers or browser-grazers intermediates, suggesting the presence of more wooded habitats. The Laetoli sample is dominated by various levels of mixed feeding, although the presence of grazing taxa suggests a complex mosaic habitat at the site. Finally, the Hadar sample, divided into three hominin-bearing members, showed an increase in the number of grazing taxa over time. This suggests that there may have been gradual aridification at the site during the occupation of the australopiths.

This dissertation is approved for

Recommendation to the

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DEDICATION

This dissertation is dedicated, with love, to my father.

Table of Contents

Chapter Outlines

This dissertation is presented as a series of three prepared articles, the standard format for the Doctoral Program in Environmental Dynamics. The first chapter introduces the project and its primary objectives. It also provides the requisite background material on the fossil sites included in the study and the use of dental microwear for dietary reconstruction. The subsequent chapters contain the three articles that comprise the body of the dissertation. Each article is presented in its entirety, including reference sections.

The first article, presented in Chapter Two, is entitled "*Dental microwear texture analysis of extant African Bovidae*". This article presents the comparative database developed to interpret the microwear signals of the fossil taxa. It addresses the significant differences among modern bovids with known diets and the amount of overlap that exists between dietary categories. This article also discusses the ability of dental microwear to detect seasonality and various levels of mixed feeding.It is the first comprehensive study on dental microwear textures of bovids, or indeed any cetartiodactyls. The paper is currently in press in the De Gruyter journal *Mammalia: International Journal of the Systematics, Biology and Ecology of Mammals*.

Chapter Three presents the second article, "*Dental microwear texture analysis of fossil bovids from Hadar, Ethiopia: implications for the paleoenvironment ofAustralopithecus afarensis*". In this article, the diets of the fossil bovids from the Sidi Hakoma, Denen Dora and Kada Hadar Members of the Hadar Formation are reconstructed. The paper also addresses environmental change over the timespan during which*Australopithecus afarensis*lived in the Afar triangle.This paper has been submitted to The Journal of Vertebrate Paleontology, published by Taylor and Francis.

The last of the articles is presented in Chapter Four and titled, "*Paleoenvironmental change in Pliocene eastern Africa as inferred from dental microwear texture analysis of fossil Bovidae*". This article expands on the previous paper by adding dietary reconstructions of the bovids from Allia Bay, Kanapoi and Laetoli to the Hadar data. The paper explores what these reconstructions tell us about local environments at the four sites and the implications of this project for paleoenvironmental change during the middle Pliocene, when the early australopiths roamed eastern Africa. This paper will be submitted to The Journal of Human Evolution, published by Elsevier.

Chapter One: Introduction

My research to date has focused broadly on late Neogene habitat reconstruction and the ways in which organisms interact with their local environments. While I have worked with a wide variety of taxa, including living and fossil primates, carnivores, modern humans and early hominins, I selected bovids for my dissertation work because of their frequent use as paleoenvironmental proxies. Due to their abundance at hominin fossil sites, these taxa have been used to infer habitat based on presumed ecological similarity to their closest living relatives. The goal of this project was to reconstructthe diets of fossil bovids from some of the most important early hominin sites in eastern Africa, using a non-genetic dietary signal. The resulting dietary reconstructions were then used tomake inferences about the types of habitats that would have been available to the local bovid populations.

In order to understand relationships between hominin evolution and environmental change, it is first necessary to have the best possible interpretations of the habitats occupied by our early forbearers. Techniques for reconstructing local paleoenvironments include the study of floral remains and geochemical analyses of paleosols. There have also been various types of studies focused on the faunal assemblages as proxies for paleohabitat, including taxonomic uniformitarianism, stable isotope analyses, ecomorphology and dental mesowear. These have unfortunately not offered consistent reconstructions for paleoenvironments at many important fossil sites, including the four Pliocene localities that are the focus of this dissertation. This dissertation uses dental microwear analysis of local fauna to evaluate the competing hypotheses. Microwear offers direct evidence of diet and can therefore provide important indications of the types of resources available during the occupation of the early hominins.

Objectives

The goal of this dissertation project was to reconstruct the diets of bovids from hominin-bearing deposits at Kanapoi, Allia Bay, Laetoli and Hadar using dental microwear texture analysis to better understand the environmental contexts of the early hominins *Australopithecus anamensis* and *A. afarensis*, a putative lineage in eastern Africa persisting between about 4.2 and 3.0 million years ago.In order to interpret the microwear textures of these fossil bovids, the results were compared with an extant database that includes a broad range of modern ruminants with known dietary and habitat preferences. This has allowed me to evaluate previous reconstructions of the habitats occupied by the margins homininsand how their environmental milieu may have changed through the middle Pliocene. The results have been used in conjunction with previously published paleoecological and paleoclimatological data to provide finer resolution habitat reconstructions.

In sum, this project had three primary objectives. First, I sought to develop a large database of extant bovid dental microwear that could be used to interpret the microwear signatures of the fossil samples and be applied to other sites and time periods in Africa during future projects. Second, I set out to use this comparative database to reconstruct the diets of the fossil bovids from Kanapoi, Allia Bay, Laetoli and Hadar. An important component of this objective was to infer local habitat types based on the dietary preferences of the associated fauna and to compare these results with previously published habitat reconstructions. Finally, I aimed to test the principle of taxonomic uniformitarianism and determine whether or not it could be reliably applied to the fossil bovids from eastern Africa.

Objective 1. Dental microwear texture analysis of extant African bovids

Pilot work on extant bovids suggested that microwear texture analysis could separate not only grazers from browsers, but that it also held the promise of finer dietary distinctions, including obligate versus occasional graze, leaf versus fruit browse, etc. However, microwear texture analyses of living and fossil bovids have been limited to date (Ungar et al, 2007), and a larger baseline series was necessary to improve the resolution enough to reliably place fossil bovids into the number of diet categories typically used to separate and categorize living ruminants.

The resulting database includes 25 extant taxa representing all of the dietary classifications for bovids proposed by Gagnon and Chew (2000). The comparative sample also includes taxa reflecting seasonal and/or geographic variation in diet, in the hope of recognizing these patterns in the fossil species. In addition to extensive dietary variation, the taxa also represent a wide variety of habitat preferences, ranging from closed forest to open savanna grasslands. While it is always possible that environments existed in the past that are no longer present today, the baseline includes specimens from most modern African habitat types and should therefore provide a reliable basis for paleoenvironmental reconstruction.

Objective 2. Diet and habitat reconstruction of fossil bovids

The four sites selected for this study represent the temporal span of *A. anamensis* and *A. afarensis*. The fossil bovids from the hominin bearing deposits have been previously studied with techniques including taxonomic uniformitarianism and ecomorphology, with the aim of better understanding the adaptations of the taxa (for examples, see Kappelman et al., 1997; Spencer, 1997; Reed, 1997, 2008; Bobe et al., 2002; Kovarovic and Andrews, 2007). The results of these studies, while valuable, are more reflective of the evolutionary adaptations of the bovid taxa than the actual diet, which can change rapidly with environmental conditions. Nongenetic signals, including dental mesowear and stable isotopes, have also been previously studied, but have generally been restricted to single sites and thus preventing a more regional look at *Australopithecus* paleohabitat (for example, see Schoeninger et al., 2003; Kingston and Harrison, 2007). This study aimed to reconstruct the diets of these taxa using anongenetic signal that reflect the actual diet of the animal during its lifetime.

To interpret the diets of the fossil bovids, the dental microwear signatures were compared to the extant comparative database. All of the fossil taxa analyzed fell within the range of one of Gagnon and Chew's six dietary categories: obligate and variable grazers, browser-grazer intermediate, generalist, browser or frugivore. This suggests that while different resources may have been available in the past, the bovids at these sites were processing foods in similar ways to those consumed by living ruminants.

The dietary reconstructions of the fossil taxa were also used to infer local paleoenvironment. While the relationship between dental microwear and habitat type is not exact, an abundance of browsing or grazing taxa does imply the presence of woodland forest or open grassland, respectively. The taxa from Kanapoi, Allia Bay, Laetoli and Hadar all suggest the presence of mosaic habitats during the occupation of the early australopiths. The earlier sites have higher numbers of bovids with microwear signatures similar to modern browsers, suggesting more heavily wooded habitats. Even at these sites though, at least some grazing taxa are present, indicting the inclusion of, or proximity to, more open grassland. These graze-adapted bovids are more common at the later sites associated with *A. afarensis*, suggesting a gradual aridification trend may have been present. However, the evidence presented here is not consistent with the dominance of wide open grassland habitats, as previously suggested by 'the savanna hypothesis' (Dart, 1925).

Objective 3. Testing taxonomic uniformitarianism of fossil bovids

The principle of taxonomic uniformitarianism is often utilized by studies that rely on faunal assemblages for environmental reconstruction. This approach relies on the assumption that fossil species share the ecological preferences of their closest living relatives. The advantage of dental microwear is that it gives insights into what animals actually ate in the past rather than what they were capable of eating, as suggested by the sizes, shapes and structures of their teeth. Microwear mitigates the basic adaptationist assumptions that animals today eat the foods to which their ancestors were evolved, and that morphology reflects dietary preference.

Previous work by Sponheimer et al. (1999) at Makapansgat, South Africa, tested this assumed relationship using stable isotope analysis, also a non-genetic signal for diet. Their results suggested that the assumed diet was inconsistent with the isotopic signature in approximately 30% of the analyzed taxa. The results presented here suggest that this number may be even higher at the sites in eastern Africa. While most inconsistencies were only a matter of degree (i.e., variable grazer instead of obligate grazer), several were much more dramatic. For example, the Alcelaphini sample from Allia Bay is presumed to be most closely related to modern alcelaphines that practice obligate and variable grazing. The dental microwear signature of the fossils, however, is most similar to that of modern browsers.

Paleoclimate and Human Evolution

Researchers have long hypothesized a relationship between Pliocene hominin evolution and global climate change (for examples, see Dart, 1925; Robinson, 1963; Howell, 1978; Laporte and Zihlman, 1983; Vrba, 1985, 1988, 1992, 1995a, 1995b, 2000; Stanley, 1992; deMenocal, 1995; Hill, 1995; Potts, 1996, 1998, 2007; Bobe et al., 2002; Trauth et al., 2005). The "savanna hypothesis" (Dart, 1925, 1953; Bartholomew and Birdsell, 1953; Washburn, 1960; Robinson, 1963; Jolly, 1970; Laporte and Zihlman, 1983; Vrba et al., 1989) suggested that bipedality and other morphological features of early hominins reflected adaptations for open, arid savanna habitats. However, more recent paleoenvironmental reconstructions have revealed a shift towards more variable environments (Kingston et al., 1994; Kappelman et al., 1997; Reed, 1997; Schoeninger et al., 2003).

Australopithecus anamensis is the earliest identified member of its genus, first appearing in the Turkana Basin 4.2 mya (Leakey et al., 1995, 1998) and represented by more than 80 fossil specimens from the Kenyan sites of Kanapoi and Allia Bay (Figure 1). *Australopithecus afarensis* first appears in the fossil record 3.6 mya, and possibly as early as 3.85-3.89 mya at Belohdelie, Ethiopia (Asfaw, 1987; Renne et al., 1999). The species is represented by more than 400 fossils, over 95% of which were found at the sites of Laetoli, Tanzania and Hadar, Ethiopia (Leakey and Harris, 1987; Lockwood et al., 2000; White et al., 2000) (Figure 1). *Australopithecus anamensis* is accepted by many paleoanthropologists as being ancestral to *A. afarensis* (Leakey et al., 1995; Wolpoff, 1999; Ward et al., 2001; Kimbel et al., 2006), and some have even argued that the two taxa represent a single chronospecies (Senut, 1996; Wolpoff, 1999). This view is primarily supported by the facts that *A. anamensis* predates *A. afarensis* with no known overlap between species and that the former is the more plesiomorphic taxa (Ward et al., 2001; Kimbel et al., 2006).

Most of the characteristics reflecting evolutionary change in *Australopithecus* between 4.1 and 3.0 mya are related to dental and locomotor adaptations. The molarization of premolars associated with *A. anamensis* and *A. afarensis* has been linked to Pliocene expansion of dry, open savanna; however, modern studies of marine sediment cores suggest that widespread C4 grasslands did not develop in eastern Africa until after 3.0 mya and would not have influenced the habitats of *A. anamensis* and *A. afarensis* (deMenocal, 1995; Leakey et al., 1995). Recent paleoenvironmental models instead suggest that a wide range of habitats were available to early hominins, including closed and open woodland, gallery forest, bushland, and wet and dry grassland habitats (Leakey et al., 1995; Reed, 1997; Wynn, 2000; Kingston and Harrison, 2001; Bonnefille et al., 2004; Campisano and Feibel, 2007). Therefore, the morphological adaptations of *A. anamensis* and *A. afarensis* could instead reflect increasingly fluctuating seasonal conditions across a range of locally available habitats, where the ability to utilize lower-quality foods as needed during “crunch times” would be advantageous (Teaford and Ungar, 2000; Ungar, 2004; Reed and Fish, 2005; Kimbel et al., 2006). The mosaic nature of reconstructed Pliocene sites also accords well with the inferred locomotor adaptations of the australopiths. Both *A. anamensis* and *A. afarensis* are characterized by postcranial adaptations allowing for both terrestrial bipedality and arboreal climbing (e.g., Rodman and McHenry, 1980; Johanson et al. 1987). This unique locomotor adaptation has been hypothesized to be the result of an environmental shift towards mosaic habitats, where the ability to walk bipedally and yet retain climbing proficiency would have been beneficial.

The hominin fossils themselves have been studied in an attempt to reconstruct their trophic adaptations and by extension, their paleoenvironments. Previous examination of the dental microwear of *A. anamensis* and *A. afarensis*, for example, has revealed no consistent changes in diet over time and suggested a narrow range of fracture properties (Grine et al., 2006; Ungar et al., 2010). This is surprising given the paleoclimatic reconstructions of Pliocene eastern Africa as a world of increasing climate variability, which would suggest an accompanying change in resource use. There are several possible explanations for the lack of variation in the dietary signature of these early hominins. It is possible that *A. anamensis* and later *A. afarensis* showed no significant directional change in diet during this period of climatic instability. It is also possible that the environmental change previously reported for middle Pliocene eastern Africa was not entirely regional, and that the basins occupied by early hominins may not have been as strongly affected by the climatic fluctuations. Finally, *A. anamensis* and later *A. afarensis* may have adopted a foraging strategy similar to modern chimpanzees, maintaining large territories and ranging long distances to acquire preferred resources.

Previous Paleoenvironmental Reconstructions of Hominin Habitats

The Kanapoi fossil site is located on the southwest side of Lake Turkana, Kenya and includes fluvial and deltaic sediments accumulated during a major lacustrine phase dated between 4.2-4.17 mya (Harris and Leakey, 2003). As the earliest known site for *A. anamensis*, an understanding of associated paleoenvironments is important, though reconstructions have sometimes been inconsistent (See Table 1 for a summary). A study of paleosol stratigraphy by Brown and Feibel (1991) suggested that the Omo River flowed through the basin and into the Indian Ocean for much of the Pliocene, and that a series of temporary lakes were created when tectonics disrupted the river outflow. The presence of this river system, combined with the results of stable isotope and palynological studies, has led researchers to interpret Kanapoi as a mosaic habitat (Brown and Feibel, 1991; Cerling, 1992; Bonnefille, 1995; Wynn, 2000). Ecological diversity analysis of the faunal assemblages from the hominin-bearing strata indicate that at least a portion of the site was closed woodland forest during its accumulation, similar to the reconstructed environment for the slightly older hominin *Ardipithecus ramidus* from Ethiopia (Reed, 1997). However, taxonomic uniformitarianism of the fossil bovids recovered from Kanapoi has suggest a drier and more arid habitat, and studies of the associated paleosols liken the paleohabitat to the savanna environment of the modern Omo Delta (Harris and Leakey, 2003).

The Allia Bay hominin site is also located in the Turkana Basin of Kenya, on the eastern shore of the modern lake. The site is dated to approximately 3.9 mya and the fossils were likely accumulated during a relatively short period of time (Leakey et al., 1995). As at Kanapoi, previous attempts to reconstruct the paleoenvironment have suggested a mosaic habitat with the presence of floodplain grassland, woodland forest and dry bushland around the site margins (Cerling et al., 1988; Feibel et al., 1991; Coffing et al., 1994; Leakey et al., 1995) (See Table 1 for a summary). Stable isotope analysis of the associated paleosols suggests a highly seasonal environment (Raymo et al., 1996; Wynn, 2000), with rainfall levels that remained virtually unchanged through the Pliocene and Pleistocene (Feibel, 1999). In fact, a study comparing stress lines in the teeth of fossil bovids to modern bovids from a variety of environments suggests that the paleoenvironment at Allia Bay was likely similar to the modern seasonal mosaic ecosystem of the Masai Mara (Macho et al., 2003).

The Laetoli site is located in northern Tanzania and consists of sediments that span the time range between 4.3 mya and 120 kya. *Australopithecus afarensis* has been found in the Upper Laetolil Beds dated to 3.7-3.5 mya. Several paleoecological reconstructions of Laetoli have been conducted and the results have been very inconsistent (See Table 1 for a summary). Reconstructions based on taxonomic uniformitarianism of mammal assemblages found in association with *A. afarensis* indicate fairly closed woodland (Andrews, 1989; Reed, 1997) or woodland with patches of forest (Kingston and Harrison, 2007), thoughinterpretations of the bovid assemblages recovered from the site have been confusing. Kaiser and Solounias (2003) used dental mesowear of fossil bovids to suggest multiple habitat types but few arid-adapted grazing taxa. However, other researchers have argued that the presence of grazing bovids including dik-diks and wildebeest, indicates a more open, arid habitat, as does the complete absence of aquatic species at the site (Harris, 1987).

The Hadar hominin site is located in the Afarregion of Ethiopia and has yielded more than 370 numbered specimens of *A. afarensis* to date, the most found at any site in eastern Africa. The site has four identified geologic members associated with early hominins: Basal (~3.8-3.42 mya), Sidi Hakoma (~3.42-3.26 mya), Denen Dora (~3.26-3.2 mya), and Kada Hadar (<~3.2 mya) (Taieb et al., 1976; Campisano, 2007), each bounded by radioisotopically dated tephras. Horizons associated with *A. afarensis* have been dated to 3.4-3.0 mya and contain the last known individuals of the species. Previous paleoenvironmental reconstructions of Hadar have suggested a mosaic of microhabitats with slight fluctuations throughout the temporal range of *A. afarensis* that indicate a general trend towards drier and more open settings (See Table 1 for a summary). This reconstruction is supported by a wide variety of studies, including those of palynological remains (Radosevich et al., 1992; Bonnefille et al., 2004), ecomorphological and diversity analyses of faunal assemblages (Bobe and Eck, 2001; Reed, 2008) and stable isotope data (Hailemichael, 2000). Isotopic analysis of paleosols at Hadar also suggest periodic shifts from wetter to drier environments suggestive of, according to Hailemichael (2000), a general trend from more closed to open habitats.

In sum, the reconstructions for these four important Pliocene hominin sites have been inconsistent and have, in some cases, yielded inconsistent results. These local habitat types have been used to explain the adaptations that distinguish *A. anamensis* and *A. afarensis* from one another, as well as from other hominins, and it is therefore critical that the reconstructions are as accurate as possible. Additionally, given the morphological and apparent dietary stasis of *A. anamensis* and *A. afarensis*, evaluating variation in food availability may improve our understanding of the adaptations of these anagenetic taxa. Therefore, if we hope to develop a clearer understanding of the adaptations of the early australopiths, one of the first steps must be clarifying our interpretations of their local environments, and one way of doing this is to look to the local fauna.

Bovids as Paleoenvironmental Indicators

Bovids are generally considered to be reliable indicator species for environmental reconstruction both because they are ubiquitous at fossil hominin sites, and because modern ruminants fall into discrete dietary categories that reflect habitat preferences. These dietary categories refer to the percentages of monocotyledons (grasses, sedges and roots) and dicotyledons (fruits, seeds, flowers, buds, leaves, tubers and shoots). The commonly used dietary classifications are: obligate grazers, which inhabit open environments and eat >90% monocotyledons; browsers, which inhabit more closed environments and eat >90% dicotyledons;

and mixed feeders, which include species with highly localized and/or seasonal diets that alternate between grazing and browsing (Fortelius and Solounias, 2000). Actual bovid diets are often more complex than these categories suggest though, and many intermediate classifications have been proposed, including the subdivision of mixed-feeding taxa and the recognition of a separate frugivore category (Gagnon and Chew, 2000). Even given the oversimplification of a three category system (grazer versus browser versus mixed feeder), such a classification has proven valuable for interpreting the diets and habitat preferences of fossil bovids (e.g., Fortelius and Solounias, 2000; Merceron and Ungar, 2005; Schubert et al., 2006). Finer dietary distinctions for fossil taxa may be possible through dental microwear texture analysis, as suggested by a recent study on the fossil bovids from Langebaanweg by Ungar et al. (2007).

Habitats occupied by extant bovids range from deserts and rainforests. These allow us to determine microwear-environment associations for a broad variety of habitats. The use of bovid assemblages to make inferences about Pliocene hominin habitats is widespread in the paleoanthropological literature, and has been applied to sites in both eastern and South Africa (Kappleman, 1984; Vrba, 1980, 1985; Shipman and Harris, 1988; Harris, 1991; Plummer and Bishop, 1994; Spencer, 1997; Sponheimer et al., 1999; Merceron and Ungar, 2005; Reed, 2008).

Fossil bovids recovered from eastern African hominin sites include members of 12 biological tribes, often the most specific identification available for bovid specimens not accompanied by the distinctive horn cores. Aepycerotini (impala), Tragelaphini (kudu and browsing antelope), Reduncini (reedbucks and lechwe) and Bovini (cattle and spiral horned antelope) are typically browsers and associated with closed, moist habitats dominated by woodlands and fresh grasslands (Kingdon, 1982). Alcelaphini (wildebeest), Antilopini (gazelles), and Hippotragini (oryx antelopes and their kin) are predominantly grazers considered to be indicators of open and seasonally arid environments dominated by grasslands (Kingdon, 1982; Gagnon and Chew, 2000). The other tribes, Cephalophini (duikers), Neotragini (dwarf antelope), Caprini (sheep and goats), Boselaphini (four-horned antelope), and Ovibovini (takin) are mixed feeders associated with various types of mixed habitats (Kingdon, 1982).

Taxonomic uniformitarianism

Studies of faunal assemblages as proxies for the paleoenvironment of a fossil site typically apply the principle of taxonomic uniformitarianism, which is based on the assumption that fossil species share the same ecological preferences as their closest living relatives. Although this assumption is rarely questioned for recent faunas, its utility for reconstructing the paleoecology of long extinct species is uncertain. The primary problems with taxonomic uniformitarianism are that it is not applicable to fossil taxa with few or no living relatives, and that it assumes that groups remain constant in their ecological preferences over long periods of time. While taxonomic uniformitarianism is relatively straightforward and requires minimal effort beyond a quick glance at a faunal list, critics have questioned many of its inherent assumptions (Solounias et al., 1988; Reed, 1996; Sponheimer et al., 1999; Schubert et al., 2006). For example, Sponheimer et al. (1999) demonstrated that more than one-third of the Makapansgat fossil bovids had diets that differed from the assumed diets based on taxonomic uniformitarianism. While *Aepyceros sp.* and *Gazella vanhoepeni* were both assumed to be mixed/seasonal feeders like their closest living relatives, for example, isotopic signatures and ecomorphological data suggested that both were obligate browsers, and showed no evidence of C4 grass consumption. Due to these discrepancies between inferred and actual diet, it is critical that ecological similarities of extant and fossil taxa be tested in some reliable way in order to have confidence in these assumed relationships.

Dietary Reconstruction

Diet is the most direct way that an organism interacts with its environment. Attempts to reconstruct diet in fossil forms have included the use of tooth size, shape and structure. However these are all genetic signals that reflect only what a species capable of eating, not what individuals actually ate. The diet of an individual may vary over its lifetime, but it can take many generations for the morphology of species to change in response to selective pressures. In order to reconstruct what an animal actually ate at a moment in time in the past, a non-genetic signal is needed. Dental microwear, or the microscopic pits and scratches created on the enamel surface during mastication, is one such line of evidence.

Differences in the dental microwear between grazing and browsing ungulates have been noted in previous studies of extant and fossil species (for examples, see Solounias et al., 1988; Solounias and Moelleken, 1993; Merceron and Ungar, 2005; Merceron et al., 2005; Schubert et al., 2006; Ungar et al., 2007), with browsers having more pits and grazers having more scratches. Mixed-feeding taxa tend to have intermediate microwear signatures, or patterns overlapping with browsers and grazers. This has important implications for reconstructing paleoenvironments, as while the connection between diet and habitat are not exact, grazing and browsing microwear signatures do imply the availability of grasses and woody plants respectively.

Dental Microwear Analysis

Conventional methods of studying dental microwear, including scanning electron microscopy and light microscopy, are subject to high rates of observer measurement error and a lack of depth data in two dimensional surface characterizations. Dental microwear texture analysis was developed to be a solution to these problems. It combines white-light confocal profilometry with scale-sensitive fractal analysis, resulting in the quantitative description of surfaces at a range of scales. This offers a suite of objective and repeatable measures of microwear surface textures in three dimensions that can be compared between groups with differing diets. Further, white-light confocal profilometry is quicker, easier to use, and less costly than scanning electron microscopy, and automated analysis requires less time and effort from researchers than does identification and measurement of individual features. The most important advance of texture analysis is the reduction of observer error in measurement, which allows direct comparisons between studies, as well as the establishment of a large database that researchers can access for interpretation of their results. Dental microwear texture analysis has been successfully used to distinguish dietary differences between species of extant and fossil taxa including humans and non-human primates, carnivores, bovids, kangaroos and wallabies (Scott et al., 2005, 2006; Ungar et al., 2008; Prideaux et al., 2009; Scott et al., 2009; Schubert et al., 2010).

Teeth are relatively common in the fossil record, as they are almost entirely mineralized and more durable than any other part of the skeleton. For this reason, diet reconstructions of extinct species, including early hominins, center on what data can be gathered and inferred from teeth. Teeth provide the most direct evidence of diet since they are the only part of the body to come into direct contact with food. Additionally, much information can be gained from teeth in relation to jaw movement and diet. For example, form-function relationships have been described between tooth shape and diet in bovids. Grazing species tend to be more hypsodont, or high crowned, and this has been linked to offsetting the added wear caused by abrasives in grass forage (Fortelius, 1985; Janis, 1988, 1995; Mendoza and Palmqvist, 2008). Studies of these form-function relationships have also been conducted on primates. Species with sharp molar crests are associated with folivory and the need for shearing of tough foods, whereas those eating hard or brittle foods typically have flat, thick enameled surfaces for crushing and grinding (Kay, 1975; Kay and Hylander, 1978; Lucas, 1979, 2004). These studies have been complicated by the difficulty in studying teeth with worn cusps, yet wear often begins very early in life- sometimes even *in utero* (Teaford and Walker, 1983). Ungar and M'Kirera (2003) proposed a solution to this problem using GIS software, but even with this technology to reconstruct the occlusal surface, simply knowing what a species was capable of eating does not definitely indicate that this was their primary source of food. The diet of a species may change relatively quickly, but it can take many generations for the morphology of the tooth to follow.

One of the most reliable methods for reconstructing what an individual actually ate in the past is dental microwear analysis. This consists of examining the occlusal or buccal surface of a tooth with a microscope to document the scratches, pits, and gouges caused by foods of different properties during the mastication process. Microwear is created when the teeth come into occlusion during chewing. Scratches are formed on the enamel during the mastication of tough foods like fibrous plant material, much in the same way a pair of scissors would be scratched by abrasives on paper dragged between its blades during slicing. In this case, teeth come into contact at a steeper angle relative to the wear facet for shearing. Both maxillary and mandibular molars can be examined for microwear. Previous studies have demonstrated no significant difference between them as an indicator of diet related wear (Teaford and Walker, 1984). It is standard to look for bovid microwear on the disto-buccal enamel band of the mesial cuspid of the M_1 and M_2 or the mesio-buccal enamel band of the mesial cusp of the M^1 or M^2. (Janis, 1990; Merceron et al., 2005b).

Microwear Signatures on Living Species

Dental microwear studies have been conducted on many living species, including bovids, and a direct connection has been made between the type of wear found on the teeth and the known and observed diets of the species. Moderate pit counts on the surface of a tooth indicate that the animal was likely a frugivore or specialized in soft foods. Scratches can also be found on the teeth of these animals if the soft food they eat is coated in dirt or other gritty material (Silcox and Teaford, 2002). If the pit counts are very high, the animal was probably a hard-object feeder, specializing in items like seeds or nuts (Strait, 1993; Silcox and Teaford, 2002). Folivores are usually distinguished by high counts of scratches on the molar surface from plant material being scraped across the tooth by the opposing molar (Teaford and Walker, 1984; Teaford, 1988a).

Because of the connection between food type and microwear pattern, the study of the dental microwear of fossils can reveal important clues about the diet and ecology of extinct species. Studies have been conducted on many types of fossil species, including rodents (Rensberger, 1978), ungulates (Solounias and Hayek, 1993; Solounias and Moelleken, 1992a, b, 1994; Solounias and Semprebon, 2002), carnivores (Van Valkenburgh et al., 1990), horses (MacFadden et al., 1999), giraffids (Solounias et al., 1988), tyrannosaurids (Schubert and Ungar, 2005), non-human primates (Teaford and Walker, 1984; Lucas and Teaford, 1994; Ungar, 1996;

Ungar and Teaford, 1996; King et al., 1999; Leakey et al., 2003; El-Zaatari et al., 2006), and human bioarchaeological populations (Rose and Marks, 1985; Harmon and Rose, 1988; Krueger and Ungar, 2010). There have also been studies of microwear in early hominin species in an attempt to answer questions about our own dietary heritage (Walker, 1981; Grine, 1981, 1986; Puech et al., 1983, 1986; Puech, 1986; Grine and Kay, 1988; Kay and Grine, 1989; Grine et al., 2006a, 2006b; Ryan and Johanson, 1989; Ungar and Grine, 1991; Lalueza Fox and Pérez-Pérez, 1993; Lalueza et al., 1996; Pérez-Pérez et al., 1999, 2003; Ungar et al., 2006; Teaford et al., 2007).

The Development of Dental Microwear Studies

An interest in the markings left on teeth during mastication developed in 1933, when Simpson noted a correlation between the movement of the jaw and the principles of molar occlusion in mammals (Simpson, 1933). He suggested that the wear evinced on the teeth should correspond to specific movements of the jaw during mastication and should be indicative of diet. Later work demonstrated that molar facets, created by the occlusion of the upper and lower teeth, can be used to reconstruct the motions of the jaw. The preferred orientations of striations (if any) created on these surfaces reflect the direction of jaw movement (Butler, 1952; Mills, 1955, 1963, 1967; Butler and Mills, 1959).

While the first studies of microwear on the occlusal surfaces of teeth were focused on understanding jaw movements during mastication, studies soon began to emphasize the association between food types eaten by a species and microscopic wear patterns. These early microwear studies were conducted using binocular light microscopy and primarily qualitative analysis, and emphasized the link between diet and wear on the enamel (Baker et al., 1959;

Dahlberg and Kinzey, 1962; Walker, 1976). Baker et al. (1959) studied the microwear of caprine teeth to determine the impact of silica in grass and found that these abrasives contributed significantly to wear. Young (1986) later confirmed the contribution of abrasives by conducting SEM analysis on the incisors of Canadian moose. Despite the lack of quantitative data, these studies showed the potential of microwear for the reconstruction of diet in fossil species (Ungar et al., 2007).

Dahlberg and Kinzey (1962) suggested that studies of dental microwear might be used to study interspecific and intraspecific variation among populations. It was not until the late 1970s, however, that interest in microwear and diet really began to take off. Walker (1976) hypothesized that arboreal and terrestrial monkeys exhibited different microwear patterns because or foods available in different substrates. Combined with studies by Rensberger on rodents (1978) and Walker (1978) on hyraxes, a strong connection was inferred between microwear on the occlusal surfaces of teeth and the mechanical properties of foods.

With all of this potential, it quickly became apparent that a better approach than light microscopy, with its limited depth of focus, was needed. Rensberger (1978) and Walker et al. (1978) began using scanning electron microscopy (SEM) to look at microwear. Early SEM images taken of microwear surfaces on the teeth of small mammals were much clearer and allowed forobservation of more detail on the enamel surfaces. Researchers soon began to measure wear features on photomicrograph images, and standardized procedures were developed in an attempt to make these studies comparable (Peters, 1982; Gordon and Walker, 1983; Kay and Covert, 1983). These methods included using calipers or a digitizing table and later PC based measuring software (Ungar, 1995) to count and measure individual microwear features.

Small mammals were not the only subjects of early SEM studies. The hypothesized connections between dental microwear and food properties were being investigated using the teeth of fossil hominins (Grine, 1977, 1981; Puech, 1979; Ryan, 1980a, 1980b; Walker, 1981). While these studies were still qualitative, comparisons were made between fossil species and often included modern primate taxa. Walker (1981) speculated that similarities between early hominin microwear and that found on modern chimpanzees and orangutans suggested a frugivorous diet for*Paranthropus boisei*. Similar studies conducted on anterior tooth wear (Ryan, 1980a, 1980b; Ryan and Johanson, 1989) also included comparative samples, both nonhuman primates and recent human populations (Inuit and Micronesians), and suggested that early hominins might have used their incisors to strip away gritty plant parts like roots and seeds.

While much about the diets of extinct species has been learned from SEM-based microwear studies, these studies suffer from two primary criticisms. First, identification and measurement of wear features are highly subject to observer error. Intraobserver measurement error rates have been estimated at 7% and interobserver error rates at 9% (Grine, 2002). Secondly, SEM studies produce two dimensional images based on three dimensional surfaces, which causes the image to be affected the angle of the specimen on the microscope stage relative to the light or electron source (i.e., depth is sensed by shadows, so the dip and strike of the surface will affect the pattern of shadows) and the instrument settings (Gordon, 1988). Finally, these SEM studies are time-consuming due to the necessity of identifying and measuring up to hundreds of individual features on a single surface.

In the 1980s, several studies critiqued microwear techniques and their ability to differentiate between dietary patterns. Covert and Kay (1981) conducted a controlled experiment and attempted to control for diet. They used test groups of opossums, feeding them cat food supplemented with insect chitin, plant fibers, or no additives. After the study, Covert and Kay were unable to distinguish between the groups eating different foods. They used this study to cite the inability of microwear techniques to distinguish between herbivory and insectivory. These conclusions were later questioned by Gordon and Walker (1983), who critiqued the Covert and Kay study due to inappropriate dietary mediums, the use of additives and insufficient quantification of the results. Gordon (1982, 1984) predicted that future refinements of microwear techniques would reveal differences in the opossums that were not seen by Covert and Kay and noted that her own studies of chimpanzee teeth had revealed that variation in microwear features could be partially accounted for by facet type, tooth position and individual information like age (Gordon, 1982). The Covert and Kay experiments called for a reevaluation of the limitations of dental microwear studies and the importance of a dietary control when categorizing specimens. Later studies focused on the necessity of standardizing the portion to the tooth scanned (Gordon, 1982, 1984), reducing interobserver and intraobserver error through automated practices (Kay, 1987; Grine and Kay, 1987; Walker et al., 1987), and the effect of enamel structure on tooth wear (Boyde 1984; Boyde and Fortelius, 1986; Maas, 1991).

The work of Covert and Kay also challenged researchers to demonstrate the ability of microwear studies to distinguish animals based on their diets. The work of Teaford and Walker (1984) utilized anthropoid primates to demonstrate that frugivorous species had more pits on their “Phase II” wear facets, while folivorous species had more scratches. Among frugivores, these authors recorded even higher percentages of pits for species that consumed hard objects, making three distinct dietary categories distinguishable through microwear studies of primates. Teaford and Oyen (1989) also conducted long-term studies on vervet monkeys, altering their diet and examining the microwear on the teeth. They have recorded differences in microwear signals between animals eating hard monkey chow and soft wet chow. Animals eating the hard, dry chow showed significantly more microwear features than those eating soft foods. Their research also confirmed that pit frequency is related to the hardness of the food source.

New and more automated methods of image processing were introduced in an attempt to minimize interobserver error (Kay, 1978), but these still relied on SEM photomicrographs and the two dimensional images. A semi-automated analysis technique using these images was developed by Ungar et al. (1991) and Ungar (1995) and has been used consistently over the years, but is not immune to the problems associated with SEM, because it still requires time-consuming observer identification of microwear features (Teaford, 2006). Therefore, studies performed using these methods are still prone to subjectivity and high rates of observer error (Grine et al., 2002).

SEM-based analysis of microwear has been the most commonly used approach to dental microwear study. Recent investigations have used this technique with emphasis on reconstructing the diets of fossil species and other primates by using large comparative databases of modern species with known diets. SEM studies of Eocene omomyids (Strait, 1991), Egyptian Oligocene primates (Teaford et al., 1996), Miocene apes (Walker et al., 1994; Ungar and Teaford, 1996; Ungar et al., 1996), subfossil Malagasy lemurs (Rafferty et al., 2002), and early hominins (Grine et al., 2006a, 2006b; Ungar et al., 2006) have been conducted and yielded new information on the diets of fossil species. However, even with its continued use and the efforts to automate and standardize the technique, it has been suggested that SEM-based analysis has reached its limitations and that new methods must be sought (Teaford, 2006).

As noted by Rose and Ungar (1998), taking a single specimen through the process from preparation to data collection from SEM photomicrographs can take hours. This, predictably, limits the number of specimens that can be included in a single study. In an effort to improve sample sizes, Solounias and Semprebon (2002) returned to low-magnification light microscopy, which involves the tallying of microwear features while viewing specimens though a binocular light microscope. This approach has been applied to a variety of taxa in recent years, including primates, bovids, equids, mammoths and even squirrels (Solounias and Semprebon, 2002; Kaiser, 2003; Godfrey et al., 2004; Semprebon et al., 2004; Nelson et al., 2005; Green et al., 2005; Godfrey et al., 2005; Rivals and Semprebon, 2006). Merceron and his colleagues have used a variant of this approach, combining light microscopy with the quantification of features on a computer screen (Merceron, 2003a, 2003b, 2004, 2005a, 2005b). The advantage to low magnification light microscopy is that itallows for the processing of large samples comparatively quickly and studies have reported low rates of interobserver error among experiences observers (Solounias and Semprebon, 2002). However, as Ungar et al. (2008) observed, this revived technique has not solved the problems with depth of field and magnification that led researchers away from light microscopy in the 1970s.

Dental microwear texture analysis combines white-light confocal profilometry with scale-sensitive fractal analysis, resulting in the quantitative description of surfaces at a range of scales. This offers a suite of objective and repeatable measures of microwear surface textures in three dimensions that can be compared between groups with differing diets. The technique has been successfully used to distinguish dietary differences between species of extant and fossil taxa including humans and non-human primates, carnivores, and bovids (for examples, see Scott et al., 2005, 2006; Krueger et al., 2008; Ungar et al., 2007, 2008, 2010; Scott et al., 2009; Krueger and Ungar, 2010; Schubert et al., 2010).

Limitations of Dental Microwear Research

A factor considered early on to be a problem for microwear studies of fossils was that surface patterns might have been affected by postmortem or taphonomic damage. Taphonomic processes are those that affect the remains after death. Fossil teeth can sustain several different types of postmortem damage. Acid etching, damage from excavation tools or preservatives, water transport, and weathering are well established taphonomic agents that can easily obliterate microwear features. As the microwear scratches can be less than a single micron deep, they can be easily destroyed by taphonomic processes and even obscured by fingerprints. However this is not the complicating factor it was once thought to be. It is relatively easy for researchers to tell actual microwear from postmortem scratching of the tooth surface by rocks and dirt. Microwear is regular and found predictably on specific areas of the tooth, whereas damage to the enamel caused by being in the ground is randomly placed and not at all uniform (Teaford, 1988; King, 1999). In fact, the problem with postmortem wear is not that it confuses microwear researchers, but that it limits the number of useable samples for study. For example, according to Teaford (2006), only about 20% of the monkey specimens found at Koobi Fora, and only 60% of Olduvai material have been determined to be useable for microwear. A recent study on early hominin microwear supports this conclusion, suggesting that only approximately 23% of the hominin molars found throughout Ethiopia, Tanzania, Kenya, Malawi and South Africa display useable antemortem microwear (Ungar et al., 2006). This number also corresponds to similar estimates of Plio-Pleistocene monkey fossils from South Africa (El-Zaatari et al., 2005). The percentages could be even lower with bovid taxa, as the narrow bands of enamel that preserve microwear are easily damaged. Thus, the most serious complication of dental microwear studies on fossils is the small sample sizes for many species, and the limited number within these collections that are suitable for microwear analysis.

Dental microwear research has other limitations. While microwear studies have been successfully used to differentiate between short and long term diets and therefore the presence of seasonal diets, the microwear on a single tooth is not necessarily indicative of the overall dietary pattern of the animal's lifetime. It has been demonstrated that microwear only reflects a few days diet because recently created microwear overlays earlier wear (Walker et al, 1978). This is commonly known as the "Last Supper" phenomenon and is a complicating factor which must be considered in all microwear studies (Grine, 1986). Knowing this, seasonal variation in diet and the limited temporal range of what microwear can reveal can be taken into consideration. The potential to reveal dietary breadth makes the collection of large samples especially important in microwear studies, particularly when we can assume limited bias in the sample.

Summary

Environmental change is widely accepted to have been a motive force in human evolution and because of this, it is critical that our paleoenvironmental reconstructions are as detailed and robust as possible. Dental microwear, as direct evidence of actual diets of individuals, is an established method used in paleoenvironmental reconstruction free from assumptions inherent with taxonomic uniformitarianism. Further, because bovids are the most common taxa found at fossil sites and are known to have diets that vary with habitat, they are wellsuited to serve as environmental proxies. The results of this study not only test previous assessments of diets of fossil bovids from Pliocene hominin sites, but they provide more robust interpretations of early hominin habitats in eastern Africa based on faunal assemblages.

This project has generated the largest database of microwear textures for both extant and fossil bovids yet assembled, and will provide a substantial comparative collection for future research. It also serves as an important test of the principle of taxonomic uniformitarianism, which is often assumed in the use of faunal assemblages as paleoenvironmental proxies. The results of this study confirm previous work by Sponheimer et al. (1999) which suggests that taxonomic uniformitarianism may not be a consistently reliable predicator of bovid dietary preferences.

Bibliography

Andrews, P., 1989. Paleoecology rof Laetoli. J. Hum. Evol. 18, 173-181.

Asfaw, B., 1987. The Belohdelie frontal: new evidence of early hominid cranial morphology from the Afar of Ethiopia. J. Hum. Evol. 16, 611-624.

Baker, G., Jones, L.H.P., Wardrop, I.D., 1959. Cause of wear in sheeps teeth. Nature, 184, 1583-1584.

Bartholomew, G.A., Birdsell J.B., 1953. Ecology and the protohominids. Am. Anthropol. 55, 481- 498.

Bobe, R., Behrensmeyer, A.K., 2002. Faunal change, environmental variability and late Pliocene hominin evolution. J. Hum. Evol. 42, 475-497.

Bobe, R., Eck, G.G., 2001. Responses of African bovids to Pliocene climatic change.Paleobiology 27 (Suppl. to No. 2). Paleobiology Memoirs 2, 1-47.

Bonnefille, R., 1995. A reassessment of the Plio-Pleistocene pollen record of East Africa. In: Vrba, E. S., Denton, G. H., Partridge, T. C. and Burckle, L. H. (Eds.), Paleoclimate and Evolution, with Emphasis on Human Origins. Yale University Press, New Haven, CT, pp. 299-310.

Bonnefille, R., Potts, R., Chalié, F., Jolly, D., Peyron, O., 2004. High-resolution vegetation and climate change associated with Pliocene *Australopithecus afarensis*. Proc. Natl. Acad. Sci. 101, 12125-12129.

Boyde, A. Fortelius, M., 1986. Development, structure and function of rhinoceros enamel. Zoological Journal of the Linnean Society 87:181-214.

Boyde, A., Fortelius, M., 1991.New confocal LM method for studying local relative microrelief with special references to wear studies. Scanning, 13, 429-430.

Brown, F.H., Feibel, S.S., 1991. Stratigraphy, depositional environments, and palaeogeography of the Koobi Fora Formation. In: Harris, J.H. (Ed.), Koobi Fora Research Project, Vol. 3. The fossil ungulates: geology, fossil artiodactyles and palaeoenvironments. Clarendon Press, Oxford, pp. 1-30.

Butler, P.M., 1952. The milk molars of Perissodactyla, with remarks on molar occlusion. Proc. Zool. Soc. Lond., 121, 777-817.

Butler, P.M., Mills, J.R.E., 1959 A contribution to the odontology of *Oreopithecus.* Bull. Brit. Mus. Nat. Hist. (Geology), 4: 3-26.

Campisano, C.J., 2007. Tephrostartigraphy and hominin paleoenvironments of the Hadar Formation, Afar Depression, Ethiopia. Ph.D. Dissertation, Rutgers, The State University of New Jersey.

Campisano, C.J., Feibel, C.S., 2007. Connecting local environmental sequences to global climate patterns: evidence from the hominin-bearing Hadar Formation, Ethiopia. J. Hum. Evol 53, 515-527.

Cerling, T.E., 1992. Development of grasslands and savannas in East Africa during the Neogene.Palaeogeogr.Palaeoclimatol.Palaeoecol. 97, 241-247.

Cerling, T.E., Bowman, J.R., O'Neil, J.R., 1988. An isotopic study of a fluvial-lacustrine sequence: the Plio-Pleistocene Koobi Fora sequence, East Africa. Palaeogeo.Palaeoclimatol.Palaeoecol. 63, 335-356.

Coffing, K., Feibel, C., Leakey, M., Walker, A., 1994.Four-million year old hominid from East Lake Turkana, Kenya. Am. J. Phys. Anthrop. 93, 55-65.

Covert, H.H., Kay, R.F., 1981.Dental microwear and diet - implications for determining the feeding behaviors of extinct primates, with a comment on the dietary pattern of *Sivapithecus.* Am. J. Phys. Anthropol., 55, 331-336.

Dahlberg, A.A., Kinzey, W., 1962. Étude microscopique de l'abrasion et de l'attrition sur la surface des dents. Bull. Gr. Int. Rech. Sci. Stomatol., 5, 242-251.

Dart, R.A., 1925.*Australopithecus africanus*: The man ape of South Africa. Nature 115, 195-199.

Dart, R.A., 1953. Faunal and climatic fluctuations in Makapansgat Valley: their relation to the geologic age and Promethean status of *Australopithecus*. In: Leakey, L.S.B., Cole, S., (Eds.) Proceedings of the 1st Pan African Congress on Prehistory, Nairobi, 1947, pp. 96-106.

deMenocal, P.B., 1995. Plio-Pleistocene African climate. Science 270, 53-59.

El Zaatari, S., Grine, F.E., Teaford, M.F., Smith, H.F., 2005.Molar microwear and dietary reconstruction of fossil Cercopithecoidea from the Plio-Pleistocene deposits of South Africa. J. Hum. Evol. 51, 297-319

Feibel, C.S., 1999. Basin evolution, sedimentary dynamics, and hominid habitats in East Africa. In: Bromage, T.G., Schrenk, F. (Eds.), African Biogeography, Climate Change and Human Evolution, pp. 276-281. Oxford University Press, New York.

Fortelius, M., 1985. Ungulate cheek teeth: developmental, functional and evolutionary interrelations. Acta Zool. Fenn. 180, 1-76.

Fortelius, M., Solounias, N., 2000. Functional characterization of ungulate molars using the abrasion-attrition wear gradient: a new method for reconstucting diets. Am. Mus. Nov. 3301, 1-36.

Gagnon, M., Chew, A.E., 2000. Dietary preferences in extant African Bovidae. J. Mammal. 81:2, 490-511.

Godfrey, L.R., Semprebon, G.M., Jungers, W.L., Sutherland, M.R., Simons, E.L., Solounias, N., 2004. Dental use wear in extinct lemurs: evidence of diet and niche differentiation. J. Hum. Evol., 47, 145-169.

Godfrey, L.R., Semprebon, G.M., Schwartz, G.T., Burney, D.A., Jungers, W.L., Flanagan, E.K., Cuozzo, F.P., King, S.J., 2005. New insights into old lemurs: the trophic adaptations of the Archaeolemuridae. Int. J. Primatol., 26, 825-854.

Gordon, K.D., 1982. A study of microwear on chimpanzee molars: implications for dental microwear analysis. Am. J. Phys. Anthropol., 59, 195-215.

Gordon, K.D., 1984. Hominoid dental microwear: complications in the use of microwear analysis to detect diet. J. Dent. Res., 63, 1043-1046.

Gordon, K.D., 1988. A review of methodology and quantification in dental microwear analysis.Scanning Microsc. 2, 1139-1147.

Gordon, K.D., Walker, A.C., 1983. Playing 'possum: a microwear experiment. Am. J. Phys. Anthropol., 60, 109-112.

Green, J.L., Semprebon, G.M., Solounias, N., 2005. Reconstructing the palaeodiet of Florida *Mammut americanum* via low-magnification stereomicroscopy.Palaeogeogr.Palaeoclimatol.Palaeoecol., 223, 34-48.

Grine, F.E., 1977. Analysis of early hominid deciduous molar wear by scanning electron microscopy: a preliminary report. Proceedings of the Electron Microscopy Society of South Africa, 7, 157-158.

Grine, F.E., 1981. Trophic differences between 'gracile' and 'robust' australopithecines: a scanning electron microcope analysis of occlusal events. S. Afr. J. Sci., 77, 203-230.

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., Kay, R.F., 1987. Quantitative analysis of occlusal microwear in *Australopithecus* and *Paranthropus*. Scanning Microsc., 1, 647-656.

Grine, F.E., Ungar, P.S., Teaford, M.F., 2006a. Was the Early Pliocene hominin *'Australopithecus' anamensis* a hard object feeder? S. Afr. J. Sci. 102, 301-310.

Grine, F.E., Ungar, P.S., Teaford, M.F., 2002. Error rates in dental microwear quantification using scanning electron microscopy. Scanning, 24, 144-153.

Grine, F.E.; Ungar, P.S.; Teaford, M.F.; El Zaatari, S, 2006b. Dental microwear of *Praeanthropus afarensis.* J. Hum. Evol., 51: 297-319.

Hailemichael, M., 2000. The Pliocene environment of Hadar, Ethiopia: a comparative isotopic study of paleosol carbonates and lacustrine mollusk shells of the Hadar Formation and of modern analogs. Ph.D. Dissertation, Case Western Reserve University.

Harmon, A.M., Rose, J.C., 1988.The role of dental microwear analysis in the reconstruction of prehistoric diet. In: Kennedy, B.V., Le Moine, G.M. (Eds.), Diet and Subsistence: Current Archaeological Perspectives, pp. 267-272. Calgary: Archaeological Association of the University of Calgary.

Harris, J.M., 1987. Fossil Giraffidae and Camelidae from Laetoli and summary. In: Leakey, M.D., Harris, J.M. (Eds.), Laetoli: A Pliocene Site in Northern Tanzania, pp. 358-377. Oxford University Press, Oxford.

Harris, J.M., 1991. The Fossil Ungulates: Geology, Fossil Artiodactyls, and Paleoenvironments. Koobi Fora Research Project, vol. 3. Clarendon Press, Oxford.

Harris, J.M., Leakey, M.G. (Eds.), 2003. Geology and Vertebrate Paleontology of the Early Pliocene Site of Kanapoi, Northern Kenya.Natural History Museum of Los Angeles County, Los Angeles.

Hillson, S., 1996.Dental Anthropology. Cambridge University Press, London.

Janis, C.M., 1988. An estimation of tooth volume and hyposodonty indices in ungulate mammals. In: Russell, D.E., Santoro, J.P., Sigogneau-Russel, D. (Eds.), Teeth revisited. Proceedings of the 7th Annual International Congress of Dental Morphology.Mem. Mus. Hist. Nat. 53, 367-387.

Janis, 1990.The correlation between diet and dental wear in herbivorous mammals and its relationship to the determination of diets of extinct species. In: Boucot, A.J. (Ed.), Evolutionary Paleobiology of Behavior and Coevolution, p. 241-259.

Johanson, D., Masao, F.T., Eck, G.G., White, T.D., Walter, R.C., Kimbel, W.H., Asfaw, B., Manega, P., Ndessokia, P., Suwa, G., 1987. New partial skeleton of *Homo habilis* from Olduvai Gorge, Tanzania. Nature 327, 205-209.

Jolly, C.J., 1970. The seed eaters: a new model of hominid differentiation based on a baboon analogy. Man 5, 5-26.

Kaiser, T.M., Solounias, N., 2003. Extending the tooth mesowear method to extinct and extant equids. Geodiversitas 25, 321-345.

Kappelman, J., 1984. Plio-Pleistocene environments of Bed I and Lower Bed II, Olduvai Gorge, Tanzania.Palaeogeo.Palaeoclimatol.Palaeoecol. 48, 171-196.

Kappelman, J., Plummer, T., Bishop, L., Duncan, A., Appleton, S., 1997.Bovids as indicators of Plio-Pleistocene paleoenvironments in East Africa. J. Hum. Evol. 32, 229-256.

Kay, R.F., 1975. The functional adaptations of primate molar teeth. Am. J. phys. Anthrop. 43, 195–216.

Kay, R.F., 1987. Analysis of primate dental microwear using image processing techniques. Scanning Microsc., 1, 657-662.

Kay, R.F., Covert, H.H., 1983. True grit: a microwear experiment. Am. J. Phys. Anthropol., 61, 33-38.

Kay, R.F., Grine, F.E., 1989. Tooth morphology, wear and diet in *Australopithecus* and *Paranthropus* from southern Africa . In: The Evolutionary History of the Robust Australopithecines. New York : Aldine de Gryter. pp. 427-444.

Kay, R.F., Hiiemae, K.M., 1974. Jaw movement and tooth use in recent and fossil primates. Am. J. Phys. Anthropol., 40:227-256.

Kay, R.F., Hylander, W.L., 1978. The dental structure of mammalian folivores with special reference to primates and Phalangeroidea (Marsupialia). In: Montgomery, G.G., (Ed.). The ecology of arboreal folivores. Washington, DC: Smithsonian Institution, p. 173-191.

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., Aiello, L.C., Andrews, P., 1999.Dental microwear of *Griphopithecus alpani*. J. Hum. Evol., 36, 3-31.

Kingdon, J., 1982. East African Mammals: Bovids, vol. IIID. University of Chicago Press, Chicago.

Kingston, J.D., Harrison, T., 2007. Isotopic dietary reconstructions of Pliocene herbivores at Laetoli: implications for early hominin paleoecology. Palaeogeogr.Palaeoclimatol.Palaeoecol. 243, 272-306.

Kingston, J.D., Marino, B.D., Hill, A., 1994. Isotopic evidence for Neogene hominid paleoenvironments in the Kenya Rift Valley. Science 264, 955-959.

Kovarovic, K., Andrew, P., 2007. Bovid postcranial ecomorphological survey of the Laetoli paleoenvironment. J. Hum. Evol. 52, 663-680.

Krueger, K., Scott, J.R., Kay, R., Ungar, P., 2008. Comparisons of dental microwear texture attributes between facets in three primate taxa. Am. J. Phys. Anthropol. 137, 485-490.

Krueger, K.L., Ungar, P.S., 2010. Incisor microwear textures of five bioarcheological groups. Int. J. Osteoarch. 20:549-560.

Lalueza Fox, C., Pérez-Pérez, A., 1993.The diet of the Neanderthal child Gibralter 2 (Devils' Tower) through the study of the vestibular striation pattern. J. Hum. Evol. 24, 29-41.

Lalueza, C., Pérez-Pérez, A., Turbon, D., 1996.Dietary inferences through buccal microwear analysis of middle and upper Pleistocene human fossils.Am J Phys Anthropol 100, 367-387.

Laporte L.F., Zihlman A.L., 1983. Plates, climate and hominoid evolution. S. Afr. J. Sci. 79, 96-110.

Leakey, M.G., Feibel, C.S., McDougall, I., Walker, A., 1995. New four million-year-old hominid species from Kanapoi and Allia Bay, Kenya. Nature 376, 565-571.

Leakey, M.G., Feibel, C.S., McDougall, I., Ward, C., Walker, A., 1998. New specimens and confirmation of an early age for *Australopithecus anamensis*. Nature 393, 62-66.

Leakey, M., Harris, J.M. (Eds.), 1987. Laetoli: A Pliocene Site in Northern Tanzania. Clarendon, Oxford.

Leakey, M. G., Teaford, M. F., Ward, C. V., 2003. Cercopithecidae from Lothagam. In Lothagam, ed. Leakey, M. G. and Harris, J., pp. 130-177. New York: Columbia University Press.

Lockwood, C.A., Kimbel, W.H., Johanson, D.C., 2000.Temporal trends and metric variation in the mandibles and dentition of *Australopithecus afarensis*. J. Hum. Evol. 39, 23-55.

Lucas, P.W., 1979. The dental-dietary adaptations of mammals. N JB Geol Palaontol Mh 8:486-512.

Lucas, P.W., 2004. Dental functional morphology: How teeth work. Cambridge University Press, London.

Lucas, P. W. and Teaford, M. F., 1994.Functional morphology of colobine teeth. In Colobine Monkeys: Their Ecology, Behaviour and Evolution, ed. Davies, A. G. and Oates, J. F., pp. 173-203. Cambridge: Cambridge University Press.

Maas, M.C., 1991. Enamel structure and microwear: an experimental study of the response of enamel to shearing force. Am. J. Phys. Anthropol., 85, 31-49.

MacFadden, B.J., Solounias, N., Cerling, T.E., 1999. Ancient diets, ecology, and extinction of 5-million-year-old horses from Florida. Science, 283, 824-827.

Macho, G.A., Leakey, M.G., Williamson, D.K., Jiang, Y., 2003. Palaeoenvironmental reconstruction: evidence for seasonality at Allia Bay, Kenya, at 3.9 million years. Palaeogeo.Palaeoclimatol.Palaeoecol. 199, 17-30.

Mendoza, M., Palmqvist, P., 2008. Hypsodonty in ungulates: an adaptation for grass consumption or for foraging in open habitat? J. Zool. 274, 134-142.

Merceron, G., 2003a. Dental microwear analysis of primates and ungulates from the late Miocene of eastern Mediterranean: paleobiological and paleoenvironmental implications. Ph.D. Univ. of Poitiers, France.

Merceron, G., 2003b. Une nouvelle méthodologie pour la quantification de la micro-usure dentaire : application à l'hominoïde fossile *Ouranopithecus macedoniensis* (Miocène, Grèce). Bulletin et Mémoires de la Société d'Anthropologie de Paris, 15, 300-301.

Merceron, G., Blondel, C., Brunet, M., Sen, S., Solounias, N., Viriot, L., Heintz, E., 2004. The Late Miocene paleoenvironment of Afghanistan as inferred from dental microwear in artiodactyls. Palaeogeogr.Palaeoclimatol. Palaeoecol., 207, 143-163.

Merceron, G., Blondel, C., de Bonis, L., Koufos, G.D., Viriot, L., 2005a. A new method of dental microwear analysis: Application to extant primates and *Ouranopithecus macedoniensis* (Late Miocene of Greece). Palaios, 20, 551-561.

Merceron, G., deBonis, L., Viriot, L., Blondel, C., 2005b. Dental microwear of fossil bovids from northern Greece: paleoenvironmental conditions in the eastern Mediterranean during the Messinian. Palaeogeo.Palaeoclimatol.Palaeoecol. 217, 173-185.

Merceron, G., Ungar, P.S., 2005. Dental microwear and palaeoecology of bovids from the Early Pliocene of Langebaanweg, Western Cape province, South Africa. S. Afr. J. Sci. 101, 365-370.

Mills, J.R.E., 1955. Ideal dental occlusion in primates. Dent. Pract., 6, 47-51.

Mills, J.R.E., 1963. Occlusion and malocclusion of the teeth of primates. In: Brothwell, D.R. (Ed.) Dental Anthropology. Oxford, Pergamon.

Mills, J.R.E, 1967. A comparison of lateral jaw movements in some mammals from wear facets on the teeth.Archs. Oral Biol., 12: 645-661.

Nelson, S., Badgley, C., Zakem, E., 2005.Microwear in modern squirrels in relation to diet. Palaeontologia Electronica, 8.

Pérez-Pérez, A., Bermudez de Castro, J.M., Arsuaga, J.L., 1999.Nonocclusal dental microwear analysis of 300,000-year-old *Homo heidelbergensis* teeth from Sima de los Huesos (Sierra de Atapuerca, Spain). Am. J. Phys. Anthropol., 108, 433-457.

Pérez-Pérez, A., Espurz, V., Bermudez de Castro, J.M., de Lumley, M.A., Turbon, D., 2003.Non-occlusal dental microwear variability in a sample of Middle and Late Pleistocene human populations from Europe and the Near East. J. Hum. Evol., 44, 497-513.

Peters, C.R., 1982. Electron-optical microscopic study of incipient dental microdamage from experimental seed and bone crushing. Am. J. Phys. Anthropol., 57, 283-301.

Plummer, T.W., Bishop, L.C., 1994. Hominid paleoecology at Olduvai Gorge, Tanzania as indicated by antelope remains. J. Hum. Evol. 27, 47-75.

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 Pleistocene kangaroo. PNAS 106:11646-11650.

Puech, P.F., 1979. Diet of early man - evidence from abrasion of teeth and tools.Curr. Anthrop., 20, 590-592.

Puech, P.F., 1986. *Australopithecus afarensis* Garusi-1, variability and specialization of early hominids in their masticatory apparatus. C. R. Acad. Sci. Ser. II, 303, 1819.

Puech, P.F., Albertini, H., Serratrice, C., 1983. Tooth microwear and dietary patterns in early hominids from Laetoli, Hadar and Olduvai. J. Hum. Evol., 12, 721-729.

Puech, P.F., Cianfarani, F., Roth, H., 1986.Reconstruction of the maxillary dental arcade of Garusi Hominid 1. J. Hum. Evol., 15, 325-332.

Radosevich, S.C., Retallack, G.J., Taieb, M., 1992.Reassessment of the paleoenvironment and preservation of hominid fossils from Hadar, Ethiopia. Am. J. Phys. Anthrop. 87, 15-27.

Rafferty, K.L., Teaford, M.F., Jungers, W.L., 2002. Molar microwear of subfossil lemurs: improving the resolution of dietary inferences. J. Hum. Evol., 43, 645-657.

Raymo, M.E., Grant, B., Horowitz, M., Rau, G.H., 1996. Mid-Pliocene warmth: stronger greenhouse and stronger conveyor. Marine Micropaleontol. 27, 313-326.

Reed, K.E., 1996. The paleoecology of Makapansgat and other African Pliocene Hominid Localities.Ph.D. Dissertation.State University of New York, Stony Brook.

Reed, K.E., 1997. Early hominid evolution and ecological change through the African Plio-Pleistocene. J. Hum. Evol. 40, 289-322.

Reed, K.E., 2008. Paleoecological patterns at the Hadar hominin site, Afar Regional State, Ethiopia. J. Hum. Evol. 54, 743-768.

Reed, K.E., Fish, J.L., 2005. Tropical and temperate seasonal influences on human evolution. In: Brockman, D., van Schaik, C. (Eds.), Primate Seasonality and Human Evolution. Cambridge University Press, Cambridge.

Renne, P.R., WoldeGabriel, G., Hart, W.K., Heiken, G., White, T.D., 1999. Chronostratigraphy of the Miocene-Pliocene Sagantole Formation, Middle Awash Valley, Afar rift, Ethiopia. Geol. Soc.Am. Bull. 111, 869-885.

Rensberger, J. M., 1978. Scanning electron microscopy of wear and occlusal events in some small herbivores. In Development, Function, and Evolution of Teeth, ed. Butler, P. M. and Joysey, K. A., pp. 415-438. New York: Academic Press.

Rivals, F., Semprebon, G.M., 2006. A comparison of the dietary habits of a large sample of the Pleistocene pronghorn *Stockoceros onusrosagris* from the Papago Springs Cave in Arizona to the modern *Antilocapra americana*. Journal of Vertebrate Paleontology, 26, 495-500.

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, Chicago, Aldine, 385-416.

Rodman, P.S., McHenry, H.M., 1980.Bioenergetics and the origin of hominid bipedalism. Am. J. Phys. Anthropol. 52, 103-106.

Rose, J.C. , Marks, M.K., 1985. Bioarcheology of the Alexander Site.In The Alexander Site, ed. Arkansas Archeological Survey, pp. 76-98. Fayetteville, AR.

Rose, J.C., Ungar, P.S., 1998. Gross wear and dental microwear in historical perspective. In: Alt, K.W., Rosing, F.W., Teschler-Nicola, M. (Eds.), Dental Anthropology: Fundamentals, Limits, Prospects, pp. 349-386. Stuttgart: Gustav-Fischer.

Ryan, A. S., 1980a. Anterior dental microwear in hominid evolution: comparisons with human and nonhuman primates. Ph.D. University of Michigan.

Ryan, A.S., 1980b. Anterior dental microwear in Neanderthals. Am. J. Phys. Anthropol., 52, 274.

Ryan, A.S., Johanson, D.C., 1989. Anterior dental microwear in *Australopithecus afarensis*: comparisons with human and nonhuman primates. J. Hum. Evol., 18, 235-268.

Schoeninger, M.J., Reeser, H., Hallin, K., 2003. Paleoenvironment of *Australopithecus anamensis* at Allia Bay, East Turkana, Kenya: evidence from mammalian herbivore enamel stable isotopes. J. Anthrop. Archaeo. 22, 200-207.

Schubert, B., Ungar, P.S., 2005. Wear facets and enamel spalling in tyrannosaurid dinosaurs. Acta Palaeontologica Polonica, 50, 93-99.

Schubert, B.W., Ungar, P.S., DeSantis, L.R.G. 2010. Carnassial microwear and dietary behaviour in large carnivorans. J Zool 280:257-263.

Schubert, B.W., Ungar, P.S., Sponheimer, M., Reed, K.E., 2006. Microwear evidence for Plio-Pleistocene bovid diets from Makapansgat Limeworks Cave, South Africa.Palaeogeo.Palaeoclimatol.Palaeoecol. 241, 301-319.

Scott, J.R., Ungar, P.S., Jungers, W.L., Godfrey, L.R., Scott, R.S., Simons, E.L., Teaford, M.F., Walker, A., 2009. Dental microwear texture analysis of the archaeolemurids and megaladapids, two families of subfossil lemurs from Madagascar.Submitted to the Journal of Human Evolution 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., Ungar, P.S., Bergstrom, T.S., Brown, C.A., Grine, F.E., Teaford, M.F., Walker, A., 2005. Dental microwear texture analysis reflects diets of living primates and fossil hominins. Nature 436, 693-695.

Semprebon, G.M., Godfrey, L.R., Solounias, N., Sutherland, M.R., Jungers, W.L., 2004. Can low-magnification stereomicroscopy reveal diet? J. Hum. Evol., 47, 115-144.

Senut, B., 1996. Pliocene hominid systematics and phylogeny. S. Afr. J. Sci. 92, 165-167.

Shipman, P., Harris, J.M., 1988.Habitat preference and paleoecology of *Australopithecus boisei* in Eastern Africa. In: Grine, F.E. (Ed.), Evolutionary History of the Robust Australopithecines. Aldine, New York, pp. 343-381.

Silcox, M.T., Teaford, M.F., 2002. The diet of worms: An analysis of mole dental microwear. J. Mammal., 83, 804-814.

Simpson, G.G., 1933. Paleobiology of Jurassic mammals. Paleobiologica, 5, 127-158.

Solounias, N., Hayek, L.A.C., 1993. New methods of tooth microwear analysis and application to dietary determination of two extinct antelopes. J. Zool., 229, 421-445.

Solounias, N., Moelleken, S.M.C., 1992a. Dietary adaptations of two goat ancestors and evolutionary considerations. Geobios, 25, 797-809.

Solounias, N., Moelleken, S.M.C., 1992b. Tooth microwear analysis of *Eotragus sansaniensis* (Mammalia: Ruminantia), one of the oldest known bovids. Journal of Vertebrate Paleontology, 12, 113-121.

Solounias, N., Moelleken, S.M.C., 1994. Dietary differences between two archaic ruminant species from Sansan, France. Historical Biology, 7, 203-220.

Solounias, N., Teaford, M.F.,Walker, A.C., 1988. Interpreting the diet of extinct ruminants: the case of a non-browsing giraffid.Paleobio. 14, 287-300.

Solounias, N., Moelleken, S.M.C., 1993. Determination of dietary adaptations of extinct ruminants through premaxillary analysis. J. Mammal. 74, 1059-1074.

Solounias, N., Semprebon, G., 2002. Advances in the reconstruction of ungulate ecomorphology with application to early fossil equids. Am. Mus. Nov., 1-49.

Spencer, L.M., 1997. Dietary adaptations of Plio-Pleistocene Bovidae: implications for hominid habitat use. J. Hum. Evol. 32, 210-228.

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 Limeworks hominin locality. J. Hum. Evol. 36, 705-718.

Strait, S. G., 1991.Dietary reconstruction in small-bodied fossil primates.Ph.D. State University of New York at Stony Brook.

Strait, S.G., 1993. Molar microwear in extant small-bodied faunivorous mammals: an analysis of feature density and pit frequency. Am. J. Phys. Anthropol., 92, 63-79.

Taieb, M., Johanson, D.C., Coppens, Y., Aronson, J.L., 1976.Geological and paleontological background of Hadar hominid site, Afar, Ethiopia. Nature 260, 289-293.

Teaford, M.F., 1988. Scanning electron microscope diagnosis of wear patterns versus artifacts on fossil teeth. Scanning Microsc. 2:1167-1175.

Teaford, M. F., 2006. What do we know and not know about dental microwear and diet? In: Ungar, P.S. (Ed.) Evolution of the Human Diet: The Known, the Unknown, and the Unknowable. New York: Oxford University Press.

Teaford, M.F., Mass, M.C., Simons, E.L., 1996. Dental microwear and microstructure of early Oligocene Fayum primates: Implications for diet. Am. J. Phys. Anthropol. 101, 527-543.

Teaford, M.F., Oyen, O.J., 1989. Differences in rate of molar wear between monkeys raised on different diets. J. Dent. Res. 68, 1513-1518.

Teaford, M.F., Ungar, P.S., 2000. Diet and the evolution of the earliest human ancestors. Proc. Natl. Acad. Sci. USA 97, 13506-13511.

Teaford, M. F., Ungar, P. S., and Grine, F. E, 2007. Dental microwear and hominin paleoecology. In: Sponheimer, M., Ungar, P., Reed, K., and Lee-Thorp, J. (Eds.), Early Hominin Paleoecology, Boulder: University of Colorado Press.

Teaford, M.F., Walker, A.C., 1983. Dental microwear in adult and stillborn guinea pigs (*Cavia porcellus*). Arch. Oral Biol. 28, 1077-1081.

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., 1995. A semiautomated image analysis procedure for the quantification of dental microwear .Scanning, 17, 57-59.

Ungar, P.S., 1996. Dental microwear of European Miocene catarrhines: evidence for diets and tooth use. J. Hum. Evol., 31, 335-366.

Ungar, P.S., 2004. Dental topography and diets of *Australopithecus afarensis* and early *Homo*. J. Hum. Evol. 46, 605-622.

Ungar, P.S., Grine, F.E., 1991. Incisor size and wear in *Australopithecus africanus* and *Paranthropus robustus*. J. Hum. Evol., 20, 313-340.

Ungar, P.S., Grine, F.E., Teaford, M.F., 2006. Diet in early *Homo*: A review of the evidence and a new model of adaptive versatility. Ann. Rev. Anthrop., 35.

Ungar, P.S., Merceron, G., Scott, R.S. 2007. 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., M'Kirera, F, 2003. A solution to the worn tooth conundrum in primate functional anatomy. Proc. Natl. Acad. Sci., USA, 100, 3874-3877.

Ungar, P.S., Scott, R.S., Grine, F.E., Teaford, M.F., 2010. Molar microwear textures and the diets of *Australopithecus anamensis* and *A. afarensis*. Phil. Trans. Roy. Soc., B. 365:3345-3354.

Ungar, P.S., Scott, R.S., Scott, J.R., Teaford, M.F., 2008. Dental microwear analysis: historical perspectives and new approaches. In: Irish, J.D. (Ed.), Technique and Application in Dental Anthropology. Cambridge University Press, Cambridge, 389-425.

Ungar, P.S., Simon, J.C., Cooper, J.W., 1991. A Semiautomated Image-Analysis Procedure for the Quantification of Dental Microwear. Scanning, 13, 31-36.

Ungar, P.S., Teaford, M.F., 1996. Preliminary examination of non-occlusal dental microwear in anthropoids: implications for the study of fossil primates. Am. J. Phys. Anthropol., 100, 101-113.

Van Valkenburgh, B., Teaford, M.F., Walker, A.C., 1990. Molar microwear and diet in large carnivores: inferences concerning diet in the sabretooth cat, Smilodon fatalis. J. Zool., 222, 319-340.

Vrba, E.S., 1980. The significance of bovid remains as indicators of environment and predation patterns. In: Behrensmeyer, A.K., Hill, A. (Eds.), Fossils in the Making, Vertebrate Taphonomy and Paleoecology. University of Chicago Press, Chicago, pp. 247-271.

Vrba, E.S., 1985. African Bovidae: Evolutionary events since the Miocene. S. Afr. J. Sci. 81, 263-266.

Vrba, E.S., Denton, G.H., Prentice, M.L., 1989. Climatic influences on early hominid behavior. Ossa 14, 127-156.

Walker, A., 1981. Diet and teeth.Dietary hypotheses and human evolution. Philos. Trans. R. Soc. Lond B Biol. Sci., 292, 57-64.

Walker, A., Hoeck, H.N., Perez, L., 1978. Microwear of mammalian teeth as an indicator of diet. Science, 201, 908-910.

Walker, A., Teaford, M.F., Ungar, P.S., 1994. Enamel microwear differences between species of *Proconsul* from the early Miocene of Kenya. Am. J. Phys. Anthropol., Suppl. 18, 202-203.

Walker , P.L., 1976. Wear striations on the incisors of cercopithecoid monkeys as an index of diet and habitat preference. Am. J. Phys. Anthropol., 45, 299-308.

Walker, P.L., Bernstein, S.A., Gordon, K.D., 1987. An image processing system for the quantitative analysis of dental microwear. Am. J. Phys. Anthropol., 72, 267.

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.

Washburn, S.L., 1960. Tools and human evolution. Sci. Am. 203, 3-15.

White, T.D, Suwa, G., Simpson, S., Asfaw, B., 2000.Jaws and teeth of *Australopithecus afarensis* from Maka, Middle Awash, Ethiopia. Am. J. Phys. Anthop. 111, 45-68.

Wolpoff, M.H., 1999. Paleoanthropology, second ed. McGraw-Hill.

Wynn, J.G., 2000. Paleosols, stable carbon isotopes, and paleoenvironmental interpretation of Kanapoi, northern Kenya. J. Hum. Evol. 39, 411-432.

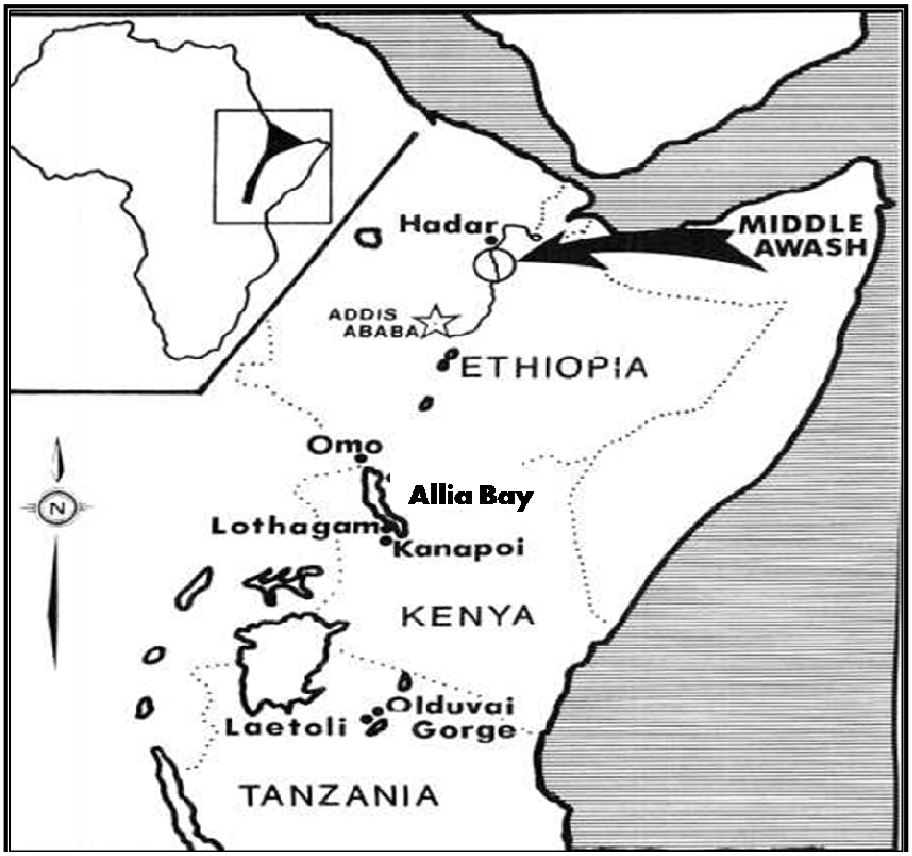
Young, W.G., 1986. Wear and microwear on the teeth of a moose (*Alces alces*) population in Manitoba, Canada.Canadian J. Zool. 64, 2467-2479.

TABLE 1. Summary table of previous paleoenvironmental reconstructions at fossil sites

Method of Reconstruction	Hypothesized Paleoenvironment	Source
Kanapoi, Kenya		
Paleosols- carbon isotopes	Mosaic with semi-arid, seasonal climate	Wynn, 2000
Paleosols- stratigraphy	Mosaic with gallery forest and edaphic grasslands	Cerling, 1992; Brown & Feibel, 1986, 1991
Faunal assemblages	Mosaic with gallery forest and dry, open bushlands	Leakey et al., 1995; Reed, 1997
Bovid Taxonomy	Arid savanna grassland	Harris & Leakey, 2003
Pollen assemblages	Included forest or woodland habitats	Bonnefille, 1995
Allia Bay, Kenya		
Paleosols- carbon isotopes	Mosaic, but with dominant open savanna	Wynn, 2000; Raymo et al., 1996
Paleosols- stratigraphy	Mosaic and highly seasonal	Brown & Feibel, 1991
Floral assemblages	Open woodland with expanses of grassland	Cerling et al., 1988
Faunal assemblages	Mosaic with gallery forest, bushland, open floodplain and riparian woodland	Coffing et al., 1994; Feibel et al., 1991
Organic stable isotopes	Mosaic with woodland and grassland	Schoeninger & Reeser, 1991
Laetoli, Tanzania		
Paleosols- carbon isotopes	Closed, deciduous woodland forest	Cerling, 1992
Paleosols- stratigraphy	At least a seasonal dry, arid climate	Hay, 1987
Paleosols- stratigraphy	Closed woodland to bushland	Verdcourt, 1987
Faunal assemblages	Mosaic with heavy woodland	Andrews, 1989; Reed, 1997
Faunal assemblages	Patch woodland and grassland	Harrison, 2005; Andrews, 2006, Kingston & Harrison, 2007
Faunal taxonomy	Savanna grassland and open woodland	Hay, 1980; Harris, 1985
Bovid Taxonomy	Open arid savanna	Harris, 1987
Pollen assemblages	Mosaic with grassland and open woodland	Bonnefille & Riollet, 1987
Hadar, Ethiopia		

Paleosols- carbon isotopes	Seasonal habitats and shifts from open and closed woodlands	Hailemichael, 2000
Paleosols- stratigraphy	Grassy woodland and semi-arid climate	Radosevich et al., 1992
Faunal assemblages	Physiognomic habitat with habitats ranging from scrub to edaphic grassland	Reed, 2008 Bobe & Eck, 2001
Pollen assemblages	Mosaic habitat that trended towards dry open environments	Bonnefille et al., 1987 Bonnefille et al., 2004

FIGURE 1. Map of East African fossil sites



Chapter Two: Dental Microwear Texture Analysis of Extant African Bovidae

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Abstract

Bovids are often used as paleoenvironmental proxies because they are among the most commonly recovered large mammals at many fossil hominin sites and because modern African bovids occupy a wide range of dietary and environmental niches. This study uses dental microwear texture analysis to examine 25 species of extant African bovids, representing 6 dietary categories and with an emphasis on various levels of mixed feeding. The results show significant differences among the dietary classifications and confirm previous work suggesting that grazing taxa have less complex, more anisotropic surfaces with smaller features than browsing taxa. The results also indicate that dental microwear texture analysis can distinguish beyond the classic grazer-browser-mixed feeder trichotomy and accurately separate variable grazers, generalists, browser-grazer intermediates and frugivores from obligate grazers and browsers, as well as from one another. Some differences among taxa within dietary categories were also found, likely reflecting seasonal and/or geographic differences in diet. In addition to demonstrating the effectiveness of the technique at differentiating between different levels of mixed feeding in bovids, this study also provides a comprehensive comparative dataset of extant bovid microwear textures that can be applied to fossil taxa from sites and time periods across Africa.

Key Words: microwear, bovid, grazer, browser, diet

Introduction

The Family Bovidae is an ecologically diverse group of ungulates represented by more than 45 genera spread across Africa, Asia, Europe and North America (Wilson and Reeder, 2005). African bovids are particularly varied and include 27 extant genera and 79 species, making them one of the dominant herbivorous mammals on the continent (Kingdon, 1997). They inhabit a broad variety of ecosystems- from desert to tropical rainforest (Grzimek, 1990). The diets of African bovids are equally varied and range from habitual grass grazers such as the common tsessebe (*Damaliscus lunatus*), to browse specialists like the gerenuk (*Litocranius walleri*), to highly frugivorous taxa such as the blue duiker (*Philantomba monticola*). Even as ubiquitous as these bovids are today, the fossil record shows that they were even more abundant in the past, with over 100 fossil taxa from the Pliocene and Pleistocene described to date (Gentry, 1990; Vrba, 1995). An understanding of both modern and fossil bovid ecology is therefore crucial if we hope to better understand the paleoenvironments associated with human evolution.

Reconstructions of paleoenvironment that utilize faunal remains are only as strong as the extant baseline used to interpret them. There is a wealth of literature available on modern bovid diets and considerable work has been done to compile this information into a comprehensive system of classification (Gagnon and Chew, 2000). This system distinguishes not only grazing and browsing taxa, but also recognizes several levels of mixed feeding, an important advance that can be useful in informing habitat preference. However, even with clearer dietary categories for extant species, distinguishing between various levels of mixed feeding in the fossil record is difficult using traditional methods of dietary reconstruction. Dental microwear texture analysis, which combines white-light confocal microscopy with scale-sensitive fractal analysis, is an objective and repeatable method for characterizing microwear surfaces. Most importantly, this technique has the potential to get beyond the classic grazer-browser-mixed feeder trichotomy and distinguish taxa that engage in various levels of mixed feeding, as suggested by a previous study on the fossil bovids at Langebaanweg, South Africa (Ungar et al., 2007). In this paper, I test this hypothesis using a new comparative baseline series of extant bovid dental microwear textures. This dataset includes 25 species of modern African bovids, representing a wide variety of dietary preferences. These data provide a baseline series that can be used to interpret the microwear signatures of fossil bovids from sites and time periods across Africa.

The dietary categories typically used to classify bovids refer to the percentages of monocotyledons (grasses and sedges) and dicotyledons (fruits, seeds, flowers, buds, leaves, twigs, tubers and shoots) that make up their diet. Traditionally, these percentages have been used to divide bovids into three distinct dietary classifications: grazers, browsers and mixed feeders (Vesey-Fitzgerald, 1960; MacNaughton and Georgiadis, 1986; Hoffman, 1989; Estes, 1991; Fortelius and Solounias, 2000). The grazer and browser categories reflect specific dietary and habitat preferences, with the former including taxa that inhabit open environments and eat mostly monocotyledons, and the latter representing taxa that inhabit more closed environments and primarily eat dicotyledons. The generalized mixed feeder category, however, refers to a highly diverse group of bovids that display a myriad of environmental and dietary preferences. These taxa are not static in the foods that they consume and many have highly localized and/or seasonal diets that alternate between grazing and browsing.

Actual bovid diets are more complex than this grazer-browser-mixed feeder category scheme suggests, and several more detailed classifications have been proposed. Hofmann and Stewart (1972), for example, proposed a three category system based on differences in extant bovid stomach structure. Taxa were classified as bulk-roughage eaters (grazers), concentrated herbage selectors (browsers) or intermediate feeders, and were further subdivided based on consumed percentages of each food type. Langer (1988) built on these categories by adding three more levels of intermediate feeding. A later re-classification by Bodmer (1990) recognized the importance of fruit in the diet of many African bovids and proposed a dietary continuum ranging from grazing to dedicated frugivory, with browsing being the intermediate form. More recently, Gagnon and Chew (2000) described a comprehensive system of dietary classification for African bovids based on food type, seasonality, geographic variation and body mass. Their system proposed six primary dietary categories: obligate grazers (> 90% monocots), variable grazers (60-90% monocots), browser-grazer intermediates (30-70% monocots and dicots, < 20% fruit), browsers (> 70% dicots), generalists (> 20% all food types) and frugivores (> 70% fruits). Sponheimer et al. (2003) successfully used stable carbon isotope analysis to test the dietary information for 24 of the taxa classified by Gagnon and Chew and found that, with a few exceptions that could be explained based on sample population differences, the results of the two studies yielded similar dietary classifications.

Diet is the most direct way that an organism interacts with its environment and has had significant influence on the evolutionary adaptations of grazing and browsing ungulates. Previous attempts to identify morphological indicators of diet have included taxonomic uniformitarianism and ecomorphological proxies like the configuration of the masticatory structure, as well as the use of tooth size, shape and structure (Solounias et al, 1995; Pèrez-Barberia and Gordon, 2001; Archer and Sanson, 2002). However, these are all genetic signals that reflect only what a species is capable of eating, not what individuals actually ate. The diet of an individual may vary over its lifetime, but it can take many generations for the morphology of a species to change in response to selective pressures (Solounias and Moelleken, 1999). In order to reconstruct what an animal actually ate at a moment in time, epigenetic signals must be examined. Dental microwear, or the microscopic pits and scratches created on the enamel surface during mastication, is one such line of evidence.

Differences in the dental microwear of grazing and browsing ungulates have been noted in previous studies of extant and fossil species (e.g. Solounias et al., 1988; Solounias and Moelleken, 1993; Merceron and Ungar, 2005; Merceron et al., 2005; Schubert et al., 2006; Ungar et al., 2007), with browsers having more pits and grazers having more scratches. Mixed-feeding taxa tend to have intermediate microwear signatures, or patterns overlapping with both browsers and grazers. This has important implications for understanding the relationship between bovid diet and habitat preference, as while the connection between diet and habitat are not exact, grazing and browsing microwear signatures do imply the availability of grasses and woody plants respectively.

Bovids are generally considered to be reliable indicator species for environmental reconstruction because modern ruminants fall into discrete dietary categories that reflect habitat preferences. The relationship between bovid diet and habitat has been long established in the literature (e.g., Vrba, 1980, 1985; Wing et al., 1992, Bobe and Eck, 2001) and their fossils are frequently used to infer the ecological context of a site (e.g. Gentry, 1970; Solounias and Dawson-Saunders, 1988; Merceron et al., 2004a, 2005; Merceron and Ungar, 2005; Ungar et al., 2007). This is especially true for early hominin localities where fossil bovids tend to be among the most commonly recovered large mammals (e.g. Vrba, 1980, 1995; Kappelman, 1984; Shipman and Harris, 1988; Harris, 1991; Plummer and Bishop, 1994; Kappelman et al., 1997; Reed, 1997, 2008; Spencer, 1997; Sponheimer et al., 1999, 2003; Schoeninger et al., 2003; Schubert et al., 2006; Kingston and Harrison, 2007).

Most models for paleoenvironmental reconstruction using bovids apply the principle of taxonomic uniformitarianism, the assumption that fossil species share the same ecological preferences as their closest living relatives. Although this assumption is rarely questioned for recent faunas, its utility in reconstructing the paleoecology of long extinct species is uncertain. One of the principal issues with taxonomic uniformitarianism is that it assumes groups remain constant in their ecological preferences over long periods of time. While taxonomic uniformitarianism is relatively straightforward and requires minimal effort beyond a glance at a faunal list, critics have questioned many of its inherent assumptions (Solounias et al., 1988; Reed, 1996; Sponheimer et al., 1999; Schubert et al., 2006). In a study of fossil bovid diets utilizing stable isotopes and ecomorphology, Sponheimer et al. (1999) demonstrated that half of the included taxa had diets that differed from the assumed diets based on taxonomic uniformitarianism. For example, although *Aepyceros sp.* and *Gazella vanhoepeni* had been previously assumed to be mixed/seasonal feeders like their closest living relatives, the isotopic signatures and ecomorphological data suggested that both were obligate browsers, and revealed no evidence of C4 grass consumption. Due to these discrepancies between dietary signals, it is critical that ecological similarities of extant and fossil taxa be tested in some reliable way in order to have confidence in these assumed relationships.

Materials and Methods

Specimens

575 specimens were included in this study, representing 25 extant bovid taxa. The taxa used in this study were selected because they represent a wide variety of ecological adaptations, with diets ranging from open-country-adapted obligate grazers to closed-habitat browsers to

dedicated frugivores. Special emphasis was placed on including taxa that engage in various levels of mixed feeding, including variable grazers, browser-grazer intermediates and generalists. Finally, most of the included taxa have well-understood diet and habitat preferences that have been documented during field studies. Table 1 lists the included extant taxa and summarizes their dietary preferences.

The specimens examined for this study are housed at the American Museum of Natural History (AMNH), New York; the Field Museum (FMNH), Chicago; the Smithsonian National Museum of Natural History (NMNH), Washington D.C.; and the Royal Museum of Central Africa (RMCA), Tervuren, Belgium. All are wild-shot specimens with known provenience data. Only specimens that preserved unobscured antemortem microwear were included in the dataset. The criteria used to determine suitability for microwear analysis were those of Teaford (1988) and King et al. (1999).

Both upper and lower second molars were included in this study and have been shown in previous projects to yield similar results (Merceron et al., 2004a, 2004b). High-resolution casts were prepared following conventional procedures for microwear analysis (Grine, 1986, Ungar, 1996). The original specimens were cleaned with cotton swabs soaked in acetone and then molded using a polyvinylsiloxane dental impression material (Presidents Jet Regular Body, Coltene-Whaledent Corp.). Casts were then made using high-resolution epoxy (Epotek), which has been demonstrated to produce replicas that are precise to a fraction of a micron (Beynon, 1987; Teaford and Oyen, 1989).

Dietary Classifications

The dietary categories used in this study are those of Gagnon and Chew (2000) and expand on the traditional grazer-browser-mixed feeder continuum. This classification system was selected because it recognizes various levels of mixed feeding and allows for categorization of all African bovid taxa. The categories are determined by the percentages of fruits, dicotyledons and monocotyledons included in the diet, as recorded during observations in the wild. Inarguably, consideration of these various levels of mixed feeding improves the resolution of dietary reconstructions and can aid in our understanding of behavior and habitat preference in fossil taxa. However, it is also important to note that extensive ecological observation and fecal analyses have not been conducted for many taxa classified as mixed feeders (Gagnon and Chew, 2000, Fortelius and Solounias, 2002). Further field work is needed to better determine the influence of seasonal and geographic variation on the diets of these mixed feeding bovids.

The species included in the study were classified using the Gagnon and Chew model (2000) and are listed in Table 1. Taxa classified as obligate grazers have a diet consisting of more than 90% monocotyledons, with no seasonal or geographic variation. Variable grazers consume 60-90% monocotyledons, but vary in diet seasonally and geographically. The diet of bovids classified as browser-grazer intermediates consists of 30-70% monocotyledons and dicotyledons and always includes some fruit, although never more than 20%. Browsers have a diet that includes more than 70% dicotyledons. Fruit accounts for more than 70% of the diet of bovids classified as frugivorous and these taxa rarely, if ever, consume monocotyledons. Taxa classified as dietary generalists are widely variable by season and locality, but always consume more than 20% of each of the three food types.

Data Collection

Conventional methods of studying dental microwear, including scanning electron microscopy and light microscopy are subject to observer measurement error and a lack of depth data due to two dimensional surface characterizations (Grine et al., 2002). Dental microwear texture analysis was developed to be a solution to these problems (Ungar et al., 2003). It combines white-light confocal profilometry with scale-sensitive fractal analysis, resulting in the quantitative description of surfaces at a range of scales. This offers a suite of objective and repeatable measures of microwear surface textures in three dimensions that can be compared between groups with differing diets. Further, white-light confocal profilometry is quicker, easier to use, and can be less costly than scanning electron microscopy; and automated analysis requires less time and effort from researchers than does identification and measurement of individual features. The most important advance of texture analysis is the reduction of observer error in measurement, which allows direct comparisons between studies, as well as the establishment of a large database that researchers can access for interpretation of their results. Dental microwear texture analysis has been successfully used to identify dietary differences between species of extant and fossil taxa including humans and non-human primates, marsupials, carnivores, and bovids (R. Scott et al., 2005, 2006; Ungar et al., 2008a, 2008b, 2010, in press; Krueger and Ungar, 2009; Merceron et al., 2009; Prideaux et al., 2009; J. Scott et al., 2009; Ungar and Scott, 2009; Schubert et al., 2010; Schultz et al., 2010) and to detect differences in diet by season and even gender (Merceron et al., 2010).

As is conventional for studies of bovid dental microwear, texture data were collected on the disto-buccal enamel band of the mesial cuspid of M_2 and the mesio-buccal enamel band of the mesial cusp of M^2 (Janis, 1990; Merceron, 2005; Schubert, 2006; Ungar et al., 2007). These areas are illustrated in Figure 1. The casts were scanned using a Sensofar PLμ white-light confocal profiler (Solarius Development Inc., Sunnyvale, CA). This instrument collects 3-D point clouds from the wear surface of the tooth to create photo simulations and digital elevation models.

Each specimen was scanned using a 100x objective, resulting in the generation of a point cloud with a lateral sampling interval of 0.18 μm, a vertical resolution of 0.005 μm, and a field of view of 102 x 138 μm. Data were collected for four adjoining fields, resulting in a total work envelope of 204 x 276 μm for each specimen. The scans were then leveled using Solarmap Universal software (Solarius Development Inc., Sunnyvale, CA). Prior to analysis, defects such as dust or other adherents were removed from the scan using the erase or thresholding function in Solarmap and/or the slope-filtering function in Sfrax (Surfract Corporation). The resulting data files were saved in ".sur" format in preparation for analysis.

Scale-Sensitive Fractal Analysis

Point clouds were analyzed using Toothfrax and Sfrax scale-sensitive fractal analysis software packages (Surfract Corporation). Scale-sensitive fractal analysis originates from studies of fractal geometry, and is based on the principle that the texture of a surface changes with the scale of observation. Thus, a surface that appears smooth at a coarse scale may seem rough when viewed at a fine scale. These apparent changes in surface texture across scales can be examined for entire surfaces or for profiles across a surface. Several texture variables generated during these analyses have been identified as particularly informative for dental microwear studies (Ungar et al., 2003; Scott et al., 2005, 2006). Data for five of these variables are presented here. They are area-scale fractal complexity, length-scale anisotropy of relief, scale of maximum complexity, textural fill volume and heterogeneity of area-scale fractal complexity. These variables have been described in detail elsewhere (Ungar et al., 2003, 2007, 2008; Scott et al., 2005, 2006) and will be summarized briefly here.

Complexity (Asfc) - Area-scale fractal complexity is measured as the change in surface roughness across different scales of observation. *Asfc* is calculated by taking the slope of the steepest part of a curve fit to a plot of relative area over the range of scales at which the measurements are taken. The value for *Asfc* will be higher for steeper slopes, indicating more complex surfaces. For example, a surface dominated by pits of various sizes or pits and scratches overlaying one another will result in high values for *Asfc*.

Scale of Maximum Complexity (Smc)- Earlier studies using dental microwear texture analysis have suggested that range of scales at which *Asfc* is calculated may be informative (Scott et al., 2005, 2006). This is calculated by taking the range of scales where the relative area versus scale curve is the steepest. *Smc* likely corresponds in some measure with the scale of wear-causing particles. Values for this variable will be highest for surfaces that display less wear at finer scales and will be lowest for those with more wear at fine scales.

Anisotropy (epLsar)- Length-scale anisotropy of relief is a measure of the orientation concentration of surface roughness. This variable is calculated by taking profiles of the wear surface at different orientations at a given scale. This study employed a sampling interval of 5°and a scale of 1.8 μm. Highly anisotropic surfaces have relative profile lengths that differ with orientation. The relative lengths at given orientations can be defined as vectors and normalized to create a rosette diagram. Values for *epLsar* are calculated by taking the length of the mean vector. Surfaces that feature parallel scratches will have a high value for *epLsar*.

Textural Fill Volume (Tfv)- The textural fill volume algorithm calculates the volume of square cuboids at a given scale that can fill a surface. *Tfv* is defined as the difference in summed volume for fine cuboids (2 µm per side) and large cuboids (10 µm per side). This removes the impact of overall surface structure, such as facet curvature, and allows for the characterization of the microwear features themselves. Surfaces dominated by large pits or deep scratches will have high values for *Tfv*.

Heterogeneity (HAsfc) - The variables mentioned above all help to provide accurate descriptions of microwear textures; however, the values for adjoining areas of the facet may vary. This variation for a given variable across a surface may be important in characterizing the surface. In order to better study this variation, the heterogeneity of area-scale fractal complexity variable measures the difference in *Asfc* across a surface. *HAsfc* is calculated through the use of the Auto-Split function in Toothfrax. This computation divides the scanned area of the facet into successively smaller sub-regions with equal numbers of rows and columns, beginning with 2 x 2 and ending with 11 x 11. The value for *HAsfc* is defined as the median absolute deviation of *Asfc* divided by the median of *Asfc*.

Statistical Analysis

Following analysis, median values were calculated for the four scans representing each specimen (Scott et al., 2006). The resulting data were then rank transformed prior to analysis because unranked microwear texture data typically violate assumptions inherent in parametric statistical tests (Conover and Iman, 1981). A nested analysis of variance model was used in this study, with taxon as the subordinate level of classification, nested within assigned dietary category, specifically obligate grazer, variable grazer, browser-grazer intermediate, generalist, browser, or frugivore (Gagnon and Chew, 2000). The data were then analyzed using a general linear model to determine whether there were overall differences in microwear among the six dietary categories. Analyses of variance for individual texture attributes and pairwise comparisons tests were then used to determine the sources of significant variation both between dietary categories and among taxa within the dietary categories. Both Tukey's Honestly Significant Difference and Fisher's Least Significant Difference tests were used to balance the risks of Type I and Type II errors (Cook and Farewell, 1996).

Results

Examples of the microwear surfaces of extant bovid taxa are illustrated in Figures 2 and 3. Descriptive and analytical statistics are presented in Tables 2, 3 and 4 and Figures 4 and 5. There is significant variation in the overall general linear estimate model, indicating that the microwear textures varied among the dietary classifications in all six variables. Additionally, some significant variation was also identified among taxa within the dietary categories.

Results by variable

Asfc – Tukey's HSD pairwise comparisons indicate significant differences in surface complexity among all pairs of dietary categories except browser-grazer intermediates versus generalists. These tests indicate that frugivores had significantly higher microwear complexity values than all other dietary categories. Predictably, browsers had higher complexityvalues than the grazing and mixed feeding taxa. Browser-grazer intermediates and generalists had similar values for complexity and were not significantly different using Tukey's HSD or Fisher's LSD tests. Of the grazing taxa, variable grazers had significantly higher complexity values than obligate grazers.

epLsar – Significant differences were found among all taxa except browser-grazer intermediates versus generalists, and browsers versus frugivores. Fisher’s LSD test also indicated significant differences between browser-grazer intermediates versus generalists. Obligate grazers had the highest values for anisotropy, while frugivores and browsers had the lowest. Among the mixed feeding taxa, browser-grazer intermediates had higher values than generalists and variable grazers.

Smc - Tukey’s HSD pairwise comparisons indicate significant differences among all dietary categories, with the exception of browsers versus variable grazers, and frugivores versus generalists, which were distinguished by Fisher’s LSD test. Obligate grazers had the highest values for *Smc*, while frugivores had the lowest. Variable grazers had the highest values among mixed feeding taxa, with browser-grazer intermediates and generalists having comparatively low values.

Tfv- Significant differences in textural fill volume were found between all pairs of dietary categories when analyzed with Tukey’s HSD pairwise comparisons test. Frugivores had the highest values for textural fill volume, followed by browsers. Among the mixed feeding taxa, generalists had higher values for fill volume than browser-grazer intermediates. Obligate grazers had the lowest recorded values.

HAsfc$_9$- Tukey’s HSD pairwise comparisons indicate significant differences between all pairs of dietary categories except frugivores versus browser-grazer intermediates, and generalists versus variable grazers. Fisher’s LSD test also reported significant differences for browser-grazer intermediates versus frugivores. Browsers had the highest values for heterogeneity, while obligate grazers have the lowest values. Among mixed feeders, browser-grazer intermediates and frugivores have higher values than variable grazers and generalists.

$HAsfc_{81}$– Tukey's HSD pairwise comparisons indicate significant variation in heterogeneity between all pairs of dietary categories except browser-grazer intermediates versus frugivores, browser-grazer intermediates versus generalists, frugivores versus generalists, and obligate grazers versus variable grazers. A Fisher's LSD test also indicated significant differences for browser-grazer intermediates versus generalists and obligate grazers versus variable grazers. Browsers have the highest values forheterogeneityand obligate and variable grazers have the lowest values.

Results by diet category

The trends by dietary category are summarized in Table 5. In general, frugivores have high values for complexity and fill volume, low values for anisotropy and mid-range values for heterogeneity and the scale of maximum complexity. Browsers have high values for complexity, fill volume and heterogeneity, low values for anisotropy and mid-range values for scale of maximum complexity. Obligate grazers have high values for anisotropy and the scale of maximum complexity, and low values for complexity, fill volume and heterogeneity. Variable grazers have low complexity and heterogeneity, and mid-range values for anisotropy, fill volume and the scale of maximum complexity. Browser-grazer intermediates have relatively low values for anisotropy and mid-range values for complexity, the scale of maximum complexity, fill volume and heterogeneity. Generalists have high values for fill volume, low values for anisotropy and the scale of maximum complexity, and mid-range values for complexity and heterogeneity.

Variation within dietary category

In addition to clear differences among the dietary categories, some significant variation among taxa within dietary category was also indicated. Significant differences among obligate grazers, variable grazers, browser-grazer intermediates and browsers were present for all texture attributes. There was significant variation among generalists in *epLsar* and among frugivores in *epLsar*, *Smc*, *Tfv*, $HAsfc_9$.

Obligate grazers- Among obligate grazing taxa, *Redunca fulvorufula*has significantly higher values for complexityand significantly lower values for the scale of maximum complexitythan any other species. *Damaliscus lunatus* and *Redunca fulvorufula*both have significantly higher values for anisotropy and heterogeneity 3 x 3, as well assignificantly lower values for fill volumeand heterogeneity 9 x 9than *Kobus leche*, and *Redunca fulvorufula*also has higher values for this variable than *Redunca arundinum*.

Variable grazers- Significant differences were also present among variable grazers in all texture attributes. *Tragelaphus spekii* and *Gazella granti* have significantly higher values for complexity than the other four taxa. *Gazella granti*, *Damaliscus pygargus* and *Tragelaphus spekii*have significantly lower values for anisotropythan the other variable grazing taxa. *Gazella granti* and *Hippotragus niger*both have significantly lower values for the scale of maximum complexitythan the other four taxa, and *Damaliscus pygargus* has significantly higher values for this variable than *Gazella granti*, *Hippotragus niger*, *Kobus ellipsiprymnus* and *Syncerus caffer*. *Damaliscus pygargus* and *Hippotragus niger*have significantly higher values for fill volumethan the other four taxa, none of which differ significantly from one another. *Hippotragus niger*and *Kobus ellipsiprymnus*group together in heterogeneity 3 x 3and have significantly higher values than any of the other four taxa. *Damaliscus pygargus* and *Gazella granti* have significantly lower values than *Hippotragus niger*, *Kobus ellipsiprymnus*, and *Syncerus caffer*. *Damaliscus pygargus* and *Gazella granti* have significantly lower values for heterogeneity 9 x 9 than *Kobus ellipsiprymnus* and*Tragelaphus spekii*.

Browsers- Browsing taxa also showed some significant differences among taxa in all variables. *Tragelaphus euryceros* and *Neotragus batesi* have significantly higher complexityvalues than *Sylvicapra grimmia*, *Litocranius walleri*. *Sylvicapra grimmia* has significantly lower values for complexity than any of the other browsers. *Tragelaphus euryceros* has significantly lower anisotropy values than any of the other browsing taxa, while *Sylvicapra grimmia* has significantly higher values for this variable than *Neotragus batesi* or *Tragelaphus euryceros*. *Tragelaphus euryceros* has significantly higher fill volumethan *Neotragus batesi*. *Litocranius walleri* has significantly higher scale of maximum complexity values than *Sylvicapra grimmia*, as well as higher values for both heterogeneity variables than any of the other browsers.

Browser-grazer intermediates- Among browser-grazer intermediates, *Aepyceros melampus* and *Tragelaphus imberbis* have significantly lower complexityvalues than the other four taxa, while *Raphicerus campestris* has significantly lower anisotropyvalues. *Tragelaphus imberbis* and *Antidorcas marsupialis* have significantly lower values for the scale of maximum complexity. *Raphicerus sharpei* has significantly lower fill volumevalues than all five other taxa in this category, while *Raphicerus campestris* has significantly higher values for this variable than *Aepyceros melampus*, *Antidorcas marsupialis*, and *Raphicerus sharpei*. Finally, *Raphicerus sharpei* has significantly higher values for both heterogeneity variables than all of the other browser-grazer intermediates.

Generalists and frugivores- There was generally less significant variation among frugivores and generalists than the more dedicated grazing and browsing taxa. Of the generalist taxa, the only significant difference was in anisotropy and all three taxa were significantly different from one another, with *Tragelaphus strepsiceros* having the highest values and *Oreotragus oreotragus* having the lowest. Frugivores differed in anisotropy,the scale of maximum complexity, fill volume and heterogeneity 3 x 3, with *Cephalophus sylvicultor* having significantly higher values for anisotropy and the scale of maximum complexityand significantly lower values for fill volumeand heterogeneity 3 x 3.

Discussion and Conclusion

The dataset presented here allowed me to test the hypothesis that dental microwear texture analysis can distinguish between taxa that fall into different dietary categories, particularly those that engage in various levels of mixed feeding. By including large sample sizes, by microwear standards, and multiple taxa representing each dietary category, testing the ability of dental microwear texture analysis to differentiate taxa could be done with much more confidence. The results of the analysis confirm that the technique is capable of finer dietary distinctions than previously demonstrated and suggest that, with additional testing, more specific information still may be gleaned. These results have important implications for the use of dental microwear textures to distinguish bovid taxa with different dietary categories and to reconstruct the diets, and by extension habitats, of fossil bovids.

Bovid diets and dental microwear analysis – As previous studies have suggested, the classic dietary categories used to describe bovids (grazers, browsers, mixed feeders) are obvious oversimplifications (Bodmer, 1990; Gordon and Illius, 1994; Gagnon and Chew, 2000). Even so, these classifications do have substantive heuristic value. In addition to differing in their nutritional content, grasses and browse also differ in their physical properties (Shipley, 1999), which are essentially what is being measured by dental microwear analysis. Monocotyledonous grasses are distinguished by dense cell walls composed primarily of cellulose (Demment and Vansoest, 1985) and veins that typically run parallel to the long axes of their blades. This structure causes the grass blades to be highly resistant to stress and difficult to fracture (Vincent, 1990). It has also been long hypothesized that the tissues found in grasses are denser and more homogenous than those found in browse, thus resulting in a difference in the overall fracture pattern between the two food types (Spalinger et al., 1986; Kay, 1993; Van Wieren, 1996). Additionally, grasses tend to have high concentrations of abrasives, such as endogenous phytoliths, and/or exogenous grit adhering to the surfaces of individual blades (Baker et al., 1959; Dougall et al., 1964; NcNaughton et al., 1985; Sanson et al., 2007). While they cannot fuel the body, these abrasives are harder than dental enamel and contribute to the microwear signature of grazing taxa by scratching the surface of the teeth during mastication (Baker, 1959).

Dicotyledonous browse can include a wide variety of foods, making it difficult to characterize. In general, however, items classified as browse have thinner cell walls resulting in greater ease of access to nutrient content than grasses (Spalinger et al., 1986). Browse components are also more variable than grasses in their physical properties (Caswell et al., 1973). Some browse resources tend to be more brittle and therefore less resistant to fracture than grass blades. Others, however, are much harder and require greater stress to fracture, possibly due to the higher percentages of bundle sheaths characteristic of C3 browse (Caswel et al., 1973; Heckathorn et al., 1999).

These contrasts between hard and tough foods have important implications for interpreting patterns of dental microwear because they reflect the biomechanical adaptations needed to process foods with different fracture properties (Lucas, 2004). Tough foods, such as grass blades, tend to require shearing or grinding, with the lateral movement of opposing occlusal surfaces relative to one another. This process results in abrasives being dragged across the surface of the teeth, causing microscopic striations on the enamel (Rensberger, 1973; Walker et al., 1978). Parallel tooth-food-tooth processing can also cause ‘prism plucking’, or small prism-sized pits on the enamel surface (Walker, 1984; Teaford and Runestad, 1992).

Hard and/or brittle foods, on the other hand, necessitate crushing, or vertical contact of opposing surfaces with food items fractured between them, a process that results in the production of microscopic pits. Because of the range of food types and fracture properties in items categorized as browse, the resulting pits can vary widely in size and shape. Larger pits, for example, are thought to result from concentrated pressure on hard foods between the enamel surfaces, whereas smaller pits may be caused by strict tooth-tooth wear (Walker, 1984; Teaford and Oyen, 1989a, b; Teaford and Runestad, 1992)

The ability of dental microwear analysis to distinguish grazing and browsing bovids is well documented in the literature. The earliest studies of bovid dental microwear were conducted using a scanning electron microscope (e.g. Solounias et al., 1988; Solounias and Moelleken, 1992a, 1992b, 1993). Microwear surfaces were imaged at 500x and individual features were digitized and measured. These studies demonstrated that grazing taxa tend to have occlusal surfaces dominated by scratches, while browsers had more pits. Mixed feeding bovids usually show intermediate percentages of pits and scratches.

More recent studies have approached the characterization of bovid dental microwear using feature-based or texture-based analysis techniques to identify finer subdivisions within the basic grazer-browser-mixed feeder categories. Low-magnification light microscopy, a feature-based microwear technique, requires the examination of wear facets using a standard stereomicroscope at 35x. Microwear features are then quantified and divided into six categories: scratches, pits, scratch textures, cross scratches, large pits and gouges (e.g. Solounias and Semprebon, 2002; Rivals and Deniaux, 2003; Semprebon et al., 2004). Studies employing this method have reported clear differences between dedicated grazing and browsing taxa, and have described two distinct variations in the microwear signatures of mixed feeders- seasonal/regional mixed feeders and meal-by-meal mixed feeders. Other studies have applies combinations of various techniques to successfully distinguish between grazing and browsing bovids, including low magnification light microscopy with semi-automated image analysis (Merceron et al., 2004a, b, 2005, 2007) and white-light confocal microscopy with feature-based measurement techniques has also been applied to the study of bovid dental microwear (Merceron and Ungar, 2005; Schubert et al., 2006).

Most recently, texture-based analysis, which utilizes three-dimensional characterization of the microwear surface and semi-automated image analysis, has been employed in the study of dental microwear. While to date there have been only limited applications of this technique to bovids, the results have clearly demonstrated the effectiveness of texture analysis in distinguishing grazing, browsing and mixed feeding taxa and the technique shows promise for more specific dietary distinction. Ungar and colleagues (2007) have suggested that dental microwear texture analysis has the potential to differentiate among finer dietary categories and called for further study of extant bovids with known subtle differences in diet.

A new database of bovid dental microwear textures- The extant African bovids included in this study show a wide variety of microwear texture patterns that reflect a correspondingly broad range of known diets. The results presented here confirm the previous observation of Ungar and colleagues (2007) that bovids classified as browsers have complex microwear surfaces with low anisotropy, whereas those classified as obligate grazers have highly anisotropic surfaces, with low complexity. In fact, there is no overlap between obligate grazers and browsers in an anisotropy-complexity bivariate space, as illustrated in Figure 4. In addition to supporting the previous work, this study adds data for four additional variables: *Smc*, *Tfv*, $HAsfc_9$, and $HAsfc_{81}$, to that previously described by Ungar et al. (2007). The present work also greatly expands sample sizes, and the number and dietary range of extant bovid taxa available for the baseline to interpret wear signatures of fossil taxa.

Variation among dietary categories- Diet clearly explains a significant fraction of the overall variation in the microwear patterns, with browsers having higher values for complexity, fill volume, and both heterogeneity variables and grazers having higher values for anisotropy and scale of maximum complexity. In fact, when taxa were grouped by dietary category and compared, significant differences were present for all six variables. The only consistent overlap in microwear signature was between taxa classified as browser-grazer intermediates and those classified as generalists.

Beginning with the extremes of the classic browser-grazer continuum, significant differences were present between browsers and obligate grazers for all six variables and in fact, there was no overlap recorded between the ranges of these taxa for any of the texture attributes

(Figure 4). The difference between these two dietary categories is clearly visible when viewed in a bivariate space contrasting complexityand anisotropy (Figure 5), with browsers having higher values for *Asfc* and lower values for *epLsar* and grazers falling at the opposite end of both distributions. Taxa that have been classically categorized as mixed feeders, including browser-grazer intermediates and generalists, fall in between these two extremes.

One of the primary goals of this study was to determine whether or not dental microwear texture analysis could differentiate between various levels of grazing, browsing and mixed feeding, as previously suggested by Ungar et al. (2007). In addressing this question, comparisons between obligate grazers and variable grazers; browsers and frugivores; and browser-grazer intermediates and generalists were of particular import. Beginning with the grazing taxa, some overlap was documented in the ranges of obligate and variable grazers; however, there were significant differences between the two groups for all texture attributes with the exception of $HASFC_{81}$. Bovids classified as obligate grazers have more limited ranges than variable grazers, particularly for complexity and anisotropy. This lack of variation in the microwear signature of obligate grazers is unsurprising. These bovids have diets that consist of >90% monocots and are not variable by season or region. Although monocots also make up the largest component of the diets of variable grazers, these taxa consume more dicots and/or fruit than obligate grazers. The diets of variable grazers also change as herds move from one region to another and can also be altered seasonally. The wider value ranges for texture attributes like complexity, anisotropy and fill volume is likely reflective of this seasonal and/or regional shift in food types evinced by variable grazers.

Browser-grazer intermediates and generalists had more overlap in microwear signature than any of the other groups, with no significant differences in complexity or anisotropyand only suggestive differences in scale of maximum complexity or heterogeneity. This lack of variation is not surprising given that both groups regularly consume a combination of hard and tough foods in somewhat equal parts. Browser-grazer intermediates typically consume 30-70% monocots and dicots and slightly less than 20% fruit, while generalists regularly consume >20% of all food types. Even given these dietary similarities, some differences were present. Significant differences in fill volume were found between the two groups, although some overlap was present in the ranges. This may be reflective of differences in hard fruit consumption by the taxa included in this study. Fruit makes up >20% of the diets of all three species classified as generalists, whereas it only makes up 10% or less of the diets of all six browser-grazer intermediates. Since frugivores have the highest values for fill volume recorded in this study, it is possible that higher inclusions of this food type may explain why this is the only significant difference between browser-grazer intermediate and generalist taxa.

It is interesting to note that non-fruit browsers and frugivores, often lumped together into a single dietary classification, show significant differences in microwear signature for all variables, with the exception of anisotropy. In general, the values for the frugivorous bovids were higher than those of the browsing taxa, suggesting that regular fruit consumption by bovids results in even more complex microwear surfaces with larger and deeper features than those resulting from the consumption of other dicot plant parts. Fruit, as a dietary category, includes fruits, bulbs, tubers, succulents, pods, and seeds. Many of these food types are protected by tough or hard shells that require considerable processing to open and would result in increased pitting on the enamel surface. For example, fruit is frequently protected by a tough exocarp and seeds are often surrounded by a thick, hard endocarp.

Frugivorous bovids also display lower degrees of seasonal and/or geographic variation than browsing taxa. For example, both frugivores included in this study have documented diets consisting of >75% fruit with no recorded seasonal variation (Kingdon, 1982, Perrin et al., 1992), while browsers like *Sylvicapra grimmia* and *Tragelaphus euryceros* include >75% other dicots and vary by season. The distinct differences in microwear textures recorded here between frugivorous and browsing bovids supports previous arguments by Bodmer (1990) and Gagnon and Chew (2000) that frugivory should be recognized as a distinct dietary category for bovids, as it is for primates, and that bovid diets should be considered as a grazer-frugivore continuum rather than a grazer-browser continuum.

Variation within dietary categories- In addition to considering the higher-order factor "dietary classification", variation among taxa nested within dietary categories was also explored. Some significant differences were found among species classified as obligate grazers, variables grazers, browsers and browser-grazer intermediates.

Among obligate grazing taxa, *Redunca fulvorufula*differed significantly from the other three taxa in with higher values for complexity and scale of maximum complexity, as well as lower values for anisotropy. These differences can be best explained by differences in fruit consumption. This species has been reported to include fruit as nearly 5% of its regular diet, while *Damaliscus lunatus*, *Kobus leche*, and *Redunca arundinum* consume little to no fruit (Hofmann and Stewart, 1972). This addition of hard fruit to a diet of primary grazing may be responsible for the significant increases in microwear surface complexity and feature size, as well as the decrease in feature anisotropy, when compared to the other taxa.

Significant differences were also found among variable grazers in all texture attributes. *Tragelaphus spekii*, *Gazella granti*, and *Syncerus caffer* generally group together away from the other taxa, with higher values for complexity and lower values for anisotropy. This distinction may be related to increased dicot consumption by these species. Dicots make up 20-30% of the diet of these three taxa, whereas they only account for <10% of the diet in *Damaliscus pygargus*, *Kobus ellipsiprymnus* or *Hippotragus niger* (Skinner and Smithers, 1990; Gagnon and Chew, 2000).

Browsing taxa also showed some significant differences among taxa in anisotropy, scale of maximum complexity and heterogeneity 9 x 9. *Tragelaphus euryceros* has significantly lower anisotropy values than *Litocranius walleri*, *Neotragus batesi* or *Sylvicapra grimmia*. *Tragelaphus euryceros* consumes slightly more monocots than the other three taxa and this could explain the lower values for anisotropy. Additionally, *Sylvicapra grimmia* has significantly lower values for scale of maximum complexity and heterogeneity 9 x 9 than the other three taxa. This could be reflective of the somewhat more catholic diet reported for the species. Dicots make up >83% of the diet of *Sylvicapra grimmia*, with a combination of fruits and monocots comprising the rest. This is in contrast to *Neotragus batesi* and *Tragelaphus euryceros*, the diets of which consist of only 75% monocots.

Significant differences among taxa were also recorded for browser-grazer intermediates in anisotropy and fill volume. *Raphicerus campestris* has significantly lower values for anisotropy and higher values for fill volume than the other browser-grazer intermediates. This may reflect the fact that *Raphicerus campestris* has been reported to consume higher percentages of fruits and dicots that most of the other browser-grazer intermediates. Combined, these two food types comprise >65% of the diet for *Raphicerus campestris*, while accounting for approximately 55% in *Antidorcas marsupialis*, *Raphicerus sharpei* and *Tragelaphus imberbis* and only 50% in *Taurotragus oryx* and *Aepyceros melampus* (Gagnon and Chew, 2000). Interestingly, this supports previous work by Sponheimer et al. (2003), which suggested that *Raphicerus campestris* included considerably less grass in its diets than previously thought.

The differences between taxa within dietary categories were not always as predicted but seem to have some biological relevance when considered alongside known differences in diet. All of this suggests that dental microwear texture analysis has the potential to distinguish between taxa with more subtle differences in diet and the within category differences reported here will certainly be a source of hypotheses for further testing. While this obviously requires further investigation, the possibility of being able to identify these subtle dietary distinctions in the fossil record is a tantalizing one. If further study confirms that the technique can, in fact, identify dietary differences to this level, the application of dental microwear texture analysis to the study extinct bovids could strongly enhance what we know about the niche differentiation and habitat preference of fossil taxa.

Implications for habitat reconstruction- Because many of the extant bovids included in this study utilize multiple habitat types seasonally and/or depending on geographic range, comparisons of taxa by habitat type were not practical. However, the results do have implications for the study of bovid habitat preference that can be cautiously applied to the fossil record. Obviously, the connection between diet and habitat are not exact, but grazing and browsing microwear signatures do imply the availability of grasses and woody plants respectively (Schubert et al., 2006). The obligate grazing taxa, for example, all occupy some type of grassland. *Redunca arundinum* lives in both moist lowland savanna grassland and short shrubland (Kingdon, 1982; Skinner and Smithers, 1997), *Redunca fulvorufula*occupies grassy mountain ridges (Hofmann and Stewart, 1972; Kingdon, 1997; Skinner and Smithers, 1990), *Damaliscus lunatus* is found in both open grassland and floodplain (Kingdon, 1982; Skinner and Smithers, 1997), and *Kobus leche* (Kingdon, 1982; Sayer and Van Lavieren, 1975) typically inhabits wet grassy marshland. Dedicated browsing taxa, on the other hand, occupy forest or shrubland. *Litocranius walleri* inhabits both bushland and woodland (Kingdon, 1982; Leuthold, 1978), *Sylvicapra grimmia* lives in savanna and bushland (Kingdon, 1982; Skinner and Smithers, 1990), while *Neotragus batesi* and *Tragelaphus euryceros* are both typically found in closed forest habitats. Both frugivorous species included here inhabit closed forests (Hofmann and Stewart, 1972; Ralls, 1978; Kingdon, 1982; Emmons et al., 1983).

The relationship between diet and habitat is even less exact for mixed feeding taxa that consume a variety of food types. Even so, dietary reconstruction using microwear analysis can still inform habitat preference. All of the variable grazers included in this study occupy some type of primary or peripheral grassland, with the exception of *Hippotragus niger*, which is usually associated with open woodland habitats (Kingdon, 1992). The taxa classified as browser-grazer intermediates are all found in forest or bushland habitats, except *Aepyceros melampus*, sometimes found in savannas (Skinner and Smithers, 1990; Kingdon, 1992), and *Antidorcas marsupialis*, which occupy grasslands (Hofmann and Stewart, 1972; Kingdon, 1982). The three generalist taxa occupy a combination of bushland, open woodland and closed forest habitats (Dunbar and Dunbar, 1974; Kingdon, 1982, 1992). In sum, while there is no one-to-one relationship between dental microwear and habitat, the ability to accurately classify diet, and especially to classify beyond the traditional grazer-browser-mixed feeder continuum, can help narrow down habitat preferences to a likely range of local environments.

Summary and concluding remarks- This study builds on previous work by others, and features 25 extant African bovid taxa from six known dietary categories. Analysis nesting species within dietary classifications proposed by Gagnon and Chew (2000) was employed in order to better understand differences in microwear signatures resulting from the consumption of different combinations of monocots, dicot plant parts and fruits. The results indicate that dental microwear texture analysis can successfully distinguish between bovid taxa with differing diets, including those that reflect different levels of mixed feeding. Additionally, the fact that nearly all dietary categories were significantly different from one another supports the accuracy of the dietary classification system proposed by Gagnon and Chew (2000).

The dataset described here can be used as a baseline for interpreting microwear in fossil bovids from a variety of sites and time periods across Africa. The clear separation between dietary categories indicates that this comparative database will be useful in reconstructing diet and possibly even habitat preference. Significant differences among species within dietary categories confirm the previous assertion by Ungar et al. (2007) that finer dietary distinctions between taxa may be possible with texture analysis. Continued work on extant ruminants and the inclusion of taxa with even finer distinctions in diet and habitat preference will be necessary to assess the ultimate potential resolution of dental microwear texture analysis.

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References

Archer, D., Sanson, G., 2002. Form and function of the selenodont molar in southern African ruminants in relation to their feeding habits. J. Zool. 257, 13-26.

Baker, G., Jones, L.H.P., Wardrop, I.D. 1959. Cause of wear in sheeps teeth. Nature 184:1583-1584.

Beynon, A.D. 1987. Replication technique for studying microstructure of fossil enamel. Scanning Micro 1:663-669.

Bobe, R., Eck, G.G., 2001. Responses of African bovids to Pliocene climatic change.Paleobiology27 (Suppl. to No. 2).Paleobiology Memoirs 2, 1-47.

Bodmer, R.E. 1990. Ungulate frugivores and the browser grazer continuum. Oikos 57:319-325.

Caswell, H., Reed, F., Stephenson, S.N., Werner, P.A. 1973. Photosynthetic pathways and selective herbivory: a hypothesis. Am. Nat. 107:465-480.

Conover, W.J., Iman, R.L. 1981. Rank transformations as a bridge between parametric and nonparametric statistics. Am Stat 35:124-129.

Cook, R.J., Farewell, V.T. 1996. Multiplicity considerations in the design and analysis of clinical trials.J R Stat Soc Ser A, 159:93-110.

Demment, M.W., Vansoest, P.J. 1985. A nutritional explanation for body size patterns of ruminant and nonruminant herbivores. Am Nat 125:641-672.

Dougall, H.W., Drysdale, V.M., Glover, P.E. 1964. The chemical composition of Kenya browse and pasture herbage. E. Afr. Wildl. J. 2, 86-121.

Dunbar, R.I.M., Dunbar, P. 1974. Social organization and ecology of the klipspringer (*Oreotragus oreotragus*) in Ethiopia. Zeitschrift fur Tierpsychologie 35:481-493.

Emmons, L.H., Gauthier-Hion, A., Dubost, G. 1983.Community structure of the frugivorous-folivorous forest mammals of Gabon. J. Zool. (London) 199:209-222.

Estes, R.D., 1991. Behavior Guide to African mammals. The University of California Press, Los Angeles.

Fortelius, M., Solounias, N. 2000. Functional characterization of ungulate molars using the abrasion-attrition wear gradient: a new method for reconstructing diets. Am Mus Nov 3301:1-36.

Franz-Odendaal, T.A., Kaiser, T.M., Bernor, R.L. 2003.Systematics and dietary evaluation of a fossil equid from South Africa.S. Afr. J. Sci. 99:553-559.

Gagnon, M., Chew, A.E. 2000. Dietary preferences in extant African Bovidae. J Mammal 8:490-511.

Gentry, A.W. 1970.The Bovidae (Mammalia) of the Fort Ternan fossil fauna. Leakey, L.S.B. Savage, R.J.G. (Eds.) Fossil Vertebrates of Africa. Vol. 2, pp. 243-323. Academic Press, London.

Gordon I.J., Illius A.W. 1994. The functional significance of the browser-grazer dichotomy in African ruminants. Oecologia 98:167-175.

Grine, F.E. 1986. Dental evidence for dietary differences in *Australopithecus* and *Paranthropus*. J Hum Evol 15:783-822.

Grine, F.E., Ungar, P.S., Teaford, M.F., 2002. Error rates in dental microwear quantification using scanning electron microscopy. Scanning 24, 144-153.

Grzimek, B. (Ed.) 1990. Grzimek's encyclopedia of mammals. McGraw-Hill, New York.

Harris, J.M. 1991. The Fossil Ungulates: Geology, Fossil Artiodactyls, and Paleoenvironments. Koobi Fora Research Project, vol. 3. Clarendon Press, Oxford.

Heckathorn, S.A., McNaughton, S.J., Coleman, J.S. 1999.C4 plants and herbivory. In: C4 plant biology. Sage, R.F., Monson, R.K. (Eds.). Academic Press, San Diego, 285-312.

Hofmann, R.R., 1989. Evolutionary steps of ecophysiological and diversification of ruminants: a comparative view of their digestive system. Oecologia, 78,443-457.

Hofmann, R.R., Stewart, D.R.M. 1972. Grazer or browser: a classification based on the stomach structure and feeding habits of East African ruminants. Mammalia 36:226-240.

Janis, C. 1990. The correlation between diet and dental wear in herbivorous mammals, and its relationship to the determination of diets of extinct species. Boucot, A.J. (Ed.), Evolutionary paleobiology of behavior and coevolution. Elsevier, Amsterdam, pp 241-259.

Kappelman, J. 1984. Plio-Pleistocene environments of Bed I and Lower Bed II, Olduvai Gorge, Tanzania. Palaeogeogr Palaeoclimatol Palaeoecol 48:171-196.

Kappelman, J., Plummer, T., Bishop, L., Duncan, A., Appleton, S. 1997.Bovids as indicators of Plio-Pleistocene paleoenvironments in East Africa. J Hum Evol 32:229-256.

Kay, R.N.B. 1993. Digestion in ruminants at pasture.World Conf. Anim. Prod. Edmonton, Canada, 461-474.

King T., Andrews P., Boz B. 1999. Effect of taphonomic processes on dental microwear.Am J Phys Anthrop 108:359-373.

Kingdon, J. 1982. East African mammals: an atlas of evolution in Africa. The University of Chicago Press, Chicago, Illinois.

Kingdon, J. 1997. The Kingdon field guide to African mammals. Academic Press, London, United Kingdom.

Kingston, J.D., Harrison, T. 2007. Isotopic dietary reconstructions of Pliocene herbivores at Laetoli: implications for early hominin paleoecology. Palaeogeogr.Palaeoclimatol.Palaeoecol. 243:272-306.

Krueger, K.L., Ungar, P.S. 2009. Incisor microwear textures of five bioarcheological groups. Int J Osteoarcheol 20:549-560.

Langer, P. 1988. The mammalian herbivore stomach.Comparative anatomy, function, and evolution. G. Fischer, New York.

Leuthold, W. 1978.On the ecology of the gerenuk *Litocranius walleri*. J. Animal Ecol. 47:561-580.

Lucas, P.W. 2004. Dental functional morphology: How teeth work. Cambridge University Press, New York.

McNaughton, S. J., Georgiadis, N.J., 1986. Ecology of African grazing and browsing animals. Annual Review of Ecoology and Systematics 17:39-65.

McNaughton, S.J., Tarrants, J.L., McNaughton, M.M., Davis, R.H. 1985. Silica as a defense against herbivory and a growth promotor in African grasses. Ecol 66:528-535.

Merceron, G., Ungar, P.S. 2005. Dental microwear and palaeoecology of bovids from the Early Pliocene of Langebaanweg, Western Cape province, South Africa. S. Afr. J. Sci. 101:365-370.

Merceron, G., Blondel, C., Brunet, M., Sen, S., Solounias, N., Viriot, L., Heintz, E. 2004a. The late Miocene paleoenvironments of Afghanistan as inferred from dental microwear in artiodactyls. Palaeogeo, Palaeoclimatol, Palaeoecol 207:143-163.

Merceron, G., Escarguel, G., Angibault, J-M., Verheyden-Texier, H., 2010. Can dental microwear textures record inter-individual dietary variations? Plos One 5, 9542.

Merceron, G., Viriot, L., Blondel, C. 2004b. Tooth microwear pattern in roe deer (*Capreolus capreolus* L.) from Chizé (Western France) and relation to food composition. Small Ruminant Res 53:125-132.

Merceron G., de Bonis L., Viriot L., Blondel C. 2005. Dental microwear of fossil bovids from northern Greece: paleoenvironmental conditions in the eastern Mediterranean during the Messinian. Palaeogeogr Palaeoclimatol, Palaeoecol 217:173-185.

Merceron, G., Schulz, E., Kordos, L., Kaiser, T.M. 2007. Paleoenvironment of *Dryopithecus brancoi* at Rudabànya, Hungary: evidence from dental meso- and micro-wear analyses of large vegetarian mammals. J. Hum. Evol. 53, 331-349.

Merceron, G.M., Scott, J.R., Scott, R.S., Geraads, D., Spassov, N., Ungar, P.S. 2009. Folivary or fruit/seed predation for *Mesopithecus*, an earliest colobine from the late Miocene of Eurasia? J Hum Evol 57:732-738.

Nowak, R.M. 1991. Walker's mammals of the world. 5th ed. The Johns Hopkins University Press, Baltimore, Maryland.

Pérez-Barberia, F.J., Gordon, I.J., 2001. Relationships between oral morphology and feeding style in the Ungulata: a phylogenetical controlled evaluation. Proc. Royal Soc. London. B. 268, 1021-1030.

Perrin, M.R., Bowland, A.E., Fauries, A.S. 1992. Niche segregation between the blue duiker *Philantomba monticola* and the red duiker *Cephalophus natalensis*. In: Ongules 91. Spitz, F., Janeau, G., Gonzalez, G., Aulagnier, S., (Eds.). Societe Francaise pour l'Etude et la Protection des Mammiferes, Paris, France, 201-204.

Plummer, T.W., Bishop, L.C. 1994. Hominid paleoecology at Olduvai Gorge, Tanzania as indicated by antelope remains. J Hum Evol 27:47-75.

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 Pleistocene kangaroo. PNAS 106:11646-11650.

Ralls, K. 1978. Tragelaphus eurycerus. Mammalian Species 111:1–4.

Reed, K.E. 1996. The paleoecology of Makapansgat and other African Pliocene Hominid Localities.Ph.D. Dissertation.State University of New York, Stony Brook.

Reed, K.E. 1997. Early hominid evolution and ecological change through the African Plio-Pleistocene. J Hum Evol 40:289-322.

Reed, K.E. 2008. Paleoecological patterns at the Hadar hominin site, Afar Regional State, Ethiopia. J Hum Evol 54:743-768.

Rensberger, J.M. 1973. Occlusion model for mastication and dental wear in herbivorous mammals. J. Paleontol. 47:515-528.

Rivals, F., Deniaux, B. 2003. Dental microwear analysis for investigating the diet of an argali population (*Ovis ammon antiqua*) of mid-Pleistocene age, Caune de I'Arago cave, eastern Pyrenees, France. Palaeogeogr Palaeoclimatol Palaeoecol 193:443-455.

Sanson, G.D., Kerr, S.A., Gross, K.A. 2007. Do silica phytoliths really wear mammalian teeth? J Arch Sci 34:526-531.

Sayer, J.A., Van Lavieren, L.P. 1975.The ecology of the Kafue lechwe population of Zambia before the operation of hydroelectric dams on the Kafue River. East African Wildlife Journal 13, 9-37.

Schoeninger, M.J., Reeser, H., Hallin, K. 2003. Paleoenvironment of *Australopithecus anamensis* at Allia Bay, East Turkana, Kenya: evidence from mammalian herbivore enamel stable isotopes. J. Anthrop. Archaeo. 22:200-207.

Schubert, B.W., Ungar, P.S., DeSantis, L.R.G. 2010. Carnassial microwear and dietary behaviour in large carnivorans. J Zool 280:257-263

Schubert, B.W., Ungar, P.S., Sponheimer, M., Reed, K.E. 2006. Microwear evidence for Plio-Pleistocene bovid diets from Makapansgat Limeworks Cave, South Africa. Palaeogeogr, Palaeoclimatol, Palaeoecol 241:301-319.

Schulz, E., Calandra, I., Kaiser, T.M., 2010. Applying tribology to teeth of hoofed animals.Scanning 32, 162-182.

Scott, J.R., Ungar, P.S., Jungers, W.L., Godfrey, L.R., Scott, R.S., Simons, E.L., Teaford, M.F., Walker, A. 2009. Dental microwear texture analysis of the archaeolemurids and megaladapids, two families of subfossil lemurs 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., Ungar, P.S., Bergstrom, T.S., Brown, C.A., Grine, F.E., Teaford, M.F., Walker, A. 2005. Dental microwear texture analysis reflects diets of living primates and fossil hominins. Nature 436:693-695.

Semprebon, G., Janis, C., Solounias, N. 2004. The diets of the Dromomerycidae (Mammalia : Artiodactyla) and their response to miocene vegetational change. J Vertebr Paleontol 24:427-444.

Shipley, L.A. 1999. Grazers and browsers: how digestive morphology affects diet selection. In: Launchbaugh, K.L., Sanders, K.D., Mosley, J.C. (Eds.) Grazing behavior of livestock and wildlife. Idaho Forest, Wildlife and Range Experimental Station Bulletin #70. University of Idaho, Moscow, ID, pp 20-27.

Shipman, P., Harris, J. 1988.Habitat preference and paleoecology of *Australopithecus boisei* in eastern Africa. Grine, F.E. (Ed.) Evolutionary History of the ‘‘Robust’’ Australopithecines, pp. 343-381. Aldine de Gruyter, New York.

Skinner, J.D., Smithers, R.H.N. 1990. The mammals of the southern African subregion.2nd ed. University of Pretoria, Pretoria, South Africa.

Solounias, N., Dawson-Saunders, B. 1988.Dietary adaptations and palaeoecology of the late Miocene ruminants from Pikermi and Samos in Greece. Palaeogeogr Palaeoclimatol Palaeoecol 65:149-172.

Solounias, N., Moelleken, S.M.C. 1992a. Dietary adaptations of two goat ancestors and evolutionary considerations. Geobios 25:797-809.

Solounias, N., Moelleken, S.M.C. 1992b. Tooth microwear analysis of *Eotragus sansaniensis* (Mammalia:Ruminantia), one of the oldest known bovids. J Vert Paleontol 12:113-121.

Solounias, N., Moelleken, S.M.C. 1993. Determination of dietary adaptations of extinct ruminants through premaxillary analysis. J Mammal 74, 1059-1074.

Solounias, N., Moelleken, S.M.C., 1999. The Miocene gazelle from Greece as a model for detecting Darwinian evolutionary change. Ann. Musei Goulandris 10, 291-308.

Solounias, N., Moelleken, S.M.C., Plavcan, J.M., 1995. Predicting the diet of extinct bovids using masseteric morphology. J. Vert. Paleo. 15, 795-805.

Solounias, N., Semprebon, G. 2002. Advances in the reconstruction of ungulate ecomorphology with application to early fossil equids.Am Mus Nov 1-49.

Solounias, N., Teaford, M.F.,Walker, A. 1988. Interpreting the diet of extinct ruminants: the case of a non-browsing giraffid. Paleobio 14, 287-300.

Spalinger, D.E., Robbins, C.T., Hanley, T.A. 1986. The assessment of handling time in ruminants: the effect of plant chemical and physical structure on the rate of breakdown in plant particles in the rumen of mule deer and elk. Can. J. Zool. 64:312-321.

Spencer, L.M. 1997. Dietary adaptations of Plio-Pleistocene Bovidae: implications for hominid habitat use. J Hum Evol 32:210-228.

Sponheimer, M., Lee-Thorp, J.A., DeRuiter, D.J., Smith, J.M., van der Merwe, N., Reed, K., Grant, C.C., Ayliffe, L.K., Robinson, T.F., Heidelberger, C. and Marcus, W. 2000. Diets of Southern African Bovidae: Stable Isotope Evidence. Journal of Mammalogy. 84 (2): 471-479.

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 Limeworks hominin locality. J Hum Evol 36:705-718.

Teaford, M.F. 1988. A review of dental microwear and diet in modern mammals.Scanning Microsc 2:1149-1166.

Teaford, M.F., Oyen, O.J. 1989a. Live primates and dental replication: new problems and new techniques. Am J Phys Anthrop 80:73-81.

Teaford, M.F., Oyen, O.J. 1989b. *In vivo* and *in vitro* turnover in dental microwear. Am. J. Phys. Anthrop. 80:447-460.

Teaford, M.F., Runestad, J.A. 1992. Dental microwear and diet in Venezuelan primates. Am. J. Phys. Anthrop. 88:347-364.

Ungar, P.S. 1996. Dental microwear of European Miocene catarrhines: evidence for diets and tooth use. J Hum Evol 31:335-366.

Ungar, P.S., Krueger, K.L, Blumenschine, R.J. Njao, J. Scott, R.S. in press.Dental microwear texture analysis of hominins recovered by the Olduvai Landscape Paleoanthropology Project, 1995-2007. J Hum Evol.

Ungar, P.S., Scott, J.R., Schubert, B., Stynder, D. 2010. Carnivoran dental microwear textures: comparability of carnassial facets and functional differentiation of the postcanine teeth. Mammalia 74:219-224.

Ungar, P.S., Scott, R.S. 2009. Dental evidence for diets of Early *Homo*. The First Humans: Origins of the Genus *Homo*. Grine, F.E. Leakey, R.E., Fleagle, J.G., (Eds.) Springer-Verlag, New York, pp. 121-134.

Ungar, P.S., Scott, R.S., Scott, J.R., Teaford, M.F. 2008a. Dental microwear analysis: historical perspectives and new approaches. In: Irish, J.D. (Ed.), Technique and Application in Dental Anthropology. Cambridge University Press, Cambridge, 389-425.

Ungar, P.S., Grine, F.E., Teaford, M.F. 2008b. Dental microwear indicates that *Paranthropus boisei* was not a hard-object feeder. PLoS 2044:1-6.

Ungar, P.S., Merceron, G., Scott, R.S. 2007. 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., Brown, C.A., Bergstrom, T.S., Walker, A. 2003. A quantification of dental microwear by tandem scanning confocal microscopy and scale-sensitive fractal analysis.Scanning 25:189-193.

Van Wieren, S.E. 1996. Digestive strategies in ruminants and non-ruminants.Thesis, University of Wageningen.

Vesey-Fitzgerald, D.F., 1960.Grazing succession among east African game animals. J. Mammal. 41, 161-172.

Vincent, J.F.V. 1990. Fracture properties of plants. Adv Bot Res Inc Adv Plant Pathol 17:235-287.

Vrba, E.S. 1980. The significance of bovid remains as indicators of environment and predation patterns, pp. 247-271. Behrensmeyer, A.K., Hill, A.P. (Eds.), Fossils in the making. University of Chicago Press, Chicago.

Vrba, E.S. 1985. Paleoecology of early Hominidae, with special reference to Sterkfontein, Swartkrans and Kromdraai, pp. 345-369 iii. M. Beden et al. (Eds.), L'environnement des hominides au Plio-Pleistocene. Masson, Paris.

Vrba, E.S. 1995. The fossil record of African antelopes (Mammalia, Bovidae) in relation to human evolution and paleoclimate. In: Vrba, E.S., Denton, G.H., Partridge, T.C., Burckle, L.C. (Eds.), Paleoclimate and Evolution with Emphasis on Human Origins, pp. 385-424. Yale University Press, New Haven.

Walker, A. 1984.Mechanisms of honing in the male baboon canine. Am. J. Phys. Anthrop. 65:47-60.

Walker, A., Hoeck, H.N., Perez, L., 1978. Microwear of mammalian teeth as an indicator of diet. Science 201, 908-910.

Walker, E.P. 1975. Mammals of the world. 3rd ed. The Johns Hopkins University Press, Baltimore, Maryland.

Wilson, D.E., Reeder, D.M. (Eds.) 2005. Mammal species of the world. Johns Hopkins Press, Washington, D.C.

Wing, S.L., Sues, H.D., Potts, R., DiMichele, W.A., Behrensmeyer, A.K. 1992.Evolutionary paleoecology. Behrensmeyer, A.K., Damuth, J.D., DiMichele, W.A., Potts, R., Sues, H.D., Wing, S.L. (Eds.). Terrestrial ecosystems through time: evolutionary paleoecology of terrestrial plants and animals. University of Chicago Press, Chicago.

Figure Legends

Figure 1. Occlusal view of bovid M2, illustrating the shearing facets where microwear was examined (Illustration courtesy of Gildas Merceron). A = left m^2, B= right m_2

Figure 2. Examples of dental microwear surfaces for extant bovids from different dietary categories. These images are photosimulations based on data collected using the confocal imaging profiler, and each represents an area of 276 x 204 µm. A) obligate grazer; B) variable grazer; C) browser-grazer intermediate; D) generalist; E) browser; and F) frugivore.

Figure 3. Examples of dental microwear surfaces for extant bovids from different dietary categories. These images are 3-D meshed axonometrics based on data collected using the confocal imaging profiler, and each represents an area of 138 x 102 µm. A) obligate grazer; B) variable grazer; C) browser-grazer intermediate; D) generalist; E) browser; and F) frugivore.

Figure 4. Box and whisker plots comparing extant taxa. A) mean complexity (*Asfc*); mean anisotropy (*epLsar*); C) mean scale of maximum complexity (*Smc*); mean textural fill volume (*Tfv*); mean heterogeneity 3x3 ($HAsfc_9$); mean heterogeneity 9x9 ($HAsfc_{81}$). Lines associated with each bar indicate standard error above and below the mean.

Figure 5. Bivariate plot of M_1 shear facet microwear texture anistropy and complexity. Data are plotted for individuals with species as indicated by the markers.

Tables

TABLE 1. Extant bovid taxa included in this study, along with associated diets

Taxon	Common Name	Diet
Obligate Grazers (>90% monocots, little to no seasonal or geographic variation)		
Damaliscus lunatus	Tsessebe	Savanna and floodplain grasses
Kobus leche	Lechwe	Aquatic marsh grasses
Redunca arundinum	SouthernReedbuck	Tall grass specialist
Redunca fulvorufula	Mountain Reedbuck	Seasonal grasses
Variable Grazers (60-90% monocots, varies seasonally)		
Damaliscus pygargus	Bontebok	Short Highveld grasses, some fynbos consumption
Gazella granti	Grant’s Gazelle	Short grasses, seasonal herbs and shrub foliage
Hippotragus niger	Sable Antelope	Grasses in wet season and forbs and foliage in dry season
Kobus ellipsiprymnus	Waterbuck	Medium to short grasses, reeds and some rushes
Synceos caffer	African Buffalo	Pasture grasses year-round and swamp vegetation during dry season
Tragelaphus spekii	Sitatunga	Swamp grasses, sedges, leaves and low-level vegetation
Browser-Grazer Intermediates (30-70% monocots, <20% fruit)		
Aepyceros melampus	Impala	Grazes on grasses when green, also browses on seedpods, foliage, forbs and shoots
Antidorcas marsupialis	Springbok	Shrubs and succulents in dry season, young grasses during wet season
Raphicerus campestris	Steenbok	Low herbaceous plants, seeds and pods during dry season, young grass in wet season
Raphicerus sharpei	Sharpe’s Grysbok	Mature plants, fruit pods and roots
Taurotragus oryx	Eland	Seasonal young grasses, small herbaceous plants, roots, and tubers, highly seasonal
Tragelaphus imberbis	Lesser Kudu	Succulents, buds, leaves, pods and grasses, pronounced seasonal variation
Browsers (>70% dicots)		
Litocranius walleri	Gerenuk	Pure browsers, focuses on flowers and leaves of shrubs, not known to eat grass or herbs
Neotragus batesi	Bate’s Pygmy Antelope	Ground-level herbaceous vegetation

Sylvicapra grimmia	Common Duiker	Leaves, shoots, fruit pods and seeds, tubers, insects, rarely known to consume grasses
Tragelaphus euryceros	Bongo	High-concentrate green herbage, including shrubs and creeping plants

Generalists (>20% of all three food types, highly variable by season and region)

Oreotragus oreotragus	Klipspringer	Leaves, buds, pods, bark, short grasses and some fruit
Tragelaphus angasi	Nyala	Mixed grasses and leaves
Tragelaphus strepsiceros	Greater Kudu	Herbs, leaves, vines, fruit, tubers and some grass

Frugivores (>70% fruit, rarely consumes monocots)

Cephalophus sylvicultor	Yellowback Duiker	Forbs and shrubs
Philantomba monticola	Blue Duiker	Fallen fruit, leaves, buds, seeds and mushrooms

Diet information based on Walker, 1975; Kingdon, 1982, 1997; Grzimek, 1990; Nowak, 1991. Gagnon and Chew, 2000

TABLE 2. Descriptive microwear texture statistics for extant African Bovidae

Taxon	Statistic	*n*	*Asfc*	*epLsar*	*Smc*	*Tfv*	*HAsfc9*	*HASFC81*
A. melampus	Mean	20	1.868	0.004	2.842	5878.293	0.498	0.831
	Median		1.809	0.004	0.512	5719.810	0.455	0.749
	Standard Deviation		0.482	0.002	10.071	1062.347	0.145	0.237
	Skewness		0.815	0.480	4.467	0.927	1.475	0.377
A. marsupialis	Mean	21	2.382	0.004	4.082	6038.774	0.510	0.786
	Median		2.064	0.004	0.267	5733.700	0.480	0.799
	Standard Deviation		1.138	0.001	17.085	1269.053	0.136	0.138
	Skewness		1.896	-0.271	4.581	0.424	0.725	-0.115
C. sylvicultor	Mean	25	4.617	0.003	0.253	12405.420	0.494	0.801
	Median		4.628	0.003	0.267	13081.060	0.498	0.811
	Standard Deviation		1.263	0.001	0.048	1790.455	0.052	0.052
	Skewness		0.396	-0.140	-0.788	-0.375	-0.204	-0.481
D. lunatus	Mean	22	0.952	0.007	1.474	2174.730	0.435	0.657
	Median		0.909	0.007	1.417	1912.030	0.440	0.672
	Standard Deviation		0.247	0.001	0.437	944.932	0.065	0.074
	Skewness		0.164	0.505	0.580	0.698	0.036	-0.171
D. pygargus	Mean	22	1.281	0.005	1.316	5013.254	0.381	0.608
	Median		1.265	0.005	1.330	4917.000	.0389	0.609
	Standard Deviation		0.390	0.001	0.207	1663.663	0.091	0.076
	Skewness		0.443	-0.070	-0.170	0.625	-0.469	0.334
G. granti	Mean	25	1.680	0.004	0.525	3193.148	0.358	0.676
	Median		1.816	0.004	0.532	3070.000	0.364	0.692
	Standard Deviation		0.448	0.001	0.309	1243.082	0.073	0.118
	Skewness		-0.276	0.623	0.623	0.747	0.068	-.0.102
H. niger	Mean	22	1.464	0.006	0.271	5001.706	0.525	0.735
	Median		1.530	0.006	0.267	4929.280	0.536	0.740
	Standard Deviation		0.478	0.001	0.102	1047.802	0.087	0.097
	Skewness		-.0751	-0.243	0.206	0.127	-0.123	0.045
K. ellipsypry.	Mean	23	1.299	0.006	0.803	3608.550	0.622	1.110
	Median		1.361	0.006	0.816	3473.530	0.535	0.803
	Standard Deviation		0.452	0.001	0.125	1077.223	0.267	0.768
	Skewness		0.352	-1.264	-0.182	0.007	1.365	2.709
K. leche	Mean	24	0.986	0.006	1.598	2913.420	0.379	0.790
	Median		0.954	0.006	1.558	2975.175	0.378	0.751
	Standard Deviation		0.267	0.001	0.544	980.589	0.056	0.119
	Skewness		0.823	0.353	0.452	-0.007	-0.072	0.793
L. walleri	Mean	25	3.410	0.002	0.990	11136.860	0.754	1.076
	Median		3.265	0.002	0.965	10685.150	0.699	0.994
	Standard Deviation		1.099	0.001	0.350	1874.815	0.181	0.196
	Skewness		0.473	-0.001	1.036	0.476	0.830	0.841
N. batesi	Mean	22	3.833	0.002	0.833	10254.340	0.601	0.964
	Median		4.121	0.002	0.764	9875.320	0.599	0.932
	Standard Deviation		1.099	0.001	0.283	1603.675	0.112	0.127

	Skewness		-0.255	-0.104	1.259	0.389	0.338	1.067
O. oreotragus	Mean	24	2.239	0.004	0.344	8975.312	0.435	0.791
	Median		2.223	0.003	0.313	8587.210	0.446	0.742
	Standard Deviation		0.573	0.001	0.129	1851.004	0.084	0.183
	Skewness		0.851	0.339	0.470	0.678	-0.703	1.088
P. monticola	Mean	21	4.526	0.002	0.201	14629.710	.0551	0.813
	Median		4.215	0.002	0.203	14597.540	0.570	0.836
	Standard Deviation		1.036	0.001	0.046	1881.079	0.089	0.119
	Skewness		0.400	0.198	0.177	-0.270	-0.483	0.027
R. campestris	Mean	21	2.296	0.003	0.690	8376.412	0.456	0.863
	Median		2.355	0.003	0.668	7420.810	0.488	0.874
	Standard Deviation		0.543	0.001	0.181	1617.150	0.088	0.155
	Skewness		0.138	0.023	1.056	-0.188	-0.649	-0.296
R. sharpei	Mean	25	2.350	0.004	0.527	4816.287	0.577	0.937
	Median		2.523	0.004	0.433	4862.960	0.583	0.932
	Standard Deviation		0.429	0.001	0.218	1354.920	0.100	0.150
	Skewness		-0.417	2.586	1.213	-0.186	-0.235	1.221
R. arundinum	Mean	25	0.922	0.006	1.585	3349.817	0.371	0.784
	Median		0.865	0.006	1.698	3497.230	0.367	0.794
	Standard Deviation		0.216	0.001	0.530	1001.484	0.041	0.088
	Skewness		0.666	0.137	0.092	-0.307	0.336	-0.087
R. fulvorufula	Mean	24	1.199	0.008	1.084	1717.802	.0413	0.845
	Median		1.184	0.007	1.192	1657.615	0.414	0.620
	Standard Deviation		0.241	0.001	0.236	515.621	0.094	1.155
	Skewness		-0.097	0.729	-0.164	0.670	0.487	4.851
S. grimmia	Mean	25	3.076	0.003	0.629	11690.790	0.725	0.884
	Median		3.201	0.003	0.567	11599.350	0.608	0.884
	Standard Deviation		0.774	0.001	0.242	3233.051	0.289	0.157
	Skewness		-0.128	-0.086	1.136	0.039	0.813	1.026
S. caffer	Mean	22	1.490	0.005	0.775	2847.686	0.434	0.719
	Median		1.483	0.005	0.743	2872.690	0.440	0.731
	Standard Deviation		0.454	0.001	0.259	1184.979	0.085	0.139
	Skewness		0.397	0.557	1.771	0.146	-0.106	-0.035
T. oryx	Mean	21	2.123	0.004	0.455	7101.973	0.539	0.950
	Median		2.133	0.004	0.416	6829.630	0.504	0.842
	Standard Deviation		0.453	0.001	0.289	1289.774	0.164	0.218
	Skewness		0.540	-0.048	0.845	0.260	0.841	0.501
T. angasi	Mean	22	2.091	0.004	0.296	9741.029	0.446	0.810
	Median		1.876	0.004	0.267	9882.410	0.441	0.794
	Standard Deviation		0.730	0.001	0.117	1506.152	0.089	0.153
	Skewness		0.574	0.635	0.253	-0.200	0.180	0.801
T. euryceros	Mean	22	3.779	0.002	.0816	12568.670	0.611	0.986
	Median		3.799	0.002	0.854	12740.510	0.624	0.969
	Standard Deviation		0.817	0.000	0.265	2306.309	0.110	0.183
	Skewness		-0.092	-0.937	-0.144	-0.037	0.126	0.301
T. imberbis	Mean	23	2.038	0.004	0.234	7206.095	0.481	0.884

	Median		1.960	0.004	0.267	7127.730	0.461	0.873
	Standard Deviation		0.606	0.001	0.057	2062.956	0.088	0.227
	Skewness		1.316	-0.386	-0.009	-0.151	0.195	0.232
T. spekei	Mean	22	1.897	0.005	1.046	2773.355	0.406	0.917
	Median		1.885	0.004	1.009	2545.770	0.400	0.879
	Standard Deviation		0.450	0.001	0.206	1020.237	0.061	0.131
	Skewness		0.344	-0.331	0.405	0.314	0.501	.0514
T. strepsiceros	Mean	25	2.328	0.004	0.263	8836.616	0.450	0.882
	Median		2.388	0.004	0.267	9027.370	0.465	0.866
	Standard Deviation		0.654	0.001	0.087	1914.357	0.070	0.176
	Skewness		-0.263	0.331	0.432	-0.194	0.269	0.943

TABLE 3. Nested analyses of variance

Source	SS	*df*	MS	*F*	*p*
Complexity (*Asfc* ranked data)					
Diet	11114250	5	2222850	296.488	0.00
Species (diet)	540529.7	19	28448.930	3.795	0.00
Error	4115996	549	7,497.261		
Anisotropy (*epLsar* ranked data)					
Diet	9967934	5	1993587	228.161	0.00
Species (diet)	60423.02	19	60423.02	6.915	0.00
Error	4796959	549	8737.631		
Maximum Complexity (*Smc* ranked data)					
Diet	8697416	5	1739483	249.868	0.00
Species (diet)	3253916	19	171258.8	24.600	0.00
Error	3921917	549	6961.597		
Fill Volume (*Tfv* ranked data)					
Diet	12784997	5	2556999	662.002	0.00
Species (diet)	908875.9	19	47835.57	12.385	0.00
Error	2120527	549	3862.526		
Heterogeneity 3x3 (*$HAsfc_9$* ranked data)					
Diet	5026810	5	1005362	64.357	0.00
Species (diet)	2037744	19	107249.7	6.865	0.00
Error	8573277	549	15621.63		
Heterogeneity 9x9 (*$HAsfc_{81}$* ranked data)					
Diet	3473674	5	694734.8	39.810	0.00
Species (diet)	2685031	19	141317.4	8.098	0.00
Error	9580677	549	17451.14		

TABLE 4. Pairwise comparisons test of dietary categories

Categories		*Asfc*	*epLsar*	*Smc*	*Tfv*	*HAsfc9*	*Hasfc81*
B-G Int.	**Browser**	-147.829 **	142.73 **	-136.633 **	-171.974 **	-137.736 **	-88.847 **
B-G Int.	**Frugivore**	-208.329**	114.949 **	129.234 **	-225.374 **	-40.521	43.049
B-G Int.	**Generalist**	-7.037	-32.485	84.865 **	-105.897 **	77.087 **	42.203
B-G Int.	**Obl. Grazer**	236.792 **	-245.575 **	-272.592 **	209.901 **	153.011 **	146.922 **
B-G Int.	**Var. Grazer**	124.517 **	-145.656 **	-112.54 **	142.105 **	86.074 **	107.406 **
Browser	**Frugivore**	-60.500 **	-27.781	265.867 **	-53.400 **	97.215 **	131.896 **
Browser	**Generalist**	140.792 **	-175.216 **	221.498 **	66.076 **	214.824 **	131.05 **
Browser	**Obl. Grazer**	384.621 **	-388.305 **	-135.959 **	381.874 **	290.748 **	235.769 **
Browser	**Var. Grazer**	272.346 **	-288.386 **	24.093	314.079 **	223.811 **	196.254 **
Frugivore	**Generalist**	201.292 **	-147.435 **	-44.369	119.476 **	117.608 **	-0.846
Frugivore	**Obl. Grazer**	445.121 **	-360.524 **	-401.826 **	435.274 **	193.532 **	103.873 **
Frugivore	**Var. Grazer**	332.846 **	-260.605 **	-241.774 **	367.479 **	126.595 **	64.358 *
Generalist	**Obl. Grazer**	243.829 **	-213.09 **	-357.457 **	315.798 **	75.924 **	104.719 **
Generalist	**Var. Grazer**	131.554 **	-113.171 **	-197.405 **	248.003 **	8.987	65.203 *
Obl. Grazer	**Var. Grazer**	-112.275 **	99.919 **	160.052 **	-67.795 **	-66.937 **	-39.516

* indicates significant differences using Fisher's Least Significant Difference test, ** indicates significant differences using both Tukey's Honest Significant Difference Test and Fisher's Least Significant Difference test.

TABLE 5. Median values for all microwear variables by dietary category.

	Complexity (*Asfc*)	Anisotropy (*epLsar*)	Scale of Maximum Complexity (*Smc*)	Fill Volume (*Tfv*)	Heterogeneity 3 x 3 (*HAsfc9*)	Heterogeneity 9 x 9 (*HAsfc81*)
Obligate Grazer	0.9845	0.0065	1.3425	2306.8516	0.3871	0.698
Variable Grazer	1.5015	0.0053	0.7741	3691.8629	0.4291	0.7368
Browser-Grazer Intermediate	2.0632	0.0037	0.4173	6248.3253	0.4968	0.8655
Generalist	2.2553	0.0038	0.2671	2736.0549	0.4482	0.8174
Browser	3.6115	0.0022	0.7665	10975.1446	0.6215	0.9513
Frugivore	4.3993	0.0023	0.2346	13569.5572	0.5162	0.8117

Chapter Three: Dental microwear texture analysis of fossil bovids from Hadar, Ethiopia: implications for the paleoenvironment of *Australopithecus afarensis*

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Abstract

Considerable paleoecological research has focused on the Pliocene locality of Hadar in Ethiopia, due to the long occupation by *Australopithecus afarensis*. In order to better understand the adaptations of these early hominins, it is necessary that reconstructions of the paleoenvironment be as accurate as possible. This study employs dental microwear texture analysis to reconstruct the diets of the local bovid fauna, frequently used as indicator taxa for habitat. To interpret the microwear signatures, the Hadar taxa are compared to a database including 25 extant bovid species with well-documented diet and habitat preferences. This paper also addresses the paleoenvironments of the Sidi Hakoma, Denen Dora and Kada Hadar Members, as inferred from the dietary data. Clear differences in bovid microwear textures were found between members. The Sidi Hakoma bovids are reconstructed as browsers or browser-grazer intermediates, suggesting the presence of woodland resources, and closed habitats. The Denen Dora bovids evince microwear textures ranging from obligate grazers to browser-grazer intermediates, indicating access to both browse and graze and a mosaic habitat. The Kada Hadar bovids primarily have variable or obligate grazing signatures, although a few browsing taxa are present. This suggests open habitats for grazing, although the presence of browsing taxa supports a mosaic reconstruction for this member. The results presented here are consistent with a trend toward increasing aridification over time at Hadar. The microwear signatures of the fossil bovids suggest a transition from closed habitats during accumulation of the Sidi Hakoma Member to a more open environment by the time of Kada Hadar deposition.

Keywords: *Australopithecus afarensis*, microwear, paleoenvironment, diet, Hadar, bovid

Introduction

An important goal of paleoanthropology is to understand the ecological backgrounds in which early hominins lived, and the climatic and environmental changes that likely influenced their evolution. In order to understand the relationships between hominin evolution and environmental change, it is first necessary to have the most robust possible interpretations of the habitats occupied by our early forbearers. Techniques for reconstructing these paleoenvironments include the use of floral and faunal assemblages as proxies and geochemical analysis of paleosols. However, these techniques address paleoecological questions of different temporal and geographic scales and frequently do not offer consistent results.

Considerable recent research has focused on reconstructing local habitats at the Hadar in Ethiopia, during the long occupation period of *Australopithecus afarensis*. Although a wide variety of studies, including those utilizing palynological remains (Radosevich et al., 1992; Bonnefille et al., 2004), ecomorphological and diversity analyses of faunal assemblages (Bobe and Eck, 2001; Reed, 2008) and stable isotope data (Hailemichael, 2000), have suggested a mosaic of microhabitats at Hadar throughout the temporal range of *A. afarensis*, some disagreement exists about the amount of fluctuation in habitat type, rainfall and humidity.

In this paper, I address paleoecological change at Hadar by reconstructing the diets of fossil bovids from the Sidi Hakoma, Denen Dora and Kada Hadar Members using dental microwear texture analysis. The microwear data for the fossil taxa are compared with a large database of texture signatures for extant African bovids, with results discussed in relation to other paleoecological reconstructions of the site. I also address variation in the diets of Hadar bovid taxa found in multiple members and its implications for habitat change over time. Finally, I discuss the reconstructed habitats for Hadar as compared to the *A. afarensis* localities at Laetoli and Koobi Fora.

Hadar

The Hadar hominin site in the Afar Region of Ethiopia dates to ~3.42-2.9 mya and includes the last known locality associated with *A. afarensis* (Walter et al., 1984; Walter and Aronson, 1993; Walter, 1994; Campisano and Feibel, 2007). Approximately 370 specimens of *A. afarensis* have been recovered from the site, along with more than 7500 other vertebrate specimens (Reed, 2008). The Hadar faunal assemblage is both diverse and extensive, including camels, hippos, antelopes, pigs, giraffes, rhinos, true and false saber-toothed cats, jackals, lions, hyenas, mongooses, weasels, rabbits, horses, civets, monkeys, elephants, deinotheres, and rodents.

The Afar triangle was occupied by *A. afarensis* for more than 500 ky and the remains of fossil hominins have been recovered from three of the four recognized members: Sidi Hakoma, Denen Dora and Kada Hadar. Each of the Hadar members is composed of geologic layers bound by a radioisotopically dated tephra (Taieb et al., 1976; Campisano, 2007). These members are then subdivided into smaller stratigraphic units based on the presence of marker beds. There are ten submembers that make up the Hadar Formation: Basal, Sidi Hakoma 1-4, Denen Dora 1-3, and Kada Hadar 1-2. Studies of local geology have revealed that these strata were deposited during periods of high fluvial activity of a large river system associated with the site, as well as incursions of a reoccurring paleolake (Aronson and Taieb, 1981).

The Basal Member has been reliably dated to 3.8-3.42 mya and has not produced hominin remains, although they have been recovered from the formation and the same time period at the nearby site of Dikika, Ethiopia (Alemseged et al., 2005). The composition of faunal remains from this member has suggested a mosaic habitat composed of woodland and shrubland. The bovid assemblages contain congeners of modern taxa adapted to both open and closed environments. This includes abundances of alcelaphins, typically adapted to open grassland today; tragelaphins, which inhabit a variety of partially or totally closed environments; and aepycerotins, which occupy woodlands (Skinner and Smithers, 1990). Palynological studies have inferred a closed forest habitat, although it is possible that floral sampling was limited to a forested area of a more complex environment. Regardless, most reconstructions agree that the local habitat was more closed during the formation of the Basal Member than is evidenced later at the site (Bonnefille et al., 2004).

The Sidi Hakoma Member was deposited between ~3.42-3.26 mya (Campisano, 2007). Previous studies suggest some subtle differences in the paleoenvironments between the four submembers. The rarity of grazing bovid taxa suggests a more closed habitat and the reconstructed locomotor and dietary adaptations of the local mammalian fauna suggest that there was higher annual rainfall and less seasonality during the deposition of the lower Sidi Hakoma submembers than any other time at the site (Reed, 2008). A study of the local mollusks by Hailemichael (2000) supports this reconstruction, with carbon and oxygen isotope analyses consistent with a three month annual dry season during this time. The upper Sidi Hakoma Member has been reconstructed as more mosaic, including scrub woodlands and floodplain grasslands. The local faunal assemblages include both grazing and browsing bovids, as well as wetland taxa like reduncins and hippotamids (Reed, 2008). Additionally, the pollen record from these upper members suggests slightly drier conditions than those recorded for SH-1 and SH-2 and is consistent with closed to open woodland and wet grassland (Bonnefille et al., 2004).

Overall, both the palynological data and the faunal record from throughout the member have suggested a shift from wetter, more closed conditions to slightly drier, more open ones (Hailemichael, 2000; Bonnefille et al., 2004; Reed, 2008).

The Denen Dora Member of the Hadar Formation dates between ~3.26-3.2 mya and is composed of three submembers. In general, composition of the faunal assemblages within Denen Dora suggests that Hadar became drier and more seasonal over this comparatively brief interval (Reed, 2008). The oldest fauna in the Denen Dora Member, including reduncin, aepycerotin and tragelaphin bovids, are associated with highly mosaic habitats, including gallery forest, bushland and woodland. Evidence suggests that there was a lake incursion during the DD-2 phase and the faunal assemblages reflect an increase in the abundance of wetland adapted taxa. Finally, a slight faunal shift is evident in the more recent layers of the Denen Dora Member, with open woodland and wooded grassland adapted taxa like Alcelaphini becoming more common (Reed, 2008). Analysis of fossil pollen has revealed a corresponding increase in C3 grasses and a decrease in annual precipitation (Bonnefille et al., 2004). All of this suggests that Hadar was mosaic and fluctuating during the formation of the Denen Dora Member.

The Kada Hadar Member dates from ~3.2 mya-2.94 mya and contains the last known occurrences of *A. afarensis*. The member is divided into two submembers, both of which have been generally reconstructed as drier and more open than the earlier deposits at Hadar. Fauna from the hominin-bearing strata share adaptations for habitats ranging from open woodlands to savanna grasslands (Reed, 2008). For example, the predominant bovid genera found in the deposit are Antilopini and Alcelaphini, both associated with dry, open environments (Vrba, 1980; Kingdon, 1982a,b). In contrast, however, studies of fossil pollen from the Kada Hadar Formation have suggested a shift back to a wetter woodland habitat (Bonnefille et al., 2004).

Reed (2008) suggested that this discrepancy might be indicative of multiple closed physiognomies within the geologic member.

Previous paleoecological reconstructions at Hadar

Paleoenvironmental reconstructions based on associated fauna, sedimentology and paleosols at Hadar have generally indicated a temporary mosaic of habitats that fluctuated between open and closed and woodland and grassland (Johanson et al., 1982; Radosevich et al., 1992). The presence of these different habitat types can indicate the presence of subterranean water, changes in soil type, or even incursions from river systems or lakes (Puhakka et al., 1992; Dodds, 1997). All of these factors, related to the source of water and the amount available, can alter vegetation patterns at a site dramatically and account for modern sites where disparate habitat types are found in the immediate vicinity of one another (Archibold, 1995; O'Brien, 1998, 2006; Andrews, 2006; Reed, 2008).

The examination of the faunal assemblages from each individual member provides a unique opportunity to assess paleoecological change during the occupation of *A. afarensis*. However, reconstructions of mammalian paleoecology have traditionally relied upon taxonomic uniformitarianism, a principle based on the assumption that fossil taxa shared the same ecological preferences as their closest living relatives. In most cases, this is probably accurate; however, Sponheimer et al. (1999) have suggested that the principle deserves further scrutiny. In their study on dietary reconstruction of the Makapansgat bovids using stable isotopes and ecomorphology, these authors concluded that two of the seven fossil bovid taxa had isotopic signatures consistent with different diets than those suggested using only phylogenetic similarities. Thus, while taxonomic uniformitarianism may be generally reliable, it must be independently verified in some reliable way in order to have confidence in the assumed relationships.

In addition to comparisons within the site, studies of the Hadar fauna in relation to other Pliocene localities have also been useful for understanding the local paleoenvironment. Reed (2008) used the absence and presence of specific mammalian taxa to characterize the local community ecology at Hadar and compared the results to reconstructions of other known *A. afarensis* localities, including Maka and Laetoli. Adaptations of fossil taxa were assumed based on taxonomic uniformitarianism and/or previous dietary reconstructions using stable isotope analysis. In general, these data suggest that the environment at Hadar was highly mosaic and included intermediate cover habitats like scrubland, bushland, and open woodland, with occasional incursions of wetlands or edaphic grasslands over time (See Table 1 for a description of the habitat categories referenced in this study). Bobe and Eck (2001) also suggested a mosaic habitat at the site. They compared the abundance of bovid remains from Hadar and compared them to those recovered from the Shungura Formation in the lower Omo Valley, Ethiopia, where a distinct shift toward more open, arid habitats has been recorded. The study concluded that there is no evidence for a faunal shift towards open grassland habitats at Hadar. Instead, the assemblage of bovid taxa suggests that the overall habitat at the site was composed primarily of open grassland and woodland.

Hadar, like the other early hominin habitats in eastern Africa, has a paleoenvironmental signature that is not completely understood. Different analyses have returned results ranging from primary wetlands to a mosaic habitat of open savanna and closed woodland forest. Improving the paleoecological assumptions made about the fauna recovered from the site is an important step in achieving an accurate understanding of the Pliocene environment at Hadar and determining how it might have shaped the evolutionary adaptations of *A. afarensis*.

Bovid diets and paleodiets

African bovids have long been used as paleoenvironmental indicator species because modern taxa can be grouped into categories based on specific diet and habitat preferences. Even though the literature on bovid ecology is extensive, it is also often contradictory, resulting in considerable debate about how to best classify bovids by diet. One early attempt to improve classification of bovids was based on consumption of roughage versus herbage. This system, described by Hofmann and Stewart (1972), divided taxa into three dietary categories: grazers, browsers and intermediate feeders. Taxa in the latter category were then subdivided based on the relative percentages of food types included in the diet. Bodmer (1990) argued that fruit is a staple dietary component for many bovid species and proposed a new continuum ranging from grazer to frugivore, with browsing as an intermediate category. In an effort to address the lack of consensus on the dietary classifications of bovids, Gagnon and Chew (2000) offered a system based on a synthesis of field research on 78 African bovid diets. Their six dietary classifications were based on the observed percentages of monocotyledons and dicotyledons included in the diet, with fruit considered separately from other dicots. The Gagnon and Chew system also takes into account the effect of seasonality and geographic changes on diet.

In this study, I employ the system of Gagnon and Chew (2000) because it not only distinguishes grazing and browsing, but also fruit from leaf browse, and recognizes various levels of mixed feeding. These categories have been determined by the percentages of fruits versus non-fruit vegetation, and dicotyledons versus monocotyledons included in the diet, as recorded during observations in the wild. While the inclusions of these various levels of mixed feeding cannot help but improve the resolution of dietary and habitat reconstructions of fossil taxa, extensive ecological observations and fecal analyses have not been conducted for many mixed-feeding taxa (Gagnon and Chew, 2000, Fortelius and Solounias, 2002). Therefore, further field work will eventually be required if we are to fully understand the influence of seasonal and geographic variation on the diets of these bovids.

Gagnon and Chew (2000) distinguish obligate grazers, variable grazers, browser-grazer intermediates, browsers, generalists and frugivores. Obligate grazing taxa have a diet made up of more than 90% monocotyledons, with no seasonal or geographic variation. Taxa classified as variable grazers consume 60-90% monocotyledons, but may vary in diet seasonally and geographically. Browser-grazer intermediates have diets consisting of 30-70% monocotyledons and dicotyledons, always including some fruit, although never more than 20%. Browsing bovids consume more than 70% dicotyledons. Fruit accounts for at least 70% of the diet of frugivorous bovids and these taxa rarely, if ever, consume monocotyledons. Finally, generalist taxa classified are highly variable by both locality and season, but they consistently consume more than 20% of each of the three food types.

Implications of diet for habitat reconstruction

The selection and consumption of food is the most direct way that an organism interacts with its environment; therefore the reconstruction of diet holds the potential to tell us much about that animals preferred habitat. However, many extant bovids utilize multiple habitat types seasonally and/or depending on geographic range, so it is not reasonable to expect a one-to-one correspondence between diet and habitat. However, dietary reconstruction does have implications for bovid habitat preference that can be cautiously applied to the fossil record. Even though the correlation between diet and habitat is not exact, grazing and browsing microwear signatures do have implications for availability of grasses and woody plants respectively (Schubert et al., 2006). For example, all obligate grazing taxa occupy some type of grassland, although this category includes dry and moist savanna, floodplain grassland and marshland. Dedicated browsing taxa, on the other hand, always live in or near forest or shrubland, which can also include open and closed woodland, bushland and closed forest. Dedicated frugivorous species either inhabit or have ready access to closed forests or open woodlands (Hofmann and Stewart, 1972; Kingdon, 1982a,b; Skinner and Smithers, 1990).

The relationship between diet and habitat is less exact for taxa that consume a variety of food types. Even so, dietary reconstruction of these "mixed feeders" can still inform habitat preference. Variable grazers are typically found in some type of grassland, although a few inhabit open woodland (Kingdon, 1997). Browser-grazer intermediate taxa all occupy forest or bushland habitats for at least part of the year, although some range into savannas and grasslands during dry seasons. Generalist taxa are unsurprisingly the most difficult to classify, occupying a wide range of environments, including grassland, bushland, open woodland and closed forest habitats (Hofmann and Stewart, 1992; Dunbar and Dunbar, 1974; Kingdon, 1982a,b, 1997; Skinner and Smithers, 1990). In sum, while there is no exact correlation between diet and habitat, the ability to accurately classify diet beyond the traditional grazer-browser-mixed feeder continuum can help us narrow down habitat preferences to a likely range of local environments.

Dental microwear analysis

Conventional methods of studying dental microwear include scanning electron microscopy and light microscopy, both subject to observer measurement error and a lack of three-dimensional surface characterizations. Dental microwear texture analysis was developed to address these issues and provide an objective and replicable method for characterizing surfaces. The technique combines white-light confocal profilometry and scale-sensitive fractal analysis, allowing for quantitative descriptions of microwear surfaces over a range of scales. White-light confocal profilometry is also faster, less expensive and easier to use than scanning electron microscopy; and the automated analysis is less time consuming and requires less effort for quantification than identification and measurement of individual features. Most importantly, the automated nature of texture analysis reduces the amount of observer error in measurement, which allows direct comparisons between studies, as well as the establishment of a large database that researchers can access for interpretation of their results. Dental microwear texture analysis has previously been used to successfully identify dietary differences between species of extant and fossil taxa including humans and non-human primates, marsupials, carnivores, and bovids (R. Scott et al., 2005, 2006; Ungar et al., 2008a, 2008b, 2010, in press; Krueger and Ungar, 2009; Merceron et al., 2009; Prideaux et al., 2009; J. Scott et al., 2009; Ungar and Scott, 2009; Schubert et al., 2010).

Materials and Methods

Specimens

This study includes 121 fossil bovid specimens from the Sidi Hakoma, Denen Dora and Kada Hadar geologic members of the Hadar Formation (summarized in Table 2). The fossil bovids represent 12 taxonomic tribes, often the most specific identification available for bovid specimens not accompanied by distinctive horn cores. Taxa identifiable to the level of genus were considered both inclusive and exclusive of other members of the tribe. Molds of upper and lower first and second molars were collected at the Ethiopian National Museum (NME) in June 2010. Microwear analysis of these different tooth types has been shown to yield similar results (Merceron et al., 2004a, b). All available bovid specimens from the Hadar Formation were examined and the vast majority had to be excluded due to postmortem damage, following the criteria of Teaford (1988) and King et al. (1999). Unworn teeth and those with extreme wear were also excluded from the study. Ideally, comparisons would have been made among the individual Hadar submembers rather than the members themselves. Unfortunately, the sample sizes were not consistently large enough when divided out by submember, so the analysis presented here contrasts the Sidi Hakoma, Denen Dora and Kada Hadar bovids exclusive of submember.

In order to interpret the microwear signatures of the fossil taxa, the study also includes a comparative sample of 575 specimens, representing 25 extant African bovid species (Scott, in press). These extant specimens are housed at the American Museum of Natural History (AMNH), New York; the Field Museum (FMNH), Chicago; the Smithsonian National Museum of Natural History (NMNH), Washington D.C.; and the Royal Museum of Central Africa (RMCA), Tervuren, Belgium. All extant specimens were wild-shot and have known provenience data. The extant taxa were selected because they vary widely in ecological adaptations, ranging from open-country-adapted obligate grazers to closed-habitat browsers to dedicated frugivores. The included species have well-documented diet and habitat preferences, and special emphasis was placed on including taxa that engage in various levels of mixed feeding, including variable grazers, browser-grazer intermediates and generalists. Table 3 lists the included extant taxa and summarizes their dietary preferences.

High-resolution casts were prepared following conventional procedures for microwear analysis, a process described in detail elsewhere (Rose, 1983; Grine, 1986, Ungar, 1996). The original specimens were cleaned with acetone or alcohol soaked cotton swabs and then molded using a polyvinylsiloxane dental impression material (Presidents Jet Regular Body, Coltene-Whaledent Corp.). The casts were then made using a high-resolution epoxy polymer (Epotek, Epoxy technologies Inc.) This process has been previously demonstrated to produce replicas that precisely reproduce microwear features with a resolution to a fraction of a micron (Beynon, 1987; Teaford and Oyen, 1989).

Data Collection

A Sensofar PLμ white-light confocal profiler (Solarius Development Inc., Sunnyvale, CA) was used to collect the microwear texture data. This instrument allows for the collection of data points which form a 3-dimensional point cloud reproducing the surface of the tooth. These point clouds can be used to create photo simulations and digital elevation models of the wear surface. As in previous studies of bovid dental microwear, texture data were collected on the disto-buccal enamel band of the mesial cuspid of M_2 and the mesio-buccal enamel band of the mesial cusp of M^2 (Janis, 1990; Merceron, 2005; Schubert, 2006; Ungar et al., 2007), as illustrated in Figure 1.

The occlusal surface of each specimen was scanned with 100x objective, resulting in a point cloud with a lateral sampling interval of 0.18 µm, a vertical resolution of 0.005 µm, and a field of view of 102 x 138 µm. Texture data were collected for four adjoining fields of view for a total work envelope of 204 x 276. Solarmap Universal software (Solarius Development Inc., Sunnyvale, CA) was then used to level each scan. Surface defects, including dust and other adherents, were removed from the scan using the erase or thresholding function in Solarmap.

The resulting point clouds were analyzed using Toothfrax and Sfrax scale-sensitive fractal analysis software (Surfract Corporation). Scale-sensitive fractal analysis is based on the principle that surfaces may appear different when viewed from different scales. Thus, a surface that appears smooth at a coarse scale may seem rough when viewed at a finer scale. Previous studies employing texture analysis have identified several variables as particularly informative for dietary reconstruction (Ungar et al., 2003; Scott et al., 2005, 2006). I present data for five of these variables here. They are area-scale fractal complexity, length-scale anisotropy of relief, scale of maximum complexity, textural fill volume and heterogeneity of area-scale fractal complexity. These variables will be summarized briefly here, as they have been described extensively elsewhere (Ungar et al., 2003, 2007, 2008; Scott et al., 2005, 2006).

Area-scale fractal complexity (*Asfc*) is a measure of change in surface roughness across a range of scales. This variableis calculated by taking the slope of the steepest part of a curve fit to a plot of relative area over the range of scales at which the measurements are taken. Specimens with steeper slopes will have correspondingly higher values for *Asfc*, indicating a more complex surface. For example, surfaces dominated by overlying features of various sizes will result in high values for *Asfc*.

The scale of maximum complexity (*Smc*) refers to the fine scale limit of the *Asfc* line (Scott et al., 2005, 2006). This variable is calculated as the fine-scale limit of the steepest part of the curve described for the *Asfc* measure. It has been suggested that *Smc* corresponds with the size of wear-causing particles. Surfaces with less wear at finer scales will have the highest values for *Smc* and those with more wear at fine scales will have the lowest values.

The length-scale anisotropy of relief variable (*epLsar*)measures the orientation concentration of surface roughness. *EpLsar* is calculated by taking profiles of the wear surface at different orientations at a given scale. The sampling interval employed for this study was 5°and a scale of 1.8 μm. Anisotropic surfaces have relative profile lengths that differ with orientation and these relative lengths at given orientations are defined as vectors and normalized, resulting in a rosette diagram. Mean values for the mean vector lengths are then calculated for *epLsar*. Microwear surfaces characterized by parallel scratches will have higher values for *epLsar* than those dominated by pits or scratches with different orientations.

Textural fill volume (*Tfv*)describes the volume of cuboids of various sizes that can digitally fill the microwear surface. The *Tfv* variableis the difference in summed volume for 2 μm cuboids and 10 μm cuboids, which removes the impact of facet curvature and allows for the characterization of the microwear features themselves. Microwear surfaces that have high values for this variable are typically those characterized by moderate size features.

While all the variables help to describe the overall texture of the microwear surface, surfaces themselves vary in their textures. The heterogeneity (*HAsfc*)variables can help quantify the extent of this variation and may be important in accurately characterizing the surface. This variable is calculated through the use of the Auto-Split function in Toothfrax and measures the difference in *Asfc* across a surface. The scanned area of the facet is divided into successively smaller sub-regions with equal numbers of rows and columns, beginning with 2 x 2 and ending with 11 x 11. The value for *HAsfc* is defined as the median absolute deviation of *Asfc* divided by the median of *Asfc*.

Statistical Analysis

Following scale-sensitive fractal analysis, median values were calculated for each of the four scans collected for each specimen (Scott et al., 2006). Resulting data were rank transformed prior to statistical analysis because unranked microwear texture data typically violate assumptions inherent in parametric statistical tests (Conover and Iman, 1981). I employed a nested analysis of variance model in this study, with taxon as the subordinate level of classification, nested within Hadar Member- Denen Dora, Sidi Hakoma and Kada Hadar. The data were then analyzed using a general linear model to determine whether there were overall differences in microwear among the taxa within the members, as well as among the members themselves. Analyses of variance for individual texture attributes and pairwise comparisons tests were then used to determine the sources of significant variation both among taxa within members and among the individual members. Both Tukey's Honestly Significant Difference and Fisher's Least Significant Difference tests were used to balance the risks of Type I and Type II errors (Cook and Farewell, 1996).

Results

Examples of the microwear textures of the extant and fossil taxa are pictured in Figures 2 and 3. Median values for each texture variable by taxon are presented in Table 3. Descriptive and analytical statistics are presented in Tables 4, 5 and 6, as well as Figures 4, 5 and 6. To summarize, there are significant differences among the taxa, among the members, and among some of the taxa within each of the members. There is also significant variation between members for some individual taxa found in more than one member.

The general linear estimate model revealed significant differences among the three Hadar members in all texture variables except *Smc*. When considered as a group, the bovid taxa within the Sidi Hakoma Member have significantly higher values for *Asfc*, *Tfv* and $HAsfc_9$,and the lowest recorded values for *epLsar*. The Denen Dora bovids have the lowest values for *Tfv*, and intermediate values for *Asfc*, *epLsar and* $HAsfc_9$. The bovids associated with the Kada Hadar Member have significantly lower values for *Asfc* and $HAsfc_9$, intermediate values for *Tfv*, and the highest recorded values for *epLsar*.

Results by member

Sidi Hakoma Member- Significant variation was found among the eight bovid taxa from the Sidi Hakoma Member for all texture variables, with the exception of $HAsfc_{81}$.

Asfc- Alcelaphini, *Gazella* sp. and *Kobus* sp.cluster together and have significantly lower values for this variable than the other Sidi Hakoma taxa. *Tragelaphus kyaloae* and *Ugandax coryndonae* have similar *Asfc* values and are only significantly different from *Aepyceros* sp., Antilopini and Neotragini using a Fisher's LSD test.

epLsar-*Gazella* sp. has significantly higher values for this variable than any other taxon, while *Aepyceros* sp., *Kobus* sp. and Neotragini have the lowest values. *Tragelaphus kyaloae*, Alcelaphini and Antilopini all group together with intermediate values and are significantly different from the other taxa.

Smc- *Aepyceros* sp., Alcelaphini and *Ugandax coryndonae* have significantly lower values for this variable than the other taxa, while *Kobus* has the highest recorded value. Antilopini, *Gazella* sp., Neotragini and *Tragelaphus kyaloae* all cluster together with intermediate values.

Tfv- *Kobus* sp. has significantly lower *Tfv* values than any other taxon, while *Aepyceros* sp.,Antilopini, Neotragini and *Tragelphus* sp.have the highest values. Alcelaphini, *Gazella* sp. and *Ugandax coryndonae* all have intermediate values for this variable.

$HAsfc_{9}$- The Sidi Hakoma bovids vary significantly in the $HAsfc_{9}$ variable, though this can primarily be explained by a few taxa with extreme values. There are not significant differences between most of the individual taxa, with the exception of *Kobus* sp., which has the lowest recorded values for this variable and differs significantly from all other taxa. The other notable taxa are Antilopini and Neotragini, both of which differ significantly from *Gazella* sp.

$HAsfc_{81}$- Although there is no significant variation in the overall model for this variable, significant differences in $HAsfc_{81}$ are present between some of the individual taxa. *Gazella* sp. has the lowest recorded values for this variable and is significantly different than those of Neotragini and Antilopini, the taxa with the highest values for $HAsfc_{81}$.

<u>Denen Dora Member</u>- Significant variation was found among the ten bovid taxa from Denen Dora for all variables.

Asfc- *Aepyceros* sp., Alcelaphini, Hippotragini, *Tragelaphus kyaloae* and *Ugandax coryndonae* group together with intermediate values for this variable, with Antilopini and *Gazella* sp. having significantly higher complexity values and Reduncini, *Pelorovis* sp. and *Kobus* sp. having significantly lower values than the other taxa.

epLsar-*Aepyceros* sp., Antilopini, Alcelaphini and *Kobus* sp. have significantly lower values for this variable than the other taxa, with Antilopini having the lowest recorded values. *Gazella* sp., *Tragelaphus kyaloae* and *Ugandax coryndonae* all cluster together with intermediate values and Hippotragini, *Pelorovis* sp. and Reduncini have the highest values.

Smc- *Aepyceros* sp., Alcelaphini, Antilopini, *Gazella* sp., Hippotragini and *Ugandax coryndonae* cluster together with significantly lower values than *Kobus* sp., *Pelorovis* sp., Reduncini and *Tragelaphus kyaloae*

Tfv- Antilopini has the highest values for this variable, while *Pelorovis* sp. and Reduncini have significantly lower values for this variable than any of the other taxa. *Aepyceros* sp., Alcelaphini, *Gazella* sp., *Tragelaphus kyaloae* and *Ugandax coryndonae* have intermediate values similar to one another, while Hippotragini and *Kobus* sp. cluster together with slightly, but still significantly, lower values.

$HAsfc_9$- The Denen Dora bovids vary significantly in the $HAsfc_9$ variable, however, this difference is primarily accounted for by the significant difference between the values for Antilopini and *Gazella* sp. The taxa with the lowest recorded values for this variable are *Gazella* sp., *Aepyceros* sp., Hippotraginiand *Kobus* sp., while the taxa with the highest values are Antilopini, *Pelorovis* sp. and *Ugandax coryndonae*

$HAsfc_{81}$- *Tragelaphus kyaloae* and *Aepyceros* sp. have similar $HAsfc_{81}$ values that are significantly lower than those of the other taxa, while Alcelaphini and Antilopini cluster together with values that are significantly higher than those of any other bovid taxa.

<u>Kada Hadar Member</u>- Significant variation was reported among the ten bovid taxa from the Kada Hadar Member for all variables.

Asfc- Antilopini, *Gazella* sp. and Neotragini are similar to one another and have significantly higher values for surface complexity than the other seven taxa. Hippotragini, *Kobus* sp., *Oryx* sp. and *Pelorovis* sp.group together with significantly lower values than *Aepyceros* sp. and Alcelaphini using a Fisher's LSD test.

epLsar-Aepyceros sp., Antilopini, *Kobus* sp. and Neotraginihave significantly lower values than the other taxa, with *Kobus* sp. andNeotragini having the lowest recorded values for this variable. Alcelaphini, Bovini, *Oryx* sp. and *Pelorovis* sp. are not significantly different from one another and cluster together with significantly higher values for this variable than the other Kada Hadar taxa. *Gazella* sp. and Hippotragini have intermediate values for *epLsar* that are significantly different from *Kobus* sp., Neotragini, *Oryx* sp. and *Pelorovis* sp.

Smc- *Aepyceros* sp., Alcelaphini and Hippotragini cluster together with significantly lower values for this variable than any other taxa. Bovini, *Kobus* sp. and *Oryx* sp. have the highest recorded values, while Antilopini, *Gazella* sp., Neotragini and *Pelorovis* sp. have intermediate values.

Tfv- This variable divided the Kada Hadar bovids into two groups, with *Aepyceros* sp., Antilopini and Neotragini having significantly higher values for this variable than the other taxa. *Kobus* sp. and *Oryx* sp. have the lowest values for *Tfv*, while Antilopini and Neotragini have the highest.

$HAsfc_9$- Antilopini, Neotragini and *Oryx* sp. have the highest recorded values for this variable and are significantly different from the remaining seven taxa. There are no significant differences in the $HAsfc_9$ variable among *Aepyceros* sp., Alcelaphini, Bovini, *Gazella* sp., Hippotragini, *Kobus* sp. and *Pelorovis* sp.

$HAsfc_{81}$- Antilopini, Hippotragini, Neotragini and *Oryx* sp. group together and have the highest recorded values for this variable. This group is significantly different from all six other taxa in this member. *Gazella* sp. has an intermediate value for this variable and is significantly different from *Kobus* sp., Neotragini, Bovini, *Oryx* sp., *Pelorovis* sp. and Antilopini *Aepyceros* sp., Alcelaphini, Bovini, *Kobus* sp. and *Pelorovis* sp. are not significantly different from one another and have $HAsfc_{81}$ values that are significantly lower than those of the other Kada Hadar bovids.

Results for taxa in multiple members

Aepyceros sp.- This taxon was found in all three Hadar members used in this study, as well as the earlier Basal Member, and showed significant variation among members in all of the texture variables, with the exception of $HAsfc_{81}$. The specimens from the Denen Dora and Kada Hadar members are similar in *Asfc*, *epLsar* and *Tfv*, while the Sidi Hakoma specimens are significantly different from the other two, with higher values for *Asfc*, *Tfv* and $HAsfc_{9}$, and lower values for *epLsar*. The Kada Hadar and Sidi Hakoma specimens are not significantly different from one another in *Smc*, but both have significantly lower values than the specimens from Denen Dora.

Alcelaphini- This taxon has been recovered from all three hominin-bearing members at Hadar, as well as the Basal Member, and there are significant differences among the members for all of the texture variables. The specimens from Kada Hadar have significantly lower values for *Asfc*, *Smc*, *Tfv*, $HAsfc_{9}$ and $HAsfc_{81}$and higher values for *epLsar* than those from Sidi Hakoma and Denen Dora. The specimens from Denen Dora have the highest values for *Smc* and $HAsfc_{81}$.

Antilopini- This taxon is reported for all four Hadar members. There were no significant differences among the Sidi Hakoma, Denen Dora and Kada Hadar specimens reported for any of the texture variables.

Gazella sp.- This taxon has been identified from the Sidi Hakoma, Denen Dora and Kada Hadar members. The only significant difference among *Gazella* specimens from these three members is in the $HAsfc_9$ variable. The specimens with the highest values for heterogeneity are those from the Sidi Hakoma Member, while those with the lowest values were recovered from the Denen Dora Member.

Hippotragini- This taxon is found in the all of the Hadar members included in this study; however only specimens from the Denen Dora and Kada Hadar members were suitable for microwear analysis. There are no significant differences between these members for any of the texture variables according to Tukey's HSD tests, although some suggestive differences were present according to Fisher's LSD test results. The Hippotragini specimens from the Kada Hadar Member have lower values for *epLsar* than those from Denen Dora, but again, this only significant when using a Fisher's LSD test.

Kobus sp.- This taxon has been recovered in the Sidi Hakoma, Denen Dora and Kada Hadar members. There were no significant differences among the members for any of the texture variables, although suggestive differences are present when analyzed with a Fisher's LSD test. This test suggests that the *Kobus* sp. specimens from Kada Hadar had lower values for *Tfv* than those from the Sidi Hakoma and Denen Dora members. Additionally, the $HAsfc_9$ values for *Kobus* sp.specimens from Sidi Hakoma were significantly lower than those of the Sidi Hakoma and Denen Dora specimens.

Neotragini- This taxon has been found in small quantities in the Sidi Hakoma, Denen Dora and Kada Hadar members. Only specimens from the Sidi Hakoma and Kada Hadar members were suitable for microwear analysis though there are suggestive differences between the members according to Fisher's LSD test. The *Asfc* values for the specimens from the Sidi Hakoma Member have marginally higher complexity values than those from Kada Hadar.

Pelorovis sp.- This taxon has been recovered from the Denen Dora and Kadar Hadar members. Significant differences are only present for the $HAsfc_9$variable. The specimens from Denen Dora have higher values for this variable than those from Kada Hadar.

Tragelaphus kyaloae- This taxon has been recovered from all of the geologic members at Hadar, however only specimens from Sidi Hakoma and Denen Dora preserve unobscured microwear. Significant differences between specimens from these two members were identified in *Asfc*, *epLsar*, *Smc* and $HAsfc_{81}$. The Sidi Hakoma specimens have significantly higher values for *Asfc* and $HAsfc_{81}$ and significantly lower values for *epLsar* and *Smc* than those from Denen Dora. A Fisher's LSD test also suggests significant differences in $HAsfc_9$ between the Sidi Hakoma and Denen Dora specimens, with individuals from Sidi Hakoma having higher values for this variable.

Ugandax coryndonae- This taxon has been recovered from all of the hominin-bearing members at Hadar, although this study only included specimens from the Sidi Hakoma and Denen Dora members. There are significant differences between the members reported for *Asfc*, *epLsar* and *Tfv*. The Sidi Hakoma specimens have significantly higher values for *Asfc* and *Tfv* and lower values for *epLsar* than those from Denen Dora.

Discussion

The results presented here have important implications for the ability of dental microwear texture analysis to reconstruct the diets of fossil bovid taxa, and by extension, local paleoenvironments.

Extant Taxa

The extant database used in this study has previously been used to demonstrate the presence of significant differences among the six dietary classifications identified by Gagnon and Chew (Scott, in review). Overall, grazing taxa had less complex, more anisotropic surfaces with smaller features than browsing taxa. In addition to clearly differentiating between obligate grazers and browsers, the data strongly indicate that dental microwear texture analysis can distinguish beyond the classic bovid dietary trichotomy and accurately separate variable grazers, generalists, browser-grazers intermediates and frugivores from obligate grazers and browsers, as well as from one another (Figure 4). Some differences among taxa within dietary categories were also identified, likely reflecting seasonal and/or geographic differences in diet.

Dietary reconstruction of the Hadar bovids by tribe

Overall, the Hadar bovids evince a range of microwear texture patterns comparable to the comparative extant taxa, suggesting similar levels of dietary variation in the taxa.

<u>Aepycerotini</u>- *Aepyceros* is the only genus within the tribe Aepycerotini and includes two extant subspecies: the common impala, *Aepyceros melampus melampus* and the black-faced impala, *Aepyceros melampus petersi*. Both of these modern taxa are classified as browser-grazer

intermediates, consuming equal proportions of monocots and dicots and including fruit as approximately 10% of their regular diet (Kingdon, 1997; Gagnon and Chew, 2000). Aepycerotine bovids typically inhabit a combination of thick bushveld and open savanna (Kingdon, 1992 a,b). Fossil specimens of *Aepyceros* sp. have been recovered from the Sidi Hakoma, Denen Dora and Kada Hadar members at Hadar and there is evidence of a change in the dietary signature over time at the site.

The *Aepyceros* sp. specimens from the Sidi Hakoma Member display microwear textures similar to modern dedicated browsing taxa, with high values for *Asfc* and *Tfv* and low values for *epLsar*. The overall microwear signature for these specimens is most similar to that of *Litocranius walleri*, the modern gerenuk, which consumes no monocots and only a small percentage of fruit. These specimens from Sidi Hakoma have significantly different microwear signatures from the specimens from the Denen Dora and Kada Hadar members. These later *Aepyceros* sp. specimens have texture values that fall clearly within the range of modern browser-grazer intermediates, a dietary category that includes the extant congener, *Aepyceros melampus*. Overall, the microwear evidence suggests that *Aepyceros* sp. consumed little to no grass during the Sidi Hakoma time period at Hadar, but began including grasses during the Denen Dora period, carrying that through the formation of the Kada Hadar Member.

Alcelaphini- The tribe Alcelaphini includes hartebeests, wildebeests, bonteboks and tsessebes. All modern alcelaphines are primarily classified as grazers and consume little to no fruit (Kingdon, 1997; Gagnon and Chew, 2000). The extant alcelaphine species included in the study are the tsessebe, *Damaliscuslunatus*, which occupies open savannas and floodplains and the bontebok, *Damaliscus pygargus*, commonly found in the coastal highveld (Kingdon, 1992a, b). These taxa are classified as an obligate grazer and variable grazer respectively. *Damaliscus* *pygargus* is classified as an obligate grazer and consumes more dicots, but varies its diet on a seasonal basis. *Damaliscus lunatus* is categorized as a variable grazer, and while it consumes a wider variety of food types than the tsessebe, the bontebok has a diet that apparently does not vary seasonally or geographically.

Fossil alcelaphines are found in all three Hadar members and differences in microwear texture were found between the members. The fossil Alcelaphini specimens from the Sidi Hakoma and Denen Dora members all display indications of frequent browsing and are most similar to modern browser-grazer intermediates. The fossil specimens from these members have microwear signatures that cluster with the modern eland, a species with a diet consisting of nearly equal amounts of browse and graze, with some seasonal fruit consumption (Kingdon, 1982; Skinner and Smithers, 1990; Gagnon and Chew, 2000). Microwear evidence for more dedicated grazing by the Hadar alcelaphines doesn't occur until the Kada Hadar Member, for which the specimens have microwear signatures similar to those of extant variable grazers like *Damaliscus pygargus* and *Kobus ellipsiprymnus*. Browse makes up less than 15% of the diet for both of these modern taxa (Hofmann and Stewart, 1972; Skinner and Smithers, 1990; Gagnon and Chew, 2000).

Antilopini- The tribe Antilopini is composed of gazelles, gerenuks and springboks. Modern taxa subscribe to a wide range of diets, from the browsing *Litocranius walleri*, to the dedicated grazer, *Gazella granti* (Kingdon, 1997; Gagnon and Chew, 2000). The habitats occupied by antilopines are mostly semi-arid scrubland, savanna and even desert (Kingdon, 1992a, b). The Hadar fauna includes fossil species of *Gazella* sp., as well as unclassified Antilopini. Both of these taxa have been recovered from the Sidi Hakoma and Kada Hadar members and *Gazella* specimens have also been found in the Denen Dora Member.

The fossil *Gazella* sp. specimens from the three Hadar members are not significantly different and share microwear signatures most closely resembling those of modern browser-grazer intermediates. The fossil specimens have texture values that group with modern *Raphicerus sharpei*, the grysbok, and *Antidorcas marsupialis*, the springbok. Both of these extant taxa consume a variable diet that includes more than 55% browse and seasonal fruit consumption (Kingdon, 1982; Skinner and Smithers, 1990). Some subtle differences in dietary signature among the Hadar members are present, but the only statistically significant difference is in the heterogeneity variable. Unfortunately, the sample sizes for *Gazella* sp. are simply not large enough to draw many conclusions about potential change in diet over time at the site.

The Antilopini fossil specimens from the Sidi Hakoma and Kada Hadar members all have microwear signatures closely resembling those of the modern browsers *Litocranius walleri* and *Neotragus batesi*. While no significant differences were present between the representatives from these two members, the Sidi Hakoma specimens had higher values overall for *Asfc* and *Tfv*, as well as lower values for *epLsar* than those from Kada Hadar. When these specimens are compared to modern taxa, they fall well within the uppermost ranges of browsing taxa and overlap with the frugivorous bovids.

Bovini- The tribe Boviniis composed of large bovids that are classified as variable or obligate grazers (Kingdon, 1997; Gagnon and Chew, 2000). This includes domestic cattle, bison and the African buffalo, *Syncerus caffer*, which is part of the comparative database used here.Modern members of this tribe are highly successful grazers and found in habitats ranging from open grassland to more closed woodland (Kingdon, 1992a, b). Bovini specimens from Hadar include *Pelorovis* sp. and *Ugandax coryndonae*, as well as a number of specimens that cannot be classified past the level of tribe and are therefore considered separately here.

Bovinifossils have been recovered from all three Hadar members- *Ugandax coryndonae*in the Sidi Hakoma and Denen Dora members, *Pelorovis* in the Denen Dora and Kada Hadar members, and Bovini in the Kada Hadar Member. Differences in microwear textures are present both among and within the Hadar members.

*Ugandax coryndonae*is the only Bovini taxon present in the Sidi Hakoma Member, and its microwear signature is comparable to those of modern browser-grazer intermediates, like *Raphicerus sharpei*. This suggests that *Ugandax* engaged in a diet very different from its closest living relative, *Syncerus caffer*, which is classified as variable grazer. *Ugandax coryndonae*and *Pelorovis* sp.are both present in the Denen Dora Member, and although the microwear evidence suggests that both were variable grazers, the two taxa fall at the opposite extremes of the category, suggesting some subtle differences in diet. For example, *Ugandax coryndonae*has texture values for complexity and textural fill volume that are at the highest end of the range for extant variable grazers, and actually overlap with browser-grazer intermediates, while *Pelorovis* has complexity and anisotropy values similar to modern obligate grazers. These results suggest that while grass was probably the staple resource for both taxa, browse may have been a more important component of the diet of *Ugandax coryndonae*.

The Kada Hadar assemblage includes both *Pelorovis* sp. and specimens classified only as Bovini. The microwear signature of the Bovini falls well within the range of modern obligate grazing taxa and clusters closely with *Redunca arundinum*, a species that consumes a diet of nearly all grass with no seasonal variation. *Pelorovis* sp., on the other hand, has a microwear texture nearly identical to that of *Syncerus caffer* and similar to fossils of the same genus from Denen Dora. While the sample for Bovini specimens is not large, the evidence presented here suggests an increase in grazing over time by these taxa at Hadar.

Hippotragini- Examples of modern hippotragines include the grazing oryx, a desert-dweller, and sable antelope, commonly found in savanna woodlands and grasslands (Kingdon, 1992a, b; Gagnon and Chew, 2000). Members of the genus *Oryx* have been found at Hadar, along with fossil bovids identified only as hippotragines. Both Hippotragini and *Oryx* sp. have been recovered from all three hominin-bearing members at Hadar; however, specimens with well-preserved microwear were only identified from Denen Dora and Kada Hadar. The *Oryx* sp. specimens used in this study were all recovered from the Kada Hadar Member and these specimens have significantly higher anisotropy values than the Hippotragini specimens. This could be indicative of more dedicated grazing by *Oryx*. The specimens classified as Hippotragini have similar texture values to both variable and obligate grazers, suggesting the possibility of a seasonal shift in preferred resource availability. The *Oryx* sp. specimens clearly fall into the same range as obligate grazers including *Damaliscus lunatus* and *Redunca fulvorufula*, two taxa that consume almost no browse or fruit (Hofmann and Stewart, 1972).

Neotragini- Modern neotragines include the African dwarf antelopes including dik-diks, grysboks, oribis, and klipspringers. These taxa are primarily browsers and dietary generalists, consuming a wide variety of food types (Kingdon, 1997; Gagnon and Chew, 2000). Neotragines also occupy a variety of habitats, from moist closed forests to open savanna (Kingdon, 1992a, b). Fossil specimens belonging to the tribe Neotragini have been identified from all three hominin-bearing members at Hadar, but only specimens from the Sidi Hakoma and Kada Hadar members were suitable for microwear analysis.

The Sidi Hakoma and Denen Dora neotragin specimens are significantly different from one another, although both have microwear texture signatures similar to those of modern browsers. The microwear texture values of the Sidi Hakoma specimens are nearly identical to those of the modern neotragin, *Neotragus batesi*, while those from Kada Hadar are most similar to the browsing gerenuk, *Litocranius walleri*. These similarities with different modern taxa may indicate subtle differences in browsing strategy. For example, fruit accounts for more than 20% of the diet of *Neotragus batesi*, while only making up about 5% of the diet of *Litocranius*.

Reduncini- Modern reduncines primarily inhabit watery environments including marshes, floodplains and swamps (Kingdon 1992a, b). The comparative database used in this study includes data on four members of this tribe: the waterbuck, *Kobus ellipsiprymnus*,the lechwe, *Kobus leche*, the southern reedbuck, *Redunca arundinum*, and the mountain reedbuck, *Redunca fulvorufula*. Nearly all members of Reduncini are classified as obligate grazers, with only *Kobus ellipsiprymnus*engaging in more variable grazing (Gagnon and Chew, 2000). Both *Kobus* sp. and Reduncini fossils have been found in all three hominin-bearing members at Hadar, however the only Reduncini specimens preserving well-preserved microwear were those from the Denen Dora Member.

While the differences between the *Kobus* fossils from the three members are only marginally significant (Fishers test, p-value=0.048), there is subtle variation among the specimens from each member. This becomes more apparent when the values are plotted in a multivariate space alongside the modern taxa (Figure 5). The microwear textures of the *Kobus* sp. specimens from Sidi Hakoma most closely resemble those of modern browser-grazer intermediates like *Raphicerus sharpei*, which consumes mostly dicots, while the Denen Dora specimens generally fall into a different space, overlapping variable grazing taxa like *Gazella granti*. The Kada Hadar *Kobus* sp. specimens fall on the border of obligate and variable grazing taxa and have a microwear signature that most closely resembles that of *Damaliscus pygargus*, a species that consumes primarily grass, with seasonal inclusion on dicots. This suggests that browse and/or fruit may have always been an important component to the diet of *Kobus* sp. throughout the Hadar Formation, but that it may have become a seasonal component rather than a year-round staple by the time of Denen Dora and Kada Hadar deposition.

The Reduncini specimens from the Denen Dora Member have microwear textures consistent with those of modern obligate grazers. In fact, the taxon clusters most closely with the modern reduncines, *Redunca fulvorufula*and *Kobus leche*. This suggests that, at least during the Denen Dora period, Reduncinifavored a somewhat catholic diet primarily composed of grasses, with very occasional consumption of fruit or other dicots.

Tragelaphini- The spiral-horned antelopes include the genera *Tragelaphus* and *Taurotragus*. The tragelaphines recovered from Hadar have all been identified as members of the genus *Tragelaphus*. This genus also includes modern bovids representing nearly all dietary specializations, ranging from *Tragelaphus spekii*, a variable grazer, to *Tragelaphus euryceros*, a dedicated browser (Gagnon and Chew, 2000). All modern tragelaphines occupy forest habitats, although within this category, they range dramatically from open woodland to swamp forest to rainforest (Kingdon, 1992a, b).

Tragelaphus sp. has been identified in all three Hadar members, but only specimens from the Sidi Hakoma and Denen Dora members preserve suitable microwear for analysis. The specimens from Sidi Hakoma have a microwear texture signature similar to modern browsers, specifically the congener, *Tragelaphus euryceros*; while results for later Denen Dora specimens suggest a diet like that of extant browser-grazer intermediates. In fact, the microwear signature of the Denen Dora *Tragelaphus* sp. specimens is nearly identical to that of *Tragelaphus imberbis*, a species for which grass makes up more than one-third of its diet (Hofmann and Stewart, 1972). This suggests that graze may have become more important as a staple resource for *Tragelaphus* at Hadar over time. It is worth noting, however, that modern tragelaphines engage in a wide variety of dietary strategies and that since the fossil taxa cannot be identified past the level of genus, there is a possibility that we are combining multiple taxa into a single sample.

Implications for paleoenvironment at Hadar

Dental microwear is a nongenetic signal that provides direct evidence of what an animal ate during its lifetime, rather than a prediction of what an animal was adapted to eat based on morphology. This is an important step in reconstructing diet because resource availability can change rapidly, but it can take many generations for morphology to follow suit. Therefore, microwear can be an excellent indicator of the types of resources available to local fauna. Dental microwear texture analysis of the Hadar bovids is an important step toward better understanding the local paleoenvironment throughout the occupation of *Australopithecus afarensis*.

<u>Sidi Hakoma Member</u>- The Sidi Hakoma Member was deposited between 3.43-3.26 mya and is composed of four submembers known as SH-1 through SH-4 (Campisano, 2007). Previous analyses of local fauna (Reed, 2008), as well as oxygen and carbon isotope studies (Hailemichael, 2000), have suggested that Hadar was made up of woodland and shrubland during this time, with low seasonal variation. This may not have been the case consistently, however, as palynological studies at the site have indicated that the local environment was a frequently changing mosaic (Bonnefille et al., 2004) during the time of Sidi Hakoma deposition.

Overall, the dietary reconstructions of the Sidi Hakoma taxa included in this study suggest a relatively closed habitat, or at least, regular access to regular fruit and browse. The microwear evidence presented here suggests that no obligate or variable grazers were present in the assemblage and that the bovid taxa found in the Sidi Hakoma deposits primarily consumed browse. Additionally, there appears to have been less overall variation in the diets of the Sidi Hakoma bovids than in the Denen Dora or Kada Hadar members, where the bovids evince both dedicated grazing and browsing signatures. The absence of wear signatures similar to open country adapted grazers, along with the presence of so many browsing taxa, strongly suggests that the Sidi Hakoma paleoenvironment was more closed than that of the later Hadar members.

<u>Denen Dora Member</u>- The Denen Dora Member dates from 3.26-3.2 mya (Campisano, 2007), and is divided into three submembers, DD-1 through DD-3. Analysis of the fauna has suggested a local paleoenvironment comparable to that of modern mosaic woodlands that include both gallery forest and bushland (Reed, 2008). An overall increase in the number of alcelaphine bovids also suggests the presence of, or proximity to, grassland during this time period and this is also consistent with high levels of grass pollen collected in the lower strata of the member by Bonnefille et al. (2004). However, evidence of other habitat types are also present in the Denen Dora Member, including sedge and reed pollen (Bonnefille et al., 2004) and the presence of reduncin and aepycerotin bovids, all of which is suggestive of a browse-rich woodland environment.

The microwear textures of the Denen Dora bovids suggest a variety of dietary strategies, and are most similar to modern taxa with diets that depend on a substantial graze component. Most of the Denen Dora fossil taxa cluster with modern browser-grazer intermediates, variable grazers and/or obligate grazers. This is consistent with reconstructions of Hadar as a mosaic woodland habitat where both grasses and woody browse were available. The microwear data also suggest a shift in paleoenvironment between the deposition of Sidi Hakoma and Denen Dora. In contrast to the Sidi Hakoma Member, none of the Denen Dora bovids have microwear signatures similar to those of modern dedicated browsers or frugivores. Additionally, the dietary signatures of several of the bovid taxa change between the two members. For example, Sidi Hakoma specimens of *Aepyceros* sp. and *Tragelaphus* sp. display microwear consistent with browsing, while Denen Dora members of the same taxa resemble modern browser-grazer intermediates that consume higher quantities of grass. *Kobus* sp. also shifts between these two members, going from a browser-grazer intermediate signature to one more consistent with variable grazing. All of these transitions suggest the availability of multiple resource types and access to both open and closed habitats.

Kada Hadar Member- The two collection units that make up the Kada Hadar Member were deposited between ~3.2-2.94 mya and are known as KH-1 and KH-2 (Campisano, 2007). Reed (2008) noted that the fauna from this member resembles the assemblages typical of modern open woodland/edaphic grassland environments such as in Amboseli National Park in Kenya. Antilopin and alcelaphin bovids are common in both of the submembers, indicating a drier and more open habitat (Vrba, 1980). However, pollen data suggests a humid woodland habitat (Bonnefille et al., 2004), although it has been suggested that this could be reflective of one of several types of closed physiognomies comprising the mosaic local environment and not an indicator of habitat for the whole site (Campisano and Reed, 2007).

The microwear evidence presented in the current study supports a more open habitat reconstruction for the Kada Hadar Member, although there is still evidence suggesting that local fauna had access to woodland resources. The majority of the bovid taxa have microwear textures consistent with an obligate or variable grazing strategy, although some browsing taxa are still present. This suggests the availability of a range of food types, including both significant graze and browse, and could indicate a mosaic environment including both grassland and woodland.

The difference in the paleoenvironmental signal between Denen Dora and Kada Hadar is not as pronounced as that between Sidi Hakoma and Denen Dora, but evidence of some change is present nonetheless. Bovids reconstructed as obligate grazers are more common in the Kada Hadar assemblages than those from Denen Dora, and while evidence of browse consumption is still present, it appears to have only been a primary resource for three of the ten taxa. There is also evidence to suggest that graze became more of a staple resource for some of the Kada Hadar bovids than it was for their predecessors. *Kobus* sp. specimens appear to transition from a variable grazing signature in the Denen Dora Member to an obligate grazing signature in the Kada Hadar Member, and both Alcelaphini and Hippotragini shift from browser-grazer intermediate to variable grazer. These changes in diet suggest that the Kada Hadar bovids had access to open habitats for grazing, although the presence of a few browsing taxa support mosaic reconstructions for this member.

In general, the microwear evidence is consistent with a gradual aridification trend at Hadar during the occupation of *A. afarensis*. This suggests that the local environment transitioned from closed woodland dominated by browsing bovids during the Sidi Hakoma Member, to more open, mosaic habitats with both woodland and grassland available to the local bovid populations by the time of the Kada Hadar deposition. It is necessary to note that because the sample sizes did not allow for comparison among submembers, changes in habitat availability within the members themselves cannot be commented on here. However, the differences in bovid diets reported between the Hadar members are sufficient to suggest that the overall environment changed considerably during the time in which *A. afarensis* inhabited the site.

Paleoenvironments of *Australopithecus afarensis*

The results of this study are generally consistent with previous reconstructions of Hadar as a mosaic of localized environments during the occupation of *Australopithecus afarensis*. In addition to Hadar, *A. afarensis* specimens have also been recovered from East African sites where the paleoenvironments appear to have ranged from open shrubland to closed woodland, with no evidence of specific habitat preference (Andrews, 1989, 2006; White et al., 1993; Reed, 1997). The fact that these early hominins have been found in such a variety of paleoenvironmental conditions has led to the suggestion that *A. afarensis* was ecologically plastic and could successfully inhabit a wide variety of habitat types (White et al., 1993).

Conclusions

The dental microwear of the Hadar bovids indicates a wide range of dietary variation, and by extension, food availability. This suggests that local habitat at Hadar were not entirely open or closed, but instead included a variety of habitat types that changed during the occupation of *A. afarensis*. Dental microwear data agree with other lines of evidence that these may have ranged from intermediate cover physiognomies including bushland and woodland, to more open habitats like shrubland and edaphic grasslands. The dental microwear signatures of the fossil bovids indicate a gradual transition from the more closed habitats comprising the Sidi Hakoma Member to more open environments by the time of Kada Hadar deposition.

This research contributes to the large body of information on the paleoecology at Hadar and suggests that dental microwear texture analysis about a valuable additional proxy for the diet and habitat preferences of fossil mammals.

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References

Alemseged, Z., 2003. An integrated approach to taphonomy and faunal change in the Shungura Formation (Ethiopia) and its implication for hominid evolution. J. Hum. Evol. 44, 451-478.

Andrews, P., 1989. Paleoecology of Laetoli. J. Hum. Evol. 18, 173-181.

Andrews, P., 2006. Taphonomic effects of faunal impoverishment and faunal mixing.Palaeogeogr.Palaeoclimatol.Palaeoecol. 241, 572-589.

Archibold, O.W., 1995. Ecology of World Vegetation.Chapman Hall, London.

Aronson, J., Taieb, M., 1981.Geology and paleogeography of the Hadar hominid site, Ethiopia. In: Rapp, G., Vondra, C.F. (Eds.), Hominid Sites: Their Geological Setting. Westview Press, Boulder, pp. 165-195.

Bobe, R., Behrensmeyer, A.K., Eck. G.G., Harris, J.M., 2007. Patterns of abundance and diversity in late Cenozoic bovids from the Turkana and Hadar Basins, Kenya and Ethiopia. In: Bobe, R., Alemseged, Z., Behrensmeyer, A.K., (Eds.) Hominin Environments in the East African Pliocene: An Assessment of the Faunal Evidence, pp. 129-157. Springer, Dordrecht.

Bobe, R., Eck, G.G., 2001. Responses of African bovids to Pliocene climatic change.Paleobiology27 (Suppl. to No. 2).Paleobiology Memoirs 2, 1-47.

Bonnefille, R., 1995. A reassessment of the Plio-Pleistocene pollen record of East Africa. In: Vrba, E. S., Denton, G. H., Partridge, T. C. and Burckle, L. H. (Eds.), Paleoclimate and Evolution, with Emphasis onHuman Origins, pp. 299-310. Yale University Press, New Haven, CT.

Bonnefille, R., Potts, R., Chalié, F., Jolly, D., Peyron, O., 2004. High-resolution vegetation and climate change associated with Pliocene *Australopithecus afarensis*. Proc. Natl. Acad. Sci. 101, 12125-12129.

Bonnefille, R., Riollet, G., 1987. Palynological spectra from the Upper Laetolil Beds. In: Leakey, M.D., Harris, J.M. (Eds.), Laetoli, a Pliocene Site in Northern Tanzania, pp. 52-61. Clarendon Press, Oxford.

Campisano, C.J., 2007. Tephrostartigraphy and hominin paleoenvironments of the Hadar Formation, Afar Depression, Ethiopia. Ph.D. Dissertation, Rutgers, The State University of New Jersey.

Campisano, C.J., Feibel, C.S., 2007. Connecting local environmental sequences to global climate patterns: evidence from the hominin-bearing Hadar Formation, Ethiopia. J. Hum. Evol 53, 515-527.

Campisano, C.J., Reed, K.E., 2007. Spatial and temporal patterns of *Australopithecus afarensis* habitats at Hadar, Ethiopia.Paleoanthropology Society Annual Meeting, Philadelphia, Pennsylvania, Abstracts, p. A6.

Conover, W.J., Iman, R.L., 1981. Rank transformations as a bridge between parametric and nonparametric statistics. Am Stat 35:124-129.

Cook, R.J., Farewell, V.T., 1996. Multiplicity considerations in the design and analysis of clinical trials.J R Stat Soc Ser A, 159:93-110.

Dodds,W.K., 1997. Distribution of runoff and rivers related to vegetative characteristics, latitude and slope: a global perspective. J. N. Am. Benthol. Soc. 16, 162-168.

Dunbar, R.I.M., Dunbar, P. 1974. Social organization and ecology of the klipspringer (*Oreotragus oreotragus*) in Ethiopia. Zeitschrift fur Tierpsychologie 35:481-493.

Fortelius, M., Solounias, N., 2000. Functional characterization of ungulate molars using the abrasion-attrition wear gradient: a new method for reconstructing diets. Am Mus Nov 3301:1-36.

Gagnon, M., Chew, A.E., 2000. Dietary preferences in extant African Bovidae. J Mammal 8:490-511.

Gifford, D.P., 1981. Taphonomy and paleoecology: a critical review of archaeology's sister disciplines. Advances in Archaeological Methods and Theory 4, 365-438.

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.

Hailemichael, M., 2000. The Pliocene environment of Hadar, Ethiopia: a comparative isotopic study of paleosol carbonates and lacustrine mollusk shells of the Hadar Formation and of modern analogs. Ph.D. Dissertation, Case Western Reserve University.

Harris, J.M., 1987. Fossil Giraffidae and Camelidae from Laetoli and summary. In: Leakey, M.D., Harris, J.M. (Eds.), Laetoli: A Pliocene Site in Northern Tanzania, pp. 358-377. Oxford University Press, Oxford.

Harrison, T., 2005. Fossil bird eggs from the Pliocene of Laetoli, Tanzania: their taxonomic and paleoecological relationships. J. Afr. Earth Sci. 41, 289-302.

Hofmann, R.R., Stewart, D.R.M. 1972. Grazer or browser: a classification based on the stomach structure and feeding habits of East African ruminants. Mammalia 36:226-240.

Janis, C., 1990. The correlation between diet and dental wear in herbivorous mammals, and its relationship to the determination of diets of extinct species. Boucot, A.J. (Ed.), Evolutionary paleobiology of behavior and coevolution. Elsevier, Amsterdam, pp 241-259.

Johanson, D., Masao, F.T., Eck, G.G., White, T.D., Walter, R.C., Kimbel, W.H., Asfaw, B., Manega, P., Ndessokia, P., Suwa, G., 1987. New partial skeleton of *Homo habilis* from Olduvai Gorge, Tanzania. Nature 327, 205-209.

Kimbel, W.H., 1988. Identification of a partial cranium of *Australopithecus afarensis* from the Koobi Fora Formation. J. Hum. Evol. 17, 647-656.

King T., Andrews P., Boz B., 1999. Effect of taphonomic processes on dental microwear.Am J Phys Anthrop 108:359-373.

Kingdon, J. 1997. The Kingdon field guide to African mammals. Academic Press, London, United Kingdom.

Kingdon, J., 1982a. East African Mammals: Bovids, vol. IIIC. University of Chicago Press, Chicago.

Kingdon, J., 1982b. East African Mammals: Bovids, vol. IIID. University of Chicago Press, Chicago.

Krueger, K.L., Ungar, P.S., 2009. Incisor microwear textures of five bioarcheological groups. Int J Osteoarcheol 20:549-560.

Merceron, G., Ungar, P.S., 2005. Dental microwear and palaeoecology of bovids from the Early Pliocene of Langebaanweg, Western Cape province, South Africa. S. Afr. J. Sci. 101:365-370.

Merceron, G., Blondel, C., Brunet, M., Sen, S., Solounias, N., Viriot, L., Heintz, E., 2004a. The late Miocene paleoenvironments of Afghanistan as inferred from dental microwear in artiodactyls. Palaeogeo, Palaeoclimatol, Palaeoecol 207:143-163.

Merceron, G., Viriot, L., Blondel, C., 2004b. Tooth microwear pattern in roe deer (*Capreolus capreolus* L.) from Chizé (Western France) and relation to food composition. Small Ruminant Res 53:125-132.

Merceron, G.M., Scott, J.R., Scott, R.S., Geraads, D., Spassov, N., Ungar, P.S., 2009. Seed predation for an early Colobine as a link between frugivory and folivory?Evidence from dental microwear texture analysis of Mesopithecus (Late Miocene of Eurasia). J Hum Evol 57:732-738.

Musiba, C.M., Magori, C., Stoller, M., Stein, T., Branting, S., Vogt, M., Tuttle, R., Hallgrímsson, B., Killindo, S., Mizambwa, F., Ndunguru, F., Mabulla, A., 2007. The Taphonomy and paleoecological context of the Upper Laetolil Beds (Localities 8 and 9), Laetoli in northern Tanzania. In: Bobe, R., Alemseged, Z., Behrensmeyer, A.K., (Eds.)

Hominin Environments in the East African Pliocene: An Assessment of the Faunal Evidence, pp. 257-278. Springer, Dordrecht.

O'Brien, E.M., 1998. Water-energy dynamics, climate, and prediction of woody plant species richness: an interim general model. J. Biogeogr. 25, 379-398.

O'Brien, E.M., 2006. Biological relativity to water-energy dynamics. J. Biogeogr. 33, 1868-1888.

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 Pleistocene kangaroo. PNAS 106:11646-11650.

Puhakka, M., Kalliola, R., Rajasilta, M., Salo, J., 1992.River types, site evolution and successional vegetation patterns in Peruvian Amazonia. J. Biogeogr. 19, 651-665.

Radosevich, S.C., Retallack, G.J., Taieb, M., 1992.Reassessment of the paleoenvironment and preservation of hominid fossils from Hadar, Ethiopia. Am. J. Phys. Anthrop. 87, 15-27.

Reed, K.E., 1997. Early hominid evolution and ecological change through the African Plio-Pleistocene. J. Hum. Evol. 40, 289-322.

Reed, K.E., 2008. Paleoecological patterns at the Hadar hominin site, Afar Regional State, Ethiopia. J. Hum. Evol. 54, 743-768.

Rose, J.J., 1983. A replication technique for scanning electron microscopy: applications for anthropologists. American Journal of Physical Anthropology 62, 255–261.

Schubert, B.W., Ungar, P.S., DeSantis, L.R.G., 2010. Carnassial microwear and dietary behaviour in large carnivorans. J Zool 280:257-263

Schubert, B.W., Ungar, P.S., Sponheimer, M., Reed, K.E., 2006. Microwear evidence for Plio-Pleistocene bovid diets from Makapansgat Limeworks Cave, South Africa. Palaeogeogr, Palaeoclimatol, Palaeoecol 241:301-319.

Scott, J.R., in review.Dental microwear texture analysis of extant African Bovidae.Mammalia.

Scott, J.R., Ungar, P.S., Jungers, W.L., Godfrey, L.R., Scott, R.S., Simons, E.L., Teaford, M.F., Walker, A., 2009. Dental microwear texture analysis of the archaeolemurids and megaladapids, two families of subfossil lemurs 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., Ungar, P.S., Bergstrom, T.S., Brown, C.A., Grine, F.E., Teaford, M.F., Walker, A., 2005. Dental microwear texture analysis reflects diets of living primates and fossil hominins. Nature 436:693-695.

Skinner, J.D., Smithers, R.H.N. 1990. The mammals of the southern African subregion.2nd ed. University of Pretoria, Pretoria, South Africa.

Taieb, M., Johanson, D.C., Coppens, Y., Aronson, J.L., 1976.Geological and paleontological background of Hadar hominid site, Afar, Ethiopia. Nature 260, 289-293.

Teaford, M.F., 1988. A review of dental microwear and diet in modern mammals.Scanning Microsc 2:1149-1166.

Teaford, M.F., Oyen, O.J., 1989. Live primates and dental replication: new problems and new techniques. Am J Phys Anthrop 80:73-81.

Ungar, P.S., 1996. Dental microwear of European Miocene catarrhines: evidence for diets and tooth use. J Hum Evol 31:335-366.

Ungar, P.S., Krueger, K.L, Blumenschine, R.J. Njao, J. Scott, R.S., in press.Dental microwear texture analysis of hominins recovered by the Olduvai Landscape Paleoanthropology Project, 1995-2007. J Hum Evol.

Ungar, P.S., Scott, J.R., Schubert, B., Stynder, D., 2010. Carnivoran dental microwear textures: comparability of carnassial facets and functional differentiation of the postcanine teeth. Mammalia 74:219-224.

Ungar, P.S., Scott, R.S., 2009. Dental evidence for diets of Early *Homo*. The First Humans: Origins of the Genus *Homo*. Grine, F.E. Leakey, R.E., Fleagle, J.G., (Eds.) Springer-Verlag, New York, pp. 121-134.

Ungar, P.S., Scott, R.S., Scott, J.R., Teaford, M.F., 2008a. Dental microwear analysis: historical perspectives and new approaches. In: Irish, J.D. (Ed.), Technique and Application in Dental Anthropology. Cambridge University Press, Cambridge, 389-425.

Ungar, P.S., Grine, F.E., Teaford, M.F., 2008b. Dental microwear indicates that *Paranthropus boisei* was not a hard-object feeder. PLoS 2044:1-6.

Ungar, P.S., Merceron, G., Scott, R.S., 2007. 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., Brown, C.A., Bergstrom, T.S., Walker, A., 2003. A quantification of dental microwear by tandem scanning confocal microscopy and scale-sensitive fractal analysis.Scanning 25:189-193.

Verdcourt, B., 1987. Mollusca from the Laetolil and Upper Ndolanya Beds. In: Leakey, M.D., Harris, J.M. (Eds.), Laetoli: A Pliocene Site in Northern Tanzania, pp. 438-450. Oxford Science Publications, Oxford.

Vrba, E.S., 1980. The significance of bovid remains as indicators of environment and prediction patterns. In: Behrensmeyer, A.K., Hill, A. (Eds.), Fossils in the Making, Vertebrate Taphonomy and Paleoecology. University of Chicago Press, Chicago, pp. 247-271.

Walter, R.C., 1994. Age of Lucy and the First Family: single-crystal 40Ar/39Ar dating of the Denen Dora and lower Kada Hadar Members of the Hadar Formation, Ethiopia. Geology 22, 6-10.

Walter, R.C., Aronson, J.L., 1993. Age and source of the Sidi Hakoma Tuff, Hadar Formation, Ethiopia. J. Hum. Evol. 25, 229-240.

Walter, R.C., Westgate, J.A., Hart, W.K., Aronson, J.L., 1984. Tephrastratigraphic correlation of the Sidi Hakoma and Tulu Bor tuffs; Nd isotope and new trace element data.Geol. Soc. Am. Abstracts with Programs 16, 686.

White, F., 1983. The vegetation of Africa: a descriptive memoir to accompany UNESCO/AETFAT/UNSO vegetation maps of Africa. UNESCO, Paris.

White, T.D., Suwa, G., Hart, W.K., Walter, R.C., WoldeGabriel, G., de Heinzelin, J., Clark, J.D., Asfaw, B., Vrba, E.S., 1993. New discoveries of *Australopithecus* at Maka in Ethiopia. Nature 366, 261-265.

TABLES

Table 1. Descriptions of habitat categories discussed in this paper. (White, 1983; Reed, 1997, 1998).

Habitat Types	Characteristics
FORESTS	
Lowland rainforest	tall columnar with multi-structured canopies and a shrub layer and sparse ground cover
Montane forest	dominated by deciduous and evergreen trees, high annual rainfall
Dry or seasonal forest	single closed canopy forest, prolonged dry seasons
SAVANNAS	
Open woodland	deciduous trees comprise 20-25% of vegetation, grass and herb ground cover
Medium density woodland	deciduous trees comprise 30-45% of vegetation, grass and herb ground cover
Closed woodland	deciduous trees comprise more than 50% of vegetation, grass and herb ground cover
Shrubland or scrub woodland	shrubs constitute more than 20% of ground cover, poor quality grass, very few trees
Secondary or open grassland	dominated by grasses and herbs, with widely scattered trees and shrubs
Edaphic grassland or wetland	seasonally or permanently waterlogged soil, aquatic grasses
BUSHLAND	
Bushland	bushes constitute 40% of ground cover, also some trees, few grasses
DESERT	

Desert	low rainfall, dominated by succulent plants

Table 2.Sample sizes and median texture values for fossil taxa by member.

TAXON	*n*	*ASFC*	*epLSAR*	*SMC*	*TFV*	*HASFC9*	*HASFC81*
SIDI HAKOMA							
Aepyceros	3	3.526147	0.0024	0.29761	8752.488	0.52981	0.94515
Alcelaphini	4	2.239167	0.003966	0.405793	6598.503	0.524273	0.884276
Antilopini	5	4.817109	0.003345	0.631563	11977.21	0.661216	1.155878
Gazella	2	2.288603	0.004937	0.6128	6071.115	0.498515	0.729166
Kobus	3	2.491008	0.002117	0.972458	4184.89	0.326508	0.837516
Neotragus	3	4.265469	0.001865	0.686543	9763.845	0.693515	0.953135
Tragelaphus	5	3.076213	0.003149	0.644873	8062.735	0.544011	0.855305
Ugandax	6	2.987175	0.003452	0.453171	5578.615	0.579619	0.840578
DENEN DORA							
Aepyceros	4	1.74854	0.00385	0.504261	5371.542	0.426949	0.750294
Alcelaphini	10	2.237113	0.004795	0.425972	6239.596	0.500645	0.924125
Gazella	4	2.791705	0.005235	0.505698	5333.485	0.4076	0.807513
Hippotragini	3	1.978451	0.005978	0.436846	3984.685	0.450178	0.813547
Kobus	9	1.598745	0.003698	1.187655	4462.355	0.419865	0.861324
Pelorovis	2	1.232126	0.006082	0.7799	2328.855	0.506156	0.855029
Reduncini	14	0.991558	0.006	1.215434	2593.004	0.444572	0.815354
Trgelaphus	10	1.963995	0.004993	0.855291	6539.146	0.482329	0.720312
Ugandax	9	2.068764	0.004933	0.502647	4267.688	0.513265	0.894055
KADA HADAR							
Aepyceros	5	1.484654	0.0041	0.26845	5972.351	0.386515	0.85441
Alcelaphini	4	1.485766	0.007602	0.322352	3331.107	0.400018	0.793935
Antilopini	5	3.587647	0.002977	0.618765	9597.235	0.698785	1.064988
Bovini	5	0.926677	0.00698	1.066665	3564.102	0.427961	0.724178
Gazella	4	2.281361	0.005181	0.534876	4276.6	0.451222	0.86058
Hippotragini	2	1.315717	0.00493	0.40046	2626.581	0.404886	0.921388
Kobus	3	0.987651	0.002976	1.135454	1103.832	0.432497	0.76133
Neotragus	4	2.698746	0.001985	0.624687	10268.15	0.626487	0.988435
Oryx	3	0.998747	0.007698	1.264877	1168.655	0.598465	0.975454
Pelorovis	4	1.315469	0.006076	0.753212	2677.005	0.427806	0.753905

Table 3.Sample size, diet and habitat preferences of the extant taxa. The habitat categories are those of White, 1983 and preferences by taxon are summarized in Kingdon, 1982 and 1997. The diet categories are those assigned by Gagnon and Chew, 2000.

TAXON	*n*	PREFERRED HABITAT
BROWSERS		
Litocranius walleri	*25*	scrubland
Neotragus batesi	*22*	bushland and dry forest
Sylvicapra grimmia	*25*	scrubland and woodland
Tragelaphus euryceros	*22*	dense forest
OBLIGATE GRAZERS		
Damaliscus lunatus	*22*	open woodland and grassland
Redunca fulvorufula	*24*	forest and medium-closed woodland
Kobus leche	*24*	edaphic grassland
Redunca arundinum	*25*	edaphic grassland and woodland
VARIABLE GRAZERS		
Damaliscus pygargus	*22*	open grassland
Gazella granti	*25*	shrubland and open grassland
Hippotragus niger	*22*	open-medium density woodland
Kobus ellipsiprymnus	*23*	scrubland and edaphic grassland
Syncerus caffer	*22*	edaphic grassland and dry forest
Tragelaphus spekii	*22*	edaphic grassland
BROWSER-GRAZER INTERMEDIATES		
Aepyceros melampus	*20*	bushland and open woodland
Antidorcas marsupialis	*21*	open grassland, shrubland and desert
Raphicerus campestris	*21*	open woodland, shrubland and grassland
Taurotragus oryx	*21*	open woodland, shrubland and grassland
Tragelaphus imberbis	*23*	bushland and open-medium density woodland
Raphicerus sharpei	*25*	shrubland and open grassland
GENERALISTS		
Oreotragus oreotragus	*24*	open-medium density woodland
Tragelaphus angasi	*22*	dense forest
Tragelaphus strepsiceros	*25*	bushland and closed woodland
FRUGIVORES		
Cephalophus sylvicultor	*25*	rainforest
Philantomba monticola	*21*	rainforest

Table 4. Statistical results of the general linear estimate model.

	SS	df	MS	F	p
Asfc	122927.657	27	4552.876	17.148	0.000
epLsar	110533.863	27	4093.847	10.267	0.000
Smc	136819.248	27	5067.380	43.633	0.000
Tfv	128649.096	27	4764.781	23.359	0.000
HAsfc9	88424.771	27	3274.992	5.145	0.000
HAsfc81	78937.456	27	2923.609	3.959	0.000

Table 5.Nested analysis of variance of fossil taxa within member.

SIDI HAKOMA					
	SS	df	MS	F	p
Asfc	5487.927	7	783.990	5.087	0.002
epLsar	7741.130	7	1105.876	5.760	0.001
Smc	16921.250	7	2417.321	44.103	0.000
Tfv	12481.102	7	1783.015	15.445	0.000
HAsfc9	13690.133	7	1821.029	5.460	0.003
HAsfc81	13914.774	7	1987.825	2.438	0.058
DENEN DORA					
Asfc	34597.524	9	3844.169	11.338	0.000
epLsar	23746.513	9	2638.501	4.710	0.000
Smc	64426.516	9	7158.502	44.785	0.000
Tfv	46997.090	9	5221.899	21.496	0.000
HAsfc9	19571.584	9	4597.251	9.784	0.007
HAsfc81	33479.190	9	3719.910	5.113	0.000
KADA HADAR					
Asfc	34658.500	9	3850.944	22.292	0.000
epLsar	41285.692	9	4587.299	28.828	0.000
Smc	44858.833	9	4984.315	88.385	0.000
Tfv	41061.588	9	4562.399	24.952	0.000
HAsfc9	34268.015	9	3948.264	16.264	0.004
HAsfc81	28289.500	9	3143.278	4.521	0.002

Table 6.Nested analysis of variance among members by taxon.

	SS	*df*	MS	F	*p*			SS	*df*	MS	F	*p*
AEPYCEROS							KOBUS					
Asfc	8326.833	2	4163.417	30.429	0.000		*Asfc*	3994.861	2	1997.431	3.104	0.094
epLsar	2831.363	2	1415.681	8.077	0.010		*epLsar*	2352.250	2	1176.125	2.422	0.144
Smc	3111.450	2	1555.725	23.305	0.000		*Smc*	111.111	2	55.556	0.325	0.731
Tfv	2698.675	2	1349.338	14.543	0.002		*Tfv*	1439.361	2	719.681	3.386	0.080
HAsfc9	7029.633	2	3514.817	19.616	0.001		*HAsfc9*	2041.944	2	1020.972	1.985	0.193
HAsfc81	5408.133	2	2704.067	2.596	0.129		*HAsfc81*	1372.861	2	686.431	0.640	0.550
ALCELAPHINI							NEOTRAGUS					
Asfc	4296.444	2	2148.222	6.712	0.008		*Asfc*	456.333	1	456.333	48.893	0.020
epLsar	11501.594	2	5750.797	9.397	0.002		*epLsar*	16.333	1	16.333	0.122	0.761
Smc	901.150	2	450.575	3.605	0.053		*Smc*	4.033	1	40.333	2.327	0.267
Tfv	6766.065	2	3383.033	9.086	0.003		*Tfv*	0.333	1	0.333	0.007	0.940
HAsfc9	7561.194	2	3780.597	7.185	0.006		*HAsfc9*	0.333	1	0.333	0.002	0.969
HAsfc81	5635.000	2	2817.500	6.671	0.008		*HAsfc81*	70.083	1	70.083	0.255	0.663
ANTILOPINI							PELOROVIS					
Asfc	138.375	2	69.187	1.855	0.250		Asfc	0.000	1	0.000	0.000	1.000
epLsar	20.700	2	10.350	0.030	0.970		epLsar	16.000	1	16.000	0.087	0.796
Smc	1.800	2	0.900	0.013	0.987		Smc	1.000	0	0.000	0.011	0.926
Tfv	106.575	2	53.287	2.530	0.174		Tfv	25.000	1	25.000	0.240	0.672
HAsfc9	456.675	2	228.338	4.031	0.091		HAsfc9	1681.000	1	1981.000	6.657	0.123
HAsfc81	258.800	2	129.400	0.300	0.753		HAsfc81	1260.250	1	1260.250	2.793	0.237

GAZELLA							TRAGELAPHUS					
Asfc	490.083	2	245.042	1.170	0.421		*Asfc*	5713.200	1	5713.200	14.117	0.002
epLsar	112.333	2	56.167	0.077	0.927		*epLsar*	7776.300	1	7776.300	12.819	0.003
Smc	330.333	2	165.167	4.112	0.138		*Smc*	1598.700	1	1598.700	15.569	0.002
Tfv	1334.333	2	667.167	3.390	0.170		*Tfv*	1203.333	1	1203.333	4.104	0.064
HAsfc9	1702.583	2	851.292	24.886	0.014		*HAsfc9*	1360.133	1	1360.133	1.256	0.283
HAsfc81	2071.000	2	1035.500	1.101	0.438		*HAsfc81*	6720.033	1	6720.033	11.904	0.004
HIPPOTRAGINI							UGANDAX					
Asfc	952.033	1	952.033	8.471	0.062		*Asfc*	3324.544	1	3324.544	15.794	0.002
epLsar	572.033	1	572.033	6.725	0.081		*epLsar*	4579.600	1	4579.600	17.555	0.001
Smc	38.533	1	38.533	0.332	0.605		*Smc*	208.544	1	208.544	2.098	0.171
Tfv	264.033	1	264.233	1.349	0.329		*Tfv*	1232.100	1	1232.100	6.611	0.023
HAsfc9	388.800	1	388.800	0.347	0.597		*HAsfc9*	1020.100	1	1020.100	3.158	0.099
HAsfc81	1642.800	1	1642.800	5.380	0.103		*HAsfc81*	298.844	1	298.844	0.532	0.479

Figure Legends

Figure 1. Occlusal view of bovid M2, illustrating the shearing facets where microwear was examined (Illustration courtesy of Gildas Merceron). A = left m^2, B= right m_2

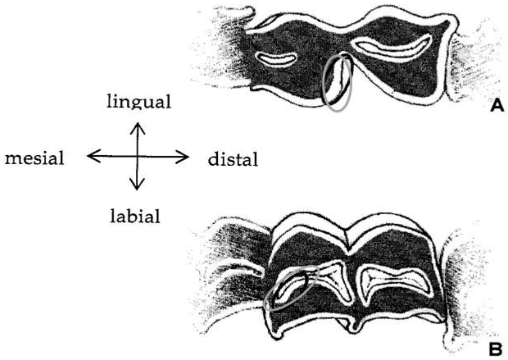


Figure 2. Examples of dental microwear surfaces for extant bovids from different dietary categories. These images are photosimulations based on data collected using the confocal imaging profiler, and each represents an area of 276 x 204 µm. A) obligate grazer; B) variable grazer; C) browser-grazer intermediate; D) generalist; E) browser; and F) frugivore.

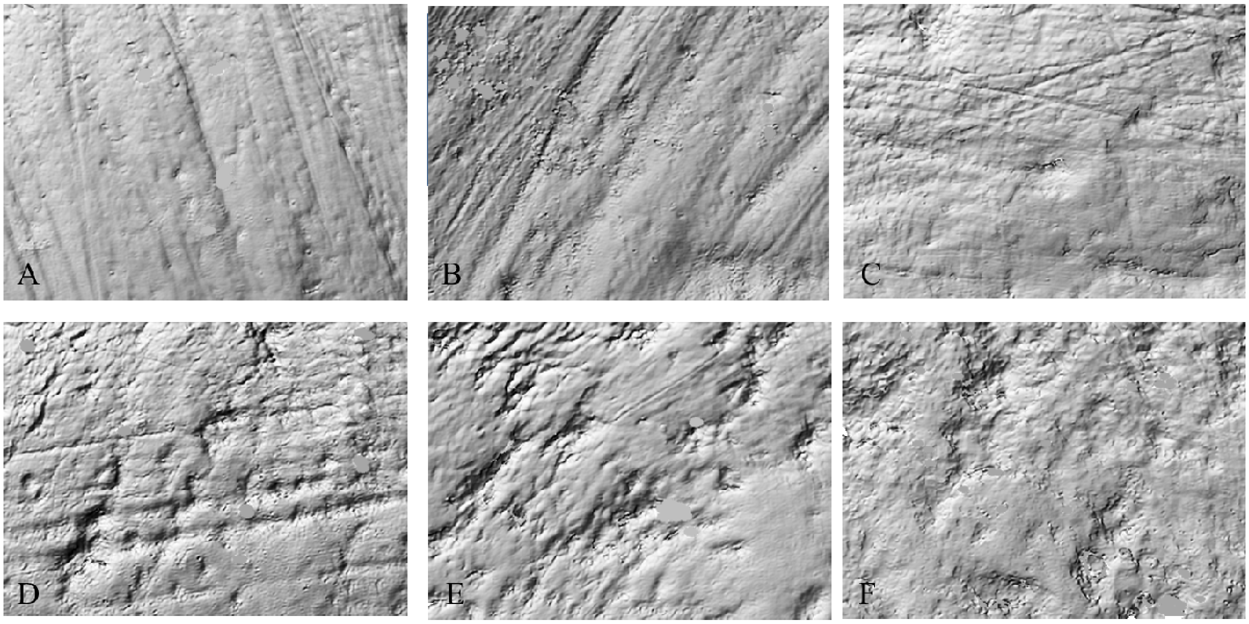
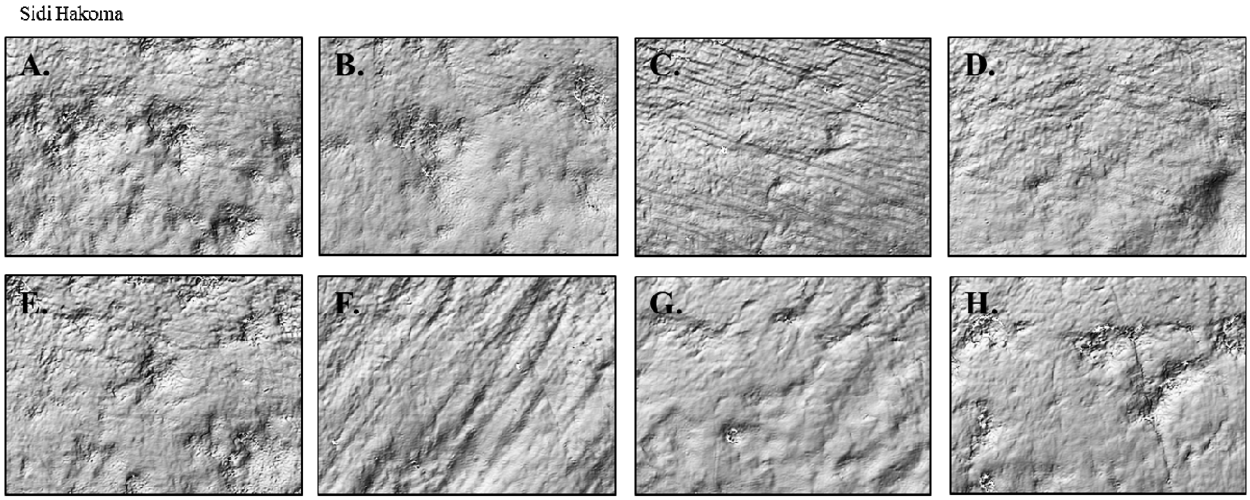
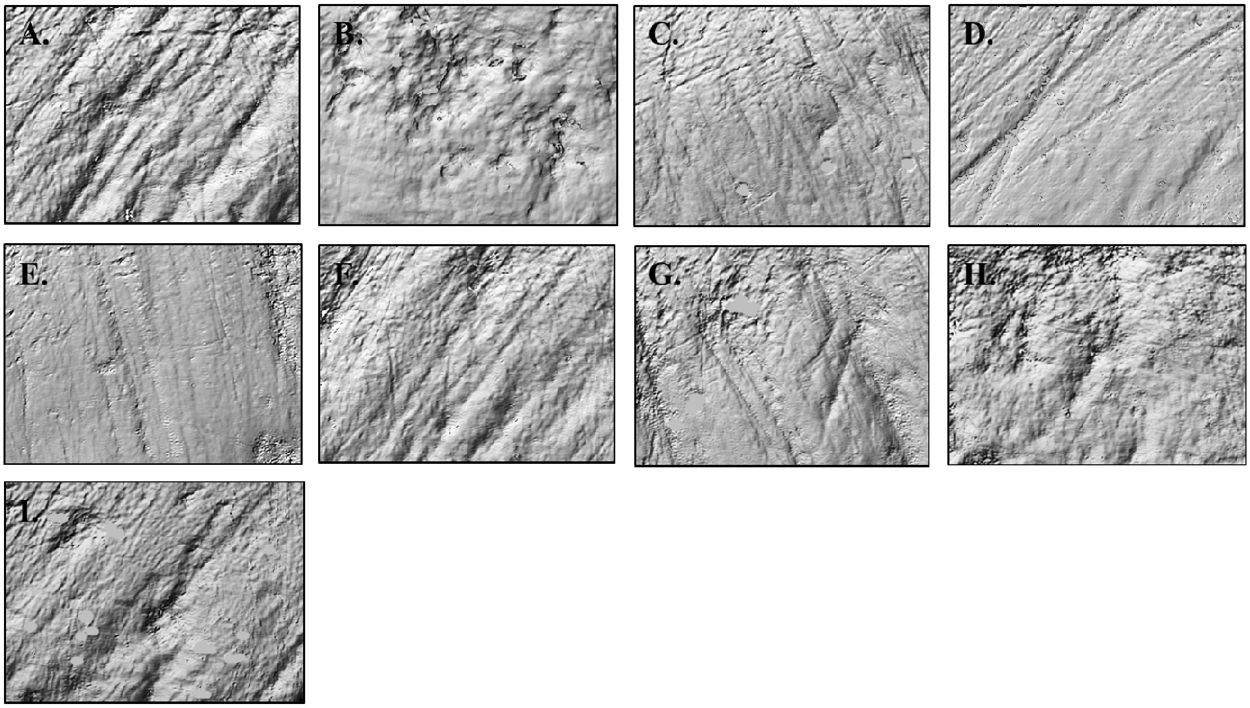


Figure 3. Examples of dental microwear surfaces for the Hadar bovids by member. These images are photosimulations based on data collected using the confocal imaging profiler, and each represents an area of 138 x 102 µm. Sidi Hakoma: A) *Aepyceros*; B) Alcelaphini; C) Antilopini; D) *Gazella*; E) *Kobus*; F) *Neotragus*; G) *Tragelaphus*; H) *Ugandax*. Denen Dora: A) *Aepyceros*; B) Alcelaphini; C) *Gazella*; D) Hippotragini; E) *Kobus*; F) *Pelorovis*; G) Reduncini; H) *Tragelaphus*; I) *Ugandax*. Kada Hadar: A) *Aepyceros*; B) Alcelaphini; C) Antilopini; D) Bovini; E) *Gazella*; F) Hippotragini; G) *Kobus*; H) *Neotragus*;I) *Oryx*; J) *Pelorovis*.



Denen Dora



Kada Hadar

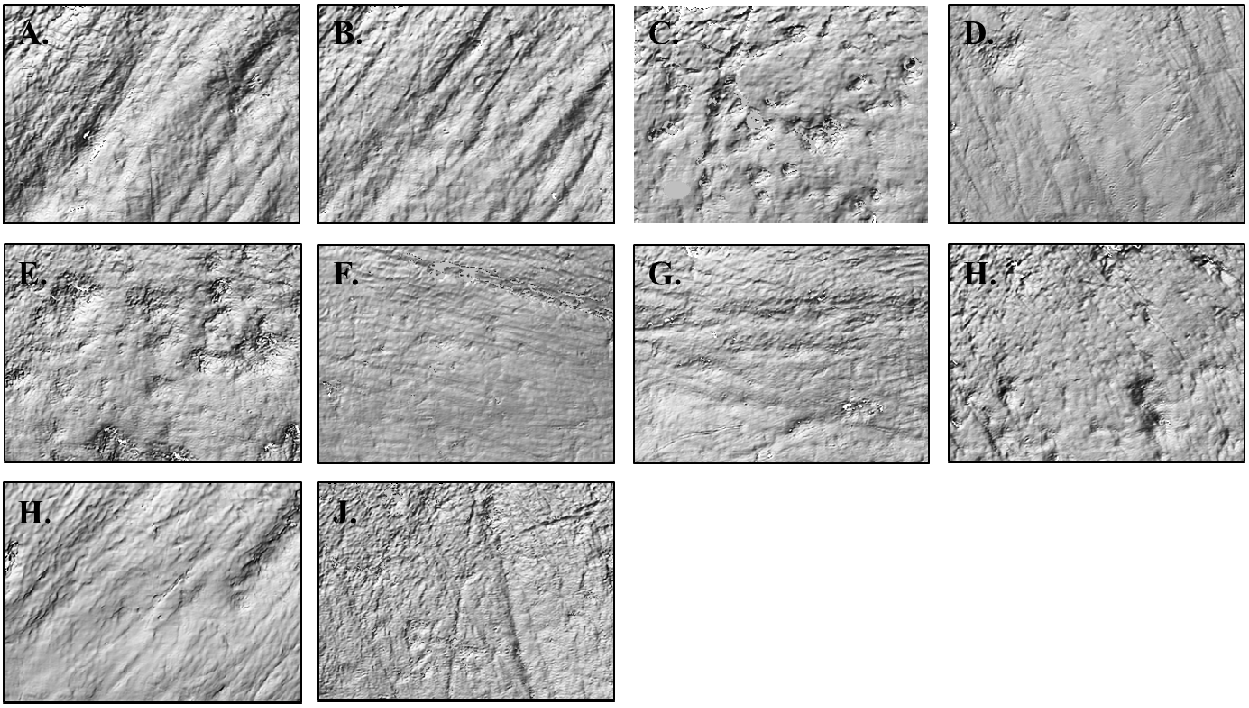


Figure 4. Bivariate plot of M_1 shear facet microwear texture anistropy and complexity for extant taxa by dietary category. Data are plotted for individuals with species as indicated by the markers.

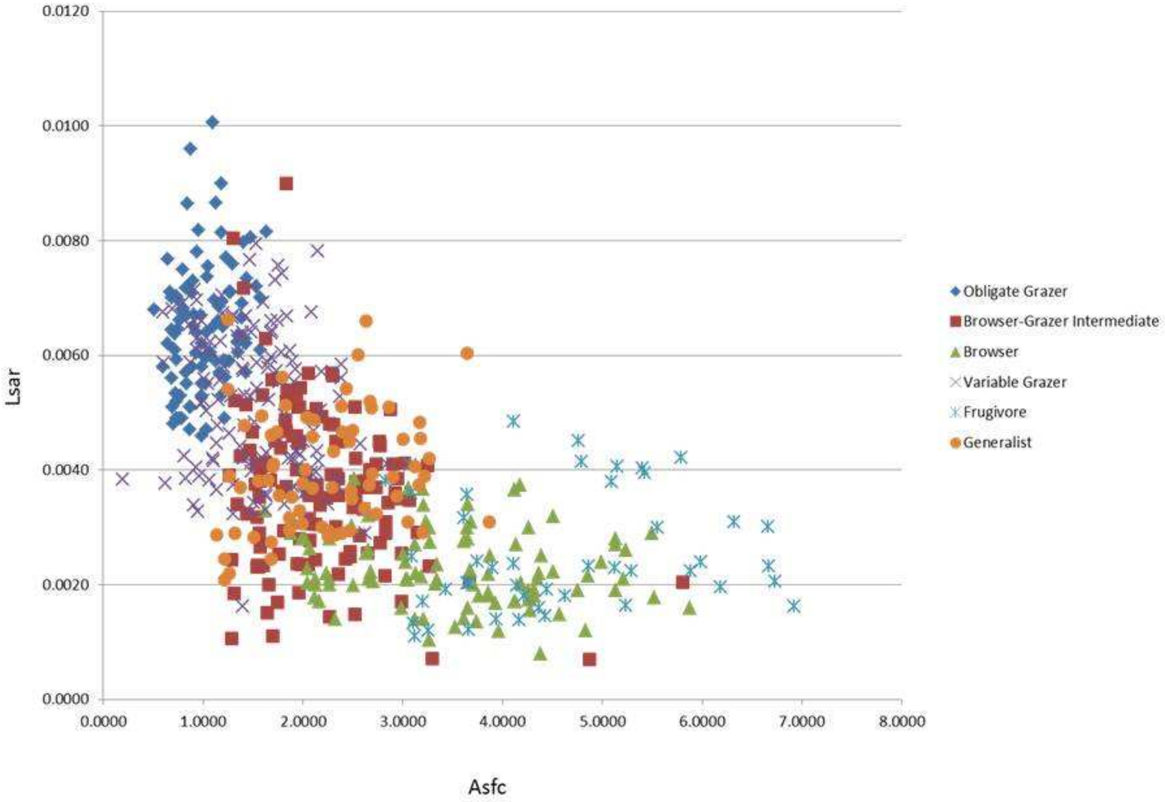


Figure 5. Bivariate plot of M_1 shear facet microwear texture anistropy and complexity for Hadar fossil taxa by member.

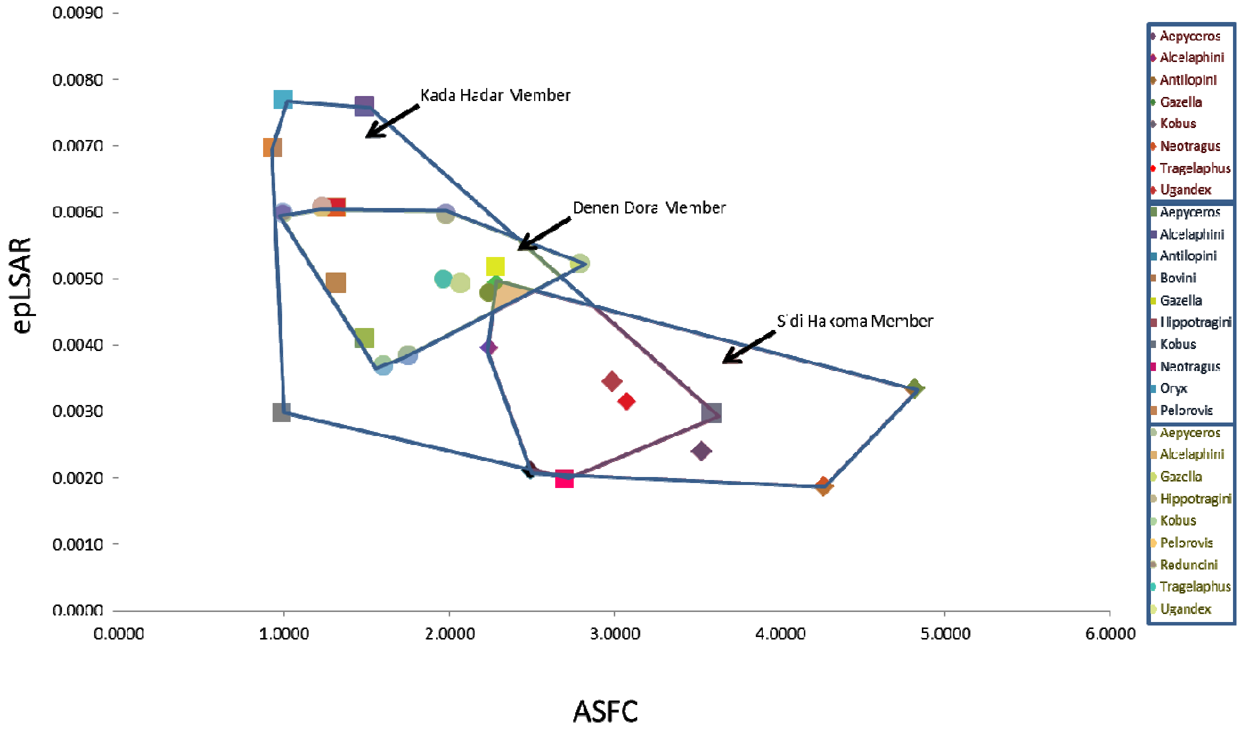
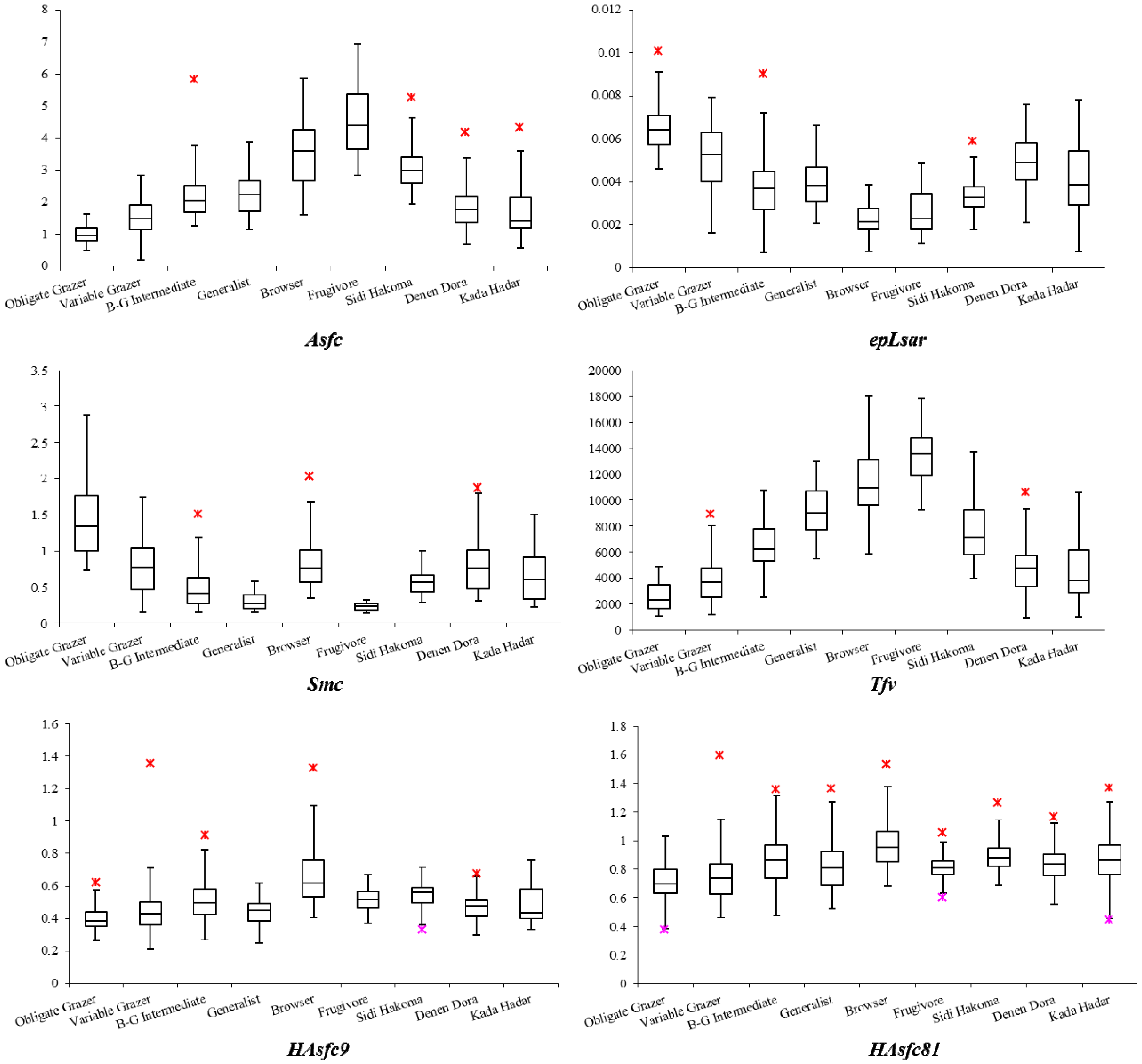


Figure 6. Box and whisker plots



Chapter Four: Paleoenvironmental change in Pliocene eastern Africa as inferred from dental microwear texture analysis of fossil Bovidae

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Abstract

Environmental hypotheses of Pliocene hominin evolution state that key ecological adaptations of early hominins are directly linked to shifts in local or regional climate. In order to determine relationships between climate change and human evolution, it is first necessary to reconstruct the habitats in which early hominins lived. This is especially important for Pliocene sites where increasing bipedality has been linked to a shift from closed woodland forests to more open, arid habitats. Many techniques have been used to refine our understanding of the Pliocene paleoenvironments of eastern Africa; however these have not led to consensus reconstructions. Here, I bring a new, independent dataset for the inference of diet, and by extension habitats, of individual bovids in the days before death. This study applies dental microwear texture analysis to reconstruct the diet, and therefore ecological contexts, of specimens from Kanapoi, Allia Bay and Laetoli. The microwear signatures of the fossils are interpreted using a comparative database of 25 extant species of African Bovidae and are compared to previously published data on the bovids from the Hadar hominin site in Ethiopia. Results indicate that the fossil bovid assemblages from all four sites included both browsing and grazing taxa, suggesting access to a wide variety of resources. The earlier sites include higher proportions of browsing taxa, suggesting more closed habitats on average. In general, the results presented here indicate that all of these sites associated with the early australopiths were mosaic and primarily composed of semi-closed habitats like woodland and bushland, with incursions of open savanna grassland.

Introduction

Many researchers have argued that climate change was a motive force for human evolution and that key ecological adaptations of australopiths were directly linked to shifts in local or regional climate (for examples, see Dart, 1925; Robinson, 1963; Howell, 1978; Vrba, 1985, 1988, 1992, 1995a, 1995b, 2000; Stanley, 1992; deMenocal, 1995; Hill, 1995; Potts, 1996, 1998, 2007; Bobe et al., 2002; Trauth et al., 2005). The "savanna hypothesis" (Dart, 1925, 1953; Bartholomew and Birdsell, 1953; Robinson, 1954; Washburn, 1960; Jolly, 1970; Laporte and Zihlman, 1983) and "turnover pulse hypothesis" (Vrba et al., 1989; Vrba, 1995a,b) both suggest that a shift toward drier, more open settings led to adaptations for bipedality and the consumption of savanna resources, including large grazing mammals. However, recent studies of marine sediment cores suggest that widespread C4 grasslands did not develop in eastern Africa until after 3.0 mya and therefore, would not have influenced the habitats of australopiths or earlier probable hominins (deMenocal, 1995; Leakey et al., 1995; White et al., 1994, 2009). Recent paleoclimatological models instead suggest that a wide range of habitats were available to early hominins, including closed and open woodland, gallery forest, bushland, and wet and dry grassland habitats (Kingston et al., 1994; Kappelman et al., 1997; Leakey et al., 1995; Reed, 1997; Wynn, 2000; Kingston and Harrison, 2001; Schoeninger et al., 2003; Bonnefille et al., 2004; Campisano and Feibel, 2007).

The Pliocene australopiths from eastern Africa, *Australopithecus anamensis* and *A. afarensis*, form a putative single anagenetic lineage suggesting changing adaptations over time (Kimbel et al., 2006). *Australopithecus anamensis* is best known from the sites of Kanapoi and Allia Bay in Kenya, and the largest collections of *A. afarensis* fossils have been found at Laetoli in Tanzania and Hadar in Ethiopia. The middle Pliocene dates associated with these chronologically distinct sites cover a span from 4.1-3.0 mya and represent a period of changing, variable habitats (deMenocal, 1995; Leakey et al., 1995). The proposed mosaic nature of these habitats has led to the suggestion that concomitant variation in available foods and diets might be considered a possible driving force behind evolutionary changes within the hominin lineage (Teaford and Ungar, 2000; Ungar, 2004; Reed and Fish, 2005; Kimbel et al., 2006). *Australopithecis anamensis* and *A. afarensis* are characterized by morphological adaptations for at least facultative bipedalism and more robust dentition than earlier taxa like *Ardipithecus ramidus* (White et al., 1994). The mosaic nature of reconstructed Pliocene sites accords well with the locomotor adaptations of the australopiths. *Australopithecus anamensis* and *A. afarensis* are characterized by postcranial adaptations allowing for both terrestrial bipedality and arboreal climbing (e.g., Rodman and McHenry, 1980; Johanson et al. 1987). This unique locomotor pattern has been hypothesized to be the result of an environmental shift towards mosaic habitats, where the ability to walk bipedally and yet retain climbing proficiency would have been beneficial.

The reconstruction of past environments often centers on the paleoecology of a single taxon or several taxonomic groups (e.g., Robinson, 1963; Vrba, 1974, 1975, 1980, 1988; Kay, 1975, 1978; Grine, 1981; Stern and Susman, 1983; Kappelman, 1988; Benefit and McCrossin, 1990, Ciochon, 1990; Spencer, 1995; Lewis, 1997). Paleoecological research on these fossil faunas has involved two principal approaches. Some have focused on the ecomorphology, or relationship between morphological adaptations and ecological preferences, of a single taxon (Vrba, 1974, 1975, 1980, 1988; 1995b; Grine, 1981; Kappelman, 1988; Spencer, 1995). Others have concentrated on analyses of fossil communities as a whole by using entire faunal assemblages from a fossil site to identify major locomotor and trophic adaptations, thus implying local environmental conditions (Dodd and Stanton, 1990; Behrensmeyer et al., 1997; Reed and Rector, 2006; Reed, 1998, 2007, 2008). Fossil bovids are frequently used as paleoenvironmental indicator species because they are ubiquitous at fossil sites and modern taxa can be placed into discrete dietary categories that reflect habitat preference (Kappleman, 1984; Vrba, 1980, 1982, 1985; Shipman and Harris, 1988; Harris, 1991; Plummer and Bishop, 1994; Spencer, 1997; Sponheimer et al., 1999).

In this paper, I evaluate previous reconstructions of paleohabitats associated with *A. anamensis* and *A. afarensis* by reconstructing the diets of the fossil bovids from the Pliocene sites of Kanapoi, Allia Bay and Laetoli in Tanzania using dental microwear texture analysis. This technique provides a measurement-error-free method for studying microwear, incorporating automated data collection and three-dimensional surface analysis. The fossil bovid data are considered in relation to an established microwear texture database featuring 25 extant African bovid taxa with known diet and habitat preferences (Scott, in press), as well as previously described fossil bovid taxa from the Sidi Hakoma, Denen Dora and Kada Hadar members of the Hadar Formation in Ethiopia, associated with *A. afarensis* (Scott, in review). This paper also addresses implications of inferred fossil bovid diets for paleoenvironments at the sites. Finally, I discuss how the ecological settings at these important sites may have changed over the temporal span of *A. anamensis* and *A. afarensis*.

Bovid paleoecology and habitat

Studies of faunal assemblages as paleoenvironmental proxies for a fossil site typically apply the principle of taxonomic uniformitarianism, which is based on the assumption that fossil species had the same ecological preferences as their closest living relatives. Although this assumption is rarely questioned for recent faunas, its utility for reconstructing the paleoecology of long extinct species is uncertain. The primary problems with taxonomic uniformitarianism are that it is not applicable to fossil taxa with few or no living relatives, and that it assumes that groups remain constant in their ecological preferences over long periods of time. While the concept of taxonomic uniformitarianism is relatively straightforward, critics have questioned many of its inherent assumptions (Solounias et al., 1988; Reed, 1996; Sponheimer et al., 1999; Schubert et al., 2006). For example, Sponheimer et al. (1999) demonstrated in a study of fossil bovid isotopes and ecomorphology that half of the included taxa had food preferences that differed from their assumed diets based on taxonomic uniformitarianism. While *Aepyceros* sp. and *Gazella vanhoepeni* were both assumed to be mixed/seasonal feeders like their closest living relatives, for example, isotopic signatures and ecomorphological data suggested that both were obligate browsers, and showed no evidence of C4 grass consumption. Another diet proxy that considers actual diets of individuals would certainly prove valuable for interpreting these discrepancies, and that is where dental microwear comes in.

Diet is the most direct way that an organism interacts with its environment. Attempts to reconstruct diets of fossil forms have included the use of tooth size, shape and structure. However these are all genetic signals that reflect only what a species capable of eating, not what individuals actually ate on a daily basis. The diet of an individual may vary over its lifetime, but it can take many generations for the morphology of species to change in response to selective pressures. Additionally, adaptation does not always imply food preference and less than optimal solutions given phylogenetic inertia may complicate interpretation. In order to reconstruct what individuals actually ate in the past, a non-genetic signal is needed. Dental microwear is direct line evidence of the foods eaten and, by extension, of the environments inhabited by extinct bovids. It can therefore be a valuable tool for habitat reconstruction.

Bovid diets have traditionally been classified as grazing, browsing and mixed feeding. These categories refer to the proportions of monocotyledons (grasses, sedges and roots) and dicotyledons (fruits, seeds, flowers, buds, leaves, tubers and shoots) included in their diets. Grazers consume more than 90% monocotyledons and inhabit open, arid environments (Fortelius and Solounias, 2000). Modern grazing bovids include Alcelaphini (wildebeest), Antilopini (gazelles), and Hippotragini (grazing antelopes) (Kingdon, 1982). Browsers eat more than 90% dicotyledons and live in closed, moist habitats like woodlands and forests (Fortelius and Solounias, 2000). Examples of modern browsing taxa include Aepycerotini (impala), Tragelaphini (kudu, eland, bongo, nyala and sitatunga), Reduncini (reedbucks and lechwe) and Bovini (buffalo and their relatives) (Kingdon, 1982). Finally, species classified as mixed feeders alternate between grazing and browsing and tend to inhabit seasonal and/or mosaic environments (Fortelius and Solounias, 2000). Extant mixed feeders include Cephalophini (duikers), Neotragini (dwarf antelope), Caprini (sheep and goats), and Boselaphini (four-horned antelope) (Kingdon, 1982). It should be noted, however, that actual bovid diets are often more complex than these categories suggest, and many intermediate classifications have been proposed (Gagnon and Chew, 2000). Even given the over-simplicity of the grazer-browser-mixed feeder categories, they have been proven useful in interpreting the diets and associated habitats of fossil bovids (Fortelius and Solounias, 2000; Merceron et al., 2004a, 2004b).

Differences in the dental microwear of grazing and browsing ungulates have been noted in previous studies of extant and fossil species (for examples, see Solounias et al., 1988; Solounias and Moelleken, 1993; Merceron and Ungar, 2005; Merceron et al., 2005; Schubert et al., 2006; Ungar et al., 2007), with browsers having more pits and grazers having more scratches. Mixed-feeding taxa tend to have intermediate microwear signatures, or patterns overlapping with browsers and grazers. This has important implications for reconstructing paleoenvironments, as while the connection between diet and habitat are not exact, grazing and browsing microwear signatures do imply the availability of grasses and woody plants respectively.

Hominin paleoenvironments in eastern Africa

Many techniques have been used to refine our understanding of the paleoenvironments of eastern Africa; however these have not led to consensus reconstructions. At Kanapoi, ecological diversity analysis indicates that at least part of the site was composed of closed woodland forest; however, taxonomic uniformitarianism of bovid taxa suggests a dry arid habitat. Similarly contradictory reconstructions exist for Allia Bay, with paleosol analysis and palynology suggesting a mosaic habitat dominated by savanna, and taxonomic uniformitarianism of faunal assemblages suggesting an environment composed of gallery forest, open woodland, floodplains and edaphic grasses. The Laetoli faunal assemblages have also led to varying reconstructions, with some suggesting habitats as disparate as open grassland and closed woodland. Here I test these opposing hypotheses using a new, independent dataset for the inference of diet by extension habitats of actual individuals in the days before death.

Although the link between dental microwear and paleoenvironment has been explored (Merceron et al., 2004a, 2005; Schubert et al., 2006; Ungar et al., 2007), few studies have used dental microwear to resolve conflicting interpretations of paleohabitat. This is surprising given the recognition of bovids as excellent paleoenvironmental indicators (Vrba, 1980, 1985; Kappelman, 1984; Plummer and Bishop, 1994; Spencer, 1997; Sponheimer et al., 1999). Due to the prevalence of fossil bovids at early australopith sites in eastern Africa, available bovid specimens from the sites of Kanapoi, Allia Bay and Laetoli are the focus of this study.

Materials and Methods

The fossil specimens used in this study are housed at the National Museums of Ethiopia (NME), Tanzania (NMT) and Kenya (NMK). All available maxillary and mandibular first and second molars were examined, as previous studies have not revealed significant differences in the microwear signals preserved on these teeth (Merceron et al., 2004a, 2004b). The teeth were assessed using the criteria of Teaford (1988) and King et al. (1999). The majority of fossil specimens examined were not suitable for microwear analysis, which is unsurprising given that bovid molars have thin enamel bands that are frequently damaged or broken. A total of 15 specimens from Allia Bay, 35 specimens from Kanapoi and 49 specimens from Laetoli possessed unobscured antemortem microwear and were included in the fossil sample, along with 124 specimens from Hadar that have been previously described (Scott, submitted). Table 2 details the fossil taxa and sample sizes. Only one tooth per individual was included to avoid bias in the sample.

This study uses a large microwear texture database of extant African bovids, previously published by Scott (in press) for comparison with the fossil taxa. This database includes 575 specimens representing 25 modern bovid taxa with well-understood diets and habitats. Original specimens are housed at the American Museum of Natural History (AMNH), New York; the Field Museum (FMNH), Chicago; the Smithsonian National Museum of Natural History (NMNH), Washington D.C.; and the Royal Museum of Central Africa (RMCA), Tervuren, Belgium. All are wild-shot specimens with known provenience. To ensure that the dietary reconstructions of the fossils are as precise as possible, extant bovids from all six diet categories of Gagnon and Chew (2000) were included in the comparative database. Particular emphasis was placed on the selection of taxa that engage in various levels of mixed feeding, as mosaic habitats have been suggested for all four fossil sites included in this study. The modern taxa considered here are equally variable in habitat preference, ranging from open-country grazers (e.g., *Damaliscus lunatus*, *Redunca arundinum*) to closed-forest frugivores and browsers (eg. *Cephalophus sylvicultor*, *Neotragus batesi*).

The extant taxa included in the comparative database as listed in Table 1, along with their dietary category as assigned by Gagnon and Chew (2000). This system for classifying diet was selected because it expands on the traditional browser-grazer-mixed feeder trichotomy to include multiple levels of mixed feeding. As in traditional classification systems for bovids, the dietary categories used here are determined by the approximate percentages of monocotyledons and dicotyledons consumed during observation in the wild, although fruit is considered separately from other dicotyledons. When applied to fossil taxa, the incorporation of these various levels of mixed feeding improves the overall resolution of dietary reconstruction and the usefulness of microwear texture data as a proxy for habitat preference.

Gagnon and Chew (2000) recognized six dietary categories, defined by the amount of monocotyledons and dicotyledons included in the diet, with fruit considered separately. Obligate grazers have uniform diets consisting of at least 90% monocotyledons. These taxa typically occupy more open habitats like grasslands and savanna. Browsers consume more than 70% dicotyledons, while frugivores restrict at least 70% of their diet to fruit. Bovids belonging to these categories are usually found in closed or semi-closed habitats like forest or woodland. Variable grazing taxa can vary diets both seasonally and geographically, but always include 60-90% monocotyledons. Browser-grazer intermediates also have variable diets, but regularly consume 30-70% monocotyledons and dicotyledons, always including some fruit. Generalist bovids have more catholic diets that consist of more than 20% of each of the three food types.

Bovids that consume a wide variety of resources are frequently found in environments that consist of multiple habitat types.

The molding and casting procedures used in this study are those of Ungar (1996). As is standard in studies of bovid dental microwear, data were collected from the disto-buccal enamel band of the mesial cuspid of $M1_{1\text{-}2}$ and the mesio-buccal enamel band of the mesial cusp of $M^{1\text{-}2}$ (Janis, 1990; Merceron, 2005; Schubert, 2006; Ungar et al., 2007), as illustrated in Figure 1. The teeth were cleaned with acetone-soaked cotton swabs and then molded with President's Jet regular body polyvinylsiloxane dental impression material (Coltène-Whaledent Corp.). The casts were poured using Epotek 301 high-resolution epoxy resin and hardener (Epoxy Technologies Corp.). This process has been demonstrated to produce surface replicas that are accurate to a fraction of a micron (Beynon, 1987; Teaford and Oyen, 1989).

The casts were scanned using a Sensofar PLµ white-light confocal profiler (Solarius Development Inc., Sunnyvale, CA). This instrument uses 3-D point clouds to create digital elevation models of microwear surfaces. Each specimen was scanned with a 100x objective to generate a point cloud with a lateral sampling interval of 0.18 µm, a vertical resolution of 0.005 µm, and a field of view of 102 x 138 µm. Four adjoining scans were collected for each specimen, for a total work envelope of 204 x 276 µm. Solarmap Universal software (Solarius Development Inc., Sunnyvale, CA) was then used to level each scan. Dust particles and other adherents were removed from the scans using the erase and/or thresholding functions in Solarmap. The resulting point clouds were analyzed with Sfrax and Toothfrax scale-sensitive fractal analysis software (Surfract Corp, Worcester, MA.).

Scale-sensitive fractal analysis is based on the principle that apparent surface textures change with scale of observation. A surface that appears smooth when viewed at a coarse scale may appear quite rough when examined at a fine scale. Apparent surface texture can be quantitatively characterized using several texture variables. Data were generated for five of these variables previously identified as informative for dietary reconstruction: area-scale fractal complexity (*Asfc*), length-scale anisotropy of relief (*epLsar*), scale of maximum complexity (*Smc*), textural fill volume (*Tfv*) and heterogeneity of area-scale fractal complexity (*HAsfc*). Specific details concerning these variables are well-documented in the literature (Ungar et al., 2003, 2007, 2008; Scott et al., 2005, 2006).

In general, taxa that consume hard or brittle foods tend to hard higher values for *Asfc*, *Tfv* and *HAsfc* as well as lower values for *epLsar* and *Smc* than do closely-related species that consume soft resources (Scott et al., 2006; Ungar et al., 2007, 2010; Prideaux et al., 2009; Schubert et al., 2010, Scott, in press; submitted). Complexity is a measure of surface roughness; and individuals with microwear surfaces dominated by pits will have high values for this variable. Anisotropy measures tendency toward directionality of surface features. Microwear surfaces dominated parallel striations should have high values for anisotropy. Previous studies have suggested that the range of scales at which complexity is calculated may be informative (Scott et al., 2005, 2006) and those scales yield the *Smc* variable. Higher *Smc* values correspond with fewer small features. Texture fill volumeis a three-dimensional measure of feature size, so surfaces with higher values for this variable tend to have many features in the 2-10 µm diameter range. Finally, *HAsfc* measures the overall heterogeneity of the surface by dividing each scan area into progressively smaller subsections and comparing the complexity of each. Two heterogeneity variables that have been used for distinguishing extant taxa with known differences in diet are $HAsfc_9$, which divides in surface into a 3 x 3 gridand $HAsfc_{81}$, which divides the surface into a 9 x 9 grid.Individuals with features that vary across a surface typically have higher values for this variable than more surface homogeneity.

Statistical Analyses

Statistical analyses of the baseline sample have been previously published (Scott, in press), so the analyses here were focused on determining the extent of dietary variation found both within and among the fossil bovids at the four sites. The three Hadar submembers were considered independently since previous analysis has determined that the paleoenvironmental signals between them vary significantly (Scott, in preparation). Five variables showed significance in the overall model and included in the remaining statistical analyses: 1) *Asfc*,2) *epLsar*, 3) *Smc*, 4) *Tfv*, and 5) $HAsfc_9$.

Differences among fossil sites

The fossil bovid microwear data were analyzed using a general linear model to determine the extent of differences in microwear among the taxa within, as well as among, the sites. Data were rank transformed because raw microwear data typically violate assumptions inherent to parametric tests (Conover and Iman, 1981). I also employed analyses of variance for the individual texture attributes and pairwise comparisons tests to determine the sources of significant variation both among taxa within individual fossil assemblages and between sites. Tukey's Honestly Significant Difference (HSD) and Fisher's Least Significant Difference (LSD) tests were both used to balance the risks of Type I and Type II errors (Cook and Farewell, 1996). Where, $p<0.05$ for Fisher's but not Tukey's test, the result was considered of marginal significance and suggestive.

Comparisons of extant and fossil taxa

Hierarchical cluster analysis was also used to cluster fossil groups with extant bovids, using each of the microwear variables that showed significant variation among taxa in the ANOVA models. Each of the texture variables was considered separately because they reflect different scales. Euclidean distance and complete linkage were used, following Fortelius and Solounias (2000). In each case, the extant taxa were grouped by dietary category and the fossil taxa were grouped by site and/or member.

Results

Microwear texture summary statistics for individual taxa are presented in Table 2. Analytical statistics are presented in Tables 3 and 4. Examples of photosimulations and three-dimensional reconstructions of microwear surfaces of the fossil taxa are pictured in Figure 2. Similar images for the comparative taxa are presented in Figures 3.

Statistical analyses of the comparative sample can be found in Scott (in press). The MANOVA results for the fossil bovid sample indicate significant variation in the overall model. Individual ANOVA tests reveal significant variation in all microwear variables except $HAsfc_{81}$. Pairwise comparisons tests reveal that the Kanapoi, Allia Bay and Sidi Hakoma samples do not differ significantly from one another in any attributes, although there are suggestive differences between these sites. These samples generally have high values for *Asfc*, *Tfv* and $HAsfc_9$. The samples from the Laeotil Beds and the Denen Dora and Kada Hadar Members also cluster together, with higher values for *epLsar* and *Smc*.

Significant differences among sites by microwear variable

Asfc- Bovids from the sites fall into two discrete complexity groups when analyzed with a Tukey's HSD test- Kanapoi, Allia Bay, the Sidi Hakoma Member and the Laeotil Beds in one group and the Denen Dora and Kada Hadar Members in the other. Kanapoi and Allia Bay have the highest values for this variable, while the Denen Dora and Kada Hadar Members of the Hadar Formation have the lowest value.

Smc- When analyzed with a Tukey's HSD test, only bovids from the Sidi Hakoma Member of the Hadar Formation, which has the lowest value for this variable, and from the Laeotil Beds, which has the highest value, vary significantly in the *Smc* variable. However, a Fisher's LSD test also suggests marginal differences between bovids in the Sidi Hakoma and Denen Dora Members, as well as between those from Kanapoi and the Laeotil Beds.

epLsar- The anisotropy variable also clearly differentiates bovids by site using ANOVA and Tukey's tests. The Kanapoi, Allia Bay and Sidi Hakoma Member of Hadar bovids group together with the lowest values for this variable and are significantly different those from the Denen Dora and Kada Hadar Members of Hadar. The Laeotil Bed bovids have mid-range anisotropy values and are significantly different from Allia Bay, Denen Dora and Kada Hadar.

Tfv- Tukey's HSD analyses of the textural fill volume variable suggests significant differences among the sites, resulting in two primary groups. The Kanapoi, Allia Bay and Sidi Hakoma Member bovids cluster together with the highest values for this variable, while the Denen Dora and Kada Hadar bovids have the lowest values. Additionally, the bovids from the Laeotil Beds are significantly different from the Allia Bay sample when analyzed with Tukey's tests, and are marginally different according to Fisher's LSD tests compared with those from Kanapoi and the Denen Dora Member.

$HAsfc_9$- The bovids from Allia Bay have the highest value for this variable and are significantly different from those from all of the other included sites, with the exception of Sidi Hakoma. A Fisher's test also suggests differences among the Sidi Hakoma Member, Kanapoi and Denen Dora.

Hierarchical cluster analysis

The results of the hierarchical cluster analyses for each variable are depicted in Figure 4. In sum, the Kanapoi, Allia Bay and Sidi Hakoma Member samples cluster together for most variables, along with modern frugivorous, browsing and/or browser-grazer intermediate taxa. On the other hand, the fossil samples from the Laeotil Beds and the Denen Dora and Kada Hadar Members generally cluster with the extant obligate and/or variable grazers.

Results by variable

Asfc-There are two distinct clusters for microwear complexity (*Asfc*). The taxa with the highest values for this variable, including the fossils from Kanapoi, Allia Bay and Sidi Hakoma, and the extant browsers and frugivores, are clearly separate from all other taxa. There is also a second-order division for this variable, with the bovids from the Laeotil Beds and the extant generalists and browser-grazer intermediates separating from the Kada Hadar and Denen Dora fossils and the modern obligate and variable grazers.

Smc- There are also two primary divisions for scale of maximum complexity (*Smc*) variable. The modern browser-grazer intermediates, generalists and frugivores are separated from the other taxa. The latter group contains two main subdivisions: the Allia Bay, Denen Dora and Laeotil Bed fossils with the modern browsers and variable grazers, and the Kanapoi, Kada Hadar and Sidi Hakoma bovids. None of the fossil bovids cluster with modern obligate grazers for this variable.

epLsar- The anisotropy variable (*epLsar*) divides the taxa into two primary clusters, with the Denen Dora and Kada Hadar fossils, along with the modern obligate and variable grazers, having higher values for this variable than the other groups. The taxa with the lower values further divide into two clusters. The Allia Bay fossils group with the modern browsers and frugivores, while the Kanapoi, Sidi Hakoma and Laetoli fossils are most similar to extant browser-grazer intermediates and generalists.

Tfv- There are also two primary clusters for textural fill volume (*Tfv*). The group with the highest values for this variable includes the Kanapoi and Allia Bay fossils and the modern generalists, browsers, and frugivorous taxa. The remaining group contains two secondary divisions. The first is comprised of the Denen Dora and Kada Hadar fossils and the extant obligate and variable grazers, while the second contains the bovids from Laetoli and Sidi Hakoma, along with modern browser-grazer intermediates.

$HAsfc_9$- Finally, the heterogeneity variable ($HAsfc_9$) separates the taxa into two primary groups. The fossils from Kanapoi and Allia Bay cluster with the extant browsers, frugivores and generalists. The second cluster is further divided. The Sidi Hakoma and Laetoli fossils group with the modern browser-grazer intermediates while the Denen Dora and Kada Hadar fossils cluster with the extant obligate and variable grazers.

Discussion

The dental microwear data presented here provide a strong basis for the reconstruction of fossil bovid paleoecology, including habitat preference. These data offer an opportunity to evaluate previous paleoenvironmental reconstructions for Kanapoi, Allia Bay and Laetoli. When they are considered alongside the data from Hadar, these data can contribute to the larger discussion of the ecological context of hominin evolution.

Paleoenvironmental reconstructions

Kanapoi- The site of Kanapoi is located in the Kerio River Valley of northern Kenya and has been dated to 4.2-4.17 mya (Leakey et al., 1995). It is composed of fluvial and deltaic sediments accumulated during a major lacustrine phase (Harris and Leakey, 2003). The dating and stratigraphy of Kanapoi are well established and provide solid temporal constraints for the *A. anamensis* fossil material found there (Leakey et al., 1995, 1998). While Pickford's (2001) study of the hominins from the site has called into question the integrity of the deposit (Pickford, 2001), Leakey et al.'s (1998) descriptions of specimen preservation as carnivore-damaged, fragmented and weathered, indicates that the assemblages are the result of attritional accumulation rather than mixing by taphonomic processes.

The Kanapoi paleosols provide an excellent opportunity for paleoenvironmental reconstruction, because the majority of the early hominin material is derived from two distinct strata, the Dite paleosols (Wynn, 2000). Stable carbon isotope analysis of these paleosols suggests a semi-arid and seasonal climate (Cerling, 1992). The Dite paleosols have high concentrations of carbonates that are only formed during arid periods, and this combined with fossilized seasonal vegetation has led to the hypothesis that *A. anamensis* at Kanapoi inhabited a mosaic environment that ranged from gallery woodlands to forb-dominated edaphic grasslands (Cerling, 1992; Kingston, 1994). Pollen data also suggest that Kanapoi was a highly mosaic habitat. Bonnefille (1995) found large percentages of Gramineae pollen, usually associated with clearings in forest or woodland environments, in the hominin-bearing strata at the site. Most recently, Cerling et al. (2011) reexamined $^{13}C/^{12}C$ ratio data from hominin-bearing sites at

Kanapoi, as well as many other early hominin localities, and argued that open habitats like wooded grassland would have composed a significant portion of these sites during the late Pliocene.

Analyses of the fossil fauna have suggested that Kanapoi comprised variety of microhabitats. Leakey et al. (1995), categorized the majority of the assemblage from the Dite paleosols as adapted for dry, open bushland, based on taxonomic uniformitarianism, with some browse-adapted bovid taxa like reduncin and aepycerotin indicating the presence of gallery forest in the region, probably along river channels. Reed (1997), on the other hand, used ecomorphological analyses of the fauna and ecological structure analysis to conclude that early australopith habitats were fairly static and tightly constrained by annual rainfall and tree cover. In general, although all lines of evidence have led to the conclusion that a variety of habitats and food resources would have been available to early *A. anamensis*, disagreement remains about the degree of ecological mosaicism at Kanapoi.

The microwear texture data support the previous reconstructions that indicate the presence of both closed forest and open gallery woodland at Kanapoi (Cerling, 1992; Kingston, 1994; Bonnefille, 1995; Cerling et al., 2011). The overall microwear values for the Kanapoi bovids, deposited between 4.2-4.17 mya, are similar to those from Allia Bay at 3.9 mya and the Sidi Hakoma Member at Hadar, dating to 3.42~3.26 mya. This suggests that *A. anamensis* and early *A. afarensis* probably occupied, or at least had regular access to, somewhat closed habitats.

The overall dental microwear of the Kanapoi bovids most closely resembles that of modern browser-grazer intermediates and generalists. When broken down into individual fossil taxa, a range of dietary preferences is indicated. Three of the seven fossil taxa have reconstructed diets similar to those of their closest living relatives. *Madoqua* sp., for example, has a microwear signature consistent with a browser-grazer intermediate diet, comparable to that of the modern antilopine, *Neotragus batesi*, a species whose diet consists of 80% dicots with some monocot and fruit consumption (Skinner and Smithers, 1990). This extant species is most commonly found in dry forest and thick bushland (Kingdon, 1997). The microwear of *Tragelaphus* sp.is not distinguishable from that of the extant *T. euryceros*, which consumes 75% dicots, along with some fruit and monocots and prefers dense forest habitats (Hofmann and Stewart, 1972). The remaining taxa, however, have wear patterns that suggest a different dietary strategy than that practiced by their modern congeners, suggesting that taxonomic uniformitarianism is not a reliable indicator of food preference for these bovids. For example, the microwear of the Alcelaphini sp. specimens from Kanapoi most closely resembles that of modern browser-grazer intermediates, but most modern alcelaphines are variable grazers. Likewise, *Raphicerus* sp. has a similar microwear pattern to modern browsers, but the three modern species are all classified as either browser-grazer intermediates or generalists.

When considered as a group, the Kanapoi bovids present a picture of a local environment with considerable forest habitat, or at least one with consistent access to nearby forest resources. The results of this study are consistent with the preliminary paleoenvironmental reconstruction of Kanapoi by Leakey et al. (1995). These authors suggested that australopiths at the site occupied a mosaic habitat composed of dry bushland and gallery forest. The microwear texture values for all but two of the bovid taxa from the site fall into the range of browser or browser-grazer intermediate species and are most similar to modern taxa that prefer forest or woodland habitats. However, there are indications of more open habitats at Kanapoi. Wynn (2000) utilized paleosols analysis to suggest that the environment at Kanapoi was more open than previously thought, including open low tree-shrub savanna. The presence of *Simatherium* sp. and *Hippotragus* sp.,two bovids with microwear signatures similar to modern open-country adapted grazers, suggests the presence of at least some grassland and supports previous reconstructions of Kanapoi as a mosaic habitat (Wynn, 2000; Cerling et al., 2011).

Allia Bay- The Allia Bay hominin site is located on the eastern shore of Lake Turkana in northern Kenya, and associated with the Omo River Drainage Basin. This site, which has been dated to 3.9 mya, is the last known locality associated with *A. anamensis* (Coffing et al., 1994; Leakey et al., 1995). Although the modern environment at Allia Bay is not riverine, five million years ago, this site was located on the banks of the Omo River (Coffing et al., 1994). The modern habitat is arid grassland, and previous reconstructions have suggested that temperatures during the occupation of *A. anamensis* were probably similar to the present (Dowsett et al., 1996). Reconstructions of ancient sea level, however, suggest that precipitation would have been higher during the Pliocene, making more closed habitats possible (Dowsett et al., 1996).

Most reconstructions of the Allia Bay paleoenvironment suggest a mosaic habitat of open woodland forest with expanses of grassland. The fossil plant composition at the site is primarily C3 trees and shrubs, with only 20-40% C4 grasses associated with open savanna (Cerling et al., 1988). The fossil fauna from the sites also suggests a mosaic paleoenvironment. These assemblages contain mammalian taxa that have been associated with habitats as diverse as gallery forest, bushland and open floodplain (Coffing et al., 1994; Feibel et al., 1991). Feibel et al. (1991) combined both floral and faunal data to suggest that the Turkana Basin was dominated by riparian woodland and gallery forest during the Pliocene, and that grassland probably existed on floodplains and on the borders of the extensive seasonal stream systems. Carbon and oxygen isotope analysis of fossil herbivore tooth enamel also indicates a variety of habitat types and eurytopic adaptations for all documented taxa (Schoeninger and Reeser, 1999; Schoeninger et al., 2003).

While most studies have suggested a mosaic habitat dominated by woodland, some have opined that savanna was a more important component of the overall environment than previously thought. Using a study of pedogenic carbonates, Wynn (2000) suggested that open savanna was the predominant habitat type at Allia Bay during the occupation of *A. anamensis*. Carbon isotope ratios of marine samples also hint at a drier, more arid climate, similar to that at the site today (Raymo et al., 1996). In sum, while most studies agree that the early hominins had access to a variety of resources at Allia Bay, there is a lack of consensus on the importance of open versus closed habitats at the site.

Studies of stable isotopes (Cerling et al., 1988), palynology and faunal composition (Feibel et al., 1991; Coffing et al., 1994) suggested that Allia Bay was dominated by more closed habitat; and the bovid microwear data presented here are consistent with this hypothesis. The alcelaphin and *Tragelaphus* sp. specimens have dental microwear signatures that overlap with modern browsers and browser-grazer intermediates. While these data do not support previous reconstructions of Allia Bay as composed entirely of dry savanna, it does leave open the possibility of a mosaic habitat that included open grassland.

The alcelaphin sample from Allia Bay, while small, has a microwear signature that is very different from that of their modern relatives, *Damaliscus lunatus* and *D. pygargus*, which are classified as obligate and variable grazers respectively (Gagnon and Chew, 2000). In fact, the microwear textures of alcelaphins from this site are most similar to the extant steenbok, *Raphicerus campestris*, which consumes mostly browse and fruit, and grazes less than 30% of the time (Skinner and Smithers, 1990). This diverse diet is supported by preferred habitats that include woodland and acacia savanna. Kingdon (1997) suggested that these bovids prefer transitional or even ecologically unstable habitats, and this may indicate that the Allia Bay paleohabitat had similar mosaic qualities.

Reconstructions based on taxonomic uniformitarianism are more consistent with microwear textures for other bovids from Allia Bay. The *Tragelaphus* sp. specimens from Allia Bay have a microwear signature that is indistinguishable from that of the modern tragelaphine, *T. euryceros*. The modern bongo occupies dense forests and is typified by a diet that consists primarily of browse from shrubs and low-hanging trees (Kingdon, 1982, 1997). The similarity between the microwear textures of these congeners strongly implies the presence of some forest coverage in or near the Allia Bay site.

While the previous reconstructions for Allia Bay have suggested a relatively closed habitat, there are also indicators of a highly seasonal environment. Macho et al. (2003) reported dental stress lines in the teeth of fauna from the site, including bovids, and that these strongly suggested seasonal fluctuations similar to those found in parts of Africa today (Feibel, 1999). Research on the relationship between dental microwear and seasonality are limited for bovids (Merceron et al., 2010), but study to date does suggest that seasonal changes in diet are reflected in the dental microwear texture. The results of the current study suggest that seasonal variation was present at Allia Bay, as all of the fossil bovid taxa have microwear signatures that are most similar to modern taxa with highly seasonal diets.

<u>Laetoli</u>- The Laetoli hominin site is located in northern Tanzania and is composed of an extensive series of outcrops that date from 4.2 mya-120 kya (Leakey and Harris, 1987). The strata associated with *A. afarensis*, the Upper Laetolil Beds,are dated to 3.7-3.5 mya. These beds are composed of several localities separated by volcanic tuffs that have been reliably dated to 3.6

mya (Hay, 1987). In general, reconstructions of Laetoli during the occupation of *A. afarensis* have been inconsistent, with inferred habitat ranging from open savanna to closed wetland (Leakey and Harris, 1987; Radosevich et al., 1992).

Early ecological studies hypothesized that the environment inhabited by the australopiths at Laetoli was similar to the modern savanna grassland habitat at the site (Hay, 1980; Harris, 1985; Bonnefille and Riollet, 1987; Leakey and Harris, 1987). This conclusion was supported by sediment cores that revealed extensive aeolian deposits of sand-sized ash particles, indicating a habitat with xeric vegetation (Hay, 1980). Paleosol analysis by Hay (1987) also revealed high frequencies of ash and phillipsite, commonly formed in dry, arid climates. Finally, pollen analysis and assemblages of preserved leaves and twigs from the hominin-bearing strata were reported to contain floral taxa closely related to modern species found in savanna grassland habitats (Bonnefille and Riollet, 1987; Hay, 1987).

Faunal assemblages have also been cited as support a savanna grassland reconstruction. Gentry (1981) observed that the Laetoli bovid assemblage is composed primarily of alcelaphin, antilopin, and neotragin taxa whose modern congeners inhabit more open habitats. Other taxa have also been utilized for paleoenvironmental reconstructions at Laetoli. Suid species associated with dry, open conditions, like *Nyanzachoerus euilus*, are among the more common fauna recovered from the site (Harris, 1987). Additionally, two arid-adapted species of tortoise (*Geochelone laetoliensis* and *Geochelone brachygularis*) are also found in the assemblages, as well as several genera of gastropods not common outside of dry environments (Meylan and Auffenberg, 1987; Verdcourt, 1987). All of these lines of evidence have led to the conclusion that dry savanna grassland and open woodland were dominant habitat types at Laetoli during the occupation of *A. afarensis*.

However, other analyses have suggested the Laetoli was a more complex environment than previously thought and might have included closed, deciduous woodland forest as an important part of the ecosystem (Cerling, 1992; Reed, 1997; Musiba, 1999; Harrison, 2005, Musiba et al., 2007; Su and Harrison, 2007). Andrews' (1989) study of ecological diversity at the site was the first to suggest a forested habitat, concluding that the frequency of arboreal fauna at Laetoli was best explained by a heavily wooded setting. He did note, however, that the presence of these taxa could also be the result of faunal mixing from a mosaic ecosystem or habitat changes during the late Pliocene. However, more recent studies of the Laetoli fauna have also supported the closed woodland/mosaic hypothesis. For example, Reed (1997) argued that the diverse assemblages of frugivorous and arboreal mammals are strong indicators of the presence of closed woodland habitats at the site.

Studies of bovid ecomorphology have also suggested that the initial reconstructions of Pliocene Laetoli as similar to the modern savanna grassland might be too simplistic. In fact, modern congeners of many of the bovid taxa represented in the fossil assemblage are not currently found in the Serengeti region. Although some taxa are associated with open habitats, others are more often found in wooded or mosaic habitats. These include Tragelaphini, Bovini and Cephalophini (Gentry, 1987; Bobe et al., 2002). Indicator taxa common in modern savanna ecosystems, like Hippotragini, are not abundant at Laetoli, while the bushland-adapted *Madoqua* is among the most common taxa at the site (Gentry, 1987; Kingdon, 1997). Additionally, the presence of forest adapted pythons and elephant shrews contradict the savanna model and suggest the presence of mosaic woodland habitats (Meylan and Auffenberg, 1987; Butler, 1987). The emerging picture of Laetoli as a complex environment is also supported by evidence from isotopes and palynological studies. Cerling (1992) conducted stable isotope analysis of the paleosols from the hominin-bearing strata and found evidence for substantial quantities of C3 plants, suggesting that wooded habitats were common at Laetoli during the time of *A. afarensis*. Palynological comparisons of the modern and fossil pollen assemblages at the site are also consistent with more closed forests in the Pliocene than today (Bonnefille and Riollet, 1987).

The conflicting results from various studies of floral and faunal assemblages at Laetoli have been interpreted as indicators of a complex environment composed of a wide range of open and closed microhabitats. The dramatically different interpretations of the site may reflect a sampling bias or misinterpretation of the stratigraphically indistinguishable tuffs that make up the hominin-bearing strata (Gifford, 1981; Musiba et al., 2007). Another possible explanation for the confusing signal is taphonomic bias, and previous studies have suggested both sediment mixing and extensive bioturbation as potential contributing factors (Andrews, 1989; Harrison, 2005).

The reconstructions of paleoenvironment of the Upper Laetolil Beds have been more conflicting than those for any of the other sites addressed in this study, with inferred habitat ranging from closed woodland forest to open, arid savanna. If we assume that the faunal assemblages collected are not the result of taphonomic bias (Andrews, 1989; Harrison, 2005) or ill-defined stratigraphy (Gifford, 1981), the picture that emerges for the Upper Laetolil Beds is one of a mosaic environment even more complex than the one found at the modern site. The microwear evidence supports this hypothesis with dietary reconstructions for local bovid fauna including dedicated browsers/frugivores and variable grazers.

The Laetoli bovids evince a wide variety of microwear signals, suggesting a myriad of available resource types. Most of the fossil bovids from Laetoli have microwear signatures that overlap with modern browser-grazer intermediates. The alcelaphin and *Simatherium* sp.

specimens are most similar to the extant eland, *Taurotragus oryx*. This taxon inhabits grassland, bushland and open woodland and is known for a highly seasonal diet alternating between grazing and browsing (Skinner and Smithers, 1990; Kingdon, 1997). The microwear of the bovinspecimens overlaps with *Raphicerus sharpei*, the modern grysbok. This taxon lives in shrub and tall grasslands, consuming approximately 70% browse/fruit and 30% grasses (Kingdon, 1982). Finally, the specimens of *Gazella* sp. from Laetoli have a texture signature similar to that of the modern springbok, *Antidorcas marsupialis*,which occupies shrub and grasslands and consumes a variable diet (Skinner and Smithers, 1990).

Although many of the Laetoli bovids have been reconstructed as consuming a wide variety of resources, others appear to have had narrower diets. For example, *Antidorcas* sp., *Madoqua* sp., and *Tragelaphus* sp. all have microwear signatures that overlap with modern dedicated browsers and/or frugivores, suggesting regular access to forest resources. *Antidorcas* sp. most closely resembles the modern pygmy antelope, *Neotragus batesi*, which occupy dense forest and thick bushland habitats (Kingdon, 1982). The *Tragelaphus* sp. sample has a texture signal similar to that of their modern congener, *T. euryceros*, the bongo. This species lives in dense forest habitats and consumes more than 85% browse and fruit resources (Hofmann and Stewart, 1973; Kingdon, 1982). The *Madoqua* sp. specimens from Laetoli cluster with extant frugivorous duikers, *Philantomba monticola*, that inhabit rainforest (Kingdon, 1982).

Other fossil taxa appear to have focused on grazing. The *Hippotragus* sp. sample has a microwear signature nearly identical to that of the modern variable grazer, *Damaliscus pygargus*, which occupies open highveld grasslands. The fossil *Parmularius* sp. also has a grazing signature, most similar to *Kobus ellipsiprymnus*. These modern waterbucks prefer open savanna and scrub habitats, which provide year-round access to grasses (Kingdon, 1997). The fact that these likely grazers are common in the faunal assemblage at Laetoli suggests the presence of, or at least proximity to, more open grassland environments.

The presence of bovids exhibiting a wide variety of dietary strategies suggests that the Laetoli hominin site was highly mosaic in nature. The dental microwear evidence presented here indicates that the local bovid taxa had regular access to resources found in both open and closed microhabitats. This supports and strengthens the previous reconstructions of Laetoli as containing closed forest (Andrews, 1989; Cerling, 1992; Reed, 1997; Musiba, 1999; Harrison, 2005, Musiba et al., 2007; Su and Harrison, 2007), but does not rule out the presence of grasslands, given to the presence of at least two grazing species. The predominance of browse-adapted taxa suggests, however, that closed habitats made up a significant component of the paleoenvironment at the site.

<u>Hadar</u>- The Hadar hominin locality in the Afar Region of Ethiopia dates to 3.42-2.9 mya and is the last known site associated with *A. afarensis* (Walter et al., 1984; Walter and Aronson, 1993; Walter, 1994; Campisano and Feibel, 2007). Approximately 370 *A. afarensis* individuals have been recovered from the site, along with more than 7500 other vertebrate specimens (Reed, 2008). As at Laetoli, paleoenvironmental reconstructions based on the associated fauna, sedimentology and paleosols at Hadar have generally indicated the presence of a mosaic of habitats that fluctuated between open and closed and woodland and grassland (Johanson et al., 1982; Radosevich et al., 1992).

The Hadar Formation was occupied by *A. afarensis* for more than 400 ky, and remains of these fossil hominins have been recovered from the Sidi Hakoma (~3.42-3.26 mya), Denen Dora (~3.26-3.2 mya), and Kada Hadar (<~3.2 mya) members (Taieb et al., 1976; Campisano, 2007). Studies of local geology have revealed that these formations were deposited during periods of high fluvial activity of a large river system associated with the site, as well as incursions of a reoccurring paleolake (Aronson and Taieb, 1981). Comparison of preserved floral and faunal assemblages from the various members provides a unique opportunity to assess habitat change over time at Hadar during the occupation of *A. afarensis*.

Details of the dental microwear of the bovids from the Hadar hominin locality are detailed elsewhere (Scott, in review), and will be considered here in relation to results from the other sites. In general, significant differences were found between the microwear textures of the bovid samples from the three hominin-bearing strata: the Sidi Hakoma Member, the Denen Dora Member and the Kada Hadar Member. While all three faunal assemblages evidently contain both grazers and browsers, there is a general trend toward increasing numbers of variable and obligate grazers in the more recent strata.

Dental microwear texture analysis as a test of taxonomic uniformitarianism

One of the advantages of dental microwear analysis is that it provides direct evidence of what an animal actually ate during its lifetime. Many other forms of dietary reconstruction rely on morphology alone, resulting in conclusions based on what the animal may have been adapted to eat. However, diet can change quickly due to shifts in available resources and it can take many generations for morphology to change accordingly. Sponheimer et al. (1999) used stable isotope analysis to compare dietary reconstructions of fossil bovids from the South African site of Makapansgat based on taxonomic uniformitarianism to those resulting from the isotopes. Their results indicated inconsistencies between the reconstructions for nearly half of the taxa they studied. If bovids are going to be used as paleoenvironmental indicators, accurate reconstructions of diet must be available.

The current study offers similar results for the fossil bovids of Allia Bay, Kanapoi, Laetoli and Hadar. Only three of the seven taxa from Kanapoi, two of the three at Allia Bay, and five of the nine at Laetoli have reconstructed diets similar to their modern counterparts. Morphology is an important factor in how we understand and interpret paleoecology and should therefore continue to be a major component in dietary reconstruction. However, as this study and that of Sponheimer et al. (1999) have demonstrated, a combined approach including direct evidence of diet like microwear or isotopes, as well as morphology should be applied whenever possible.

African Pliocene Climate Dynamics and Human Evolution

Early studies of hominin paleoenvironments have suggested that the changes in locomotion and dentition associated with *A. anamensis* and *A. afarensis* were adaptations to receding forests and spreading savannas. However, marine sediment cores have revealed that increases in aridity and the spread of extensive grasslands did not occur in East Africa until after 3.0 mya and would not have influenced the habitats of the gracile australopiths (Tiedemann et al., 1994; deMenocal, 1995; deMenocal and Bloemendal, 1995). Thus, other explanations for how the morphological adaptations of early hominins correlate to environmental change at fossil sites must be sought.

Although disagreement over the interpretation of paleoenvironmental data from the hominin sites in eastern Africa exists, previous reconstructions of the Kanapoi-Allia Bay-Laetoli-Hadar chronology have generally suggested a predominance of mosaic environments and a possible increase over time in the frequency of open habitats. Both Kanapoi and Allia Bay have paleoenvironmental signals that suggest the presence of seasonal habitats during the Pliocene occupation of *A. anamensis*. These habitats were likely composed of mosaic woodland with some incursions of grassland, although disagreement remains on the degree to which open habitats were present. Reconstructions of the paleoenvironment at Laetoli have not reached a consensus, with interpretations varying from open grassland and closed woodland. However, most recent studies have suggested that the site was composed of several microhabitats during the occupation of *A. afarensis* and that both forest and savanna biomes were important parts of the local ecology. Finally, the Pliocene environment at Hadar has also been reconstructed as mosaic, including closed-forest, bushland, open-woodland and edaphic-grassland habitats. Open habitats appear to have been more common at Hadar than at other sites.

These reconstructions have been used to suggest that the morphological adaptations of *A. anamensis* and *A. afarensis* were not responses to directional increases in the prevalence of open, dry environments, but could instead reflect increasingly fluctuating seasonal conditions across a range of locally available habitats, where the ability to occasionally utilize lower-quality foods could be advantageous (Teaford and Ungar, 2000; Ungar, 2004; Reed and Fish, 2005; Kimbel et al., 2006). If this is the case, other local species should also be affected. This suggests that the use of faunal assemblages may be essential in understanding the relationship between human evolution and environmental change in East Africa.

The results presented here support the presence of these highly mosaic habitats, as well as an increase in the amount of available grassland at the sites associated with *A. afarensis*. This suggests that the habitats associated with *A. anamensis* were more closed than those of the later hominins.The microwear signatures of fossil taxa from Kanapoi and Allia Bay are most similar to those of modern taxa that inhabit closed forest, open woodland and bushland. The presence of a few taxa with grazing signatures suggests that some edaphic grassland may have been present either within or near the fossil sites. However, these grazing taxa have been recovered in small quantities and may have been migratory or seasonal members of the local faunal assemblages. The microwear evidence also suggests that *A. afarensis* occupied highly mosaic environments that included both open and closed habitat types. This would account for the presence of both grazing and browsing adapted bovid taxa. Even with some evidence of graze-adapted taxa at australopith sites, open and closed woodlands appear to have important components to the habitats. While habitat reconstructions alone cannot conclusively demonstrate that the adaptations of the australopiths were in response to specific environmental conditions, anatomical studies of these hominins suggest morphological adaptations for terrestrial bipedality, but that they also retained attributes associated with arboreal locomotion (Stern and Susman, 1983; Susman et al., 1984, Ward et al., 2001).

While there are some indications that the Laetoli and later Hadar members included drier, more open habitats, the overall results of this study suggest that both of these early australopith species occupied highly mosaic environments. The results presented here generally agree with Stanley (1992) that Pliocene hominin environments did not shift dramatically; however, there is some evidence for an increase in the number of grazing taxa at Laetoli and the later Hadar member. This supports the observation by Reed (1997) that the overall composition of the mammalian communities at these sites indicates a gradual aridification trend in eastern Africa that may have resulted in drier, more open habitats and the presence of a more pronounced dry season. This could explain why these early australopith taxa disappear around 2.8-2.5 mya and are replaced by members of the more ecologically adaptable genus *Homo*.

Conclusions

The ability of dental microwear texture analysis to separate modern bovids with known diets and to assign dietary categories to fossil taxa has been demonstrated in previous papers (Ungar et al., 2007; Scott, in press, in review). This study applies the technique to fossil taxa from four of the sites occupied by *A. anamensis* and *A. afarensis*, with the goal of inferring paleoenvironment at the sites. In general, the dental microwear signatures of the fossil bovids from Kanapoi, Allia Bay, Laetoli and Hadar all reflect an array of dietary preferences and suggest access to a variety of resource types. Specifically, all of these sites have bovid taxa with microwear signatures similar to modern species that occupy wooded or thick bushland habitats, but grazers are still present in small but increasing numbers. This suggests that the early australopiths may have preferred mosaic environments that would have provided both protection from predation and access to an assortment of food types.

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References

Andrews, P., 1989. Paleoecology of Laetoli. J. Hum. Evol. 18, 173-181.

Andrews, P., 2006. Taphonomic effects of faunal impoverishment and faunal mixing.Palaeogeogr.Palaeoclimatol.Palaeoecol. 241, 572-589.

Andrews, P., Humphrey, L., 1999. African Miocene environments and the transition to early hominins. In: Bromage, T., Schrenk, F. (Eds.), African Biogeography, Climate Change, and Early Hominid Evolution. Oxford University Press, Oxford, pp. 282-300.

Aronson, J.L., Taieb, M., 1981.Geology and paleogeography of the Hadar hominid site, Ethiopia. In: Rapp, G., Vondra, C. (Eds.) Hominid Sites, their geologic settings, pp. 165-195. Westview Press, Boulder, CO.

Bartholomew, G.A., Birdsell J.B., 1953. Ecology and the protohominids. Am. Anthropol. 55, 481- 498.

Benefit, B.R., McCrossin, M.L., 1990. Diet, species diversity, and distribution of African fossil baboons. Kroeber Anthrop. Soc. Papers 71–72, 79–93.

Beynon, A.D., 1987. Replication technique for studying microstructure of fossil enamel.Scanning Micro. 1:663-669.

Bobe, R., Behrensmeyer, A.K., Chapman, R., 2002. Faunal change, environmental variability and late Pliocene hominin evolution. J. Hum. Evol.42, 475.

Bonnefille, R., 1995. A reassessment of the Plio-Pleistocene pollen record of East Africa. In: Vrba, E. S., Denton, G. H., Partridge, T. C. and Burckle, L. H. (Eds.), Paleoclimate and Evolution, with Emphasis on Human Origins. Yale University Press, New Haven, CT, pp. 299-310.

Bonnefille, R., Potts, R., Chalié, F., Jolly, D., Peyron, O., 2004. High-resolution vegetation and climate change associated with Pliocene Australopithecus afarensis. Proc. Natl. Acad. Sci. 101, 12125-12129.

Bonnefille, R., Riollet, G., 1987. Palynological spectra from the Upper Laetolil Beds. In: Leakey, M.D., Harris, J.M. (Eds.), Laetoli, a Pliocene Site in Northern Tanzania, pp. 52-61. Clarendon Press, Oxford.

Brown, F.H., Feibel, S.S., 1991. Stratigraphy, depositional environments, and palaeogeography of the Koobi Fora Formation. In: Harris, J.H. (Ed.), Koobi Fora Research Project, Vol. 3. The fossil ungulates: geology, fossil artiodactyles and palaeoenvironments. Clarendon Press, Oxford, pp. 1-30.

Butler, P.M., 1987. Fossil insectivores from Laetoli. In: Leakey, M.D., Harris, J.M. (Eds.), Laetoli: A Pliocene Site in Northern Tanzania, pp. 62-78. Clarendon Press, Oxford.

Campisano, C.J., Feibel, C.S., 2007. Connecting local environmental sequences to global climate patterns: evidence from the hominin-bearing Hadar Formation, Ethiopia. J. Hum. Evol 53, 515-527.

Cerling, T.E., 1992. Development of grasslands and savannas in East Africa during the Neogene.Palaeogeogr.Palaeoclimatol.Palaeoecol. 97, 241-247.

Cerling, T.E., Bowman, J.R., O'Neil, J.R., 1988. An isotopic study of a fluvial-lacustrine sequence: the Plio-Pleistocene Koobi Fora sequence, East Africa. Palaeogeo.Palaeoclimatol.Palaeoecol. 63, 335-356.

Cerling, T.E.., Wynn, J.G., Andanje, S.A., Bird, M.I., Korir, D.K., Levin, N.E., Mace, W., Macharia, A.N., Quade, J., Remien, C.H., 2011. Woody cover and hominin environments in the past 6 million years. Nature 476, 51-56.

Ciochon, R.L., 1990. Evolution of the Cercopithecoid forelimb: Phylogenetic and Functional Implications from Morphometric Analysis. California: University of California Publications in Geological Science, 135.

Coffing, K., Feibel, C., Leakey, M., Walker, A., 1994.Four-million year old hominid from East Lake Turkana, Kenya. Am. J. Phys. Anthrop. 93, 55-65.

Cook, R.J., Farewell, V.T., 1996. Multiplicity considerations in the design and analysis of clinical trials.J R Stat Soc Ser A, 159:93-110.

Conover, W.J., Iman, R.L., 1981. Rank transformations as a bridge between parametric and nonparametric statistics. Am Stat 35:124-129.

Dart, R.A., 1925.*Australopithecus africanus*: The man ape of South Africa. Nature 115, 195-199.

Dart, R.A., 1953. Faunal and climatic fluctuations in Makapansgat Valley: their relation to the geologic age and Promethean status of *Australopithecus*. In: Leakey, L.S.B., Cole, S., (Eds.) Proceedings of the 1st Pan African Congress on Prehistory, Nairobi, 1947, pp. 96-106.

DeGusta, D., Vrba, E.S., 2003. A method for inferring paleohabitats from the functional morphology of bovid astragali. J. Archaeol. Sci. 30, 1009-1022.

deMenocal, P.B., 1995. Plio-Pleistocene African climate. Science 270, 53-59.

deMenocal, P.B., 2004. African climate change and faunal evolution during the Plio-Pleistocene.Earth Planet. Sci. Let. 220, 3-24.

deMenocal, P.B., Bloemendal, J., 1995. Plio-Pleistocene climatic variability in subtropical Africa and the paleoenvironment of hominid evolution: A combined data-model approach. In: Vrba, E. S., Denton, G. H., Partridge, T. C. and Burckle, L. H. (Eds.), Paleoclimate and

Evolution, with Emphasis on Human Origins, pp. 262–288. New Haven: Yale University Press.

deMenocal, P.B., Brown, F.H., 1999. Pliocene tephra correlations between East African hominid localities, the Gulf of Aden and the Arabian Sea. In: Hominoid evolution and climatic change in Eurasia, pp. 23-59.

Dowsett, H., Barron, J., Poore, R., 1996. Middle Pliocene sea surface temperatures: a global reconstruction. Marine Micropaleontol. 27, 13-25.

Ehleringer, J.R., Cerling, T.E., Heliker, B.R., 1997. C4 photosynthesis, atmospheric CO2, and climate. Oecologia 112, 285-299.

Feibel, C., Harris, J.M., Brown, F.H., 1991. Paleoenvironmental context for the Late Neogene of the Turkana Basin. In: Harris, J.M. (Ed.), Koobi Fora Research Project, vol. 3. Clarendon Press, Oxford, pp. 321-370.

Fernández-Jalvo, Y., Denys, C., Andrews, P., Williams, T., Dauphin, Y., Humphrey, L., 1998.Taphonomy and paleoecology of Olduvai Bed-I (Pleistocene, Tanzania). J. Hum. Evol. 34, 137-172.

Fortelius, M., Solounias, N., 2000. Functional characterization of ungulate molars using the abrasion-attrition wear gradient: a new method for reconstucting diets. Am. Mus. Nov. 3301, 1-36.

Gagnon M., Chew, A.E., 2000. Dietary preferences in extant African Bovidae. J. Mammal. 8:490-511.

Gentry, A.W., 1981.Notes on Bovidae from the Hadar Formation, Ethiopia, vol. 33. Kirtlandia, Cleveland. 1-30.

Gentry, A.W., 1987.Fossil Bovidae from Laetoli. In: Leakey, M.G., Harris, J.M. (Eds.) Laetoli: A Pliocene site in northern Tanzania, pp. 378-408. Clarendon Press, Oxford.

Gifford, D.P., 1981. Taphonomy and paleoecology: a critical review of archaeology's sister disciplines. Adv. Arch. Methods and Theory 4, 365-438.

Grine, F.E., 1981. Trophic differences between ‘‘gracile’’ and ‘‘robust’’ australopithecines, a scanning electron microscope analysis of occlusal events. S. Afr. J. Sci. 77, 203–230.

Grine, F.E., Ungar, P.S., Teaford, M.F., 2006a. Was the Early Pliocene hominin '*Australopithecus*' *anamensis* a hard object feeder? S. Afr. J. Sci. 102, 301-310.

Grine, F.E., Ungar, P.S., Teaford, M.F., El-Zaatari, S., 2006b. Molar microwear in *Praeanthropus afarensis*: evidence for dietary stasis through time and under diverse paleoecological conditions. J. Hum. Evol. 51, 297-319.

Harris, J.M., 1985. Age and paleoecology of the Upper Laetolil Beds, Laetoli, Tanzania. In: Delson, E. (Ed.), Ancestors: The Hard Evidence, pp. 76-81. Alan Riss, New York.

Harris, J.M., Leakey, M.G. (Eds.), 2003. Geology and Vertebrate Paleontology of the Early Pliocene Site of Kanapoi, Northern Kenya.Natural History Museum of Los Angeles County, Los Angeles.

Harrison, T., 2005. Fossil bird eggs from the Pliocene of Laetoli, Tanzania: their taxonomic and paleoecological relationships. J. Afr. Earth Sci. 41, 289-302.

Hay, R.L., 1980. Paleoenvironment of the Laetolil Beds, northern Tanzania. In: Rapp, G., Vondra, C.F. (Eds.), Hominid Sites: Their Geologic Settings. AAAS Selected Symposium 63, pp. 7-24. Westview Press, Boulder, CO.

Hay, R.L., 1987. Geology of the Laetolil Beds. In: Leakey, M.D., Harris, J.M. (Eds.), Laetoli, A Pliocene Site in Northern Tanzania. Clarendon Press, Oxford, pp. 23-47.

Hill, A., 1995. Faunal and environmental change in the Neogene of east Africa: Evidence from the Tugen Hills sequence, Baringo District, Kenya. In: Vrba, E.S., Denton, G.H., Partridge, T.C., Burkle, L.H., (Eds), Paleoclimate and Evolution, with Emphasis on Human Origins, Yale University Press, New Haven, pp. 178–193.

Hofmann, R.R., Stewart, D.R.M. 1972. Grazer or browser: a classification based on the stomach structure and feeding habits of East African ruminants. Mammalia 36:226-240.

Howell, F.C., 1978. Hominidae. In: Maglio V.J., Cooke, H.B.S. (Eds.), Evolution of African Mammals. Cambridge, Harvard University Press, 152-248.

Jacob, B., 1999. Estimation of rainfall variables from leaf characters in tropical Africa.Palaeogeogr.Palaeoclimatol.Palaeoecol. 145, 231-250.

Janis, C. 1990. The correlation between diet and dental wear in herbivorous mammals, and its relationship to the determination of diets of extinct species. Boucot, A.J. (Ed.), Evolutionary paleobiology of behavior and coevolution. Elsevier, Amsterdam, pp 241-259.

Jolly, C.J., 1970. The seed eaters: a new model of hominid differentiation based on a baboon analogy. Man 5, 5-26.

Johanson, D., Masao, F.T., Eck, G.G., White, T.D., Walter, R.C., Kimbel, W.H., Asfaw, B., Manega, P., Ndessokia, P., Suwa, G., 1987. New partial skeleton of Homo habilis from Olduvai Gorge, Tanzania. Nature 327, 205-209.

Johanson, D., Taieb, M. Coppens, Y., 1982. Pliocene hominids from the Hadar Formation, Ethiopia (1973-1977): stratigraphic chronologic, and paleoenvironmental contexts, with notes on hominid morphology and systematic. Am. J. Phys. Anthrop. 57:4, 373-402.

Kappelman, J., 1988. Morphology and locomotor adaptations of the bovid femur in relation to habitat. J. Morphol. 198, 119–130.

Kappelman, J., Plummer, T., Bishop, L., Duncan, A., Appleton, S., 1997.Bovids as indicators of Plio-Pleistocene paleoenvironments in East Africa. J. Hum. Evol. 32, 229-256.

Kay, R.F., 1975. The functional adaptations of primate molar teeth. Am. J. phys. Anthrop. 43, 195–216.

Kay, R.F., 1978. Molar structure and diet in extant Cercopithecidae. In: Joysey, K., Butler, P., (Eds.) Development, Function, and Evolution of Teeth, pp. 309–339. London: Academic Press.

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., 1982. East African Mammals: Bovids, vol. IIID. University of Chicago Press, Chicago.

Kingdon, J., 1997. The Kingdon Field Guide to African Mammals.Academic Press, San Diego, CA.

Kingston, J.D., Harrison, T., 2007. Isotopic dietary reconstructions of Pliocene herbivores at Laetoli: implications for early hominin paleoecology. Palaeogeogr.Palaeoclimatol.Palaeoecol. 243, 272-306.

Kingston, J.D., Marino, B.D., Hill, A., 1994. Isotopic evidence for Neogene hominid paleoenvironments in the Kenya Rift Valley. Science 264, 955-959.

Kovarovic, K., Andrews, P., Aiello, L., 2002. The palaeoecology of the Upper Ndolanya Beds at Laetoli, Tanzania. J. Hum. Evol. 43, 395-418.

Laporte L.F., Zihlman A.L., 1983. Plates, climate and hominoid evolution. S. Afr. J. Sci. 79, 96-110.

Leakey, M.G., Feibel, C.S., McDougall, I., Walker, A., 1995. New four million-year-old hominid species from Kanapoi and Allia Bay, Kenya. Nature 376, 565-571.

Leakey, M.G., Feibel, C.S., McDougall, I., Ward, C., Walker, A., 1998. New specimens and confirmation of an early age for Australopithecus anamensis. Nature 393, 62-66.

Leakey, M., Harris, J.M. (Eds.), 1987. Laetoli: A Pliocene Site in Northern Tanzania. Clarendon, Oxford.

Lewis, M.E., 1997. Carnivoran paleoguilds of Africa: implications for hominid food procurement strategies. J. Hum. Evol. 32, 257-288.

Merceron, G., Blondel, C., Brunet, M., Sen, S., Solounias, N., Viriot, L., Heintz, E., 2004a. The late Miocene paleoenvironments of Afghanistan as inferred from dental microwear in artiodactyls. Palaeogeo, Palaeoclimatol, Palaeoecol 207:143-163.

Merceron, G., Viriot, L., Blondel, C. 2004b. Tooth microwear pattern in roe deer (Capreolus capreolus L.) from Chizé (Western France) and relation to food composition. Small Ruminant Res. 53:125-132.

Merceron G., de Bonis L., Viriot L., Blondel C. 2005. Dental microwear of fossil bovids from northern Greece: paleoenvironmental conditions in the eastern Mediterranean during the Messinian. Palaeogeogr Palaeoclimatol, Palaeoecol 217:173-185.

Meylan, P.A., Auffenberg, W., 1987. The chelonians from the Laetolil Beds. In: Leakey, M.D., Harris, J.M. (Eds.), Laetoli: A Pliocene Site in Northern Tanzania, pp. 62-78. Clarendon Press, Oxford.

Musiba, C.M., 1999. Laetoli Pliocene paleoecology: a reanalysis via morphological and behavioral approaches. Ph.D. Dissertation, University of Chicago.

Musiba, C.M., Magori, C., Stoller, M., Stein, T., Branting, S., Vogt, M., Tuttle, R., Hallgrímsson, B., Killindo, S., Mizambwa, F., Ndunguru, F., Mabulla, A., 2007. The Taphonomy and paleoecological context of the Upper Laetolil Beds (Localities 8 and 9), Laetoli in northern Tanzania. In: Bobe, R., Alemseged, Z., Behrensmeyer, A.K., (Eds.) Hominin Environments in the East African Pliocene: An Assessment of the Faunal Evidence, pp. 257-278. Springer, Dordrecht.

Pickford, M., 2001.The geological context of the Kanapoi fossil hominids. Hum. Evol. 16, 45-48.

Plummer, T.W., Bishop, L.C., 1994. Hominid paleoecology at Olduvai Gorge, Tanzania as indicated by antelope remains. J. Hum. Evol. 27, 47-75.

Potts, R., 1996. Humanity's Descent: The Consequences of Ecological Instability. Morrow Press, New York.

Potts, R., 1998. Environmental hypotheses of hominin evolution.Yrbk. Phys. Anthropol. 41, 93-136.

Potts, R., 2007. Environmental hypotheses of Pliocene human evolution. In: In: Bobe, R., Alemseged, Z., Behrensmeyer, A.K., (Eds.) Hominin Environments in the East African Pliocene: An Assessment of the Faunal Evidence, pp. 25-49. Springer, Dordrecht.

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 Pleistocene kangaroo. PNAS 106:11646-11650.

Radosevich, S.C., Retallack, G.J., Taieb, M., 1992.Reassessment of the paleoenvironment and preservation of hominid fossils from Hadar, Ethiopia. Am. J. Phys. Anthrop. 87, 15-27.

Raymo, M.E., Grant, B., Horowitz, M., Rau, G.H., 1996. Mid-Pliocene warmth: stronger greenhouse and stronger conveyor. Marine Micropaleontol. 27, 313-326.

Reed, K.E., 2008. Paleoecological patterns at the Hadar hominin site, Afar Regional State, Ethiopia. J. Hum. Evol. 54, 743-768.

Reed, K.E., 1996. The paleoecology of Makapansgat and other African Pliocene Hominid Localities.Ph.D. Dissertation.State University of New York, Stony Brook.

Reed, K.E., 1997. Early hominid evolution and ecological change through the African Plio-Pleistocene. J. Hum. Evol. 40, 289-322.

Reed, K.E., Fish, J.L., 2005. Tropical and temperate seasonal influences on human evolution. In: Brockman, D., van Schaik, C. (Eds.), Primate Seasonality and Human Evolution. Cambridge University Press, Cambridge.

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, Chicago, Aldine, 385-416.

Rodman, P.S., McHenry, H.M., 1980.Bioenergetics and the origin of hominid bipedalism. Am. J. Phys. Anthropol. 52, 103-106.

Schoeninger, M.J., Reeser, H., 1999. Paleoenvironment of Allia Bay, East Turkana, Kenya 3.9 ma: the stable isotope data. J. Hum. Evol.33, A21-A22.

Schoeninger, M.J., Reeser, H., Hallin, K., 2003. Paleoenvironment of *Australopithecus anamensis* at Allia Bay, East Turkana, Kenya: evidence from mammalian herbivore enamel stable isotopes. J. Anthrop. Archaeo. 22, 200-207.

Schubert, B.W., Ungar, P.S., DeSantis, L.R.G. 2010. Carnassial microwear and dietary behaviour in large carnivorans. J Zool 280:257-263

Schubert, B.W., Ungar, P.S., Sponheimer, M., Reed, K.E. 2006. Microwear evidence for Plio-Pleistocene bovid diets from Makapansgat Limeworks Cave, South Africa. Palaeogeogr, Palaeoclimatol, Palaeoecol 241:301-319.

Scott, J.R., in review.Dental microwear texture analysis of extant African Bovidae. Mammalia

Scott, J.R., in preparation.Dental microwear texture analysis of fossil Bovidae from the Hadar hominin site.

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., Ungar, P.S., Bergstrom, T.S., Brown, C.A., Grine, F.E., Teaford, M.F., Walker, A. 2005. Dental microwear texture analysis reflects diets of living primates and fossil hominins. Nature 436:693-695.

Sikes, N.E., 1994. Early hominid habitat preferences in East Africa: paleosols carbon isotope evidence. J. Hum. Evol. 27, 25-45.

Skinner, J.D., Smithers, R.H.N. 1990. The mammals of the southern African subregion.2nd ed. University of Pretoria, Pretoria, South Africa.

Soligo, C., Andrews, P., 2005. Taphonomic bias, taxonomic bias and historical non-equivalence of faunal structure in early hominin localities. J. Hum. Evol. 49, 206-229.

Solounias, N., Moelleken, S.M.C., 1993. Determination of dietary adaptations of extinct ruminants through premaxillary analysis. J. Mammal. 74, 1059-1074.

Solounias, N., Teaford, M.F.,Walker, A.C., 1988. Interpreting the diet of extinct ruminants: the case of a non-browsing giraffid.Paleobio. 14, 287-300.

Spencer, L.M., 1995. Antelope and Grasslands: Reconstructing African Hominid Environments. Ph.D. Dissertation, State University of New York at Stony Brook.

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 Limeworks hominin locality. J. Hum. Evol. 36, 705-718.

Stanley, S.M., 1992. An ecological theory for the origin of Homo.Paleobio. 18, 237-257.

Stern, J.T., Susman, R.L., 1983. The locomotor anatomy of *Australopithecus afarensis*. Am. J. Phys. Anthropol. 60, 279-317.

Su, D., Harrison, T., 2007. The paleoecology of the Upper Laetolil Beds at Laetoli: a reconsideration of the large mammal evidence. Shackleton, N.J., 1995. New data on the evolution of Pliocene climate variability. In: Vrba, E.S., Denton, G.H., Partridge, T.C., Burckle, L.H. (Eds.), Paleoclimate and Evolution, with Emphasis on Human Origins, pp. 243-248. Yale University Press, New Haven, CT.

Susman, R.L., Stern, J.T., Jungers, W.L., 1984. Arboreality and bipedality in the Hadar hominids.Folia Primatol. 43, 113-156.

Taieb, M., Johanson, D.C., Coppens, Y., Aronson, J.L., 1976.Geological and paleontological background of Hadar hominid site, Afar, Ethiopia. Nature 260, 289-293.

Teaford, M.F., 1988. Scanning electron microscope diagnosis of wear patterns versus artifacts on fossil teeth. Scanning Microsc. 2:1167-1175.

Teaford, M.F., Oyen, O.J., 1989. Live primates and dental replication: new problems and new techniques. Am. J. Phys. Anthrop. 80:73-81.

Teaford, M.F., Ungar, P.S., 2000. Diet and the evolution of the earliest human ancestors. Proc. Natl. Acad. Sci. USA 97, 13506-13511.

Tiedemann, R., Sarnthein, M., Shackleton, N.J., 1994. Astronomical timescale for the Pliocene Atlantic δ18O and dust flux records of ODP Site 659. Paleoceanography 9, 619-638.

Trauth, M.H., Maslin, M.A., Deino, A., Strecker, M.R., 2005. Late Cenozoic moisture history of East Africa.Science 309, 2051.

Ungar, P.S., 1996. Dental microwear of European Miocene catarrhines: evidence for diets and tooth use. J. Hum. Evol. 31:335-366.

Ungar, P.S., 2004. Dental topography and diets of *Australopithecus afarensis* and early *Homo*. J. Hum. Evol. 46, 605-622.

Ungar, P.S., Merceron, G., Scott, R.S. 2007. 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, F.E., 2010. Molar microwear textures and the diets of *Australopithecus anamensis* and *Australopithecus afarensis*. Philosophical Transactions of the Royal Society B: Biological Sciences 365 (1556): 3345-3354.

Ungar, P.S., Scott, R.S., Scott, J.R., Teaford, M.F. 2008. Dental microwear analysis: historical perspectives and new approaches. In: Irish, J.D. (Ed.), Technique and Application in Dental Anthropology. Cambridge University Press, Cambridge, 389-425.

Ungar, P.S., Scott, R.S., Grine, F.E., Teaford, M.F., 2010. Molar microwear textures and the diets of *Australopithecus anamensis* and *A. afarensis*. Phil. Trans. Roy. Soc., B. 365:3345-3354.

Ungar, P.S., Brown, C.A., Bergstrom, T.S., Walker, A. 2003. A quantification of dental microwear by tandem scanning confocal microscopy and scale-sensitive fractal analysis.Scanning 25:189-193.

Verdcourt, B., 1987. Mollusca from the Laetolil and Upper Ndolanya Beds. In: Leakey, M.D., Harris, J.M. (Eds.), Laetoli: A Pliocene Site in Northern Tanzania, pp. 438-450. Oxford Science Publications, Oxford.

Vrba, E.S., 1974. Chronological and ecological implications of the fossil Bovidae at the Sterkfontein australopithecine site. Nature 250, 19-23.

Vrba, E.S., 1975. Some evidence of chronology and palaeocology of Sterkfontein, Swartkrans, and Kromdraai from the fossil Bovidae. Nature 254, 301-304.

Vrba, E.S., 1980. The significance of bovid remains as indicators of environment and prediction patterns. In: Behrensmeyer, A.K., Hill, A., (Eds.) Fossils in the making, Vertebrate Taphonomy and Paleoecology, pp. 247–271. Chicago: University of Chicago Press.

Vrba, E.S., 1985. African Bovidae: Evolutionary events since the Miocene. S. Afr. J. Sci. 81, 263-266.

Vrba, E.S., 1988. Late Pliocene climatic events and hominid evolution. In: Grine, F.E. (Ed.), Evolutionary History of the “Robust” Australopithecines, pp. 405-426. Aldine, New York.

Vrba, E.S., 1992. Mammals as the key to evolutionary theory. J. Mammal. 73, 1-28.

Vrba, E.S., 1995a. The fossil record of African antelopes (Mammalia, Bovidae) in relation to human evolution and paleoclimate. In: Vrba, E.S., Denton, G.H., Partridge, T.C., Burckle, L.C. (Eds.), Paleoclimate and Evolution with Emphasis on Human Origins, pp. 385-424. Yale University Press, New Haven.

Vrba, E.S., 1995b. On the connection between paleoclimate and evolution. In: Vrba, E.S., Denton, G.H., Partridge, T.C., Burckle, L.C. (Eds.), Paleoclimate and Evolution with Emphasis on Human Origins, pp. 24-45. Yale University Press, New Haven.

Vrba, E.S., 2000. Major features of Neogene mammalian evolution in Africa. In: Partridge, T.C., Maud, R.R. (Eds.), The Cenozoic of Southern Africa, pp. 277-304. Oxford University Press, Oxford.

Vrba, E.S., Denton, G.H., Prentice, M.L., 1989. Climatic influences on early hominid behavior. Ossa 14, 127-156.

Walter, R.C., 1994. Age of Lucy and the First Family: single-crystal 40Ar/39Ar dating of the Denen Dora and lower Kada Hadar Members of the Hadar Formation, Ethiopia. Geology 22, 6-10.

Walter, R.C., Aronson, J.L., 1993. Age and source of the Sidi Hakoma Tuff, Hadar Formation, Ethiopia. J. Hum. Evol. 25, 229-240.

Walter, R.C., Westgate, J.A., Hart, W.K., Aronson, J.L., 1984. Tephrastratigraphic correlation of the Sidi Hakoma and Tulu Bor tuffs; Nd isotope and new trace element data.Geol. Soc. Am. Abstracts with Programs 16, 686.

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.

Washburn, S.L., 1960. Tools and human evolution. Sci. Am. 203, 3-15.

White, T.D, Ambrose, S.H., Suwa, G., Su, D.F., DeGusta, D., Bernor, R.L., Boisserie, J-R, Brunet, M., Delson, E., Frost, S., Garcia, N., Giaourtsakis, I.X., Haile-Selassie, Y., Howell, F.C., Lehmann, Likius, A., Pehlevan, C., Saegusa, H., Semprebon, G., Teaford, M., Vrba, E., 2009. Macrovertebrate paleontology and the Pliocene habitat of *Ardipithecus ramidus*. Science, 326, 87-93.

White, T.D., Suwa, G., Asfaw, B., 1994. *Ardipithecus ramidus*, a new species of early hominid from Aramis, Ethiopia. Nature 317, 306-312.

White, T.D, Suwa, G., Simpson, S., Asfaw, B., 2000.Jaws and teeth of *Australopithecus afarensis* from Maka, Middle Awash, Ethiopia. Am. J. Phys. Anthop. 111, 45-68.

Wynn, J.G., 2000. Paleosols, stable carbon isotopes, and paleoenvironmental interpretation of Kanapoi, northern Kenya. J. Hum. Evol. 39, 411-432.

Figures

Figure 1. Occlusal view of bovid M2, illustrating the shearing facets where microwear was examined (Illustration courtesy of Gildas Merceron). A = left m^2, B= right m_2

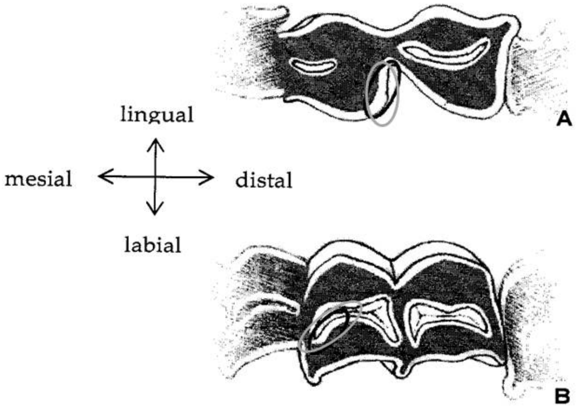
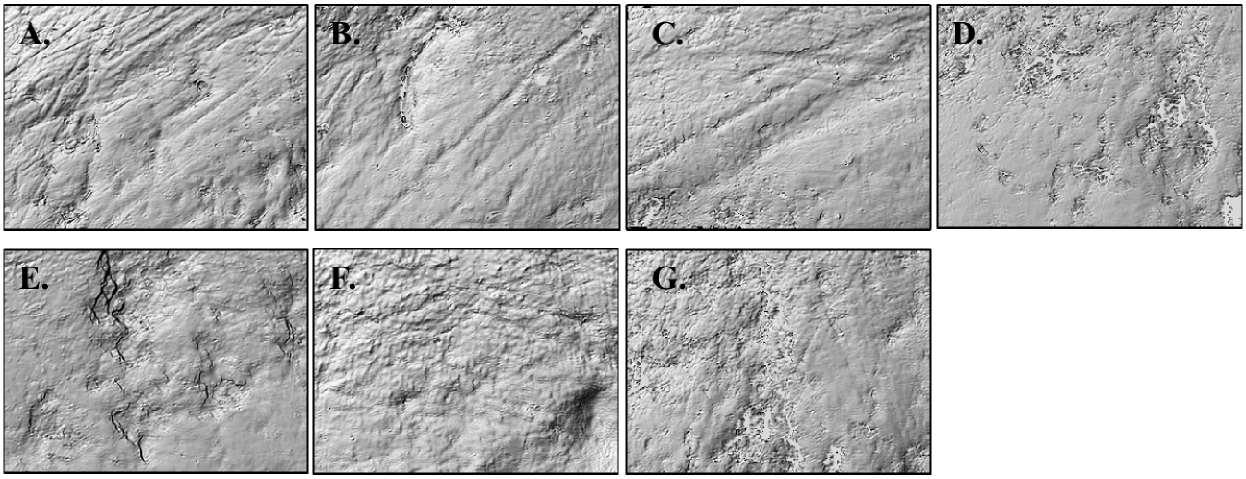
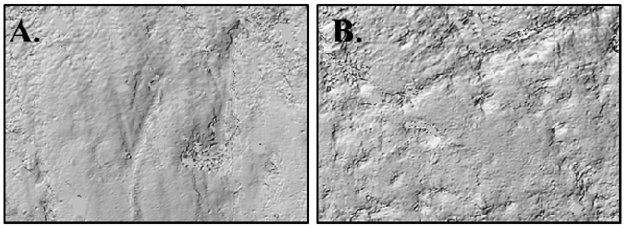


Figure 2. Examples of dental microwear surfaces of taxa from (a) Kanapoi, (b) Allia Bay, (c) Laetoli. These images are photosimulations based on data collected using the confocal imaging profiler, and each represents an area of 276 x 204 µm. Kanapoi: A) *Aepyceros*; B)Alcelaphini; C) Hippotragini; D) *Madoqua*; E) Raphicerus; F) *Simatherium*; G) *Tragelaphus*. Allia Bay: A) Alcelaphini; B) *Tragelaphus*. Laetoli: A) Alcelaphini; B) *Antidorcas*;C) Bovini; D) *Gazella*; E) Hippotragini; F) *Madoqua*;G) *Parmularius*; H) *Simatherium*;I) *Tragelaphus*.

Kanapoi



Allia Bay



Lactoli

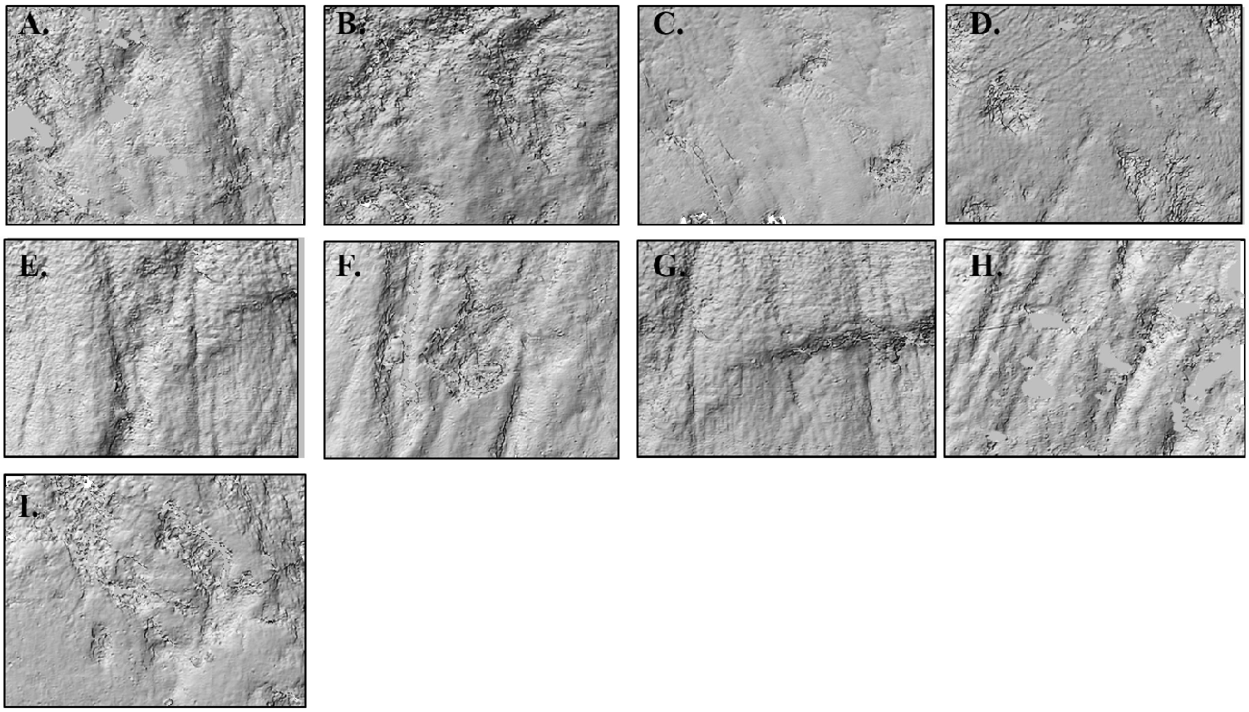


Figure 3. Examples of dental microwear surfaces for extant bovids from different dietary categories. These images are 3-D photosimulations based on data collected using the confocal imaging profiler, and each represents an area of 138 x 102 µm. a) obligate grazer; b) variable grazer; c) browser-grazer intermediate; d) generalist; e) browser; and f) frugivore.

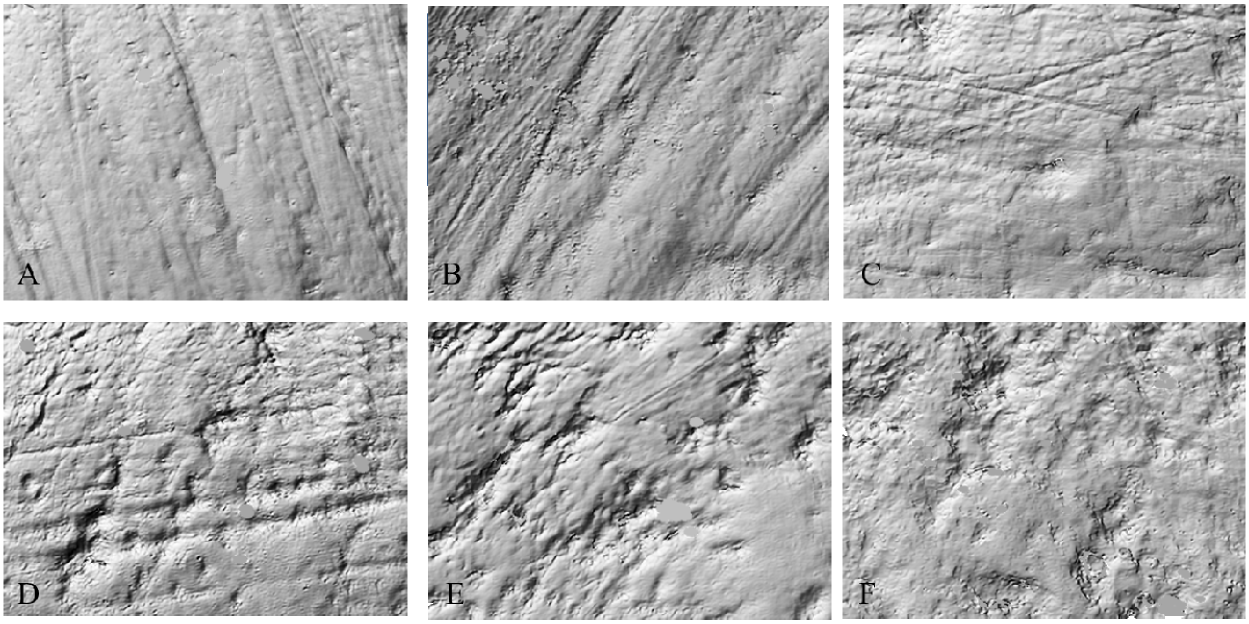
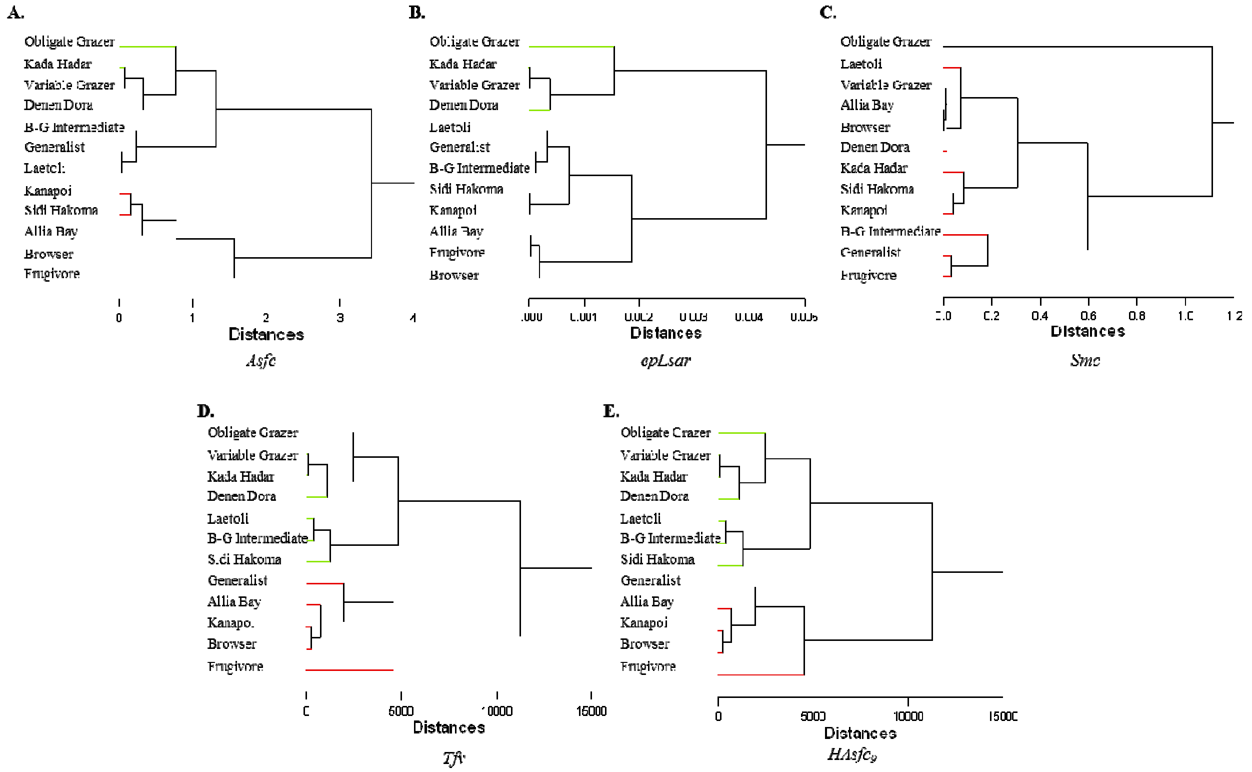


Figure 4. Hierarchical cluster analysis of fossil and extant taxa by site or dietary category. These results are organized by microwear texture variable: (a) *Asfc*,surface complexity; (b) *epLsar*, anisotropy; (c) *Smc*, scale of maximum complexity; (d) *Tfv*, fill volume; *HAsfc$_9$*, heterogeneity.



Tables

TABLE 1. Extant bovid taxa included in this study, along with associated diets

Taxon	Common Name	Diet
Obligate Grazers		
Damaliscus lunatus	Tsessebe	Savanna and floodplain grasses
Kobus leche	Lechwe	Aquatic marsh grasses
Redunca arundinum	SouthernReedbuck	Tall grass specialist
Redunca fulvorufula	Mountain Reedbuck	Seasonal grasses
Variable Grazers		
Damaliscus pygargus	Bontebok	Short Highveld grasses, some fynbos consumption
Gazella granti	Grant's Gazelle	Short grasses, seasonal herbs and shrub foliage
Hippotragus niger	Sable Antelope	Grasses in wet season and forbs and foliage in dry season
Kobus ellipsiprymnus	Waterbuck	Medium to short grasses, reeds and some rushes
Synceos caffer	African Buffalo	Pasture grasses year-round and swamp vegetation during dry season
Tragelaphus spekii	Sitatunga	Swamp grasses, sedges, leaves and low-level vegetation
Browser-Grazer Intermediates		
Aepyceros melampus	Impala	Grazes on grasses when green, also browses on seedpods, foliage, forbs and shoots
Antidorcas marsupialis	Springbok	Shrubs and succulents in dry season, young grasses during wet season
Raphicerus campestris	Steenbok	Low herbaceous plants, seeds and pods during dry season, young grass in wet season
Raphicerus sharpei	Sharpe's Grysbok	Mature plants, fruit pods and roots
Taurotragus oryx	Eland	Seasonal young grasses, small herbaceous plants, roots, and tubers, highly seasonal
Tragelaphus imberbis	Lesser Kudu	Succulents, buds, leaves, pods and grasses, pronounced seasonal variation
Browsers		
Litocranius walleri	Gerenuk	Pure browsers, focuses on flowers and leaves of shrubs, not known to eat grass or herbs
Neotragus batesi	Bate's Pygmy Antelope	Ground-level herbaceous vegetation

Sylvicapra grimmia	Common Duiker	Leaves, shoots, fruit pods and seeds, tubers, insects, rarely known to consume grasses
Tragelaphus euryceros	Bongo	High-concentrate green herbage, including shrubs and creeping plants

Generalists

Oreotragus oreotragus	Klipspringer	Leaves, buds, pods, bark, short grasses and some fruit
Tragelaphus angasi	Nyala	Mixed grasses and leaves
Tragelaphus strepsiceros	Greater Kudu	Herbs, leaves, vines, fruit, tubers and some grass

Frugivores

Cephalophus sylvicultor	Yellowback Duiker	Forbs and shrubs
Philantomba monticola	Blue Duiker	Fallen fruit, leaves, buds, seeds and mushrooms

Diet information based on Walker, 1975; Kingdon, 1982, 1997; Grzimek, 1990; Nowak, 1991.

Table 2. Median values by fossil taxon.

KANAPOI

Alcelaphini	*5*	1.4196	0.0037	0.7667	5740.80	0.4381	0.6433
Aepyceros sp.	*1*	2.3279	0.0030	0.4502	8649.56	0.6444	1.0553
Simatherium sp.	*3*	1.4262	0.0064	0.5015	1485.66	0.5266	0.9517
Hippotragus sp.	*2*	2.0592	0.0054	0.3283	2636.06	0.3148	0.7553
Madoqua sp.	*9*	3.9542	0.0035	0.9171	16220.87	0.4999	0.7307
Raphicerus sp.	*3*	3.6907	0.0021	0.3645	5799.58	0.6612	1.1978
Tragelaphus sp.	*12*	3.9042	0.0018	0.1502	13486.87	0.4030	0.7444

ALLIA BAY

Alcelaphini	*1*	2.4609	0.0020	0.2692	4930.21	0.5960	0.6962
Tragelaphus sp.	*14*	3.2013	0.0025	0.7820	10888.61	0.6248	0.9839

LAETOLI

Alcelaphini	*10*	2.1934	0.0048	1.0958	6551.74	0.4062	0.8868
Antidorcas sp.	*3*	4.0596	0.0013	0.5302	8598.90	0.5264	1.0024
Bovini	*10*	2.2624	0.0040	0.6885	4602.28	0.4606	1.2403
Gazella sp.	*4*	2.0844	0.0030	0.5366	4287.92	0.3683	0.7620
Hippotragus sp.	*2*	1.2170	0.0050	0.3109	6871.15	0.6293	0.7855
Madoqua sp.	*3*	3.9078	0.0016	0.8505	14011.05	0.6154	1.2027
Parmularius sp.	*10*	1.2937	0.0051	1.1150	3627.816	0.3761	0.7902
Simatherium sp.	*3*	2.4788	0.0030	0.5208	7784.08	0.4644	0.7690
Tragelaphus sp.	*4*	3.8115	0.0024	0.7204	13683.39	0.6426	0.8986

SIDI HAKOMA

Aepyceros	3	3.5261	0.0024	0.2976	8752.488	0.5298	0.9452
Alcelaphini	4	2.2392	0.004	0.4058	6598.503	0.5243	0.8843
Antilopini	5	4.8171	0.0033	0.6316	11977.21	0.6612	1.1559
Gazella	2	2.2886	0.0049	0.6128	6071.115	0.4985	0.7292
Kobus	2	2.491	0.0021	0.9725	4184.89	0.3265	0.8375
Neotragus	3	4.2655	0.0019	0.6865	9763.845	0.6935	0.9531
Tragelaphus	5	3.0762	0.0031	0.6449	8062.735	0.544	0.8553
Ugandax	6	2.9872	0.0035	0.4532	5578.615	0.5796	0.8406

DENEN DORA

Aepyceros	4	1.7485	0.0039	0.5043	5371.542	0.4269	0.7503
Alcelaphini	10	2.2371	0.0048	0.426	6239.596	0.5006	0.9241
Gazella	2	2.7917	0.0052	0.5057	5333.485	0.4076	0.8075
Hippotragini	3	1.9785	0.006	0.4368	3984.685	0.4502	0.8135
Kobus	9	1.5987	0.0037	1.1877	4462.355	0.4199	0.8613
Pelorovis	2	1.2321	0.0061	0.7799	2328.855	0.5062	0.855
Reduncini	14	0.9916	0.006	1.2154	2593.004	0.4446	0.8154

Tragelaphus	10	1.964	0.005	0.8553	6539.146	0.4823	0.7203
Ugandax	9	2.0688	0.0049	0.5026	4267.688	0.5133	0.8941

KADA HADAR

Aepyceros	5	1.4847	0.0041	0.2685	5972.351	0.3865	0.8544
Alcelaphini	4	1.4858	0.0076	0.3224	3331.107	0.4	0.7939
Antilopini	5	3.5876	0.003	0.6188	9597.235	0.6988	1.065
Bovini	5	0.9267	0.007	1.0667	3564.102	0.428	0.7242
Gazella	2	2.2814	0.0052	0.5349	4276.6	0.4512	0.8606
Hippotragini	2	1.3157	0.0049	0.4005	2626.581	0.4049	0.9214
Kobus	1	0.9877	0.003	1.1355	1103.832	0.4325	0.7613
Neotragus	1	2.6987	0.002	0.6247	10268.15	0.6265	0.9884
Oryx	3	0.9987	0.0077	1.2649	1168.655	0.5985	0.9755
Pelorovis	2	1.3155	0.0061	0.7532	2677.005	0.4278	0.7539

Table 3. Nested analysis of variance.

Source	SS	*df*	MS	*F*	*p*
Complexity (*Asfc* ranked data)					
Asfc	255292.59	5	51058.52	17.28	0.00
Error	632021.41	214	2953.37		
Anisotropy (*epLsar* ranked data)					
epLsar	238143.19	5	47628.64	15.701	0.00
Error	649166.81	214	3033.49		
Maximum Complexity (*Smc* ranked data)					
Smc	83613.58	5	16722.72	4.453	0.001
Error	803701.42	214	3755.52		
Fill Volume (*Tfv* ranked data)					
Diet	226891.18	5	45378.24	14.704	0.00
Error	660422.82	214	3086.09		
Heterogeneity 3x3 (*HAsfc*$_9$ ranked data)					
Diet	121338.41	5	24267.69	6.780	0.00
Error	765975.09	214	3579.32		
Heterogeneity 9x9 (*HAsfc*$_{81}$ ranked data)					
Diet	34692.59	5	6938.52	1.742	0.126
Error	852621.9	214	3984.22		

Table 4. Pairwise comparisons of bovids by fossil site/member.*- significant with Fisher's LSD test, **- significant with Tukey's HSD test.

MEMBER	**MEMBER**	***Asfc***	***epLsar***	***Smc***	***Tfv***	***HAsfc9***
Allia Bay	Denen Dora	88.477**	-97.244**	3.004	94.46**	81.024**
Allia Bay	Kada Hadar	93.067**	-104.617**	26.933	95.683**	81.45**
Allia Bay	Kanapoi	23.6	-37.676*	34.181	24.219	83.819**
Allia Bay	Laetoli	55.51**	-57.166**	-9.178	64.631**	79.725**
Allia Bay	Sidi Hakoma	7.759	-30.57	45.844*	36.326*	39.633*
Denen Dora	Kada Hadar	4.59	-7.372	23.929	1.223	0.426
Denen Dora	Kanapoi	-64.877**	59.568**	31.177*	-70.241**	2.795
Denen Dora	Laetoli	-32.966**	40.078**	-12.182	-29.829*	-1.299
Denen Dora	Sidi Hakoma	-80.717**	66.674**	42.84*	-58.134**	-41.391**
Kada Hadar	Kanapoi	-69.467**	66.94**	7.248	-71.464**	2.369
Kada Hadar	Laetoli	-37.556**	47.451**	-36.112*	-31.052*	-1.725
Kada Hadar	Sidi Hakoma	-85.307**	74.046**	18.911	-59.357**	-41.817*
Kanapoi	Laetoli	31.91	-19.49	-43.359**	40.412**	-4.094
Kanapoi	Sidi Hakoma	-15.841	7.106	11.663	12.107	-44.186**
Laetoli	Sidi Hakoma	-47.751**	26.596*	55.023**	-28.305*	-40.092*

Chapter Five: Summary and Future Directions

Some of the most important events in early human evolution occurred during the Pliocene epoch in eastern Africa, including major taxonomic diversification of early hominins and the introduction of bipedalism, our diagnostic form of locomotion. Previous hypotheses have linked these events to environmental pressures caused by global and regional climatic shifts (Vrba, 1985, 1988, 1995a, 2000; Stanley, 1992; deMenocal, 1995), and various lines of evidence have indicated that while the earliest known hominins inhabited closed woodland habitats (WoldeGabriel et al., 1994), middle Pliocene species witnessed a shift towards more open and mosaic environments that would have made changes in locomotion and diet advantageous (Kingston et al., 1994; Kappelman et al., 1997; Reed, 1997; Schoeninger et al., 2003).

Australopithecus anamensis and *Australopithecus afarensis* are two of the earlier identified hominins in eastern Africa and have been suggested to be part of an anagenetic lineage based on subtle changes in morphology over time (Leakey et al., 1995; Wolpoff, 1999; Ward et al., 2001; Kimbel et al., 2006). These two hominins have been primarily recovered from four fossil sites that span from 4.2-3.0 mya. Two of the primary sites associated with *A. anamensis* are Kanapoi and Allia Bay, both located in the Turkana Basin of Kenya (Leakey et al., 1995, 1998). Laetoli in Tanzania is the earliest known habitat associated with *A. afarensis* and Hadar in Ethiopia is the latest known site occupied by this species (Leakey and Harris, 1987; Lockwood et al., 2000; White et al., 2000). These hominins are characterized by morphological adaptations for habitual bipedalism and more robust dentition than earlier taxa like *Ardipithecus ramidus* (White et al., 1994). Additionally, Johanson et al. (1987) observed that these middle Pliocene hominins also exhibit short legs and long arms in relation to trunk length, which indicates combined terrestrial bipedality and arboreal climbing. This adaptation has been hypothesized to be the result of environmental changes in eastern Africa that would have made such a unique locomotor pattern advantageous (Stanley, 1992).

Establishing a direct relationship between climate change and evolution presents a unique challenge because climate is generally preserved in one context and evolution in another. Proxy climate records for the Pliocene have been recovered primarily from deep-sea sediments and often represent more than one million years of continuous environmental history (Dowsett et al., 1996; deMenocal and Brown, 1999). These extensive records provide an opportunity to analyze the tempo of climatic change and compare overarching trends to major events in human evolution. Records of evolution, however, are not continuous time series, but snapshots over a wide geographic range, usually based solely on fossil remains of hominins and other fauna.

This dissertation approaches the question of Pliocene hominin paleoenvironments in eastern Africa by reconstructing the diets of the associated bovid fauna. These taxa are considered by many to be reliable indicators of paleoenvironment due to predictable relationships between diet and habitat, and this dissertation explores this relationship for both extant and fossil species. The study also serves as a test of taxonomic uniformitarianism, comparing evidence of actual diet during the lifetime of individuals to the inferred diet based on morphology alone. Finally, the reconstructed bovid diets are used to evaluate previous hypotheses for the paleoenvironments at the sites of Kanapoi, Allia Bay, Laetoli and Hadar, as well as the implications of local habitats for the adaptations of the early australopiths.

Project Objectives

From its conception, this project has had three primary objectives. First, I aimed to confirm the utility of dental microwear texture analysis as a powerful tool for bovid dietary reconstruction. The only study to date to apply this technique to bovids suggested that the method could be used reliably to reconstruct the diets of fossil taxa, and that those results had implications for local paleoenvironment (Ungar et al., 2007). However, in order for the technique to have wider applicability, it was first necessary to develop a large extant comparative database of bovid microwear textures that could be applied to the fossil samples included in this dissertation, as well as samples from other sites and time periods in Africa. In order to accomplish this, texture data were collected for 25 extant African bovid species with known dietary preferences, representing all of the dietary categories previously described by Gagnon and Chew (2000) and resulting in the largest database of microwear textures yet assembled.

The second objective was to reconstruct the diets of fossil taxa from Kanapoi, Allia Bay, Laetoli and Hadar. Microwear texture data were collected for 223 specimens from the four early hominin sites. These include 35 specimens from Kanapoi, 15 specimens from Allia Bay, 49 specimens from Laetoli, and 124 specimens from Hadar. The diets of these fossil taxa were determined by comparing their microwear signatures to those from the modern comparative sample.

In addition to dietary reconstruction, an important component of this dissertation was to explore the efficacy of dental microwear texture analysis as an indicator of paleohabitat. The sites included in this study are four of the key localities associated with the early australopiths and because of this, an accurate understanding the local environment is important. However, there has been considerable disagreement over the paleoenvironments at these sites during the occupation of the hominins, even after the application of various methods of habitat reconstructions. In an effort to evaluate these competing hypotheses on paleoenvironment, the paleoenvironmental implications of the reconstructed bovid diets were used to evaluate the previous habitat reconstructions for the four sites.

The final dissertation objective was to use the bovid dietary reconstructions as a test of the principle of taxonomic uniformitarianism. This principle assumes that fossil taxa share the ecological preferences of their modern counterparts and while this is usually reliable for recent faunas, its applicability to the distant past is questionable. While many authors have questioned the utility of taxonomic uniformitarianism, only a few have sought to test its accuracy. An examination of the fossil bovids of Makapansgat, South Africa by Sponheimer et al. (1999) used carbon stable isotopes to demonstrate that nearly half of included taxa had actual diets that were different from those of their closest living relatives. In order to assess the accuracy of taxonomic uniformitarianism at the sites included in this dissertation, the reconstructed diets for the fossil bovids from Kanapoi, Allia Bay, Laetoli and Hadar were compared to previous dietary assumptions based on this principle.

Brief summaries and concluding remarks for each goal are presented individual below.

Objective 1: Extant bovid microwear texture database

It is assumed that a relationship exists between environmental change and evolution, however these connections are difficult to discern because of the challenges involved in accurately reconstructing paleoenvironments. One of the primary ways that past habitats are determined is through the reconstruction of the paleoecology of fossil fauna. Bovids are most frequently used indicator taxa for the paleoenvironments associated with human evolution. This is because they are ubiquitous at hominin fossil sites and modern taxa have can be placed into dietary categories that reliably predict habitat preference. However, since critiques of taxonomic uniformitarianism suggest that morphology alone is not always a reliable predictor of diet, direct line evidence must be sought from other methods. Dental microwear, or the microscopic pits and scratches on the enamel surface that result from the interaction of food and teeth during chewing, is one such line of evidence.

Use of dental microwear texture analysis

The first objective was to develop a database of extant African bovid dental microwear that could be used to interpret the texture signatures of fossil bovids. This goal could be sub-divided into two further objectives. It was first necessary to confirm pilot data collected by Ungar et al. (2007), which suggested that texture analysis could successfully separate extant bovids with diets from different ends of the spectrum, i.e., obligate grazers and browsers. Previous work also suggested that microwear texture analysis has the potential for finer dietary distinctions (Ungar et al., 2007), so an important component of this study was to explore the resolution of the technique. In order to accomplish this, extant taxa classified as ‘mixed-feeders’ (i.e., variable grazers, browser-grazer intermediates, generalists) were statistically compared to identify significant differences.

The initial study of bovid microwear texture by Ungar et al. (2007) utilized two microwear texture variables, complexity (*Asfc*) and anisotropy (*epLsar*). Their data indicated that browser taxa have more complex surfaces with lower values for anisotropy than grazing bovids. These differences in complexity and anisotropy were confirmed with the increased sample. Additionally, since the original bovid microwear texture analysis study was conducted, new variables have been added to the microwear texture suite, including scale of maximum complexity (*Smc*), textural fill volume (*Tfv*), and heterogeneity 3x3 ($HAsfc_9$) and 9x9 ($HAsfc_{81}$). While these variables have proven to be strong indicators of diet in primates and hominins, this relationship had to be explored for bovids of differing diets (for examples, see Ungar et al., 2008; Scott et al., 2009; Grine et al., 2010; Merceron et al., 2010; Ungar et al., 2010; Pontzer et al., in press). All of these variables proved to be significant indicators of bovid diet, although not for all dietary categories.

Comparative sample selection

The extant taxa included in this study were selected for analysis because of their wide-ranging differences in diet and habitat preference. Gagnon and Chew (2000) identified six dietary categories for extant African bovids that are based on the percentages of monocotyledons and dicotyledons included in the diet, with separate consideration of fruit consumption. When selecting comparative taxa for this study, representative species from all six dietary categories were chosen, with specific emphasis on bovids that evince various levels of mixed feeding. The included taxa for each dietary category, along with habitat preferences are reviewed below. Dietary categories are from Gagnon and Chew (2000) and habitat preferences are from Kingdon (1982, 1997).

The browsing taxa selected were *Litocranius walleri*, *Neotragus batesi*, *Sylvicapra grimmia*, and *Tragelaphus euryceros*. Dedicated browsers focus primarily on dicots, consuming more than 70% of these resources and including small quantities of grass (Gagnon and Chew, 2000). Because of their preference for forest resources, browsing taxa tend to inhabit more closed habitats, like forest and woodland. The species included here represent a range of closed habitats, from the rainforest preferred by the common duiker, *Sylvicapra grimmia*, to the scrub forest occupied by the gerenuk, *Litocranius walleri*. Bongos, *Tragelaphus euryceros*, are found in dense forest with considerable undergrowth, and pygmy antelope, *Neotragus batesi*, inhabit woodland forest and bushland.

The grazing taxa include four obligate grazers: *Damaliscus lunatus*, *Redunca fulvorufula*, *Kobus leche*, and *Redunca arundinum*. These bovids have diets that consist almost exclusively of monocotyledonous grasses, usually consuming less than 10% of any other type of resource (Gagnon and Chew, 2000). All four of these taxa inhabit open habitats, although some variation in habitat preference is represented. *Damaliscus lunatus*, the tsessebe, prefers open savanna and floodplains. The lechwe, *Kobus leche*, is typically found in wet marshes. The two *Redunca* species, the southern and mountain reedbuck, both prefer tall, seasonal grassland.

The mixed feeders included six variable grazers: *Damaliscus pygargus*, *Gazella granti*, *Hippotragus niger*, *Kobus ellipsiprymnus*, *Syncerus caffer*, and *Tragelaphus spekii*. Taxa classified as variable grazers consume 60-90% monocots and usually have diets that vary seasonally (Gagnon and Chew, 2000). Variable grazers typically occupy mosaic habitats where they have access to a variety of resource types. In order to include a wide representation of variable grazer environments, the extant sample includes taxa that favor a range of habitat types. This includes species as diverse as *Damaliscus pygargus*, the bontebok, which occupies highveld grassland and *Hippotragus niger*, the sable antelope, which inhabits wooded savanna. Other preferred habitats include edaphic grassland (*Tragelaphus spekii*), closed forest (*Syncerus caffer*), open grassland (*Gazella granti*) and scrub forest (*Kobus ellipsiprymnus*).

The mixed-feeding taxa also included six browser-grazer intermediates: *Aepyceros melampus*, *Antidorcas marsupialis*, *Raphicerus campestris*, *Taurotragus oryx*, *Tragelphus* *imberbis*, and *Raphicerus sharpei*. Browser-grazer intermediates include bovids that eat 30-70% of dicots and monocots, and always include some fruit (Gagnon and Chew, 2000). Like variable grazers, browser-grazer intermediates prefer habitats that allow them access to a variety of resource types. Overall, these bovids are more likely to be found in highly mosaic habitats and the extant sample presented here includes taxa that a representative of the environmental preferences of the category. The taxa that prefer more open habitats include the impala, *Aepyceros melampus*, which is found in bushland and open savanna, the springbok, *Antidorcas marsupialis*, usually found in grassland and the common eland, *Taurotragus oryx*, which inhabits savannas and plains. More closed habitat taxa include the lesser kudu, *Tragelaphus imberbis*, which occupies dry bushland and closed forest, and Sharpe's grysbok, *Raphicerus sharpei*,usually found in scrubland. Some browser-grazers intermediates are also highly variable and can be found in both woodland and grassland, like the steenbok, *Raphicerus campestris*.

Three taxa classified as generalists were included in the sample. These are *Oreotragus oreotragus*, *Tragelaphus angasi*, and *Tragelaphus strepsiceros*. Generalists consume a wide variety of foods and typically include more than 20% of the primary resource types (Gagnon and Chew, 2000). Like most mixed feeders, these taxa occupy a broad range of habitats. This sample includes taxa with a range of habitat preferences. The klipspringer, *Oreotragus oreotragus*, is found in open woodland and savanna, while the nyala (*Tragelaphus angasi*) prefers dense forests. The greater kudu, *Tragelaphus strepsiceros*, is intermediate to the other two, typically inhabiting woodland forest and thick bushland.

Finally, two frugivorous bovids were sampled in order to have microwear textures from all possible extant dietary categories. The two taxa, *Cephalophus sylvicultor* and *Philantomba monticola*, both consume more than 70% fruit, with little to no inclusion of grasses (Gagnon and

Chew, 2000). These two taxa were selected because neither varies its diet seasonally and reliable dietary information based on wild studies is available (Emmons et al., 1983; Dubost, 1984). Both species occupy dense forest habitats where fruit is widespread.

Results

The second chapter of this dissertation, "*Dental microwear texture analysis of extant African Bovidae*" addresses the extant microwear texture database collected for this project. This comparative sample is the largest ever collected for bovids and includes 575 individual specimens representing 25 taxa. The technique accurately classified all 25 extant bovid taxa by dietary category, indicating that this dataset can be used to reliably assign dietary preference to the fossil taxa. Clear statistical differences were present among all dietary categories, with the exception of generalists and browser-grazer intermediates, both of which consume a wide variety of graze and browse resources. The results confirm the conclusions of Ungar et al. (2007) that grazers and browsers can be easily identified using dental microwear textures. In fact, there was no overlap between obligate grazers and dedicated browsers for any of the texture variables. In addition to examining the difference among the dietary categories, I also looked at variation within diets. Some significant differences among taxa within the dietary categories were identified. These may relate to seasonal or geographic differences in diet, and points to future research.

In sum, the construction of the extant comparative database for African bovids serves two important purposes. First, it confirms the ability of dental microwear texture analysis to distinguish among the dietary categories, including various levels of mixed feeding. Second, it provides a comprehensive dataset of bovid microwear textures that can be used to interpret the microwear signatures of fossil taxa from sites across Africa, including the eastern localities addressed in this study.

Objective 2: Bovid paleodiets and paleoenvironments

The second objective of this dissertation was to reconstruct the diets of the fossil bovids from Kanapoi, Allia Bay, Laetoli using dental microwear texture analysis and Hadar and to use these data to test competing hypotheses regarding the paleoenvironments at these important early hominin sites. Microwear texture data were collected for each of the fossil bovid taxa and the resulting wear signatures were compared to the extant comparative database. Finally, the apparent resource preferences of the fossil bovids were used to infer likely habitat types at the various sites. Previous paleoenvironmental reconstructions were then evaluated based on the microwear texture data and current paleoclimatological models.

Fossil sample selection

Inferences of diet are frequently used as proxies for paleoenvironment, so testing the ability of dental microwear texture analysis to accurately classify taxa by dietary preference was a priority (e.g., Robinson, 1963; Vrba, 1974, 1975, 1980, 1988; Kay, 1975, 1978; Grine, 1981; Stern and Susman, 1983; Kappelman, 1988; Benefit and McCrossin, 1990, Ciochon, 1990; Spencer, 1995; Lewis, 1997). Although there is undoubtedly a relationship between bovid diet and habitat, reliable predictions of paleoenvironment depend on the ability to reconstruct diet accurately. Thus, the aim of this project was to develop a large database of fossil microwear textures to insure that the dietary inferences were as well-supported as possible.

The large collections of fossil bovids from the four sites allowed for a large volume of data to be collected. This made it possible to draw inferences not only for diet, but also habitat preference. All available bovid specimens from Kanapoi, Allia Bay, Laetoli and Hadar were examined for microwear preservation. As is typical for fossils, only a small percentage of specimens preserved unobscured antemortem microwear that could be analyzed. The Kanapoi and Allia Bay samples are the smallest, with 35 total specimens from Kanapoi, representing 8 taxa, and 15 from Allia Bay, representing 2 taxa. The Laetoli sample consists of 49 individuals, representing 9 taxa. Finally, the Hadar sample includes 124 specimens: 30 from the Sidi Hakoma Member, representing 8 taxa; 63 from the Denen Dora Member, representing 9 taxa; and 31 from the Kada Hadar Member, representing 10 taxa.

Bovids as proxies for paleoenvironment

Previous studies have shown that dental microwear patterns reflect diet in extant bovids (for examples, see Solounias et al., 1988; Solounias and Moelleken, 1993; Merceron and Ungar, 2005; Merceron et al., 2005; Schubert et al., 2006, Ungar et al., 2007). Several studies have explored the implications of dietary reconstructions based on microwear for understanding paleoenvironments (Merceron et al., 2005, Merceron and Ungar, 2005; Ungar et al., 2007). The results of these studies have been promising and this dissertation furthers the exploration of the diet-habitat relationship. The Pliocene hominin sites in eastern Africa are good candidates for testing previous paleoenvironmental hypotheses, as previous research has often led to conflicting reconstructions. The microwear data presented here are consistent with some of the previous reconstructions for Kanapoi, Allia Bay, Laetoli and Hadar, particularly those that suggest the presence of mosaic habitats.

Dental microwear analysis has been used previously to evaluate competing hypotheses for paleoenvironmental reconstruction (for examples, see Ungar et al., 2007; Merceron et al., 2009). Although there is not a one-to-one relationship between habitat type and the diet of local fauna, evidence of consumption of a particular resource type indicates its local availability. For example, the presence of obligate grazers doesn't confirm that the habitat consisted solely of open savanna, but it does strongly suggest the availability of grassland resources. The dietary variability among the local fauna can indicate the different habitat types found at and near a given site, which is particularly useful for sites thought to be highly mosaic.

Results

In the third chapter, "*Dental microwear texture analysis of fossil bovids from Hadar, Ethiopia: implications for the paleoenvironment ofAustralopithecus afarensis*", the diets of the fossil bovids from Hadar were reconstructed using the new comparative database. The dietary categories assigned to the fossil taxa from the Sidi Hakoma, Denen Dora and Kada Hadar Members were then used to address implications for changing paleoenvironments at the site during the occupation of *A. afarensis*.

The reconstruction of local habitats at Hadar, Ethiopia has been the topic of considerable recent research. *Australopithecus afarensis* occupied this site from approximately 3.42-2.94 million years ago. Because the Hadar includes the last know habitat for the species, an understanding of local environment is important (Leakey and Harris, 1987; White et al., 2000). Although a wide variety of studies, including those utilizing palynological remains (Radosevich et al., 1992; Bonnefille et al., 2004), ecomorphological and diversity analyses of faunal assemblages (Bobe and Eck, 2001; Reed, 2008) and stable isotope data (Hailemichael, 2000), have suggested a mosaic of microhabitats at Hadar throughout the temporal range of *A. afarensis*, some disagreement exists about the amount of fluctuation in habitat type, rainfall and humidity.

Clear differences in bovid microwear textures were found between the members. The Sidi Hakoma bovids are reconstructed as browsers or browser-grazer intermediates, suggesting the presence of woodland resources and more closed habitats during the earliest occupation of the australopiths. The Denen Dora bovids have microwear texture signatures ranging from obligate grazer to browser-grazer intermediate, indicating access to both browse and graze and a mosaic habitat. The Kada Hadar bovids have variable or obligate grazing signatures, although a few browsing taxa are still present. This suggests open grassland habitats would have been present during the end of the Hadar occupation by *A. afarensis*, although the presence of browsing taxa supports a more mosaic habitat reconstruction. The results presented here suggest increasing aridification over time at Hadar and highlight environmental changes that might have influenced the evolution and eventual extinction of *A. afarensis*.

The fourth chapter of the dissertation, "*Paleoenvironmental change in Pliocene eastern Africa as inferred from dental microwear texture analysis of fossil Bovidae*", takes a more regional approach to the paleoenvironments of the early australopiths. This paper adds dietary reconstructions of the fossil bovids from Kanapoi, Allia Bay and Laetoli to the Hadar sample to test previous hypotheses about changing environments at the sites. It also addresses the implications of these changes for early hominins.

The *Australopithecus anamensis* habitats at Kanapoi and Allia Bay have been reconstructed as seasonally fluctuating mosaics, probably composed of woodland forest with some incursions of grassland. The primary area of disagreement stems from the degree to which grasslands contributed to the habitats. The bovids from these two sites generally have microwear signatures most similar to modern browsing taxa that inhabit closed forest, woodland and bushland habitats. However, a few taxa with grazing signatures do exist and this suggests that some edaphic grassland may have been present at or near the sites.

The Kanapoi bovids fall into two primary dietary categories. Five of the seven taxa closely resemble modern browser-grazer intermediate and generalist species. The prominence of browse-adapted bovids suggests a local environment with considerable forest habitat, or at least consistent access to forest resources. However, the remaining two taxa have microwear signatures that closely resemble those of modern variable grazers. The presence of these two grazing taxa indicates a more complex, mosaic paleoenvironment at Kanapoi, possibly including some grassland (Wynn, 2000; Cerling et al., 2011).

Although the fossil sample from Allia Bay is small, the microwear signatures are consistent with previous reconstructions of the bovids as forest-adapted browsers. The alcelaphin sample is most similar to modern browser-grazer intermediates and the tragelaphins are similar to dense forest adapted browsers. While the sample sizes are too small to draw definitive conclusions about this site, these results support previous reconstructions of Allia Bay as relatively closed forest, with the potential for seasonal fluctuations. Both of the fossil taxa have microwear signatures similar to modern taxa that inhabit seasonally variable environments.

Of all of the sites discussed in this dissertation, Laetoli has had the most inconsistent paleoenvironmental reconstructions, ranging from open savanna to closed forest. And the dental microwear of the fossil bovids reflects a wide variety of microwear signatures. As with Kanapoi and Allia Bay, most of the Laetoli fossil bovids have reconstructed diets similar to modern mixed feeding taxa, especially browser-grazer intermediates. However, there are also three taxa that have microwear signatures similar to modern browsers and two that are similar to extant grazers. The increase in the ratio of grazing to browsing taxa from the earlier sites suggests more prominent incursions of open grassland habitats by the time of *A. afarensis*. All of these signals suggest that the Laetoli paleoenvironment was highly mosaic and offered a wide variety of available niches for the local fauna, including both open and closed microhabitats. This supports previous reconstructions of the site as containing multiple habitat types (Andrews, 1989; Cerling, 1992; Reed, 1997; Musiba, 1999; Harrison, 2005, Musiba et al., 2007; Su and Harrison, 2007).

Previous reconstructions have suggested that Hadar was highly mosaic, including edaphic grassland, open woodland, bushland and closed forest. Based on faunal assemblages, open habitats appear to have been more common at Hadar than at the other sites. The highly mosaic nature of the site is confirmed by the bovid microwear data. The bovids from the Sidi Hakoma and Denen Dora Members have microwear signatures like modern browsers and browser-grazers intermediates, similar to the assemblages from Kanapoi and Allia Bay. The Kada Hadar bovids include more grazing taxa, suggesting the presence of more open habitats. The largest percentage of the fossil taxa at Hadar overall are similar to mixed feeding taxa, including browser-grazer intermediates and generalists, however grazing taxa become increasingly common throughout the formation, with the largest numbers occurring in the Kada Hadar Member.

When viewing these sites over the occupation of *Australopithecus,* a general trend emerges. The dietary reconstructions reveal greater frequency of dedicated browser and/or browser-grazer intermediate taxa at the earlier sites, i.e. Kanapoi, Allia Bay and the Sidi Hakoma Member at Hadar. Later sites, particularly the Kada Hadar Member and Laetoli, have higher numbers of bovids that grouped with modern obligate or variable grazers. While none of the sites appear to have been dominated by open grassland, the results of this dissertation are consistent with previous hypotheses that suggest a gradual aridification trend in eastern Africa during the occupation of the early australopiths.

In sum, the bovid microwear texture data agree with previous reconstructions of theaustralopith habitats as highly mosaic, with increasingly open habitats during the time of *A. afarensis*. This evidence of gradual aridification in eastern Africa supports previous observations by Reed (1997) that the fossil mammalian communities at these sites display increasing percentages of terrestrial species. In general, the results of this dissertation agree with the suggestion by Stanley (1992) that Pliocene hominin habitats did not change drastically over time, but rather that the morphological adaptations that characterize *Australopithecus afarensis* made them ecologically flexible enough to thrive in seasonally shifting mosaic habitats (Stern and Susman, 1983; Ward et al., 2001).

Objective 3: Dental microwear as a test of taxonomic uniformitarianism

Many studies of bovid paleoecology apply the principle of taxonomic uniformitarianism to fossil species, in an attempt to classify their dietary and habitat preferences by assuming that they are similar to closely related modern taxa (for examples, see Kappleman, 1984; Vrba, 1980, 1985, 2003; Shipman and Harris, 1988; Harris, 1991; Plummer and Bishop, 1994; Spencer, 1997; Sponheimer et al., 1999; Kovarovic et al., 2002; DeGusta and Vrba, 2003, 2005; Reed, 2008). Although this assumption is rarely questioned for recent faunas, its utility in reconstructing the paleoecology of long extinct species is uncertain. The primary problems with taxonomic uniformitarianism are that it is not applicable to fossil taxa with few or no living relatives, and that it assumes that groups remain constant in their ecological preferences over long periods of time. While taxonomic uniformitarianism is relatively straight-forward and requires minimal effort beyond a review of a faunal list, critics have questioned many of its inherent assumptions (Solounias et al., 1988; Reed, 1996; Sponheimer et al., 1999; Schubert et al., 2006). For example, in their study of fossil bovids from Makapansgat, Sponheimer et al. (1999) demonstrated that half of the included taxa had diets that differed from the assumed diets based on taxonomic uniformitarianism. For example, while *Aepyceros* sp. and *Gazella vanhoepeni* were both assumed to be mixed/seasonal feeders like their closest living relatives, carbon isotopic signatures and ecomorphological data suggested that both were obligate browsers, and showed no evidence of C4 grass consumption. Due to such discrepancies between inferred adaptations and inferred diet, it is critical that ecological similarities of extant and fossil taxa be tested in some reliable way in order to have confidence in these assumed relationships.

This study set out to test these previous dietary reconstructions for the fossil bovids of Kanapoi, Allia Bay, Laetoli and Hadar using dental microwear texture analysis. As in the Sponheimer et al. (1999) study, approximately half of the included taxa had microwear texture signatures that did not conform to expectations based on the dietary preferences of their modern counterparts. For both the Kanapoi sample, taxonomic uniformitarianism was an unreliable predictor of diet, with only three of the seven fossil taxa at Kanapoi having reconstructed diets similar to their closest living relatives. For the Allia Bay bovids, the *Tragelaphus* sp. specimens have a texture signature very similar to modern browsing tragelaphins. However, the microwear signatures of the fossil alcelaphin specimens are very different from those of modern taxa like *Damaliscus*. Taxonomic uniformitarianism was slightly more reliable at Laetoli, with five of the nine taxa having similar dietary preferences to their modern counterparts. Finally, the Hadar sample became more predictable over time. Only two of the eight fossil taxa from the Sidi Hakoma Member had microwear signatures similar to modern relatives. However, within the more recent deposits, five of the nine Denen Dora taxa and seven of the ten Kada Hadar taxa had texture signatures that matched the dietary predictions made using taxonomic uniformitarianism.

In sum, this dissertation confirmed the opinion of Sponheimer et al. (1999), that taxonomic uniformitarianism is not always a reliable indicator of bovid diet, especially for ancient deposits. Given how frequently fossil bovid samples are used as paleoenvironmental proxies, it is critical that their diets be reconstructed accurately. This is especially important since diet can change rapidly, but it can take many generations for morphology to change. This suggests that morphology alone cannot be considered a reliable predictor of diet and should be confirmed using direct line evidence, like dental microwear or stable isotope analysis.

Future Goals

My future goals related to this project are two-fold. First, I intend to expand the study to include additional and later sites in eastern Africa, such as Olduvai Gorge and Koobi Fora. The extant sample collected for this study has the potential to be applied to a many different sites and time periods in Africa. In fact, the comparative database presented here is already being used to interpret the microwear signatures of fossil tragulids from the Miocene sites of Rusinga Island and Songhor. Carbon isotope analyses are not an option for these sites, because C4 plants had not yet spread through Africa. The results suggest that ruminant dental microwear may be able to serve as a paleoenvironmental proxy at sites where stable carbon isotope data are not an option.

In the near future, I also hope to collaborate with other researchers to better integrate microwear with isotope and ecomorphological data to strengthen interpretations of diet and paleoecology. Stable isotopes and dental mesowear can provide complementary information on diet reflecting a longer time interval than microwear, which only reflects the last few days or weeks of an individual’s life. Carbon, oxygen, strontium and other isotopes hold the potential to provide a broad range of information about diets and mesowear informs on diet over the lifetime of the individual. Ecomorphology, depends on relationships between morphology and adaptation, and is another widely accepted method of dietary reconstruction that has been successful in distinguishing taxa. This provides a much longer time frame for diet, as it results from selective pressures over generations. These approaches taken together can complement one another in both the resolution of diet categorization, and provide important time-scale information for foods available and eaten, and by extension habitat setting.

The first of these projects is already underway. As part of a collaborative project with Dr. Francis Kirera, I am comparing dental microwear data of fossil bovids from the site of Ileret, Kenya with stable isotope data for the same specimens. While previous studies have compared these types of data for the same taxa, none have utilized the same specimens; an important step given the short lifespan of microwear data. We hope that this project will be an important step forward in understanding the relationship between isotope and microwear data and how they can be used to complement and enhance one another.

Finally, I hope to include more diverse taxa into future studies of paleoecology and habitat. Environments are complex and not perfectly represented by any single type of inhabitant. Therefore, reconstructing the paleoecological preferences of multiple taxa should provide a more complete picture of how a past ecosystem operated. Our research group has begun applying this principle with the faunal assemblage from Langebaanweg, South Africa and to date we have analyzed the dental microwear of fossil bovids, carnivores, giraffes and elephants. In future studies, I would like to apply this multi-taxon approach to further analyze the faunal assemblages of the Hadar Formation. Hopefully, this detailed analysis would provide even more complete information about changes in habitat availability during the occupation of *Australopithecus afarensis*.

References

Andrews, P., 1989. Paleoecology of Laetoli. J. Hum. Evol. 18, 173-181.

Benefit, B.R., McCrossin, M.L., 1990. Diet, species diversity, and distribution of African fossil baboons. Kroeber Anthrop. Soc. Papers 71–72, 79–93.

Bobe, R., Eck, G.G., 2001. Responses of African bovids to Pliocene climatic change.Paleobiology27 (Suppl. to No. 2).Paleobiology Memoirs 2, 1-47.

Bonnefille, R., Potts, R., Chalié, F., Jolly, D., Peyron, O., 2004. High-resolution vegetation and climate change associated with Pliocene *Australopithecus afarensis*. Proc. Natl. Acad. Sci. 101, 12125-12129.

Cerling, T.E., 1992. Development of grasslands and savannas in East Africa during the Neogene.Palaeogeogr.Palaeoclimatol.Palaeoecol. 97, 241-247.

Cerling, T.E.., Wynn, J.G., Andanje, S.A., Bird, M.I., Korir, D.K., Levin, N.E., Mace, W., Macharia, A.N., Quade, J., Remien, C.H., 2011. Woody cover and hominin environments in the past 6 million years. Nature 476, 51-56.

Ciochon, R.L., 1990. Evolution of the Cercopithecoid forelimb: Phylogenetic and Functional Implications from Morphometric Analysis. California: University of California Publications in Geological Science, 135.

DeGusta, D., Vrba, E., 2003. A method for inferring paleohabitats from the functional morphology of bovid astragali. J. Archaeol. Sci. 30, 1009-1022.

DeGusta, D., Vrba, E.S., 2005. Methods for inferring paleohabitats from the functional morphology of bovid phalanges. J. Archaeol. Sci. 32, 1099-1113.

DeMenocal, P.B., 1995. Plio-Pleistocene African climate. Science 270, 53-59.

DeMenocal, P.B., Brown, F.H., 1999. Pliocene tephra correlations between East African hominid localities, the Gulf of Aden and the Arabian Sea. In: Hominoid evolution and climatic change in Eurasia, pp. 23-59.

Dowsett, H., Barron, J., Poore, R., 1996. Middle Pliocene sea surface temperatures: a global reconstruction. Marine Micropaleontol. 27, 13-25.

Dubost, G., 1984. Comparisons of the diets of frugivorous forest ruminants of Gabon. J. Mammal. 65, 298-316.

Emmons, L.H., Gauthier-Hion, A., Dubost, G., 1983.Community structure of the frugivorous-folivorous forest mammals of Gabon. J. Zool. (London) 199, 209-222.

Gagnon M., Chew, A.E., 2000. Dietary preferences in extant African Bovidae. J. Mammal. 8:490-511.

Grine, F.E., 1981. Trophic differences between ‘‘gracile’’ and ‘‘robust’’ australopithecines, a scanning electron microscope analysis of occlusal events. S. Afr. J. Sci. 77, 203–230.

Grine, F.E., Judex, S., Daegling, D.J., Ozcivici, E., Ungar, P.S., Scott, R.S., Scott, J.R., Teaford, M.F., Sponheimer, M., Walker, A., 2010. Modeling craniofacial biomechanics, and the limitations of functional and dietary inference in hominin paleontology. J. Hum. Evol.

Hailemichael, M., 2000. The Pliocene environment of Hadar, Ethiopia: a comparative isotopic study of paleosol carbonates and lacustrine mollusk shells of the Hadar Formation and of modern analogs. Ph.D. Dissertation, Case Western Reserve University.

Harris, J.M., 1991. The Fossil Ungulates: Geology, Fossil Artiodactyls, and Paleoenvironments. Koobi Fora Research Project, vol. 3. Clarendon Press, Oxford.

Harrison, T., 2005. Fossil bird eggs from the Pliocene of Laetoli, Tanzania: their taxonomic and paleoecological relationships. J. Afr. Earth Sci. 41, 289-302.

Johanson, D., Masao, F.T., Eck, G.G., White, T.D., Walter, R.C., Kimbel, W.H., Asfaw, B., Manega, P., Ndessokia, P., Suwa, G., 1987. New partial skeleton of Homo habilis from Olduvai Gorge, Tanzania. Nature 327, 205-209.

Kappelman, J., 1984. Plio-Pleistocene environments of Bed I and Lower Bed II, Olduvai Gorge, Tanzania.Palaeogeo.Palaeoclimatol.Palaeoecol. 48, 171-196.

Kappelman, J., 1988. Morphology and locomotor adaptations of the bovid femur in relation to habitat. J. Morphol. 198, 119–130.

Kappelman, J., Plummer, T., Bishop, L., Duncan, A., Appleton, S., 1997.Bovids as indicators of Plio-Pleistocene paleoenvironments in East Africa. J. Hum. Evol. 32, 229-256.

Kay, R.F., 1975. The functional adaptations of primate molar teeth. Am. J. Phys. Anthrop. 43, 195–216.

Kay, R.F., 1978. Molar structure and diet in extant Cercopithecidae. In: Joysey, K., Butler, P., (Eds.) Development, Function, and Evolution of Teeth, pp. 309–339. London: Academic Press.

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.

Kingdon, J., 1982. East African Mammals: an atlas of evolution in Africa. The University of Chicago Press, Chicago, IL.

Kingdom, J., 1997. The Kingdon field guide to African mammals. Academic Press, London.

Kingston, J.D., Marino, B.D., Hill, A., 1994. Isotopic evidence for Neogene hominid paleoenvironments in the Kenya Rift Valley. Science 264, 955-959.

Kovarovic, K., Andrews, P., 2007. Bovid postcranial ecomorphological survey of the Laetoli palaeoenvironment. J. Hum. Evol. 52, 663-680.

Leakey, M.G., Feibel, C.S., McDougall, I., Walker, A., 1995. New four million-year-old hominid species from Kanapoi and Allia Bay, Kenya. Nature 376, 565-571.

Leakey, M.G., Feibel, C.S., McDougall, I., Ward, C., Walker, A., 1998. New specimens and confirmation of an early age for *Australopithecus anamensis*. Nature 393, 62-66.

Leakey, M.D., Harris, J.M. (Eds.), 1987. Laetoli: A Pliocene Site in Northern Tanzania. Clarendon, Oxford.

Lewis, M.E., 1997. Carnivoran paleoguilds of Africa: implications for hominid food procurement strategies. J. Hum. Evol. 32, 257-288.

Lockwood, C.A., Kimbel, W.H., Johanson, D.C., 2000.Temporal trends and metric variation in the mandibles and dentition of *Australopithecus afarensis*. J. Hum. Evol. 39, 23-55.

Merceron, G., deBonis, L., Viriot, L., Blondel, C., 2005. Dental microwear of fossil bovids from northern Greece: paleoenvironmental conditions in the eastern Mediterranean during the Messinian. Palaeogeo.Palaeoclimatol.Palaeoecol. 217, 173-185.

Merceron, G.M., Scott, J.R., Scott, R.S., Geraads, D., Spassov, N., Ungar, P.S., 2009. Seed predation for an early Colobine as a link between frugivory and folivory?Evidence from dental microwear texture analysis of *Mesopithecus* (Late Miocene of Eurasia). J. Hum. Evol. doi:10.1016/j.jhevol.2009.06.009

Merceron, G., Ungar, P.S., 2005. Dental microwear and palaeoecology of bovids from the Early Pliocene of Langebaanweg, Western Cape province, South Africa. S. Afr. J. Sci. 101, 365-370.

Musiba, C.M., 1999. Laetoli Pliocene paleoecology: a reanalysis via morphological and behavioral approaches. Ph.D. Dissertation, University of Chicago.

Musiba, C.M., Magori, C., Stoller, M., Stein, T., Branting, S., Vogt, M., Tuttle, R., Hallgrímsson, B., Killindo, S., Mizambwa, F., Ndunguru, F., Mabulla, A., 2007. The Taphonomy and paleoecological context of the Upper Laetolil Beds (Localities 8 and 9), Laetoli in northern Tanzania. In: Bobe, R., Alemseged, Z., Behrensmeyer, A.K., (Eds.) Hominin Environments in the East African Pliocene: An Assessment of the Faunal Evidence, pp. 257-278. Springer, Dordrecht.

Plummer, T.W., Bishop, L.C., 1994. Hominid paleoecology at Olduvai Gorge, Tanzania as indicated by antelope remains. J. Hum. Evol. 27, 47-75.

Pontzer, H., Scott, J.R., Lordkipanidze, D., Ungar, P.S., in press. Dental microwear and diet in the Dmanisi hominins.Journal of Human Evolution.

Radosevich, S.C., Retallack, G.J., Taieb, M., 1992.Reassessment of the paleoenvironment and preservation of hominid fossils from Hadar, Ethiopia. Am. J. Phys. Anthrop. 87, 15-27.

Reed, K.E., 1996. The paleoecology of Makapansgat and other African Pliocene Hominid Localities.Ph.D. Dissertation.State University of New York, Stony Brook.

Reed, K.E., 1997. Early hominid evolution and ecological change through the African Plio-Pleistocene. J. Hum. Evol. 40, 289-322.

Reed, K.E., 2008. Paleoecological patterns at the Hadar hominin site, Afar Regional State, Ethiopia. J. Hum. Evol. 54, 743-768.

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, Chicago, Aldine, 385-416.

Schoeninger, M.J., Reeser, H., Hallin, K., 2003. Paleoenvironment of *Australopithecus anamensis* at Allia Bay, East Turkana, Kenya: evidence from mammalian herbivore enamel stable isotopes. J. Anthrop. Archaeo. 22, 200-207.

Schubert, B.W., Ungar, P.S., Sponheimer, M., Reed, K.E., 2006. Microwear evidence for Plio-Pleistocene bovid diets from Makapansgat Limeworks Cave, South Africa.Palaeogeo.Palaeoclimatol.Palaeoecol. 241, 301-319.

Scott, J.R., Ungar, P.S., Jungers, W.L., Godfrey, L.R., Scott, R.S., Simons, E.L., Teaford, M.F., Walker, A., 2009. Dental microwear texture analysis of the archaeolemurids and megaladapids, two families of subfossil lemurs from Madagascar. J. Hum. Evol. 56, 405-416.

Shipman, P., Harris, J.M., 1988.Habitat preference and paleoecology of *Australopithecus boisei* in Eastern Africa. In: Grine, F.E. (Ed.), Evolutionary History of the Robust Australopithecines. Aldine, New York, pp. 343-381.Spencer, L.M., 1995. Antelope and

Grasslands: Reconstructing African Hominid Environments. Ph.D. Dissertation, State University of New York at Stony Brook.

Solounias, N., Moelleken, S.M.C., 1993. Determination of dietary adaptations of extinct ruminants through premaxillary analysis. J. Mammal. 74, 1059-1074.

Solounias, N., Teaford, M.F.,Walker, A.C., 1988. Interpreting the diet of extinct ruminants: the case of a non-browsing giraffid.Paleobio. 14, 287-300.

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 Limeworks hominin locality. J. Hum. Evol. 36, 705-718.

Stanley, S.M., 1992. An ecological theory for the origin of Homo.Paleobio. 18, 237-257.

Stern, J.T., Susman, R.L., 1983. The locomotor anatomy of *Australopithecus afarensis*. Am. J. Phys. Anthropol. 60, 279-317.

Su, D., Harrison, T., 2007. The paleoecology of the Upper Laetolil Beds at Laetoli: a reconsideration of the large mammal evidence. Shackleton, N.J., 1995. New data on the evolution of Pliocene climate variability. In: Vrba, E.S., Denton, G.H., Partridge, T.C., Burckle, L.H. (Eds.), Paleoclimate and Evolution, with Emphasis on Human Origins, pp. 243-248. Yale University Press, New Haven, CT.

Ungar, P.S., Merceron, G., Scott, R.S. 2007. 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, F.E., 2010. Molar microwear textures and the diets of *Australopithecus anamensis* and *Australopithecus afarensis*. Philosophical Transactions of the Royal Society B: Biological Sciences 365 (1556): 3345-3354.

Ungar, P.S., Scott, R.S., Scott, J.R., Teaford, M.F. 2008. Dental microwear analysis: historical perspectives and new approaches. In: Irish, J.D. (Ed.), Technique and Application in Dental Anthropology. Cambridge University Press, Cambridge, 389-425.

Vrba, E.S., 1974. Chronological and ecological implications of the fossil Bovidae at the Sterkfontein australopithecine site. Nature 250, 19-23.

Vrba, E.S., 1975. Some evidence of chronology and palaeocology of Sterkfontein, Swartkrans, and Kromdraai from the fossil Bovidae. Nature 254, 301-304.

Vrba, E.S., 1980. The significance of bovid remains as indicators of environment and prediction patterns. In: Behrensmeyer, A.K., Hill, A., (Eds.) Fossils in the making, Vertebrate Taphonomy and Paleoecology, pp. 247–271. Chicago: University of Chicago Press.

Vrba, E.S., 1985. African Bovidae: Evolutionary events since the Miocene. S. Afr. J. Sci. 81, 263-266.

Vrba, E.S., 1988. Late Pliocene climatic events and hominid evolution. In: Grine, F.E. (Ed.), Evolutionary History of the "Robust" Australopithecines, pp. 405-426. Aldine, New York.

Vrba, E.S., 1995a. The fossil record of African antelopes (Mammalia, Bovidae) in relation to human evolution and paleoclimate. In: Vrba, E.S., Denton, G.H., Partridge, T.C., Burckle, L.C. (Eds.), Paleoclimate and Evolution with Emphasis on Human Origins, pp. 385-424. Yale University Press, New Haven.

Vrba, E.S., 2000. Major features of Neogene mammalian evolution in Africa. In: Partridge, T.C., Maud, R.R. (Eds.), The Cenozoic of Southern Africa, pp. 277-304. Oxford University Press, Oxford.

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.

White, T., Suwa, G., Asfaw, B., 1994.Australopithecus ramidus, a new species of early hominid from Aramis, Ethiopia. Nature 371, 306-312.

White, T.D, Suwa, G., Simpson, S., Asfaw, B., 2000.Jaws and teeth of *Australopithecus afarensis* from Maka, Middle Awash, Ethiopia. Am. J. Phys. Anthop. 111, 45-68.

WoldeGabriel, G., White, T.D., Suwa, G., Renne, P., de Heinzelin, J., Hart, W.K., Heiken, G., 1994. Ecological and temporal placement of Early Pliocene hominids at Aramis, Ethiopia.Nature 371, 330-333.Wynn, J.G., 2000.Paleosols, stable carbon isotopes, and paleoenvironmental interpretation of Kanapoi, northern Kenya. J. Hum. Evol. 39, 411-432.

Wolpoff, M.H., 1999. Paleoanthropology, second ed. McGraw-Hill.

Appendix I: Specimen numbers and raw data for extant taxa

FMNH34471	Aepyceros melampus	B-G INT	1.8399825	0.005397	0.416516	5984.135487	0.478879642	0.757029596
FMNH34472	Aepyceros melampus	B-G INT	1.628754	0.0062915	0.647108	6234.15487	0.32673844	0.514555649
FMNH34473	Aepyceros melampus	B-G INT	1.403186	0.007169	45.613882	8126.03154	0.440646851	0.673717485
FMNH34474	Aepyceros melampus	B-G INT	1.320738	0.005207	0.434875	5648.32154	0.545798068	0.955443019
FMNH34475	Aepyceros melampus	B-G INT	2.127167	0.003054	0.37871	7328.646879	0.368347142	0.689688248
FMNH34476	Aepyceros melampus	B-G INT	1.5395735	0.002312	0.8843845	6139.687685	0.318901991	0.897099476
FMNH34477	Aepyceros melampus	B-G INT	2.1760725	0.003391	1.5093715	4926.878647	0.548925398	1.008837187
FMNH34478	Aepyceros melampus	B-G INT	1.2853225	0.0010635	0.8405915	5306.613203	0.462894505	1.168098188
FMNH34479	Aepyceros melampus	B-G INT	1.942438	0.0023595	0.515229	6280.465787	0.604546055	1.175986342
FMNH34770	Aepyceros melampus	B-G INT	2.267912	0.001442	0.5082065	4872.031647	0.378007143	0.491130727
FMNH95838	Aepyceros melampus	B-G INT	2.187294	0.004935	0.4173365	5139.354867	0.530561553	0.691069594
FMNH95841	Aepyceros melampus	B-G INT	1.5278015	0.0037535	0.6785885	5791.303566	0.910872564	1.289708096
FMNH98534	Aepyceros melampus	B-G INT	2.878133	0.005054	0.2707935	6138.457553	0.654825144	1.047273161
FMNH34790	Aepyceros melampus	B-G INT	1.7786945	0.0043815	0.5101575	8304.031547	0.453660527	0.575883342
FMNH34782	Aepyceros melampus	B-G INT	2.0699555	0.002776	0.5084	5595.103155	0.45657353	0.648503386
FMNH134359	Aepyceros melampus	B-G INT	2.9253	0.003593	0.762073	6065.843164	0.756173167	1.041371792
FMNH34480	Aepyceros melampus	B-G INT	1.549095	0.0023385	0.4738425	5603.506157	0.432413068	0.592614069
FMNH34781	Aepyceros melampus	B-G INT	1.2995065	0.008038	0.5336365	4408.673501	0.420712906	0.697793045
FMNH34791	Aepyceros melampus	B-G INT	1.472572	0.0043445	0.431578	4291.242405	0.433826096	0.740819063
FMNH34784	Aepyceros melampus	B-G INT	2.137925	0.003738	0.5142555	5381.37551	0.440550298	0.958137737
FMNH140861	Antidorcas marsupialis	B-G INT	2.614542	0.003805	0.1501285	6806.224023	0.31144188	0.638758604
FMNH34482	Antidorcas marsupialis	B-G INT	2.2922365	0.0056925	0.266493	4390.564865	0.850087885	0.798751564

FMNH34483	Antidorcas marsupialis	B-G INT	1.2622145	0.0039055	0.708244	5708.687808	0.641929846	0.798370595
FMNH34488	Antidorcas marsupialis	B-G INT	4.870195	0.000703	0.149882	4417.101144	0.408187068	0.729498909
FMNH34490	Antidorcas marsupialis	B-G INT	2.7712995	0.004428	0.8160825	6470.251084	0.345910161	0.522250395
FMNH34494	Antidorcas marsupialis	B-G INT	3.247638	0.004081	0.1502405	8317.677593	0.496767238	0.783561875
FMNH34496	Antidorcas marsupialis	B-G INT	1.676729	0.0038185	0.434672	5376.119861	0.582861919	0.981588347
FMNH34487	Antidorcas marsupialis	B-G INT	1.5656895	0.003523	1.276719	4520.824627	0.715157933	1.075978167
FMNH34428	Antidorcas marsupialis	B-G INT	2.94996	0.0038455	0.150592	7106.85564	0.480186234	0.813142231
FMNH34328	Antidorcas marsupialis	B-G INT	1.2848905	0.002441	0.3421295	4428.743964	0.606344308	0.820483526
FMNH34386	Antidorcas marsupialis	B-G INT	1.6940775	0.0055705	0.508052	5390.366566	0.465419015	0.57060634
FMNH34392	Antidorcas marsupialis	B-G INT	2.064117	0.0031465	0.150371	6286.463817	0.407186675	0.699732226
FMNH34471	Antidorcas marsupialis	B-G INT	2.566063	0.0028545	0.34211	5922.663362	0.409579459	0.800097844
FMNH34476	Antidorcas marsupialis	B-G INT	2.232951	0.003521	78.6355245	7836.607059	0.603202071	0.878067745
FMNH34481	Antidorcas marsupialis	B-G INT	1.954265	0.005097	0.2666325	5733.702048	0.35513256	0.572355562
FMNH129730	Antidorcas marsupialis	B-G INT	1.7942415	0.0036325	0.2676775	4838.83536	0.437143884	0.693861922
FMNH140882	Antidorcas marsupialis	B-G INT	2.611354	0.0033205	0.1504445	7169.301855	0.581756163	0.766069542
FMNH140888	Antidorcas marsupialis	B-G INT	1.5701145	0.0038145	0.266714	8428.413034	0.517645294	0.906349943
FMNH34484	Antidorcas marsupialis	B-G INT	5.803359	0.002042	0.150285	7008.957918	0.472007532	0.879169333
FMNH34493	Antidorcas marsupialis	B-G INT	1.657824	0.002004	0.267978	5561.437955	0.645917378	0.892905452
FMNH34495	Antidorcas marsupialis	B-G INT	1.5370595	0.0031835	0.267378	5094.467467	0.375930171	0.884827079
RMCA 83-006M492	Cephalophus sylvicultor	FRUG	6.670257	0.0023195	0.245239	13817.38681	0.553043323	0.811119908
RMCA10150	Cephalophus sylvicultor	FRUG	3.938943	0.0013985	0.2691015	10142.07688	0.517485365	0.792249506
RMCA19569	Cephalophus sylvicultor	FRUG	5.148326	0.004068	0.2160635	10881.05492	0.41032014	0.837688514
RMCA2700	Cephalophus sylvicultor	FRUG	5.092673	0.0037985	0.2665385	14158.30005	0.519463937	0.748059783

RMCA27769	Cephalophus sylvicultor	FRUG	4.1138935	0.004846	0.260228	11272.66039	0.448645227	0.800371031
RMCA37696	Cephalophus sylvicultor	FRUG	4.866296	0.0023205	0.292876	13820.64053	0.572121646	0.742821816
RMCA4087	Cephalophus sylvicultor	FRUG	3.0750255	0.0040855	0.3090895	13081.05878	0.526133798	0.775522407
RMCA83-006M490	Cephalophus sylvicultor	FRUG	2.8322415	0.0038115	0.3207975	9258.920862	0.532809885	0.813366481
RMCA83006-M491	Cephalophus sylvicultor	FRUG	3.0884285	0.002493	0.2988395	9552.781267	0.512500812	0.710419302
RMCA83-006M493	Cephalophus sylvicultor	FRUG	6.921407	0.0016295	0.2253655	14916.55155	0.496671328	0.830779121
RMCA83-006M494	Cephalophus sylvicultor	FRUG	3.6105785	0.003168	0.1708535	11762.78912	0.536920863	0.837526439
RMCA83-006M495	Cephalophus sylvicultor	FRUG	4.7926345	0.004146	0.284616	14861.91373	0.493909534	0.691998357
RMCA83-006M496	Cephalophus sylvicultor	FRUG	3.4302775	0.0019195	0.1518705	12316.54968	0.485350216	0.777849413
RMCA89024M12	Cephalophus sylvicultor	FRUG	4.168408	0.00139	0.2740735	13326.36803	0.559248572	0.707640429
RMCA89024M15	Cephalophus sylvicultor	FRUG	5.7891505	0.0042215	0.150323	13161.94976	0.498396007	0.807288018
RMCA83-006M483	Cephalophus sylvicultor	FRUG	3.103333	0.0013235	0.2693415	10326.52966	0.564707569	0.871848007
RMCA83-006M484	Cephalophus sylvicultor	FRUG	5.3990085	0.0040375	0.268002	13813.58029	0.415227932	0.857785098
RMCA83-006M485	Cephalophus sylvicultor	FRUG	6.7293805	0.0020585	0.258415	14438.21677	0.518895033	0.76213315
RMCA83-006M486	Cephalophus sylvicultor	FRUG	3.6431485	0.003577	0.263682	13246.7359	0.464524787	0.872641064
RMCA83-006M488	Cephalophus sylvicultor	FRUG	5.4295545	0.003947	0.209171	10922.42045	0.457379418	0.880531061
RMCA83-006M489	Cephalophus sylvicultor	FRUG	4.4478045	0.001924	0.233258	13527.90933	0.427762244	0.858387933
RMCA83-006M497	Cephalophus sylvicultor	FRUG	4.7594625	0.0045135	0.318459	12691.64647	0.560114807	0.780965401
RMCA83-006M498	Cephalophus sylvicultor	FRUG	4.6280135	0.001803	0.2082335	9497.049822	0.426397879	0.81639333
RMCA83-006M499	Cephalophus sylvicultor	FRUG	6.658063	0.0030035	0.29439	14279.2165	0.427210612	0.812328065
RMCA93-006M487	Cephalophus sylvicultor	FRUG	3.0810795	0.003602	0.2668355	11061.10869	0.42652359	0.824481001
FMNH104428	Damiliscus lunatus	OG	1.188699	0.0053155	1.4171795	2786.219049	0.434844591	0.532562317
FMNH104429	Damiliscus lunatus	OG	0.644721	0.0076775	0.907952	1998.075311	0.457514252	0.640179566

FMNH127913	Damiliscus lunatus	OG	0.7465805	0.006463	1.6000965	3527.032211	0.338481019	0.606858185
FMNH127915	Damiliscus lunatus	OG	1.113989	0.0069655	2.266841	3993.1422	0.435544594	0.522746891
FMNH127917	Damiliscus lunatus	OG	0.908991	0.0067065	1.3424585	3453.483693	0.460711355	0.64079327
FMNH127918	Damiliscus lunatus	OG	0.7608595	0.006606	1.4332235	3603.397394	0.561752956	0.691704045
FMNH127919	Damiliscus lunatus	OG	1.2752405	0.007105	1.3431635	1326.615354	0.444213312	0.609026122
FMNH127920	Damiliscus lunatus	OG	0.8453665	0.008639	1.065896	1547.050014	0.386982595	0.555790278
FMNH27477	Damiliscus lunatus	OG	0.726458	0.005336	0.8140125	1906.761451	0.507956643	0.678307565
FMNH29529	Damiliscus lunatus	OG	0.733701	0.0059315	1.071581	3673.834317	0.395432687	0.547179698
FMNH29531	Damiliscus lunatus	OG	1.3501465	0.0060535	1.732713	1048.869303	0.395680164	0.674393446
FMNH29532	Damiliscus lunatus	OG	0.7189515	0.0063725	2.2086705	1917.302852	0.368146457	0.693013021
FMNH34527	Damiliscus lunatus	OG	0.909497	0.0065015	1.2665825	1785.91323	0.314271277	0.670637222
FMNH39483	Damiliscus lunatus	OG	1.225762	0.0056235	1.5912955	1123.177318	0.380388644	0.647409181
FMNH39489	Damiliscus lunatus	OG	1.1579135	0.006856	2.2666805	1506.692188	0.458415489	0.714990577
FMNH135326	Damiliscus lunatus	OG	1.347053	0.006221	1.4342825	1248.782114	0.488455744	0.748196099
FMNH135327	Damiliscus lunatus	OG	0.9341945	0.0060405	1.150486	1270.078704	0.476801194	0.673322721
FMNH27481	Damiliscus lunatus	OG	1.038574	0.0073685	2.1409975	2771.000033	0.522783777	0.766888357
FMNH34526	Damiliscus lunatus	OG	0.7329735	0.0070385	1.742269	1353.09745	0.355971412	0.797972943
FMNH34530	Damiliscus lunatus	OG	0.5123225	0.0068015	1.2689295	2395.848276	0.526560028	0.732391462
FMNH34593	Damiliscus lunatus	OG	1.210541	0.00591	1.417367	1934.717118	0.399589089	0.630513305
FMNH34597	Damiliscus lunatus	OG	0.8555065	0.007213	0.9441255	1672.97646	0.467155886	0.678416228
FMNH13265	Damiliscus pygargus	VG	0.62034175	0.003772	1.60113	5000.894419	0.372589569	0.616902725
FMNH13266	Damiliscus pygargus	VG	1.7364035	0.0045725	1.4467525	4529.874261	0.306376769	0.50439929
FMNH13525	Damiliscus pygargus	VG	1.906413	0.0031695	1.2094175	5504.183468	0.240710027	0.557334983

FMNH34565	Damiliscus pygargus	VG	1.075136	0.006231	1.421984	5243.300845	0.334682697	0.652084819
FMNH34566	Damiliscus pygargus	VG	0.9488495	0.0032835	1.599968	3169.254588	0.211678184	0.525455951
FMNH34567	Damiliscus pygargus	VG	1.1979345	0.006743	1.344247	5417.155721	0.439897202	0.717879219
FMNH34606	Damiliscus pygargus	VG	1.406781	0.005735	1.208595	8450.443965	0.462510218	0.68603258
FMNH37615	Damiliscus pygargus	VG	1.630403	0.003585	0.919594	3424.481287	0.466847549	0.651187287
FMNH39154	Damiliscus pygargus	VG	1.2987285	0.006697	1.4646565	4456.454168	0.463320476	0.779879943
AMNH82984	Damiliscus pygargus	VG	0.80929645	0.00425	1.28261875	8959.398296	0.309330231	0.512256858
AMNH82648	Damiliscus pygargus	VG	1.691624	0.006431	1.438629	3470.329225	0.307423142	0.597382057
AMNH83594	Damiliscus pygargus	VG	1.511477	0.003437	1.7440655	4156.687159	0.283508085	0.585009497
AMNH82649	Damiliscus pygargus	VG	0.937826	0.0062885	1.3610975	5923.871279	0.394271213	0.626928963
AMNH87594	Damiliscus pygargus	VG	0.9322015	0.0040425	1.3149735	4411.868577	0.485206935	0.690275479
AMNH83459	Damiliscus pygargus	VG	1.292846	0.0066495	1.2693455	3590.999473	0.429259446	0.601070706
AMNH84597	Damiliscus pygargus	VG	1.631068	0.003549	1.385749	1690.889911	0.360395185	0.590143106
NMNH16483	Damiliscus pygargus	VG	0.87828	0.0058655	1.110468	4002.631669	0.460505675	0.67193488
NMNH18495	Damiliscus pygargus	VG	1.301803	0.0032295	1.2681495	5068.606153	0.471607888	0.619021708
NMNH19842	Damiliscus pygargus	VG	1.236952	0.00662	0.9334155	5986.79752	0.470040061	0.528806628
NMNH20348	Damiliscus pygargus	VG	1.02454	0.0061	1.2654	4833.109736	0.384282489	0.51291107
NMNH21648	Damiliscus pygargus	VG	2.13648	0.0039625	1.370485	6597.162828	0.495322058	0.643864474
NMNH21647	Damiliscus pygargus	VG	0.984617	0.0066055	0.9999155	6403.205833	0.227577232	0.504915139
FMNH127932	Gazella granti	VG	2.3680835	0.005279	0.1500785	2699.657586	0.450524852	0.876414888
FMNH134313	Gazella granti	VG	1.1393815	0.00447	0.6643135	6374.3142	0.486923834	0.744954415
FMNH29595	Gazella granti	VG	1.9548485	0.0040635	0.266507	5177.031861	0.340330289	0.687663969
FMNH29596	Gazella granti	VG	1.302947	0.003738	0.2664865	3052.566522	0.393719771	0.87893847

FMNH29598	Gazella granti	VG	1.934649	0.004316	0.2087325	2340.864853	0.298644873	0.516224572
FMNH29599	Gazella granti	VG	1.8160155	0.0033985	0.6086515	4743.694918	0.491493389	0.640150466
FMNH29600	Gazella granti	VG	1.4811555	0.0041355	0.547841	4345.894489	0.28936413	0.814075934
FMNH29604	Gazella granti	VG	1.01296	0.005587	1.035285	3496.984815	0.43954105	0.51918365
FMNH29605	Gazella granti	VG	1.647628	0.005785	0.5322895	2459.057563	0.37736376	0.737023683
FMNH32911	Gazella granti	VG	1.929781	0.005751	0.5499715	1511.114275	0.342108431	0.570807613
FMNH32913	Gazella granti	VG	1.9977925	0.0031245	0.2083235	3070.002093	0.414668609	0.632787295
FMNH32914	Gazella granti	VG	0.9071	0.0033925	0.5996475	1889.193374	0.364084873	0.50811037
RMCA83-006M795	Gazella granti	VG	2.0317085	0.0039	0.1500675	2472.739663	0.304881122	0.571840692
RMCA83-006M496	Gazella granti	VG	2.183069	0.005037	1.2158495	2073.642176	0.388305524	0.769716113
RMCA83-006M794	Gazella granti	VG	2.2539265	0.0033975	0.8312	1746.695454	0.339779332	0.731458226
RMCA80-006-M487	Gazella granti	VG	1.6367535	0.004296	0.482906	3332.39179	0.397604125	0.518047342
RMCA83-006M846	Gazella granti	VG	1.171141	0.0055565	0.836778	4866.355263	0.291221259	0.591535544
FMNH84628	Gazella granti	VG	1.4771245	0.003256	0.2085625	2331.725165	0.223399203	0.792665717
FMNH49781	Gazella granti	VG	2.006977	0.003581	0.4085115	4253.364348	0.261634677	0.476278085
FMNH26487	Gazella granti	VG	1.137683	0.0036585	0.266821	3456.133165	0.369833977	0.730617751
FMNH49875	Gazella granti	VG	2.145278	0.0043335	0.342435	3096.9314	0.300469356	0.755937048
FMNH82648	Gazella granti	VG	1.262603	0.004634	0.208421	3120.916915	0.435388721	0.784149931
FMNH84625	Gazella granti	VG	2.0055875	0.004503	0.60547585	4023.220215	0.315793319	0.639100273
FMNH26498	Gazella granti	VG	1.0659675	0.003818	0.9627325	1353.636387	0.243867804	0.691551513
FMNH26845	Gazella granti	VG	2.141911	0.0037285	0.965903	2540.596105	0.391046442	0.729472791
FMNH1166	Hippotragus niger	VG	1.7634745	0.0055315	0.4331795	5013.910017	0.461377743	0.755801343
FMNH134360	Hippotragus niger	VG	1.3902385	0.0063385	0.1522105	4288.108204	0.393476192	0.739835765

FMNH34514	Hippotragus niger	VG	1.538723	0.005419	0.208255	6877.024095	0.652076392	0.855659588
FMNH34517	Hippotragus niger	VG	0.1923125	0.003831	0.1505185	3042.671161	0.385265309	0.769168815
FMNH34605	Hippotragus niger	VG	1.81661	0.0049575	0.151845	4929.276177	0.505984396	0.929587744
FMNH98111	Hippotragus niger	VG	2.109119	0.0046845	0.1507065	3904.404539	0.535795297	0.820915995
FMNH56482	Hippotragus niger	VG	1.530215	0.007947	0.435399	5534.058008	0.454143633	0.779571034
FMNH98745	Hippotragus niger	VG	1.68119	0.0065945	0.3422015	4846.00692	0.471174223	0.586321932
FMNH64863	Hippotragus niger	VG	1.1473055	0.004782	0.2089555	6227.537395	0.547857128	0.697943873
FMNH49785	Hippotragus niger	VG	1.0514755	0.005504	0.267373	3493.686877	0.523254273	0.627700764
FMNH16486	Hippotragus niger	VG	1.7542775	0.007572	0.266895	3921.288865	0.572454879	0.640910376
FMNH26485	Hippotragus niger	VG	1.789392	0.007422	0.150431	4569.87071	0.644674304	0.886850159
FMNH97516	Hippotragus niger	VG	1.179479	0.0062485	0.341671	3998.187867	0.579341123	0.813756889
FMNH16488	Hippotragus niger	VG	0.915165	0.007143	0.343115	4049.357266	0.510873467	0.833450651
AMNH97846	Hippotragus niger	VG	1.4955175	0.0072045	0.3416845	6650.019712	0.570441267	0.717089761
AMNH36484	Hippotragus niger	VG	1.682579	0.0063825	0.4193985	4582.170104	0.599619872	0.653472897
AMNH64846	Hippotragus niger	VG	0.919643	0.0064755	0.271291	5892.682569	0.420055571	0.741557875
AMNH79548	Hippotragus niger	VG	2.1532515	0.0078185	0.341804	4716.894046	0.383804785	0.673393367
AMNH15486	Hippotragus niger	VG	0.825724	0.003858	0.1506695	5091.642845	0.621929908	0.736272299
AMNH64856	Hippotragus niger	VG	2.154472	0.0041635	0.150331	6193.543239	0.580093862	0.751274757
AMNH84975	Hippotragus niger	VG	1.4657535	0.007665	0.267177	5567.164694	0.670685775	0.736500097
AMNH29456	Hippotragus niger	VG	1.281452	0.005279	0.4184545	5170.412253	0.549995627	0.59424223
AMNH87496	Hippotragus niger	VG	1.836986	0.006677	0.266859	6479.32915	0.42897573	0.563352409
FMNH127946	Kobus ellipsyprymnus	VG	1.538099	0.0058695	0.866551	3113.324437	0.536530358	0.673086554
FMNH1279	Kobus	VG	1.9052	0.0037	0.7007	4028.7	1.1780	2.71162

48	ellipsyprymnus		875	175	375	88714	31612	2225
FMNH127952	Kobus ellipsyprymnus	VG	2.3850805	0.005837	0.94294	4321.208131	0.856962042	1.304917308
FMNH127953	Kobus ellipsyprymnus	VG	1.3479535	0.006017	0.76674	4330.612514	0.334224022	1.069476172
FMNH20661	Kobus ellipsyprymnus	VG	0.8044825	0.006925	0.724403	3977.34692	0.707760679	1.179078383
FMNH24321	Kobus ellipsyprymnus	VG	1.149678	0.0052225	0.835002	3081.449793	0.815507193	1.30365912
FMNH24322	Kobus ellipsyprymnus	VG	0.603549	0.0058765	0.9770875	1459.435166	0.498097047	0.579780556
FMNH27199	Kobus ellipsyprymnus	VG	1.397921	0.006398	0.943772	5345.906738	0.528096761	0.765923418
FMNH29542	Kobus ellipsyprymnus	VG	1.6799215	0.0059705	0.8321485	5389.469843	1.354317774	1.59748047
FMNH85433	Kobus ellipsyprymnus	VG	0.6943705	0.0068085	0.616792	3099.965436	0.736176824	1.165503274
FMNH64856	Kobus ellipsyprymnus	VG	1.7401065	0.005736	0.973816	3787.582828	0.887585653	3.824949696
NMNH87492	Kobus ellipsyprymnus	VG	0.993197	0.0062265	0.761759	2449.034552	0.510766054	0.824387615
NMNH21648	Kobus ellipsyprymnus	VG	1.5075095	0.0065175	0.6417585	2217.241508	0.465248596	0.9297031
NMNH97516	Kobus ellipsyprymnus	VG	1.7829445	0.006057	0.883015	4881.927964	0.362944884	0.7817179
NMNH78468	Kobus ellipsyprymnus	VG	1.204878	0.0058055	0.601148	2571.633798	0.56853676	0.761803619
FMNH1091	Kobus ellipsyprymnus	VG	1.3977085	0.0057775	0.708209	2837.507848	0.440430078	0.754904722
FMNH27200	Kobus ellipsyprymn	VG	1.374694	0.004412	0.617213	5066.745343	0.334018466	0.703575632

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FMNH7225	Kobus ellipsyprymnus	VG	0.983139	0.0051505	0.941958	3159.481996	0.5760158	0.699555967
FMNH85432	Kobus ellipsyprymnus	VG	0.8553535	0.0065235	0.8004705	3073.539046	0.533853664	0.627785919
FMNH85441	Kobus ellipsyprymnus	VG	1.1898405	0.007049	0.7083425	4483.600501	0.346825901	0.627777283
NMNH48756	Kobus ellipsyprymnus	VG	0.599161	0.006758	0.917827	2542.100079	0.691292265	0.837399019
NMNH51254	Kobus ellipsyprymnus	VG	1.432206	0.0066865	0.899882	4170.203641	0.417452495	0.685767008
FMNH468765	Kobus leche	OG	0.826548	0.0057	1.53154	3468.32153	0.42154	0.831354
FMNH13546	Kobus leche	OG	1.26484	0.0071	1.03215	1678.36	0.386545	0.76545684
FMNH23684	Kobus leche	OG	0.9874564	0.0046	0.96541352	3268.3215	0.35875	0.832154
FMNH34987	Kobus leche	OG	0.6898745	0.0051	0.8984521	4685.132	0.310548	0.632154
FMNH65435	Kobus leche	OG	0.987451	0.0058	1.5321354	1735.3215	0.459875	0.73154
FMNH52154	Kobus leche	OG	1.10325	0.0065	1.66845	3594.18	0.426548	0.9987654
FMNH48754	Kobus leche	OG	0.784151	0.0049	2.13454	1832.13125	0.468845	1.031545
FMNH165684	Kobus leche	OG	0.889451	0.0058	1.86456	2975.16	0.2913545	0.643154
FMNH55955	Kobus leche	OG	1.025486	0.0055	1.33154	2384.2721	0.3615648	0.7321354
FMNH164845	Kobus leche	OG	0.86548	0.0047	2.135454	1972.14	0.324687	0.6977845
FMNH49784	Kobus leche	OG	0.975154	0.0067	0.998451	3942.37815	0.283645	0.632135
FMNH16485	Kobus leche	OG	1.56878	0.0061	0.9135154	1267.3215	0.413236	0.73245
FMNH164876	Kobus leche	OG	0.6987465	0.0048	1.035135	2975.1924	0.452648	0.835468
FMNH198451	Kobus leche	OG	0.98451	0.0055	1.16846	4268.3215	0.366878	0.798764
FMNH764813	Kobus leche	OG	1.43215	0.0062	1.76451	2781.21	0.412654	0.832154

FMNH68461	Kobus leche	OG	1.26548	0.0059	2.1648	4038.6548	0.3031354	0.687845
FMNH78461	Kobus leche	OG	0.8784151	0.0051	2.368451	3058.215	0.426548	1.0322
FMNH97846	Kobus leche	OG	0.932165	0.0064	1.4687751	1682.1824	0.331354	0.721345
AMNH7164	Kobus leche	OG	0.76548	0.0049	2.87751	3451.1214	0.3946545	0.73648
AMNH1648	Kobus leche	OG	1.532154	0.0072	2.065484	2854.3215	0.40315	0.8365451
AMNH7953	Kobus leche	OG	0.7321534	0.0049	0.9874	1753.215	0.3487	0.7321354
AMNH4878	Kobus leche	OG	0.5987845	0.0058	1.698451	4038.1654	0.4568786	0.965451
AMNH19784	Kobus leche	OG	1.1548	0.0066	2.16845	3951.321	0.3687454	0.832153
AMNH76848	Kobus leche	OG	0.732154	0.0052	1.5841151	2267.1324	0.326548	0.6878453
RMCA83-008M485	Litocranius walleri	BROW	4.7548	0.0019	1.13454	13594.32156	0.76515	1.1548
RMCA83-008M468	Litocranius walleri	BROW	3.2648	0.003	1.368452	9857.32156	0.62154	0.9635432
RMCA83-008M483	Litocranius walleri	BROW	2.265168	0.0028	0.587451	12684.1654	1.16548	1.2548
RMCA83-008M451	Litocranius walleri	BROW	3.654878	0.0034	0.864521	14875.32156	1.06548	1.532135
RMCA83-008M489	Litocranius walleri	BROW	1.9874	0.0028	0.468451	10685.15468	0.587451	0.965432
RMCA83-008M462	Litocranius walleri	BROW	2.16548	0.0017	0.76451	8627.35468	0.8857451	0.868465
RMCA83-008M493	Litocranius walleri	BROW	4.36548	0.0022	1.13545	11975.1654	0.76845	0.9315
RMCA83-008M459	Litocranius walleri	BROW	3.848465	0.0018	0.987451	13294.6548	0.56845	1.1548
RMCA83-008M454	Litocranius walleri	BROW	5.49878	0.0029	0.813212	10584.3156	0.86453	1.33548
RMCA83-008M491	Litocranius walleri	BROW	3.032168	0.0021	0.5897451	12394.32156	0.5874451	0.8320325
RMCA83-008M492	Litocranius walleri	BROW	4.316548	0.0018	1.03545	9751.3215	0.83548	0.96545
RMCA83-008M456	Litocranius walleri	BROW	3.65487	0.0016	0.68451	14952.1354	0.584531	0.978451
RMCA83-006M473	Litocranius walleri	BROW	4.387845	0.0025	0.964512	11684.32156	0.868484	1.06548
RMCA83-006M497	Litocranius walleri	BROW	4.265498	0.003	0.887451	9824.32165	0.913545	1.23548

FMNH64876	Litocranius walleri	BROW	1.87845	0.0029	1.13548	8734.1354	1.0325	1.432135
FMNH13548	Litocranius walleri	BROW	3.1265468	0.0027	1.4987456	12846.1654	0.6321354	0.96543
FMNH46877	Litocranius walleri	BROW	2.26548	0.002	1.36548	8736.6548	0.7315	0.998423
FMNH14465	Litocranius walleri	BROW	3.765465	0.0018	0.53154	9521.3215	0.598451	0.898451
AMNH164854	Litocranius walleri	BROW	2.65486	0.0032	0.8968452	10684.1654	0.6215485	1.0326
AMNH164859	Litocranius walleri	BROW	5.87984	0.0016	1.225486	9824.65468	1.032153	1.36848
AMNH164853	Litocranius walleri	BROW	2.26548	0.0021	2.035435	10834.6548	0.632157	1.26548
AMNH164785	Litocranius walleri	BROW	3.6876845	0.0031	0.69845	12168.65465	0.5832435	0.965452
AMNH164798	Litocranius walleri	BROW	3.02654	0.0024	0.9684521	11762.1354	0.598784	0.9942315
AMNH164856	Litocranius walleri	BROW	2.026548	0.0028	0.86541321	8762.65846	0.69874512	0.898745
AMNH164795	Litocranius walleri	BROW	3.213546	0.0014	1.23545	9762.1354	0.5987854	0.833215
NMNH45486	Neotragus batesi	BROW	4.265154	0.0019	1.12365	9587.2315	0.59315	0.96545
NMNH46784	Neotragus batesi	BROW	2.6568	0.0026	0.7645	11268.26548	0.431854	1.0654
NMNH164856	Neotragus batesi	BROW	5.21546	0.0021	0.687451	9123.348	0.52148	0.86542
NMNH164875	Neotragus batesi	BROW	4.131564	0.0017	0.86421	8395.2354	0.684215	0.98451
NMNH464856	Neotragus batesi	BROW	2.125468	0.002	0.91548	12759.2156	0.432548	0.813546
NMNH497846	Neotragus batesi	BROW	5.2356	0.0026	1.03544	12157.1654	0.52146468	1.16548
NMNH264856	Neotragus batesi	BROW	4.1345	0.0027	1.38751	10268.35468	0.546878	0.9513215
NMNH164887	Neotragus batesi	BROW	2.65487	0.0021	0.532151	8628.3215	0.62548	0.8545
NMNH45816	Neotragus batesi	BROW	5.132154	0.0019	0.835412	9258.3215	0.6865421	1.26548
NMNH464857	Neotragus batesi	BROW	3.64687	0.003	0.687451	10284.1324	0.7315	1.0654
NMNH45978	Neotragus batesi	BROW	4.98754	0.0024	0.95841	9685.5468	0.63154	0.9456123
NMNH164872	Neotragus batesi	BROW	4.121354	0.0017	0.58451	12584.16547	0.8657	0.93245

NMNH164978	Neotragus batesi	BROW	2.321354	0.0014	0.68451	9851.3215	0.4562132	0.865432
NMNH48726	Neotragus batesi	BROW	5.132156	0.0028	0.487451	8627.32156	0.4987561	0.9132415
NMNH59782	Neotragus batesi	BROW	3.87684	0.0025	0.6684521	7925.6548	0.713548	0.93215
NMNH46587	Neotragus batesi	BROW	2.232654	0.0022	0.8351321	12958.1546	0.59875	0.79451
NMNH132648	Neotragus batesi	BROW	4.32154	0.0019	0.6845132	10285.6548	0.698751	0.8321534
NMNH134856	Neotragus batesi	BROW	2.124874	0.0021	1.065465	8637.165465	0.61548	0.93215
NMNH48792	Neotragus batesi	BROW	3.65487	0.0028	1.6321354	9875.321564	0.543249	1.235485
NMNH46597	Neotragus batesi	BROW	3.23548	0.0031	0.568745	10975.1354	0.69845	1.06548
NMNH164875	Neotragus batesi	BROW	5.135487	0.0027	0.4987451	12752.3215	0.53154	0.92154
NMNH164972	Neotragus batesi	BROW	2.98487	0.0016	0.9654121	11695.11354	0.712236	0.932154
NMNH164978	Neotragus batesi	BROW	4.8321564	0.0012	0.684521	8267.26468	0.472545	0.86545
AMNH80884	Oreotragus oreotragus	GEN	2.0907745	0.0045775	0.537062	9315.135714	0.510136769	0.82124964
AMNH81023	Oreotragus oreotragus	GEN	1.86365	0.003167	0.2668755	7670.869766	0.581445087	0.906949342
AMNH81028	Oreotragus oreotragus	GEN	2.190026	0.003012	0.2666695	5792.269424	0.517771683	0.768226966
FMNH110945	Oreotragus oreotragus	GEN	2.89897	0.0038735	0.2124255	7681.582914	0.250404112	0.62498469
FMNH135081	Oreotragus oreotragus	GEN	2.481	0.00364	0.4522755	9452.894277	0.472090453	0.675890933
FMNH19582	Oreotragus oreotragus	GEN	1.966489	0.0032975	0.150596	9152.092558	0.489634071	1.283687617
FMNH19583	Oreotragus oreotragus	GEN	1.4100885	0.004775	0.308055	12976.39999	0.448224865	0.912028384
FMNH19613	Oreotragus oreotragus	GEN	2.2550055	0.002947	0.401451	7073.145954	0.41800118	0.521399613
FMNH26957	Oreotragus oreotragus	GEN	1.6806515	0.002452	0.2385345	8840.634245	0.4379158	0.640331447
FMNH26960	Oreotragus oreotragus	GEN	2.7369385	0.0032395	0.542752	7815.664	0.493530145	0.617481233
FMNH27166	Oreotragus oreotragus	GEN	1.7037905	0.0041035	0.2456285	11614.34505	0.369807556	0.627686525
FMNH7470	Oreotragus oreotragus	GEN	1.2135805	0.002087	0.5522235	12405.69758	0.45954339	1.060597858

FMNH81008	Oreotragus oreotragus	GEN	2.3979205	0.0046645	0.210354	10781.72619	0.31586269	0.676526952
AMNH97847	Oreotragus oreotragus	GEN	2.0907745	0.0036775	0.347062	8315.135714	0.310136769	0.83624964
AMNH94878	Oreotragus oreotragus	GEN	1.987365	0.003067	0.5768755	8270.789766	0.491445087	0.921493423
AMNH13486	Oreotragus oreotragus	GEN	2.390026	0.005112	0.2766695	6892.279424	0.437771683	0.775226966
AMNH64851	Oreotragus oreotragus	GEN	1.99897	0.0037735	0.2324255	8681.632914	0.310404112	0.635198469
AMNH64853	Oreotragus oreotragus	GEN	2.4681	0.00294	0.4822755	11552.91428	0.493090453	0.695289093
AMNH21648	Oreotragus oreotragus	GEN	3.866489	0.0030975	0.190596	8162.902558	0.519634071	1.133687617
AMNH97816	Oreotragus oreotragus	GEN	2.3200885	0.002875	0.318055	10976.44999	0.443424865	0.936028384
AMNH21478	Oreotragus oreotragus	GEN	2.2550055	0.002847	0.411451	7513.165954	0.42830118	0.685996135
AMNH16483	Oreotragus oreotragus	GEN	3.1806515	0.004552	0.2485345	8652.754245	0.4429158	0.678933145
AMNH64856	Oreotragus oreotragus	GEN	2.6169385	0.0033395	0.332752	8521.674	0.298530145	0.716581233
AMNH78426	Oreotragus oreotragus	GEN	1.6837905	0.0046035	0.4556285	7295.335047	0.502807556	0.823686525
FMNH1289	Philantomba monticola	FRUG	4.142388	0.0019835	0.2667615	15935.25756	0.630827058	0.602576061
FMNH134311	Philantomba monticola	FRUG	3.663514	0.001218	0.267959	12983.95727	0.622748968	0.851293954
FMNH135322	Philantomba monticola	FRUG	5.88253	0.0022345	0.2561075	14533.073	0.467642749	0.793262144
FMNH186672	Philantomba monticola	FRUG	6.184616	0.001965	0.1513445	12214.82153	0.441689594	0.918330539
FMNH27543	Philantomba monticola	FRUG	3.67265	0.0020345	0.150108	14335.81519	0.494958047	0.6291591
FMNH27548	Philantomba monticola	FRUG	6.3192125	0.0030955	0.2097585	16135.71384	0.370827978	0.836301541
FMNH34281	Philantomba monticola	FRUG	5.2394585	0.00163	0.149953	16378.51354	0.65006411	0.712951645
FMNH34285	Philantomba monticola	FRUG	4.432642	0.001458	0.153012	12860.79432	0.554539415	0.62039423
FMNH81603	Philantomba monticola	FRUG	4.113722	0.002368	0.2358625	14597.5401	0.629379945	0.88700564
FMNH87164	Philantomba monticola	FRUG	3.750027	0.0024105	0.1366405	15507.25694	0.483957163	1.056775105
FMNH16485	Philantomba monticola	FRUG	3.647898	0.0020255	0.1509735	13611.192	0.634726461	0.696755112

FMNH87169	Philantomba monticola	FRUG	5.2941865	0.002238	0.2243835	12182.95993	0.594002336	0.773883095
FMNH87264	Philantomba monticola	FRUG	5.5493825	0.0030005	0.2101255	16884.98806	0.492471527	1.01918007
RMCA83-006M972	Philantomba monticola	FRUG	4.214451	0.0018	0.185632	17852.3625	0.632569	0.8547926
RMCA83-006M267	Philantomba monticola	FRUG	3.89554	0.0023	0.203514	16598.2654	0.575448	0.865921
RMCA83-006M384	Philantomba monticola	FRUG	3.121548	0.0011	0.156847	11658.21	0.569587	0.769852
RMCA83-006M982	Philantomba monticola	FRUG	5.98451	0.0024	0.189562	15358.0235	0.51487	0.912354
RMCA83-006M458	Philantomba monticola	FRUG	3.25417	0.0012	0.165478	14526.3258	0.669581	0.7658214
RMCA83-006M973	Philantomba monticola	FRUG	5.123548	0.0023	0.22568	15265.2565	0.498521	0.875624
RMCA83-006M977	Philantomba monticola	FRUG	4.36589	0.0016	0.268547	11256.36547	0.652617	0.845263
RMCA83-006984	Philantomba monticola	FRUG	3.20365	0.0017	0.2541665	16547.2658	0.395871	0.7865214
FMNH110946	Raphicerus campestris	B-G INT	2.818294	0.00215	0.5664675	6915.373691	0.270964816	0.671581814
FMNH127977	Raphicerus campestris	B-G INT	2.5197675	0.001486	0.5674305	8420.8106	0.563695494	0.767123972
FMNH134364	Raphicerus campestris	B-G INT	2.043816	0.0036335	0.6518245	7471.582682	0.404919932	1.055619315
FMNH134365	Raphicerus campestris	B-G INT	2.121666	0.0024325	0.8501715	5705.033737	0.431920484	0.857381374
FMNH140859	Raphicerus campestris	B-G INT	3.26635415	0.0023175	0.4174165	10693.41693	0.492638011	0.670814704
FMNH17827	Raphicerus campestris	B-G INT	2.4764695	0.002569	0.7091815	10791.35374	0.386728206	0.940936359
FMNH34509	Raphicerus campestris	B-G INT	2.0576685	0.0023475	0.7086775	9944.223036	0.530596696	1.13919729
FMNH34510	Raphicerus campestris	B-G INT	2.6467335	0.0025515	0.667962	7648.628919	0.526652519	0.953935446
FMNH34511	Raphicerus campestris	B-G INT	1.758698	0.0025365	0.808646	8724.645868	0.528071125	0.522443075
FMNH85999	Raphicerus campestris	B-G INT	1.5751215	0.0039285	0.6082135	9724.158241	0.410846428	0.705044282
FMNH54956	Raphicerus campestris	B-G INT	2.850027	0.003435	0.5689075	8293.178717	0.416054306	0.959467871
FMNH16485	Raphicerus campestris	B-G INT	1.5574885	0.0023135	0.8571335	10545.97653	0.581385685	0.897879669
AMNH97856	Raphicerus campestris	B-G INT	3.0671515	0.0034715	0.7085795	9057.905827	0.298072632	0.826066884

AMNH16485	Raphicerus campestris	B-G INT	2.3549065	0.0035535	0.6088735	7620.544291	0.510433992	0.932514101
AMNH46485	Raphicerus campestris	B-G INT	1.639916	0.0015155	0.554698	8854.772553	0.526137007	0.783979284
AMNH97815	Raphicerus campestris	B-G INT	2.425448	0.002456	0.850817	9712.076998	0.532567154	0.942356462
AMNH97485	Raphicerus campestris	B-G INT	1.642819	0.004071	0.541786	6736.389633	0.513406566	1.094663089
AMNH97826	Raphicerus campestris	B-G INT	2.772677	0.002729	0.416524	7098.074985	0.407617579	0.874272389
AMNH87456	Raphicerus campestris	B-G INT	1.9322285	0.0040115	0.74166	6829.769029	0.487974367	0.970838616
AMNH16485	Raphicerus campestris	B-G INT	2.9914665	0.0025465	1.2164535	5292.412487	0.436057002	0.872082124
AMNH97858	Raphicerus campestris	B-G INT	1.6972945	0.001102	0.8669665	9824.333663	0.319300296	0.67777702
NMNH485446	Raphicerus sharpei	B-G INT	2.36548	0.0045	0.698456	5103.1324	0.5132135	0.7613154
NMNH494515	Raphicerus sharpei	B-G INT	1.832135	0.009	0.364561	3625.1313	0.396541351	0.813154
NMNH48794	Raphicerus sharpei	B-G INT	2.732135	0.0037	1.0351564	5873.38	0.6731354	0.9321354
NMNH47516	Raphicerus sharpei	B-G INT	1.53215	0.0041	0.8315	4862.962	0.50064	0.731354
NMNH47852	Raphicerus sharpei	B-G INT	2.93154	0.0035	0.56874651	3587.11	0.536545	0.8321354
NMNH49721	Raphicerus sharpei	B-G INT	2.5231534	0.0051	0.432656548	2951.135	0.623135	0.9354353
NMNH49751	Raphicerus sharpei	B-G INT	1.968452	0.0028	0.76454	4951.32135	0.491354	0.865468
NMNH47961	Raphicerus sharpei	B-G INT	2.83215	0.0031	0.7323154	6756.84	0.5732135	0.9878435
NMNH48758	Raphicerus sharpei	B-G INT	1.93215	0.0046	1.06454	4761.35	0.3865456	0.765468
NMNH49781	Raphicerus sharpei	B-G INT	2.535468	0.0037	0.39845	2542.48	0.4232135	0.864867
NMNH48561	Raphicerus sharpei	B-G INT	2.89845	0.0041	0.59899	5435.65	0.53654165	1.025415
NMNH47846	Raphicerus sharpei	B-G INT	2.832135	0.0029	0.29848	4526.31	0.679845	1.3545
NMNH476465	Raphicerus sharpei	B-G INT	2.635468	0.0037	0.3987484	3129.23251	0.593545	0.954351
NMNH47816	Raphicerus sharpei	B-G INT	2.33215	0.0045	0.4265486	6534.3215	0.72315	0.9687878
NMNH47815	Raphicerus sharpei	B-G INT	2.532135	0.0042	0.469877	5975.13215	0.583154	0.764654

NMNH48759	Raphicerus sharpei	B-G INT	2.032135	0.0039	0.598454	6429.6915	0.561354	0.865451
NMNH48752	Raphicerus sharpei	B-G INT	2.668454	0.004	0.41648	3824.3215	0.473154	0.968754
NMNH48576	Raphicerus sharpei	B-G INT	1.565456	0.0029	0.298784	4624.3215	0.531654	0.851454
NMNH48782	Raphicerus sharpei	B-G INT	1.96845	0.0051	0.3216548	6948.35	0.5931543	0.913215
NMNH48759	Raphicerus sharpei	B-G INT	2.5315	0.0038	0.37446546	6248.3215	0.653154	1.13545
NMNH42846	Raphicerus sharpei	B-G INT	2.732135	0.0041	0.398484	2842.1354	0.713154	1.26845
NMNH42861	Raphicerus sharpei	B-G INT	2.765132	0.0045	0.498784	5361.661	0.733515	1.0648
NMNH42875	Raphicerus sharpei	B-G INT	1.835132	0.0052	0.516484	2762.32135	0.69654153	0.95645
NMNH42597	Raphicerus sharpei	B-G INT	1.96513	0.0045	0.298784	5934.1324	0.593154	0.8654321
NMNH42871	Raphicerus sharpei	B-G INT	2.265465	0.0048	0.364848	4816.44	0.643154	0.96845
AMNH56876	Redunca arundinum	OG	0.68549	0.00645	1.761654	4132.782	0.413154	0.861554
AMNH46546	Redunca arundinum	OG	0.984132153	0.0053	2.68451	1975.1231	0.3568754	0.63213534
AMNH75948	Redunca arundinum	OG	1.232654	0.0077	2.18451	4458.3215	0.384651	0.731354
AMNH79536	Redunca arundinum	OG	0.71354	0.0061	0.99841521	4658.6521	0.4032546	0.8651451
AMNH79428	Redunca arundinum	OG	1.165468	0.0057	1.8987451	3157.1124	0.36845	0.8641564
AMNH79285	Redunca arundinum	OG	0.835135	0.0055	1.913545	3497.234	0.383215	0.79451
AMNH79281	Redunca arundinum	OG	0.93515	0.0078	1.4987541	3024.324	0.4265468	0.868784
AMNH79583	Redunca arundinum	OG	0.64878654	0.0062	1.351654	4521.215	0.3648678	0.798454
AMNH79580	Redunca arundinum	OG	0.687845	0.0056	1.1845216	3751.124	0.386451	0.865154
AMNH70348	Redunca arundinum	OG	1.21548	0.0049	2.184654	2975.324	0.362154	0.76158486
AMNH40984	Redunca arundinum	OG	1.03548	0.0064	2.08765416	1578.64	0.35321354	0.6979845
AMNH72064	Redunca arundinum	OG	1.4321354	0.0057	1.86487	4168.27	0.293515	0.598784
AMNH72194	Redunca arundinum	OG	0.8654321	0.0051	1.69845	3284.534	0.303215	0.684845

AMNH73485	Redunca arundinum	OG	0.987654	0.0062	1.168474	2751.6924	0.366845	0.79845
AMNH72945	Redunca arundinum	OG	0.832135	0.0067	1.043154	3975.5424	0.3764541	0.792654
AMNH48746	Redunca arundinum	OG	0.76874351	0.0053	0.984332165	1851.954	0.42548	0.8654561
AMNH47159	Redunca arundinum	OG	1.03215	0.0047	0.83154	4861.8424	0.336548	0.69874854
AMNH15482	Redunca arundinum	OG	0.6687451	0.0071	0.954531	2834.1324	0.346845	0.7651564
AMNH46586	Redunca arundinum	OG	0.798435	0.0068	1.3984564	3752.48	0.34065468	0.7135145
AMNH16482	Redunca arundinum	OG	1.132145	0.0059	2.1845	1985.467	0.416484	0.865121
AMNH16485	Redunca arundinum	OG	0.89845	0.0073	1.96546	4297.58	0.3268451	0.7645
AMNH16487	Redunca arundinum	OG	0.7984561	0.0075	1.93254	3685.248	0.3865121	0.9846513
AMNH42648	Redunca arundinum	OG	1.23215	0.0059	2.063154	4397.546	0.363215	0.698784
AMNH42687	Redunca arundinum	OG	0.784651	0.0068	0.96545	1862.4586	0.4731235	0.7984541
AMNH42894	Redunca arundinum	OG	0.687451	0.007	0.815648	2306.85	0.323515	0.831545
FMNH127989	Redunca fulvorfula	OG	1.3857345	0.0066565	1.3420845	1892.224607	0.299900988	0.473318097
FMNH127990	Redunca fulvorfula	OG	1.1321645	0.008655	1.2666665	1811.571008	0.310496452	0.608229883
FMNH127991	Redunca fulvorfula	OG	1.0742785	0.0060585	1.41827	1163.440413	0.615112236	0.573864017
FMNH127992	Redunca fulvorfula	OG	1.6332485	0.008157	1.2664905	1676.549445	0.264648469	0.378477259
FMNH127993	Redunca fulvorfula	OG	0.8723305	0.009593	0.918397	1715.411128	0.53071263	0.553767309
FMNH18973	Redunca fulvorfula	OG	1.1828795	0.0081465	0.8414585	1593.366169	0.417047865	0.657307249
FMNH19589	Redunca fulvorfula	OG	1.4216295	0.006294	1.344485	1531.258576	0.436536172	0.641853988
FMNH19591	Redunca fulvorfula	OG	1.2960185	0.007599	1.13461525	2722.294797	0.502210664	0.61964115
FMNH19593	Redunca fulvorfula	OG	0.951748	0.00818	1.267359	2088.832416	0.572366611	0.620995272
FMNH19595	Redunca fulvorfula	OG	1.4381405	0.0073365	0.734817	1925.948551	0.448007239	0.63563952
FMNH19596	Redunca fulvorfula	OG	1.478986	0.0080555	0.8096295	2425.319608	0.436751383	0.674969897

FMNH19597	Redunca fulvorfula	OG	1.09723	0.010055	1.3457115	1207.181232	0.443359833	0.673623089
FMNH32916	Redunca fulvorfula	OG	0.891834	0.00709	0.945612	1202.273098	0.465401769	0.620209662
FMNH32917	Redunca fulvorfula	OG	1.185205	0.0089995	1.2689665	1609.543905	0.411822931	0.560061449
FMNH7041	Redunca fulvorfula	OG	1.18193	0.006921	1.249646	1243.24669	0.361521754	6.251967753
NMNH31648	Redunca fulvorfula	OG	1.5677385	0.006998	0.7960875	1056.675015	0.398775464	0.729390302
NMNH84648	Redunca fulvorfula	OG	1.047984	0.00755	0.845351	1638.678558	0.347104179	0.675804481
NMNH84628	Redunca fulvorfula	OG	1.2017425	0.006504	0.868444	2496.789124	0.56292832	0.857718576
NMNH84975	Redunca fulvorfula	OG	0.8282355	0.0071695	0.767168	1885.523072	0.323575729	0.588577267
NMNH84878	Redunca fulvorfula	OG	1.4033455	0.007973	1.26773	1036.767889	0.416555965	0.60266146
NMNH31674	Redunca fulvorfula	OG	1.385785	0.0069115	0.807614	2836.437782	0.303466008	0.595926782
NMNH31978	Redunca fulvorfula	OG	1.022531	0.005954	1.2915685	1144.502632	0.360425238	0.620074565
NMNH31854	Redunca fulvorfula	OG	1.35018	0.0063395	0.933724	1920.523414	0.379036989	0.510834646
NMNH84925	Redunca fulvorfula	OG	0.7501465	0.00698	1.27229	1402.885014	0.308302719	0.548734277
FMNH127998	Sylvicapra grimmia	BROW	2.0500505	0.002282	0.636712	18006.07053	0.40779242	0.884392643
FMNH127999	Sylvicapra grimmia	BROW	2.5138545	0.003856	0.807927	15213.06576	0.523202301	0.734448797
FMNH17789	Sylvicapra grimmia	BROW	3.611534	0.001417	1.141453	9428.883912	0.60795212	1.265870932
FMNH17790	Sylvicapra grimmia	BROW	3.343193	0.0020855	0.501272	16031.60848	0.929658022	0.90598036
FMNH27139	Sylvicapra grimmia	BROW	4.12132	0.0036585	0.7333985	12368.77115	0.44011526	0.892439224
FMNH28489	Sylvicapra grimmia	BROW	1.6169195	0.0032955	0.383116	15816.13497	0.614827255	1.048959348
FMNH34540	Sylvicapra grimmia	BROW	3.1845135	0.0021385	0.4669335	7839.525332	0.518221199	0.89666592
FMNH8166	Sylvicapra grimmia	BROW	2.045196	0.002035	0.508834	8257.821808	0.467107338	0.858089012
FMNH84006	Sylvicapra grimmia	BROW	3.9328925	0.001683	1.109075	10112.42845	0.555815357	0.713471115
FMNH85426	Sylvicapra grimmia	BROW	3.343323	0.0023455	0.4066035	11580.44965	0.985927184	0.739465318

FMNH49872	Sylvicapra grimmia	BROW	2.486413	0.0030255	0.766547	8367.83358	1.213425675	0.836781444
FMNH49876	Sylvicapra grimmia	BROW	2.6319635	0.002554	0.3414735	13818.71182	0.742412794	0.961791543
FMNH97859	Sylvicapra grimmia	BROW	3.6134305	0.002757	1.200078	15307.56705	0.44443176	0.759733748
FMNH74859	Sylvicapra grimmia	BROW	3.2113225	0.003392	0.5997495	10017.67539	0.852518137	0.758933868
FMNH49658	Sylvicapra grimmia	BROW	3.962034	0.0011885	0.5996265	7720.214279	0.770234269	1.263282816
FMNH98105	Sylvicapra grimmia	BROW	3.0043925	0.0025325	0.3427425	10070.19987	0.497960378	0.733336386
NMNH49846	Sylvicapra grimmia	BROW	4.1754515	0.0037455	0.509419	11599.34859	1.302860292	0.913396438
NMNH49859	Sylvicapra grimmia	BROW	4.5078655	0.0031925	0.434771	14949.67774	1.324144045	0.73163748
NMNH49785	Sylvicapra grimmia	BROW	3.325536	0.0020095	0.7422115	10964.57491	0.89085846	0.881815256
NMNH48759	Sylvicapra grimmia	BROW	3.2013345	0.003664	0.4423685	14007.36695	0.60347707	0.956336849
NMNH49787	Sylvicapra grimmia	BROW	2.066297	0.0026265	0.6019035	5890.815983	0.474299246	0.889442923
NMNH49852	Sylvicapra grimmia	BROW	1.9087175	0.0030775	0.867014	6858.074502	0.932544122	0.684691927
NMNH49158	Sylvicapra grimmia	BROW	2.7052375	0.002059	0.5672295	13329.67597	0.4852949	1.022216532
NMNH49875	Sylvicapra grimmia	BROW	3.0628085	0.00368	0.5110535	11620.74159	0.434819833	0.717699377
NMNH49787	Sylvicapra grimmia	BROW	3.270702	0.002745	0.509875	13092.61391	1.099302644	1.039634919
FMNH105033	Synceros caffer	VG	1.403316	0.004195	0.7499655	3165.2604	0.328857912	0.52162925
FMNH128001	Synceros caffer	VG	1.487007	0.0039725	0.501275	1788.390473	0.305015028	0.897840656
FMNH140854	Synceros caffer	VG	1.410394	0.0047755	0.919617	2105.726392	0.575220711	0.969632053
FMNH140855	Synceros caffer	VG	2.390261	0.005604	0.669611	3649.500183	0.394992258	0.647717299
FMNH20680	Synceros caffer	VG	1.513335	0.0048295	0.743059	3287.31197	0.260985439	0.461899613
FMNH21148	Synceros caffer	VG	2.3356	0.003866	0.508488	1416.983726	0.395749006	0.755097684
FMNH21149	Synceros caffer	VG	1.603264	0.0069145	1.2618569	4913.185286	0.389292343	0.884763339
FMNH21150	Synceros caffer	VG	1.8847965	0.0036535	0.8132859	2913.23353	0.496340376	0.743802786

FMNH24324	Synceros caffer	VG	0.936531	0.0060905	0.6727153	3113.799584	0.454778326	0.804474952
FMNH34547	Synceros caffer	VG	1.9005645	0.0042065	0.7814935	2832.150291	0.404576633	0.817011565
FMNH44063	Synceros caffer	VG	1.107427	0.004155	0.849889	4272.494192	0.347693256	0.554288879
AMNH46579	Synceros caffer	VG	1.9153605	0.005533	0.5996345	3918.776672	0.426965578	0.807185008
AMNH98468	Synceros caffer	VG	1.974186	0.0042785	1.17086665	4135.014902	0.559315767	0.675633593
AMNH48759	Synceros caffer	VG	0.9647795	0.0038945	0.51201	1980.513799	0.456538607	0.532616662
AMNH47954	Synceros caffer	VG	1.0304045	0.005024	0.6020075	4087.319285	0.558097736	0.666210604
AMNH49785	Synceros caffer	VG	1.0937845	0.0041995	0.6053505	1171.242875	0.457724385	0.727382528
AMNH48752	Synceros caffer	VG	1.478519	0.0052795	0.688528	1236.946571	0.541247712	0.585798048
AMNH98749	Synceros caffer	VG	1.7228025	0.0073075	0.74586	2609.280039	0.418070454	0.780527277
AMNH97845	Synceros caffer	VG	1.7422615	0.0066125	0.6034795	4762.214682	0.452702044	0.933415434
AMNH96584	Synceros caffer	VG	0.957928	0.006648	1.56166085	1316.544993	0.358785519	0.709814067
AMNH94826	Synceros caffer	VG	0.935437	0.0069635	0.7421955	2440.37152	0.500146852	0.61608987
AMNH94854	Synceros caffer	VG	1.0004495	0.0052065	0.743926	1532.848436	0.462939499	0.735215211
FMNH128003	Taurotragus oryx	B-G INT	2.295827	0.005639	0.150767	7943.366344	0.559267859	1.235638355
FMNH182002	Taurotragus oryx	B-G INT	1.772151	0.00561	0.3419435	5601.140831	0.535091514	0.801028739
FMNH34335	Taurotragus oryx	B-G INT	1.835633	0.0037095	0.210114	6829.629325	0.709522794	1.23792262
FMNH34532	Taurotragus oryx	B-G INT	1.984596	0.002358	0.4164155	6529.622807	0.437046572	0.813725227
FMNH34534	Taurotragus oryx	B-G INT	1.7447845	0.0016965	0.5081015	5435.796314	0.515888932	0.944303662
FMNH34599	Taurotragus oryx	B-G INT	1.9524355	0.0044625	0.7062475	8380.147767	0.432780249	0.841835736
FMNH49785	Taurotragus oryx	B-G INT	1.8341905	0.004681	1.065974	9080.336939	0.449133542	0.749100014
FMNH38495	Taurotragus oryx	B-G INT	2.1406635	0.003552	0.941415	8745.888058	0.330249835	0.793427681
FMNH42948	Taurotragus oryx	B-G INT	2.50162	0.003342	0.940989	9373.215265	0.398047689	0.831524505

FMNH48795	Taurotragus oryx	B-G INT	2.1329575	0.0050695	0.816254	6785.017311	0.388593546	0.691588538
FMNH49879	Taurotragus oryx	B-G INT	2.35499	0.003852	0.63489955	8774.359309	0.477519898	0.790751365
FMNH19489	Taurotragus oryx	B-G INT	1.4277655	0.005138	0.2090855	5609.265711	0.722162699	1.158006383
FMNH49859	Taurotragus oryx	B-G INT	2.3558305	0.002181	0.4167615	6149.710887	0.551540178	0.968839296
FMNH47858	Taurotragus oryx	B-G INT	1.8054665	0.002946	0.341548	5898.525379	0.837861314	1.139971889
FMNH20649	Taurotragus oryx	B-G INT	2.309797	0.00479	0.269862	7895.306196	0.336073405	0.764362765
FMNH20664	Taurotragus oryx	B-G INT	2.3323705	0.003017	0.151136	7824.202539	0.800221572	1.356778142
FMNH20750	Taurotragus oryx	B-G INT	3.1454775	0.002907	0.1499215	5847.025776	0.606146123	1.214590387
FMNH20755	Taurotragus oryx	B-G INT	1.3409085	0.0034045	0.2677895	6615.354493	0.504395178	0.676479054
FMNH35114	Taurotragus oryx	B-G INT	1.82808	0.004869	0.4346025	5306.422416	0.445739001	0.970002623
FMNH40849	Taurotragus oryx	B-G INT	2.47457	0.0024885	0.1504945	7317.723911	0.401939213	0.721585179
FMNH20876	Taurotragus oryx	B-G INT	3.0203835	0.0041135	0.4362125	7199.355896	0.884519879	1.239451013
FMNH134327	Tragelaphus angasi	GEN	1.86729	0.0029495	0.450489	9816.525136	0.486600825	1.18038025
FMNH30238	Tragelaphus angasi	GEN	3.647961	0.0060365	0.1536675	10481.39136	0.36096696	0.726776338
FMNH26158	Tragelaphus angasi	GEN	1.7943635	0.0056125	0.4218005	7764.861537	0.425442373	0.823964274
FMNH26485	Tragelaphus angasi	GEN	1.3734075	0.0037	0.15052	11019.58504	0.494283153	0.985661954
FMNH36154	Tragelaphus angasi	GEN	1.214266	0.002447	0.3503735	8250.893464	0.399970737	0.650743117
FMNH61526	Tragelaphus angasi	GEN	1.2632575	0.0021965	0.250135	10351.87431	0.322816279	0.647021623
FMNH42159	Tragelaphus angasi	GEN	1.680136	0.0027495	0.4819905	10577.79867	0.376402196	0.821449841
AMNH94519	Tragelaphus angasi	GEN	2.4937105	0.0046885	0.209442	8129.529326	0.541813501	0.96381297
AMNH92648	Tragelaphus angasi	GEN	2.6315985	0.006597	0.4439645	9929.672413	0.491408025	1.118619272
AMNH82496	Tragelaphus angasi	GEN	2.0237565	0.0040045	0.2011355	8821.549956	0.547973105	0.881662083
AMNH49536	Tragelaphus angasi	GEN	2.552136	0.00601	0.267363	8936.417317	0.39385178	0.838599087

AMNH84952	Tragelaphus angasi	GEN	1.139301	0.002874	0.190069	10437.83267	0.400254153	0.647520823
AMNH18294	Tragelaphus angasi	GEN	1.884228	0.003529	0.150923	11545.62743	0.325374345	0.732026767
AMNH29485	Tragelaphus angasi	GEN	1.505669	0.00283	0.4507545	12636.83523	0.31680385	0.56346964
AMNH19825	Tragelaphus angasi	GEN	1.316859	0.002893	0.1503845	11283.29722	0.581939945	0.757743849
AMNH49785	Tragelaphus angasi	GEN	1.7612065	0.0035555	0.2669005	7116.062027	0.584571536	0.799513515
AMNH15476	Tragelaphus angasi	GEN	1.5561135	0.0038055	0.3505765	11499.7955	0.457055124	0.754654006
RMCA83-006M475	Tragelaphus angasi	GEN	3.26548	0.0042	0.38547	9835.1548	0.3598745	0.8265847
RMCA83-006M496	Tragelaphus angasi	GEN	3.21654	0.0039	0.452301	6987.26484	0.528745	0.8965844
RMCA83-006M685	Tragelaphus angasi	GEN	2.46878	0.0045	0.241254	10658.23651	0.584125	0.7851254
RMCA83-006M985	Tragelaphus angasi	GEN	2.865487	0.0051	0.1985236	9563.1548	0.38454	0.625484
RMCA83-006M698	Tragelaphus angasi	GEN	2.48776	0.0035	0.298754852	8659.2657	0.45684	0.78954
FMNH35106	Tragelaphus euryceros	BROW	3.261591	0.00104	0.7081855	10659.91743	0.565713982	0.951944315
FMNH35107	Tragelaphus euryceros	BROW	3.738787	0.0013595	0.411488	9022.874742	0.416394806	0.800939684
FMNH35108	Tragelaphus euryceros	BROW	4.1842795	0.002034	0.567914	12424.7385	0.665373682	0.991972042
FMNH97846	Tragelaphus euryceros	BROW	4.5045545	0.002219	1.0437985	15965.16457	0.564701118	0.737149167
FMNH21546	Tragelaphus euryceros	BROW	4.2614865	0.001735	0.9474605	15666.39715	0.546209313	1.144765017
FMNH97816	Tragelaphus euryceros	BROW	3.6741795	0.00226	0.85414164	13793.0638	0.674583967	0.738755144
RMCA83-006M978	Tragelaphus euryceros	BROW	5.519954	0.0017805	0.358696377	10407.30745	0.833025423	1.176690199
RMCA83-006M548	Tragelaphus euryceros	BROW	4.383803	0.0008025	1.110759	13508.74607	0.685245594	1.315460231
RMCA-006M956	Tragelaphus euryceros	BROW	3.1264865	0.001404	0.98525404	11622.47498	0.513237876	0.813334031
RMCA83-006M876	Tragelaphus euryceros	BROW	3.0509475	0.002082	1.04128255	15701.45271	0.643881079	0.996111473
RMCA83-006-M548	Tragelaphus euryceros	BROW	4.570233	0.0014895	0.70869635	13696.31189	0.714739554	1.172905911
RMCA83-006M872	Tragelaphus euryceros	BROW	2.677101	0.0022285	0.89547876	9358.327995	0.510110416	0.96569692

RMCA83-006-M648	Tragelaphus euryceros	BROW	3.70783	0.0020015	0.5207965	15149.95463	0.627156059	1.274969762
RMCA83-006M318	Tragelaphus euryceros	BROW	3.8597	0.002183	0.432438	15251.58376	0.713272012	1.209901026
RMCA83-006M264	Tragelaphus euryceros	BROW	2.505407	0.001986	1.03984015	13962.39552	0.654464974	0.972536148
RMCA83-006M856	Tragelaphus euryceros	BROW	2.119026	0.001771	0.9813485	10148.64298	0.490197946	0.792467921
RMCA83-006M361	Tragelaphus euryceros	BROW	4.277681	0.001551	0.854077495	11887.17106	0.757661973	1.207257637
RMCA83-006M879	Tragelaphus euryceros	BROW	3.128836	0.0021965	1.28172665	9561.105741	0.53270095	0.802624041
AMNH16485	Tragelaphus euryceros	BROW	4.352157742	0.00210325	0.5632514	13056.2658	0.621125468	0.95123548
AMNH49881	Tragelaphus euryceros	BROW	3.85945	0.00185945	0.798517	11215.2648	0.7598421	1.0215484
AMNH16476	Tragelaphus euryceros	BROW	3.52485	0.0012548	1.20547	9826.32518	0.456876	0.853168465
AMNH64826	Tragelaphus euryceros	BROW	4.859642	0.0021548	0.645136	14625.32518	0.4876513	0.798511324
FMNH1417	Tragelaphus imberbis	B-G INT	1.9599655	0.0018555	0.223076	6104.343952	0.422716757	0.622071501
FMNH1418	Tragelaphus imberbis	B-G INT	1.571634	0.0026605	0.2083365	3586.989323	0.411759596	1.159388114
FMNH26939	Tragelaphus imberbis	B-G INT	1.3108795	0.001844	0.341601	7127.732995	0.565205796	1.073218597
FMNH27132	Tragelaphus imberbis	B-G INT	1.8968895	0.004594	0.2664975	7583.615289	0.454494398	0.693339727
FMNH1420	Tragelaphus imberbis	B-G INT	1.7233095	0.0045085	0.266658	6139.71137	0.661634046	0.950467421
FMNH1423	Tragelaphus imberbis	B-G INT	1.6017645	0.002333	0.208315	7072.637796	0.450829854	1.178161069
FMNH1427	Tragelaphus imberbis	B-G INT	2.990987	0.0017085	0.1499495	9161.984062	0.58232256	0.954677416
FMNH27164	Tragelaphus imberbis	B-G INT	1.932816	0.005245	0.2664575	5225.796011	0.509253979	0.632828157
FMNH27918	Tragelaphus imberbis	B-G INT	1.4893025	0.004671	0.266676	8327.943005	0.552060228	0.753388965
FMNH1416	Tragelaphus imberbis	B-G INT	1.630802	0.0041335	0.3417355	9427.944431	0.471131255	0.701728552
FMNH1412	Tragelaphus imberbis	B-G INT	1.4385965	0.0032375	0.266894	9864.26584	0.589840478	0.914279805
FMNH27948	Tragelaphus imberbis	B-G INT	1.973723	0.0054415	0.266905	7702.113033	0.535730954	0.873409116
FMNH27658	Tragelaphus imberbis	B-G INT	2.0524825	0.0056895	0.267149	3814.198208	0.460633746	0.936602756

FMNH1425	Tragelaphus imberbis	B-G INT	1.3700775	0.004241	0.267002	5589.444536	0.525227132	1.058232644
FMNH1431	Tragelaphus imberbis	B-G INT	2.3332525	0.0039265	0.2089145	10309.69833	0.493751695	0.824042974
FMNH19002	Tragelaphus imberbis	B-G INT	2.529572	0.00355685	0.1518095	8048.13503	0.6152931	1.144500106
FMNH26933	Tragelaphus imberbis	B-G INT	3.6666935	0.002057	0.150161	6559.842741	0.423602341	1.331727358
FMNH26935	Tragelaphus imberbis	B-G INT	3.2950585	0.0007095	0.1499255	10572.15926	0.371218114	0.671854237
AMNH49782	Tragelaphus imberbis	B-G INT	1.5940385	0.005308	0.151316	4920.503133	0.431923045	0.806993514
AMNH19748	Tragelaphus imberbis	B-G INT	2.0623735	0.0035535	0.2098035	6835.786327	0.41290433	0.727749659
AMNH19452	Tragelaphus imberbis	B-G INT	2.105131	0.004932	0.267472	8561.2659	0.355667022	0.477930721
AMNH24876	Tragelaphus imberbis	B-G INT	2.063233	0.0030705	0.2083365	4089.818011	0.311235058	1.202162144
AMNH29875	Tragelaphus imberbis	B-G INT	2.285831	0.0039235	0.266452	9114.25412	0.444551081	0.635266192
FMNH186677	Tragelaphus spekii	VG	1.8740175	0.0060845	1.37448	1458.925904	0.359413996	0.673054437
FMNH26077	Tragelaphus spekii	VG	2.082185	0.0039545	0.8200685	1467.431414	0.449373186	1.067554232
FMNH26078	Tragelaphus spekii	VG	1.487345	0.0064075	1.466321	2374.672746	0.45630626	0.962259406
FMNH26074	Tragelaphus spekii	VG	2.5787055	0.004461	1.2450365	4227.868149	0.306329461	0.925195407
FMNH20681	Tragelaphus spekii	VG	1.07055	0.00607125	1.0850835	2750.608435	0.326490572	0.829809507
FMNH20686	Tragelaphus spekii	VG	2.1927055	0.0057145	1.1504895	1634.063668	0.414271718	0.855198645
FMNH26079	Tragelaphus spekii	VG	1.648309	0.0058695	0.9668915	4534.198456	0.328939439	0.849039044
FMNH186672	Tragelaphus spekii	VG	2.0883555	0.006753	1.3504805	1875.63843	0.381426419	0.893529452
RMCA83-006M846	Tragelaphus spekii	VG	1.411539	0.005315	0.9503025	2406.37545	0.489626336	0.808406765
RMCA83-006M538	Tragelaphus spekii	VG	1.3388315	0.00633	1.213861	2234.678133	0.550281923	1.081927703
RMCA83-006M978	Tragelaphus spekii	VG	1.4011005	0.0016235	0.920955	3734.214894	0.464335062	1.223583372
RMCA83-006M154	Tragelaphus spekii	VG	2.84695	0.0041	0.98514	1985.15487	0.34879	0.759587
RMCA83-006M876	Tragelaphus spekii	VG	2.02154	0.0038	1.03265	3528.26548	0.42658	0.86548

RMCA83-006M654	Tragelaphus spekii	VG	1.89526	0.0059	1.232648	4125.2884	0.365487	0.765468
NMNH46875	Tragelaphus spekii	VG	1.658784	0.00522	0.85154	1587.1684	0.398787	0.965468
NMNH54876	Tragelaphus spekii	VG	2.36518	0.0037	0.716548	1984.3518	0.401226	0.921245
NMNH26486	Tragelaphus spekii	VG	1.59784	0.0042	1.08749	3287.548	0.369874	0.85468
NMNH16485	Tragelaphus spekii	VG	1.62558	0.0033	0.91254	3164.588	0.415987	1.07154
NMNH64856	Tragelaphus spekii	VG	1.9874	0.004	0.79815	4120.4878	0.429857	1.09784
NMNH16489	Tragelaphus spekii	VG	2.06958	0.0037	0.832154	3987.5487	0.487515	0.987654
NMNH56975	Tragelaphus spekii	VG	1.85478	0.0042	0.86887	2685.16498	0.35487	0.85487
NMNH59753	Tragelaphus spekii	VG	2.62648	0.0029	1.1547	1859.5468	0.398787	0.851546
FMNH134367	Tragelaphus strepsiceros	GEN	3.2011955	0.0029055	0.41932	10955.18074	0.418433418	0.646903696
FMNH1414	Tragelaphus strepsiceros	GEN	1.249269	0.006632	0.341519	8971.173574	0.523577837	1.200328269
FMNH27198	Tragelaphus strepsiceros	GEN	2.6645715	0.003742	0.267522	5952.417071	0.420791923	0.753095769
FMNH34432	Tragelaphus strepsiceros	GEN	2.290922	0.0037035	0.2666855	10924.86206	0.492451993	1.03730595
FMNH34433	Tragelaphus strepsiceros	GEN	2.6903655	0.0050855	0.2082945	11592.87352	0.465428536	0.96055804
FMNH34434	Tragelaphus strepsiceros	GEN	2.6988305	0.0039395	0.208825	9565.376522	0.414918924	0.703586295
FMNH34435	Tragelaphus strepsiceros	GEN	1.6964965	0.0040555	0.3432385	10660.10025	0.618266522	0.801080257
NMNH589200	Tragelaphus strepsiceros	GEN	1.650986	0.003819	0.433702	6952.52186	0.504003078	0.768391207
NMNH589204	Tragelaphus strepsiceros	GEN	1.590659	0.0049445	0.416673	7469.671163	0.384113473	0.865524597
AMNH46875	Tragelaphus strepsiceros	GEN	2.944144	0.003536	0.34261	9123.067742	0.30575827	0.928535071
AMNH68468	Tragelaphus strepsiceros	GEN	1.827085	0.0051285	0.2679435	7866.196922	0.382123804	0.990079444
AMNH47861	Tragelaphus strepsiceros	GEN	1.2440275	0.0054105	0.2670605	6565.563078	0.561640779	0.817353028
AMNH49784	Tragelaphus strepsiceros	GEN	2.1123065	0.004872	0.266602	5471.532293	0.369942073	0.646588103
AMNH49876	Tragelaphus strepsiceros	GEN	2.31034	0.0043255	0.2664915	10745.8282	0.494729861	1.363412105

AMNH47896	Tragelaphus strepsiceros	GEN	3.120328	0.0040645	0.1508395	6005.721573	0.368801915	0.833481426
AMNH49785	Tragelaphus strepsiceros	GEN	1.73528	0.004667	0.1499695	9027.365846	0.474562255	0.832558192
FMNH129732	Tragelaphus strepsiceros	GEN	3.0050065	0.004533	0.2083125	11281.43092	0.41083212	0.962236676
FMNH16487	Tragelaphus strepsiceros	GEN	2.037084	0.00492	0.1500655	9718.764167	0.477993358	1.109874629
FMNH64856	Tragelaphus strepsiceros	GEN	3.165543	0.0037435	0.150014	11083.5564	0.491794063	0.692185345
FMNH69485	Tragelaphus strepsiceros	GEN	2.4314055	0.0054265	0.2666885	7276.562026	0.473415628	0.873740413
FMNH46876	Tragelaphus strepsiceros	GEN	3.1664385	0.0048268	0.150008	8459.255567	0.484514805	1.030756851
FMNH59484	Tragelaphus strepsiceros	GEN	2.38751215	0.0029487	0.27895154	7526.31548	0.5126498	0.865484545
FMNH46856	Tragelaphus strepsiceros	GEN	2.66878154	0.00524878	0.34648512	9875.216547	0.39874628	0.6987894545
RMCA83-006M497	Tragelaphus strepsiceros	GEN	1.26568132	0.00395651	0.19887412	10859.65685	0.416548621	0.9315781545
RMCA83-006M648	Tragelaphus strepsiceros	GEN	3.054842365	0.003156465	0.215487515	6985.165426	0.387984612	0.732165448

Appendix II: Specimen numbers and raw data for fossil specimens

Specimen	Taxon	Member	ASFC	EPLSAR	SMC	TFV	HASFC9	HASFC81
KNM-ER17889	Alcelaphini sp.	Allia Bay	2.460901	0.001961	0.269202	4930.211117	0.595976053	0.696223764
KNM-ER17890	Tragelaphus sp.	Allia Bay	2.4299795	0.0032715	0.6794645	12460.65812	0.746371761	1.21906948
KNM-ER42604	Tragelaphus sp.	Allia Bay	3.1566165	0.003683	0.8082775	8132.485875	0.551600035	1.48145984
KNM-ER42655	Tragelaphus sp.	Allia Bay	3.4778045	0.0026015	0.69316183	12887.30307	0.710383818	0.806825485
KNM-ER42663	Tragelaphus sp.	Allia Bay	3.9480215	0.002059	0.7499035	10128.28305	0.578067292	1.123152467
KNM-ER42673	Tragelaphus sp.	Allia Bay	3.245959	0.003007	0.9086825	12353.39044	0.523098438	0.812073315
KNM-ER42685	Tragelaphus sp.	Allia Bay	4.1230465	0.0037085	0.869335	8304.026325	0.618631097	0.882882928
KNM-ER42686	Tragelaphus sp.	Allia Bay	2.6580805	0.0023265	0.79692327	12625.34027	0.626725316	0.657711386
KNM-ER42689	Tragelaphus sp.	Allia Bay	4.738863	0.002071	0.6505555	7968.076129	0.626912731	1.197678889
KNM-ER42694	Tragelaphus sp.	Allia Bay	3.151646	0.0017685	0.80854	10256.51326	0.730613434	0.791911924
KNM-ER42823	Tragelaphus sp.	Allia Bay	2.3995925	0.001658	0.7667375	9739.217806	0.605309416	1.084847547
KNM-ER42831	Tragelaphus sp.	Allia Bay	2.721119	0.003024	0.8671925	13694.89911	0.622909262	0.700407349
KNM-ER42953	Tragelaphus sp.	Allia Bay	3.718931	0.0028035	0.93411511	11755.99358	0.707275427	1.252934552
KNM-ER42974	Tragelaphus sp.	Allia Bay	2.6978245	0.0017515	0.609199	9026.794839	0.810129851	0.856526755
KNM-ER794654	Tragelaphus sp.	Allia Bay	4.315648	0.0019955	0.7671655	11520.70831	0.499896807	1.14371602
AL114-7	Aepyceros sp.	Denen Dora	2.132468	0.00428	0.481648	5317.651465	0.481354	0.8354
AL 385-1	Aepyceros sp.	Denen Dora	1.6984545	0.004	0.526874	4921.515	0.398454	0.76515
AL794-1	Aepyceros sp.	Denen Dora	1.798465	0.0034	0.414878	6108.6546	0.4356987	0.692648
AL158-16	Aepyceros sp.	Denen Dora	1.698615	0.0037	0.566487	5425.431797	0.4182	0.735437477
AL450-1	Aepyceros sp.	Kada Hadar	1.287845	0.0041	0.247813	6264.3548	0.375931	0.98451
AL 463-1	Aepyceros sp.	Kada Hadar	1.484654	0.0037	0.26845	5627.315	0.412264	0.85441

AL870-1	Aepyceros sp.	Kada Hadar	2.065648	0.0049	0.316845	7345.98454	0.406548	0.864206
AL939-2	Aepyceros sp.	Kada Hadar	1.865465	0.0037	0.2845156	5972.35145	0.3865152	0.75481
AL479-6	Aepyceros sp.	Kada Hadar	1.4813945	0.004611	0.2665435	5482.87357	0.331255662	0.635437477
AL50-35	Aepyceros sp.	Sidi Hakoma	3.5261468	0.0021	0.29715	8185.3515	0.52981	0.94515
AL 222-2	Aepyceros sp.	Sidi Hakoma	3.958451	0.0033	0.29761	9815.6548	0.496545	0.82312
AL1242-1	Aepyceros sp.	Sidi Hakoma	2.9884515	0.0024	0.301548	8752.48765	0.5598745	0.996821
AL135-17	Alcelaphini sp.	Denen Dora	2.166291	0.004921	0.4220665	4564.101844	0.421586349	0.860151003
AL310-2	Alcelaphini sp.	Denen Dora	2.489078	0.005933	0.312189	5766.116738	0.473661604	0.963211544
AL55-35	Alcelaphini sp.	Denen Dora	1.680395	0.004789	0.4095705	5600.704758	0.671814019	0.898530909
AL116-146	Alcelaphini sp.	Denen Dora	2.15465	0.0031	0.465486	8731.1254	0.513135	0.951324
AL181-4	Alcelaphini sp.	Denen Dora	2.878465	0.0048	0.44513251	6264.545	0.5103515	1.032645
AL196-5	Alcelaphini sp.	Denen Dora	2.16484	0.0033	0.4298784	8206.646	0.498754	0.90315
AL162-2	Alcelaphini sp.	Denen Dora	2.31654	0.0042	0.38633515	6214.646	0.4265468	0.875431
AL398-18	Alcelaphini sp.	Denen Dora	2.598784	0.0021	0.384544	7628.6465	0.46871	0.9451
AL310-3	Alcelaphini sp.	Denen Dora	1.7045605	0.005949	0.5736945	6989.198931	0.623636446	1.049856342
AL406-25	Alcelaphini sp.	Denen Dora	2.3079355	0.005221	0.4820165	4873.81992	0.50253542	0.834783203
AL451-1a	Alcelaphini sp.	Kada Hadar	1.657886	0.007704	0.3382505	3148.55864	0.350376082	0.772409091
AL451-1b	Alcelaphini sp.	Kada Hadar	1.3136455	0.006295	0.3131645	5425.431797	0.456849741	0.872184375
AL485-1	Alcelaphini sp.	Kada Hadar	1.184651	0.0075	0.23154	3513.6545	0.398465	0.761654
AL406-26	Alcelaphini sp.	Kada Hadar	1.98451	0.0086	0.33154	2846.3515	0.40157	0.81546
AL225-6	Alcelaphini sp.	Sidi Hakoma	1.9261635	0.0040315	0.319059	5179.828894	0.535606318	0.776756269

AL126-58	Alcelaphini sp.	Sidi Hakoma	2.3095654	0.003508	0.3984541	6849.35145	0.498764	0.87945
AL325-12	Alcelaphini sp.	Sidi Hakoma	2.1687684	0.0039	0.413132	6347.6548	0.51294	0.90265468
AL597-1	Alcelaphini sp.	Sidi Hakoma	3.308112	0.004421	0.442031	7612.441309	0.577772237	0.88910245
AL773-3	Antilopini sp.	Denen Dora	4.15978	0.003284656	0.62544879	10597.36588	0.56841354	1.164879
AL452-2	Antilopini sp.	Kada Hadar	4.3165468	0.003549878	0.68761654	9834.548755	0.5988745	1.368487
AL496-2	Antilopini sp.	Kada Hadar	3.864654	0.004165487	0.59784654	10587.31655	0.6865461	1.0649879
AL452-15	Antilopini sp.	Kada Hadar	3.164987	0.002976547	0.61876454	8268.648785	0.69878545	0.8616487
AL444-27	Antilopini sp.	Kada Hadar	2.9846513	0.002678465	0.71326468	9597.234687	0.7364878	0.98134
AL807-1	Antilopini sp.	Kada Hadar	3.58764654	0.002187465	0.56846513	9234.87845	0.75987545	1.3264845
AL251-5	Antilopini sp.	Sidi Hakoma	5.146563	0.003764651	0.6755126	13685.66587	0.605948	1.046878
AL255-6	Antilopini sp.	Sidi Hakoma	4.48765465	0.002925513	0.58761315	10268.74688	0.716484654	1.26487864
AL535-2	Bovini sp.	Kada Hadar	0.926677	0.00698	1.0680705	3564.101844	0.473661604	0.863211544
AL587-5	Bovini sp.	Kada Hadar	1.5092765	0.006278	0.8346135	4821.667768	0.418799156	0.724177844
AL716-3	Bovini sp.	Kada Hadar	0.835608	0.006631	1.066665	2989.198931	0.427961115	0.577862749
AL717-1	Bovini sp.	Kada Hadar	1.0368687	0.007066	0.9425405	1414.23049	0.524718888	0.837593961
AL1251-4	Bovini sp.	Kada Hadar	0.5844045	0.0080995	1.214932	3980.941995	0.353201023	0.450286345
AL161-4	Gazella sp.	Denen Dora	3.0846545	0.006184546	0.5135487	5684.624651	0.39871313	0.89845645
AL613-1	Gazella sp.	Denen Dora	2.4987545	0.00428465	0.497846545	4982.34451	0.416486	0.716569
AL713-2	Gazella sp.	Kada Hadar	2.1978465	0.004763512	0.489874654	5168.114513	0.43256846	0.82654687
AL713-3	Gazella sp.	Kada Hadar	2.3648751	0.005598746	0.579876547	3385.084515	0.469875465	0.89461313
AL132-7	Gazella sp.	Sidi	2.5987	0.0058	0.5987	6157.9	0.4982	0.6898

		Hakoma	546	74545	5465	34654	648	7846
AL666-24	Gazella sp.	Sidi Hakoma	1.9784513	0.003998465	0.626845645	5984.295144	0.49876545	0.768454
AL1043-1	Hippotragini sp.	Denen Dora	1.5846545	0.006348784	0.31654687	2197.785485	0.450178465	0.81354654
AL427-2	Hippotragini sp.	Denen Dora	2.08454	0.005978454	0.45987545	3984.684651	0.31927854	0.7946513
AL133-37	Hippotragini sp.	Denen Dora	1.9784513	0.005531355	0.436845642	4129.198785	0.51987846	0.887413213
AL810-2	Hippotragini sp.	Kada Hadar	1.34687	0.00489465	0.38465465	2894.31548	0.3878946	0.897645351
AL610-1	Hippotragini sp.	Kada Hadar	1.2845645	0.004965132	0.41626548	2358.846545	0.421876847	0.945131
AL157-4	Kobus sp.	Denen Dora	1.264878	0.00513487	0.7651321	3826.32154	0.4198654	0.85513
AL155-2	Kobus sp.	Denen Dora	0.9846512	0.00294645	1.1876546	5394.345	0.3987654	0.796531
AL1334-1	Kobus sp.	Denen Dora	1.5987451	0.00489765	0.8654351	4462.35456	0.40298984	0.831546
AL155-7	Kobus sp.	Denen Dora	2.1546578	0.00369845	1.265487	4862.31545	0.499878	0.926548
AL1227-1	Kobus sp.	Denen Dora	1.6984513	0.002487545	1.346878	3051.3554	0.51654867	0.98456
AL1230-1	Kobus sp.	Denen Dora	0.8465487	0.003698454	1.498784	3945.21524	0.35321548	0.7561654
AL1276-1	Kobus sp.	Denen Dora	1.34654687	0.003168456	0.9846545	5192.3548	0.3987684	0.86132354
116-191	Kobus sp.	Denen Dora	2.398456	0.004168465	0.9984654	4592.13245	0.451798	0.91265487
AL210-1	Kobus sp.	Denen Dora	1.9846545	0.003796465	1.39687654	2976.761354	0.45387684	0.86374654
AL1352-2	Kobus sp.	Kada Hadar	0.987651321	0.002976453	1.135454	1103.831545	0.4324965	0.76133
AL1311-1	Kobus sp.	Sidi Hakoma	2.1654687	0.00236878	0.99846545	3975.13215	0.32654687	0.9762664
AL1218-1	Kobus sp.	Sidi Hakoma	2.81654687	0.00186487	0.946451	4394.6487	0.3264687	0.6987654
AL454-9	Neotragus sp.	Kada Hadar	2.698745641	0.00198453	0.624687	10268.15465	0.6264867	0.988435132
AL200-5	Neotragus sp.	Sidi Hakoma	5.2354687	0.001865431	0.656876546	9763.845468	0.712646786	1.0336548

AL211-2	Neotragus sp.	Sidi Hakoma	3.968454	0.001763214	0.716487846	12648.26487	0.69351454	0.89535132
AL249-7	Neotragus sp.	Sidi Hakoma	4.2654687	0.003154687	0.686543213	8753.654658	0.569875456	0.95313548
AL515-1	Oryx sp.	Kada Hadar	0.998746514	0.008165469	1.2648765	986.354587	0.5984651	1.0264867
AL447-3	Oryx sp.	Kada Hadar	1.3688754	0.00598454	1.0631254	1168.6548	0.679846545	0.9754543
AL447-2	Oryx sp.	Kada Hadar	0.798451321	0.007698452	1.4987656	1987.32154	0.4879131	0.92646867
AL167-2	Pelorovis sp.	Denen Dora	1.3987654	0.00536487	0.6943132	2168.354548	0.4987654	0.81354576
AL116-39	Pelorovis sp.	Denen Dora	1.065487	0.006798465	0.865487	2489.35454	0.5135457	0.89651321
AL709-3	Pelorovis sp.	Kada Hadar	1.365451	0.006164876	0.71654687	1972.35454	0.39684654	0.713264568
AL713-1	Pelorovis sp.	Kada Hadar	1.265487	0.005987651	0.78987654	3381.654687	0.458765456	0.794545315
AL 116-6	Reduncini sp.	Denen Dora	0.984651	0.0073	1.2654	2984.2654	0.49878654	0.894513
AL134-15	Reduncini sp.	Denen Dora	1.1648	0.0056	1.035486	1026.351454	0.365487	0.97641351
AL156-1	Reduncini sp.	Denen Dora	1.598784	0.0059	0.865431	2873.16584	0.412684768	1.03548
AL154-57	Reduncini sp.	Denen Dora	0.835154	0.0058	0.97654	3821.864	0.4632648	0.7652513
AL118-13	Reduncini sp.	Denen Dora	0.687451	0.0071	1.3568476	3384.654	0.34978465	0.699846513
AL118-20	Reduncini sp.	Denen Dora	1.03269	0.0069	1.8645	2493.3545	0.297845	0.989451
AL524-6	Reduncini sp.	Denen Dora	0.971546	0.0063	1.498745	3935.654444	0.425879	0.864513
AL116-77	Reduncini sp.	Denen Dora	0.759842	0.0041	1.69845	921.8736	0.4978131	0.7984654
AL158-76	Reduncini sp.	Denen Dora	1.38746	0.0052	0.864135	1138.6543	0.53698751	0.83216547
AL341-10	Reduncini sp.	Denen Dora	1.39874	0.0069	0.97351	2462.87651	0.6198784	0.836484
AL279-8	Reduncini sp.	Denen Dora	1.36548	0.0046	0.76513	2069.6846	0.597846	0.798543
AL153-5	Reduncini sp.	Denen Dora	0.998465	0.0061	1.165468	1576.687461	0.4987846	0.712648
AL181-6	Reduncini sp.	Denen Dora	0.814487	0.0048	1.268787	3358.65548	0.3654687	0.697664

AL169-7	Reduncini sp.	Denen Dora	0.86874315	0.0064	1.3684654	2692.654	0.3884651	0.7065846
AL116-94	Tragelaphus sp.	Denen Dora	1.264974	0.0026815	0.767607	10652.85091	0.503894066	0.753414207
AL154-59	Tragelaphus sp.	Denen Dora	1.9451175	0.005112	0.809713	5566.25568	0.431548011	0.683886041
AL158-17	Tragelaphus sp.	Denen Dora	2.3794405	0.0061095	0.7499215	7720.332497	0.516132501	0.582950261
AL158-5	Tragelaphus sp.	Denen Dora	1.481118	0.0042965	0.9698355	6551.127628	0.474934198	0.557002915
AL158-6	Tragelaphus sp.	Denen Dora	2.1764825	0.0048745	1.0382335	6527.16338	0.307356036	0.675437447
AL161-30	Tragelaphus sp.	Denen Dora	1.626847	0.0055965	0.884982	5469.214604	0.626661264	0.753025096
AL167-28	Tragelaphus sp.	Denen Dora	2.644847	0.0075995	1.112672	7907.775471	0.582256758	0.748480789
AL185-12	Tragelaphus sp.	Denen Dora	1.982873	0.0039065	0.833879	4722.03982	0.489724215	0.857778914
AL567-1	Tragelaphus sp.	Denen Dora	2.5501945	0.00548	0.6997695	7059.592552	0.46739309	0.705753969
AL86-1	Tragelaphus sp.	Denen Dora	1.4850805	0.0044805	0.8767035	6001.212512	0.374964349	0.734869539
AL146-2	Tragelaphus sp.	Sidi Hakoma	3.2201705	0.0033215	0.740933	8062.73506	0.497326206	0.880236322
AL222-12	Tragelaphus sp.	Sidi Hakoma	3.076213	0.0029095	0.5638425	7126.101481	0.584066825	0.996107172
AL25-17	Tragelaphus sp.	Sidi Hakoma	2.858706	0.0031485	0.7079155	11614.78684	0.426586679	0.838358138
AL539-12	Tragelaphus sp.	Sidi Hakoma	3.1118525	0.002757	0.6448725	7529.983075	0.544011206	0.70700521
AL885-1	Tragelaphus sp.	Sidi Hakoma	2.6043	0.003685	0.619546	10487.15134	0.618877217	0.855305241
AL133-12	Ugandex sp.	Denen Dora	2.346867864	0.004164879	0.498786465	5134.984651	0.49765451	0.916354
AL169-3	Ugandex sp.	Denen Dora	2.165487	0.005598755	0.51354876	4031.64513	0.5543265	0.82646548
AL185-9	Ugandex sp.	Denen Dora	1.8646513	0.004613548	0.559765465	5752.71513	0.5132648	0.80354567
AL185-30	Ugandex sp.	Denen Dora	2.068764	0.003765451	0.61865456	4983.35158	0.487612531	0.894054564
AL158-	Ugandex	Denen	1.6874	0.0049	0.4364	4267.6	0.4626	0.9034

100	sp.	Dora	513	75451	6876	87646	4687	6876
AL362-9	Ugandex sp.	Denen Dora	2.684513	0.004933154	0.52845645	3357.96626	0.536148	0.8164876
AL907-2	Ugandex sp.	Denen Dora	1.9846513	0.005598765	0.459845465	5384.976513	0.58461526	0.759654
AL279-13	Ugandex sp.	Denen Dora	1.79465132	0.005684654	0.50264688	4137.02154	0.49876545	0.916468764
AL1305-3	Ugandex sp.	Denen Dora	2.7975121	0.004268764	0.416879846	3982.313546	0.63105154	0.912046846
AL265-1	Ugandex sp.	Sidi Hakoma	2.98456435	0.003164654	0.426546879	5826.84513	0.5749751	0.93058464
AL327-24	Ugandex sp.	Sidi Hakoma	3.087545	0.003416469	0.489786545	5034.654651	0.61326448	0.79203664
AL224-15	Ugandex sp.	Sidi Hakoma	3.29825454	0.003764513	0.436465413	6138.684513	0.5031544	0.85794654
AL332-5	Ugandex sp.	Sidi Hakoma	2.989786456	0.004316548	0.51364687	4873.321655	0.58426254	0.8264878
AL237-12	Ugandex sp.	Sidi Hakoma	2.498768465	0.002978646	0.469876463	5394.264874	0.56845166	0.85466846
AL886-1	Ugandex sp.	Sidi Hakoma	2.775165	0.003487865	0.431648798	5762.96513	0.59876565	0.81264876
KNM-KP106	Aepyceros sp.	Kanapoi	2.3278519	0.003038	0.4502065	8649.557176	0.644422804	1.055287541
KNM-KP31733	Alcelaphini sp.	Kanapoi	1.786175	0.005524	0.7505735	3166.861599	0.384743197	0.615145643
KNMKP73C	Alcelaphini sp.	Kanapoi	1.308454	0.003455	0.809034	5740.804173	0.302237359	0.643315361
KNMKP4684	Alcelaphini sp.	Kanapoi	1.419596	0.004008	1.266529	6615.523163	0.503210614	0.62040796
KNMKP1648	Alcelaphini sp.	Kanapoi	1.2916365	0.0032485	0.5664755	4496.544482	0.438122689	0.702783721
KNMK01645	Alcelaphini sp.	Kanapoi	1.7732445	0.0037045	0.766709	5969.288811	0.445728588	0.818201827
KNM-KP29274	Hippotragus sp.	Kanapoi	2.8316815	0.006502	0.2675445	3106.921376	0.314965682	0.79358124
KNM-KP32526	Hippotragus sp.	Kanapoi	1.2866645	0.0042465	0.3890635	2165.203595	0.314653099	0.71696124
KNM-KP103	Madoqua sp.	Kanapoi	5.304795	0.0045475	1.03508	5956.263898	0.499865145	0.878371543
KNM-	Madoqua	Kanapo	4.6155	0.0044	0.8510	16220.	0.5034	0.7068

KP30206	sp.	i	985	125	23	87274	88497	37529
KNM-KP30207	Madoqua sp.	Kanapoi	2.8354315	0.003294	0.9170895	17759.14335	0.623476176	0.910287001
KNM-KP30416	Madoqua sp.	Kanapoi	2.6203535	0.00277	0.767272	17580.3078	0.464567433	0.678307352
KNM-KP30427	Madoqua sp.	Kanapoi	4.0728415	0.003511	159.3248995	6775.254756	0.86609766	1.762701094
KNM-KP30537	Madoqua sp.	Kanapoi	3.9541955	0.00370105	0.837041	17634.00437	0.397770092	0.730676057
KNM-KP36832	Madoqua sp.	Kanapoi	2.306034	0.002955	1.1551315	14040.57707	0.507672705	0.784999177
KNM-KP36835	Madoqua sp.	Kanapoi	1.8347345	0.0024025	0.8900285	14903.81333	0.309955302	0.541455649
KNM-KP36840	Madoqua sp.	Kanapoi	4.732209	0.0034915	0.9501895	19250.72913	0.448127289	0.609230377
KNM-KP30273	Raphicerus sp.	Kanapoi	3.690708	0.0043755	0.211286	4931.560042	0.661235727	0.758243616
KNM-KP30443	Raphicerus sp.	Kanapoi	2.6917205	0.002149	0.364501	5799.582372	0.747752354	1.211992446
KNM-KP93	Raphicerus sp.	Kanapoi	4.469182	0.001629	0.52394	72203.21969	0.480304244	1.197819262
KNM-KP29265	Simatherium sp.	Kanapoi	1.986231	0.006309	0.501475	1485.655024	0.526615502	1.137184905
KNM-KP96	Simatherium sp.	Kanapoi	1.426238	0.007799	0.7753525	2137.172914	0.675736075	0.872762666
KNM-KP8746	Simatherium sp.	Kanapoi	0.738269	0.0064205	0.450168	953.6069815	0.370702738	0.951715851
KNM-ER30395	Tragelaphus sp.	Kanapoi	3.529008	0.0030675	0.150638	13242.35152	0.514841696	1.409075416
KNM-KP109	Tragelaphus sp.	Kanapoi	4.4025735	0.002038	117.5771395	13268.23962	0.910206601	1.104415547
KNM-KP29273	Tragelaphus sp.	Kanapoi	3.8073665	0.003221	0.1500715	13705.49366	0.404878526	0.766636045
KNM-KP30421	Tragelaphus sp.	Kanapoi	4.9993875	0.001282	0.150382	16610.678	0.253327419	0.453291166
KNM-KP32545	Tragelaphus sp.	Kanapoi	12.2181905	0.0014855	0.150004	17649.16246	0.151729583	0.306731334
KNM-KP32570	Tragelaphus sp.	Kanapoi	3.662624	0.0018865	0.150203	13897.55428	0.701999726	1.017728737
KNM-KP32573	Tragelaphus sp.	Kanapoi	4.9199885	0.001223	0.149906	8655.803027	0.40120644	0.674446812
KNM-KP32574	Tragelaphus sp.	Kanapoi	4.0011275	0.0036135	0.150221	15139.10903	0.465740501	0.958006844
KNM-KP32829	Tragelaphus sp.	Kanapoi	2.1932755	0.004346	0.1499835	9706.804205	0.265166705	0.42949546
KNM-	Tragelaphu	Kanapo	2.1045	0.0008	0.1500	10711.	0.3379	0.7770

KP32881	s sp.	i	91	1	63	22821	55359	8943
KNM-KP67	Tragelaphus sp.	Kanapoi	3.339045	0.0018095	1.3387745	11329.82757	0.326699747	0.584253805
KNM-KP76	Tragelaphus sp.	Kanapoi	5.290756	0.001621	0.150342	14582.67458	0.53238821	0.722230472
LAET25-2246	Alcelaphini sp.	Laeotil Beds	1.646875	0.005465	1.1499835	6927.402754	0.371666098	0.748908174
LAET75-793	Alcelaphini sp.	Laeotil Beds	2.594672	0.006389	0.7499705	7011.054853	0.336398442	0.640731496
LAET76-7E-23	Alcelaphini sp.	Laeotil Beds	2.7913945	0.0055415	0.98203855	9492.302415	0.402029077	0.940861103
LAET76-7E-25	Alcelaphini sp.	Laeotil Beds	2.4390135	0.0048195	1.2499	5889.156774	0.573397374	0.932031295
LAET75-18-592	Alcelaphini sp.	Laeotil Beds	2.4446265	0.003909	0.83503335	6908.951455	0.410334399	1.02170111
Laet75-248	Alcelaphini sp.	Laeotil Beds	1.1672375	0.0048015	1.262541	4816.57711	0.601326088	0.886834575
LAET75-2900	Alcelaphini sp.	Laeotil Beds	1.549695	0.0059475	1.181124	8044.733116	0.315441584	0.527607726
LAET75-4624	Alcelaphini sp.	Laeotil Beds	1.9478855	0.0020735	0.8149898	3423.195817	0.529191673	1.622273819
Laet75-56	Alcelaphini sp.	Laeotil Beds	1.1672375	0.0048015	1.066541	6036.186299	0.601326088	0.886834575
LAET76-18-354	Alcelaphini sp.	Laeotil Beds	2.8632595	0.003883	1.1250646	6194.524061	0.320514019	0.591283469
LAET3373-00	Antidorcas sp.	Laeotil Beds	2.6368785	0.001759	0.530198	8598.897841	0.526359079	0.933142765
LAET75-18-596	Antidorcas sp.	Laeotil Beds	4.8409215	0.0013355	0.338177	10484.95727	0.403014162	1.002373112
LAET75-910	Antidorcas sp.	Laeotil Beds	5.248925	0.0008215	0.9817665	6976.550413	0.588573583	1.015051344
EP816-03	Bovini sp.	Laeotil Beds	3.2782485	0.004419	0.524735	3560.118978	0.460013949	1.276437001
LAET75-117	Bovini sp.	Laeotil Beds	3.9603285	0.0017595	0.710117	4816.57711	0.685120608	1.32169176
LAET75-1890	Bovini sp.	Laeotil Beds	2.1475715	0.004016	0.6667885	2235.472122	0.323113433	0.697314264
Laet75-277	Bovini sp.	Laeotil Beds	2.202664	0.000767	0.830401	4080.359523	0.804375311	1.319722659
LAET75-3052	Bovini sp.	Laeotil Beds	3.7335465	0.0058475	0.580307	6801.918438	0.419943834	0.825648195
LAET78-4760	Bovini sp.	Laeotil Beds	1.212556	0.004044	0.6611025	3431.600407	0.777667412	1.369201784
LAET78-4761	Bovini sp.	Laeotil Beds	2.6893725	0.0041845	1.00453	5177.082571	0.424699179	0.753394466
LAET78-	Bovini sp.	Laeotil	1.7509	0.0016	0.7927	4631.9	0.4612	1.2041

4763		Beds	43	56	17	42162	58014	53749
LAET78-4826	Bovini sp.	Laeotil Beds	2.136771	0.004014	0.840167	4572.626719	0.505106023	1.280764192
LAET78-5176	Bovini sp.	Laeotil Beds	2.3222155	0.0016065	0.498825	5001.678567	0.328182815	0.669633363
EP497-00	Gazella sp.	Laeotil Beds	3.3925505	0.003745	0.522615	4281.412861	0.306136192	0.576677341
LAET75-2741	Gazella sp.	Laeotil Beds	2.451238	0.001667	0.6342495	2437.260456	0.354690069	0.688110861
LAET78-5198	Gazella sp.	Laeotil Beds	1.717559	0.004945	0.4867425	4294.427981	0.382008146	0.835944301
LAET75-3520	Gazella sp.	Laeotil Beds	1.456699	0.0021715	0.550552	5856.876502	0.536675699	1.675503866
EP1268-00	Hippotragus sp.	Laeotil Beds	1.090602	0.004212	0.351484	4800.928882	0.66908798	0.84789888
LAET75-2949	Hippotragus sp. (?)	Laeotil Beds	1.3433605	0.0057055	0.2703685	8941.380548	0.589492669	0.723102041
LAET75-5287	Madoqua sp.	Laeotil Beds	3.9077655	0.001013	0.850466	12160.99281	0.421627386	0.986793913
LAET74-1982	Madoqua sp. (?)	Laeotil Beds	2.76743	0.003152	0.912646	14011.05485	0.90843698	1.929041254
LAET75-479	Madoqua sp. (?)	Laeotil Beds	4.845299	0.00163	0.6514545	15858.15926	0.615392967	1.202652864
LAET75-1417	Parmularius sp.	Laeotil Beds	1.470725	0.0047605	1.150761	2663.346649	0.354469646	0.627182659
LAET75-2829	Parmularius sp.	Laeotil Beds	2.114182	0.006568	0.9821495	5911.499064	0.432645734	0.772617773
LAET75-2855	Parmularius sp.	Laeotil Beds	0.7785805	0.0051665	1.6750559	2474.010561	0.642018139	1.069779161
LAET75-2937	Parmularius sp.	Laeotil Beds	0.95443	0.0044895	1.49961	4466.192982	0.199172321	0.469162384
LAET75-3376	Parmularius sp.	Laeotil Beds	1.2638285	0.003854	0.8506	2365.222808	0.39777613	0.8077786
LAET75-3458	Parmularius sp.	Laeotil Beds	0.820111	0.0043825	1.0800735	1187.67524	0.478490095	1.01399669
LAET75-356	Parmularius sp.	Laeotil Beds	1.556762	0.005106	1.3600565	5820.381607	0.334527639	0.941670152
LAET75-357	Parmularius sp.	Laeotil Beds	2.0223325	0.00708	0.970603	5377.318689	0.499019774	0.760638786
LAET75-832	Parmularius sp.	Laeotil Beds	1.323531	0.0065265	0.8950005	3096.170645	0.301711341	0.819779929
LAET75-1669	Parmularius sp.	Laeotil Beds	1.1258125	0.007764	1.1499	4159.460592	0.323430523	0.531403999
LAET75-616	Simatherium sp.	Laeotil Beds	3.0665905	0.003015	0.4503215	8932.12449	0.468385619	0.76901904
LAET78-	Simatheriu	Laeotil	2.4788	0.0061	0.5208	6187.0	0.3996	0.6994

2437	m sp. (?)	Beds	04	08	347	89877	01059	23408
LAET78-4623	Simatherium sp. (?)	Laeotil Beds	2.2965425	0.002212	0.6499635	7784.078839	0.464380863	1.201985378
LAET75-1300	Tragelaphus sp.	Laeotil Beds	4.016725	0.0019265	0.7502425	11169.77475	0.604263033	0.821255208
LAET76-18-622	Tragelaphus sp.	Laeotil Beds	3.1679235	0.003121	0.6415235	13351.57434	0.522673149	1.071459457
LAET752915	Tragelaphus sp.	Laeotil Beds	3.606299	0.002822	0.8301745	15714.69775	0.680868684	0.975901865
LAET75-722	Tragelaphus sp.	Laeotil Beds	5.116272	0.0018265	0.690489	14015.20803	0.770844419	0.819855393

Curriculum vitae

Jessica Renee Scott

Doctoral Program in Environmental Dynamics
University of Arkansas
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Education

University of Arkansas, Ph.D. in Environmental Dynamics, expected December 2011
Committee Chair: Peter S. Ungar
Committee Members: J. Michael Plavcan, Walter S. Manger and Rene Bobe
Dissertation: Dental Microwear Texture Analysis of Pliocene Fossil Bovids from Four Early Hominin Sites in Eastern Africa: Implications for Paleoenvironmental Dynamics and Human Evolution

University of Arkansas, M.A. in Anthropology, 2007
Committee Chair: Peter S. Ungar
Committee Members: Jerome C. Rose, Jesse Casana and Mark Teaford
Thesis: Dental Microwear Texture Analysis of the Archaeolemurids and Megaladapids, Two Families of Subfossil Lemurs from Madagascar

University of Arkansas at Little Rock, B.A. in Anthropology, 2005

Research Interests

Environmental and ecological context of human evolution in East and South Africa
Relationship between climatic and evolutionary change
Community ecology of fossil mammals
Dietary reconstruction using dental microwear and stable isotope analyses

Field Experience

Amarna, Egypt	The Amarna Project	March-April 2008
Freighter Gap, Wyoming	The Great Divide Basin Project	June-July 2007
Beza Mahafaly, Madagascar	The Ring-Tailed Lemur Project	July-August 2006
LaSuerte, Costa Rica	Advanced Primate Ecology	July-August 2005
Myakka City, Florida	Lemur Conservation Foundation	May-June 2005
Toltec Mounds, Arkansas	Arkansas Archaeological Survey	July-October 2004

Ometepe, Nicaragua Primate Ecology Field SchoolJune 2004

Collections Experience

Smithsonian National Museum of Natural History, Washington D.C.
National Museum of Ethiopia, Addis Ababa
Kenya National Museums, Nairobi
Royal Museum of Central Africa, Tervuren, Belgium
The Field Museum, Chicago
Arkansas Archaeological Survey
American Museum of Natural History, New York
The Amarna Trust, Egypt

Other Research Experience

Koobi Fora Plio-Pleistocene Bovid Project
University of Arkansas Stable Isotope Lab, Department of Biology
University of Arkansas Soil Lab, Department of Geosciences
Graduate Research Assistant, J. Michael Plavcan
Graduate Research Assistant, Peter S. Ungar

Grants and Awards

NSF Doctoral Dissertation Improvement Grant (0925822), 2009-2011, $15000
Walton Doctoral Academy Fellowship, August 2007- May 2011
University of Arkansas Conference Grant for AAPA meeting, April 2010, $1100
University of Arkansas Conference Grant for AAPA meeting, April 2009, $1100
University of Arkansas Conference Grant for AAPA meeting, April 2008, $1100
University Study Abroad Grant for work at Amarna, Egypt, March- April 2008, $500
University of Arkansas Conference Grant for AAPA meeting, April 2007, $550
Katherine J. Hardie Award for Outstanding Graduate in Anthropology, May 2005
UALR Student Fieldwork Award in Anthropology, May 2005, $1000

Professional Service

Kenya National Museum, Invited Lecturer, May 2010
Department of Biological Sciences, Brown Bag Lunch Speaker, 2010
Day of Darwin Celebration, University of Arkansas, 2009
Pearson Publishing Text Development Seminar, March 2009
Fayetteville Middle School Science Fair Judge, 2008
University Days for high school students, 2005, 2006, 2007, 2008, 2009
Department of Anthropology, Colloquium Speaker, University of Arkansas, 2007
Primate Enrichment Coordinator, Little Rock Zoo, 2003, 2004, 2005

Membership in Professional Organizations

American Association of Physical Anthropologists

Society of Vertebrate Paleontology
East African Association for Palaeoanthropology and Paleontology
Dental Anthropology Association
Sigma Xi
Phi Kappa Phi
Lambda Alpha

Publications

Scott, J.R., in press.Dental microwear texture analysis of extant African Bovidae.Mammalia.

Stynder, D., **Scott, J.R.**, Schubert, B., Ungar, P.S., in review. Dental microwear texture analysis of fossil felids and hyaenids from Langebaanweg, South Africa.

Pontzer, H., Scott, J.R., Lordkipanidze, D., Ungar, P.S., in press. Dental microwear and diet in the Dmanisi hominins.Journal of Human Evolution.

Ungar, P.S., **Scott, J.R.**, Schubert, B., Stynder, D., 2011. Carnivoran dental microwear textures: comparability of carnassial facets and functional differentiation of the postcanine teeth. Mammalia.

Grine, F.E., Judex, S., Daegling, D.J., Ozcivici, E., Ungar, P.S., Scott, R.S., **Scott, J.R.**, Teaford, M.F., Sponheimer, M., Walker, A., 2010. Modeling craniofacial biomechanics, and the limitations of functional and dietary inference in hominin paleontology.Journal of Human Evolution.

Merceron, G.M., **Scott, J.R.**, Scott, R.S., Geraads, D., Spassov, N., Ungar, P.S., 2009. Seed predation for an early Colobine as a link between frugivory and folivory?Evidence from dental microwear texture analysis of *Mesopithecus* (Late Miocene of Eurasia).Journal of Human Evolution.doi:10.1016/j.jhevol.2009.06.009

Scott, J.R., Ungar, P.S., Jungers, W.L., Godfrey, L.R., Scott, R.S., Simons, E.L., Teaford, M.F., Walker, A., 2009. Dental microwear texture analysis of the archaeolemurids and megaladapids, two families of subfossil lemurs from Madagascar. Journal of Human Evolution 56, 405-416.

Krueger, K., **Scott, J.R.**, Kay, R., Ungar, P., 2008. Comparisons of dental microwear texture attributes between facets in three primate taxa. American Journal of Physical Anthropology 137, 485-490.

Ungar, P.S., Scott, R.S., **Scott, J.R.**, Teaford, M.F., 2008. Historical Perspectives on Dental Microwear- new applications. In: Technique and Application in Dental Anthropology (Cambridge Studies in Biological Anthropology and Evolution), Irish, J.D. (Ed.), Cambridge University Press, Cambridge.

Cuozzo, F.P., Sauther, M.L., Yamashita, N., Lawler, R.R, Brockman, D.K., Godfrey, L.R., Gould, L., Youssouf, I.A.J., Lent, C., Ratsirarson, J., Richard, A.F., **Scott, J.R.**, Sussman, R.W., Villers, L.M., Weber, M.A., Willis, G., 2008. A comparison of salivary pH in sympatric wild lemurs (*Lemur catta* and *Propithecus verreauxi*) at Beza Mahafaly Special Reserve, Madagascar. American Journal of Primatology 70, 363-371.

Abstracts

Scott, J.R., 2012. Dental microwear texture analysis of the fossil Bovidae from the Hadar hominin site: implications for paleoenvironment. American Association of Physical Anthropologists.

Ungar, P.S., **Scott, J.R.**, McNulty, K.P., Harcourt-Smith, W., Dunsworth, H.M., 2012.Environments of early Miocene Rusinga Island and Songhor: evidence from the dental microwear of tragulids. American Association of Physical Anthropologists.

Scott, J.R., 2011. Dental microwear texture analysis of extant African Bovidae.Society of Vertebrate Paleontologists.

Scott, J.R., Ungar, P.S., Schubert, B.W., Stynder, D.D., 2011. Dental microwear texture analysis of fossil hyaneids from Langebaanweg, South Africa.American Association of Physical Anthropologists.

Zolnierz, M.S., Delezene, L., Kimbel, W.H., **Scott, J.R.**, Ungar, P.S., 2011. Premolar microwear in *Australopithecus afarensis* and *A. africanus*.American Association of Physical Anthropologists.

Schmitt, E., Schubert, B.W., **Scott, J.R.**, Ungar, P.S., 2010. Analysis of the bone-crushing behavior of *Canis dirus* using dental microwear texture analysis.Society of Vertebrate Paleontology 2010.

Scott, J.R., Grine, F.E., Teaford, M.F., Ungar, P.S., 2010. Premolar microwear texture analysis of *Australopithecus africanus*.American Journal of Physical Anthropology, S50.

Scott, J.R., Krueger, K.L., Kemp, B., Rose, J.C., 2009. Dental microwear texture analysis of workers from Amarna, an eighteenth dynasty site in Egypt.American Journal of Physical Anthropology S48, 223.

Krueger, K.L., **Scott, J.R.**, Kay, R.F., Ungar, P.S., 2008. Comparisons of dental microwear texture attributes between facets in three primate taxa. American Journal of Physical Anthropology S46, 135.

Scott, J.R., Ungar, P.S., Jungers, W.L., Godfrey, L.R., Scott, R.S., Simons, E.L., Teaford, M.F., Walker, A., 2007. Dental microwear texture analysis of the archaeolemurids and megaladapids, two families of subfossil lemurs from Madagascar.American Journal of Physical Anthropology S44, 212.

Cuozzo, F.P., Sauther, M.L., Lawler, R.R, Yamashita, N., **Scott, J.R.**, Ratsirarson, J., L.M., Weber, M.A., 2007. A comparison of salivary pH in sympatric lemur species (*Lemur catta* and *Propithecus verreauxi*) at Beza Mahafaly Special Reserve, Madagascar: investigating feeding ecology, dietary chemicals and primate tooth wear. American Journal of Physical Anthropology, S44, 94.