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Using Bovid Tribe Proportions to Reconstruct Paleoenvironments of Eastern African
Paranthropus

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Sciences
In Biology at Virginia Commonwealth University

By

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Abstract

There are conflicting theories about the eating habits and corresponding environmental needs of *Paranthropus boisei* and *Paranthropus aethiopicus*, two species of extinct hominins that existed ~2.8 to ~1 Ma in eastern Africa. *Paranthropus* species are well-known for their unusually large molars and sagittal crest (a bony ridge on their skulls which allowed for large chewing muscle attachments), these skeletal adaptations were once thought to be due to their feeding on hard foods; however, recent isotope data and dental microwear studies question the simplicity of this assumption. This has revealed a gap in our understanding of the environmental needs of our ancestral cousins. Fossil antelope (bovids) are often used to reconstruct environments that supported communities found at sites throughout Africa because of their extreme specialization to specific habitats. Bovids are not only the most abundant remains in the fossil record but also exhibit consistent feeding habits that have endured over time. In order to reconstruct the environments that supported eastern African *Paranthropus* an analysis of their faunal communities was necessary. Fossil faunal lists were collected from 12 sites in eastern Africa that contain the faunal community of *Paranthropus*. Multiple g-tests of independence were performed to examine and compare the proportions of antelope tribes present. A focus on key indicator species that signal known environments revealed that these sites are not statistically different. The similarity of these 12 sites allows for an understanding of the environmental features that were essential for *Paranthropus*. This analysis further supports the idea that *P. boisei* and *P. aethiopicus* had very specific environmental requirements which were met by these sites in eastern Africa. The results indicate that these two *Paranthropus* species inhabited primarily grassland environments which included nearby water source, most likely wetland or lacustrine (lakeside) areas. This reconstruction aligns with recent isotope data which highly suggests that the skeletal adaptations of these two species were not exclusively for chewing hard

food items, like nuts, and were instead consuming mixed diets of primarily tough C₄ resources which would have been plentiful in these habitats.

Introduction

Paranthropus is a genus of extinct hominin that existed ~2.8 to ~1 Ma in eastern and southern Africa. In some literature the *Paranthropus* genus is instead referred to as a member of the *Australopithecus* genus, here they will be referred to the distinct group of *Paranthropus* (Sponheimer et al., 2022; Strait et al., 2013; Wood & Constantino, 2007). The genus consists of three species: *P. aethiopicus* and *P. boisei*, which are found in eastern Africa, and *P. robustus*, found in southern Africa. Members of the *Paranthropus* genus have distinct morphology which sets them apart from all other hominins: extremely large molars and a robust skull with a prominent sagittal crest. These skeletal adaptations were once thought to relate to the chewing of hard foods; however, new discoveries have challenged the simplicity of those assumptions (Macho & Shimizu, 2009; Ungar, 2011; Strait et al., 2013).

Paranthropus was first discovered in the late 1950's and more than fifty years later there were not many studies done to understand their diet, even though their diet was widely cited as the reason they were so morphologically different from all other known hominins (Wood & Constantino, 2007). The molars of *Paranthropus* were not only extremely large, but also had a thick enamel layer, which has been suggested to resist wear and protect from cracking and were able to resist "high vertical pressures" which allowed them to consume hard foods, like nuts (Macho & Shimizu, 2009; Wood & Constantino, 2007). In comparison to their molars, the canine teeth were much smaller. This dental morphology suggests that the foods they consumed either did not need much "incisal preparation" or was prepared outside of the mouth (Wood & Constantino, 2007). Studies of both dental morphology and biomechanics, including both jaw

muscle attachments and bite force, indicate that *P. boisei* had significantly larger mandibles and could generate a higher bite force than other hominins which would imply that they were adapted for the high stress caused by chewing very hard food items (Wood & Constantino, 2007). While this above research was focused on understanding the dental and skeletal uniqueness of *Paranthropus*, there has been no consensus on what foods they were eating. Some of the suggested resources include leaves and berries, small fruits without thick husks or fleshy pulp, and/or “very hard” food items (Wood & Constantino, 2007). The diet and paleoenvironmental context that supported and shaped the morphology of *Paranthropus* is not well-understood (Sponheimer et al., 2022). New research using stable carbon isotopic analysis, which measures the C₃ and C₄ components of an animal’s diet may shed light on this perplexing question¹.

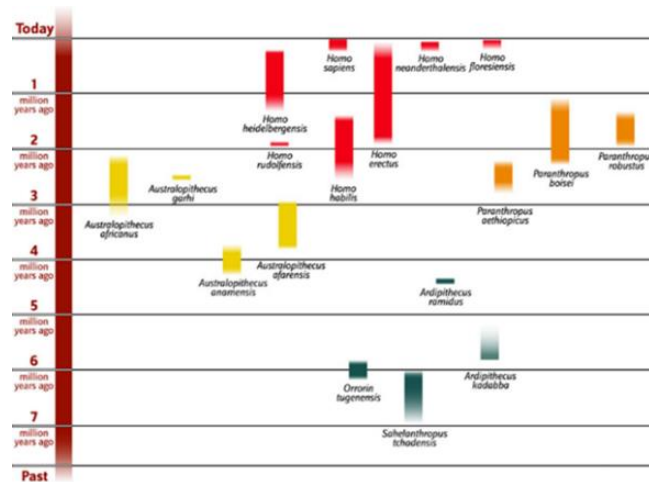
Stable carbon isotopic analysis and dental microwear suggest that although *P. boisei* and *P. robustus* had very similar morphology they were not consuming the same foods (van der Merwe et al., 2008). *P. boisei* seems to have been consuming large amounts of C₄ vegetation, which includes sedges and grasses, while *P. robustus* was consuming harder foods including nuts, which are predominantly from C₃ plants (Strait et al., 2013). The teeth of *P. robustus* specimens vary in microwear texture complexity, suggesting that they were feeding on hard food objects, while microwear evidence shows that *P. boisei* was instead consuming “tough” foods, like fibrous plant tissues (Unger, 2011). The strong isotopic C₄ signal, as much as 85% of carbon in their diet came from C₄ sources, is unlikely due to consumption of C₄-consuming animals, which at this high percentage would cause fatal protein poisoning, or from seeds which are a seasonal food source (Lee-Thorpe et al., 2012; van der Merwe et al., 2008). Instead, scientists

¹ Refers to the pathways used by plants to capture carbon dioxide during photosynthesis. C₃ plants are found mostly in cool and wet areas while C₄ plants are found in hot, often dry, areas.

suggest that a food source similar to modern day papyrus, *Cyperus papyrus*, was a large part of *P. boisei*'s diet. Species within *Cyperus* grow in both wetland areas as well drier, sandy areas with seasonal moisture and produce tubers and/or swollen bases (Lee-Thorpe et al., 2012). Lee-Thorpe et al. worked with carbon isotope data collected from an earlier hominin species, *Australopithecus bahrelghazali*, which lived in central Africa ~3.5 Ma, and suggest *A. bahrelghazali* had a similar diet to *P. boisei*. This mismatch between physical traits and isotope analyses highlights the need for an understanding of the environmental context of *P. boisei*. Therefore, this project seeks to reconstruct habitats that supported *P. boisei* and *P. aethiopicus* in eastern Africa.

While at least three new species in the genus *Homo* were coexisting at the same time and the same places as *Paranthropus*, all species of *Paranthropus* went extinct by ~1 Ma, as seen in Figure 1 (orange bars) below. Newly discovered evidence, a partial hominin mandible (LD 350-1), has pushed back the origins of early *Homo* species to ~2.8 Ma in eastern Africa (Villmoare, 2015). This new date for *Homo* overlaps the beginnings of the *Paranthropus* lineage (~2.7-2.3 Ma). The emergence of *Homo* and *Paranthropus* is often considered a response to global climatic changes between ~3.2 and 2.6 Ma, which brought forth increasing aridity across northern and eastern Africa leading to palaeoecological change (deMenocal, 1995, 2004; Trauth et al., 2007). The ability of these two species to overlap in time and space indicates differences in resource needs, while the *Paranthropus* extinction most likely indicates their inflexibility to adapt to a rapid change in the environment. In broadening our understanding of the environmental needs of *P. boisei* specifically, we will be able to add to the knowledge needed to understand what made the genus *Homo* so different.

Figure 1. Timeline of Hominin Evolution (Karen Carr, Smithsonian National Museum of Natural History.)



Marine sedimentary sequences off the African coast contain records of wind-blown dust that allow scientists to view precipitation history and environmental changes that occurred over the last five million years. Eastern African climates shifted from monsoonal, which supported closed (tree-filled) habitats, to more arid and open (grassland) habitats between 3.2 – 2.6 Ma due to the growth and expansion of glaciers in the Northern Hemisphere (deMenocal, 1995). While these broad paleoenvironmental shifts can be seen in the ocean sediment, the types of grasslands and plant materials they supported are not clear due to the rarity of paleobotanical evidence (Spencer, 1997). This period, known as the mid-Pliocene aridification shift, is thought to have had strong influences on early hominid evolution, and possibly was the pressure that led to the evolution of *Paranthropus* and the genus *Homo* (deMenocal, 2004). After ~1 Ma the marine sediment cores indicate longer and more severe periods of aridity which would have caused previously wet areas to dry out, most likely leading to devastating habitat loss (Faith & Du, 2019). These periods of increasing drying coincide with both the appearance of *Paranthropus*, around 2.8 Ma, and their extinction, around 1Ma.

Figure 2. The geologic timeline for the Cenozoic Era. Source: Encyclopedia of Earth

Era	Period	Epoch (start mya)	
Cenozoic	Quaternary	Holocene 0.01	
		Pleistocene 2.6	
	Tertiary	Neogene	Pliocene 5.3
			Miocene 23.0
		Paleogene	Oligocene 33.9
			Eocene 55.8
			Paleocene 65.5

Fossil bearing deposits dating to this time period are rarely exposed in eastern Africa, due to active faulting, erosion, and non-deposition (deMenocal, 2004). This means the shift from the Pliocene (5.3-2.6 Ma) to the Pleistocene (2.6-0.02 Ma) in eastern Africa is not well understood, although pollen data from fossil sites in northeastern Africa also support the shift to cooler and drier vegetation types after 2.5 Ma (deMenocal, 2004). The appearance of *Paranthropus* and early *Homo* at roughly the same time may signal an adaptation to more arid and varied environments (Potts, 1998). The ocean sediment cores and the pollen data both indicate a shift over millions of years towards drier and more open grasslands, however this does not mean that more closed habitats disappeared altogether. This illustrates why paleoenvironmental reconstruction is even more important to our understanding of the context in which these species evolved.

Traditional environmental reconstruction relies on the comparison of soil, plant, and animal remains found at a fossil site to modern plants and environments. The lack of fossil plant evidence at sites in eastern Africa makes it difficult to understand the resources available for faunal communities, including those that contain *Paranthropus* (Spencer, 1997). Many researchers have relied on the faunal communities, specifically the antelope, present at fossil sites across Africa to infer the types of vegetation needed to support the community (Faith et al.,

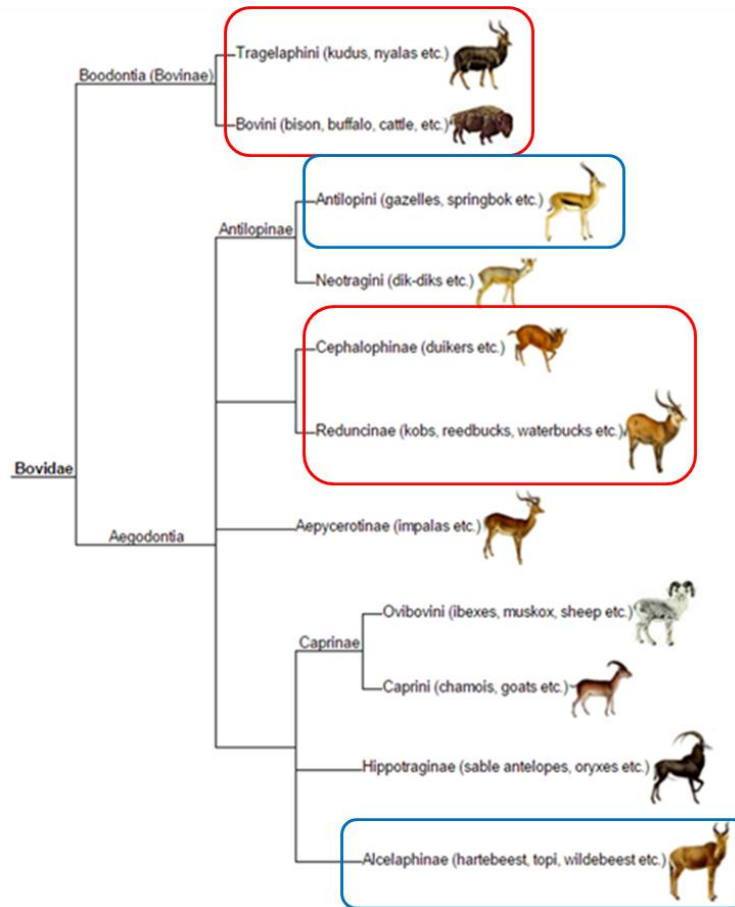
2019; Rector et al., 2017; Reed, 1998; Spencer, 2005; 2007; Vrba, 1980). In work first done by Vrba, which used modern bovid population percentages in 16 African parks and reserves, proportions of antelope belonging to key indicator subfamilies (tribes) corresponded to the predicted habitats (Vrba, 1980). Her work relied on the assumption that these tribes were adapted to the same environments millions of years ago that they live in today. This assumption is justified and strengthened by the fact that the antelope taxonomic diversity represented today by nine tribes was already established by the Pliocene (Spencer, 1997). There is uncertainty about paralleling modern environments with those of the past because taxonomic uniformitarianism, or comparison of a fossil taxon with its closest living relative to predict ecological behaviors, may not be an ideal method for ecological reconstructions. Significant problems with this method include, change over time of ecological preferences, a lack of morphological analysis of the fossils, an ecological bias that may result from the use of only one taxon or taxonomic group, and human-induced reduction of habitat (Reed, 1998). However, modern bovid enamel isotopes have been successfully matched to their known diets, providing evidence that traditional methods of environmental reconstruction are likely reliable (Sponheimer & Lee-Thorp, 2003). Further support for this method is the large number of bovid species at fossil sites which suggests that the fossil taxa present had well defined niches (Spencer, 1997). This is evidence that habitats and environmental pressures which existed millions of years ago may be inferred by studying the bovid assemblages found alongside fossil hominins in eastern Africa.

Bovidae, which includes cattle, bison, buffalo, antelopes, and caprines (sheep and goats) diverged from Cervids (deer) and Giraffids about 23 million years ago in Eurasia. As the global climate warmed in the middle and late Miocene bovids migrated onto the African continent and have been evolving and specializing there for ~18 million years. Today there are 279 known

extant species, including 72 African antelope species, about 48 species in eastern Africa alone, and at least 300 identified extinct species (Spencer, 1997; Castelló, 2016). There is some disagreement on the way they should be classified, however, most sources indicate that there are between 9 and 13 bovid tribes, or subfamilies, as illustrated in Figure 3 below (Yang et al., 2013). While experts disagree on the number of tribes there should be, the taxonomic diversity represented today was already in place by the Pliocene. Bovids have been described as sensitive indicators of environment and have been attuned to their habitat for at least the last 4 million years (Spencer, 2007; Vrba, 1980).

Bovoid species within a tribe have similar feeding habits and environmental needs allowing them to be used to indicate a known habitat. African Bovidae also “exhibit extreme dietary resource partitioning,” which allows many species to exist in the same space because they have differences in primary food, habitat, and feeding-height preferences (Spencer, 1995). These differences result in significant morphological differences depending on their diet making them extremely valuable environmental indicators, even in the absence of evidence like isotopes (Spencer, 1997). They are extremely specialized to their environments, due to strict feeding preferences, and therefore, are tied closely to environmental contexts. Bovids are also the most plentiful faunal remains at Plio-Pleistocene sites in Africa and there is often relatively complete skeletal material of extinct taxa allowing for less complicated and less expensive analyses (Spencer, 1997).

Figure 3. Cladogram of Bovid Tribes (based on Yang et al., 2013). *Bovini*, *Cephalophini*, *Tragelaphini*, and *Reduncini* (in red) are considered indicator species for wetter habitats. *Antilopini* and *Alcelaphini* (in blue) are considered indicators of grassland habitats (Rector et al., 2017).



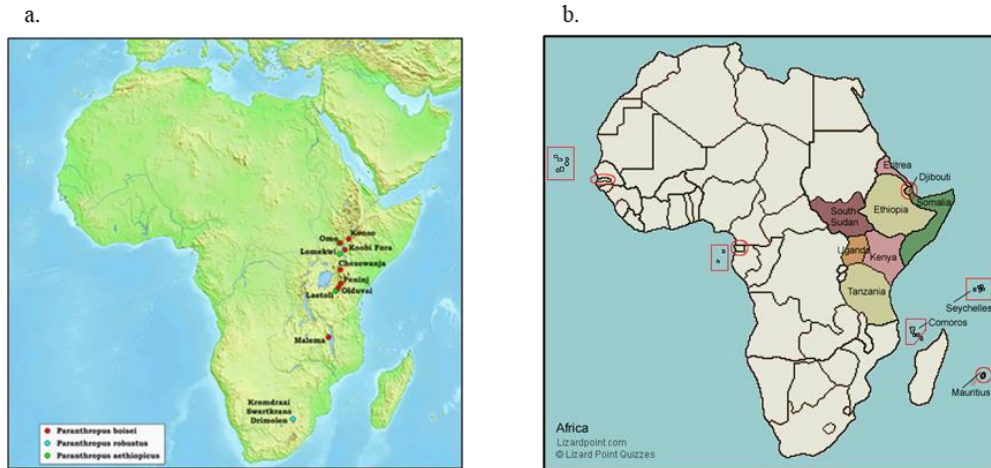
The taxa that are considered indicator species for wetter habitats and are most relevant to east African stories are: *Bovini*, which include species that are usually large, and heavy-bodied including the Cape Buffalo; *Cephalophini*, which consists of several species of duiker, small antelope, the majority of which are under 20 kg; *Tragelaphini*, a group of medium to large antelopes with spiral or twisted horns that includes kudu; and *Reduncini*, medium to large species that are strongly associated with water, like waterbuck (Castelló, 2016). *Antilopini*, which are mixed feeders, includes true gazelles and dwarf antelopes, and *Alcelaphini*, nomadic

grazers that consume C₄ vegetation and includes wildebeest, are tribes found in large numbers in eastern Africa and are considered indicators of grassland habitats.

Methods

Twelve fossil sites that contain *Paranthropus boisei* and/or *Paranthropus aethiopicus* were identified in eastern Africa, mostly along the African rift valley in the modern countries of Malawi, Kenya, Tanzania, and Ethiopia.

Figure 4. a. Map of African continent with *Paranthropus* site locations. (By Chartep - Own work, CC BY-SA 4.0, <https://commons.wikimedia.org/w/index.php?curid=47269511>) b. Map of eastern Africa. (Lizardpoint.com)



These sites and their ages are: Chiwondo 2, Northern Malawi (~2.5-2.3 Ma); Ileret 2, East Turkana, Kenya (~1.5-1.4 Ma); Kangatukuseo II, West Turkana, Kenya (2.53 Ma); Kokiselei 1, West Turkana, Kenya (~2.3-1.76 Ma); Lomekwi 1, Turkana County, Kenya (2.59-1.81 Ma); Lomekwi 3, Turkana County, Kenya (2.59-1.81 Ma); Naiyena Engol 2 and 3, West Turkana, Kenya (~3.6 - 0.781 Ma); Olduvai Bed 1, Ngorongoro Conservation Area, Tanzania (~1.9-1.8 Ma); Olduvai Bed 2, Ngorongoro Conservation Area, Tanzania (1.8-1.2); Shungura D, Lower Omo Valley, Ethiopia (2.52-2.4 Ma); Shungura E, Lower Omo Valley, Ethiopia (2.4-2.36 Ma); and Shungura G, Lower Omo Valley, Ethiopia (~2.3-1.9 Ma).

Fossil faunal assemblage lists, which list all specimens recovered at each site, were obtained from published literature and database entries from the above sites (van der Merwe,

2013; Maglio, 1971; Sandrock, 2003; Brugal et al., 2003; Boisserie et al., 2008). Data from each site was analyzed and present bovid species were assigned to their taxonomical subfamily, or tribe. The proportion of bovid tribes, specifically the indicator tribes mentioned above, present at each site has a direct relationship with the kind of habitat that was present at the time of the creation of the fossil bed. Multiple g-tests of independence were performed, looking for any statistical differences in the proportions of bovid tribes present between sites, which would show if there were major differences in the habitats of the sites. In order to perform the g-tests, the number of species in each tribe present at a site were totaled, then these site totals were compared to every other site, resulting in 66 individual tests. The resulting comparisons of proportions of tribes at individual sites enabled interpretations about the vegetation and the respective environments needed to support the faunal community.

The sites were then grouped and compared to each other to view similarities and differences in environmental needs. Sites were grouped according to: *Paranthropus* species present (solely boisei: Chiwondo, Ileret, Kangatukuseo, Kokiselei, Lomekwi 3, Naiyena Engol, Olduvai Bed 1, and Olduvai Bed 2) vs. (*P. boisei* and *P. aethiopicus*: Lomekwi 1, Shungura D, Shungura E, and Shungura G), date of the fossil beds (previous to 2.5 Ma: Chiwondo, Kangatukuseo, Shungura D, and Shungura E) vs (after 2.3 Ma: Ileret, Kokiselei, Olduvai 1, Olduvai 2, and Shungura G)², and geographical location (Ethiopia and northern Kenya: Ileret, Kangatukuseo, Kokiselei, Lomekwi 1, Lomekwi 3, Naiyena Engol, Shungura D, Shungura E, and Shungura G) vs. (southern Kenya and Tanzania: Chiwondo, Olduvai 1, and Olduvai 2). One final g-test was done to observe habitat differences between these twelve *Paranthropus* sites and

² Three sites were not included in this comparison because their date ranges did not fit within the parameter (Lomekwi 1, Lomekwi 3 and Naiyena Engol)

sites that contain the faunal communities of *Australopithecus afarensis*, which in previous similar work was shown to live in divergent habitats that might have been characterized by varying amounts of tree cover and seasonality (Rector et al., 2017). The results of these examinations, which focused on key indicator species for wet vs dry habitats along with those considered signals of open vs closed habitats, are evidence for the following reconstruction of their most likely environments (Faith et al., 2019; Rector et al., 2017; Reed, 1998; Spencer, 2005; 2007; Vrba, 1980). This analysis allows for a larger statement about habitats and vegetation needed to support bovid tribes, and the community at large, in these eastern African sites and therefore make reconstructions of past environments of these two *Paranthropus* species.

Results

Of the 66 site-to-site comparisons, 65 showed no significant statistical differences that would indicate that the sites varied in habitats, shown in Table 1 below. Only one test had a statistical difference, p-value 0.0415 (Olduvai 2 and Shungura E), discussed below.

Table 1. Results of site to site g-tests of independence. Test p-values show no statistical differences (p-value < 0.05), except one test p-value shows significant statistical difference (highlighted below).
Olduvai 2 vs Shungura E: p-value = 0.0415.

Sites Compared	D of F	G	P-value	Sites Compared	D of F	G	P-value	Sites Compared	D of F	G	P-value
Chiwondo vs Ileret	6	2.0772	0.9125	Kangatukuseo vs Lomekwi 1	6	1.526	0.9478	Lomekwi 1 vs Shungura G	7	2.2009	0.9479
Chiwondo vs Kangatukuseo	6	3.9933	0.6776	Kangatukuseo vs Lomekwi 3	5	2.2932	0.8073	Lomekwi 3 vs Naiyena Engol 2&3	6	5.89	0.4356
Chiwondo vs Kokiselei	6	4.3862	0.6246	Kangatukuseo vs Naiyena Engol 2&3	6	4.7892	0.5711	Lomekwi 3 vs Olduvai 1	7	5.0358	0.6556
Chiwondo vs Lomekwi 1	6	2.0669	0.9134	Kangatukuseo vs Olduvai 1	7	6.2782	0.5077	Lomekwi 3 vs Olduvai 2	7	9.2655	0.2341
Chiwondo vs Lomekwi 3	6	5.0658	0.5354	Kangatukuseo vs Olduvai 2	7	9.8212	0.1989	Lomekwi 3 vs Shungura D	4	5.0479	0.4101
Chiwondo vs Naiyena Engol 2&3	6	1.4754	0.9611	Kangatukuseo vs Shungura D	5	1.8106	0.8747	Lomekwi 3 vs Shungura E	4	4.0253	0.4026
Chiwondo vs Olduvai 1	7	3.2189	0.864	Kangatukuseo vs Shungura E	5	3.0051	0.6992	Lomekwi 3 vs Shungura G	7	5.1554	0.641
Chiwondo vs Olduvai 2	7	5.2122	0.6341	Kangatukuseo vs Shungura G	7	3.9867	0.7813	Naiyena Engol 2 and 3 vs Olduvai 1	7	2.6343	0.9167
Chiwondo vs Shungura D	6	4.1	0.6631	Kokiselei vs Lomekwi 1	6	5.5065	0.4807	Naiyena Engol 2 and 3 vs Olduvai 2	7	4.9868	0.6616
Chiwondo vs Shungura E	6	6.341	0.3861	Kokiselei vs Lomekwi 3	3	1.9545	0.5819	Naiyena Engol 2 and 3 vs Shungura D	5	3.0457	0.6929
Chiwondo vs Shungura G	7	1.791	0.9705	Kokiselei vs Naiyena Engol 2&3	6	3.3302	0.7664	Naiyena Engol 2 and 3 vs Shungura E	6	8.3178	0.2157
Ileret vs Kangatukuseo	6	2.5863	0.8587	Kokiselei vs Olduvai 1	7	3.7475	0.8084	Naiyena Engol 2 and 3 vs Shungura G	7	3.646	0.2692
Ileret vs Kokiselei	6	3.2081	0.7823	Kokiselei vs Olduvai 2	7	6.612	0.4704	Olduvai 1 vs Olduvai 2	7	3.0934	0.8762
Ileret vs Lomekwi 1	6	2.0664	0.9135	Kokiselei vs Shungura D	4	4.186	0.3814	Olduvai 1 vs Shungura D	7	7.129	0.4156
Ileret vs Lomekwi 3	6	4.2545	0.6423	Kokiselei vs Shungura E	4	4.186	0.3814	Olduvai 1 vs Shungura E	7	10.585	0.1578
Ileret vs Naiyena Engol 2&3	6	2.0087	0.9189	Kokiselei vs Shungura G	7	6.747	0.4557	Olduvai 1 vs Shungura G	7	3.3381	0.8521
Ileret vs Olduvai 1	7	2.9712	0.8876	Lomekwi 1 vs Lomekwi 3	6	3.9188	0.6877	Olduvai 2 vs Shungura D	7	9.5005	0.2187
Ileret vs Olduvai 2	7	5.2312	0.6318	Lomekwi 1 vs Naiyena Engol 2&3	6	3.097	0.7966	Olduvai 2 vs Shungura E	7	14.6	0.0415
Ileret vs Shungura D	6	3.2149	0.7814	Lomekwi 1 vs Olduvai 1	7	5.2404	0.6307	Olduvai 2 vs Shungura G	7	6.766	0.4536
Ileret vs Shungura E	6	7.2992	0.2941	Lomekwi 1 vs Olduvai 2	7	9.4468	0.2221	Shungura D vs Shungura E	5	4.0922	0.5362
Ileret vs Shungura G	7	3.4795	0.8374	Lomekwi 1 vs Shungura D	6	2.4403	0.8751	Shungura D vs Shungura G	7	5.4343	0.6071
Kangatukuseo vs Kokiselei	5	3.881	0.5667	Lomekwi 1 vs Shungura E	6	3.4059	0.7564	Shungura E vs Shungura G	7	6.7275	0.4578

The one site-to-site comparison that showed a statistically significant difference ($p=0.0415$), was Olduvai 2 vs. Shungura E, and is shown in Figure 5.

Figure 5. Site bovid tribe comparison (Olduvai 2 vs Shungura E).



The difference in proportions between these two sites is likely heavily influenced by the absence of *Alcelaphini* (maroon section) from the Shungura E site data. There could be multiple reasons species of this tribe are not represented in the fossil data; they could have actually not been present, there may be a lack of preservation, there could be a misidentification of a fossil species, or some other unknown reason. In any case, the absence of *Alcelaphini* does not have a major impact on the overall results because the large proportion of *Antilopini* (green section) indicates that the site supported grassland dwelling antelope. Shungura E also has a large proportion of *Reduncini* and *Tragelaphini*, both of these tribes are indicators of wetter habitats, this supports the idea that Shungura E was not different from the other *Paranthropus* sites.

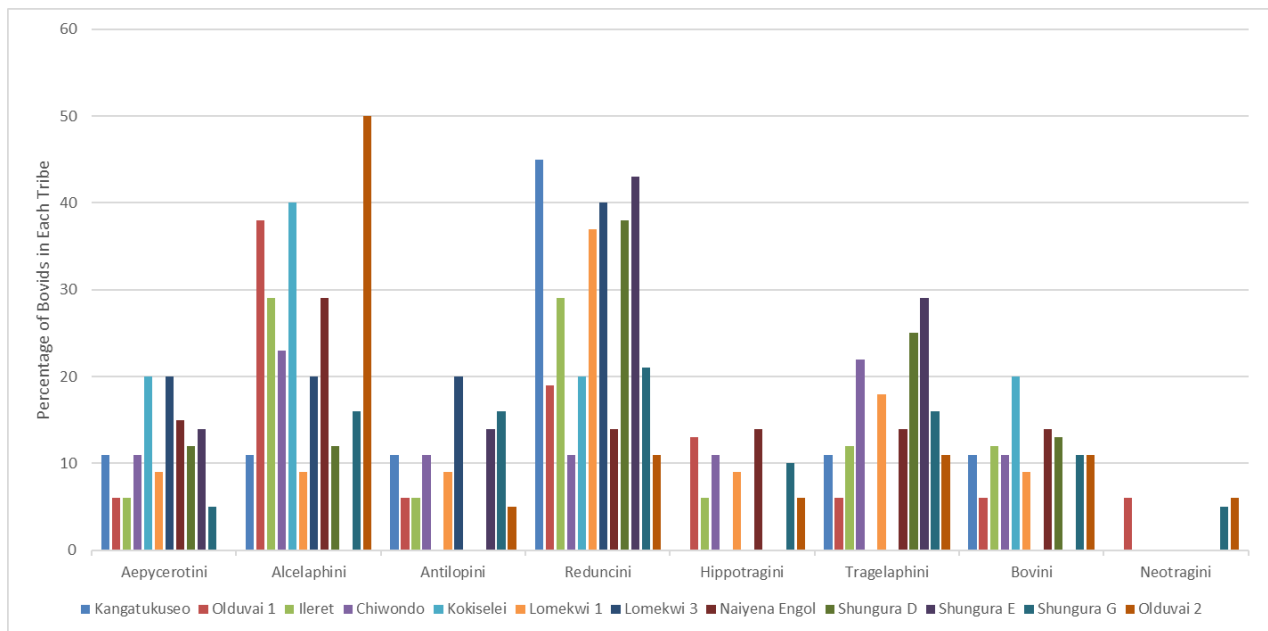
There were also no significant statistical differences indicating habitat differences in any of the groupings of sites: *Paranthropus* species present ($p=0.21$), date of the fossil beds ($p=0.0898$), or geographical location ($p=0.1008$), shown in Table 2.

Table 2. Results of g-tests of independence for grouped sites (*Paranthropus* species present (p=0.21), date of the fossil beds (p=0.0898), or geographical location (p=0.1008). Test p-values show no statistical differences (p-value < 0.05), except one test p-value shows significant statistical difference (highlighted below). Comparison of *Paranthropus* sites in this study vs *Australopithicus* sites in previous study (Rector et al., 2017).

Sites Compared	D of F	G	P-value
Time Early vs Late (Before/At 2.5 MA vs After 2.3 MA)	7	12.345	0.0898
Species (Only <i>P. boisei</i>) vs (Both <i>P. boisei</i> and <i>P. aethiopicus</i>)	7	9.6387	0.21
Geographical (Northern vs Southern)	7	11.992	0.1008
<i>Paranthropus</i> Sites vs <i>Australopithicus</i> Sites	9	21.689	0.0099

Further analysis was conducted to view the proportions of bovid tribes present at all sites to look for similarity of habitat requirements. Across all sites and groupings the tribes with the greatest proportions were *Alcelaphini*, *Reduncini*, and *Tragelaphini*, as shown below in Figure 6. The data shows a clear pattern, these three tribes not only represent the largest proportions overall, they are also the tribes most likely to be present at each site.

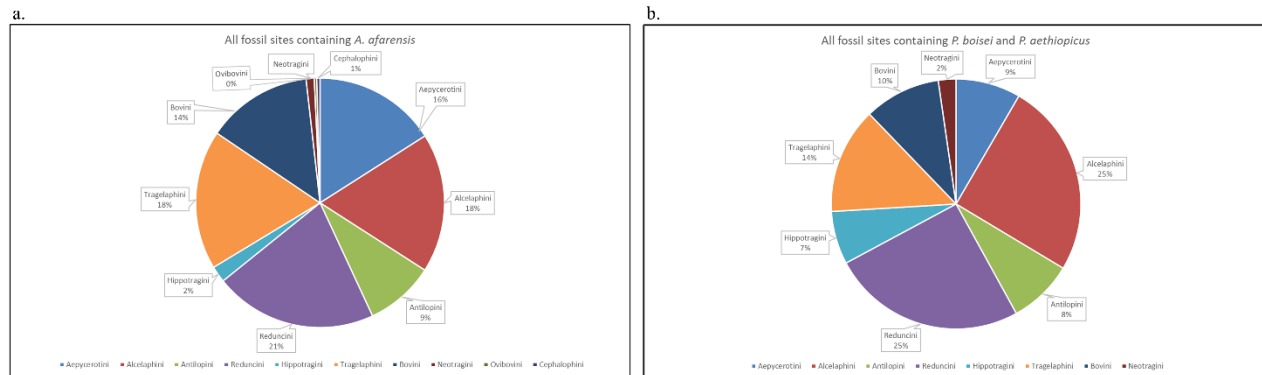
Figure 6. Bar chart representing the proportions of bovid tribes at each of the twelve *Paranthropus* sites



The data from all twelve sites was then combined and the proportions of tribes examined, shown in Figure 7a below. The proportions of tribes across all sites exhibits the same pattern shown in the individual site data. The tribe proportions, from most to least are: *Alcelaphini* and

Reduncini, both at 25%; *Tragelaphini* at 14%; *Bovini* represents 10%; *Aepycerotini* at 9%; *Antilopini* at 8%; *Hippotragini* at 7%; and *Neotragini* at just 2%.

Figure 7. a. Chart representation of bovid tribe proportions across all twelve sites in current *Paranthropus* study.
 b. Chart representation of bovid tribe proportions across all twelve sites in previous study on *Australopithecus afarensis* (Rector et al., 2017).



One final comparison was done to observe differences between the twelve *Paranthropus* sites in this study and previous work on twelve sites that contain the faunal fossil community found alongside *Australopithecus afarensis* which lived between 3.85 and 2.95 million years ago also in Eastern Africa (Ethiopia, Kenya, Tanzania), data shown for these sites in Figure 7b (Rector et al., 2017). This last comparison was done in order to see if there was a statistically significant difference between these two species as the findings of Rector et al. suggested there would be, the results of this comparison supports this conclusion ($p=0.0099$).

Discussion

The overall similarity in bovid tribe proportions between sites and across all groupings suggests that the eastern African *Paranthropus* species were only found in a very specific ecological niche, sites that included open grasslands with associated wet locations. This reconstruction is strongly supported by both the ocean sediment data and isotope test results. *P. boisei* and *P. aethiopicus* lived around the same time as the climate in eastern Africa became

more arid, coinciding with the proposed spread of grasslands (deMenocal 1995, 2004; Potts, 1998; Reed, 1997). Research done by Reed, which used faunal locomotion and morphological categories to reconstruct paleohabitats, also found that *P. boisei* lived in habitats with abundant water and edaphic grasslands, or grasslands in which the grasses grow in water-logged soils, such as wetlands or swamps (Reed, 1997). The results of the above reconstruction fit nicely with the isotope data which suggests that these two species were consuming a large amount of C₄ resources (Lee-Thorpe et al., 2012; Sponheimer et al., 2022; Sponheimer & Lee-Thorpe, 2003). Similarly, *A. bahrelghazali*, in central Africa was also found to have an extremely high C₄ signal and in a comparable reconstruction is thought to have lived in areas that supported the abundance of the same kinds of resources (Lee-Thorpe et al., 2012). Lee-Thorpe et al.'s reconstruction suggests that the earlier australopithecines may have had a more generalist approach to finding food resources and by ~3.5 Ma *A. bahrelghazali* was able to capitalize on the available C₄ resources. This suggests that as grasslands spread across eastern African landscapes, bordering areas with water sources, *Paranthropus* was able to exploit the abundance of C₄ resources. If the main C₄ resource that they were exploiting was fibrous plant tissues that relied on wet or swampy soils, the period of aridification that occurred in eastern Africa around a million years ago likely led to their extinction as they were unable to withstand the disappearance of their main food source. The above reconstruction not only helps us understand the habitats that supported eastern African *Paranthropus* species, it also illustrates how strongly tied to their environments they were.

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Vita

In the fall of 2014, Lisa attended Virginia Commonwealth University to pursue degrees of Bachelor of Science in Anthropology and Bachelor of Arts in History, graduating in December 2020. While at VCU during her undergraduate education she took part in a month-long study abroad, over the summer of 2017 and again the summer of 2018, in South Africa. This trip inspired her curiosity and shifted her focus to the study of early human ancestors, which led to an independent study and numerous conference attendances to present research posters. In the fall of 2021, she entered the Master of Science in Biology program at VCU in Dr. Rector's Paleoecology Lab and began working towards her degree. Lisa will complete this degree December of 2023 and looks forward to continuing her study in this field.