



Ecosystem evolution and hominin paleobiology at East Turkana, northern Kenya between 2.0 and 1.4 Ma



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ABSTRACT

Over the past five decades, fossil deposits within the Upper Burgi, KBS and Okote members at East Turkana in northern Kenya have provided many important insights into hominin behavior and ecology during a critical period in hominin evolution between 2.0 and 1.4 Ma. In this study, we use a large compilation of faunal abundance data from paleontological and archaeological collections at East Turkana dating to this time interval to investigate temporal patterns in large mammal taxa, ecosystem evolution and hominin ecology. Our analyses indicate that although portions of the ecosystem were dominated by mesic grasslands, the relative proportion of mesic and arid grassland environments varied through time. We document a major transition in the family Suidae with an increase in the abundance of fossils attributed to the *Metridiochoerus* lineage coeval with the local extinction of the *Notochoerus* lineage and decline in abundance of the *Kolpochoerus* lineage. Finally, by comparing the proportional representation of mammalian taxa found in paleontological collections versus those found in archaeological collections, our data suggest that archaeological sites at East Turkana, particularly those c.1.5 Ma, contain disproportionately large numbers of alcelaphin bovid remains. This could reflect 1) hominin prey choice, 2) hominin hunting/scavenging habitat choice, or 3) a combination of the two.

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1. Introduction

1.1. Plio-Pleistocene hominin ecology

Placing early Pleistocene hominin evolution within a well-defined temporal and spatial ecological framework has been a longstanding goal of paleoanthropology. Understanding the relationship between ecosystem dynamics and hominin paleobiology is critical to testing hypotheses that seek to explain the influence of the environment on the morphological and behavioral adaptations of early hominins. The Pleistocene epoch was marked by rapid oscillations in climate (deMenocal, 2004), which are frequently implicated as drivers of biotic events, particularly in the eastern African hominin fossil record (Vrba, 1985,

1995; Potts, 1998; Potts and Faith, 2015). However, differences in the type and scale of paleoenvironmental data have hampered attempts to establish causal links between environmental change and inferred adaptations in the hominin lineage (Behrensmeyer, 2006; Patterson et al., 2014).

New techniques and data compilations have increased the resolution with which the environmental context of hominin adaptation across space and through time can be understood, especially during the Pleistocene of eastern Africa (Tryon et al., 2014; Faith et al., 2015; Cerling et al., 2013, 2015; Fortelius et al., 2016). The record suggests an overall decrease in woody cover over the past 4 million years, but this trend was spatially heterogeneous depending on basin-scale differences in topography and climate (Feakins et al., 2013; Levin, 2015). The broad-scale opening of eastern African ecosystems is also evident in the mammal fossil record, which suggests an increase in the prevalence of grassland-adapted taxa at many fossil localities (Bobe and Behrensmeyer, 2004). These patterns suggest significant environmental

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dynamism and regional to sub-regional heterogeneity in eastern Africa during the Pleistocene, thus understanding how hominin taxa adapted to localized environmental conditions remains challenging.

1.2. Turkana Basin paleoecosystems

Much of the evidence for environmental change and hominin evolution in eastern Africa comes from fossil deposits in the Turkana Basin of northern Kenya and southern Ethiopia. Sediments from the Shungura, Nachukui and Koobi Fora formations (Fig. 1), to the north, west and east of Lake Turkana respectively, provide a detailed record of more than four million years of ecosystem change (Passey et al., 2010; Bobe, 2011; Levin et al., 2011; Fortelius et al., 2016). Over the past five decades, this region has been the focus of extensive paleontological research and has featured prominently in hypotheses related to the tempo and mode of evolutionary and ecological change in eastern Africa during the Pleistocene (Vrba, 1985; Behrensmeyer et al., 1997; Bobe and Behrensmeyer, 2004; Bobe, 2011; Patterson et al., 2014; Bibi and Kiessling, 2015; Fortelius et al., 2016). Paleoeological research indicates that over the past four million years Turkana Basin paleoecosystems were highly variable with environments on the east side of Lake Turkana more humid and more variable than contemporaneous environments on the west side of the Lake (Bobe and Leakey, 2009; Bobe, 2011; Hernández Fernández and Vrba, 2006; Fortelius et al., 2016). Broad-scale environmental heterogeneity is also supported by the distribution of bovid tribes across the region suggesting that seasonally-arid grasslands were more prevalent at East and West Turkana compared to contemporaneous periods in the northern portions of the Basin associated with an axial fluvial system (Bobe et al., 2007).

Plio-Pleistocene environments in the Turkana Basin consist of a succession of floodplain systems interspersed with lacustrine phases during which large portions of the Basin were under water (Feibel, 2011). One of the best-documented of the latter phases is the formation and subsequent regression of Lorenyang Lake beginning around 2.0 Ma. This lake dominated the Basin for approximately 200 Kyr until regression began around 1.8 Ma. After this, primarily riverine environments are represented in the preserved sedimentary sequences of the east, west, and northern parts of the basin (Brown and Feibel, 1991; Isaac and Behrensmeyer, 1997), but there is evidence in the East Turkana deposits that a substantial body of water persisted until 1.45 Ma (Behrensmeyer et al., 2016a, 2016b). Stable carbon isotopes collected

from pedogenic carbonates dating to this period indicate that the region contained abundant C₄ vegetation (e.g., tropical grasses and sedges) with habitats ranging from wooded-grassland-shrublands to grasslands (Cerling et al., 1988; Wynn, 2004; Quinn et al., 2007, 2013; Levin et al., 2011).

Changes in the physical environment were accompanied by alterations in the composition of mammalian communities in the Turkana Basin between 2 and 1.4 Ma. The paleontological record indicates increased faunal turnover (i.e., species origination and extinction) during this period, with a variety of bovid, suid and primate species first appearing in the region, while many others disappear (Harris, 1991; Behrensmeyer et al., 1997; Bobe and Behrensmeyer, 2004; Jablonski and Leakey, 2008). In general, there is correspondence between different lines of paleoenvironmental evidence (e.g., the pedogenic carbonate isotope record, the mammalian paleontological record) indicating that as open environments became a larger proportion of the paleolandscape, mammalian taxa indicative of open habitats also increased (Bobe and Behrensmeyer, 2004).

1.3. East Turkana hominin ecology

Of all the Turkana Basin deposits, sediments from the Koobi Fora Formation at East Turkana have received the most attention from paleoanthropologists due to the abundance of hominin remains (Wood, 1991; Wood and Leakey, 2011; Leakey et al., 2012) and archaeological evidence of their behavior in the form of lithic artifacts (Behrensmeyer, 1978; Rogers et al., 1994; Isaac and Isaac, 1997; Braun and Harris, 2003; Braun et al., 2008, 2009, 2010; Pobiner et al., 2008). Fossils attributed to the hominin genera *Australopithecus*, *Paranthropus* and *Homo* collected at East Turkana have provided many important insights into the paleobiology of these taxa during the Plio-Pleistocene (Wood, 1991; Wood and Leakey, 2011). Sediments dating to between 2.0 and 1.4 Ma from the Upper Burgi (1.98–1.87 Ma), KBS (1.87–1.56 Ma) and Okote (1.56–1.38 Ma) members (Fig. 1; McDougall and Brown, 2006) document the synchronic and sympatric coexistence of the hominin genera *Homo* and *Paranthropus* as well as the morphological transition from early *Homo* (i.e., *H. habilis*, *H. rudolfensis*) to *Homo erectus/ergaster* (Wood, 1991; Wood and Collard, 1999; Wood and Leakey, 2011; Antón et al., 2014). In addition, these deposits record significant changes in the technology produced by these hominins (Rogers et al., 1994; Isaac and Isaac, 1997; Ludwig and Harris, 1998; Braun and Harris, 2003).

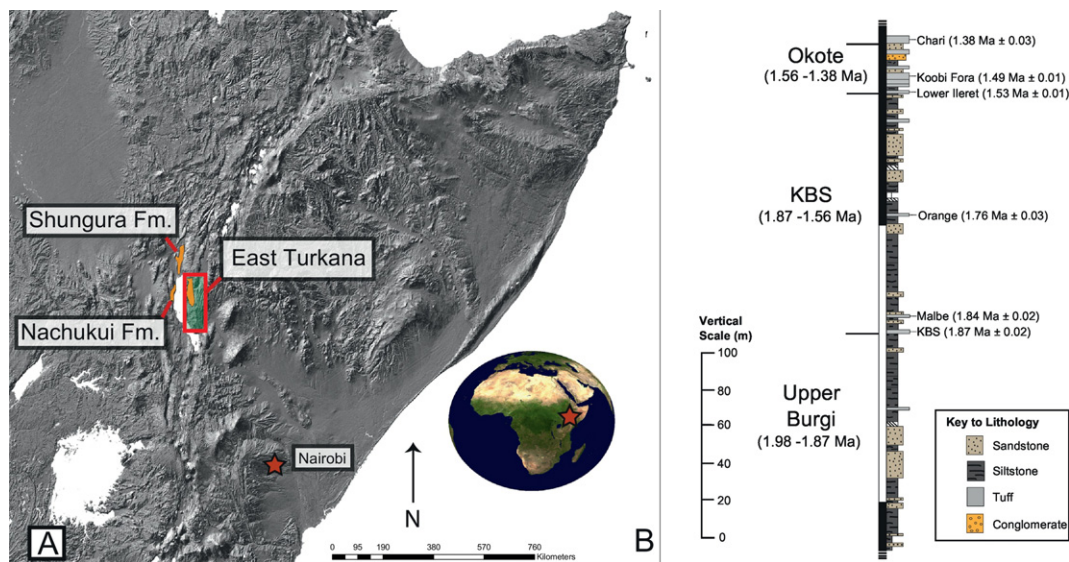


Fig. 1. A) Geographic position of East Turkana, the Shungura, Nachukui and Koobi Fora formations (highlighted in blue within East Turkana box) in eastern Africa; B) Stratigraphic section of Upper Burgi, KBS and Okote Members at East Turkana (modified from Brown and McDougall, 2011). Paleomagnetic polarity is indicated in the thin column to the left of lithologic section. Normal intervals shown in grey; reversed intervals shown in black. Names to the right of the lithologic column refer to selected tuffs with dates.

Although East Turkana fossil assemblages from between 2.0 and 1.4 Ma have been included in studies that investigate ecological changes in the Turkana Basin as a whole (Behrensmeyer et al., 1997; Bobe and Behrensmeyer, 2004; Hernández Fernández and Vrba, 2006; Bobe and Leakey, 2009; Fortelius et al., 2016), only a few of these have focused on understanding the relationship between localized ecosystem evolution and hominin adaptation at East Turkana (Behrensmeyer, 1978; Shipman and Harris, 1988), which is surprising given the prominence of East Turkana hominin remains in hypotheses that seek to explain the paleobiology of hominin lineages during this period (Wood and Strait, 2004; Cerling et al., 2011, 2013). Behrensmeyer (1978) found, based on the limited sample at that time, that at East Turkana *Paranthropus* remains were more commonly associated with fluvial depositional systems, whereas fossils attributed to the genus *Homo* were evenly distributed between both fluvial and lake margin settings. Subsequently, although on a broader geographic scale, Shipman and Harris (1988) used bovid tribe abundances from hominin localities at East Turkana to suggest that *Paranthropus* was more commonly associated with closed/wet habitats, whereas *Homo* likely possessed a broader environmental tolerance.

Most recently, stable isotopes of hominin teeth have been used to investigate patterns of resource use at East Turkana. Stable carbon isotope data from hominin enamel indicate that *Homo* and *Paranthropus* had different dietary ecologies during this period (Cerling et al., 2011, 2013). These data indicate that *Paranthropus* subsisted on almost exclusively C₄ resources (e.g., tropical grasses and sedges) throughout the Upper Burgi, KBS and Okote Members, while *Homo* incorporated a combination of C₄ and C₃ resources (e.g., bushes and trees) into its diet, particularly between 2.0 and 1.65 Ma. More importantly, however, these data also indicate that during this period *Homo* altered its resource use in a way that caused enrichment in carbon and depletion in oxygen isotopic values, a pattern not seen in *Paranthropus*.

1.4. The East Turkana hominin behavioral record

Since the late 1960s, archaeological investigations at East Turkana have yielded many insights into Early Pleistocene hominin behavior. Archaeological research began at East Turkana in 1969 with the discovery of artifacts weathering out of what would later be named the KBS (“Kay Behrensmeyer Site”) tuff (Isaac et al., 1971). Early work focused on understanding the paleogeographic context (Isaac and Behrensmeyer, 1997) and site formation processes (Schick, 1987) of archaeological localities, as well as patterns of stone tool production and discard (Toth, 1987; Harris and Isaac, 1976).

In the decades following this foundational research, many more archaeological localities bearing lithic artifacts and mammalian fossils were discovered in the Turkana Basin (Isaac and Isaac, 1997; Pobiner et al., 2008; Braun et al., 2010; Lepre et al., 2011). This research revealed that the temporal distribution of archaeological localities dating to between 2.0 and 1.4 Ma at East Turkana is uneven. To date, there is one site in the Upper Burgi Member, approximately five in the KBS Member, and more than twenty in the Okote Member. This pattern could be related to 1) increased hominin tool use and discard through this sequence, 2) taphonomic biases relating to depositional environment that limit the record of archaeological localities in the Upper Burgi and KBS members, or 3) a combination of the above. These localities at East Turkana also record the first evidence of aquatic resource exploitation by hominins in eastern Africa (Braun et al., 2010), as well as provide evidence of major transitions in hominin landscape use and tool discard patterns (Rogers et al., 1994; Braun and Harris, 2003; Braun et al., 2008, 2009). Faunal remains from East Turkana archaeological localities have also yielded insights into the carcass processing strategies of early Pleistocene hominins (Bunn, 1981, 1997; Pobiner et al., 2008) and suggest that during this period hominins systematically butchered a wide variety of mammals (Pobiner et al., 2008; Merritt, 2012). Although archaeological localities at East Turkana have already contributed to our

understanding of hominin behavior in eastern Africa between 2.0 and 1.4 Ma, they can be mined for additional information that helps to place hominin behavior within the context of the broader ecosystem.

1.5. Study objectives

This study uses new and previously published faunal abundance data to investigate ecosystem-level change and hominin ecology at East Turkana during the Upper Burgi, KBS and Okote members to address two primary research questions:

1. Does the abundance distribution of major taxonomic groups of mammals change through this period, and can this change be attributed to ecological rather than taphonomic biases?
2. Does faunal material collected from archaeological localities suggest that hominins concentrated their carnivorous foraging behavior on specific taxa or within specific habitats at East Turkana?

2. Materials and methods

To address these research questions, our analyses focus on both paleontological and archaeological collections from East Turkana dating to between 2.0 and 1.4 Ma. First, we use our paleontological dataset to assess temporal changes in the abundance of major mammalian taxonomic groups at East Turkana. Next, we compare the paleontological dataset, which samples the broader mammalian community, with the faunal composition of archaeological localities (i.e., taxa accessed as dietary resources by hominins). We describe the paleontological dataset in Section 2.1, the archaeological dataset in Section 2.2, and in Section 2.3 we set the methodology for comparing datasets that have different collection methodologies and taxonomic resolution.

2.1. Paleontological abundance data

The East Turkana region is divided into discrete spatial units called “Collecting Areas” (see Brown and Feibel, 1991). Mammal fossils from known Collecting Areas were sourced from the Turkana Basin Paleontology Database (Dataset S1; http://naturalhistory.si.edu/ete/ETE_Datasets_Turkana.html), the Turkana Basin Institute Paleontology Database (Fortelius et al., 2016) and from new field collections made by DBP. Fossils without Collecting Area information were excluded from this dataset to increase confidence in the contextual information (both spatial and temporal) associated with each specimen. Fossils with multiple elements assigned to a single museum or field number were counted as a single specimen. Specimens were only included if confidently identified to the generic level (i.e., all cf. taxa were removed), except for the family Bovidae, which were included at the tribal level, and the order Carnivora, which were included at the family level. The dataset includes specimens from 17 mammalian families representing a wide range of body sizes, comprises 4843 specimens, 1820 from the Upper Burgi Member, 2226 from the KBS Member and 797 from the Okote Member (refer to Table S1). For paleoecological analyses we focus on the abundance distributions of 11 of the most abundant and ecologically-informative (i.e., well-studied habitat preferences) taxa at East Turkana, namely the bovid tribes Aepycerotini, Alcelaphini, Antilopini, Bovini, Reduncini and Tragelaphini, the equid genera *Equus* and *Eurygnathohippus*, and the suid genera *Metridiochoerus*, *Notochoerus* and *Kolpochoerus*.

The paleosol carbonate isotope record indicates that the East Turkana ecosystem between 2.0 and 1.4 Ma contained abundant C₄ vegetation. However, this signal could be derived from plants growing along a continuum from low to high water availability (i.e., arid to mesic). To evaluate the relative proportion of these habitats through the East Turkana sequence, we compared the relative abundance of mesic grassland-indicative reduncin bovids to that of arid grassland-

adapted antilopin, alcelaphin and hippotragin bovids (AAH; Vrba, 1975, 1980; Bobe and Eck, 2001). We also used the published East Turkana paleosol carbon isotope record (Cerling et al., 1988; Levin et al., 2011; Quinn et al., 2007, 2013; Wynn, 2004) from this period, which suggests that there is a slight, but significant, increase in the prevalence of C₄ vegetation on the landscape. However, this pattern could be related to preservation or sampling biases in the pedogenic carbonate isotope record (see Levin et al., 2004 for discussion). We also investigated the relative abundance of bovid and non-bovid grassland-indicative taxa through the Upper Burgi, KBS and Okote sequence at East Turkana. Taxa were chosen based upon those described in Bobe and Behrensmeyer (2004) and included: antilopin and alcelaphin bovids, the suid *Metridiochoerus*, the cercopithecoid *Theropithecus* and the family Equidae.

We use composite chi-square and adjusted residual analyses (following Grayson and Delpech, 2003; Faith and Behrensmeyer, 2006) to compare the relative distribution of abundant and ecologically-informative taxa. Adjusted residuals represent standard normal deviates (Everitt, 1977) and allow for an investigation of the underlying differences in taxonomic distribution that are responsible for composite chi-square values.

2.2. Archaeological abundance data

To evaluate the types of taxa accessed by hominins between 2.0 and 1.4 Ma, we compiled a large faunal dataset from East Turkana archaeological localities, each of which includes fauna associated with either cut marked bone, stone artifacts or both. Our archaeological dataset, which consists of material from 13 localities: 1 site from the Upper Burgi Member, 2 from the KBS Member and 10 from the Okote Member (Table 1; Bunn, 1997; Pobiner et al., 2008; Braun et al., 2010), comprises 197 individuals from 12 mammalian families. The archaeological sites included in this analysis are identified using a nomenclature that follows the SASES system (Nelson, 1971). In this system, the prefix “Fx” is used for sites in the Karari subregion, “Fw” for those sites in the Ileret subregion and “Ga” for those in the Koobi Fora subregion (Fig. 2). During the Okote Member, which contains ten of the thirteen sites included here, the Karari subregion sites occur in fluvial floodplain and channel deposits, while Ileret subregion localities occur in fluvial to deltaic deposits that were closer to the paleo-lake than Karari deposits. The Koobi Fora subregion sites occur in fluvial to lake margin depositional environments to the south.

2.2.1. Upper Burgi member (1.98–1.87 Ma)

2.2.1.1. Fwj20. This site, the only published archaeological locality within the Upper Burgi Member, is dated to 1.95 Ma and associated sediments from the site indicate alternating fluvial and lacustrine environments (Braun et al., 2010). Artifacts and faunal material derive from a clay unit that underlies a sand and pebble-rich conglomerate. A significant portion of this assemblage consists of aquatic taxa, some

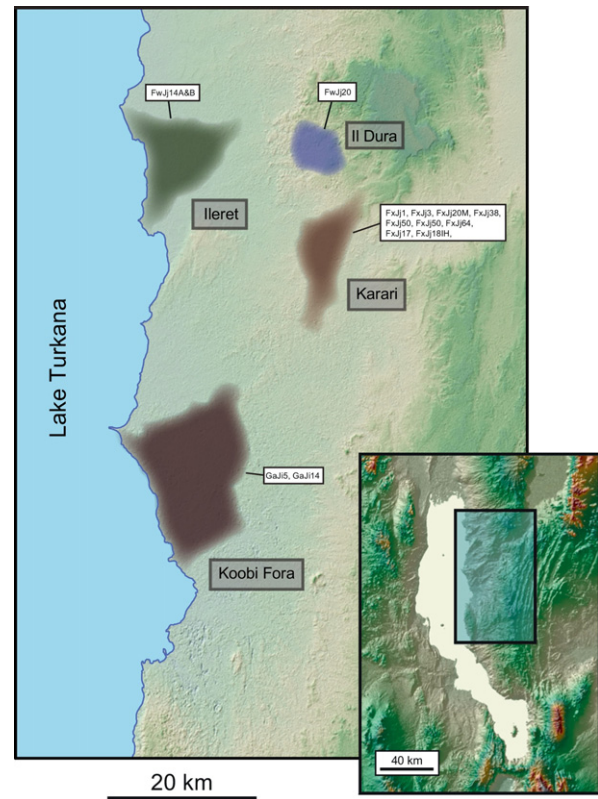


Fig. 2. Spatial distribution of archaeological localities included in this analysis.

with evidence of hominin modification, and thus it represents the first evidence in eastern Africa for the exploitation of this particular food resource by hominins (Braun et al., 2010; Archer et al., 2014).

2.2.2. KBS member (1.87–1.56 Ma)

2.2.2.1. Fxj1. Stone artifacts and faunal remains were found within the 1.87 Ka KBS Tuff dating (see Brown and McDougall, 2011). The site occurs in the upper part of a tuffaceous channel infill within a large, swampy floodplain (Isaac et al., 1997; Isaac and Behrensmeyer, 1997).

2.2.2.2. Fxj3. This site is also known as the “Hippo and Artefact Site” (HAS). The locality is stratigraphically contemporaneous with Fxj1 (Isaac et al., 1997). Artifacts and faunal remains were found in close proximity to the 1.87 Ma KBS Tuff. The faunal material from at Fxj3 is dominated by a single hippo (*Hexaprotodon karumensis*) carcass unearthed in close spatial association with stone artifacts (Isaac et al., 1997).

Table 1

Archaeological localities included in this analysis from the Upper Burgi, KBS and Okote Mbrs. at East Turkana.

Matrix #	Site Name	Age	Member	Artifacts	Cutmarked Bone	Reference
1	Fwj20	1.95	Upper Burgi	Y	Y	Braun et al. (2010)
2	Fwj14A	1.52	Okote	N	Y	Pobiner et al. (2008)
3	Fwj14B	1.5	Okote	N	Y	Pobiner et al. (2008)
4	Gaj14	1.5	Okote	N	Y	Pobiner et al. (2008)
5	Fxj17	1.5	Okote	Y	N	Bunn (1997); Isaac and Behrensmeyer (1997)
6	Fxj18IH	1.5	Okote	Y	Y	Bunn (1997); Isaac and Behrensmeyer (1997)
7	Fxj50	1.55	Okote	Y	Y	Bunn (1997); Isaac and Behrensmeyer (1997)
8	Fxj1	1.87	KBS	Y	N	Bunn (1997); Isaac and Behrensmeyer (1997)
9	Fxj3	1.87	KBS	Y	N	Bunn (1997); Isaac and Behrensmeyer (1997)
10	Fxj38	1.55	Okote	Y	N	Bunn (1997); Isaac and Behrensmeyer (1997)
11	Fxj64	1.55	Okote	Y	Y	Bunn (1997); Isaac and Behrensmeyer (1997)
12	Gaj5	1.55	Okote	N	Y	Bunn (1997); Isaac and Behrensmeyer (1997)
13	Fxj20M	1.5	Okote	Y	Y	Bunn (1997); Isaac and Behrensmeyer (1997)

2.2.3. Okote member (1.56–1.38 Ma)

2.2.3.1. Fxj20M. This site, which contains >4500 bone specimens, is one of the richest collections of faunal material at East Turkana (Bunn, 1997). The locality is part of a larger complex of sites within the Okote Member and dates to approximately 1.5 Ma. Stone artifacts and faunal remains were found heterogeneously distributed within a tuffaceous, sandy-silt layer of sediment that can be traced laterally to the other archaeological sites within the larger complex (Bunn, 1997).

2.2.3.2. Fxj38. This complex of spatially associated sites occurs within a channel setting, and it is notable for the preservation of both *Homo* and *Paranthropus* remains. Its fluvial nature led Harris (1978) to draw only a tentative behavioral association between fossils and artifacts.

2.2.3.3. Fxj50. The site, which is dated to approximately 1.57 Ma, formed under low-to-moderate energy fluvial processes and contains the remains of >20 vertebrate taxa (Bunn et al., 1980). The excellent bone preservation, compared to other localities in the area (e.g., Fxj20M), is likely due to the low-energy conditions in which the site formed.

2.2.3.4. Fxj64. This locality is one of the smallest sites at East Turkana, both in terms of the numbers of stone artifacts and mammal fossils (Bunn, 1997). Due to the high number of stone artifact refits in association with bone fragments, Isaac (1981) suggested that the locality records a short episode of hominin use.

2.2.3.5. Fxj17. The site was excavated from floodplain sediments, and the low abundance of both stone tools and fauna has been interpreted as evidence of a relatively short occupation by hominins (Harris, 1978; Bunn, 1997).

2.2.3.6. Fxj18IH. The site is one of the densest accumulations of stone tools at East Turkana (Isaac and Isaac, 1997). Harris (1978) suggested that the site was slightly winnowed, but had not moved significantly from its original position.

2.2.3.7. Fwjj14 A&B. At both sites, which are in close proximity, faunal material was deposited adjacent to a watercourse during two different depositional phases. At both sites, a large collection of faunal material was excavated but no associated stone artifacts were recovered. Hominin activity at the locality is inferred from the abundance of butchered bone (Pobiner et al., 2008).

2.2.3.8. Gaji5. This 1.45 Ma site, which is located on a lacustrine shoreline, also lacks stone artifacts. It consists of an in situ faunal assemblage associated with many butchered specimens that appear to have recently eroded from the same stratigraphic horizon (Bunn, 1997), and it suggests episodes of meat-eating also occurred in lacustrine shoreline depositional environment.

2.2.3.9. Gaji14. Like Fwjj14A&B and Gaji5, no stone tools were found at this site and hominin presence is inferred by bone modifications indicative of butchery (Pobiner et al., 2008). The faunal assemblage from this c.1.5 Ma (Pobiner et al., 2008) site consists of both in situ and surface fossils. At this site, which has been reconstructed as the infill of small tributaries leading into an antecedent of Lake Turkana, cut-marked bones were found in channel sands of the stratigraphically lower portions of the locality.

2.3. Comparison of East Turkana archaeological and paleontological assemblages

Although existing studies have considered the taxonomic composition of East Turkana archaeological localities dating to between 2.0 and 1.4 Ma, these analyses are often limited to a single (Braun et al.,

2010) site, or to a small number of sites (Bunn, 1997; Pobiner et al., 2008). Also, these analyses focused on hominin carcass processing strategies rather than on the relationship of these assemblages to the broader mammalian community during the period of accumulation. As a result, research has not previously examined whether hominins targeted particular taxa or preferentially foraged in particular environments for hunting/scavenging behaviors. To assess these possibilities, we compared the relative representation of mammalian taxa within archaeological localities to that of East Turkana paleontological assemblages. More specifically, we pooled archaeological localities by geologic member and use the minimum number of individuals (MNI) from both archaeological and paleontological collections to determine the relative representation of taxa in each assemblage. The MNI values for archaeological localities were taken from the published literature (see Section 2.2), while those for paleontological assemblages were determined by removing duplicate specimens attributed to the same individual within the paleontological datasets described in Section 2.1. Although confidently calculating MNI for non-excavated (i.e., surface collected) paleontological specimens is problematic (Badgley, 1986), the data presented here represent a conservative estimate based on well-studied fossils collected from East Turkana deposits.

Taxa with especially low frequencies (MNI < 5) in the archaeological dataset (i.e., Canidae, *Cercocebus*, *Cercopithecus*, *Colobus*, *Hippotragini*, *Notochoerus*, *Papio*, *Rhinocolobus*, *Sivatherium*) were not compared to their corresponding frequencies within paleontological collections (i.e., they were removed from both datasets). Additionally, hominin remains have been targeted for collection at East Turkana resulting in overrepresentation in the paleontological collections relative to their actual abundance in East Turkana surface fossil assemblages (see Bobe and Leakey, 2009 for discussion), so all hominin fossils were removed from both datasets. Finally, due to smaller sample sizes in archaeological collections relative to those from paleontological collections, several taxa from archaeological sites were combined to make the archaeological and paleontological abundances more comparable. Modifications are as follows: *Diceros* and *Ceratotherium* were combined into Rhinocerotidae; *Equus* and *Eurygnathohippus* were merged into Equidae; *Hexaprotodon* and *Hippopotamus* were combined into *Hippopotamus* following Boissarie (2005).

As in our analysis of temporal shifts in taxonomic abundance in the paleontological dataset included here, we use a composite chi-square and adjusted residual analysis (following Grayson and Delpech, 2003; Faith and Behrensmeyer, 2006) to compare the relative abundance of taxa within archaeological and paleontological assemblages.

2.4. Minimizing taphonomic bias

It is important to consider the effect of taphonomic biases on the abundance distributions of East Turkana mammals during this period. Factors like differential preservation of remains (relating to depositional environment or body mass), time averaging and collection biases can obscure the fidelity with which a fossil collection reflects the original animal community (Behrensmeyer et al., 2000). Throughout the analyses presented here we attempt to minimize the effect of taphonomic biases that would affect the relative frequencies of different taxa by also investigating the abundance distribution of more-or-less isotaphonomic groups (Behrensmeyer et al., 1992), focusing specifically on bovid remains. These parallel investigations were performed for our paleontological abundance analyses (Section 2.1), as well as for our comparisons of paleontological and archaeological assemblages (Section 2.3) in an attempt to corroborate the findings of the larger, more taxonomically-inclusive analyses (Section 2.1). For each of these analyses, bovid tribe abundance data were derived from the assemblages associated with their corresponding sections (i.e., Sections 2.1 and 2.3).

3. Results

3.1. Temporal shifts in the paleontological assemblage

The abundance distributions of the taxa from the paleontological collections included in our analyses are included in Table S1. Our analyses suggest significant differences ($\chi^2 = 20.00$, $p = 0.03$) in the relative proportion of ecologically-informative taxa between the Upper Burgi and KBS Members at East Turkana (Fig. 3; Table 2). Our adjusted residual analysis indicates that this pattern is largely driven by abundance shifts within the family Suidae, with *Metridiochoerus* rising in abundance between these members and *Notochoerus* decreasing to the point of local extinction. We find no significant difference ($\chi^2 = 4.58$, $p = 0.92$) between our KBS and Okote datasets. When the Upper Burgi Member abundance distribution of ecologically-informative taxa is compared to that from the Okote Member, however, we find a significant difference ($\chi^2 = 29.26$, $p = 0.001$) that is primarily driven by changes in the family Suidae, with *Notochoerus* becoming locally extinct and *Kolpochoerus* decreasing, while *Metridiochoerus* rises in abundance (Fig. 4A).

Fossils attributed to the tribe Reduncini make up 48% of the bovid assemblage from the Upper Burgi Member, and AAH bovids compose 28% of the assemblage. It should be noted that hippotragin bovid remains constitute < 0.5% of the fossil assemblage from each geologic member analyzed here. Therefore, although included in our analysis of AAH taxa relative to reduncin bovids (Fig. 4B), we do not consider them independently in the analyses that follow. Reduncins decrease in abundance in the KBS Member to 38%, while AAH bovids rise to 33% of the assemblage. This pattern is reversed between the KBS and Okote members, such that in the latter the bovid assemblage is composed of approximately 42% reduncin bovids and 30% AAH bovid taxa. Although changes in the relative proportion of reduncin AAH bovid taxa are insignificant ($p = 0.44$), these data indicate a bovid community dominated by the members of the tribe Reduncini. Our analyses of bovid and non-bovid grassland-indicative taxa suggest a temporal increase in the abundance of C₄ grassland vegetation (Fig. 4C), as represented by our faunal proxies. Grassland-indicative taxa make up 37% of the Upper Burgi sample and 42% of both the KBS and Okote Member assemblages. Finally our analyses indicate that if bovid taxa (excluding hippotragins) are analyzed individually, alcelaphin bovids, as well as the Tribe Bovini, increase while antilopin and aepycerotin bovids decrease through the sequence (Fig. 5).

3.2. Paleontological vs. archaeological assemblages

When the archaeological and paleontological data are pooled from the Upper Burgi, KBS and Okote Members, the abundance of taxa within

archaeological localities is not significantly different ($\chi^2 = 20.38$, $p = 0.09$) from what would be predicted from paleontological collections (Table 3; Fig. 6A). Only one taxon, *Theropithecus*, is significantly less abundant in archaeological localities, which could be an artifact resulting from the targeted collecting of this taxon in the surface fossil assemblage. When these collections are analyzed by geologic member we find that Upper Burgi Member archaeological sample is not significantly different ($\chi^2 = 22.24$, $p = 0.05$) from the corresponding paleontological collection, while those from the KBS ($\chi^2 = 84.20$, $p < 0.05$) and Okote Members ($\chi^2 = 30.33$, $p < 0.05$) are significantly different. In the KBS Member, alcelaphin and antilopin bovids are found more frequently in archaeological sites than in the paleontological collections, while the opposite is true of aepycerotin bovids, *Kolpochoerus*, *Metridiochoerus*, *Giraffa* and both genera of equids. In the Okote Member, alcelaphin bovids are significantly more abundant in archaeological localities, while reduncin bovids are significantly more abundant in the paleontological collections.

When the distribution of bovid tribes is compared between archaeological and paleontological collections (Fig. 6B), we find that KBS and Okote Member assemblages are significantly different ($p < 0.05$), while those from the Upper Burgi are approaching significance ($p = 0.05$). Alcelaphin bovids are consistently overrepresented in archaeological collections, while the opposite is true of reduncins, particularly during the Okote Member. (See Table 4.)

4. Discussion

4.1. Temporal shifts in abundance

4.1.1. Suid abundance through time

Our analyses indicate a major turnover event within the family Suidae at East Turkana between 2.0 and 1.4 Ma (Fig. 4A). These data imply that members of the *Notochoerus* lineage were virtually replaced by the *Metridiochoerus* lineage during the KBS and Okote members. The exception is a single *Notochoerus* specimen from the Okote Member, which, if this identification is correct, is the youngest occurrence of this genus (see Bishop, 2010 for discussion). But given the difficulties in taxonomic identification during this period of suid evolution (see Bishop, 2010), the current allocation of this specimen (KNM-ER 63272) should be treated with some caution. The replacement of *Notochoerus* by *Metridiochoerus* coincides with a general decline in abundance of the *Kolpochoerus* lineage.

Several authors have characterized the dental anatomy of earlier members of the *Notochoerus* lineage as generalized omnivores (Kullmer, 1999) that preferred more closed environments (Bishop, 1994; Bishop et al., 1999). Analyses of the carbon isotope signature

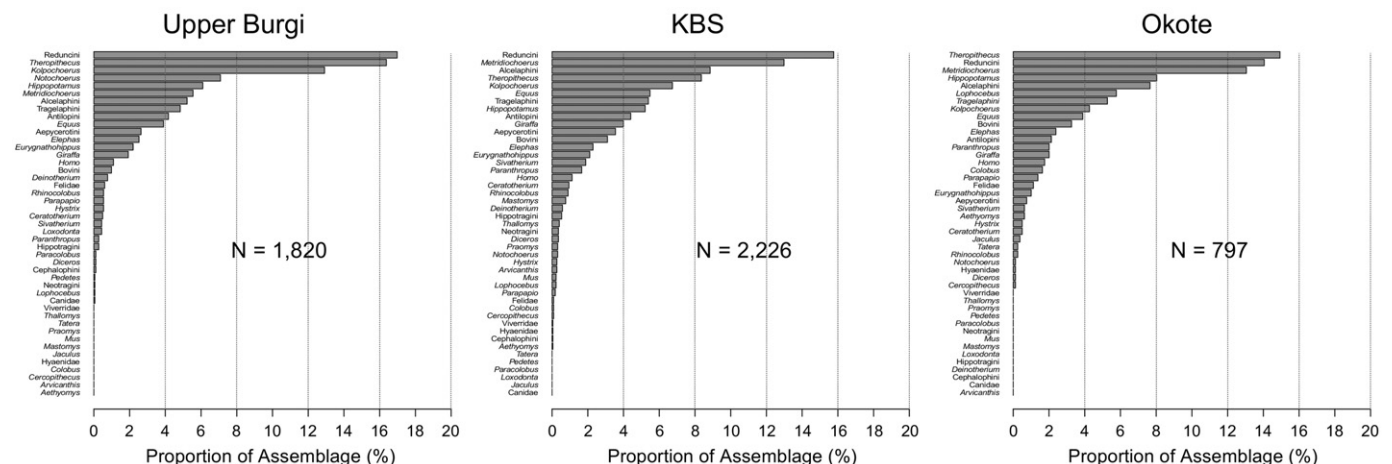


Fig. 3. Abundance distributions of Upper Burgi, KBS and Okote paleontological assemblages included in this analysis.

Table 2

Relative abundance and adjusted residual analysis of Upper Burgi, KBS and Okote Bovidae, Suidae and Equidae.

Taxon	UB % $\chi^2 = 20.00, p = 0.030$	KBS %	AR _{UB-KBS}	KBS % $\chi^2 = 4.58, p = 0.92$	OK %	AR _{KBS-OK}	UB % $\chi^2 = 29.26, p = 0.001$	OK %	AR _{UB-OK}
<i>Aepycerotini</i>	4.0	5.2	0.41	5.2	1.4	-1.52	4.0	1.4	-1.15
<i>Alcelaphini</i>	7.9	12.9	1.17	12.9	13.8	0.19	7.9	13.8	1.35
<i>Antilopini</i>	6.3	6.4	0.04	6.4	3.8	-0.82	6.3	3.8	-0.79
<i>Bovini</i>	1.5	4.5	1.25	4.5	5.9	0.44	1.5	5.9	1.65
<i>Equus</i>	5.9	8.0	0.59	8.0	7.0	-0.26	5.9	7.0	0.33
<i>Eurygnathohippus</i>	3.3	3.1	-0.09	3.1	1.8	-0.58	3.3	1.8	-0.67
<i>Kolpochoerus</i>	19.4	9.8	-1.92	9.8	7.7	-0.53	19.4	7.7	-2.42
<i>Metridiochoerus</i>	8.3	18.9	2.18	18.9	23.5	0.80	8.3	23.5	2.93
<i>Notochoerus</i>	10.7	0.5	-3.15	0.5	0.2	-0.28	10.7	0.2	-3.25
<i>Reduncini</i>	25.5	23.0	-0.43	23.0	25.3	0.39	25.5	25.3	-0.03
<i>Tragelaphini</i>	7.3	7.8	0.15	7.8	9.5	0.42	7.3	9.5	0.57

AR = Adjusted residual values. Bold values > +/- 1.96 are significant at $p < 0.05$.

Notochoerus enamel, however, indicate there that the diet contained significant amounts of open-environment, C₄-plant material (Harris and Cerling, 2002). Researchers have also suggested, based on ecomorphological evidence, that early members of the *Kolpochoerus* lineage inhabited intermediate habitats ranging from grasslands to woodlands (Bishop, 2010). Recent isotopic analyses (Harris and Cerling, 2002; Cerling et al., 2015), however, suggest that between 2.0 and

1.4 Ma, the genus was dominated by individuals subsisting almost exclusively on C₄ vegetation. This finding is intriguing given that *Kolpochoerus* was significantly less hypsodont than the contemporaneous *Notochoerus* and *Metridiochoerus* lineages (Bishop, 2010) and its microwear signature differs from that of any other suid, extant or extinct suid (Bishop et al., 2006). As for the *Metridiochoerus* lineage, although there have been some indications that *Metridiochoerus* taxa

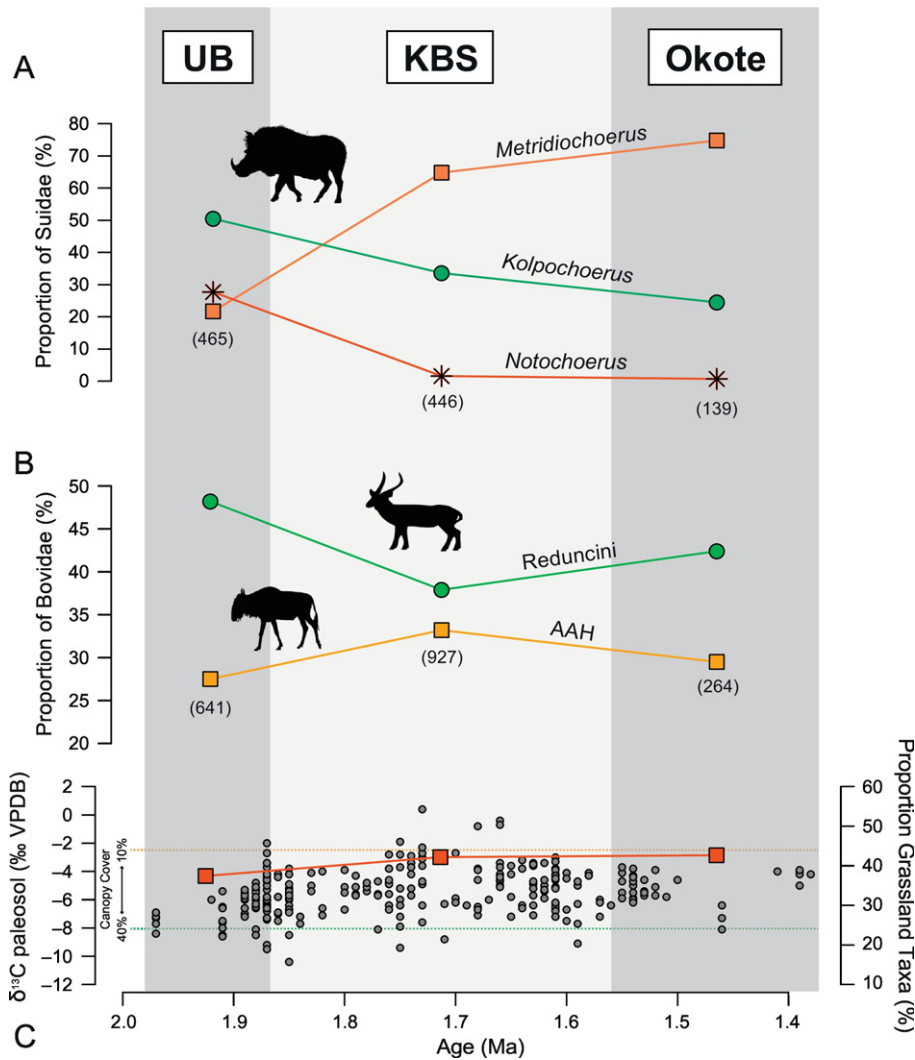


Fig. 4. A) Trends in suid abundance through time at East Turkana. Sample sizes for each interval in parentheses; B) Trends in reduncin and AAH (antilopin, alcelaphin and hippotragin) bovids through time. Sample sizes for each interval in parentheses; C) δ¹³C values of paleosol carbonates (left axis; data from Cerling et al., 1988; Levin et al., 2011; Quinn et al., 2007, 2013; Wynn, 2004) and relative abundance of grassland-indicative taxa (right axis; following Bobe and Behrensmeier, 2004) during the Upper Burgi, KBS and Okote Members at East Turkana.

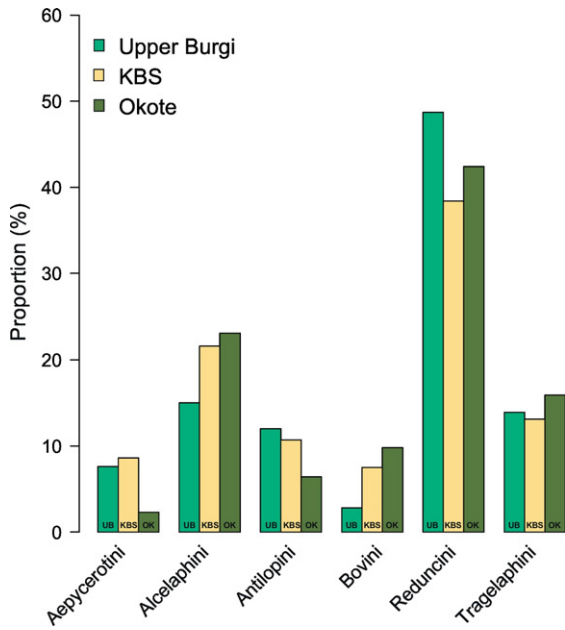


Fig. 5. Abundance of bovid tribes through the Upper Burgi, KBS and Okote Member sequence at East Turkana.

inhabited intermediate habitats (Bishop et al., 1999) and incorporated C_3 vegetation during certain periods of their evolutionary history (Harris and Cerling, 2002), it appears to have been adapted to grassland environments throughout its evolutionary history (Bishop, 2010). At East Turkana between 2.0 and 1.4 Ma *Metridiochoerus* was highly hypsodont, indicating adaptation to water-stressed, arid environments (Liu et al., 2009), and isotopic evidence that is consistent with a diet based almost exclusively on C_4 vegetation (Cerling et al., 2015). The combination of these two lines of evidence support the interpretation that the *Metridiochoerus* lineage was primarily adapted to feeding in open-grassland ecosystems.

The evidence of isotopic overlap in the diets of *Notochoerus*, *Kolpochoerus* and *Metridiochoerus* suggest strategies other than diet for niche partitioning within fossil suids at East Turkana. It is possible that suid taxa, particularly those in the *Metridiochoerus* and *Kolpochoerus* lineages, concentrated on C_4 plants characteristic of different portions of the East Turkana ecosystem. Enamel oxygen isotope analyses of Harris and Cerling (2002) indicate that *Metridiochoerus* was less water-dependent than *Kolpochoerus*. This disparity could suggest that the C_4 signature of *Kolpochoerus* indicates that it fed on well-watered (i.e., mesic) grasses in floodplain or deltaic environments, which is also consistent with the brachydont dentition of *Kolpochoerus* relative to that of *Metridiochoerus*. This is also consistent with occurrence patterns of these two taxa in different depositional environments (Behrensmeyer, 1975). If the decline in *Kolpochoerus* was related to a decrease in mesic grasslands, however, we would also expect bovid taxa characteristic of these environments (i.e., reduncins) to become less prevalent through this same interval. This does not appear to be the case because the abundance of reduncin bovids remains relatively stable throughout this sequence.

Differences in suid ecology, as described above, are a reasonable hypothesis for shifts in the abundance of the three lineages through this sequence, but taphonomic bias may have also played a part. For example, the extreme hypsodonty of the third molar of *Metridiochoerus* (Bishop, 2010) increases the likelihood of their preservation, collection and subsequent identification, thus potentially influencing the prevalence of *Metridiochoerus* dental elements in fossil assemblages relative to other suids. However, given their value as biochronological markers, all suid remains have been selectively collected at East Turkana, so it is unlikely that a preservational bias in favor of *Metridiochoerus* is

Table 3
Comparison of East Turkana archaeological and paleontological assemblages.

Taxon	Arch. All #	Arch. All %	Paleo. All #	Paleo. All %	AR _{Arch.} All-Paleo.All	Arch. OK #	Arch. OK %	Paleo. OK #	Paleo. OK %	AR _{Arch.} OK-Paleo.OK	Arch. KBS #	Arch. KBS %	Paleo. KBS #	Paleo. KBS %	AR _{Arch.} KBS-Paleo.KBS	Arch. UB #	Arch. UB %	Paleo. UB #	Paleo. UB %	AR _{Arch.} UB-Paleo.UB
Antilopini	19	9.6	191	4.5	-1.43	7	6.9	17	2.6	-1.45	7.0	33.3	98.0	4.9	-5.12	7.0	9.6	76.0	4.7	-1.33
Acelaphini	34	17.3	353	8.3	-1.91	21	20.8	61	9.2	-2.30	7.0	33.3	197.0	9.8	-4.04	7.0	9.6	95.0	5.9	-0.97
Aepycerotini	8	4.1	133	3.1	-0.36	4	4.0	6	0.9	-1.40	0.0	0.0	79.0	3.9	2.00	3.0	4.1	48.0	3.0	-0.43
Reduncini	26	13.2	772	18.1	0.95	11	10.9	112	16.9	1.22	2.0	9.5	351.0	17.5	1.65	10.0	13.7	309.0	19.3	1.06
Tragelaphini	14	7.1	250	5.8	-0.36	9	8.9	42	6.3	-0.69	1.0	4.8	120.0	6.0	0.38	5.0	6.8	88.0	5.5	-0.40
Bovini	5	2.5	113	2.6	0.05	5	5.0	26	3.9	-0.36	0.0	0.0	69.0	3.4	1.87	0.0	1.1	18.0	1.1	1.06
Kolpochoerus	13	6.6	419	9.8	0.83	4	4.0	34	5.1	0.39	0.0	0.0	150.0	7.5	2.79	7.0	9.6	235.0	14.7	1.10
Metridiochoerus	11	5.6	494	11.6	1.51	6	5.9	104	15.7	2.21	1.0	4.8	289.0	14.4	2.32	4.0	5.5	101.0	6.3	0.25
Giraffa	9	4.6	140	3.3	-0.47	4	4.0	16	2.4	-0.62	0.0	0.0	89.0	4.4	2.13	4.0	5.5	35.0	2.2	-1.21
Equidae	14	7.1	319	7.5	0.10	8	7.9	39	5.9	-0.57	0.0	0.0	169.0	8.4	2.97	6.0	8.2	111.0	6.9	-0.35
Rhinocerotidae	6	3.0	45	1.1	-0.99	3	3.0	5	0.8	-1.16	1.0	4.8	29.0	1.4	-1.35	3.0	4.1	11.0	0.7	-1.58
Hippopotamus	27	13.7	291	6.8	-1.61	14	13.9	64	9.6	-0.93	2.0	9.5	116.0	5.8	-1.00	11.0	15.1	111.0	6.9	-1.84
Elephantidae	6	3.0	151	3.5	0.19	3	3.0	19	2.9	-0.05	0.0	0.0	64.0	3.2	1.80	3.0	4.1	68.0	4.2	0.05
Theropithecus	5	2.5	603	14.1	2.96	2	2.0	119	17.9	3.77	0.0	0.0	186.0	9.3	3.12	3.0	4.1	298.0	18.6	3.23
Total	197		4274			101		664			21		2006			73		1604		

AR = Adjusted residual values - values > +/- 1.96 are significant at $p < 0.05$.

Bold values were significant at the $p < 0.05$ alpha level.

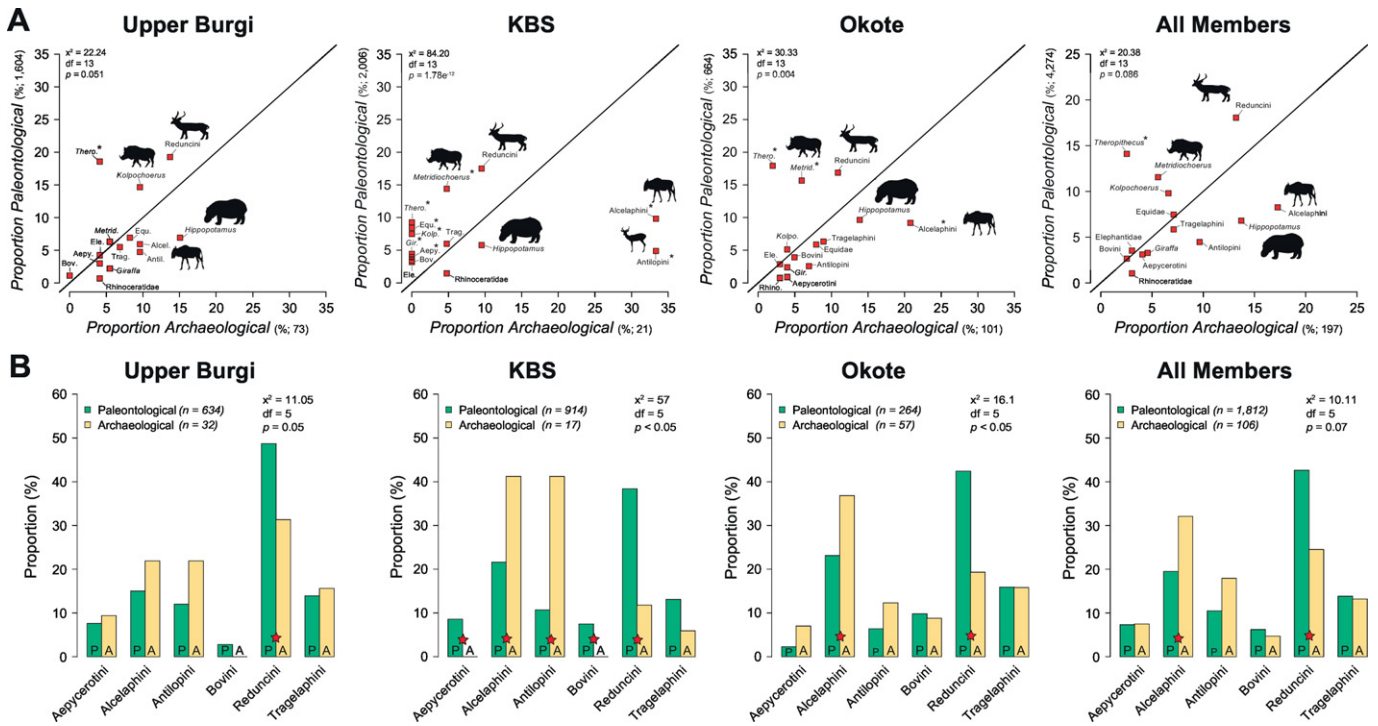


Fig. 6. Comparison of paleontological and archaeological assemblages from the Upper Burgi, KBS and Okote Members as well as all Members compiled. A) Comparison of all taxa; 1:1 line depicted in black; sample sizes in parentheses following axes labels, asterisks denote taxa with significantly different proportional representation between paleontological and archaeological assemblages. B) Comparison of bovid tribe representation in archaeological and paleontological assemblages. Red stars highlight tribes with significant differences between archaeological and paleontological collections based upon adjusted residual analyses (see [Methods](#)).

significant enough to explain the marked shift in the abundance of suid taxa (Fig. 4). Thus, we suggest that taken overall, the evidence supports an important evolutionary transition for suids during the 2.0–1.4 Ma time interval at East Turkana. Further research and standardized collection of surface fossil assemblages could further elucidate the ecological and taphonomic factors that contributed to this pattern.

4.1.2. Bovid abundance through time

Between 2.0 and 1.4 Ma the East Turkana bovid community was dominated by members of the Tribe Reduncini between 2.0 and 1.4 Ma (Fig. 5). In all three members, reduncins make up >38% of the bovid assemblage. Given that in modern ecosystems reduncins are rarely found away from permanent water sources in modern ecosystems (Kingdon, 1982), this suggests that the areas of the East Turkana paleolandscape that preserved fossil vertebrates were dominated by well-watered, mesic grassland environments. Stable carbon isotope data collected from reduncin enamel dating to this period at East Turkana show that the sampled individuals fed almost exclusively on C_4 resources. These two lines of evidence, indicate the persistence of well-watered grasslands at East Turkana during the Upper Burgi, KBS and Okote members. This is consistent with sedimentological evidence for the presence of fluvial/lacustrine environments with relatively high water tables throughout this time (Behrensmeyer, 1975, 1985).

Although we find no significant changes in the bovid abundance distribution through time, our analyses do suggest some consistent patterns. First, reduncin bovinds decrease in abundance between the Upper Burgi and KBS members, while the more arid-adapted AAH bovid tribes increase in prevalence. When AAH taxa are analyzed individually in conjunction with other tribes, alcelaphin bovinds increase at the expense of antilopins throughout the sequence. Given the well-documented dietary adaptations of alcelaphin bovinds, this could indicate an increase in seasonally arid grasslands in portions of the East Turkana paleolandscape between the Upper Burgi and KBS Members. This finding is consistent with existing geological interpretations that suggest

an increase in fluvial environments during the KBS Member (Brown and Feibel, 1991). The combined evidence suggests seasonally well-watered habitats adjacent to river channels and more permanent well-watered lake margin or deltaic habitats that provided suitable habitat for reduncins thus maintaining their populations throughout the 2.0–1.4 Ma time interval. This scenario would have also created abundant, arid-adapted grassland vegetation in portions of the landscape distal to river channels that was more suitable for alcelaphin bovinds.

4.2. Grassland dynamics at east Turkana

Several studies have used the prevalence of AAH bovid taxa as a proxy for the extent of arid grasslands in eastern Africa (e.g., Vrba, 1975, 1980; Bobe, 2011; Bibi and Kiessling, 2015). Our study demonstrates that focusing solely on the abundance of AAH taxa may conceal important information regarding the nature of these C_4 grasslands in eastern Africa during the Plio-Pleistocene. Although AAH bovinds make up a significant portion of the bovid assemblage from East Turkana, they are consistently less prevalent than reduncin bovinds. Additionally, AAH taxa rise in abundance in conjunction with a decline in antilopin bovid abundance (Fig. 5). Although there is a slight decrease between the Upper Burgi and KBS members, the abundance of reduncin bovinds remains relatively stable through the sequence. This suggests that, at least in the paleoecological window provided by the preserved faunas of East Turkana, the prevalence of seasonally arid grasslands increased within a landscape dominated by mesic grasslands. Enamel isotope data from alcelaphin, antilopin and reduncin bovinds dating to this period indicate that C_4 vegetation was a prominent component of the diet of these taxa (Cerling et al., 2015). Therefore, increased C_4 vegetation in a paleoecosystem does not necessarily indicate increased environmental aridity. We need to take into account that the mesic-adapted C_4 vegetation consumed by reduncin bovinds and the arid-adapted C_4 vegetation consumed by alcelaphin and antilopin bovid taxa could produce

Table 4
Comparison of East Turkana archaeological and paleontological bovid assemblages.

Taxon	Arch. All #	Arch. All %	Paleo. All #	Paleo. All %	AR _{Arch. All-Paleo.All}	Arch. OK #	Arch. OK %	Paleo. OK #	Paleo. OK %	AR _{Arch. OK-Paleo.OK}	Arch. KBS #	Arch. KBS %	Paleo. KBS #	Paleo. KBS %	AR _{Arch. KBS-Paleo.KBS}	Arch. UB #	Arch. UB %	Paleo. UB #	Paleo. UB %	AR _{Arch. UB-Paleo.UB}
	$\chi^2 = 10.11, p = 0.07$		$\chi^2 = 16.1, p < 0.05$			$\chi^2 = 57, p < 0.05$		$\chi^2 = 11.05, p = 0.05$			$\chi^2 = 11.05, p = 0.05$									
Antilopini	19	17.9	191	10.5	-1.5	7	12.3	17	6.4	-1.4	7.0	41.2	98.0	10.7	-4.9	7.0	21.9	76.0	12.0	-1.9
Alcelaphini	34	32.1	353	19.5	-2.0	21	36.8	61	23.1	-2.1	7.0	41.2	197.0	21.6	-3.0	7.0	21.9	95.0	15.0	-1.3
Aepycerotini	8	7.5	133	7.3	-0.1	4	7.0	6	2.3	-1.6	0.0	0.0	79.0	8.6	3.0	3.0	9.4	48.0	7.6	-0.5
Bovini	5	4.7	113	6.2	0.5	5	8.8	26	9.8	0.3	0.0	0.0	69.0	7.5	2.8	0.0	0.0	18.0	2.8	1.7
Reduncini	26	24.5	772	42.6	2.7	11	19.3	112	42.4	3.5	2.0	11.8	351.0	38.4	4.3	10.0	31.3	309.0	48.7	2.5
Tragelaphini	14	13.2	250	13.8	0.1	9	15.8	42	15.9	0.0	1.0	5.9	120.0	13.1	1.7	5.0	15.6	88.0	13.9	-0.3
Total	106		1812			57		264			17		914			32		634		

AR = Adjusted residual values - values > +/- 1.96 are significant at $p < 0.05$.

indistinguishable $\delta^{13}\text{C}$ values as documented in pedogenic carbonates from this period (Quinn et al., 2007, 2013; Levin et al., 2011).

Considering the abundance distribution of *Metridiochoerus* in conjunction with that of reduncin and alcelaphin bovids further strengthens the interpretation of an increase in the prevalence of seasonally arid habitats within a mesic grassland-dominated ecosystem between the Upper Burgi and KBS members at East Turkana. If the decline in *Kolpochoerus* between the Upper Burgi and KBS members was related to a decrease in mesic grasslands, then this should have caused a decline in reduncin bovids, which is not the case (Fig. 7). Other possible ecological factors influences on shifts in the abundance of suids remain to be explored through further standardized sampling and analysis of faunal patterns in the Okote Member. Finally, it is important to consider that these taxonomic abundance patterns likely varied across space at East Turkana, particularly given the findings of Patterson et al. (in review) that suggest elevation and distance from the central axis of the Turkana Basin were the primary drivers in determining how C_3 and C_4 vegetation and large mammals were distributed.

4.3. Implications for hominin behavior at East Turkana

The archaeological and stable isotopic record indicates that hominins went through a behavioral transition between 2.0 and 1.4 Ma at East Turkana, including changes in lithic artifact technology, landscape-scale patterns of lithic resource use and dietary ecology (Rogers et al., 1994; Braun and Harris, 2003; Braun et al., 2008; Cerling et al., 2013). Our analyses, which build upon this previous work, suggest that during the later portion of this sequence hominins disproportionately accessed a particular taxonomic subset of the broader mammalian community. When Upper Burgi, KBS and Okote archaeological fauna are pooled, the relative representation of taxonomic groups is not significantly different between the paleontological and archaeological collections. When this relationship is analyzed by geologic member, however, the archaeological fauna from later in the sequence (particularly the Okote Member) suggests that hominins accessed a greater proportion of alcelaphin bovids than would be predicted by the abundance of the latter in paleontological collection. The opposite is true of the cercopithecoid *Theropithecus*, which is relatively rare in the archaeological collections. When only bovid tribes are considered, in the archaeological collections alcelaphin bovids are overrepresented and reduncins are underrepresented.

It is important to consider these results in conjunction with the temporal distribution of archaeological localities at East Turkana. Our dataset suggests an approximately three-fold increase in the number of archaeological localities in the Okote Member relative to those in both the KBS and Upper Burgi members. Although this could reflect biases relating to the increase in fluvial floodplain deposits in the Okote Member, landscape use and inferred diet suggest that the period between the KBS and Okote members at East Turkana was a time of substantial biological evolution in hominins (Wood, 1991; Rogers et al., 1994). Further exploration for archaeological localities in the Upper Burgi and KBS members is needed to understand why there are so many more archaeological sites in the Okote Member than in the KBS and Upper Burgi members.

We consider statistically significant differences between the small KBS archaeological fossil assemblage and the much larger KBS paleontological assemblage as an artifact of low sample size (basically one site, Fxj1). This is not the case, however, for the Okote Member archaeological sample. The results indicate that hominins during this period targeted particular types of animals, or the habitats where these animals lived, within the East Turkana paleoecosystem. The abundance of alcelaphin bovids in archaeological localities during the Okote Member suggests that hominins concentrated their hunting or scavenging behaviors in the more open portions of the East Turkana paleoecosystem. Given this finding, the relative lack of *Metridiochoerus* remains in archaeological sites is interesting given the frequent association of this

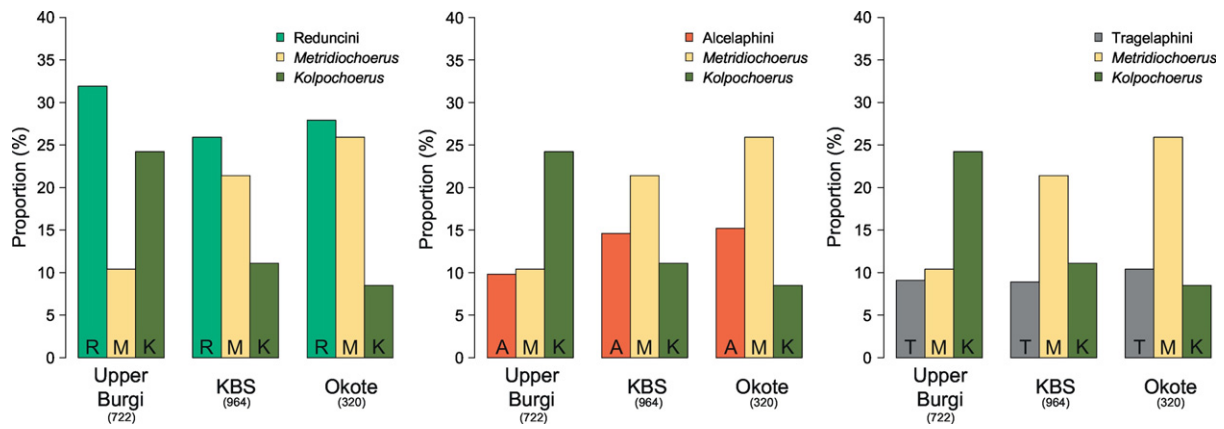


Fig. 7. Comparison of suid genera and selected bovid tribe abundance through the Upper Burgi, KBS and Okote Member sequence at East Turkana.

taxon with open environments (see Bishop, 2010) or the disparity could be related to the taphonomic biases that affect their abundance in paleontological collections (see Section 4.1.1). Existing work suggests archaeological localities dating to this period at East Turkana are more prevalent in wooded-grassland environments (Quinn et al., 2013) and some have interpreted this to indicate that while carcasses were accessed in more open habitats, they were consumed in more wooded habitats (Blumenschine, 1987; Cavallo and Blumenschine, 1989). Neotaphonomic and modern ecological studies indicate that grassland habitats often include high-levels of interspecific competition for carcass resources, suggesting that hominins, particularly during the Okote Member, may have occupied a prominent trophic position in the carnivore paleoguild (Blumenschine, 1987). Higher-resolution paleoenvironmental sampling of East Turkana archaeological localities and paleosols is needed to test this hypothesis.

Finally, these data contribute to existing interpretations of hominin dietary evolution in eastern Africa during this period. The prevalence of open-adapted bovid taxa in East Turkana archaeological localities parallels technological and dietary changes in hominins at other localities in eastern Africa (Monahan, 1996; Egeland and Domínguez-Rodrigo, 2008; de la Torre, 2011; Gallotti, 2013; Pante, 2013; de la Torre and Mora, 2014). All of this indicates that this period was one of significant ecological change in the hominin niche.

4.4. Taphonomy and archaeology

Potential taphonomic biases due to the actions of different bone-collecting agents should be taken into account when using archaeological evidence to reconstruct hominin carnivory. In this study we define an archaeological locality as a site that possesses either stone artifacts, cut marked bones or both. We also assume that hominins were responsible for all of the faunal material collected within archaeological localities, although it is possible that some of the faunal material accumulated in these sites independent of hominin behavior. More detailed analysis of bone modification features, e.g., how hominin-induced cut marks are distributed across mammal taxa, and comparison of skeletal part frequencies in controlled paleontological versus archaeological assemblages, would help assess the strength of the relationship between hominin behavior and archaeological faunal evidence.

It is also important to consider the effect of differences in sample size between our archaeological and paleontological assemblages. Although our dataset represents one of the largest compilations of archaeological faunal abundance data in the Plio-Pleistocene of eastern Africa, it is still substantially smaller than the paleontological collections. Future studies should test the interpretations presented here with additional excavations in poorly sampled temporal intervals at East Turkana.

5. Conclusion

The period between 2.0 and 1.4 Ma in eastern Africa represents an important period in the macroevolution of the morphology and inferred behavior of hominins. Much of the primary evidence comes from hominin fossils and archaeological evidence collected from the Upper Burgi, KBS and Okote members at East Turkana. We used a large compilation of faunal abundance data from paleontological and archaeological collections at East Turkana dated to between 2.0 and 1.4 Ma to investigate large mammal community dynamics and hominin behavior through this sequence. Our analyses of East Turkana bovid taxa indicate an ecosystem dominated by mesic grasslands throughout the Upper Burgi, KBS and Okote members. Changes in suid taxa indicate an increase in the abundance of fossils attributed to the *Metridiochoerus* lineage, the local extinction of the *Notochoerus* lineage and a decline in the abundance of the *Kolpochoerus* lineage. We hypothesize that this transition within Suidae may relate primarily to differences in dietary ecology, with possible amplification of the *Metridiochoerus* trend due to preservational biases. Finally, we find that the taxonomic composition of the large mammal fauna from archaeological localities in the KBS and Okote members is significantly different from contemporaneous paleontological assemblages. We attribute these differences in the KBS Member to small archaeological sample size, but hypothesize that differences in the Okote Member reflect hominin behavior. These data indicate that hominins accessed more alcelaphin carcasses than would be predicted by their representation in paleontological collections. The opposite is true of reduncin carcasses during this period. We suggest that this pattern could be related to hominin prey choice, scavenging behavior, and/or habitat use. These hypothesis needs to be tested with additional standardized paleontological and archaeological sampling at East Turkana. Our findings are consistent with interpretations that suggest the major transition in the diet of genus *Homo* during this period was potentially related to the increased ingestion of C₄-grazing ungulates (see Ungar et al., 2006 for discussion).

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