1 Paleoenvironmental change in the late Middle Pleistocene – Holocene Kibish Formation,
2 southern Ethiopia: evidence from ungulate isotopic ecology

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12 **Abstract**

13 East Africa has produced the earliest record of *Homo sapiens* ~ 200 ka and a
14 punctuated record of Middle Stone Age and Later Stone Age behaviors. We lack,
15 however, a detailed late Quaternary paleoenvironmental record for the region,
16 particularly during humid periods. Without a regional record, hypotheses about the
17 evolution and ecology of early *Homo sapiens* in East Africa remain vague and untestable.
18 The Kibish Formation of southern Ethiopia presents a long, albeit punctuated, record of
19 late Middle Pleistocene to Holocene faunal change in East Africa, which was deposited
20 during humid periods. Here we present oxygen and carbon stable isotope data of the
21 Kibish ungulates and test whether there are environmental changes within the Kibish
22 Formation. Significant differences in $\delta^{18}\text{O}$ enamel isotopes are consistent with more
23 humid conditions during the Holocene-age Member IV (~ 13-4 ka) than either

Pleistocene-age Member I (~ 196 ka) or Member III (~ 104 ka). Mesowear data document a shift towards more attritional wear among grazers in Member IV and are correlated with more depleted $\delta^{18}\text{O}$ enamel values, suggesting that the wear pattern shift is linked to the onset of more humid conditions during the Holocene. $\delta^{13}\text{C}$ enamel values show subtle variations through time, but do not suggest any major changes in diets. We propose that the paleoenvironmental differences evident in Member IV, based on $\delta^{18}\text{O}$ enamel values, mesowear, and bovid abundances, may be explained by cooler and wetter conditions at the beginning of the Holocene in the lower Omo Valley. The evidence suggesting that the Holocene humid phase is more pronounced than earlier humid phases may explain why arid-adapted grassland ungulates became extinct in East Africa by the Pleistocene-Holocene transition, but persisted through previous humid phases of the late Quaternary.

Keywords: isotopes; mesowear; ungulates; Late Quaternary; East Africa; Ethiopia

1. Introduction

We know very little about paleoenvironments in East Africa from the Middle Pleistocene through the Holocene associated with Middle Stone Age (MSA) and Later Stone Age (LSA) toolkits, and early *Homo sapiens* fossils. This is especially true compared to the Middle and Late Pleistocene cave sites in South Africa that provide rich archaeological (Henshilwood et al., 2002; d’Errico et al., 2005; Marean et al., 2007; Marean, 2010; Brown et al., 2009, 2012) and paleoenvironmental records (Klein, 1980, Klein et al., 1999; Chase and Meadows, 2007; Bar-Matthews et al., 2010; Faith, 2013).

The lack of data for East Africa is problematic, as documenting the temporal and spatial complexity of paleoenvironments during the late Quaternary is critical to contextualizing hypotheses about the ecology and evolution of early *Homo sapiens*. Understanding how early human populations responded to such changes via geographic, demographic, or behavioral shifts are central goals of paleoanthropology (Barham and Mitchell, 2008; d’Errico and Stringer, 2011; Blome et al., 2012). While fieldwork in southern and western Kenya has greatly expanded our knowledge of paleoenvironments during arid phases of the Late Pleistocene (Marean and Gifford-Gonzalez, 1991; Marean, 1992; Faith et al., 2013, 2014, 2015; Tryon and Faith, 2013; Tryon et al., 2010, 2014, 2015), the paucity of paleoenvironmental data for humid intervals confounds our ability to address these questions.

The Kibish Formation of southern Ethiopia has yielded a relatively large sample of late Middle Pleistocene to early to mid-Holocene faunal remains, including the earliest modern human fossils (McDougall et al., 2005; Fleagle et al., 2008). This record ranges in age from roughly 196 thousand years ago (ka) to ~ 13-4 ka, with three fossil-bearing members (Members I, III, and IV) deposited during humid phases linked to intensification of the African monsoon during precessional minima (Leakey, 1969; McDougall et al., 2005; Brown and Fuller, 2008; Fleagle et al., 2008; Brown et al., 2012). Although it is by no means continuous (McDougall et al., 2005; Brown and Fuller, 2008; Brown et al., 2012), the temporal span of the Kibish Formation is greater than other late Quaternary sites in East Africa (Gramly, 1976; Phillipson, 1977; Clark et al., 1984; Barham, 2000; Clark et al., 2003; Brandt et al., 2012; Gliganic et al., 2012; Tryon and Faith, 2013; Assefa et al., 2014; Tryon et al., 2014, 2015; Faith et al., 2015). Thus, the

Kibish Formation offers a potential ‘yardstick’ through which a Pleistocene-Holocene chronology of East African paleoenvironmental change can be built. Here, we present new data that better our understanding of late Quaternary paleoenvironments in East Africa using carbon and oxygen stable isotope data of the Kibish Formation ungulates (Table 1).

2. Geological context

The Kibish Formation outcrops to the north of Lake Turkana in southern Ethiopia and has been mapped over an area roughly 50 x 190 km (Figure 1) (Butzer et al., 1969; Butzer, 1971; Davidson, 1983; McDougall et al., 2005; Brown and Fuller, 2008, Brown et al., 2012). Butzer et al. (1969; Butzer, 1971) divided the Kibish Formation into Members I, II, III, and IV (McDougall et al., 2005; Brown and Fuller, 2008; Fleagle et al., 2008; Brown et al., 2012).

Deltaic deposits dominate the Kibish Formation, although fluvial and lacustrine facies do occur (Brown and Fuller, 2008). The Formation was deposited in the delta of the Omo River that empties into Lake Turkana, which extended ~ 100 km northward during humid periods of the late Quaternary (McDougall et al., 2005, 2008). During these humid periods, the Omo River swelled due to increased rainfall over the Ethiopian Highlands coincident with precessional minima and intensification of the African monsoon (Rossignol-Strick et al., 1982; McDougall et al., 2008). These periods of increased rainfall have been linked with sapropel development in the Mediterranean Sea and their correlation with the fossil-bearing layers suggests that deposition of each Kibish Member was relatively rapid (McDougall et al., 2008). Thus, here we consider each

Member to be equivalent in age to the absolute dates derived from tephra in the Formation, with little time-averaging across multiple climatic regimes (McDougall et al., 2005, 2008; Brown and Fuller, 2008; Brown et al., 2012). For each member, fossils were concentrated in discrete sedimentary lenses.

The oldest Member, Member I, is late Middle Pleistocene in age and is dated to ~ 196 ka by the Nakaa'kire Tuff (McDougall et al., 2005; Brown et al., 2012). This Member rests unconformably over the Nkalabong and Mursi Formations (Brown and Fuller, 2008). Member II has yielded little faunal remains, and is only tentatively dated to between 180 – 150 ka, although correlation with Mediterranean sapropels suggests deposition ~ 172 ka (Brown and Fuller, 2008; McDougall et al., 2008; Brown et al., 2012). Due to the lack of faunal remains recovered from Member II, it is not considered here. The Aliyo Tuff dates Member III to the Late Pleistocene, ~ 104 ka (Brown and Fuller, 2008; Brown et al., 2012). Finally, Member IV is Late Pleistocene to mid-Holocene in age, ~ 13 – 4 ka, based on ^{14}C dating of fossil mollusks (Owen and Renaut, 1986; Brown and Fuller, 2008).

3. Materials and Methods

3.1 Carbon and oxygen stable isotopes

Stable isotope characterization of fossil teeth for paleobiological, paleoecological, and paleoenvironmental reconstruction has been a well-developed method for decades (Lee-Thorp, 1989; Koch et al., 1989; Kohn, 1996; Sponheimer and Lee-Thorp, 1999a; Sponheimer and Lee-Thorp, 1999b; Schoeninger et al., 2003; Cerling et al., 2003; Kingston and Harrison, 2007; Sponheimer and Lee-Thorp, 2007; Harris et al., 2008). This is because the carbonate fraction of tooth enamel is minimally affected by

116 diagenesis and can be used as a proxy for diet, which is in turn used to infer
117 paleoenvironments (DeNiro and Epstein, 1978; Wang and Cerling, 1994; Cerling and
118 Harris, 1999; Sponheimer and Lee-Thorp, 1999a; Lee-Thorp, 2002; Lee-Thorp and
119 Sponheimer 2003). Seasonality, competition, migration, social behavior, and other factors
120 may complicate the link between diet and environmental proxies (Caswell et al., 1973;
121 Behrensmeyer and Hook, 1992). Thus, in order to minimize these factors, diets and
122 paleoenvironments are primarily interpreted and reconstructed through a community-
123 based approach (Sponheimer and Lee-Thorp, 1999a; Kingston, 2007; Kingston, 2011).

124 Terrestrial plants predominantly use two different photosynthetic pathways based
125 on differences in the fractionation of ^{12}C and ^{13}C from atmospheric CO_2 . Trees, shrubs,
126 and high-altitude grasses (>2,000 m) in tropical Africa utilize the C_3 photosynthetic
127 pathway and have a modern $\delta^{13}\text{C}$ range of -22‰ to -36‰ (mean: -27.1 ± 2.0 ‰; Tieszen et
128 al., 1979; O’Leary, 1981; Cerling et al., 2003; Passey et al., 2005; Kohn, 2010;
129 Brookman and Ambrose, 2012). This variability in C_3 plants is partially driven by
130 photosynthetic recycling of respired CO_2 in closed canopy forests, known as the canopy
131 effect, and variability in water availability, light, and temperature (van der Merwe and
132 Medina, 1991; Kohn, 2010). Most low elevation, tropical grasses in Africa employ one of
133 the C_4 subpathways and have $\delta^{13}\text{C}$ values ranging from about -14‰ to -10‰ (mean: -
134 13.1 ± 1.2 ‰; Heaton, 1999; Passey and Cerling, 2002; Cerling et al., 2003). In certain
135 environments, such as marshes, both C_3 and C_4 plants may have isotopic yields outside of
136 the average ranges cited above, but the general distinction between C_4 grasses and other
137 plants is ideal for differentiating broad dietary strategies (Cerling et al., 2003; Kingston
138 and Harrison, 2007). Succulents fix CO_2 through the CAM (Crassulacian acid

metabolism) pathway and yield isotopic values between C₃ and C₄ plants (O’Leary, 1981; Heaton, 1999). However, it is unlikely that succulents comprised a significant component of biomass in East Africa or featured prominently in ungulate diets (Cerling et al., 2003; Kingston, 2011; Garret et al., 2015).

For comparison to modern faunal enamel data, $\delta^{13}\text{C}$ enamel values are corrected based on changes in atmospheric CO₂ since the Late Pleistocene. Following established conversion methods (Tippie et al., 2010; Garret et al., 2015; Faith et al., 2015), the correction factor is calculated as -1.5‰. In addition to atmospheric CO₂, the fractionation between diet and enamel tissue must be considered. Tooth enamel of large mammals has been shown to be ~14‰ enriched in ¹³C compared to their diet (Cerling and Harris, 1999; Passey et al., 2005). Considering both the atmospheric correction and the fractionation between diet and enamel, values more depleted than -9‰ indicate C₃ dominated diets, -9‰ to -3‰ reflects mixed C₃/C₄ diets, and values more enriched than -3‰ indicate primarily C₄ diets.

Analysis of the oxygen isotope composition ($\delta^{18}\text{O}$) of tooth enamel provides a proxy for water flux and oxygen exchange in body water. This is a function of drinking water, the water from ingested foods, the $\delta^{18}\text{O}$ of metabolic and atmospheric oxygen, and animal behavioral and physiological water conservation mechanisms (Longinelli, 1984; Koch et al., 1989; Kohn, 1996; Koch, 1998; Sponheimer and Lee-Thorp, 1999b). It is used here as a proxy for aridity, as the lighter ¹⁶O is more readily evaporated in tropical low latitudes. The result of this scenario is heavier, or ¹⁸O enriched, meteoric and vegetative water sources recorded in faunal tooth enamel leading to more positive $\delta^{18}\text{O}$ enamel values (Kohn, 1996; Levin et al., 2006).

3.2 Aridity index

Levin et al. (2006) showed that taxa that rely on leaf water typically exhibit greater oxygen isotopic variability and are more evaporation sensitive (ES) than those that primarily drink from meteoric/surface sources and tend to be evaporation insensitive (EI). $\delta^{18}\text{O}$ values of tooth apatite from ES taxa increase with increasing aridity while the $\delta^{18}\text{O}$ enamel values of EI taxa track values of meteoric water (Kohn, 1996; Fricke et al., 1998; Levin et al., 2006). Under this framework, Levin et al. (2006) developed an ‘aridity index’ based on the differences between ES and EI taxa. The aridity index generates a value for water deficit, a proxy for aridity, which increases from closed canopy forest to open grasslands (Levin et al., 2006). In theory, the index eliminates the need to control for taxon-specific physiological factors affecting water consumption and retention or hydrological patterns affecting overall terrestrial aridity. The approach also accounts for changes in the $\delta^{18}\text{O}$ of meteoric water whether such changes are related to differences in aridity or not (Levin et al., 2006).

We calculated the aridity index for each of the three fossil-bearing Members of the Kibish Formation. We used *Phacochoerus* as our EI taxon, as in Levin et al. (2006). For ES taxa, we used various combinations of *Syncerus* with three other taxa (*Oryx*, *Giraffa*, and *Madoqua*), all of which were identified by Levin et al. (2006) as ES taxa. Through various combinations of taxa, we present a range of water deficit estimates for each Member of the Kibish Formation.

3.3 Materials and sampling

Stable carbon and oxygen isotopes were generated on 89 fossil teeth from the Kibish Formation that were collected during the 1999-2003 and 2012 field seasons. Collection methods for the Kibish project are discussed in Assefa et al. (2008) and Rowan et al. (2015). Of these 89 samples, 80 are confidently assigned to a specific member and are used in this analysis (supplemental information). Sampling was done in the summer of 2013 at the National Museum of Ethiopia in Addis Ababa, Ethiopia, by J.R.R. Sampling focused on five ungulate families – Bovidae, Equidae, Giraffidae, Hippopotamidae, and Suidae. When available, each member was sampled to ensure sufficient temporal spread. Enamel samples were taken from molars (preferably third molars) identified to the tribe or genus level of 87 of the 89 teeth to limit potentially confounding effects of weaning that might be evident on deciduous teeth. Two samples of Hippopotamidae tusk are included in this dataset. Each sample is identified with a unique catalogue number, suggesting that all 89 samples represent different individuals. Only one tooth was sampled from partial or complete tooth rows which were identified by one catalogue number.

Enamel was carefully cleaned of any adhering sediment and weathering rinds with a high speed Brasseler dental drill (Forza L50k) with tungsten-carbide bits. Approximately 2 mg of powdered enamel was removed from broken edges of each tooth. Powdered enamel was reacted for ~ 24 hours with ~ 2% bleach solution in 1.5 ml microcentrifuge tubes to digest any organic material and then rinsed and centrifuged to a neutral pH with double distilled water. This was followed by sample treatment with 0.1 M acetic acid for ~ 4 hours to remove any secondary carbonate, rinsed to neutrality again (Kingston and Harrison, 2007; Sponheimer and Lee-Thorp, 2007). Mass spectrometry

was performed at the Light Stable Isotope Laboratory in the Department of Geosciences at University of Florida, Gainesville using a Finnigan-MAT 252 mass spectrometer interfaced with a Kiel III carbonate extraction device. Carbon and oxygen values are reported relative to VPDB (Vienna Pee Dee Belemnite). Analytical precision was measured by repeated analysis of the international calcium carbonate standard NBS-19. All 89 samples were successfully characterized with analytical precision better than 0.1‰ for oxygen and 0.05‰ for carbon.

4. Results

4.1 Enamel isotopes

Although it is difficult to completely exclude the possibility of diagenesis, the $\delta^{13}\text{C}$ enamel values are within the expected range of modern equivalents (Cerling et al., 2003, 2015). Because the sample sizes for individual species within a member are relatively small, to provide sufficiently large sample sizes for statistical analysis we aggregate samples according to the following dietary classes based on observational (Kingdon, 1982, 2015) and isotopic (Harris and Cerling, 2002; Sponheimer et al., 2003; Cerling et al., 2003) data: grazers (Alcelaphini, Hippotragini, *Equus*, and *Phacochoerus*), fresh grass grazers (*Syncerus*, *Kobus*, and *Hippopotamus*), and browsers (*Madoqua*, *Tragelaphus*, and *Giraffa*). We note that our dietary classification of *Hippopotamus* relies more strongly on observational evidence suggesting *Hippopotamus* is an obligate grazer (Kingdon, 1979; Klingel, 2013) versus isotopic evidence suggesting a more varied mixed-feeding diet (Boissarie et al., 2005; Cerling et al., 2008). Because taxa within our dietary categories are not evenly sampled across the Kibish Formation, identifying

meaningful temporal changes in $\delta^{13}\text{C}_{\text{enamel}}$ or $\delta^{18}\text{O}_{\text{enamel}}$ require that we first ensure that
 the various species aggregated within each dietary class have similar isotopic values. For
 grazers and fresh grass grazers, we calculate 95% confidence intervals (CI) for the mean
 $\delta^{13}\text{C}_{\text{enamel}}$ and $\delta^{18}\text{O}_{\text{enamel}}$ value of each taxon by bootstrapping with replacement over
 10,000 iterations. Among the grazers, there is broad overlap in the 95% CI across taxa
 (Table 2), meaning that differential representation of taxa within this dietary category is
 unlikely to drive any temporal trends. However, among the fresh grass grazers,
Hippopotamus is significantly more depleted in $\delta^{13}\text{C}_{\text{enamel}}$ and $\delta^{18}\text{O}_{\text{enamel}}$ relative to
Syncerus and *Kobus* (Table 2). These results are similar to those of previous isotopic
 studies of *Hippopotamus* (Bocherens et al., 1996; Boissarie et al., 2005; Cerling et al.,
 2008), and we therefore exclude *Hippopotamus* from further consideration in our analysis
 of temporal trends within fresh grass grazers. The sample size for browsers is too small to
 conduct such an analysis and is limited primarily to Member I (7 of 8 specimens), which
 precludes any detailed analysis of change through time within this dietary category.

Figure 2A provides box plots illustrating $\delta^{13}\text{C}_{\text{enamel}}$ of grazers, fresh grass grazers,
 and browsers. For the grazers, the 95% CI of the means for Members I (-1.5‰ to -0.6‰)
 and III (-1.8‰ to 0.1‰) show substantial overlap, while Member IV (-3.7‰ to -1.5‰) is
 more depleted than Member I. A Kruskal-Wallis test further indicates significant
 differences in sample medians ($p = 0.044$). Among fresh grass grazers (excluding
Hippopotamus), there is overlap in 95% CI of the means across all Kibish Formation
 members (Member I: -2.5‰ to -0.7‰; Member III: -1.5‰ to 0.1‰; Member IV: -2.6‰
 to 0.7‰; Kruskal-Wallis test: $p = 0.284$). There are no browsers in our sample for

Member IV and Member III includes only a single specimen (*Giraffa*), which fits comfortably within the 95% CI of Member I.

There is overlap in the 95% CI for mean $\delta^{18}\text{O}_{\text{enamel}}$ of grazers (Member I: -0.1‰ to 1.3‰; Member III: -1.4‰ to 0.6‰; Member IV: -2.5‰ to 0.2‰), although a Kruskal-Wallis test suggests a near-significant difference in sample medians ($p = 0.069$), driven by the more depleted values in Member IV relative to Member I (Mann-Whitney U: $p = 0.022$). A similar depletion in Member IV $\delta^{18}\text{O}_{\text{enamel}}$ is also evident for fresh grass grazers (Member I: -1.8‰ to 0.7‰; Member III: -3.6‰ to 0.2‰; Member IV: -3.1‰ to -1.7‰), though this is not well supported statistically (Kruskal-Wallis: $p = 0.101$), potentially due to the relatively small sample sizes involved. However, combining both dietary classes, but excluding Alcelaphini and *Hippopotamus*, both of which have $\delta^{18}\text{O}_{\text{enamel}}$ values that differ from other grazers and fresh grass grazers (Table 2), we observe a highly significant difference in $\delta^{18}\text{O}_{\text{enamel}}$ across the sequence (Kruskal-Wallis: $p = 0.008$), with Member IV showing the most depleted values. Among browsers, the single specimen from Member III falls outside the 95% CI for Member I. Giraffes and tragelaphins have slightly more enriched $\delta^{18}\text{O}_{\text{enamel}}$ than grazers (Table 2) as has been found in other studies (Sponheimer and Lee-Thorp, 1999b), while *Madoqua* yields similar $\delta^{18}\text{O}_{\text{enamel}}$ to grazers. However, the small sample size for browsers precludes any meaningful interpretation either within browsers or between browsers and grazers.

4.2 Aridity index

The terrestrial aridity index devised by Levin et al. (2006) is meant to minimize or eliminate the difficulties in using $\delta^{18}\text{O}$ as a proxy for comparison of seasonality, rainfall,

or humidity across fossil and modern sites. While the Kibish $\delta^{18}\text{O}$ fossil data reveal a pattern of ^{18}O depletion from Member I to Member IV, simple comparisons can be complicated by faunal physiology and regional and global climatic systems controlling $\delta^{18}\text{O}$ in terrestrial ecosystems, which may change over time. The use here of taxa with modern analogs avoids the need to make any assumptions about fossil taxa. The temporal division of the Members of the Formation has the added advantage of stratigraphically constraining the samples, which minimizes the mixing of the fauna from oscillating environmental conditions. By calculating a water deficit value for various combinations of taxa (Table 3) we aim to demonstrate a trend through time. These estimates can be compared to the modern water deficit of the Kibish area today, which is calculated to be 857 mm using the equations of Thornthwaite (1948) and data from Worldclim (Hijmans et al., 2005).

We calculated a range of water deficit values for Kibish Formation Members I, III, and IV based on different combinations of ES taxa (Table 3). To provide 95% confidence limits on our estimates of the difference between ES and EI taxa (ϵ), we implemented the following bootstrap procedure: For each of 10,000 iterations, bootstrap the mean $\delta^{18}\text{O}$ of EI taxa, bootstrap the mean $\delta^{18}\text{O}$ of ES taxa, and determine the difference in means (ES – EI). Table 4 reports ϵ values with associated 95% confidence limits. The confidence limits are broad and completely overlapping for the analysis involving only *Syncerus*, the only comparison possible for all members, suggesting no significant differences. This almost certainly reflects the small sample sizes involved, although Member IV shows the most humid signal (negative ϵ values), paralleling the depleted $\delta^{18}\text{O}$ values observed among grazers and fresh grass grazers.

Converting ε value 95% confidence limits to estimates of water deficit, for Member I 95% confidence limits of water deficit ranged from 501 - 1011 mm. Member III water deficit values ranged from 563 - 1401 mm, while the 95% confidence interval for the single Member IV water deficit value was 395 - 837 mm. Confidence limits on water deficit estimates are broad – again a reflection of small sample sizes – and overlapping across members, though Member IV does show the more humid signal (Figure 3).

4.3 Isotope data and dental mesowear

Across tribes of grazing bovids, Rowan et al. (2015) documented a general shift toward less abrasive diets through time in the Kibish Formation. Here we assess whether these changes track shifts in $\delta^{13}\text{C}_{\text{enamel}}$ and $\delta^{18}\text{O}_{\text{enamel}}$. Because baseline values for both mesowear and isotope values differ across tribes, for each tribe we calculate the difference in the mean value of each member (for both mesowear score and isotope values) relative to the grand mean across the Kibish Formation sample. For mesowear scores, a positive value for a particular member indicates a more abrasive diet compared to the mean of all members, whereas a negative value indicates a relatively less abrasive diet. Likewise, for $\delta^{13}\text{C}_{\text{enamel}}$ and $\delta^{18}\text{O}_{\text{enamel}}$, a positive value for a particular member indicates a more enriched value relative to the grand mean of all members, while a negative value indicates a relatively more depleted value. In Figure 4, we plot the deviation in mean mesowear score against the deviation in mean $\delta^{13}\text{C}_{\text{enamel}}$ and $\delta^{18}\text{O}_{\text{enamel}}$ across bovid tribes and members. We observe a significant positive relationship between the deviation in mesowear scores and $\delta^{18}\text{O}_{\text{enamel}}$ ($r_s = 0.637$, $p = 0.047$), indicating that

shifts toward less abrasive diets are associated with shifts toward more depleted $\delta^{18}\text{O}_{\text{enamel}}$. In contrast, we observe no relationship between the deviation in mesowear scores and $\delta^{13}\text{C}_{\text{enamel}}$ ($r_s = -.180$, $p = 0.619$), even when we exclude the outlier represented by the Member IV Hippotragini ($r_s = -.626$, $p = 0.076$).

5. Discussion

The impact of late Quaternary climatic change on early *Homo sapiens* populations in East Africa remains unclear, as we lack a detailed record of paleoenvironmental change in the region. The new data from the Kibish Formation presented in this work greatly add to our knowledge of paleoenvironmental change in the lower Omo Valley, an area that has produced the earliest fossil evidence of *H. sapiens* (McDougall et al., 2005; Fleagle et al., 2008) and abundant Middle Stone Age artifacts (Shea, 2008; Sisk and Shea, 2008). Below we discuss these changes in the Kibish Formation record at both a local scale (the lower Omo Valley and Turkana Basin) and a regional scale (East Africa) using various paleoclimatic proxies (Figure 5).

Trends within the Kibish Formation—Our isotope data from the Kibish Formation show that Members I and III have overlapping ranges of $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ enamel values and similar mean aridity index water deficit values (915 mm and 961 mm, respectively). Bovid mesowear signatures vary relatively little between Members I and III (Figure 4), which further suggests consistent vegetation (i.e., grass species) and/or climatic conditions between these two members. Both the isotope and mesowear data, however, reveal that Member IV was characterized by significantly different conditions. Member IV has the most depleted $\delta^{18}\text{O}$ enamel values among grazers and fresh grass

grazers and the lowest, though not statistically significant, water deficit based on the aridity index (624 mm), in addition to less abrasive mesowear signals and a dominance of mesic-adapted *Kobus* in the bovid community (Rowan et al., 2015). $\delta^{13}\text{C}$ enamel values show variation across all Kibish members, with significantly more depleted values in Member IV for grazers. This could indicate the presence of different grass species with depleted $\delta^{13}\text{C}$ values in Member IV relative to the other Kibish members. This vegetation change may have included the appearance of sedges and other aquatic vegetation with depleted $\delta^{13}\text{C}$ values compared to other grass species (Hattersley, 1992; Chapman, 1996; Cerling et al., 2003). Alternatively, the $\delta^{13}\text{C}$ enamel values could indicate increased consumption of C_3 vegetation by grazers during Member IV times, although the bovid community provides no evidence for greater presence of trees or shrubs (Rowan et al., 2015). Despite these interesting possibilities, the $\delta^{13}\text{C}$ enamel values do not record any major dietary changes through the Kibish Formation, as most ungulate taxa have C_4 -dominated diets throughout the sequence. Thus, we focus here on $\delta^{18}\text{O}_{\text{enamel}}$, mesowear, and bovid abundance data.

We interpret these patterns as most likely reflecting more humid conditions and an expansion of well-watered grasslands, including species such as kikuyu grass (*Pennisetum clandestinum*; average $\delta^{13}\text{C}$: $-11.8 \pm 0.2\text{‰}$; Cerling et al., 2003), in the early Holocene (Member IV) compared to Member I and III times. More humid conditions are suggested by lower aridity index, while the abundance of *Kobus* (54.5% of all bovids) indicates mesic grassland vegetation. We also observe that less abrasive mesowear scores track $\delta^{18}\text{O}_{\text{enamel}}$ depletion among grazers and fresh grass grazers in Member IV times (Figure 4). Because modern fresh grass grazing bovids tend to have less abrasive

mesowear scores compared to dry grass grazers (Kaiser et al., 2013), the less abrasive mesowear score in the Member IV assemblage is consistent with increased consumption of fresh and well-watered grasses among all grazing species. The corresponding depletion of $\delta^{18}\text{O}_{\text{enamel}}$ may signal overall more humid conditions or grass leaf water that is less evaporated relative to Members I and III. Less humid conditions in the Pleistocene-age members are supported by the abundance of alcelaphins, which, while generally uncommon, are most abundant in Member I (10% of all bovids) and Member III (10.5%), while much rarer in Member IV (2%). Similarly, the arid-adapted hippotragin *Oryx* is present in both Members I and III but is absent in Member IV, in which the relatively more mesic-adapted *Hippotragus* is at its highest abundance (13%).

A possible mechanism for more humid conditions and expansion of mesic grasslands during the deposition of Member IV is cooler temperatures. Both climate models (Clement et al., 2004) and TEX_{86} temperature records from Lake Malawi and Lake Tanganyika (Tierney et al., 2008, 2010; Powers et al., 2011; Woltering et al., 2011) suggest that variation in equatorial African temperatures over orbital time-scales are mediated in part by northern hemisphere summer insolation. All members of the Kibish Formation were deposited during insolation maxima, but northern hemisphere summer insolation during Member IV times (13-4 ka: 478 to 511 W/m^2 at 30°N) is lower than Members I (196 ka: 529 W/m^2 at 30°N) and III times (104 ka: 529 W/m^2 at 30°N) (insolation data from Berger and Loutre, 1991), potentially translating to relatively cooler temperatures. While we are unable to directly provide a direct reconstruction of temperatures, insolation declines of this magnitude are associated with roughly $\sim 2^\circ\text{C}$ drops in surface temperatures of Lake Tanganyika (Tierney et al., 2008). Even if

precipitation were comparable across all members of the Kibish Formation, cooler conditions during the early Holocene, which are documented in lake surface temperature proxies from nearby Lake Turkana and elsewhere in tropical Africa (Berke et al., 2012), would equate with less evaporation over land, more effective precipitation, and overall more humid conditions compared to earlier depositional events of the Kibish Formation.

The more humid conditions recorded in Member IV, corresponding to the African Humid Period, are well documented in local climate archives. Evidence from nearby Lake Turkana, which is sourced by the Omo River (see Figure 1, A), shows that during the early Holocene lake levels rose to at least 100 m above their current level (Morrissey and Scholz, 2014). Paleolimnological evidence from nearby Lake Chew Bahir further indicates more humid conditions at this time (Foerster et al., 2012), and the same is observed in lake records throughout tropical Africa (Richardson and Dussinger, 1986; Tierney et al., 2008; Verschuren et al., 2009). Both Indian Ocean records of sea-surface temperature and TEX₈₆ records of lake temperatures show that these humid conditions were frequently associated with cooler temperatures (e.g., Berke et al., 2012; Weldeab et al., 2014). While none of these records extend to the same age of Members I and III of the Kibish Formation, our data suggest that conditions in the African Humid Period were unique relative to earlier wet phases of the Pleistocene. Indeed, the intensity of humid conditions associated with the early Holocene is well documented throughout North Africa and tropical Africa (e.g., deMenocal et al., 2000; Chase et al., 2010). This event has been linked with population expansion into the fringes of Sahara (Hoelzmann et al., 2001; Sereno et al., 2008) and the emergence of aqualithic cultures in East Africa (Sutton, 1977; Owen et al., 1982). Migrations into the Sahara are evident at Nabta Playa in the

Western Desert of Egypt where four early to middle Holocene humid interphases saw the flourishing of microlithic tool industries with a sudden onset of humid conditions at ~ 8.5 ka (Wendorf and Schild, 2001; Kuper and Kropelin, 2006).

Regional trends in East Africa— The Ocean Drilling Project (ODP) 721/722 terrigenous dust record reflects aridity in East Africa, as the dust record has an inverse relationship with rainfall over the region (deMenocal et al., 2000; deMenocal, 2004). Thus, periods of high dust deposition reflect arid conditions over East Africa, while periods of low dust deposition reflect relatively wetter conditions. The ODP 721/722 terrigenous dust record (Figure 5) shows that each member of the Kibish Formation was deposited during some of the least arid intervals in the Horn of Africa over the last ~ 200 ka. This is not surprising, given that it has been demonstrated that all three members were deposited during precessional minima when warmer ocean sea-surface temperatures lead to intensified monsoon circulation and more precipitation over East Africa (Fleagle et al. 2008). McDougall et al. (2008), furthermore, have linked the deposition of the members with the Mediterranean sapropel record, which provides another line of evidence suggesting increased rainfall over the region. Thus, the Kibish Formation record is capturing relatively humid periods in East Africa over the last ~ 200 ka.

Other Late Pleistocene sites, such as Rusinga Island, Mfangano Island, and Karungu in the Lake Victoria region (~ 100-35 ka) (Tryon et al., 2010, 2012, 2014, 2015; Beverly et al., 2015; Faith et al., 2015) and Lukenya Hill (~ >40 -15 ka) in south-central Kenya (Marean, 1992), were deposited during relatively more arid periods than the Kibish Formation based on the terrigenous dust record (Figure 5). This is consistent with geochemical analysis of paleosols from the Lake Victoria region, which suggest

substantial reductions in precipitation (760-960 mm/yr) compared to the present (1400 mm/yr) (Beverly et al., 2015), and with a water deficit estimate (974 mm) that is more arid than any of the Kibish members, and substantially more so than Member IV (Garrett et al., 2015). Indeed, the faunal communities of these sites are dominated by arid-adapted taxa, including the extinct alcelaphins *Damaliscus hypsodon*, *Megalotragus*, and *Rusingoryx atopocranion*, and the bovin *Syncerus antiquus*. In addition, these sites and others in northern Tanzania demonstrate range expansions of arid-adapted taxa such as *Oryx beisa* and *Equus grevyi* (Marean and Gifford-Gonzalez, 1991; Marean, 1992a; Faith et al., 2011, 2012, 2013, 2015; Tryon et al., 2010, 2014, 2015). These ungulate taxa are either rare (*D. hypsodon*, *O. beisa*, *E. grevyi*) or absent (*Megalotragus*, *R. atopocranion*, *S. antiquus*) in the Kibish Formation.

The extinction of arid-adapted grassland ungulates by the Pleistocene-Holocene transition in East Africa has been attributed in part to wetter conditions at the onset of the Holocene (Marean and Gifford-Gonzalez, 1991; Marean, 1992a; Faith et al., 2011, 2012; Faith, 2014). The evidence presented here suggesting that the Holocene humid phase is more pronounced than earlier humid phases may explain why arid-adapted grassland ungulates became extinct by the Pleistocene-Holocene transition, but persisted through previous humid phases of the late Quaternary. This is especially clear for the extinct blesbok *D. hypsodon*, which is present in low numbers in both Members I and III of the Kibish Formation. This species is abundant in the nearby Ziway-Shala Basin (Main Ethiopian Rift) during an arid phase of the very latest Pleistocene (~ 13.5 ka) (Lesur et al., in revision), and its absence from the early Holocene in Member IV of the Kibish

Formation provides a strong link between its extinction and the onset of humid conditions during the African Humid Period.

6. Conclusions

The Kibish Formation of southern Ethiopia presents a record of late Middle Pleistocene to Holocene faunal change in East Africa at ~ 196 ka, ~ 104 ka, and ~ 13-4 ka. Enamel $\delta^{18}\text{O}$ values suggest relatively more humid conditions during the Holocene-age Member IV (~ 13-4 ka) than either Pleistocene-age Member I (~ 196 ka) or Member III (~ 104 ka). Mesowear and bovid abundance data support the more depleted $\delta^{18}\text{O}$ enamel values in Member IV, which suggest wetter conditions. $\delta^{13}\text{C}_{\text{enamel}}$ do not suggest any major changes in diet with all grazing taxa consuming primarily C_4 biomass, although grazer $\delta^{13}\text{C}$ enamel values are more depleted in Member IV than earlier in time. Cooler and wetter conditions at the beginning of the Holocene in the lower Omo Valley could explain the paleoenvironmental differences evident in Member IV. Our evidence suggests that the Holocene humid phase was more pronounced than earlier humid phases and that this may explain why arid-adapted grassland ungulates became extinct in East Africa by the Pleistocene-Holocene transition, but persisted through previous humid phases of the late Quaternary.

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fig.1

A.

B.

fig.2

A.

B.

fig.3

fig.4

fig.5