Constraining time and ecology on the Zinj paleolandscape: Microwear and mesowear analyses of the archaeofaunal remains of FLK Zinj and DS (Bed I), compared to FLK North (Bed I) and BK (Bed II) at Olduvai Gorge (Tanzania)

Manuel Domínguez-Rodrigo[a,b,c,*], Antonio Jesús Sánchez-Flores[c], Enrique Baquedano[a], Mari Carmen Arriaza[d,e], Julia Aramendi[a,c], Lucía Cobo-Sánchez[a,c], Elia Organista[a,f], Rebeca Barba[a]

[a] Institute of Evolution in Africa (IDEA), University of Alcalá de Henares, Covarrubias 36, 28010, Madrid, Spain
[b] Real Complutense College at Harvard, 26 Trowbridge Street, Cambridge, MA, 02138, USA
[c] Department of Prehistory, Complutense University, 28040, Madrid, Spain
[d] School of Geography, Archaeology and Environmental Studies, University of the Witwatersrand, Private Bag 3, 2050, Johannesburg, South Africa
[e] Center of Excellence in Paleosciences, University of the Witwatersrand, Johannesburg, South Africa
[f] Department of Archaeology and Classical Studies, Stockholm University, Wallenberglaboratoriet, SE-106 91, Stockholm, Sweden

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ABSTRACT

Defining the time that any given archaeofaunal assemblage took to be accumulated is challenging. Understanding the time variable is crucial to interpret how early sites were formed and what these sites represent in terms of hominin behavior. Two complementary dental analysis techniques (microwear and mesowear) have been used to understand dietary niches of ungulates. Microwear has also specifically been used to detect the character of occupations at archaeological sites. Here, we apply these techniques to a selection of Olduvai sites. Microwear and mesowear analyses on bovid teeth from a set of anthropogenic sites (FLK Zinj, DS, BK) and a carnivore palimpsest (FLK North) yielded different results. Microwear data from the three anthropogenic sites are similar, reflecting short, seasonal occupations, in contrast with the carnivore assemblage, which suggests a more prolonged period of deposition. The similar microwear signal in the two pene-contemporaneous sites of FLK Zinj and DS is encouraging, but caution in its interpretation is applied because of limited tooth enamel preservation and the resulting small sample size. The results shown here must be considered as a baseline for future and more extensive studies. Both microwear and mesowear analyses show that the most common bovid taxa in the Bed I sites exhibit mixed feeding signals. This reinforces the caution about interpretations of dietary niches of extinct ungulates based on their modern counterparts and emphasizes that for some taxa, the adoption of a browsing or grazing diet is context (time and locus) specific.

1. Introduction

Although interpreting agency at the earliest archaeological sites has been controversial for several decades, understanding the timing and duration of specifically anthropogenic depositional processes at these sites has been even more challenging (Domínguez-Rodrigo et al., 2007). Regardless of which side of the hunting-scavenging debate one favors, current evidence suggests that a) hominin input was marginal in the accumulation of faunas at some sites, b) anthropogenic accumulations, in contrast, exist at other sites and, c) in the latter case, all or most of the fauna accumulated was transported by hominins targeting bulk defleshing and long bone marrow exploitation of small and medium-sized carcasses (Domínguez-Rodrigo and Barba, 2007; Domínguez-Rodrigo et al., 2007; Pobiner et al., 2008; Ferraro et al., 2013; Parkinson, 2013, 2018; Domínguez-Rodrigo, 2015; Domínguez-Rodrigo and Pickering, 2017). These anthropogenic *loci* remain the source of speculation regarding how much occupation time they represent and the type of depositional processes (single continuous or multiple discontinuous) that created them. Potts (1988) initially suggested that the extensively weathered assemblages from Olduvai Bed I sites indicated that deposition occurred intermittently over a time span involving many years. Domínguez-Rodrigo et al. (2007), in contrast, argued that bone weathering at these sites was mostly chemical and not subaerial, representing diagenetic modifications that were unrelated to

depositional time spans. Most bones at the anthropogenic site of FLK Zinj unaffected by chemical weathering show no traces of subaerial weathering, indicating a relatively fast accumulation over one or two years (Bunn et al., 1986; Binford et al., 1988; Domínguez-Rodrigo et al., 2007).

Olduvai Gorge has played a prominent role in all these debates since it contains the best-preserved anthropogenic sites for the early Pleistocene. Some of these are vertically discrete concentrations of stone artifacts and fossil bones from a diversity of animals, where time-averaging can be better understood than in vertically-dispersed archaeological deposits. A thin (< 20 cm) clay stratum situated under Tuff IC in Bed I contains a diverse set of pene-contemporaneous archaeological and paleontological sites over the same paleolandscape surface: FLK NN, FLK Zinj, AMK, PTK, DS and AGS (Uribelarrea et al., 2014; Aramendi et al., 2017; Domínguez-Rodrigo and Cobo-Sánchez, 2017; Domínguez-Rodrigo et al., 2017). This is a unique opportunity for understanding Oldowan hominin behavioral variability over a diverse set of habitats situated in lacustrine-alluvial ecotones.

FLK Zinj (Bed I, Olduvai Gorge, Tanzania) is famous for being the most widely debated early Pleistocene anthropogenic site. It is the second largest window onto an early Pleistocene paleo-surface occupied by hominins after DS (David's Site), which is situated on the same 1.84 Ma paleolandscape (Domínguez-Rodrigo et al., 2017). PTK (Philip Tobias Korongo) is also situated in the same paleosurface as FLK Zinj and DS (Fig. 1). At no other early Pleistocene site is there as much taphonomic evidence as at FLK Zinj and DS (work in progress) that the bulk of the faunal accumulation was carried out by hominins (see summary in Domínguez-Rodrigo, 2015; Domínguez-Rodrigo and Pickering, 2017). Interestingly, the amounts of bones and macro-mmamal animals unearthed at FLK Zinj and DS are more abundant than those documented in many modern hunter-gatherer̕scamps (Bunn, 1983a,b; Bunn et al., 1988; Bartram et al., 1991; Lupo, 2001). This could imply more prolonged time span(s) of occupation at these sites and/or bigger group sizes. Recent modeling of the spatial dispersal of food refuse at FLK Zinj and the amount of animal food represented by the animal parts excavated at the site suggest -using ethnoarchaeological referential frameworks-that the amount of time represented by the assemblage may have been large and so may the number of potential hominins who occupied that space (Domínguez-Rodrigo et al., 2019). An estimate of a minimum of four months and between 16 and 28 individuals was produced using Yellen (1977) data on Kalahari foraging camps and updated regression formulas (Domínguez-Rodrigo et al., 2019). The time estimate was conservative, since it was based on just the preserved amount of food and not the carcass parts potentially deleted by post-depositional agents. This could imply an even longer length of occupation by hominins at the site. This would also indicate that occupations at FLK Zinj were either few and prolonged or short and multiple over a short time scale, as suggested by the taphonomic preservation of bone surfaces.

The application of the same regression formulas to the spatial analysis of PTK yielded similar estimates of occupants (average = 13; maximum = 20) and length of occupation ranging between one and five months (Cobo-Sánchez et al., 2018). Data from both sites suggest that group sizes were bigger than traditionally assumed for Oldowan hominins and that the occupation of the sites was not ephemeral. This similarity between both sites for the two types of estimates can also be applied to the similar spatial configuration of both assemblages, indicating a common behavioral pattern (Domínguez-Rodrigo and Cobo-Sánchez, 2017)

The Olduvai sites have been used to model seasonal foraging by hominins within lacustrine habitats, mostly during the dry season (Peters and Blumenschine, 1995; Blumenschine and Peters, 1998). If hominins were behaving as these models suggest, it would be expected that the occupation of sites by the paleo-lake would have been seasonal (i.e., short and possibly redundant). In contrast, if hominins were exploiting resources on the lacustrine basin all year round, it would be

expected that the occupation of the Bed I sites would have been more prolonged and multi-seasonal. Evidence against the formation of FLK Zinj and DS[1] during the dry season could be inferred from the taxonomic composition of both faunal assemblages, dominated by *Kobus, Parmularius* and *Antidorcas*, all of them potentially classifiable as local fauna. The virtual lack or underrepresentation of migratory taxa (i.e., wildebeest) argues against an intensive occupation during the dry season, unless these taxa were already migrating like they do today in the Serengeti, returning to the region during the short wet season.

Tooth enamel microwear analyses have been used to interpret diets from fossil ungulates (Solounias and Semprebon, 2002; Rivals and Deniaux, 2003; Rivals et al., 2007b; Solounias et al., 2010, 2013; Rivals and Semprebon, 2011; Uno et al., 2018). This technique has also been used to study seasonality and types of occupations by hominins during site formation (Rivals and Deniaux, 2005; Rivals et al., 2009, 2015a; 2015b; Sánchez-Hernández et al., 2014; Rodríguez-Hidalgo et al., 2016). A substantial amount of microwear research has been done via two-dimensional imaging under high or low magnification and identification and quantification of relevant enamel alteration features (namely, pits and scratches). This has been considered by some to involve a high degree of subjectivity (Scott et al., 2006). An alternative 3D method called microwear texture analysis (MTA) has been built with the intention of not involving any subjective assessment of enamel alteration features and has been applied in order to identify the diets of a wide array of faunal taxa (Scott et al., 2005; Ungar et al., 2007; Scott, 2012; Merceron et al., 2014; Williams, 2014; Souron et al., 2015; Calandra and Merceron, 2016; Ragni et al., 2017). However, the focus of MTA has been mostly on diet breadth and dietary niche reconstruction rather than on seasonality and length of occupation at anthropogenic sites. Importantly, microwear texture analyses have been applied to the artiodactyl faunas of some of the Olduvai Bed I sites, with results suggesting a prolonged year-round deposition of faunal materials at these sites (Gurtov, 2016).

Constraining the temporal framework during which site formation took place is of utmost relevance to interpret what these early Oldowan sites represent in terms of the behavior of those early humans. Rivals et al. (2015a,b), using alternative methods of microwear scoring and quantification of feature variability, elaborated a type of microwear analysis aimed at determining the duration of faunal depositional events in archaeological assemblages. We believe this approach is currently more adequate for assessing time and number of occupations in any given archaeofaunal assemblage than available techniques of MTA, since it has successfully been tested for this purpose with controlled samples.[2] This is why we will adopt this technique here for testing alternative scenarios of site formation (single or multiple occupations involving short or prolonged time spans) in the anthropogenic sites of the Zinj paleolandscape; namely at FLK Zinj and DS. Although not pertaining to the Zinj paleolandscape, comparisons will also be made with fauna from the FLK N faunal assemblage (Upper Bed I), mostly created by carnivores (Domínguez-Rodrigo et al., 2007), to contrast hominin and non-hominin agency in site formation and use. Comparisons will be also extended to BK5, which corresponds to Leakey's (1971) excavation of this upper Bed II site where a "herd" of 24 *Pelorovis* was found. This large bovid assemblage was recently interpreted as a time-averaged deposit, therefore purportedly spanning carcass deposition at different intervals during a long time span (Organista et al., 2016).

A second target in the present work is to present new dietary inferences for the taxa most widely represented in these Bed I assemblages: *Antidorcas recki, Kobus sigmoidalis,* and *Parmularius altidens.*

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[1] PTK has not been studied yet.

[2] In addition, MTA models vary depending on the confocal microscope model and lack of calibration makes this method of limited application when analogs have been derived with different microscope types (Gurtov, 2016).
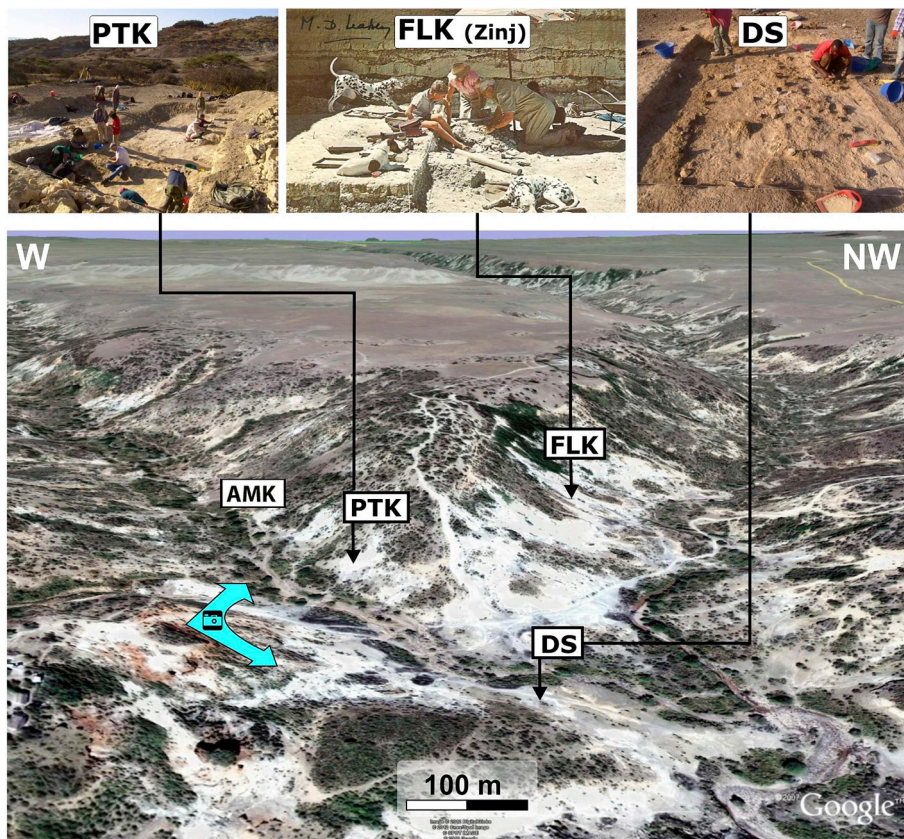
Fig. 1. Location of the sites cited in the text on the FLK Zinj paleolandscape, in relation to the modern topography of the junction between the main and the side gorges at Olduvai (by D. Uribelarrea).

Additional taxa from Bed I (e.g., *Connochaetes*) and Bed II (*Pelorovis*) *oldowayensis* were also included for comparative reasons. For this purpose, we will combine microwear and mesowear techniques. Microwear analysis uses the proportion of abrasive features (i.e., pits and scratches) to differentiate between grazing, browsing, and mixed diets on short-term temporal frameworks (Grine, 1986; Solounias and Moelleken, 1992; Solounias and Hayek, 1993; Solounias and Semprebon, 2002; Rivals and Deniaux, 2003; Rivals et al., 2007b; Solounias et al., 2010, 2013; Rivals and Semprebon, 2011; Uno et al., 2018). Mesowear analysis focuses on the attritional and abrasive wear of teeth, which is reflected on the particular topography of their occlusal surfaces (Kaiser and Solounias, 2003; Fortelius and Solounias, 2000; Franz-Odendaal and Kaiser, 2003; Clauss et al., 2007; Louys et al., 2011; Kaiser et al., 2013). The springbok (*Antidorcas marsupialis*) is the closest living relative of the prehistoric *Antidorcas recki. Antidorcas marsupialis* is mainly a browser, feeding on leaves, shrubs, and succulents. It lives in dry areas occupying grasslands, bushlands, and shrublands. Modern waterbucks (*i.e.,Kobus ellipsiprymnus*) are the closest modern phenetic relatives to Olduvai's *Kobus sigmoidalis. Kobus ellipsiprymnus* is highly dependent on water and leaves in riverine and lacustrine settings, although it feeds mainly on grasses. *Parmularius altidens* is an extinct Pleistocene alcelaphini genus/species, which has been compared to modern topi (*Damaliscus*), hartebeest (*Alcelaphus*), and hirola (*Beatragus hunteri*). These three alcelaphines are mainly grazers adapted to open habitats, but they resort to browsing substantially during the dry season. Here, we will test if these fossil taxa fed like their modern counterparts and were adapted differently to the savannah biome. This has important repercussions for our understanding of the environments where hominins lived at Olduvai Gorge and also for the timing of interaction between hominins and these ungulates.

2. Sample and methods

2.1. Microwear analysis and type of site occupation

Standard analytical approaches to the study of tooth enamel microwear were initially based on the use of only the upper and/or lower second molar for quantifying microwear features (Solounias and Moelleken, 1992, Solounias and Semprebon, 2002; Rivals and Deniaux, 2003; Semprebon et al., 2004b; Rivals and Semprebon, 2011; Rivals, 2012; Sánchez-Hernández et al., 2014). Subsequently, it has also been applied to other molars (e.g., Rivals and Deniaux, 2005; Rivals et al., 2009, 2015a; 2015b; Sánchez-Hernández et al., 2014; Rodríguez-Hidalgo et al., 2016; Rivals et al., 2015b; Xafis et al., 2017). In the present work, we followed a strict approach to microwear analysis involving the selection of one tooth per individual represented in the faunal assemblage. The reason is that we believe that microwear can be more effective when it is not biased by differential representation of dentition from multiple carcasses. Whether targeting all molars or only second molars, it is not clear that some protocols applied to date have considered not mixing more than one tooth from the same individual. This could have a negative effect on the estimated distribution of the sample. For example, a theoretical sample of 3 teeth from one individual mixed with two teeth from two different individuals deposited in different times of the year would produce biased coefficients of variation (CV), since in this example one single depositional event of a single carcass monopolizes more than 50% of the sample and yields a lower variance than when considering single teeth from each individual carcass. To test this assumption, we carried out computer modeling of different scenarios involving uneven samples of teeth of different carcasses from real examples and the resulting CVs were systematically

different from the estimates derived from single tooth per carcass samples. Fortunately, the use of second molars (especially in those cases when only either upper or lower molars were used) reduces drastically the effect of this bias, because each carcass has only one pair of upper and lower second molar teeth. Given that we intended to measure microwear feature variation according to depositional moment, we reinforced the protocol of ensuring that only one tooth per carcass was represented in the analytical sample. For this purpose, MNI estimates comparing all teeth simultaneously preceded the selection of dentition for analysis. This protocol was also used by Gurtov (2016). Here, only one molar tooth from each adult individual identified was used for analysis from the FLK Zinj, FLK North 1–2, and BK5 collections. At DS, we also used the deciduous lower premolar of two late juvenile individuals, which showed much better enamel preservation than their molars.

The occlusal surface of each specimen was cleaned with acetone and 96% ethanol and then molded using a high-resolution polyvinylsiloxane silicone (Provil Novo Light C.D.; Heraeus Kulzer) within a support made of Provil Novo Putty. Casts were then made from these molds using a high-resolution transparent epoxy resin (Camarós et al., 2016). Casts were analyzed with a stereomicroscope (Optika SMZ-1) at $35\times$ magnification using transmitted light on the transparent refractive characteristics of the cast, which enabled the detection of the micro-features of the enamel's surface.

Micro-taphonomic assessment of the enamel surface was carried out prior to feature counting to determine the impact of diagenetic processes affecting feature preservation. In the Olduvai assemblages, diagenesis has seriously affected a large part of the tooth surfaces and chemical weathering was widely documented on the enamel of a large part of the sample. The depositional environment of the Olduvai archaeofaunas occurred on the lacustrine alluvial floodplain where humidity was important due to a high water table and the surface being frequently flooded. This resulted in a large amount of biochemical modifications on bone surfaces, caused mainly by plant-associated fungi and bacteria (Domínguez-Rodrigo et al., 2007). This was especially noticeable on tooth enamel. A large part of the dental sample used for the present study was strongly affected by microscopic biochemical etching caused by acid-producing micro-organisms (namely, colonies of bacteria) (Fig. 2). Chemical modifications caused by pH properties of the soil may also have impacted the faunal remains (Fernández-Jalvo et al., 2002; Fernandez-Jalvo and Andrews, 2016). The poor preservation of the enamel made us reject a large part of the original dental sample. Due to the impact of this taphonomic alteration, areas of enamel containing pits and scratches unaffected by these taphonomic processes were screened not only on the same enamel spot

for each tooth, but all along the medial and distal infoldings. This high impact of taphonomic damage on tooth enamel had previously been documented in primate dentition (Teaford, 2007). Only about half of the Olduvai primate dentitions can be used for microwear analysis (Teaford, 2007). It is no surprise that the narrowed enamel bands of bovid dentitions are more severely affected by diagenetic processes.

The initial Olduvai tooth sample consisted of 99 molded teeth from 77 individuals. After careful screening of the enamel surface, the analytical sample was reduced to teeth from 4 *Antidorcas* and 3 *Kobus* from FLK Zinj, 4 *Parmularius* from FLK N, 5 *Pelorovis* from BK5, and 3 *Parmularius* from DS (Table 1). The other individuals and bovid taxa represented at the archaeofaunal assemblages of these sites by second molars show strong taphonomic alterations and were discarded from the analysis. Given that most of the sample involved lower second molars, as was originally suggested for the method (upper and/or lower M2) (Solounias and Semprebon, 2002; Rivals and Deniaux, 2003; Rivals and Semprebon, 2011), it is advisable in the future to extend the analysis to other teeth of the dental series in all the discarded individuals looking for well-preserved areas of enamel. Xafis et al. (2017) reported that the microwear signal is not significantly different from P4 to M3 (both upper and lower), but not in P2 and P3.

Enamel features (namely, pits and scratches) were quantified in a square area of $0.16\ mm^2$ using a gridded reticule. Scratches were analyzed following Rivals et al. (2009, 2015a,b) method, which involves the combined use of CV and standard deviation (SD). A single observer made the count to avoid inter-observer errors. Feature counting included at least two different areas on the same grid and results were averaged for each specimen. When plotted on a graph that includes a modified heat map that displays the error bands, this bivariate combination shows three major areas (Fig. 3). Area A (low CV and SD) indicates one single short-term occupation or several repeated occupations during the same time of the year (one season or a shorter event). Area B (moderate CV and SD) shows a long continued event spanning more than one season (i.e., several months). Area C (high CV and SD) would result from two separate short events in different times of the same year or different times of different years (Rivals et al., 2015a,b). The graph of the ratio of pits to scratches was based on the open access code created by Rivals (2019).

The samples used here are, obviously, insufficient to detect the true CV and dispersal values (i.e., SD) of the bigger population that they represent. Therefore, inferences made from microwear analyses of this few individuals can only be interpreted as preliminary awaiting larger samples. To nuance data spread more realistically in this small sample, a joint bootstrapped function of CV and SD was programmed in R (n = 500, with replacement), which is inspired by bootstrapping and
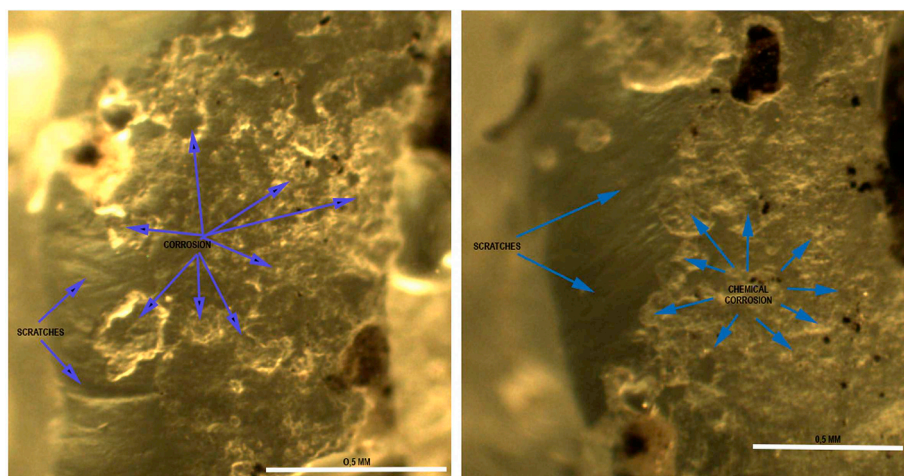

Fig. 2. Taphonomic modifications of the enamel overprinting the microwear features, namely scratches, caused by chemical etching on two specimens of *Kobus sigmoidalis* from DS and FLK Zinj.

Table 1
Microwear summary data for the Olduvai samples.

Taxa	Site	Level	Microwear													
			N	Average number of pits	Average number of scratches	%F	%C	%H	%X	%S	%L	%G	SWS	0–17% Scratch Index	Boot SD Scratches	Boot CV Scratches
Pelorovis oldowayensis	BK	5	5	13,4	17	100	100	0	20	100	0	20	0.4	60	2.41	0.14
Parmularius altidens	FLK N	L1-3	4	10	16.87	100	100	0	0	100	25	0	0.37	50	3.5	0.21
Parmularius altidens	DS	22B	3	7.62	11.75	100	100	33.3	0	100	0	33.3	0.25	100	2.32	0.17
Antidorcas recki	FLK	22	4	15.87	16.62	100	100	0	0	100	0	25	0	50	5.3	0.32
Kobus sigmoidalis	FLK	22	3	9.5	13.16	100	100	0	0	100	100	0	0.83	33.3	3.01	0.15

Abbreviations. %F: percentage of specimens with presence of fine scratches. C: percentage of specimens with presence of coarse scratches. H: percentage of specimens with presence of hypercoarse scratches. X: percentage of specimens with presence of more than 4 crossed scratches per counting area. S: percentage of specimens with presence of small pits. L: percentage of specimens with presence of more than 4 large pits per counting area. G: percentage of specimens with presence of gouges. SWS: Scratches Width Score, ranging from 0 (fine scratches only) to 2 (coarse scratches only). Boot SD/CV: Bootstrapped SD and CV. (Solounias and Semprebon, 2002; Semprebon et al., 2004).
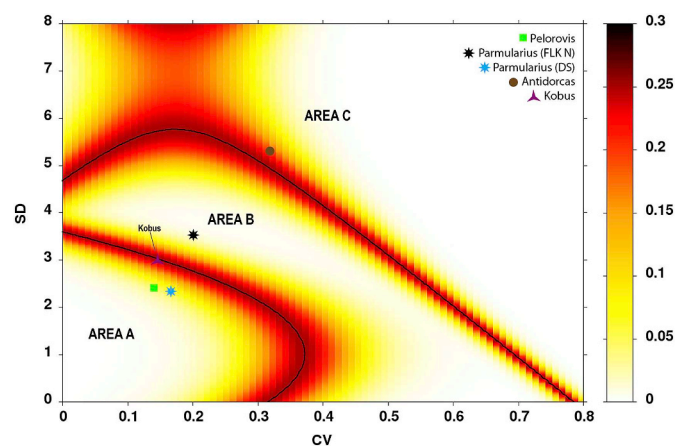

Fig. 3. Bivariate heat map showing the distribution of standard deviation (SD) and coefficient of variation (CV) of the scratches on the dental samples from the Olduvai sites. *Antidorcas* and *Kobus* are from FLK Zinj; *Pelorovis* from BK and *Parmularius* from DS and FLK North.

maximum likelihood techniques applied on triangle mortality graphs on similarly small samples (Bunn and Pickering, 2010; Weaver et al., 2011; Bunn and Gurtov, 2014) (See code in Supplementary information).

2.2. Mesowear analysis and dietary niche

First introduced by Fortelius and Solounias (2000), dental mesowear analyzes the degree of dental abrasion and attrition in ungulates, which is a reflection of their long-term diet. Dental mesowear is analysed by assessing the sharpness and relief of molar cusps. Attrition is the contact between tooth against tooth, which creates more sharpened cusps, and it is more characteristic of browsers. On the other hand, abrasion is the contact between food against tooth, and is associated with the siliceous content in grasses. Abrasion creates more blunted and rounded cusps and, consequently, it is more common in grazers (Fortelius and Solounias, 2000).

Dental mesowear analysis was applied to the buccal side of upper second molars and to the lingual side of lower second molars (Table 2). When second molars were not available for each individual analyzed, mesowear scoring was also applied to either the upper or lower first and third molars of each individual analyzed. Unworn or barely worn teeth, or those broken teeth unsuitable for dental mesowear analysis were discarded (Rivals et al., 2007a). In addition, the MNI has also been taken into account, which means that one single individual is represented by only one tooth.

Following Mihlbachler et al. (2011), teeth were classified into seven dental mesowear categories (0–6), ranging from sharp shape and high

Table 2
Mesowear summary data for the Olduvai samples.

Taxa	Site	Level	Microwear		
			N	MWS	SD
Pelorovis oldowayensis	BK	5	8	3.33	0.81
Parmularius altidens	FLK	22	5	3.5	1.22
Parmularius altidens	FLK N	L1-3	5	4	1.41
Antidorcas recki	FLK	22	6	4.80	0.47
Antidorcas recki	DS	22B	3	2.66	2.08
Kobus sigmoidalis	FLK	22	5	2.64	0.49
Kobus sigmoidalis	FLK N	L2	3	2.66	0.57
Kobus sigmoidalis	FLK N	L3	2	4	0
Kobus sigmoidalis	DS	22B	5	2	0
Connochaetes sp.	FLK	22	2	4.25	0.35
M. kattwinkeli	DS	22B	2	3.5	0.70

cusps (0) to blunt and completely flat cusps (6). Mesowear scores of single individuals from the same species were then averaged to obtain the species' mesowear score (MWS). To minimise inter-observer error, dental mesowear analysis was performed by a single, experienced researcher (AJSF), as Loffredo and DeSantis (2014) recommend. The resulting mesowear scores were compared with a large sample of modern ungulates whose diet was well-known.

The Olduvai microwear sample included 99 teeth from as many as 77 individuals, but most were discarded because of preservation issues and only 20 teeth could be analyzed. The Olduvai mesowear sample included 55 teeth from 43 individuals (Table 2). These were from FLK Zinj, FLK N, FLK NN, DS (Bed I) and BK (Bed II).

3. Results

3.1. Microwear analysis and duration of site occupation

Data on the microwear features of the selected Olduvai sample are shown in Table 1. The FLK Zinj *Antidorcas* microwear scratch pattern with high CV and SD occurs within the error zone of Area C, suggesting a probable redundant deposition in different times of the year. The FLK Zinj *Kobus* sample falls within the error zone of area A, indicating a potential (but insecure) single depositional moment, spanning no more than one season. Alternatively, it could represent several visits at the same time of the year (single-season) over consecutive years; however, the virtual lack of subaerial weathering on bones does not support this interpretation. The DS *Parmularius* sample falls within zone A clearly suggesting a single (probably seasonal at maximum) depositional process or a single-season reoccupation. This is exactly the same as is indicated by the BK *Pelorovis* data. In contrast, the FLK North carnivore-accumulated *Parmularius* sample occurs well within zone B, indicating
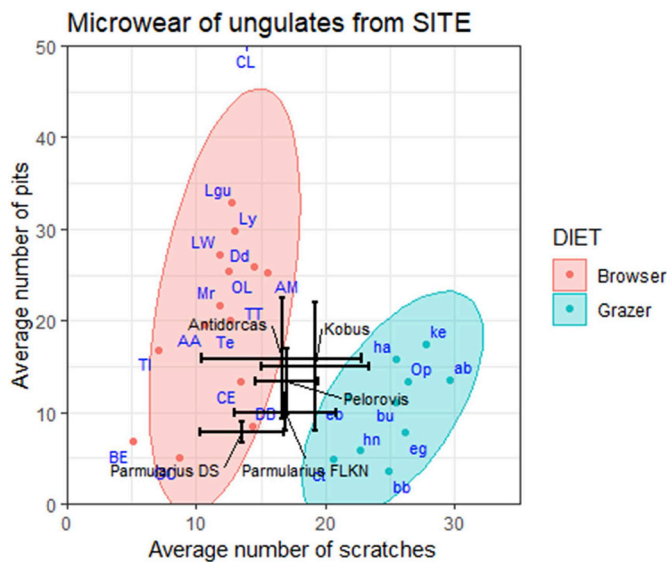
Fig. 4. Bivariate graph displaying the confidence interval of microwear features (average numbers of pit and scratches) in modern browsing and grazing taxa. The Olduvai taxa analyzed (*Kobus, Parmularius, Antidorcas, Pelorovis)* are also shown with their confidence intervals. Abbreviations: Leaf-browsers—AA, *Alces alces*; AM, *Antilocapra americana*; BE, Boocercus euryceros; CL, *Camelus dromedarius*; DB, *Diceros bicornis*; GC, *Giraffa camelopardalis*; LW, *Litocranius walleri*; OJ, Okapia johnstoni; TT, *Tragelaphus strepsiceros*. Grazers—ab, *Alcelaphus buselaphus*; bb, *Bison bison*; ct, Connochaetes taurinus; eb, *Equus burchelli*; eg, Equus grevyi; hn, *Hippotragus niger*; ke, Kobus ellipsiprymnus. Mixed-feeders—Ax, *Axis axis*; Bt, Budorcas taxicolor; Ca, Capricornis sumatraensis; Cc, *Cervus canadensis*; Cd, *Cervus duvauceli*; Ci, *Capra ibex*; Cu, *Cervus unicolor*; Gg, *Gazella granti*; Gt, Gazella thomsoni; Lg, *Lama glama*; Oc, *Ovis canadensis*; Om, *Ovibos moschatus*; Ti, Tragelaphus imberbis; To, Taurotragus oryx; Tq, Tetracercus quadricornis; Tr, *Boselaphus tragocamelus*; Ts, *Tragelaphus scriptus*; Lv, Lama vicugna.

that carnivores at that locality were occupying the area continuously for long intervals spanning several seasons (Fig. 3).

3.2. Microwear analysis and diet

It is interesting to note that all the taxa analyzed for microwear patterns cluster in the intermediate zone between browsers and grazers (Fig. 4). The average number of pits and scratches is similarly low for *Parmularius* from DS and FLK N, and slightly higher for *Pelorovis* and *Antidorcas*. *Pelorovis*, thus, shows a diet substantially different from modern buffalo, which is mainly a grazer. *Kobus* is also substantially different from its modern counterpart. Modern waterbucks are grazers and their microwear place them within the grazing spectrum (Fig. 4). *Kobus sigmoidalis*, in contrast, shows a mixed feeding pattern, between grazing and browsing. Whether this is a temporary shift of diet or a permanent dietary niche can only be approached via mesowear and isotopic analyses. *Parmularius* at DS shows a browsing signal, suggesting a variable diet according to season, like modern topis. The mixed diet signals of all these taxa, whose modern counterparts are largely grazing, would suggest a different adaptation to a mosaic environment where bush and arboreal vegetation must have been more prominent.

3.3. Mesowear analysis and dietary niche

Table 2 shows the data for mesowear scoring of the taxa analyzed. Unsurprisingly, alcelaphini taxa like *Connochaetes* and *Megalotragus* show a clear grazing adaptation, with high mesowear scores (Fig. 5). The extinct alcelaphine *Parmularius* was also a grazer. *Pelorovis* also shows a clear grazing dietary niche. The *Antidorcas* specimens from FLK Zinj also display high mesowear scores, but their interpretation must be
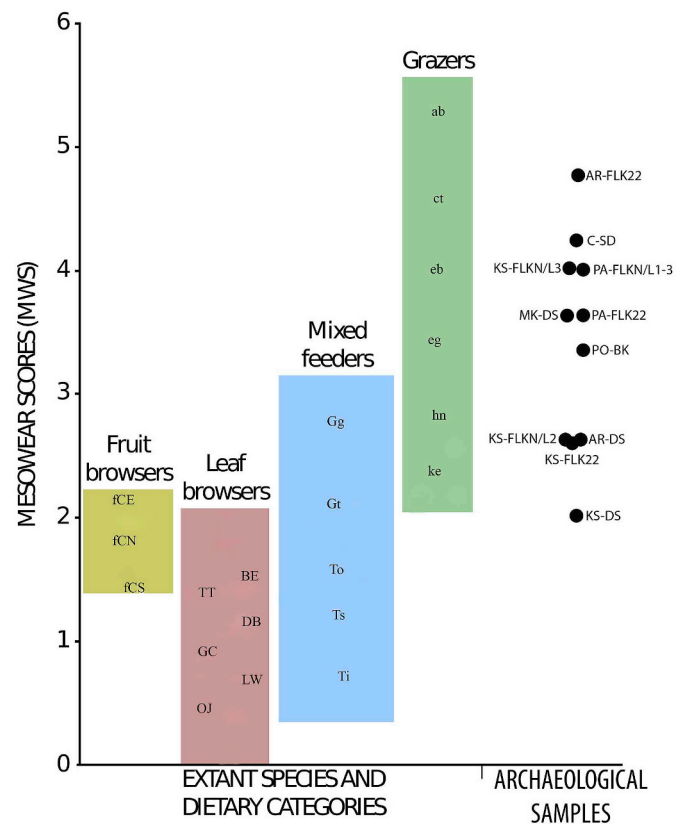

Fig. 5. Bar chart displaying mesowear scores for modern herbivores and the Olduvai selected taxa. For Olduvai: KS, *Kobus sigmoidalis*; AR, *Antidorcas recki*; PO, *Pelorovis oldowayensis*; PA, *Parmularius altidens*; C, *Connochaetes*. For modern herbivores: Leaf-browsers—CL, *Camelus dromedarius*; DB, *Diceros bicornis*; GC, *Giraffa camelopardalis*; LW, *Litocranius walleri*; OJ, Okapia johnstoni; TT, *Tragelaphus strepsiceros*. Fruit-Browsers—fCD, Cephalophus dorsalis; fCN, Cephalophus natalensis; fCS, Cephalophus silvicultor; Grazers—ab, *Alcelaphus buselaphus*; ct, Connochaetes taurinus; eb, *Equus burchelli*; eg, Equus grevyi; hn, *Hippotragus niger*; ke, Kobus ellipsiprymnus. Mixed-feeders—Gg, *Gazella granti*; Gt, Gazella thomsoni; Ti, Tragelaphus imberbis; To, Taurotragus oryx; Ts, *Tragelaphus scriptus*; Lv, Lama vicugna.

made with caution because these specimens are very old individuals who have worn out most of the crown. A similar caution should be applied to the old FLK N specimens of *Kobus*. Rivals et al. (2007) show that the ontogenetic trajectory of ungulates impact their mesowear profiles; for this reason, both very young and, especially, very old individuals do not represent the main dietary niche of the species. If focusing only on the adult non-senile individuals, all *Kobus* from FLK Zinj, FLK N, and DS cluster in the same area (Fig. 5) of low-intermediate mesowear scores (between 2 and 3), which is where mixed feeders occur. The same applies to DS non-senile *Antidorcas*.

These mesowear data indicate that the mixed feeder signal from the microwear analysis for *Pelorovis* and *Parmularius* must be a seasonal short-term shift in their diets. However, for *Antidorcas* and, especially, for *Kobus,* the microwear signal combined with their mesowear scores would suggest mixed feeding as their dietary niches.

4. Discussion

4.1. Microwear analysis and type of site occupation

MTA studies have had very limited success in determining season of death and even differentiating generalist diets from mixed diets among ungulates (Scott, 2012). MTA also has not built a proper referential analogical framework to interpret length of occupation and seasonality

efficiently. For this reason, Gurtov (2016) argued that such an analogical framework was necessary and she elaborated one using impala (*Aepyceros melampus*) from Lake Eyasi (Tanzania) as a proxy to assess potential seasonality at Olduvai sites using *Antidorcas* fossils. In her actualistic analysis, Gurtov (2016) found out that all the variables involved in MTA produced non-significant differences when comparing wet and dry seasons. She observed, though, that one of these variables (Heterogeneity Area scale fractal complexity, HAsfc) was closer to being significant than the other variables and used it to classify her sample into wet and dry season of death with mild success, since only 56% of the wet-season sample and 68% of the dry-season sample could be correctly identified. However, the probability of classifying each case correctly in most cases is lower than 80-70%. Thus, both the accuracy and probability of accurate classification are low. The reliability of this classification is also questionable for two methodological reasons. One is that there are methodological problems in the use of confocal microscopy because the enamel surface "was narrow and rounded … making confocal microscopy challenging" (Gurtov, 2016: 102). Similar problems were observed while capturing bone surface modifications on curved surfaces with the same technology (Pante et al., 2017). Subsequent remodeling of the spatial data also distorts the original properties of the surface (see critique in Courtenay et al., 2018). The other problem in Gurtov (2016) analysis is that comparisons between samples from both seasons were made using Satterthwaite (i.e., Welch) t-tests. The Welch *t*-test is a modification of the standard Student t-test to produce more reliable results when comparing samples that differ in size and variance. However, both types of t-tests require normality in the samples used for comparison. Normality was not tested in Gurtov's sample and a simple look at the values of the variable HAsfc shows that about four outliers give the wet season sample a skewed distribution. These outliers have also potentially distorted the rate of correct classification obtained via logistic regression (which is already low) by artificially increasing it. If removed, the remaining wet and dry season samples look completely identical (Gurtov, 2016: 106).

If the MTA is unable to provide statistically valid differences between carcasses that died in wet and dry seasons in Africa, the validity of the application of the method to the fossil record in that continent is more than questionable. Hence, it is not surprising that no difference was detected when comparing the dental sample of *Antidorcas recki* and *Parmularius altidens* of two different types of sites: FLK Zinj (anthropogenic) and FLK North (accumulated by carnivores). In both cases, t-tests yielded no significant differences. Given that no significant differences were found between dry- and wet season modern impalas using the same approach, the lack of difference between the fossil samples does not imply that both were accumulated all year round, as suggested by Gurtov (2016). They could have been deposited in different seasons and remain statistically similar, as in the case of the modern impalas. Alternatively, this apparent similarity could be a methodological artefact. T-tests (like most statistical tests) are highly conservative in their p-values when samples are small. Overlapping small samples (which may be different in their central values) tend to produce statistically non-significant values. Gurtov (2016) compared 5 *A. recki* and 3 *P. altidens* from FLK Zinj to 14 *Antidorcas recki* and 11 *Parmularius altidens* from FLK North. These are very small samples for any significance test.

An additional factor is that although Gurtov (2016) noticed some problems with her casts, she probably overlooked that a substantial part of the fossil sample was seriously impacted by micro-taphonomic processes. Our scrutiny of the enamel surfaces was strict and when micro-taphonomic alterations (mostly diagenetic) were found on the enamel, which would make the assessment of the original enamel features ambiguous regardless of the facet inspected, the affected specimen was discarded. We argue that part of the reason explaining the results obtained by Gurtov may be that she analyzed specimens that had micro-taphonomic chemical modifications together with specimens that were well preserved and unaffected by diagenesis. This would make her

sample highly heterogeneous and, hence, the resulting "Heterogeneity of Area Scale Fractal Complexity" being similar in both fossil samples. For example, Gurtov (2016) analyzed 3 *Parmularius* from FLK Zinj and 11 from FLK North whereas we observed that all *Parmularius* from FLK Zinj were diagenetically affected and we only analyzed 4 taphonomically-unmodified *Parmularius* from FLK North. Likewise, Gurtov (2016) analyzed 14 *Antidorcas* from FLK North, whereas we were unable to document a meaningful sample of *Antidorcas* from that site whose enamel was not diagenetically modified.

The present work has used a small fossil sample for microwear analysis limited by the well-preserved specimens. Although the size of the *Antidorcas*, *Kobus,* and *Parmularius* samples that we used are too small to be of any statistical significance, if we assume that they randomly represent the original archaeofaunal population, they indicate a similar pattern at the anthropogenic assemblages analyzed. *Parmularius* at DS, as well as *Kobus* at FLK Zinj and *Pelorovis* at BK, indicate a single short-term occupation or several short-term occupations during the same season. This latter result is surprising because, based on taphonomic analysis, the BK5 faunal assemblage was interpreted as time-averaged and corresponding to a long depositional period involving different times of the year (Organista et al., 2016). The microwear data would preliminarily support, in contrast, the original idea of Leakey (1971) that a Pelorovis "herd" was deposited either in one depositional event or spread over a single or redundant (during the exact same seasonal moment) occupational process. The only datum differing from the interpretation of a single short-term occupation for these sites is the *Antidorcas* sample from FLK Zinj. It clusters in area 3 (Fig. 2), suggesting a repeated dual short-term occupation, probably in different discontinuous seasons or different discontinuous times of the year. However, it should be emphasized that even when describing these sites as "anthropogenic" (because of the predominant anthropic agency detected by taphonomic analysis), all these sites are common-amenity *loci* as originally described by Isaac (1983). At FLK Zinj, specifically, the mismatch between the taxa identified by dental remains and by the postcrania suggest that background scatters (probably caused by non-anthropogenic agencies) are a part of the assemblage. Initially almost 50 different individuals were identified using mostly dental specimens (Bunn et al., 1986); however, only 21 bovid carcasses are represented by long bone postcrania (Domínguez-Rodrigo et al., 2007). In addition, as remarked by (Parkinson, 2013; Parkinson et al., 2015), felid damage exists on a couple of *Antidorcas* bone specimens from FLK Zinj. This is documented on a minimum of one springbok carcass that only bears damage by felids and that hominins did not exploit since the long bone impacted by felid agency was not green-broken and demarrowed. This has been argued to constitute a proof that felids (probably a leopard) transported and consumed that *Antidorcas* carcass independently from the use of other carcass remains by hominins at the site. This would confirm the common-amenity scenario described above. If hominins and medium-sized felids accumulated *Antidorcas* remains at FLK Zinj independently, that would probably indicate different times of site use to avoid overlap. This could explain the high CV-SD values for this taxon if the sample analyzed included carcasses accumulated by both agents. In such a case, the double short-term occupation pattern cautiously inferred from the data would be a taphonomic artefact. The documented pattern could be obtained if hominins had deposited *Antidorcas* remains over one single short-term event and felids would have done the same at a different moment. The double short-term occupations of *Antidorcas* at FLK Zinj probably do not correspond to the same season or time of the year because, otherwise, abrasive patterns on the enamel would have been similar and with lower SD and CV values than reported for the FLK Zinj fossils analyzed (Rivals and Solounias, 2007; Rivals et al., 2009). If they had occurred in two separate events regardless of the season, they could have taken place within the same year or over two consecutive years, in agreement with the subaerial weathering stages reported for the site (Bunn et al., 1986; 1988; Domínguez-Rodrigo et al., 2007). We admit, however, that these

interpretations are highly speculative given the small original sample size.

In contrast with the samples from the anthropogenic sites, the *Parmularius* data from FLK N indicate a long-term, probably continuous, depositional time involving several seasons. This suggests that behavioral dynamics behind site formation at FLK Zinj, DS, and FLK N differed, probably because the main accumulating agents (hominins and carnivores) were different in the intensity of occupation of these sites. Regardless of when and how many re-occupations are involved in the formation of the site, the FLK Zinj archaeofauna indicates a total use of the *locus* involving several months (Domínguez-Rodrigo et al., 2019). Therefore, when we refer to two short-term occupations, we do not imply just a few days or weeks.

If these preliminary results would be valid, they would indicate that a) hominins were not restricted in their use of the site space to just brief sporadic (i.e., hours or just few days) occupations, b) hominins were near the lacustrine basin on a seasonal basis (if admitting the felid input in the deposition of *Antidorcas* remains at FLK Zinj) or non-seasonally (if the *Antidorcas* sample was accumulated exclusively by hominins), and c) this would suggest that hominins might have been active in the lacustrine basin in a similar fashion to carnivores that seasonally occupy lacustrine wooded environments when water resources in open plains dry out. It could be argued that this would enable hominins to scavenge medium-sized carcasses from felids like lions, which occupy these habitats during (mostly at the end of) the dry season (Blumenschine, 1986; Domínguez-Rodrigo, 2001; Schaller, 1972). Several arguments contradict this speculation. First, landscape taphonomy of the Zinj paleolandscape has failed to find any compelling evidence of intense carnivore activity (and, hence, carcass productivity) on the different lacustrine habitats sampled during the formation of the FLK Zinj paleolandscape (Domínguez-Rodrigo et al., 2010; Uribelarrea et al., 2014). Secondly, ethological studies show that if medium-sized carcasses had been obtained from a large predator like the lion, these should match lions' preferences in terms of taxonomic range of their preferred prey. Multiple studies show that when lions occupy lacustrine wooded habitats, they follow their preferred prey, which usually is composed of open plain taxa, mostly zebra, wildebeest, and warthogs (Scheel, 1993). Lions do not prey on local closed-vegetation fauna only because they may potentially have higher encounter rates (Hayward et al., 2011). Lions increase encounter rates with their preferred prey by foraging more intensively in the habitats where this preferred prey lives. This explains why in ecosystems from African national parks, lions do not hunt prey according to their density or encounter rate, but by actively foraging in the habitats where their preferred prey is most active (Lamprey, 1964; Foster and Kearney, 1967; Foster and Coe, 1968; Sinclair, 1972; Kahurananga, 1981; Kahurananga and Silkiluwasha, 1997; Schaller, 1972; Hayward et al., 2011; Laizer et al., 2014; Eustace and Tarimo, 2018). For example, at Tarangire National Park (Tanzania), with a large population of waterbucks residing in the alluvial habitats that follow the Tarangire river, lions focus on zebra, wildebeest, and, to a lesser extent, buffaloes. That is, lion prides follow the game from the open plain Simanjiro ecosystem to the Tarangire river during the dry season (Lamprey, 1963, 1964) and most carcasses deposited in the alluvial Tarangire habitats are those of taxa from this allochthonous ecosystem, despite the high density of local fauna like waterbucks (Gidna et al., 2014). This has also been documented in the Serengeti, where most carcasses deposited in alluvial habitats by lion predation also correspond to open-habitat taxa (Blumenschine, 1986). This does not contradict that lions hunt waterbucks whenever conditions propitiate it (Hayward and Kerley, 2005); however, there appears to be a systematic pattern of prey preference by lions based on a significantly higher targeting of zebras, wildebeest and warthogs regardless of lion pride size (Scheel, 1993). Extraordinarily high rates of waterbuck hunting by lions in certain alluvial areas of Kruger National Park, such as that reported by (Pienaar, 1969), are an artefact of method, since they were derived from sampling just the portion of

alluvial landscape following the river, instead of all the surrounding habitats where lion predation was more intense and focused on different taxa.

Waterbucks are the most frequently processed medium-sized carcasses at FLK Zinj and DS. Wildebeests are similarly-sized ungulates from open habitats potentially preyed by lions. The presence of wildebeests in the Zinj paleolandscape and sites therein is rather marginal, suggesting that lions did not follow them to that part of the lacustrine ecosystem. *Parmularius*, as a more eclectic taxon, could also have been targeted by lions or another medium-to large-sized felid. However, the microwear signature from FLK North initially suggests that a local predator with different seasonal habits from lions (i.e., leopard-like) might have been responsible for accumulating the carcasses of this taxon at the site. That means that if hominins were acquiring *Parmularius* opportunistically from a similar locus as FLK North, they could have done so all year round. The microwear data from DS suggest they did not follow this strategy. Felid modifications on carcasses accumulated on the FLK Zinj paleo-landscape can be found at FLK NN1 (Domínguez-Rodrigo et al., 2007). They can also be documented across the stratigraphic series of Bed I; however, they are only exceptionally documented in one carcass at FLK Zinj. This taphonomic contrast would suggest lions (or felids in general) were not a source of the bulk of carcasses consumed by hominins at sites.

Unfortunately, all the interpretations from the microwear of the selected Bed I sites are rather speculative, because they rest on very small sample sizes, like those reported from microwear analysis of *Antidorcas* and *Equus* of other Olduvai sites (Rivals et al., 2018). However, the data derived from these samples may be taken as preliminary and, thus, as a null hypothesis to be tested with future extended studies.

4.2. Mesowear analysis and dietary niche

Fortelius and Solounias (2000) dataset based on the mesowear analysis of the upper M^2 was the first referential framework for dietary reconstruction of African ungulates. This dataset was expanded for modern African antilope species by Louys et al. (2011). In both studies, *Kobus ellipsiprymnus* was classified as a grazer and *A. marsupialis* as a mixed feeder. *Kobus sigmoidalis* was initially described as a grazer like its modern counterpart *Kobus ellipsiprymnus* (Gentry and Gentry, 1978; Gentry, 1985). This was further supported by Blumenschine et al. (2003) through isotopic analyses, which showed that this ungulate fits an obligate grazing C_4 diet. However (Spencer, 1997), showed that although the dentition of *Kobus sigmoidalis* and *Kobus ellipsiprymnus* is similar, these taxa differ significantly in the first two PCA components of cranial morphology, which implies some important dietary/adaptive differences between both sister taxa. These differences notwithstanding, both taxa share an adaptation to humid habitats. *Kobus ellipsiprymnus* is highly dependent on water and resides locally close to water sources. *Kobus sigmoidalis* must also have been very dependent on water not only because it is the most common bovid taxon found at the Olduvai junction sites during Bed I (at the confluence of the lake and the fluvial inputs), but more specifically, because its lower limb anatomy differed from *Kobus ellipsiprymnus* by being more elongated. The proportion of metapodials was longer compared to upper and intermediate long bones, being most similar to that of modern lechwe (*Kobus leche*) (Gentry and Gentry, 1978). The lechwe lives in marshy areas feeding on aquatic plants and use knee-deep water as protection against predators. Gentry and Gentry (1978) argued that such an elongation of the lower limb probably was an adaptation to lacustrine/palustrine watered environments, making this taxon more water-dependent than its modern relative. This different appendicular and cranial morphology of both taxa probably reflects different adaptation to the environment. In our microwear study of *Kobus sigmoidalis*, we detected a clear indication of a mixed browsing/grazing diet. The mesowear signal, more indicative of a long-term dietary niche, also suggests

that *Kobus sigmoidalis* was essentially a mixed feeder.

Plummer and Bishop's (1994) ecomorphological analysis of *Antidorcas recki* indicates that this antilope must have been adapted to an intermediate woodland-bushland habitat. Plummer et al. (2009) provide isotopic evidence that *Antidorcas recki* at Olduvai Bed I, Sterkfontein Member 4 and Kanjera had a mixed browsing and grazing diet, which indicates that its diet was not dominated by C_4 grasses (contra Blumenschine et al., 2003). This fits well with our characterization of *Antidorcas recki* as a mixed feeder using both microwear and mesowear data.

Parmularius altidens from Kanjera has been interpreted as a grazer according to its isotopic delta13C signature (Plummer et al., 2009). In our mesowear study, we support this interpretation. However, the microwear analysis showed that *Parmularius* was a mixed feeder, probably because we were sampling individuals from FLK N deposited over a long time span (Rival's SDCV region B). The uncertainty on the moment of deposition of each of these individuals probably resulted in a palimpsest of abrasive features accounting for such a mixed diet if *Parmularius* fed similarly to its modern counterparts (topi, hartebeest, and hirola) which graze during the wet season and browse more during the dry season.

The bovid fauna from the Olduvai Bed I junction sites is dominated by *Kobus* and *Antidorcas*. Given their browsing and mixed dietary niches, their abundance would imply a fairly wooded ecosystem during the formation of the Zinj paleolandscape. The virtual absence or underrepresentation of obligate bovid grazers from this landscape would further support this interpretation, which is also in agreement with the ecomorphological data of these browsing taxa (Plummer and Bishop, 1994). This wooded vegetation is well represented in the phytolith record of the Zinj paleolandscape (Arráiz et al., 2017). The presence of grasslands in the surrounding habitats is also attested by the presence of *Parmularius* and, to a much lesser extent, *Connochaetes* and *Equus*. *Kolpochoerus heseloni* is overwhelmingly the most common suid in the Zinj paleolandscape. Its ecomorphological analysis indicates adaptation to an intermediate/closed environment (from forest to bushland). The more negative δ13C values of the Olduvai specimens compared to those of Koobi Fora indicate a more reduced C_4 grass diet (Bishop et al., 2006), further supporting adaptation to a wooded lacustrine habitat.

5. Conclusions

Hominins responsible for the anthropogenic sites of FLK Zinj and DS were not determined by vegetation in their selection of *loci* to process animal carcasses and make stone artifacts in the lacustrine ecosystem. Most of the fauna that they exploited was local and probably underwent very little transportation. This is supported by an analysis of skeletal abundances of elements most likely to resist attritional processes (i.e., high-survival skeletal set) (Marean and Cleghorn, 2003; Cleghorn and Marean, 2004; Cleghorn et al., 2007), which shows relatively low carcass transport costs, reflecting short-distance transportation of carcasses accumulated in the Bed I sites (Faith et al., 2009). Hominins at FLK Zinj and DS seem to have foraged for animal food more intensively within the wooded habitats of the lacustrine basin, in contrast with carnivores at FLK N higher in the sequence, which seem to have been more actively hunting in the woodland/open grassland ecotones, as shown in their combination of *Parmularius-Antidorcas* specialized profile. No indication exists that hominins may have obtained these carcasses from lion kills, since waterbucks are not usually preferred prey by lions (Schaller, 1972).The marginal presence of other, presumably more seasonal, taxa such as *Connochaetes* and *Equus,* also argues against an opportunistic strategy by hominins, since such taxa are more commonly preyed upon by lions.

The combined evidence of microwear and mesowear on the selected sites indicates that the main taxa at Bed I sites may have had a slightly different dietary niche when compared to their modern counterparts. In this regard, it is surprising to find that a taxon like *Kobus sigmoidalis*

exhibited such a low mesowear score and also a low presence of scratches, both features commonly associated with mixed feeders and browsers. Future analyses of this taxon should compare wear patterns across the Bed I and Bed II time intervals to determine if vegetation availability (more wooded habitats in Bed I and more open environments in Bed II) conditioned dietary shifts through time.

These preliminary data on depositional processes and time-associated inferences are the first ones made for the Bed I sites and should constitute a testing hypothesis for more extensive future analyses targeting the study of complete dentitions and a larger sample of individuals. Despite the limited size of the sample used here, it is interesting to notice that at anthropogenic sites like FLK Zinj, DS, and BK, the selected medium-sized and large taxa cluster in Area A, indicating the possibility of short seasonal occupations of those sites. Particularly surprising is the information collected in the only surviving dental remains from Leakey's *Pelorovis* "herd", which does not support a long time-averaged deposition, as suggested by Organista et al. (2016, 2017) and brings back the possibility of being the result of a single depositional event; although possible repeated events during the same season over different years cannot be discarded. However, once again, this is unsupported by taphonomic data of the postcranium, which should reflect widely variable subaerial weathering stages of bones had that been the case. Instead, most bones are unweathered. This supports the single-event hypothesis. On-going excavations at this site with newer individuals should further test this controversial interpretation.

Conflict of interest

Authors have no conflict of interest.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quaint.2019.05.041.

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