Paleoecological implications of dental mesowear and hypsodonty in fossil ungulates from Kanapoi

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ABSTRACT

The Pliocene site of Kanapoi is key to our understanding of the environmental context of the earliest species of *Australopithecus*. Various approaches have been used to reconstruct the environments of this site, and here we contribute new data and analyses using mesowear and hypsodonty. The dental traits of 98 bovids, suids and rhinocerotids from Kanapoi were analyzed using these proxies. Results indicate that most of the animals analyzed had a relatively abrasive diet. Bovids in the assemblage incorporated more grass into their diet than do modern species of the same tribe or genus. Although Pliocene Kanapoi likely had complex environments, our analysis indicates that grassy habitats were a dominant component of the ecosystem, a conclusion that supports the results of previous investigations of the paleoecology of the site.

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1. Introduction

Understanding the environments of Kanapoi during the Pliocene is critical to understanding the ecology and adaptations of *Australopithecus anamensis*, the earliest species of the genus. Previous approaches include analyses of sedimentology (Feibel, 2003), paleosols (Wynn, 2000; Cerling et al., 2011), fossil vertebrate taxonomic composition (Winkler, 1998; Harris et al., 2003; Stewart, 2003; Manthi, 2008; Bobe, 2011; Werdelin and Manthi, 2012; Geraads et al., 2013), and mammalian dental enamel stable isotopes (Harris et al., 2003; Cerling et al., 2015; Manthi et al., in press). Although authors have reached somewhat different conclusions regarding Kanapoi paleoenvironments, the consensus seems to be that the site was dominated by relatively open, low tree-shrub vegetation during the Pliocene. Here we contribute new ecometric data and analysis to test previous hypotheses of Kanapoi paleoenvironments.

Dental mesowear denotes the macroscopic dental wear facets created on the molars of ungulates during the lifetime of an animal. They vary in size and shape according to the properties of the foods ingested (abrasion) and the tooth-on-tooth wear during mastication (attrition) (Fortelius and Solounias, 2000). Studies indicate that the shapes of the facets differ between grazing (grass-eating), browsing (leaf-eating) and mixed-feeding taxa. This is because of differences in the properties of the food types and the relative amount of grit they contain (Ungar, 2015). Thus mesowear facets can be used to reconstruct the diets and, therefore, the environments in which these animals lived.

The relative height of the tooth crown, or hypsodonty, has often been used in conjunction with the evaluation of mesowear to reconstruct past habitats (Jernvall and Fortelius, 2002; Andrews and Hixson, 2014) and it has been shown that using these methods in combination improves their accuracy (Fraser and Theodor, 2011). Studies have shown that a large prevalence of high-crowned teeth in herbivores can be related to decreased rainfall (Eronen et al., 2010). This is because in a drier environment, the vegetation tends to be rougher and more abrasive. An animal's teeth wear out as it feeds, and food items that contain grit and other abrasives wear down the tooth crown faster than softer foods, such as leaves. A tooth with a higher crown is therefore favorable in a drier environment because it will last longer. We will use the hypsodonty index to infer diet and environments in Kanapoi Pliocene mammals: a high hypsodonty index is likely to indicate a more grazing diet and feeding at ground level in open habitats, whereas a low one is linked to a more browsing diet (Damuth and Janis, 2011).

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However, hypsodonty is also a genetic trait linked to the "lifetime" of the tooth (Jernvall and Fortelius, 2002) which informs long-term evolutionary adaptation, and several studies have shown that it is not always directly indicative of the diet of the living animal (Feranec, 2003).

Mesowear and hypsodonty have been used increasingly in recent years to study questions related to human evolution. Mesowear was mentioned as one of the lines of evidence used in a multi-proxy framework to reconstruct the paleoenvironments at the As Duma fossiliferous deposits of Gona (4.51–4.32 million years ago (Ma)), but results were not explained in details in the article (Semaw et al., 2005). At the upper Busidima Formation (1.7 Ma – <0.64 Ma), Ethiopia, mesowear contributed to identifying two shifts in the paleoenvironment through time (Everett, 2010). The approach was also used to demonstrate the presence of grass patches around 7 Ma at the site of Toros-Menalla in Chad where *Sahelanthropus tchadensis* remains were found. The authors linked the presence of these grass patches to the development of bipedality in early hominins (Blondel et al., 2010). White and colleagues (White et al., 2009) included mesowear in their multi-proxy reconstruction of the paleoecology of *Ardipithecus ramidus* at Aramis around 4.4 Ma. The resulting mesowear scores showed that browsing or frugivorous species dominated at the site. Similarly, Curran and Haile-Selassie used mesowear in their paleoecological analysis of Woranso-Mille (3.8–3.6 Ma), where remains of various *Australopithecus* species were uncovered (Curran and Haile-Selassie, 2016). The results from their mesowear analyses helped highlight the mosaic nature of the paleoenvironments at the site. Both hypsodonty and mesowear have been used to shed light on the paleoecology of *Australopithecus africanus* around 3.2–2.5 Ma at Makapansgat, in South Africa (Schubert, 2007). The authors ruled the hypsodonty results as unable to accurately reconstruct the diet in their study, but mesowear results correlated well with stable isotope results and were further used to distinguish C_3 browsers from C_3 grazers at the site. Uno and colleagues (Uno et al., 2011) report the results of a mesowear analysis on equids from the Nakali Formation and the Namurungule Formation at Samburu Hills during the Miocene, which correlate with the results of their stable isotope analyses. They documented a transition from browsing to grazing at the site starting at 9.9 Ma.

Mesowear studies have also been used more specifically on bovids at African sites from the Miocene to the Holocene. At Laetoli, mesowear was used to investigate dietary shifts and niche diversity in ungulates between two time periods separated by a million years: the Upper Laetolil Beds (ULB) at 3.85–3.63 Ma and the Upper Ndolanya Beds (UNB) at 2.66 Ma (Kaiser et al., 2011). Similarly, Faith and collaborators (Faith et al., 2011) have also used this proxy to investigate the paleoecology of a previously poorly known bovid species from Rusinga Island in Kenya. Most recently, the identification of bovid remains from the Kibish Formation (~196-8Ka),

Ethiopia, included the evaluation of mesowear (Rowan et al., 2015). The authors used this approach to document changes in dietary ecology in different bovid species from the Middle Pleistocene to the Middle Holocene, and demonstrated that dental abrasion levels were almost systematically higher in the past. Similarly, bovid mesowear data were used in conjunction with postcranial ecomorphology to reconstruct the paleoenvironments at the Omo Shungura Formation (Barr, 2014). The author thus documented multiple ecological shifts between geological members, which he argues is linked to either migration or eurytopicity in the Omo Shungura hominins.

Finally, a recent large-scale ecometric analysis of the Turkana Basin over time showed that the west side of Lake Turkana as a whole was more arid than the east side starting around 4 Ma (Fortelius et al., 2016), about the age of the sediments of Kanapoi (Feibel, 2003). The present study provides a more localized ecological analysis focused specifically on the site of Kanapoi. The purpose of this article is to explore the paleoecology of Pliocene Kanapoi in the Turkana Basin using a 'taxon-free' approach to reconstruct habitat and diet of the large mammalian herbivores and to complement the existing data on the paleoecology of the site, particularly the results of Fortelius and colleagues' recent investigation.

2. Material and methods

Ninety-eight large herbivore specimens from the Kanapoi collection (1994–2015) were used for this study. All individuals belonging to the orders Artiodactyla, Perissodactyla and Proboscidea (APP taxa) (Eronen et al., 2010) were examined (Table 1 and Supplementary Online Material (SOM)). We only used teeth that were taxonomically identified to the genus level, or the tribe level for bovids. Only complete or nearly complete adult upper and lower molars were used. If more than one tooth of the same position was available for an individual, the average was used. Molars from older individuals (heavily worn) and subadults were not included. We used both isolated teeth and teeth still in place in the jaw. Unfortunately, no giraffids, equids or proboscideans met the criteria we set. The data on extant East African species is from Kaiser and colleagues (Kaiser et al., 2013). The bovid species in the modern dataset were gathered by tribe in order to make the data more directly comparable to the fossil sample. We used published data from other sites relevant to hominin evolution in Africa to provide further contextualization of our results: the Kibish Formation (Rowan et al., 2015), Makapansgat (Schubert, 2007), Laetoli (Kaiser, 2011), Toros-Menalla (Blondel et al., 2010) and Aramis (White et al., 2009). We only selected data generated from second molars. When necessary, we also reframed the data using Kaiser et al.'s (2009) "0 to 4" summary system described below.

Table 1
Mesowear and hypsodonty in Kanapoi ungulates. %high = percentage of teeth with high cusps, %low = percentage of teeth with low cusps, %sharp = percentage of teeth with sharp cusps, %round = percentage of teeth with rounded cusps, %blunt = percentage of teeth with blunt cusps, HYP = hypsodonty index, Category = hypsodonty index categories: b = brachydont, m = mesodont, h = hypsodont.

Taxon	n	%high	%low	%sharp	%round	%blunt	HYP	Category
Aepycerotini	14	7.14	92.86	0.0	50.0	50.0	2.41	m
Alcelaphini	11	63.64	36.36	45.45	45.45	9.09	2.25	m
Antilopini	8	12.5	87.5	50.0	25.0	25.0	1.94	m
Bovini	6	80.0	20.0	40.0	60.0	0.0	1.75	m
Hippotragini	4	25.0	75.0	25.0	75.0	0.0	1.59	m
Neotragini	7	42.86	57.14	71.43	14.29	14.29	1.51	m
Tragelaphini	15	53.33	46.67	53.33	46.67	0	1.41	b
Notochoerus	7	–	–	–	–	–	0.95	b
Nyanzachoerus	16	–	–	–	–	–	0.84	b
Rhinocerotidae	1	0	100	0	0	100	–	–

2.1. Mesowear

Mesowear (MSW) is scored according to two main criteria: cusp shape (sharp, rounded or blunt) and occlusal relief (high or low cusps) (Fig. 1.; Fortelius and Solounias, 2000). Following the original method, upper second molars (and ?M2) were used. Similarly to Blondel et al. (2010), we also expanded our sample size to include lower second molars (and ?m2) (total $n = 68$). It has been suggested that mandibular molars reflect a more grazing signal compared to the upper molars (Franz-Odendaal and Kaiser, 2003). In our sample, no significant differences between upper and lower molars were found at the $p < 0.05$ level using a two-way ANOVA.

We used the combined score as developed by Kaiser et al. (2009) in which the two traits are converted into mesowear stages from 0 to 4. This combined score was also used to describe the modern comparative dataset used here (Kaiser et al., 2013). The score can be interpreted as the combined effect of abrasion and attrition on the teeth. Mesowear scores are useful for comparative purposes, but their downside is that they muddle the relative contribution of both phenomena. Animals that mostly feed on leaves will exhibit higher and sharper cusps than those that feed on grass. In browsers, the wear is caused mainly by tooth-on-tooth contact. A stage "0" (sharp and high cusps) is a hyper browser. Grazers tend to have blunt or round cusps that tend to be low. However, some grazers also exhibit high relief (Fortelius and Solounias, 2000). The shape of their teeth is influenced mostly by the action of tooth-to-food wear during mastication. We interpret a stage "4" (blunt cusps and low relief) as hypergrazer. Mesowear has been tested for inter-observer and intra-observer biases, which were found to be negligible (Kaiser, 2000).

2.2. Hypsodonty

Hypsodonty (HYP) was evaluated using the ratio of height to width for every lower third molar in the collection (Fig. 1; Janis, 1988). Then, lightly worn lower third molar (m3s and ?m3s) from the Kanapoi assemblage were classified by tribe or genus ($n = 50$).

Some teeth are from the same individuals as the teeth used for the mesowear analysis ($n = 19$), but most are not. A note about these particular individuals is included in the Results section. Next, the tribe or genus average was computed and classified as one of three possible categories: individuals are categorized as mesodont when their hypsodonty ratio is between 1.5 and 3, brachydont when the score is less than 1.5, and hypsodont when it is higher than 3 (Damuth and Janis, 2011).

3. Results

The teeth of bovids from the Kanapoi Formation, dated to ~4 Ma, were clearly affected by a diet containing abrasive elements, as seen in the relatively high mesowear scores in Figure 2. There was a statistically significant difference between tribes across all sites according to an ANOVA, $F (6, 41) = 4.018$, $p = 0.00296$. Pairwise comparisons of the means according to Tukey HSD's test showed significant differences between three pairs: Tragelaphini-Hippotragini ($p = 0.01$), Neotragini-Hippotragini ($p = 0.02$) and Tragelaphini-Alcelaphini ($p = 0.04$). There were also significant differences between sites (ANOVA, $F (9, 38) = 2.487$, $p = 0.024$), but the differences were not maintained when examined through pairwise comparisons at the $p = 0.05$ level using Tukey HSD's test. The ANOVA was not significant at the $p = 0.05$ level when the site or the period was used as an interactive factor in addition to tribal differences.

There was a moderate correlation between hypsodonty and mesowear in bovids in our dataset (Pearson: $r = 0.57$). This is expected since both a higher hypsodonty index and a higher mesowear score are indicative of a grazing diet. We suggest that the lack of a strong correlation between hypsodonty and mesowear in our bovid sample can be explained by the difference in scale between the two proxies. Hypsodonty is strongly influenced by genetics and does not necessarily reflect the current diet of an animal in a given environment (Davis and Pineda Munoz, 2016). Nineteen specimens consisted of individuals with at least a second molar suited for the mesowear analysis and a third molar that could be used to calculate hypsodonty. There was a weak positive correlation between hypsodonty index and mesowear score when measured in these specimens (Pearson: $r = 0.28$, Fig. 3). In addition to also being biased by the different scales of the proxies, the fact that this correlation was less strong than for the tribal averages reinforces the notion that proxies like mesowear and hypsodonty need to be used at the assemblage level, which reduces the influence of individual variation. With such a low sample size, it is difficult to discern any tribal pattern, but this would be an interesting area of future investigation if the sample size were to increase.

Fossil Aepycerotini had an attrition-dominated diet at Kanapoi. With an average of 3.36 ± 0.84, they show the strongest grazing signal in the assemblage. In addition, aepycerotins have the highest hypsodonty indices among the Kanapoi fossils (HYP = 2.41), which is expected in grazing animals. They also have the lowest standard deviation in the sample, indicating low within-tribe variability. This is not surprising, considering that all individuals scored have been attributed at least tentatively to a single genus (*Aepyceros* sp.($n = 12$). or cf. *Aepyceros* ($n = 2$)) (Geraads and Bobe, in press). The enamel of three specimens used in this study, KNM-KP 32546, 29259 and 32823, have also been analyzed isotopically and show grazing or graze-dominated mixed diets (Cerling et al., 2015). Amongst the fossil Aepycerotini included here, Kanapoi aepycerotins stand out as having a much stronger grazing signal, completely out of the range of the individuals from the same tribe at other sites. Other sites show mesowear signals in the browsing

Figure 1. Illustration of traits used in the evaluation of mesowear and hypsodonty. (A) Tragelaphini, KNM-KP 58605, mesowear score (MSW) 0: sharp and high; (B) Tragelaphini, KNM-KP 30421, MSW 1: round and high; (C) Tragelaphini, KNM-KP 58607, MSW 2: sharp and low; (D) Tragelaphini, KNM-KP 56847, MSW 3: round and low; (E) Alcelaphini, KNM-KP 58608, MSW 4: blunt and low. All specimens are from the Kenya National Museums, Nairobi.
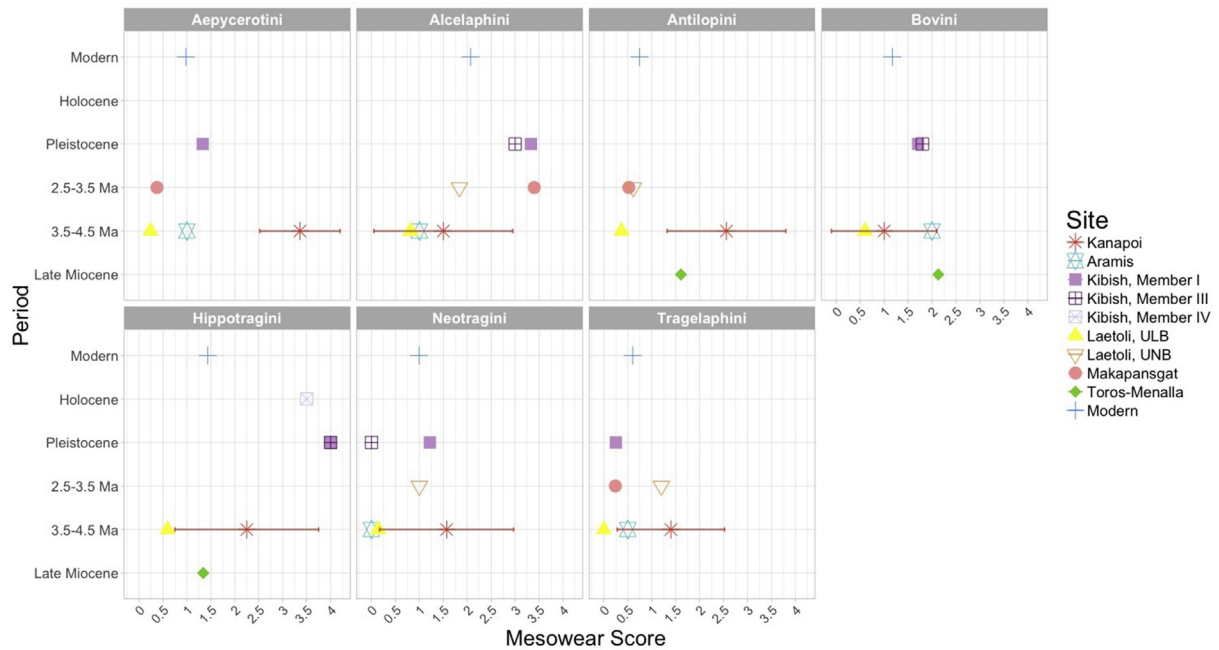
Figure 2. Distribution of mesowear scores in the Kanapoi fossils, extant eastern African bovids (Kaiser et al., 2013) and other fossil localities: Aramis (White et al., 2009), Kibish (Rowan et al., 2015), Laetoli (Kaiser, 2011), Makapansgat (Schubert, 2007) and Toros-Menalla (Blondel et al., 2010).
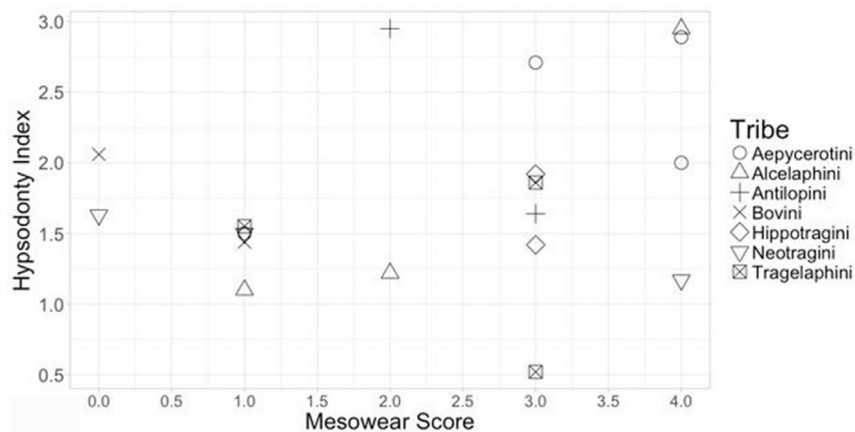
Figure 3. Distribution of the mesowear score and hypsodonty index for the 19 Kanapoi bovid specimens for which both measurements were possible.

range for the aepycerotin second molars, the highest being at Kibish member I (MSW = 1.33) and the lowest being the Upper Laetolil Beds (MSW = 0.24) (Kaiser, 2011; Rowan et al., 2015) (Fig. 2). As reflected in their mesowear score (MSW = 0.98), even modern impalas (*Aepyceros melampus*) are classified as abrasion-dominated mixed feeders (Franz-Odendaal and Kaiser, 2003; Cerling et al., 2015).

Fossil antilopins at Kanapoi are mixed-feeders that incorporated some graze into their diets and have an average mesowear score of 2.5 ± 1.31. They tend to have low cusps that are sharp or rounded. They also have relatively hypsodont teeth (HYP = 1.94). Among the antilopins analyzed, specimens were identified as *Gazella* sp. (*n* = 4), cf. *Gazella* (*n* = 1) or indeterminate (*n* = 3). *Gazella* cf. *janenshi* and a species with affinities to *Dytikodorcas* sp. are additional antilopins identified within the Kanapoi fossil assemblage but they could not be analyzed for this study (Geraads and Bobe, in press). Antilopin mesowear results overlap with those of their tribe members inhabiting the earlier site of Toros-Menalla, in Chad

(Blondel et al., 2010). In contrast, the tribe has an attrition-dominated diet at Laetoli (MSW = 0.37−0.62) and Makapansgat (MSW = 0.52) (Schubert, 2007; Kaiser, 2011). In addition, the modern members of this tribe, *Litocranius walleri* (gerenuk, MSW = 0.87), *Nanger granti* (Grant's gazelle, MSW = 0.65) and *Ammodorcas clarkei* (dibatag, MSW = 0.71), all have much more of a browsing signal despite being described as browse-dominated mixed feeders in the behavioral literature (Gagnon and Chew, 2000). This is also confirmed by isotopic studies of animals in the wild (Ngugi et al., 2014; Cerling et al., 2015).

Kanapoi Hippotragini have rounded or sharp cusps and the cusps tend to be low, which is interpreted as a mixed-feeding signal. Their hypsodonty score is 1.59 and their mesowear score is 2.25 ± 1.5. They also have the highest standard deviation in the dataset, denoting variability within the tribe, a characteristic also detected by isotopic studies at Laetoli (Kingston and Harrison, 2007). However, hippotragins are rare in the assemblage and it is unclear how many species there were at Kanapoi. All remains are

attributed to either cf. *Tchadotragus* ($n = 1$) or indeterminate ($n = 3$) (Geraads et al., 2013; Geraads and Bobe, in press). Amongst fossils, hippotragins from the Chadian site of Toros-Manella have the mean mesowear score most similar to that of Kanapoi (MSW = 1.34), but their signal is more attrition dominated (Blondel et al., 2010). Hippotragins have a browsing diet at the Upper Laetolil Beds (MSW = 0.6) (Kaiser, 2011), but a much more graze-dominated diet throughout all members of the Kibish formation (MSW = 3.5 to 4) (Rowan et al., 2015), a testament of the tribe's dietary flexibility. The modern Hippotragini used in Kaiser and colleague's study (Kaiser et al., 2013), the roan (*Hippotragus equinus*) and sable antelopes (*Hippotragus niger*), are classified as mixed feeders by the meso-wear analysis. The individuals sampled incorporated some browse in their diets, with an average mesowear score of 1.44 ± 0.21. This is particularly unexpected for the roan antelope, typically a more grazing taxon (Gagnon and Chew, 2000). Studies have shown that seasonality can significantly influence this species' diet (Havemann et al., 2016). It is thus possible that the relatively large difference between the fossil and living specimens is attributable to the fall-back foods integrated in the diets of the individuals sampled. Their teeth are also relatively hypsodont (Kaiser et al., 2013), which is more in line with what is known about the behavioral record of the members of this tribe.

Neotragins form a paraphyletic clade (Matthee and Robinson, 1999; Bibi et al., 2009), but we use this nomenclature here to refer to ecologically similar small sized antelopes that cannot be classified as Antilopini, as is typical in paleoecological literature. The specimens used here are classified as either *Raphicerus* ($n = 1$), cf. *Raphicerus* ($n = 2$) or indeterminate ($n = 4$) and no additional neotragin taxon has been identified in the Kanapoi collection in general (Geraads and Bobe, in press). Their hypsodonty index is 1.51, one of the lowest amongst Kanapoi bovids. With an average mesowear score of 1.57 ± 1.4, they are classified as attrition-influenced mixed feeders. This score was the most similar to that of neotragins from the Member I of the Kibish Formation (MSW = 1.22) (Rowan et al., 2015). Fossil Neotragini from Laetoli, Woranso-Mille, the Kibish Formation Member III and Aramis as well as the modern species (*Raphicerus campestris*, the steenbok, and *Oreotragus oreotragus*, the klipspringer) are obligate browsers (MSW< 1), as confirmed by observational studies in the wild (White et al., 2009; Kaiser, 2011; Kingdon et al., 2013b; Rowan et al., 2015; Curran and Haile-Selassie, 2016). A similar conclusion was reached about the Laetoli neotragins in a study of their isotopic signals (Kingston and Harrison, 2007). In sum, the Kanapoi neo-tragins would have grazed more frequently than any other neo-tragin included in this study, including the modern species.

Similarly, the results indicate that fossil tragelaphins display a mixed, but attrition-influenced signal, with an average of 1.4 ± 1.12. Their hypsodonty index is 1.41 and is the lowest in the assemblage. Tragelaphini are the only bovids in the Kanapoi assemblage classified as brachydont. None of the specimens used here could be identified beyond the tribe level, although *Tragelaphus* cf. *kyaloi* is currently the only tragelaphin recognized at Kanapoi (Geraads and Bobe, in press). Isotopic studies have shown the presence of a mixed, but attrition dominated diet in tragelaphins during the Plio-Pleistocene (Cerling et al., 2015). This represents a major difference from their modern counterparts. *Tragelaphus strepsiceros* (greater kudu), *Tragelaphus imberbis* (lesser kudu) and *Tragelaphus scriptus* (bushbuck) are browsers (Gagnon and Chew, 2000; Cerling et al., 2015). *Tragelaphus oryx* (common eland) typically have a more flexible diet, switching from grazing to browsing between seasons (Gagnon and Chew, 2000). But, together, the modern Tragelaphini have a browsing mesowear signal (0.6 ± 0.27). Tragelaphins are also considered browsers at most of the other fossil sites for which mesowear data are published. The two individuals studied in the Laetoli collection are a hyper browser (MSW = 0) in the Upper Laetoli Bed and an attrition-influenced mixed feeder (MSW = 1.2) in the Upper Ndolanya Beds (Kaiser, 2011). The tragelaphins from the earliest member of the Kibish Formation have an average mesowear score of 0.25, which also corresponds to a browsing signal (Rowan et al., 2015). Tragelaphins are also considered browsers at Aramis (MSW = 0.5) (White et al., 2009), Woranso-Mille (Curran and Haile-Selassie, 2016) and Makapansgat (MSW = 0.24) (Schubert, 2007).

With an average of 1.3 ± 1.4, the alcelaphin fossils from the Kanapoi collection are interpreted as having a mixed diet, which incorporates some browse. This is similar to the values seen in alcelaphins from the Laetoli succession (MSW at ULB = 0.82 and UNB = 1.84), Aramis (MSW = 1) and Woranso-Mille (White et al., 2009; Kaiser, 2011; Curran and Haile-Selassie, 2016). The values for the Kibish Formation (MSW = 3 to 3.33) and Makapansgat (MSW = 3.4) stand out as displaying a definite grazing signal in members of this tribe (Schubert, 2007; Rowan et al., 2015). At the same time, alcelaphins have one of the highest hypsodonty levels within the fossil bovid sample, a trait related to a grazing diet (HYP = 2.25). None of the Alcelaphini specimens ($n = 11$) we analyzed has been identified beyond the tribe level, despite the fact that at least four distinct species have been recognized in the Kanapoi collection: *Damalacra harrisi*, cf. *Damalborea* n. sp. and two additional ones which have not been formally attributed to a taxon (Geraads and Bobe, in press). Alcelaphini is also one of the rare tribes that show increased grazing in more modern lineages. The same relationship is also shown through isotopic analyses (Cerling et al., 2015). Although the average mesowear signal of the modern Alcelaphini species is that of a mixed-feeder (MSW = 2.07), *Connochaetes gnou* (the black wildebeest), *C. taurinus* (the blue wilde-beest), *Alcelaphus buselaphus* (the hartebeest) and *Damaliscus lunatus* (the topi) would be even more accurately described as grazers or variable grazers (Gagnon and Chew, 2000; Kingdon et al., 2013b).

And finally, fossil Bovini display a browsing signal, with a score of 1 ± 1.1, which is very close to the signal of 1.17 of the extant African buffalo (*Syncerus caffer*) (Kaiser et al., 2013). All the teeth attributed to Bovini have been identified to either *Simatherium* sp. ($n = 3$) or indeterminate ($n = 4$), as is the case for all Bovini remains recovered so far at Kanapoi (Geraads and Bobe, in press). The mesowear analysis scores can seem unexpected both for the extant and extinct specimens of this tribe. However, in their description of the original mesowear method, Fortelius and Solounias (2000) note that cusp sharpness is the variable that specifically reflects abra-sion. Mesowear studies have consistently revealed high and rounded cusps for both extant and extinct African Bovini (Fortelius and Solounias, 2000; Rivals et al., 2007; White et al., 2009; Blondel et al., 2010; Kaiser, 2011; Rowan et al., 2015; Curran and Haile-Selassie, 2016), which is also the case for Kanapoi Bovini fossils. The scores obtained reflect the downside of using the mesowear summary scoring system, which muddles the effects of abrasion and attrition. A similar pattern is observable in another Bovini, the American bison (*Bison bison*) (Rivals et al., 2007). The authors of the study acknowledge the possibility that the American fossil Bovini were integrating browse into their diet. However, Rivals and col-leagues further suggest that the low mesowear signature might also be explained by the consumption of different types of grass or to a particularly low level of abrasive particles in the food the an-imals select. A similar conclusion was reached for Bovini at Laetoli (Kaiser, 2011). In summary, Kanapoi Bovini were likely grazers and other proxies support this. Isotope analyses have classified both fossil and extant Bovini as grazers (Cerling et al., 2015). Similarly, the fossil Bovini from Kanapoi have a moderate hypsodonty index (HYP = 1.75). Furthermore, the living African buffalo is typically

classified as a "variable grazer", although studies have shown that its diet can differ significantly with geography and seasonality (Gagnon and Chew, 2000; Kingdon et al., 2013b).

Although Fortelius and Solounias (2000) have observed that high relief and round cusps are not strictly limited to browsers and thus that the Kanapoi Bovini are not necessarily browsing, more thorough investigations into the diet of Plio-Pleistocene bovins would certainly shed light on this pattern. Until then, other proxies may be more successful in predicting the tribe's diet.

Suids at Kanapoi are all brachydont. *Notochoerus jaegeri* has more hypsodont teeth (HYP = 0.95) than *Nyanzachoerus kanamensis* (HYP = 0.84), which is indicative of a more grazing diet. Isotopic analyses reveal that both fossil genera were mixed-feeders that included graze into their diets (Harris and Cerling, 2002; Cerling et al., 2015). A recent study of the microwear of the molars of both genera present similar results (Ungar et al., in press). Modern East African suids (*Potamochoerus*, *Hylochoerus*) are mostly versatile mixed feeders that integrate browse into their diets, with the exception of the grazing *Phacochoerus* (Kingdon et al., 2013b). There is currently no suid-focused mesowear method. The development of such a method could add nuance to these results but is out of the scope of this paper.

Only one Rhinocerotidae could be studied for this paper. The tooth belongs to a *Ceratotherium* (white rhinoceros) specimen. The rhinoceros has blunt and low cusps, and thus is considered an extreme grazer with its score of 4. This sample is too small to attribute patterns to the genus. The modern *Ceratotherium* is indeed a grazer (Kingdon et al., 2013a).

4. Discussion

The mesowear and hypsodonty data presented here indicate that the environments at Kanapoi were relatively grassy and dominated by ungulates with a grazing or mixed diet. This conclusion is similar to that of the study of the dental microwear in Kanapoi bovids (Ungar et al., in press). Notably, the sites closest in age and geography to Kanapoi and for which mesowear data are published — Aramis, the Upper Laetolil Beds and Woranso-Mille — show generally a more browsing diet for each bovid tribe. The bovids from Kanapoi had frequent overlaps with those of Toros-Menalla, a site with relatively open paleoenvironments including gallery forests, open grasslands and even desert conditions (Vignaud et al., 2002).

Aepycerotins were the most grazing taxon at Kanapoi, but were either browse-dominated intermediate feeders or browsers at every other site included in this study. Antilopins are systematically categorized as browsers in the African Plio-Pleistocene record, and only incorporate graze into their diets at Kanapoi, and possibly at Woranso-Mille. In both hippotragins and alcelaphins, Kanapoi bovids are at the center of the distribution. Kanapoi tragelaphins had similar diets to those of Aramis and Laetoli (UNB). Both neotragins and tragelaphins were classified as browsers at most sites except Kanapoi, where they are characterized as browse-dominated mixed-feeders. Bovini in this study are systematically classified as mixed-feeders or browsers (although, as we discussed, the signal may lead to different interpretations).

However, the mesowear results of the fossil specimens in our sample all have large standard deviations. This denotes significant within-tribe variation, which may be due to variation between the different genera or species within the tribe, as well as to individual variation. In addition, there is some discordance between the diet of living taxa as described in the behavioral literature and their mesowear score, which we attribute to the underestimation of the importance of fallback food in the diets of these animals in the behavioral literature. In addition, at least

in the case of Bovini, the mesowear summary scoring system shows limitations: it muddles the relative contributions of attrition and abrasion to the mesowear score. The two suid genera, *Notochoerus* and *Nyanzachoerus*, seem to integrate grazing in their diet.

Finally, bovids at Kanapoi are clearly dominated by taxa with a more abrasion-dominated diet than their modern counterparts. These results echo the study by Rowan and colleagues (Rowan et al., 2015) of the Kibish bovids, which suggests that modern taxa recently began integrating more browse in their diets. Our results also support Fortelius and colleagues' portrayal of West Turkana as having relatively open vegetation around 4 Ma (Fortelius et al., 2016). The results of Cerling and colleagues' stable isotope study of dietary changes in APP taxa in the Turkana Basin from 4 Ma to the present also closely mirrors our own findings (Cerling et al., 2015).

5. Conclusion

Our results corroborate previous paleoecological analyses of the Pliocene Kanapoi site using different methods. Previous studies have demonstrated the presence of Dite paleosols as well as open-adapted mammals at the site, and thus the paleoenvironments and vegetation at Kanapoi have been reconstructed as being heterogeneous, but relatively open (Wynn, 2000; Geraads et al., 2013; Ungar et al., in press). Renewed fieldwork would allow the accumulation of more fossil specimens, which would be particularly helpful to expand the sample size of Rhinocerotidae as well as to include other taxa such as Giraffidae in the analysis of dental mesowear. One major caveat of this study is that the taxonomic resolution of the data did not allow us to analyze bovids beyond the tribe level, as is recommended in the literature (Louys et al., 2015). Additional analytical methods such as postcranial ecomorphology would also help refine the results of this study.

Nevertheless, the results presented here contribute new data to our understanding of early *Australopithecus* environments. Although Pliocene environments at Kanapoi were undoubtedly complex, dental mesowear and hypsodonty in Kanapoi APP mammals indicate that the geographic distribution of early *Australopithecus* included fairly open and grassy environments. Despite this, the δ^{13}C values of the enamel of *A. anamensis* indicate that this species had a diet dominated by browse, whereas later hominins exploited a much larger range of resources, which included both C_3 and C_4 plants (Sponheimer et al., 2013). C_3 resources were undoubtedly available at Kanapoi. Dental characteristics of *A. anamensis* such as its post-canine megadontia, thick enamel, robust mandibles and dental microwear signature, demonstrate that these early australopiths likely exploited harder and more abrasive food within the C_3 spectrum (Ward et al., 2001; Macho et al., 2005; Ungar et al., in press). The realized niche of all animals, including hominins, cannot solely be explained by dietary preferences. Other factors known to influence habitat selectivity in primates include predation risk, disease, weather, the presence of appropriate shelter or sleeping sites, access to water and activity patterns as well as various topographic and vegetative factors (distance between trees, size of trees, etc.) (Barton et al., 1992; Wong et al., 2006; Rovero and Struhsaker, 2007). We can thus suggest that *A. anamensis* perhaps inhabited Kanapoi for reasons linked to other aspects of their ecology, such as locomotion. Further research on paleoenvironments at additional *A. anamensis*-bearing sites such as Allia Bay (Koobi Fora Formation, Kenya) is necessary to shed light on the breadth of environments inhabited by hominins around 4 million years ago.

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Supplementary Online Material

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