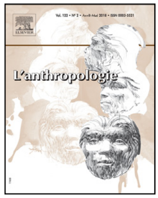
L'anthropologie 127 (2023) 103211

Available online at www.sciencedirect.com
ScienceDirect
et également disponible sur www.em-consulte.com



Original article

The Zambia Rift Valley research project: Exploring human evolution at the crossroads of Africa

Projet de recherche sur la Vallée du Grand Rift de la Zambie : explorer l'évolution humaine au croisement de l'Afrique

Amy L. Rector [a,*], Lucas K. Delezene [b], Thierra K. Nalley [c], Amelia Villaseñor [b]

[a] *Anthropology, School of World Studies, Virginia Commonwealth University, 312, N. Shafer Street, Richmond, VA 23284, United States*
[b] *Department of Anthropology, University of Arkansas, 330, Old Main, Fayetteville, AR 72701, United States*
[c] *Department of Medical Anatomical Sciences, Western University of Health Sciences, 309, E. Second Street, Pomona, CA 91766, United States*

ARTICLE INFO

Article history:
Available online 20 November 2023

Keywords:
Zambia
Pliocene
Pleistocene
Paleoanthropology
Mammal communities
Paleoecology

ABSTRACT

Key evolutionary events in hominin evolution occurred between 3.5 and 2.4 Ma, including the origins of flaked tool technology and the first appearance of the genera *Homo* and *Paranthropus*. This period remains poorly understood, however, because deposits of this age are rarely exposed across Africa. The Luangwa River Valley of eastern Zambia is part of the southernmost extension of the East African Rift System; a fossil femur from South Luangwa, identified as *Theropithecus* cf. *darti*, hints at the presence of fossiliferous beds of this age in the Luangwa Valley. Additionally, Middle Pleistocene fossils and Early and Middle Stone Age artifacts have also been recovered in sediments adjacent to the Luangwa River. Fossils from these deposits could contribute data on the diversification of hominins and mammals that occurred during the Plio-Pleistocene. The Luangwa River also supports a rich modern mammalian

* Corresponding author.
E-mail address: alrector@vcu.edu (A.L. Rector).

https://doi.org/10.1016/j.anthro.2023.103211

community that represents a critical analogue for reconstructing hominin paleoenvironments. However, no systematic ecological characterizations of living or past mammalian communities of the Luangwa River Valley have been completed. The newly initiated Zambia Rift Valley Research Project (ZRVRP) will analyze the ecology of modern and fossil Luangwa River mammalian and human communities using dental microwear, enamel and collagen isotopic composition, the distribution of bones, fossils, and vegetation on the landscape, and archaeological materials. Patterns of paleoenvironmental change, climatic seasonality, and hominin landscape use over time will provide important comparative context for other Plio-Pleistocene sites. Here, we describe the goals, methods, and community engagement of the ZRVRP, and some challenges involved in launching new paleoanthropological field research.

Mots clés :
Zambie
Pliocène
Pléistocène
Paléoanthropologie
Communautés de grands mammifères
Paléoécologie

RÉSUMÉ

Les événements évolutifs, clés de l'évolution des hominines, se sont produits entre 3,5 et 2,4 millions d'années, y compris les origines de la technologie oldowayenne, des industries sur éclats et la première apparition des genres *Homo* et *Paranthropus*. Cette période est encore peu comprise, car les gisements de cet âge sont rarement exposés à travers l'Afrique. La vallée de la rivière Luangwa, dans l'Est de la Zambie, fait partie de l'extension la plus au sud du système du rift Est-Africain ; un fémur fossile découvert dans la partie sud de la rivière Luangwa, identifié comme *Theropithecus* cf. *darti*, suggère la présence de gisements fossilifères de cet âge dans la vallée de la Luangwa. De plus, des fossiles du Pléistocène moyen et des artefacts du Paléolithique inférieur et moyen ont également été retrouvés dans les sédiments adjacents de la rivière Luangwa. Les fossiles de ces gisements pourraient apporter des données sur la diversité des hominines et des mammifères au cours du Plio-Pléistocène. La rivière Luangwa abrite également une riche communauté de mammifères modernes qui représente un parallèle important pour la reconstruction des paléoenvironnements des hominidés. Cependant, aucune caractérisation écologique systématique des communautés de mammifères vivantes ou passées de la vallée de la rivière Luangwa n'a été réalisée. Le projet de recherche sur la vallée du Rift en Zambie (ZRVRP), récemment lancé, analysera l'écologie des communautés de mammifères et d'humains modernes et fossiles de la rivière Luangwa à l'aide de micro-usures dentaires, de la composition isotopique de l'émail et du collagène, des distributions des os, des fossiles et de la végétation dans le paysage et des matériaux archéologiques. Les schémas de changement paléoenvironnemental, la saisonnalité climatique et l'utilisation du paysage par les hominidés au fil du temps fourniront un contexte comparatif important pour d'autres sites du Plio-Pléistocène. Ici, nous décrivons les objectifs, les méthodes et l'engagement communautaire du ZRVRP, ainsi que certains défis liés au lancement de nouvelles recherches paléoanthropologiques sur le terrain.

1. Introduction

Most Pliocene hominin localities are associated with East African Rift System (EARS) exposures in Ethiopia, Kenya, and northern Tanzania (Cerling et al., 2013; Feibel et al., 1989; Haile-Selassie et al., 2015). A handful of Pliocene-aged hominin bearing karstic sites are also documented in South Africa (Pickering et al., 2019). But, in the 2500 km between these two regions, there is virtually no fossil record of hominin evolution. The southern extent of the EARS – in Mozambique, Malawi, and eastern Zambia – would have been an important Pliocene biogeographic connection between eastern, western, and southern Africa; however, it remains comparatively unexplored. Intriguingly, fossils attributed to *Homo* and *Paranthropus* are known from the oldest Pleistocene sediments in Malawi (e.g., Kullmer et al., 1999; Lüdecke et al., 2018). These southernmost branches of the EARS would have been dispersal corridors, may have influenced resource availability for hominins, such as early *Homo* and *Paranthropus*, and provided paleohabitats that are distinct from those in eastern and southern Africa (Cerling et al., 2013; Lüdecke et al., 2018; Joordens et al., 2019; Martínez et al., 2016).

The Zambia Rift Valley Research Project (ZRVRP) is exploring fossil localities in the South Luangwa National Park located in the Luangwa River Valley of eastern Zambia to identify Plio-Pleistocene fossil and archaeological deposits. Additionally, the ZRVRP is systematically characterizing both the ancient and modern habitats associated with the seasonally flooded Luangwa River to provide comparative contexts for the Plio-Pleistocene movement, diversification, and adaptations of hominins. Here, we describe the goals, methods, and community engagement of the ZRVRP, and some challenges involved in launching new paleoanthropological field research.

2. Background

Major central African river valleys would have provided biogeographical connections for ancient hominins and other mammalian groups, offering dispersal corridors into and across regions with variable environments (Bishop et al., 2016; Bobe, 2006; Kingdon, 2003; Strait and Wood, 1999). One such underexplored possible corridor is the Luangwa Valley in eastern Zambia. The Luangwa River, a tributary of the Zambezi, is one the last undammed large rivers in Africa (Gilvear et al., 2000). For more than 700 km, the Luangwa flows unimpeded through a northeast/southwest-oriented valley that is a southern extension of the Eastern African Rift System (Fig. 1). To the west of the river, the rugged Muchinga Escarpment, with a high point ~1,850 m above sea level, forms a steep elevation, rainfall, and temperature gradient relative to the floor of the valley. Most human and animal populations today occupy the lower and warmer valley floor (Anderson et al., 2015). Fossil and archaeological records show that many areas of the southern part of EARS have been inhabited by rich mammalian communities, including hominins, for millennia (e.g., Bromage et al., 1995; Kullmer et al., 2011; Lüdecke et al., 2018, 2016a, 2016b). The Luangwa River Valley, though less studied, also has a rich record of prehistory (e.g., Barham et al., 2011; Bishop et al., 2016).

The Luangwa Valley is also an important center of biodiversity conservation, featuring several large national parks (e.g., South Luangwa and North Luangwa) and numerous protected areas. Given its high modern biodiversity, including numerous endemic species, the Luangwa Valley is an important resource and potential analogue for understanding the environments and ecosystems, especially seasonal riverine habitats, associated with human evolution (Chidakel et al., 2021; Child, 2012). Due to its accessibility and infrastructure, the ZRVRP is focusing on fossil and modern bone collections and mammal community analysis characterizing the stretch of the Luangwa River that is currently protected by the South Luangwa National Park.

2.1. *The Pliocene in the southern EARS*

While a gap in the hominin fossil record exists between ~2.9 and 2.5 Ma at most hominin localities in the eastern Rift (Harrison, 2011; Suwa et al., 1996; Walker et al., 1986), recent discoveries in Ethiopia have pushed the oldest evidence of *Homo* to ~2.8 Ma (Villmoare et al., 2015) and increased the known taxonomic diversity of Pliocene hominins (Haile-Selassie et al., 2015; Levin et al., 2015;

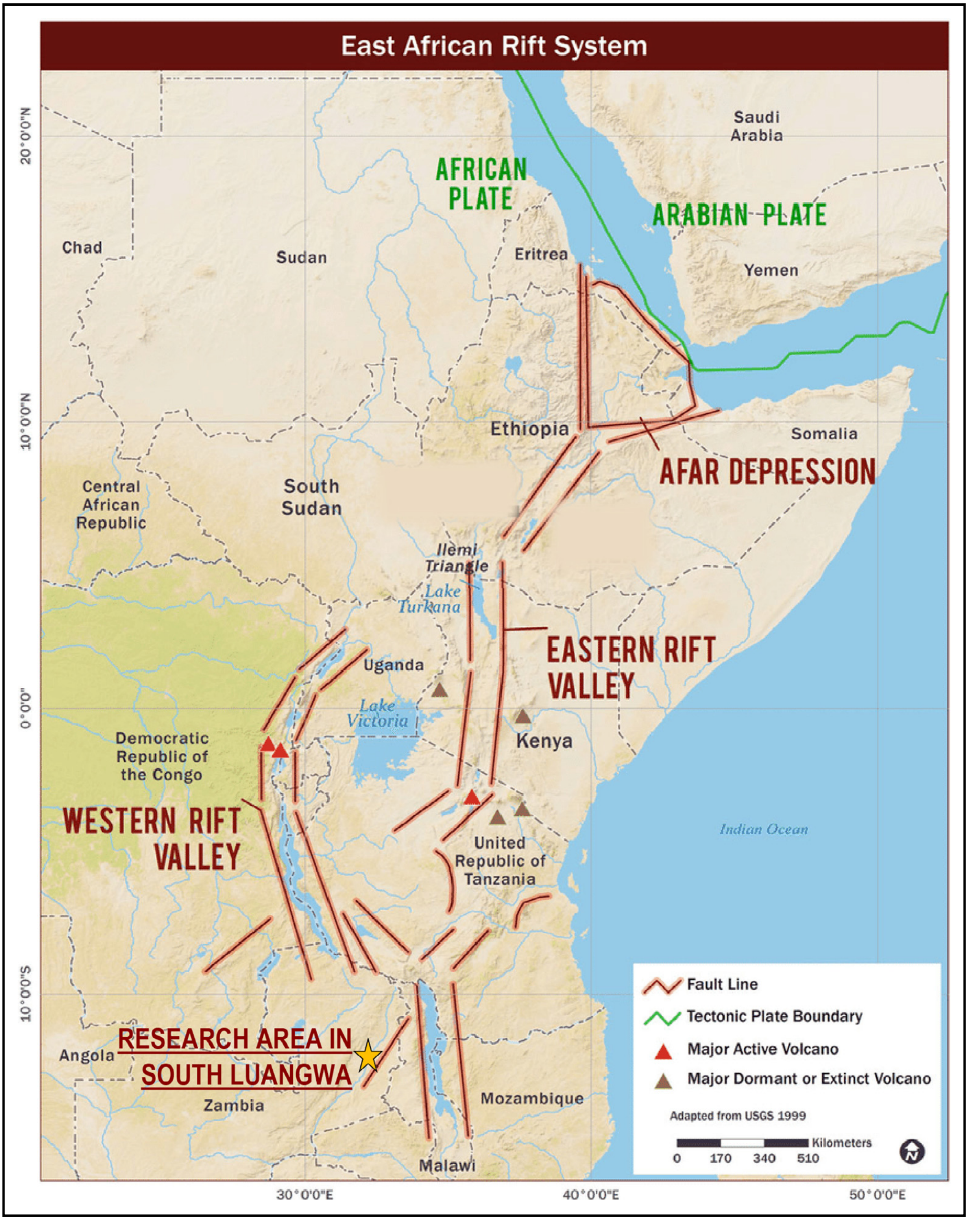


Figure 1. The full extent of the EARS, including the southernmost branch in Zambia. The Luangwa Valley is indicated on the map with a yellow star (adapted from Carr, 2017).
Étendue du système du Rift Est-Africain, y compris la partie la plus au sud de la Zambie. La vallée de Luangwa est indiquée sur la carte par une étoile jaune (adapté de Carr, 2017).

Spoor et al., 2016). Global cooling during this time interval, leading to drastic regional and local climate changes, is proposed as a catalyst for the origin of *Homo* and *Paranthropus* (deMenocal, 2004, 1995; Potts and Faith, 2015; Trauth et al., 2007; Vrba, 1988). But these new discoveries provide only a limited spatial, temporal, and ecological window into the processes that drove these genera to evolve along separate trajectories. Identifying new fossiliferous exposures in the central and southern extent of the EARS would add critical knowledge about regional environmental shifts and provide new environmental and biogeographic context for the striking morphological and phylogenetic diversification of hominins during the late Pliocene and early Pleistocene (Wood and Strait, 2004).

The Karonga Basin of Malawi, an extension of EARS (Fig. 1), provides an example of the potential for sites in central Africa to yield novel information about hominin evolution. There, representatives of early *Homo* and *Paranthropus* are found in sediments that are ~2.4 Ma (Bromage et al., 1995; Kullmer et al., 2011). Stable isotope analyses of the local paleosols and fossil tooth enamel suggest that the paleohabitats and dietary strategies of these south-central African hominins differed from those of their northern counterparts. The Malawi hominins appear to have relied on wetter, more forested habitats and consumed a higher percentage of C_3 plant resources than contemporaneous eastern African hominin taxa. Particularly striking are the carbon isotopes of *Paranthropus* in Malawi, which suggest primarily C_3 resource consumption whereas co-eval *Paranthropus* in eastern Africa specialized in C_4 resources (Lüdecke et al., 2016b). This hints at differing realized niches between *Paranthropus* in the two regions. Further, the environments of eastern Africa are associated with shifting and spreading grasslands, whereas environments in Malawi were more wooded during contemporaneous periods (e.g., Lüdecke et al., 2016b; Ségalen et al., 2007). The combined evidence from eastern Africa and Malawi thus suggests adaptations to versatile ecosystems with varying resource availability and/or selective foraging strategies in early *Homo* and *Paranthropus*. The opportunity to compare paleoenvironments of regional hominin populations provides insight into this behavioral flexibility. Questions about how early *Homo* and *Paranthropus* divided niche space – in both eastern and central Africa – remain (Wood and Strait, 2004). The ZRVRP seeks to fill this critical gap in the fossil and biogeographic record.

2.2. History of paleoanthropological research in Zambia

Relative to long-term eastern and southern Africa exploration, Zambian prehistory receives relatively less attention today. But this has not always been the case. In 1924, the Taung child provided the first fossil of *Australopithecus africanus* and revealed the potential of Africa as a center of hominin evolution, yet hominin fossil discoveries in Zambia were made even earlier. The Broken Hill (Kabwe) cranium and associated fossils were discovered in 1921 as part of mining activities in the British protectorate of Northern Rhodesia (now part of Zambia) (Woodward, 1921). Initially called *Homo rhodesiensis*, the taxonomy (and age) of the Kabwe cranium is a point of debate; it could represent an early member of our species, *Homo sapiens*, or an extinct cousin that lived around 300,000 years ago (Grün et al., 2020; McBrearty and Brooks, 2000; Millard, 2008; Rightmire, 2001). The pioneering archaeological investigations of J. Desmond Clark, based at the Livingstone Museum from 1938 to 1961, revealed stone tool cultures in Zambia that stretch from the recent to the Acheulian (e.g., Clark, 1950). Though the hominin fossil evidence is not abundant in Zambia, the archaeological record reveals the widespread presence of hominins in deep time.

The early archaeological record in Zambia is better documented than the fossil evidence, and includes both Early and Middle Stone Age (MSA) technologies (Barham, 2002; Barham et al., 2011; Barham and Smart, 1996). Indeed, some of the earliest MSA artifacts in Africa (~300 ka) have been collected from Zambian sites, including Broken Hill/Kabwe (Barham et al., 2002), Twin Rivers (Barham et al., 2000; Oakley, 1954), Mumbwa Caves (Barham, 2002; Macrae, 1926), Kalambo Falls (Barham et al., 2015; Clark, 1974, 1969; Duller et al., 2015), and in the Luangwa River Valley (Barham et al., 2015). The early MSA across Africa is noteworthy because it marks the development of new lithic technologies, including blades and backed tools linked with the development of composite tools (Barham, 2002; McBrearty and Brooks, 2000) and, in South Africa, the earliest evidence of hafting at ~300 ka (Wadley and Mohapi, 2008). However, MSA industries of Zambia tend not to be linked morphologically to those from sites located farther to the south, like the Still Bay or Howieson's Poort (Barham et al., 2002; Jacobs and Roberts, 2017), despite evidence that MSA travel and trading networks were quite large (Nash et al., 2016). The archaeological and earlier paleoanthropological records of Zambia thus fall in a uniquely south-central African space with the potential to provide important temporal and spatial continuity between the historically more productive records in southern and eastern Africa.

2.3. Paleontology and archaeology of the Luangwa Valley, Zambia

In the Luangwa River Valley, the discovery of a femur identified as *Theropithecus* cf. *darti* (Elton et al., 2003), a biochronologically sensitive species, suggests that sediments sampling the ~2.9–2.5 Ma time period – key to understanding the origins of *Homo* and *Paranthropus* – are preserved. Fossil *Theropithecus* is widespread in the African fossil record, but *T. darti* is constrained to ~3.5–2.4 Ma (Jablonski and Frost, 2010; Shapiro et al., 2016). Though Elton et al. (2003) analysis correctly highlighted the *Theropithecus* character of the Luangwa femur, our preliminary analysis reveals that it is not shaped like extant *Theropithecus*; it does, however, cluster near other purported femora of extinct *Theropithecus* in shape space (Eason et al., 2023). Additional abundant fossil faunal remains were collected from secondary surface contexts in the Luangwa River Valley through survey efforts between 1999 and 2006, including specimens identified to *Loxodonta*, *Hippopotamus*, *Phacochoerus*, *Potamochoerus*, and *Equus* (Bishop et al., 2016; Villaseñor et al., 2023). Though only the fossil femur purported to belong to *Theropithecus* may sample an extinct taxon, several taxa described by Bishop et al. (2016) do not currently range into the modern Luangwa Valley and river system, suggesting that fossil specimens are eroding from ancient deposits that may be Early and Middle Pleistocene in age.

To date, there is nearly no fossil evidence for hominins in the Luangwa Valley. Along the Luangwa River Valley in South Luangwa National Park, a relatively complete, partially fossilized hominin talus was discovered and attributed to late *Homo* (Bishop et al., 2016). Shape analyses indicate an affinity with modern populations from southern Africa, but an identification as Late Pleistocene *Homo* has not been ruled out (Bishop et al., 2016). In contrast, abundant fossil faunal remains have been recovered from secondary surface contexts on the beaches (point bar deposits) of the Luangwa River. Taxa include both modern and extinct species, suggesting that Pliocene to Middle Pleistocene deposits are sampled along with more recent fauna. The mammalian assemblage produces a paleoenvironmental signal similar to the contemporary river valley environment, although the presence of species no longer found in South Luangwa suggests past shifts in vegetation, possibly linked to environmental change (Bishop et al., 2016).

Paleolithic archaeological sites, some as ancient as one million years old, are documented in the Luangwa Valley and on its margins (Barham et al., 2011; Colton et al., 2021). These sites document the persistent presence of prehistoric "paleolithic" humans and their ancestors who engaged in a hunter/gatherer lifestyle. Iron age artifacts, like pottery, appear in the central Luangwa Valley by ca. 400 AD, and possibly earlier; these are argued to be associated with agricultural populations (Barham and Jarman, 2005), which may have co-occupied the valley with hunter-gatherer groups until the mid-19th century (Barham, 2006).

2.4. Modern environments in the Luangwa Valley

The Luangwa River Valley may serve as an important analog for Plio-Pleistocene hominin habitats. The valley is a target of biodiversity conservation and research; about 16,800 km^2 are currently set aside in four national parks (NPs): North Luangwa, South Luangwa, Luambe, and Lukusuzi. North and South Luangwa NPs are large and mostly bounded on their eastern edges by the Luangwa River; the much smaller Luambe NP sits between them on the eastern side of the river. Though the protected areas are intensely managed today, the mammalian community of the Luangwa Valley is ecologically influenced by recent events associated with the colonial and postcolonial history of Zambia. For example, during the colonial period, increased hunting in the 1800s and 1900s (Langworthy, 1971; Rangeley, 1964) led to dramatic reductions in wildlife population sizes (Marks and Fuller, 2008). Numbers eventually rebounded through conservation efforts, and tourism centered on South Luangwa National Park, established in 1938 (Kumwenda, 2021), increased in the 1990s. The area has since attracted many migrants working in the tourism industry. White and Van Valkenburgh (2022) report an estimated valley population size of 484,940 people in 2015. Today, approximately

62,000 people live within 30 km of the boundary of the South Luangwa National Park, with most settled in Mfuwe (Chidakel et al., 2021). Thus, human-wildlife interactions today are strongly influenced by the National Park and national conservation practices.

In the South Luangwa National Park, the Luangwa is a braided river with a broad floodplain lined with abandoned meanders and oxbow lakes. Though it may nearly disappear during the dry season, the Luangwa River provides water long after its wet season tributaries dry up (Ndhlovu and Balakrishnan, 1991). Modern, and likely past, habitats range from closed (e.g., riparian forests, Miombo woodlands, shrublands, thickets) to more open (e.g., wooded grasslands, grasslands, and seasonally flooded swamps called dambos) (Astle et al., 1969). More than 200 trees species are documented in the parks, including taller trees like baobab (*Adansonia digitata*), fig (*Ficus*), ebony (*Diospyros*), wild mango (*Cordyla africana*), and sausage fruit trees (*Kigelia*). Bushwillows (*Combretum*) and *Terminalia* are trees of intermediate height, and mopane (*Colophospermum mopane*) and miombo (*Brachystegia*) trees form a dense shrubby understory. Phiri (1996) records 189 species of grasses in South Luangwa. Vegetation type today is influenced by substrate such as rocky soils, alluvial deposits, and seasonally flooded oxbows, rainfall, slope, animal disturbance (e.g., elephants browsing) (Astle et al., 1969; Lewis, 1986), and human land-use patterns like agriculture, harvesting of wood for timber, and charcoal production (Gumbo et al., 2013).

The heterogeneity and diversity of habitats along the Luangwa River supports a diverse animal community. More than 400 bird and 60 mammal species are recorded in South Luangwa National Park. Among the large mammals are those of high conservation priority, including two pangolin species, lions, leopards, cheetahs, hyenas, wild dogs, black rhinos, elephants, zebras, and giraffes. The river system supports many small to large herbivores, particularly ungulates, which include more than a dozen antelope species (Ndhlovu and Balakrishnan, 1991). The Luangwa Valley may be a dispersal corridor linking eastern to southern Africa both in deep time and today (e.g., Joordens et al., 2019), but it is also characterized by endemism in several modern taxa (Curry et al., 2019). Thornicroft's giraffes (*Giraffa camelopardalis thornicrofti*), numbering 500–600 individuals, only occur in the Luangwa Valley (Berry and Bercovitch, 2016), but have also been linked genetically to a neighboring population of Masai giraffe (Fennessy et al., 2016). Cookson's wildebeest (*Connochaetes taurinus cooksoni*), numbering less than 10,000, are also a Luangwa Valley endemic (Cotterill, 2000). The Luangwa River is the western edge of the range of the endemic Crawshay's zebra (*Equus quagga crawshayi*) (Curry et al., 2019). Baboons in the region are a hybrid of two (Kinda × yellow; *Papio kindae* × *P. cynocephalus*) or three (Kinda × yellow × grayfoot; *P. kindae* × *P. cynocephalus* × *P. griseipes*) subspecies, but fall in a single mitochondrial clade, suggesting isolation after introgression (Chiou, 2017; Keller et al., 2010). This history of endemism suggests the Luangwa region is an important regional biodiversity reservoir, and likely has been since the Pliocene. Thus, the richness of the mammalian community, the deep history of human habitation, and the associated infrastructure for tourist access to the park make South Luangwa an ideal location for fossil and ecological surveys. Its location in central Africa at the crossroads of Plio-Pleistocene human evolution make it a critical area for exploration and analysis.

3. Methods

3.1. The ZRVRP

Because of its size, existing infrastructure, and conservation history, the focus of the ZRVRP is on the ecology, paleontology, and archaeology of the South Luangwa National Park. The ZRVRP uses a multiproxy approach to locate and identify fossiliferous deposits and to characterize the ecology of the modern and fossil mammalian communities associated with the Luangwa River. We employ several complementary analytical frameworks, including remote sensing and predictive modeling for identification of fossiliferous deposits, systematic surveys of fossiliferous areas, taphonomic surveys of modern skeletal remains distributed on the landscape, and isotopic sampling of dental and skeletal specimens. With the resulting data, we expect to identify patterns of paleoenvironmental change, climatic seasonality, and potential hominin landscape use over time to provide important comparative context for Plio-Pleistocene sites in other areas of the EARS.

3.2. Remote sensing

Because most fossil specimens in South Luangwa are surface finds along the exposed banks of the Luangwa River (Bishop et al., 2016), it is essential that we also locate source deposits to fully describe the lithologic and pedogenic characteristics of the fossil depositional environments. Furthermore, establishing source deposits is necessary to conduct absolute dating analyses as well as to facilitate comparisons to other sites across eastern and central Africa. A classification process was applied to multispectral satellite imagery data covering the survey area (the total area is 40 km^2) by members of the Center for Advanced Spatial Technology (CAST) at the University of Arkansas (https://cast.uark.edu/index.php). The classification process converts relevant satellite multi-band data (light wavelengths: red, blue, green, infrared, thermal infrared, black/white) into categorical classes that relate to different types of land cover (e.g., water, roads, agricultural land, scrub/tree cover, various types of geological outcrops). By using these data, analyzed images (and the subsequently produced maps) are at a higher resolution than previously available for survey. Classification analyses also involve the digitization and orthorectification of geological maps of the area. Known fossil localities from previous field seasons (Barham et al., 2011; Bishop et al., 2016; Elton et al., 2003) are input into the classification model. Similar spectral profiles based on these localities were highlighted across the region of interest and potential survey hotspots indicated for focused survey effort (Njau and Hlusko, 2010). CAST researchers performed more "supervised" classification procedures to adjust the spectral

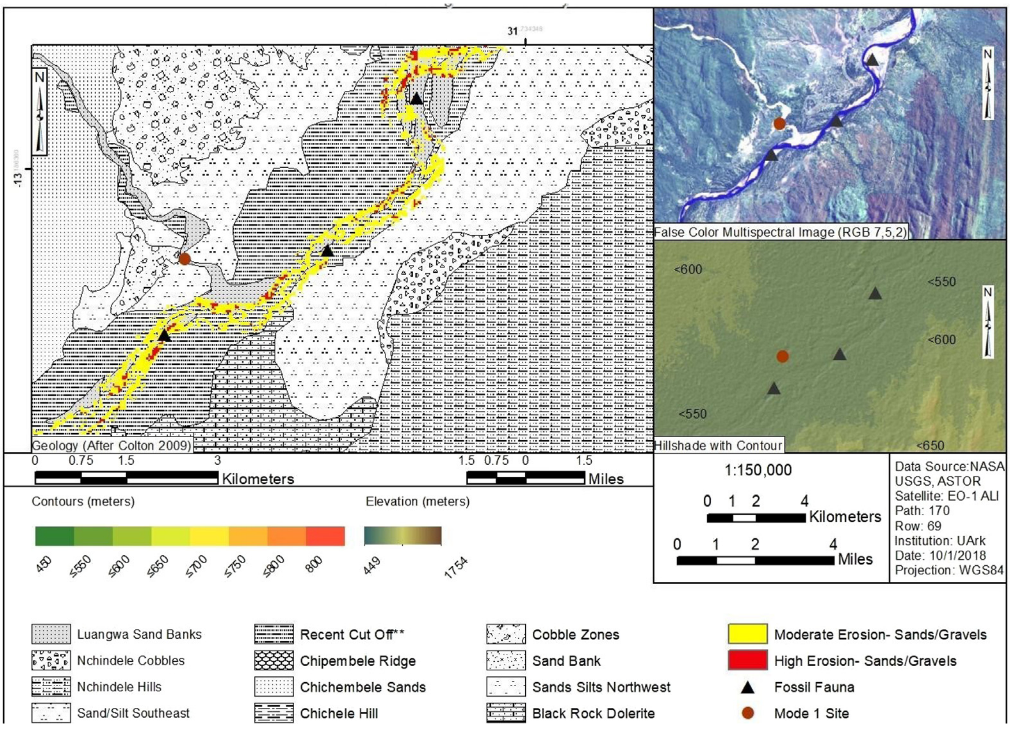


Figure 2. Results of predictive mapping showing areas of Luangwa Valley that are likely fossiliferous, based on previously recovered fossil specimens, archaeology, and landscape elevation and geomorphology (Colton, 2009; Bishop et al., 2016). Areas in yellow and red are predicted to be most highly eroded and likely to expose underlying fossiliferous deposits.

Résultats de la cartographie prévisionnelle montrant les zones de la vallée de Luangwa qui sont probablement fossilifères, sur la base des spécimens fossiles précédemment récupérés, de l'archéologie, de l'altitude du paysage et de la géomorphologie (Colton, 2009 ; Bishop et al., 2016). Les zones en jaune et en rouge sont les plus fortement érodées et sont susceptibles d'exposer des dépôts fossilifères sous-jacents.

classification system to target not only likely surface exposures of fossils, but possible Plio-Pleistocene outcrops as well (sensu Njau and Hlusko, 2010) (Fig. 2).

3.3. Paleontological investigation

Fossil surveys are designed to identify potential localities and ultimately explore the spatial patterns of paleohabitats across the landscape. For the initial ZVRVP survey seasons, we conducted traditional surveys by walking transects in likely areas of fossil recovery, primarily on exposed sandy banks in the Luangwa River (Fig. 3). Each specimen is documented, photographed, and given a unique identification number and GPS position tied to a GIS Pro data collection form that records basic collection information such as taxonomy, skeletal element, stratigraphic context, finder/collector personnel and method, etc. If collected, fossils are bagged with their barcodes so that the provenience data can be directly associated with each specimen.

3.4. Taphonomic studies

The role of taphonomic processes in the formation of bone assemblages has long been recognized as an important factor in analysis and interpretation of the fossil record (Behrensmeyer et al., 1979). However, relatively few projects have implemented long-term systematic survey with the specific goals of characterizing mammalian bone assemblages from modern habitats for use in interpreting potentially analogous paleoecological contexts of our ancestors (Badgley et al., 2018; Behrensmeyer and Miller, 2012; Behrensmeyer and Pobiner, 2004; Pobiner, 2015). The Amboseli National Park project, established in 1975 (Behrensmeyer, 1978), samples classic African savanna ecosystems and has served as the framework for all subsequent studies of modern bone assemblages (Western and

Figure 3. Map of South Luangwa localities where fossil specimens, including those used in the isotope analyses, were discovered in 2022. Photo inset features a fossil of *hippopotamus*.
Carte des localités du sud de Luangwa où des spécimens fossiles, y compris ceux utilisés dans les analyses isotopiques, ont été découverts en 2022. En encart: photo d'un fossile d'hippopotame.

Behrensmeyer, 2009). The longitudinal study at Ol Pejeta, Kenya, was fully established in 2007 (Pobiner, 2015) and builds on earlier pilot census data. The Ol Pejeta ecosystem is at a higher elevation than Amboseli, but provides a comparison of a similar range of savanna habitats as the Amboseli project (Behrensmeyer and Pobiner, 2004). The Doñana National Park project in Spain was established in 2017 to sample a Mediterranean ecosystem including various wetland habitats (Badgley et al., 2018). As yet, no seasonal riverine habitats have been sampled.

Each of these longitudinal taphonomic studies is designed around similar hypotheses testing the relationship between skeletal abundances on the landscape and presence of live mammalian species in the community. They also establish baseline data for the types of assemblages that are expected in modern habitats for comparison with those in the fossil record. Results of these studies, especially from the Amboseli Park Project in Kenya, suggest that relative abundance and distribution of species represented in modern skeletal assemblages accurately reflect the living large herbivore community on the landscape (Western and Behrensmeyer, 2009). Further, differing habitats preserve different taxa and skeletal elements, which has important implications for reconstructions of paleohabitats based on faunal assemblages (Badgley et al., 2018; Behrensmeyer and Miller, 2012). Given that many hominin paleohabitats are interpreted to be riverine contexts (e.g., Du et al., 2019; Reynolds et al., 2011), it is critical that the taphonomic processes unique to these types of habitats are fully identified and explored in undammed river valleys such as the Luangwa.

Following Behrensmeyer and Miller (2012), ZRVRP skeletal surveys are conducted by walking transects that are documented using GPS and recorded in a GIS system. GPS coordinates of beginning and end points of transects are taken, and transect locations are chosen to sample various habitat types along the spectrum of more open to more closed. Skeletal surveys are usually oriented north-south or east-west to make it easier to orient the axis of the transect path, and width of the transect path were dependent on vegetation density (~10 to 50 m on either side of the transect midline). Each transects is walked in a straight line for ~1 km. Five to six completed transects will be conducted in the coming 2023 research season; this sample should accumulate specimens that reflect the most common animals present on a landscape (Behrensmeyer and Dechant Boaz, 1980). While in this first stage of project initiation with the ZRVRP, the target was to identify two different habitat types and conduct at least three transects in each to gather pilot data on differences in relative abundances of skeletal elements in these more open and more closed habitat types (Fig. 4). These data can then be compared to results from other eastern African habitats.

Elements that are in close proximity and likely from the same animal are recorded as one occurrence, though bone scatters are given separate occurrence numbers. Data collected include taxon, age, skeletal parts present, weathering stage, breakage, tooth marks, and degree of burial. GPS coordinates are also collected for each occurrence and location.

3.5. Isotope investigations

Stable carbon and oxygen isotope signals from mammal enamel are proxies for diet and water consumption habits during the life of a mammal, and can reflect climatic conditions and resource availability (e.g., Blumenthal et al., 2017; Cerling et al., 2015). In herbivores, stable carbon isotopes from enamel primarily reflect the consumption of plants using C_3 (trees and shrubs) vs. C_4 (grasses) photosynthetic pathways (e.g., Cerling et al., 2015; Cerling and Harris, 1999). Stable oxygen isotopes from bulk samples can reflect both water dependency within a species as well as seasonality in precipitation and water usage (Blumenthal et al., 2019). Fossil and modern herbivores including pigs, antelopes, hippos, and equids from South Luangwa National Park were included in the analysis.

Samples of enamel were collected from mammal teeth after removing several micrograms of enamel from the surface of the tooth using a Kupa Mani Pro KP-55 handpiece drill with a diamond bit (Blumenthal et al., 2019). Enamel was bulk sampled along the growth axis of each tooth. Enamel samples were pretreated for 15 minutes using 3% H_2O_2 to remove organics, triple rinsed with purified and deionized water, then treated for 15 minutes with 0.1 M buffered acetic acid to remove secondary carbonates and triple rinsed again. Pretreated samples were dried overnight in an oven (~60 °C) and stable carbon and oxygen ratios were analyzed using mass spectrometer at the University of Arkansas using a Thermo Scientific Delta Plus XP isotope ratio mass spectrometer (Bremen, Germany) using

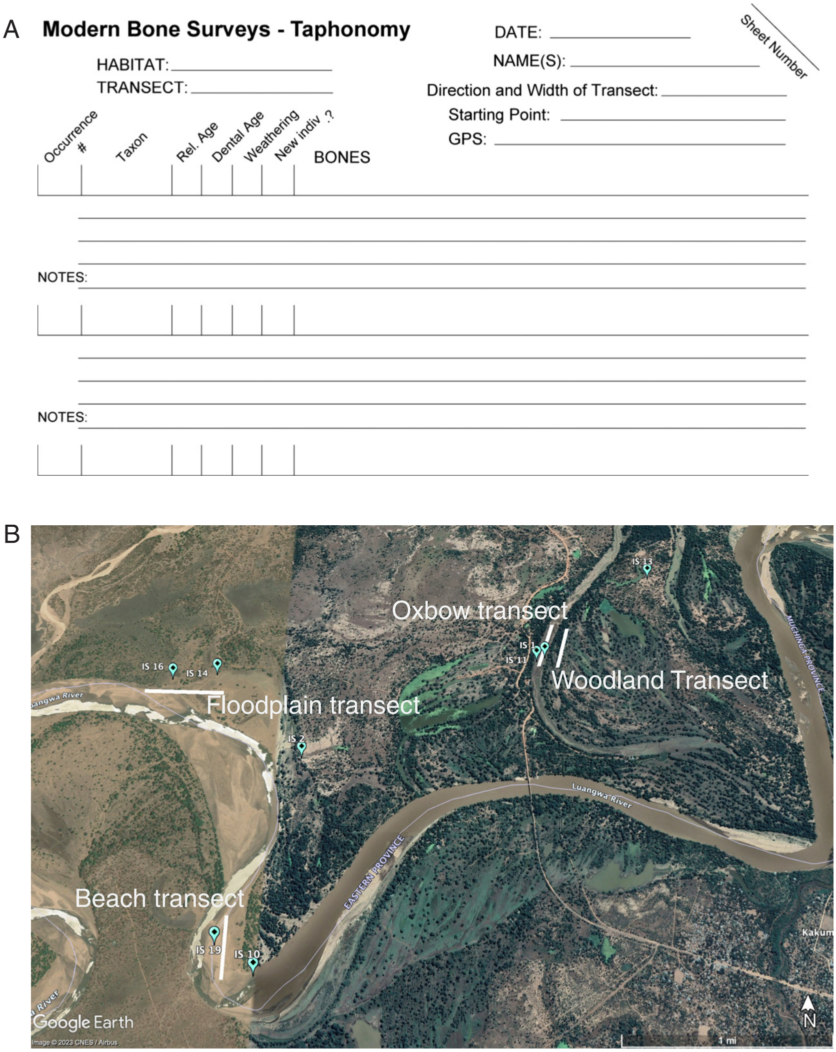


Figure 4. A. Bone Survey form that will be used for future skeletal surveys (Behrensmeyer and Miller, 2012). B. Map of taphonomic transects identified in the 2022 field season (white lines) and modern skeletal samples that were collected from these transects (blue markers).

A. Fiche de description des ossements qui sera utilisée pour les futures analyses de squelettes (Behrensmeyer and Miller, 2012). B. Carte montrant les transects taphonomiques identifiés lors de la campagne de terrain 2022 (lignes blanches) et les échantillons de squelettes modernes qui ont été prélevés à partir de ces transects (marqueurs bleus).

NBS-19 calcite standards. Isotope ratios of the heavy to light carbon isotopes are expressed using delta notation, where $\delta^{13}C = [(R_{sample} - R_{standard})/R_{standard} - 1]*1000$ and $R = {}^{13}C/{}^{12}C$.

4. Results and discussion

4.1. Finding the fossil-bearing strata

Creating predictive mapping models to aid the identification of fossiliferous deposits and ancient structures is quickly becoming a standard part of the vertebrate paleontology and archaeology toolkit (e.g., Anemone et al., 2011; Conroy, 2014). Though not as commonly employed in paleoanthropological field projects, researchers that have applied these methodologies report noteworthy success in the identification of new fossil localities (e.g., Asfaw et al., 1991; Njau and Hlusko, 2010). Predictive modeling increases the likelihood of locating fossils by identifying combinations of geological, geospatial, and spectral features that are common to productive localities. The ZRVRP used predictive mapping (Fig. 2) to correctly identify likely fossiliferous areas and collected additional fossil specimens in short 2019 and 2022 field seasons (Fig. 3). Fossils collected were primarily complete teeth and together represented several species of bovid, including *Aepyceros* and Alcelaphini and Bovini taxa, as well as multiple individual hippopotamid specimens. Fossil horse and pig teeth were also recovered. These fossils were added to the previous collection (e.g., Bishop et al., 2016), and we have sampled many of them for stable carbon and oxygen isotope analyses (Table 1, below).

While none of the Luangwa specimens recovered to date by the ZRVP were found *in situ*, many of the fossils exhibit minimal indication of rolling (Bishop et al., 2016), and in combination with Early Stone Age discoveries (Barham et al., 2011), there is strong evidence that Plio-Pleistocene fossiliferous beds exist within or upstream from the Luangwa Valley. A key area of analysis for ZRVRP is precise dating of both fossils and deposits, as well as locating the source of the fossiliferous materials.

4.2. Taphonomic insights into fluvial systems

Until now, no taphonomic sampling has been carried out in protected seasonal, riverine habitats like those of South Luangwa National Park. Results of the long-term ZRVRP censusing

Table 1
Mammalian specimens sampled for isotopes, identified to age category and taxon, along with their reported isotopic values.
Spécimens de mammifères échantillonnés pour les isotopes, identifiés selon l'âge et le taxon, ainsi que leurs valeurs isotopiques rapportées.

Family	Tribe	Genus	Species	$\delta^{13}C$	$\delta^{18}O$	Age category
Bovidae	Aepycerotini	*Aepyceros*		1.22	36.51	Fossil
	Aepycerotini	*Aepyceros*	*melampus*	−5.57	33.31	Recent
	Alcelaphini			1.14	30.73	Fossil
	Alcelaphini			−0.26	30.89	Fossil
	Bovini			0.05	30.05	Fossil
	Bovini	*Syncerus*	*caffer*	0.61	28.98	Recent
	Bovini	*Syncerus*	*caffer*	−0.93	30.85	Recent
	Bovini	*Syncerus*	*caffer*	0.18	32.15	Recent
	Cephalophini	*Sylvicapra*	*grimmia*	−14.30	31.51	Recent
	Reduncini			2.89	33.01	Fossil
	Reduncini	*Kobus*	*leche*	−4.47	30.60	Recent
	Reduncini	*Kobus*	*vardoni*	−1.55	31.33	Recent
	Reduncini	*Redunca*	*arundinum*	2.86	29.44	Recent
Equidae				2.67	29.44	Fossil
				0.02	31.51	Fossil
		Equus	*guagga*	0.88	32.39	Recent
		Equus	*guagga*	−1.58	34.55	Recent
		Equus	*guagga*	−3.57	33.69	Recent
		Equus	*quagga crawshayi*	0.22	31.65	Recent
		Equus	*quagga crawshayi*	−0.94	33.00	Recent
Hippopotamidae				−2.78	24.47	Fossil
				−3.43	25.20	Fossil
				3.20	30.00	Fossil
		Hippopotamus	*amphibius*	−3.42	24.60	Recent
		Hippopotamus	*amphibius*	−3.94	24.62	Recent
		Hippopotamus	*amphibius*	−4.25	27.52	Recent
Suidae		*Phacochoerus*	*aethiopicus*	−7.11	27.18	Fossil
		Phacochoerus	*aethiopicus*	−0.12	28.75	Recent
		Phacochoerus	*aethiopicus*	−1.11	29.13	Recent
		Phacochoerus	*aethiopicus*	−0.65	29.97	Recent
		Phacochoerus	*aethiopicus*	−5.92	30.02	Recent

project we initiated in 2022 will be directly comparable to those from other habitat types in eastern Africa and will represent a habitat that has not yet been sampled systematically in this way. In our first short field season, we identified several transects across multiple habitats including those associated with a dried oxbow, and successfully collected multiple modern skeletal specimens including crocodiles and bovids (Fig. 4). Continued taphonomic sampling in 2023 promises to be an extremely data-rich investigation in South Luangwa. Additionally, modern dental specimens we collected during taphonomic surveys are included in our isotopic investigation of modern Luangwa habitats.

4.3. Stable Isotopes

Modern and fossil herbivores from South Luangwa National Park (fossil $n = 11$; recent $n = 20$; Table 1) show isotopic differences that may be related to shifting climate patterns or shifting dietary preferences among herbivores in the Luangwa Valley.

The fossil counterparts of the C_4-dominated feeders, *Equus*, *Hippopotamus*, and Reduncini, have more positive $\delta^{13}C$ values than the modern examples by at least 2.9‰ (*Hippopotamus*) and up to 6.3‰ on average (*Equus*) (Fig. 5). The C_4 shift toward more positive values may indicate more C_4 plants in the diet of fossil C_4 specialists and in the case of *Equus* and reduncines, shifting from grazers to hypergrazers. Such differences between fossil and extant fauna have been documented in recent studies of eastern African large mammals (Cerling et al., 2015). Indeed, as found in the work of Cerling et al. (2015), the single fossil impala from Luangwa would be characterized as a hypergrazer, whereas the modern Zambian sample is a mixed feeder. However, Cerling et al. (2003) also found that mesic grasslands, such as the Aberdares in Kenya, have more positive C_4 values than do xeric systems and thus the difference may also indicate that there was a shift in the $\delta^{13}C$ of plants, where some fossil environments may have been more mesic than present environments. Certainly, not all C_4-grazing species show differences in fossil and modern $\delta^{13}C$ values. For example, fossil and modern antelopes from the Bovini tribe are very similar.

Oxygen isotope signals also differ between some of the fossil specimens and their modern representatives. Fossil equids exhibit lower oxygen isotope values than do the modern ones, while the fossil Reduncine has higher oxygen values than its modern counterpart. *Hippopotamus* specimens, whose oxygen isotope signals are thought to reflect meteoric water, show less than a per mil difference between fossil and modern averages, possibly suggesting that the Luangwa River meteoric water values are not significantly different today as compared to the past. However, oxygen isotopes from mammal enamel can be difficult to interpret since they are affected by physiology, the source of the water, temperature, and evaporation (Blumenthal et al., 2019; Levin et al., 2004). The isotope signals from mammalian herbivores presented here thus provide tantalizing differences between fossil and modern counterparts that will be explored in future data collection.

5. Future directions

With our multiproxy approach, the ZRVRP has successfully begun painting the ecological picture of the Luangwa River Valley over time. However, one of the primary challenges of initiating the ZRVRP is the lack of resolution for the dates of the recovered fossils. Evidence from stone tool typologies (Barham et al., 2011) and *Theropithecus* biochronology (Bishop et al., 2016) both suggest the presence of Plio-Pleistocene deposits. Teams working in Luangwa have yet to locate the source deposits of the recovered fossils, though stone tools are found in situ in multiple areas and deposits (Colton et al., 2021). Finding those deposits, determining the age of the fossils recovered ex situ, and confirming the taxonomic allocation of the *Theropithecus* femur are our proximate goals.

To further describe both the ancient and modern environments in Luangwa, we will be investigating mammalian adaptations further through dental microwear texture analysis. This analysis captures differences in diet related to the material properties of the foods consumed in the weeks before death (Delezene et al., 2016). Of particular relevance for studies of African mammalian communities, differences in microwear textures show that browsing and grazing

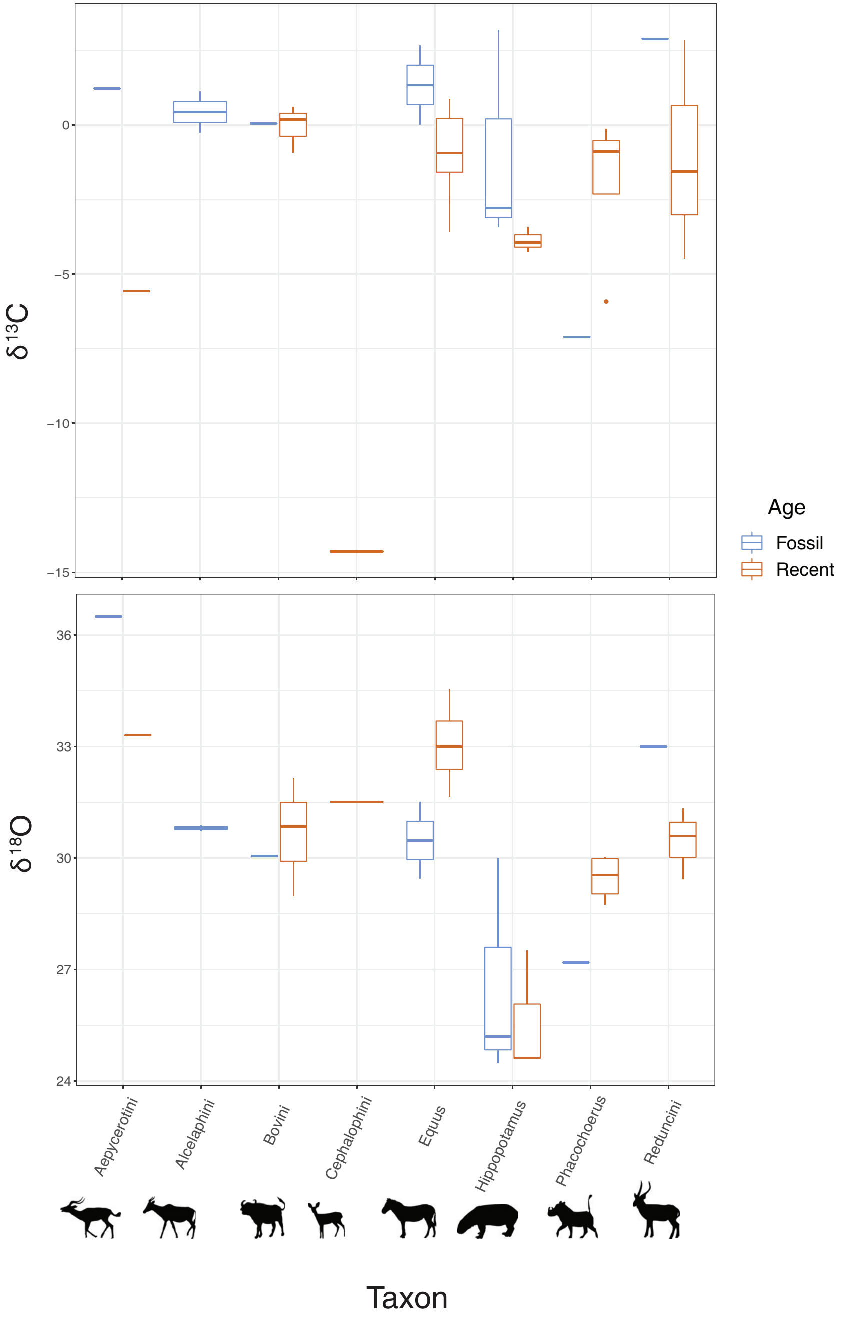


Figure 5. Results of isotopic analyses investigating carbon and oxygen isotopes of fossil and modern mammalian herbivores from South Luangwa. Several fossil taxa indicate a shift towards a more C_4 signal (top panel).

Résultats des analyses isotopiques portant sur les isotopes du carbone et de l'oxygène des fossiles et des mammifères herbivores modernes du sud de Luangwa. Plusieurs taxons fossiles indiquent une évolution vers un signal plus C_4 (panneau du haut).

bovids are easily distinguished (Ungar et al., 2016), hard object feeding African suids separate from grazing suids (Lazagabaster, 2019), and grazing and browsing perissodactyls also distinctly segregate (Hullot et al., 2019; Semprebon et al., 2016). Extensive databases of microwear textures also exist for primates, which show that leaf eating, granivorous, and frugivorous species can be teased apart (e.g., Shapiro et al., 2016). In addition to reconstructing the diets of individual taxa, analyses of fossil mammalian communities (e.g., Ungar et al., 2020), in conjunction with isotopic analyses, provide insights into community structure and niche partitioning (Sponheimer et al., 1999).

One of our overall project goals is to share results with the Luangwa community. The ZRVRP is collaborating with a local Luangwa education and wildlife conservation group, the Chipembele Wildlife Education Trust (www.chipembele.org), to design activities to engage Luangwa community members both in paleoanthropological and modern taphonomic survey. Chipembele provides conservation programs to regional schools to raise awareness about wildlife management and environment preservation, and ZRVRP will integrate their goals and activities with support from our research program. Chipembele also delivers educational and scholarship programs that encourage secondary education in science or wildlife related fields for local students, and our long-term project goals include sustained contributions to these opportunities.

6. Conclusions

The Luangwa River Valley is a productive and critical area for paleoanthropological and ecological investigations. We have discovered and collected fossils, sampled isotopes of both fossil and modern specimens, and initiated a long-term taphonomic survey that will be an important data point for comparisons with other African paleo- and modern habitats. This area is critical for exploration at the crossroads between eastern and southern Africa; there are ecological and evolutionary questions to answer about the biogeography and adaptations of Plio-Pleistocene hominins, as well as more recent question about the movements and relationships of Middle and Later Stone Age humans. The modern habitat of the Luangwa Valley is just as important: as one of the only remaining undammed major seasonal rivers in Africa, the associated mammalian communities and habitats are key analogues for paleoenvironments of our ancestors through time. Long-term goals include analyses of how Zambian mammalian communities have been structured in a seasonal riverine setting over time, how these mammalian community structures and their ecological parameters have responded to climatic shifts in the past, and the paleoecological contexts of regional mammalian diversity and the evolution of our ancestors in central Africa.

Disclosure of interest

The authors declare that they have no competing interest.

Acknowledgements

Thanks to Marie and Lydia Vergamini for assistance with translations, and to two reviewers whose comments improved our manuscript. Special thanks to Isis Mesfin and the other editors for their encouragement and engagement with our work. The Zambian Rift Valley Research project is supported by a Franklin Grant from the American Philosophical Society, and research grants from Virginia Commonwealth University, the University of Arkansas, and Western University of Health Sciences. Our work would not be possible without the active guidance, expertise, and cooperation of the Zambian National Heritage Conservation Commission (NHCC) and the Department of National Parks and Wildlife (DNPW). Joseph Museba provided critical assistance with logistics and permitting. Michael Bisson provided generous encouragement and insight into the early development of the project, for which we are grateful. We would like to give particular recognition and our appreciation to Steve and Anna Tolan for their dedication to conservation and research in the South Luangwa National Park and their steadfast support of projects like ours.

References

Anderson, N.E., Mubanga, J., Machila, N., Atkinson, P.M., Dzingirai, V., Welburn, S.C., 2015. Sleeping sickness and its relationship with development and biodiversity conservation in the Luangwa Valley, Zambia. Parasites & Vectors 8, 224, http://dx.doi.org/10.1186/s13071-015-0827-0.

Anemone, R., Emerson, C., Conroy, G., 2011. Finding fossils in new ways: An artificial neural network approach to predicting the location of productive fossil localities. Evolutionary Anthropology: Issues, News, and Reviews 20 (5), 169–180, http://dx.doi.org/10.1002/evan.20324.

Asfaw, B., Beyene, Y., Semaw, S., Suwa, G., White, T., WoldeGabriel, G., 1991. Fejej: a new paleoanthropological research area in Ethiopia. Journal of Human Evolution 21 (2), 137–143, http://dx.doi.org/10.1016/0047-2484(91)90004-F.

Astle, W.L., Webster, R., Lawrance, C.J., 1969. Land Classification for Management Planning in the Luangwa Valley of Zambia. Journal of Applied Ecology 6 (2), 143–169, http://dx.doi.org/10.2307/2401534.

Badgley, C., Domingo, M.S., Martin-Perea, D., Negro, J., 2018.In: Gateway to the fossil record: the skeletal assemblage of Donana National Park, Spain. Presented at the Society for Vertebrate Paleontology, 78th Annual Meeting. Albuquerque, New Mexico.

Barham, L., 2006. News BaTwa in the mist. Before Farming 4, 1–4, http://dx.doi.org/10.3828/bfarm.2006.4.9.

Barham, L., 2002. Backed tools in Middle Pleistocene central Africa and their evolutionary significance. Journal of Human Evolution 43 (5), 585–603, http://dx.doi.org/10.1006/jhev.2002.0597.

Barham, L.S., Smart, P.L., 1996. Current events. An early date for the Middle Stone Age of central Zambia. Journal of Human Evolution 30 (3), 287–290.

Barham, L., Jarman, C.L., 2005. New Radiocarbon Dates for the Early Iron Age in the Luangwa Valley, Eastern Zambia. Azania: Archaeological Research in Africa 40 (1), 114–121, http://dx.doi.org/10.1080/00672700509480417.

Barham, L.S., Simms, M.J., Gilmour, M., Debenham, N., 2000. Twin Rivers, excavation and behavioural record. In: Barham, L.S. (Ed.), The Middle Stone Age of Zambia, South Central Africa. Western Academic & Specialist Press, Bristol, pp. 165–216.

Barham, L., Llona, A., Stringer, C., 2002. Bone tools from Broken Hill (Kabwe) cave, Zambia, and their evolutionary significance. Before Farming 2, 1–16, http://dx.doi.org/10.3828/bfarm.2002.2.3.

Barham, L., Phillips, W.M., Maher, B.A., Karloukovski, V., Duller, G.A.T., Jain, M., Wintle, A.G., 2011. The dating and interpretation of a Mode 1 site in the Luangwa Valley, Zambia. Journal of Human Evolution 60 (5), 549–570, http://dx.doi.org/10.1016/j.jhevol.2010.12.003.

Barham, L., Tooth, S., Duller, G.A.T., Plater, A.J., Turner, S., 2015. Excavations at Site C North, Kalambo Falls, Zambia: New Insights into the Mode 2/3 Transition in South-Central Africa. Journal of African Archaeology 13 (2), 187–214, http://dx.doi.org/10.3213/2191-5784-10270.

Behrensmeyer, A.K., 1978. Taphonomic and ecologic information from bone weathering. Paleobiology 4 (2), 150–162, http://dx.doi.org/10.1017/S0094837300005820.

Behrensmeyer, A.K., Dechant Boaz, D.E., 1980. The recent bones of Amboseli National Park, Kenya, in relation to East African paleoecology. In: Behrensmeyer, A.K., Hill, A. (Eds.), Fossils in the Making. University of Chicago Press, Chicago, IL, pp. 72–93.

Behrensmeyer, A.K., Pobiner, B.L., 2004. Differing impact of carnivores on bone assemblages in two East African ecosystems. Society for American Archaeology, Montréal, Canada. , https://slideplayer.com/slide/6389856/.

Behrensmeyer, A.K., Miller, J.H., 2012. Building Links Between Ecology and Paleontology Using Taphonomic Studies of Recent Vertebrate Communities. In: Louys, J. (Ed.), Paleontology in Ecology and Conservation. Springer Berlin Heilderberg, Berlin, Heidelberg, pp. 69–91.

Behrensmeyer, A.K., Western, D., Dechant Boaz, D.E., 1979. New Perspectives in Vertebrate Paleoecology from a Recent. Source, Paleobiology 5 (1), 12–21, http://dx.doi.org/10.1017/S0094837300006254.

Berry, P.S.M., Bercovitch, F.B., 2016. Population census of Thornicroft's giraffe *Giraffa camelopardalis thornicrofti* in Zambia, 1973–2003: conservation reassessment required. Oryx 50 (4), 721–723, http://dx.doi.org/10.1017/S003060531500126X.

Bishop, L.C., Barham, L., Ditchfield, P.W., Elton, S., Harcourt-Smith, W.E.H., Dawkins, P., 2016. Quaternary fossil fauna from the Luangwa Valley, Zambia. Journal of Quaternary Science 31 (3), 178–190, http://dx.doi.org/10.1002/jqs.2855.

Blumenthal, S.A., Levin, N.E., Brown, F.H., Brugal, J.P., Chritz, K.L., Harris Jehle G.E., Cerling T.E., J.M., 2017. Aridity and hominin environments. Proceedings of the National Academy of Sciences of the United States of America 114 (28), 7331–7336, http://dx.doi.org/10.1073/pnas.1700597114.

Blumenthal, S.A., Cerling, T.E., Smiley, T.M., Badgley, C.E., Plummer, T.W., 2019. Isotopic records of climate seasonality in equid teeth. Geochimica et cosmochimica acta 260, 329–348, http://dx.doi.org/10.1016/j.gca.2019.06.037.

Bobe, R., 2006. The Evolution of arid ecosystems in eastern Africa. Journal of Arid Environments 66 (3), 564–584, http://dx.doi.org/10.1016/j.jaridenv.2006.01.010.

Bromage, T.G., Schrenk, F., Zonneveld, F.W., 1995. Paleoanthropology of the Malawi Rift: An early hominid mandible from the Chiwondo Beds, northern Malawi. Journal of Human Evolution 28 (1), 71–108, http://dx.doi.org/10.1006/JHEV.1995.1007.

Carr, C.J., 2017.In: River Basin Development and Human Rights in Eastern Africa - A Policy Crossroads. Springer Open, Berkeley, http://dx.doi.org/10.1007/978-3-319-50469-8.

Cerling, T.E., Harris, J.M., 1999. Carbon isotope fractionation between diet and bioapatite in ungulate mammals and implications for ecological and paleoecological studies. Oecologia 120, 347–363, http://dx.doi.org/10.1007/s004420050868.

Cerling, T.E., Harris, J.M., Passey, B.H., 2003. Diets of East African bovidae based on stable isotope analysis. Journal of Mammalogy 84 (2), 456–470, http://dx.doi.org/10.1644/1545-1542(2003)084<0456:DOEABB>2.0.CO;2.

Cerling, T.E., Manthi, F.K., Mbua, E.N., Leakey, L.N., Leakey, M.G., Leakey Brown F.H., Grine F.E., Hart J.A., Kaleme P., Roche H., Uno K.T., Wood B.A., Klein R.G., R.E., 2013. Stable isotope-based diet reconstructions of Turkana Basin hominins. Proceedings of the National Academy of Sciences of the United States of America 110 (26), 10501–10506, http://dx.doi.org/10.1073/pnas.1222568110.

Cerling, T.E., Andanje, S.A., Blumenthal, S.A., Brown, F.H., Chritz, K.L., Harris Hart J.A., Kirera F.M., Kaleme P., Leakey L.N., Leakey M.G., Levin N.E., Manthi F.K., Passey B.H., Uno K.T., J.M., 2015. Dietary changes of large herbivores in the Turkana Basin, Kenya from 4 to 1 Ma. Proceedings of the National Academy of Sciences of the United States of America 112 (37), 11467–11472, http://dx.doi.org/10.1073/pnas.1513075112.

Chidakel, A., Child, B., Muyengwa, S., 2021. Evaluating the economics of park-tourism from the ground-up: Leakage, multiplier effects, and the enabling environment at South Luangwa National Park, Zambia. Ecological Economics 182, 106960, http://dx.doi.org/10.1016/j.ecolecon.2021.106960.

Child, B., 2012. The Emergence of Parks and Conservation Narratives in Southern Africa. In: Child, B., Suich, H., Spenceley, A. (Eds.), Evolution Innovation in Wildlife Conservation. Routledge, London, pp. 37–52, http://dx.doi.org/10.4324/9781849771283-10.

Chiou, K.L., 2017. Population genomics of a baboon hybrid zone in Zambia. Dissertation. Washington University of St. Louis, St Louis.

Clark, J.D., 1974. Kalambo Falls Prehistoric Site II. The Later Prehistoric Cultures. Cambridge University Press, Cambridge.

Clark, J.D., 1969. Kalambo Falls Prehistoric Site I. The Geology, Palaeoecology, and Detailed Stratigraphy of the Excavations. Cambridge University Press, Cambridge.

Clark, J.D., 1950. The Stone Age cultures of Northern Rhodesia: with particular reference to the cultural and climatic succession in the upper Zambezi Valley and its tributaries, Monograph series (South African Archaeological Society). South African Archaeological Society, Claremont, Cape.

Colton, D., 2009. An Archaeological and Geomorphological Survey of the Luangwa Valley, Zambia. British Archaeological Reports Oxford Ltd, Oxford78, [coll. Cambridge Monographs in African Archaeology]

Colton, D., Whitfield, E., Plater, A.J., Duller, G.A.T., Jain, M., Barham, L., 2021. New geomorphological and archaeological evidence for drainage evolution in the Luangwa Valley (Zambia) during the Late Pleistocene. Geomorphology 392, 07923, http://dx.doi.org/10.1016/j.geomorph.2021.107923.

Conroy, G.C., 2014. Walking back the cat: Unsupervised classification as an aid in "remote" fossil prospecting. Evolutionary Anthropology: Issues, News, and Reviews 23 (5), 172–176, http://dx.doi.org/10.1002/evan.21422.

Cotterill, F., 2000. Reduncine antelope of the Zambezi basin. In: Timberlake, J.R. (Ed.), Biodiversity of the Zambezi Basin Wetlands. Biodiversity Foundation for Africa and The Zambezi Society, Bulawayo, pp. 145–199.

Curry, C.J., White, P.A., Derr, J.N., 2019. Genetic analysis of African lions (*Panthera leo*) in Zambia support movement across anthropogenic and geographical barriers. PLoS One 14 (5), e0217179, http://dx.doi.org/10.1371/journal.pone.0217179.

Delezene, L.K., Teaford, M.F., Ungar, P.S., 2016. Canine and incisor microwear in pitheciids and Ateles reflects documented patterns of tooth use. American Journal of Physical Anthropology 161 (1), 6–25, http://dx.doi.org/10.1002/ajpa.23002.

deMenocal, P.B., 2004. African climate change and faunal evolution during the Pliocene–Pleistocene. Earth and Planetary Science Letters 220 (1–2), 3–24, http://dx.doi.org/10.1016/S0012-821X(04)00003-2.

deMenocal, P.B., 1995. Plio-Pleistocene African Climate. Science 270 (5233), 53–59, http://dx.doi.org/10.1126/science.270.5233.53.

Du, A., Robinson, J.R., Rowan, J., Lazagabaster, I.A., Behrensmeyer, A.K., 2019. Stable carbon isotopes from paleosol carbonate and herbivore enamel document differing paleovegetation signals in the eastern African Plio-Pleistocene. Review of Palaeobotany and Palynology 261, 41–52, http://dx.doi.org/10.1016/j.revpalbo.2018.11.003.

Duller, G.A.T., Tooth, S., Barham, L., Tsukamoto, S., 2015. New investigations at Kalambo Falls, Zambia: Luminescence chronology, site formation, and archaeological significance. Journal of Human Evolution 85, 111–125, http://dx.doi.org/10.1016/j.jhevol.2015.05.003.

Eason, L.H., Delezene, L.K., Nalley, T.K., Rector, A.L., Getahun, D., Plavcan, J.M., 2023. Patterns of morphological variation among cercopithecid fossil femora. Presented at the American Association of Biological Anthropologists, 92nd Annual Meeting, Reno, Nevada

Elton, S., Barham, L., Andrews, P., Smith, G.H.S., 2003. Pliocene femur of *Theropithecus* from the Luangwa Valley, Zambia. Journal of Human Evolution 44 (1), 133–139, http://dx.doi.org/10.1016/S0047-2484(02)00198-7.

Feibel, C.S., Brown, F.H., McDougall, I., 1989. Stratigraphic context of fossil hominids from the Omo group deposits: Northern Turkana Basin, Kenya and Ethiopia. American Journal of Physical Anthropology 78 (4), 595–622, http://dx.doi.org/10.1002/ajpa.1330780412.

Fennessy, J., Bidon, T., Reuss, F., Kumar, V., Elkan, P., Nilsson, M.A., et al., 2016. Multi-locus analyses reveal four giraffe species instead of one. Current Biology 26 (18), 2543–2549, http://dx.doi.org/10.1016/j.cub.2016.07.036.

Gilvear, D., Winterbottom, S., Sichingabula, H., 2000. Character of channel planform change and meander development: Luangwa River, Zambia. Earth Surface Processes and Landforms 25 (4), 421–436, http://dx.doi.org/10.1002/(SICI)1096-9837(200004)25:4<421::AID-ESP65>3.0.CO;2-Q.

Grün, R., Pike, A., McDermott, F., Eggins, S., Mortimer, G., Aubert Kinsley L., Joannes-Boyau R., Rumsey M., Denys C., Brink J., Clark T., Stringer C., M., 2020. Dating the skull from Broken Hill, Zambia, and its position in human evolution. Nature 580 (7803), 372–375, http://dx.doi.org/10.1038/s41586-020-2165-4.

Gumbo, D., Moombe, K.B., Kabwe, G., Ojanen, M., Ndhlovu, E., Sunderland Kandulu M.M., T.C.H., 2013. Dynamics of the charcoal and indigenous timber trade in Zambia: A scoping study in Eastern, Northern and Northwestern provinces. Center for International Forestry Research (CIFOR), Nairobi, Kenya, http://dx.doi.org/10.17528/cifor/004113.

Haile-Selassie, Y., Gibert, L., Melillo, S.M., Ryan, T.M., Alene, M., Deino Levin N.E., Scott G., Saylor B.Z.,, A., 2015. New species from Ethiopia further expands Middle Pliocene hominin diversity. Nature 521 (7553), 483–488, http://dx.doi.org/10.1038/nature14448.

Harrison, T., 2011. Hominins from the Upper Laetolil and Upper Ndolanya Beds, Laetoli. In: Harrison, T. (Ed.), Paleontology and Geology of Laetoli: Human Evolution in Context. Volume 2: Fossil Hominins and the Associated Fauna. Springer, Dordrecht, pp. 141–188.

Hullot, M., Antoine, P.O., Ballatore, M., Merceron, G., 2019. Dental microwear textures and dietary preferences of extant rhinoceroses (Perissodactyla, Mammalia). Mammal research 64, 397–409, http://dx.doi.org/10.1007/s13364-019-00427-4.

Jablonski, N.G., Frost, S., 2010. Cercopithecoidea. In: Werdelin, L., Sanders, W. (Eds.), Cenozoic Mammals of Africa. University of California Press, Berkeley, Calif, pp. 393–428, http://dx.doi.org/10.1525/california/9780520257214.003.0023.

Jacobs, Z., Roberts, R.G., 2017. Single-grain OSL chronologies for the Still Bay and Howieson's Poort industries and the transition between them: Further analyses and statistical modelling. Journal of Human Evolution 107, 1–13, http://dx.doi.org/10.1016/j.jhevol.2017.02.004.

Joordens, J.C.A., Feibel, C.S., Vonhof, H.B., Schulp, A.S., Kroon, D., 2019. Relevance of the eastern African coastal forest for early hominin biogeography. Journal of Human Evolution 131, 176–202, http://dx.doi.org/10.1016/j.jhevol.2019.03.012.

Keller, C., Roos, C., Groeneveld, L.F., Fischer, J., Zinner, D., 2010. Introgressive hybridization in southern African baboons shapes patterns of mtDNA variation. American journal of physical anthropology 142 (1), 125–136, http://dx.doi.org/10.1002/ajpa.21209.

Kingdon, J., 2003. Lowly Origin: Where, When and Why Our Ancestors First Stood Up. Princeton University Press, Princeton, N.J.

Kullmer, O., Sandrock, O., Abel, R., Schrenk, F., Bromage, T.G., Juwayeyi, Y.M., 1999. The first *Paranthropus* from the Malawi Rift. Journal of Human Evolution 37 (1), 121–127, http://dx.doi.org/10.1006/jhev.1999.0308.

Kullmer, O., Sandrock, O., Kupczik, K., Frost, S.R., Volpato, V., Bromage Schrenk F., T.G., 2011. New primate remains from Mwenirondo, Chiwondo Beds in northern Malawi. Journal of Human Evolution 61 (5), 617–623, http://dx.doi.org/10.1016/J.JHEVOL.2011.07.003.

Kumwenda, S., 2021. Whose heritage? The state, local communities and game in South Luangwa National Park (SLNP) of eastern Zambia, 1890–2001. Thesis. The University of Zambia, Lusaka.

Langworthy, H.W., 1971. Swahili Influence in the Area between Lake Malawi and the Luangwa River. African Historical Studies 4 (3), 575–602, http://dx.doi.org/10.2307/216530.

Lazagabaster, I.A., 2019. Dental microwear texture analysis of Pliocene Suidae from Hadar and Kanapoi in the context of early hominin dietary breadth expansion. Journal of Human Evolution 132, 80–100, http://dx.doi.org/10.1016/j.jhevol.2019.04.010.

Levin, N., Quade, J., Simpson, S.W., Semaw, S., Rogers, M., 2004. Isotopic evidence for Plio-Pleistocene environmental change at Gona, Ethiopia. Earth and Planetary Science Letters 219 (1–2), 93–110, http://dx.doi.org/10.1016/S0012-821X(03)00707-6.

Levin, N.E., Haile-Selassie, Y., Frost, S.R., Saylor, B.Z., 2015. Dietary change among hominins and cercopithecids in Ethiopia during the early Pliocene. Proceedings of the National Academy of Sciences of the United States of America 112 (40), 12304–12309, http://dx.doi.org/10.1073/pnas.1424982112.

Lewis, D.M., 1986. Disturbance effects on elephant feeding: evidence for compression in Luangwa Valley, Zambia. African Journal of Ecology 24 (4), 227–241, http://dx.doi.org/10.1111/j.1365-2028.1986.tb00367.x.

Lüdecke, T., Kullmer, O., Wacker, U., Sandrock, O., Fiebig, J., Schrenk Mulch A., F., 2018. Dietary versatility of Early Pleistocene hominins. Proceedings of the National Academy of Sciences of the United States of America 115 (52), 13330–13335, http://dx.doi.org/10.1073/pnas.1809439115.

Lüdecke, T., Mulch, A., Kullmer, O., Sandrock, O., Thiemeyer, H., Fiebig, J., Schrenk, F., 2016a. Stable isotope dietary reconstructions of herbivore enamel reveal heterogeneous savanna ecosystems in the Plio-Pleistocene Malawi Rift. Palaeogeography, Palaeoclimatology, Palaeoecology 459, 170–181, http://dx.doi.org/10.1016/j.palaeo.2016.07.010.

Lüdecke, T., Schrenk, F., Thiemeyer, H., Kullmer, O., Bromage, T.G., Sandrock, O., Fiebig, J., Mulch, A., 2016b. Persistent C3 vegetation accompanied Plio-Pleistocene hominin evolution in the Malawi Rift (Chiwondo Beds, Malawi). Journal of Human Evolution 90, 163–175, http://dx.doi.org/10.1016/J.JHEVOL.2015.10.014.

Macrae, F.B., 1926. The Stone Age in Northern Rhodesia. Native Affairs Departement Annual 4, 67–68.

Marks, S.A., Fuller, R.J., 2008. Enclosure of an Important Wildlife Commons in Zambia. International Association for the Study of the Commons Conference at University of Gloucestershire, Cheltenham, UK1–21, . https://dlc.dlib.indiana.edu/dlc/handle/10535/828.

Martínez, L.M., Estebaranz-Sánchez, F., Galbany, J., Pérez-Pérez, A., 2016. Testing dietary hypotheses of East African hominines using buccal dental microwear data. PLoS One 11 (11), e0165447, http://dx.doi.org/10.1371/journal.pone.0165447.

McBrearty, S., Brooks, A.S., 2000. The revolution that wasn't: a new interpretation of the origin of modern human behavior. Journal of human evolution 39 (5), 453–563, http://dx.doi.org/10.1006/jhev.2000.0435.

Millard, A.R., 2008. A critique of the chronometric evidence for hominid fossils: I. Africa and the Near East 500–50 ka. Journal of Human Evolution 54 (6), 848–874, http://dx.doi.org/10.1016/J.JHEVOL.2007.11.002.

Nash, D.J., Coulson, S., Staurset, S., Ullyott, J.S., Babutsi, M., Smith, M.P., 2016. Going the distance: Mapping mobility in the Kalahari Desert during the Middle Stone Age through multi-site geochemical provenancing of silcrete artefacts. Journal of Human Evolution 96, 113–133, http://dx.doi.org/10.1016/j.jhevol.2016.05.004.

Ndhlovu, D.E., Balakrishnan, M., 1991. Large herbivores in Upper Lupande Game Management Area, Luangwa Valley, Zambia. African Journal of Ecology 29 (2), 93–104, http://dx.doi.org/10.1111/j.1365-2028.1991.tb00990.x.

Njau, J.K., Hlusko, L.J., 2010. Fine-tuning paleoanthropological reconnaissance with high-resolution satellite imagery: the discovery of 28 new sites in Tanzania. Journal of Human Evolution 59 (6), 680–684, http://dx.doi.org/10.1016/j.jhevol.2010.07.014.

Oakley, K.P., 1954. Study Tour of Early Hominid Sites in Southern Africa, 1953. The South African Archaeological Bulletin 9 (35), 75–87, http://dx.doi.org/10.2307/3887032.

Phiri, P.S.M., 1996. The floristic status of grasses of the South Luangwa National Park and the Lupande area. In: van der Maesen, L.J.G., van der Burgt, X.M., van Medenbach de Rooy, J.M. (Eds.), The Biodiversity of African Plants: Proceedings XIVth AETFAT Congress 22-27 August 1994, Wageningen, The Netherlands. Springer, Netherlands, Dordrecht, pp. 224–230, http://dx.doi.org/10.1007/978-94-009-0285-5_30.

Pickering, R., Herries, A.I.R., Woodhead, J.D., Hellstrom, J.C., Green, H.E., Paul Ritzman T., Strait D.S., Schoville B.J., Hancox P.J., B., 2019. U–Pb dated flowstones restrict South African early hominin record to dry climate phases. Nature 565 (7738), 226–229, http://dx.doi.org/10.1038/s41586-018-0711-0.

Pobiner, B.L., 2015. New actualistic data on the ecology and energetics of hominin scavenging opportunities. Journal of Human Evolution 80, 1–16, http://dx.doi.org/10.1016/J.JHEVOL.2014.06.020.

Potts, R., Faith, J.T., 2015. Alternating high and low climate variability: The context of natural selection and speciation in Plio-Pleistocene hominin evolution. Journal of Human Evolution 87, 5–20, http://dx.doi.org/10.1016/j.jhevol.2015.06.014.

Rangeley, W.H.J., 1964. The Portuguese. The Nyasaland Journal 17 (1), 42–71., https://www.jstor.org/stable/29545962.

Reynolds, S.C., Bailey, G.N., King, G.C.P., 2011. Landscapes and their relation to hominin habitats: case studies from *Australopithecus* sites in eastern and southern Africa. Journal of human evolution 60 (3), 281–298, http://dx.doi.org/10.1016/j.jhevol.2010.10.001.

Rightmire, G.P., 2001. Patterns of hominid evolution and dispersal in the Middle Pleistocene. Quaternary International 75 (1), 77–84, http://dx.doi.org/10.1016/S1040-6182(00)00079-3.
Ségalen, L., Lee-Thorp, J.A., Cerling, T., 2007. Timing of C4 Grass Expansion across Sub-Saharan Africa. Journal of Human Evolution 53 (5), 549–559, http://dx.doi.org/10.1016/j.jhevol.2006.12.010.
Semprebon, G.M., Rivals, F., Solounias, N., Hulbert, R.C., 2016. Paleodietary reconstruction of fossil horses from the Eocene through Pleistocene of North America. Palaeogeography, Palaeoclimatology, Palaeoecology 442, 110–127, http://dx.doi.org/10.1016/j.palaeo.2015.11.004.
Shapiro, A.E., Venkataraman, V.V., Nguyen, N., Fashing, P.J., 2016. Dietary ecology of fossil *Theropithecus*: Inferences from dental microwear textures of extant geladas from ecologically diverse sites. Journal of Human Evolution 99, 1–9, http://dx.doi.org/10.1016/J.JHEVOL.2016.05.010.
Sponheimer, M., Reed, K.E., Lee-Thorp, J.A., 1999. Combining isotopic and ecomorphological data to refine bovid paleodietary reconstruction: a case study from the Makapansgat Limeworks hominin locality. Journal of Human Evolution 36 (6), 705–718, http://dx.doi.org/10.1006/jhev.1999.0300.
Spoor, F., Leakey, M.G., O'Higgins, P., 2016. Middle Pliocene hominin diversity: *Australopithecus deyiremeda* and *Kenyanthropus platyops*. Philosophical transactions of the Royal Society of London. Series B, Biological sciences 371 (1698) , http://dx.doi.org/10.1098/rstb.2015.0231 [20150231].
Strait, D.S., Wood, B.A., 1999. Early hominid biogeography. Proceedings of the National Academy of Sciences of the United States of America 96 (96), 9196–9200, http://dx.doi.org/10.1073/pnas.96.16.9196.
Suwa, G., White, T.D., Howell, F.C., 1996. Mandibular postcanine dentition from the Shungura Formation, Ethiopia: Crown morphology, taxonomic allocations, and Plio-Pleistocene hominid evolution. American Journal of Physical Anthropology 101 (2), 247–282, http://dx.doi.org/10.1002/(SICI)1096-8644(199610)101:2<247::AID-AJPA9>3.0.CO;2-Z.
Trauth, M.H., Maslin, M.A., Deino, A.L., Strecker, M.R., Bergner, A.G.N., Dühnforth, M., 2007. High- and low-latitude forcing of Plio-Pleistocene East African climate and human evolution. Journal of Human Evolution 53 (5), 475–486, http://dx.doi.org/10.1016/j.jhevol.2006.12.009.
Ungar, P.S., Abella, E.F., Burgman, J.H.E., Lazagabaster, I.A., Scott, J.R., Delezene Manthi, F.K., Plavcan, J.M., Ward, C.V., L.K., 2020. Dental microwear and Pliocene paleocommunity ecology of bovids, primates, rodents, and suids at Kanapoi. Journal of Human Evolution 140, 102315, http://dx.doi.org/10.1016/j.jhevol.2017.03.005.
Ungar, P.S., Scott, J.R., Steininger, C.M., 2016. Dental microwear differences between eastern and southern African fossil bovids and hominins. South African Journal of Science 112 (3–4), 1–5, http://dx.doi.org/10.17159/sajs.2016/20150393.
Villaseñor, A., Delezene, L.K., Nalley, T.K., Museba, J., Rector, A.L., 2023. Zambian large mammal stable isotopes show dietary flexibility at high trophic levels: implications for the hominin niche. Presented at the American Association of Biological Anthropologists, 92nd Annual Meeting, Reno, Nevada.
Villmoare, B., Kimbel, W.H., Seyoum, C., Campisano, C.J., DiMaggio, E.N., Rowan Braun, D.R., Arrowsmith, J.R., Reed, K.E.,, J., 2015. Paleoanthropology. Early *Homo* at 2.8 Ma from Ledi-Geraru, Afar, Ethiopia. Science 347 (6228), 1352–1355, http://dx.doi.org/10.1126/science.aaa1343.
Vrba, E.S., 1988. Late Pliocene Climatic Events and Hominid Evolution. In: Grine, F.E. (Ed.), Evolutionary History of the Robust Australopithecines. Aldine de Gruyter, New York, pp. 405–426.
Wadley, L., Mohapi, M., 2008. A Segment is not a Monolith: evidence from the Howiesons Poort of Sibudu, South Africa. Journal of Archaeological Science 35 (9), 2594–2605, http://dx.doi.org/10.1016/J.JAS.2008.04.017.
Walker, A., Leakey, R.E., Harris, J.M., Brown, F.H., 1986. 2.5-Myr *Australopithecus boisei* from west of Lake Turkana, Kenya. Nature 322 (6079), 517–522, http://dx.doi.org/10.1038/322517a0.
Western, D., Behrensmeyer, A.K., 2009. Bone assemblages track animal community structure over 40 years in an African savanna ecosystem. Science 324 (5930), 1061–1064, http://dx.doi.org/10.1126/science.1171155.
White, P.A., Van Valkenburgh, B., 2022. Low-cost forensics reveal high rates of non-lethal snaring and shotgun injuries in Zambia's large carnivores. Frontiers in Conservation Science 3, 803381, http://dx.doi.org/10.3389/fcosc.2022.803381.
Wood, B., Strait, D., 2004. Patterns of resource use in early *Homo* and *Paranthropus*. Journal of Human Evolution 46 (2), 119–162, http://dx.doi.org/10.1016/j.jhevol.2003.11.004.
Woodward, A.S., 1921. A new cave man from Rhodesia, South Africa. Nature 108 (2716), 371–372, http://dx.doi.org/10.1038/108371a0.