DISTRIBUTION OF MAMMALIAN FAUNA DURING THE EARLY PLEISTOCENE OF THE KOOBI FORA FORMATION, EAST TURKANA, KENYA

by

SARAH ELIZABETH HAKALA

(Under the Direction of Elizabeth J. Reitz)

ABSTRACT

The Plio-Pleistocene is a significant period of climatic, environmental, and faunal change in the Turkana Basin. This study presents a faunal analysis among three members (Upper Burgi, KBS, and Okote) of the Koobi Fora Formation in East Turkana that date from 2.0 to 1.39 Ma (million years ago), encompassing the period when C_4 grasslands came to dominate the local vegetation and when hominins were diversifying. The Turkana Basin Paleontology Database is used to analyze temporal differences in faunal proportions among the three members. Results from fieldwork in the summer of 2011 supplement the larger-scale analysis. Bovids are the most abundant family throughout samples from the three members, and they highlight the mosaic nature of the environment. Suids, cercopithecids, and equids are the next most abundant families. These groups indicate the presence of grasslands during the KBS and Okote Members. The diversity of environments, evidenced by the diverse habitat preferences and adaptations of these mammals, provided opportunities for hominin speciation through the exploitation of different habitats and versatility in feeding niches.

INDEX WORDS: Paleoecology, Hominin evolution, East Turkana, East Africa, Climate change, Grassland expansion

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CHAPTER 1

AN INTRODUCTION TO PLIO-PLEISTOCENE CLIMATE AND THE TURKANA BASIN

The Plio-Pleistocene boundary marks the beginning of a significant period of climatic, environmental, and faunal change within the Turkana Basin in northwestern Kenya. At the same time, aridification, temperature decline, glacier onset, and grassland expansion were occurring on regional and global scales. These events all contributed to the Turkana environment, creating selective pressures on animals. The study of mammalian evolution in the Turkana Basin during the early Pleistocene links paleoenvironmental reconstructions associated with climate change to a critical time in hominin evolution: the origin and speciation of the genus *Homo*. Between 2.0 and 1.5 Ma (million years ago) as C_4 grasslands came to dominate the local vegetation and open environments expanded, many mammals evolved adaptations to grasslands while other species went extinct. The Turkana Basin is one of the most influential for hominin discoveries in Plio-Pleistocene East African research. In addition to documenting the evolution of the genus *Homo* and the emergence of the Acheulean stone tool industry, fossils from East Turkana provide evidence that four species of hominins (*Homo habilis*, *H. rudolfensis*, *H. erectus*, and *Paranthropus boisei*) lived there concurrently. Paleoecological studies can be used to reconstruct the environments in which these hominins lived during this time of environmental and evolutionary transition.

The Turkana Basin today is dominated by Lake Turkana and surrounding discontinuous deposits with dates beginning around 27.5 Ma (Fig. 1.1). Throughout the past 27.5 million years, the basin experienced continual tectonic activity and fluctuated between fluvial and lacustrine environments. Among the deposits, the Koobi Fora Formation on the eastern side of the lake contains evidence for mammalian evolution, including that of hominins (Brown and Feibel, 1991). In addition to hominins, the Koobi Fora Formation yields a diverse record of over 90 species of large mammals, over 80 species of small mammals, and a wide range of plant and invertebrate taxa (Turner and Antón, 2004:197). The Koobi Fora Formation contains deposits from the Pliocene and Pleistocene, and, therefore, the fossils reflect periods of significant environmental change.

The goal of this research is to reconstruct the paleoecology of areas within East Turkana during the early Pleistocene. This research addresses questions about faunal change and paleoenvironments in the Koobi Fora Formation: (1) do mammals show change in distribution from 2.0 to 1.5 Ma? and (2) what can the faunal distributions reveal about the environments in which hominins lived? These questions are addressed by analyzing the relative abundances of mammals over time found in the Turkana Basin Paleontology Database and through a literature review of faunal characteristics, adaptations, and evolution. Characteristics of animals coupled with previously published dietary and isotopic evidence can reveal paleoenvironmental conditions. This research also investigates the usefulness of the database for such studies and addresses whether the Turkana Basin Paleontology Database analysis agrees with previously published paleoenvironmental studies. Material collected during surface surveys, or ‘bone walks’, from the summer 2011 field season at Koobi Fora augment the larger-scale faunal analysis. The premise of this research is that faunal succession between 2.0 and 1.5 Ma reflect increases in C_4 vegetation and increases in grasslands in the Turkana Basin.

This chapter first provides an introduction to global and East African climate and environment. Second, the chapter narrows its focus to discuss the Turkana Basin: (1) geology and paleogeography, (2) climatic and environmental changes and faunal evolution during the early Pleistocene, and (3) hominins in the environment. The chapter concludes with a summary of the expected results of the research.

Global climate and evolutionary background to the Pleistocene

The Earth's climate is in continual flux, primarily as a result of orbital forcing and plate tectonics in addition to several secondary factors. Orbital forcing includes the Milankovitch cycles of eccentricity, obliquity, and precession operating at 100-ky (thousand year), 41-ky, and 23-ky periods, respectively. The net gain of insolation when these cycles are superimposed determines the distribution and intensity of solar radiation at any site on the Earth's surface. Orbital forcing explains the cyclic patterns to climate while factors such as plate tectonics, greenhouse gasses, and vegetation contribute to the variability. Tectonic activity alters continental landmass position and topography and affects ocean circulation and air currents, leading to further changes in climatic and environmental conditions at global, regional, and local scales (Zachos et al., 2001).

A decline in global temperature and an increase in climatic variability and vegetative heterogeneity began during the Eocene-Oligocene transition at 34 Ma. During the transition, continental ice-sheets appeared in the Antarctic. This trend continued until recent times with cooling, aridification, and increasing variability occurring at different scales regionally and locally (Zachos et al., 2001). Buildup of Antarctic glaciers lowered global sea levels, which decreased biological activity and led to declining CO_2 production by organisms in the ocean (Anderson et al., 2004:298). With cooling and aridification came the evolution of the C_4

photosynthetic pathway as global CO_2 levels declined. C_4 grasses are more efficient at photosynthesis than C_3 plants in atmospheres with low CO_2 concentrations (Edwards et al., 2010).

Although C_4 grasses evolved much earlier, the widespread expansion of C_4 grasslands did not occur until the late Miocene, between 8.0 to 6.0 Ma. The fossil record shows a major period of faunal turnover at that time with an increase in grassland-adapted species and shifts from C_3 to C_4 dominated diets. The expansion of C_4 grasslands during the late Miocene was a global phenomenon as CO_2 levels reached a critical threshold favoring C_4 grasses in arid environments (Cerling et al., 1997; Edwards et al., 2010).

Global cooling continued, interrupted by a brief warm period in the early Pliocene, followed by the onset of Northern Hemisphere Glaciation (Zachos et al., 2001). Marine isotope records from ocean cores reveal high latitude glacial onset in the Arctic around 2.8 Ma, and this date correlates with a shift in the dominant orbital cycle. Prior to 2.8 Ma, climate oscillated on a 23-ky precessional cycle, but after 2.8 Ma, climate oscillated on a 41-ky obliquity cycle. High latitude glaciation intensified after 1.8 Ma and, while climate continued to oscillate on a 41-ky obliquity cycle, it oscillated in higher amplitude cycles (deMenocal, 1995, 2004). In addition to intensification in aridity and variability, the development of a strong Walker Circulation in the tropical Pacific and the onset of El Niño Southern Oscillation (ENSO) also occurred near 1.8 Ma (Nicholson and Kim, 1997). Walker circulation controls ENSO (Ravelo et al., 2004). Prior to 1.8 Ma, during the early Pliocene, climatic evidence shows permanent El Niño conditions with a weak Walker Circulation: easterly winds over the tropical Pacific were weaker, the SST (sea surface temperature) gradient between the eastern and western Pacific was more uniform, and the thermocline was deeper (Molnar and Cane, 2002). After 2.0 Ma, easterly winds strengthened, and by 1.8 Ma, a strong east-west temperature gradient developed, leading to a strong Walker Circulation (Ravelo et al., 2004; Maslin and Christensen, 2007). Both Northern Hemisphere Glaciation and Pacific Ocean circulation impacted East African climate and environment.

The East African Plio-Pleistocene

Changes in East Africa were similar to events on the global scale. C_4 grasses were present in the environment by 8.0 to 7.0 Ma, with both Equidae and Elephantidae transitioning to C_4 dominated diets at this time (Cerling, 1992). Additionally, marine cores indicate a decrease in the proportion of tree pollen in East Africa after 7.0 Ma (Bonnefille, 2010). However, it was not until the late Pliocene and early Pleistocene that African aridification reached a point that C_4 grasses were the dominant vegetation. Isotopic analysis of tooth enamel from sites in Turkana and Gona shows that it is only after 4.5 Ma that Suidae, Hippopotamidae, and Bovidae shift from mixed C_3-C_4 feeders to C_4 grazers (Cerling, 1992; Ségalen et al., 2007).

In addition to Northern Hemisphere glaciation and cooling, other explanations for the causes of East African aridification include tectonic uplift and closure of the Indonesian seaway (Cane and Molnar, 2001; Haug et al., 2005; Sepulchre et al., 2006). Uplift of the East African Rift System began during the Eocene and Oligocene but reached its maximum during the Plio-Pleistocene. The changes in topography reduced the moisture and rainfall over East Africa, shifting climate from warm and moist to arid and cool. Because rainfall in the tropics is a limiting factor for plant distribution, changes in rainfall associated with uplift altered vegetation patterns (Sepulchre et al., 2006). The closure of the Indonesian seaway contributed to the climatic shift as well. New Guinea's northward movement at 4.0 to 3.0 Ma closed the deep connection between the Indian and Pacific Oceans and allowed colder northern waters to replace warmer southern waters that had previously flowed westward through the seaway. This cooled the SST in the Indian Ocean and reduced rainfall in East Africa (Cane and Molnar, 2001).

The overall trend for East African climate during the Plio-Pleistocene was continued long-term aridification superimposed on fluctuating wet-dry cycles, and low latitude African arid periods correlated with high latitude glacial periods (Table 1.1). Eolian dust records in marine sediments off the coasts of East and West Africa reveal a connection between global climate pulses and African climate pulses (deMenocal, 1995, 2004; Ravelo et al., 2004). Spikes in dust concentration and significant shifts in eolian variability occurred near 2.8 Ma, corresponding to the onset of Northern Hemisphere Glaciation. These dust concentration spikes signal an increase in wind-borne material due to increasing aridity and decreasing vegetation coverage. North Atlantic SSTs were coldest when African dust concentrations were highest (deMenocal, 1995). A marked decline in tree pollen density in East Africa indicates that forests retreated and gave way to woodlands and grasslands. In fact, no evidence for closed canopy rainforests is present at any East African Plio-Pleistocene site (Bonnefille, 2010).

The East African long-term aridification continued throughout the Quaternary, affecting environmental and ecological conditions, and leading to major evolutionary changes. Between 2.8 and 2.5 Ma, many African species experienced turnover events (Vrba, 1995, 1999; Wesselman, 1995), including hominins. The first appearance of *Paranthropus* is near 2.8 Ma, and the origin of *Homo* is near 2.5 to 2.3 Ma (Walker et al., 1986; Wood, 1992; Kimbel, 1995). Vrba (1995) notes a statistically significant number of first appearances for bovid genera and species between 2.6 and 2.4 Ma, and many of these first appearances are taxa that exhibit adaptations to cooler and open environments. Similar turnover is observed in micromammals, with the appearance of several species with specialized body plans for bipedal locomotion in open, arid habitats (Wesselman, 1995).

Around 1.8 Ma, as high latitude glaciation intensified, East African dust concentrations spiked again and eolian variability increased (deMenocal, 1995). The development of the Walker Circulation at this time had strong implications for East Africa because ENSO moderates rainfall in eastern equatorial and southeastern Africa and affects interannual variability (Nicholson and Kim, 1997). Heavy rains over East Africa are loosely correlated with El Niño events. The postulated El Niño conditions during the Pliocene may have produced the wetter setting in East Africa (Molnar and Cane, 2002), but after 1.8 Ma, when a strong Walker Circulation was in place, East Africa was much drier. Additionally, it is hypothesized that the extreme variability in rainfall after 1.8 Ma in East Africa was due to the onset of ENSO (Ravelo et al., 2004; Maslin and Christensen, 2007).

Increasing amplitude of wet-dry variability at 1.8 Ma is associated with diversification of hominins, specifically with the origin and expansion of *H. erectus* (Wood, 1991:259-261; Swisher et al., 1994; Kimbel, 1995; Gabunia et al., 2000; Antón, 2003) and the possible appearance of the Acheulean stone tool industry (Lepre et al., 2011). During this period, artifacts and archaeological fauna show that hominins repeatedly used the grassland-dominated ecosystems created by the arid climate (Plummer et al., 2009). This indicates the importance of open environments to *Homo* activity after 2.0 Ma. Regional aridity intensification combined with fluctuating wet-dry cycles was the backdrop for environmental change, grassland expansion, and faunal evolution in the Turkana Basin of East Africa.

Geology and paleogeography of the Turkana Basin

The Turkana Basin provides a unique setting to study hominin paleoecology. Hominins were present throughout the Plio-Pleistocene, and it was during this same time period that the basin underwent considerable geographic change, resulting in drastic changes to the landscape. This section describes: (1) the geologic history and topographic changes of the basin during the past 4 million years, (2) the Plio-Pleistocene deposit formations, and (3) the stratigraphy and geology of the Koobi Fora Formation.

The central feature of the Turkana Basin today is Lake Turkana, the third largest lake in Africa. However, lakes are intermittent in the basin, with the modern lake established only within the last several hundred thousand years (Harris et al., 2006). Historically, the basin's water source came principally from the Omo River, which originated in the Ethiopian highlands, and seasonally from the Turkwel and Kerio Rivers in the southwest part of the basin. These three rivers form the basin's main drainage system today. At times, smaller ephemeral rivers feed into the drainage system as well. Since the Omo River's main source is in Ethiopia, basin geography depends on the tectonics of the Ethiopian highlands in addition to local tectonic and volcanic activity (Rogers et al., 1994).

Over the past 4 million years, the basin has been dominated by fluvial systems, interrupted with the periodic development of lacustrine periods when tectonic activity altered the outflow. Lakes formed in the basin as a response to tectonic activity, but the water levels fluctuated according to precipitation and evaporation changes within the basin and in the Ethiopian highlands (Brown and Feibel, 1991; Brown, 1995; Bruhn et al., 2011). These paleolakes were much larger in size compared to the present-day Lake Turkana (Harris et al., 2006).

During the late Pliocene and Pleistocene, several events occurred in the basin: lake formation, outlet closure, and Omo River water reductions. Around 4.0 Ma, Lonyumun Lake, the oldest paleolake known in the basin, was present until it drained around 3.9 Ma. At 3.9 Ma, the Omo River outlet to the Indian Ocean, known as the Turkana River, shifted southward, and a fluvial system returned to the basin. Beginning around 2.5 Ma, major tectonic activity disrupted stability in the basin. A significant lacustrine period occurred between 1.9 and 1.7 Ma when a lake known as Lake Lorenyang or the Upper Burgi Lake formed. Formation of Lake Lorenyang coincided with tectonic activity in the southern end of the basin and closure of the basin's outlet to the Indian Ocean due to volcanism, faulting, and subsidence. Since that time, the basin has had no connection to the Indian Ocean (Brown, 1995; Bruhn et al., 2011). The presence of a lake in the Turkana Basin between 1.9 and 1.7 Ma corresponds to the presence of lakes in other East African rift localities, indicating regional trends in environmental conditions (Trauth et al., 2005, 2007). The volume of incoming water from the Omo River started to decrease around this same time, as this water was diverted to the Blue and White Nile Systems. Reduction in water volume continued until after 1.7 Ma when the basin was once again dominated by a fluvial system. Additional reductions in water volume were seen at later times, between 0.6 and 0.1 Ma (Brown and Feibel, 1991; Bruhn et al., 2011).

The Turkana Basin has a sedimentary record dating from the latest Oligocene (27.5 Ma) up to the recent Holocene, but deposits, particularly fossiliferous strata, are only present for half of this sequence (Brown, 1995). The most recent deposits can be divided into two groups: the Omo group and the Turkana group. The Omo group consists of five Plio-Pleistocene formations including the Shungura, Usno, and Mursi Formations in the Lower Omo Valley, the Nachukui Formation in West Turkana, and the Koobi Fora Formation in East Turkana (Fig. 1.1). The

Turkana group consists of two formations, the Galana Boi and Kibish Formations, containing late Pleistocene and Holocene deposits. The Turkana group disconformably overlies the Omo group (Brown and Feibel, 1991).

The combined deposits from the five formations in the Omo group are the most complete lithostratigraphic record in East Africa for the late Pliocene and early Pleistocene. Their combined total of nearly 800 m of strata provide some of the best and most complete evidence of mammalian evolution, including that of hominins, for the time period. Volcanic tuffs within the Omo group allow cross dating and correlation of paleoenvironmental events and depositional history among different regions of the basin. The deposits represent a single depositional system, enabling a more complete regional reconstruction of the Turkana Basin during the Plio-Pleistocene (Brown and Feibel, 1991).

The Mursi is the oldest formation in the Omo group, containing Pliocene sediments dating older than 5.0 Ma. Because the Shungura, Usno, and Mursi Formations are located north of the lake in the Lower Omo Valley, their depositional history has differed from the Nachukui and Koobi Fora Formations. The majority of the Shungura, Usno, and Mursi Formations record fluvial deposition when the Paleo-Omo River flowed from the Ethiopian Highlands south through the valley. The Nachukui Formation covers 500 km^2 of discontinuous deposits on the western side of Lake Turkana and documents both lacustrine and fluvial environments, corresponding with changes in the geography of the basin (Brown and Feibel, 1991; Brown, 1995).

This research focuses on the Koobi Fora Formation, which has a composite thickness of 565 m discontinuously exposed over 1,200 km^2 and was deposited between 4.35 and 0.7 Ma. It is divided into eight members (stratigraphic sections bounded by volcanic ash layers or tuffs)

(Table 1.2). The early members span from 4.35 to 2.68 Ma and include the Lonyumun, Moiti, Lokochot, and Tulu Bor Members. Deposits of the latter half of the formation include the Burgi, KBS, Okote, and Chari Members. Because of a unconformity of 0.5 million years, the Burgi Member is divided into a lower and upper section (Brown and Feibel, 1991; Brown and McDougall, 2011).

The research in this project analyzes the mammal record in the Koobi Fora Formation starting with the Upper Burgi at 2.0 Ma and continuing through the KBS and Okote Members, which have an upper boundary formed by the Chari tuff at 1.39 Ma. The deposits within the Upper Burgi, KBS, and Okote Members document a time period of tremendous change both in the environmental components and in faunal compositions and characteristics, including those in the hominin record. Therefore, these three members offer an opportunity to analyze significant events in the Turkana Basin that occurred during the early Pleistocene associated with hominin diversification (Brown and Feibel, 1991).

The Koobi Fora Formation is also broadly divided spatially into eight major regions of exposure: Ileret, Il Dura, Karari Ridge, Il Naibar Lowlands, Koobi Fora Ridge, Bura Hasuma, Sibilot, and Southern Allia Bay Plains (Fig. 1.2). These major geographic regions are further subdivided by drainage systems and ephemeral streams into collecting areas. Sibilot, the Southern Allia Bay Plains, Il Dura, and Il Naibar Lowlands have exposures predominantly of the early members of the Koobi Fora Formation while the other regions contain younger exposures. The type sections for the Upper Burgi and KBS Members are located in the Koobi Fora Ridge, and the type section for the Okote Member is located in the Karari Ridge (Brown and Feibel, 1991).

Climatic and environmental changes and faunal evolution in the Turkana Basin

Climatic and environmental changes in the Turkana Basin were associated with global cooling trends and regional aridification in addition to local tectonic activity (Table 1.1). The Plio-Pleistocene transition was a tectonically active period within the basin and saw major geographic and environmental transitions. As previously mentioned, paleogeographic reconstructions show a large, meandering fluvial system with no lake at 2.3 Ma. After 2.0 Ma, a large lake formed synchronous with the closure of the basin's outlet, and major topographic and hydrological reorganization of the Turkana Basin ensued (Bruhn et al., 2011). With global and regional climatic fluctuations around 1.8 Ma, the lake level became increasingly unstable until 1.7 Ma when the central lake disappeared and an unstable fluvial system returned to the basin (Rogers et al., 1994; Trauth et al., 2005; Trauth et al., 2007). Because of the tectonic activity and larger scale climatic changes, the period from 2.0 to 1.5 Ma was a time of shifting environmental conditions, associated with species evolution. Paleosol and faunal studies both provide evidence for localized events. These environmental changes placed different selective pressures on hominins, one of the factors influencing their evolution. The hominin record from the Turkana Basin, therefore, provides evidence for both speciation and migration events as well as behavioral developments and repeated activity in the emerging grasslands.

Non-faunal evidence: paleosols.

Using paleosol carbonates in Turkana, Wynn (2004) found stepwise increases in C_4 biomass at 2.5 Ma and 1.8 Ma that parallel high latitude glacial activity and East African increases in aridity. Paleoprecipitation decreased after 2.5 Ma, followed by a shorter, more humid phase from 1.9 to 1.8 Ma. Cerling (1992) found that C_4 plants accounted for less than 50% of the photosynthesizing biomass from 9.4 to 1.8 Ma, but after 1.8 Ma, C_4 biomass comprised 60-80% of total plant biomass. A steady increase in C_4 plants occurred over the past 4 million years, but only after 1.8 Ma did C_4 vegetation become dominant in the Turkana Basin (Cerling et al., 1988; Levin et al., 2011). Even as the environment shifted from closed woodlands to open savannas, mosaic conditions persisted (Quinn et al., 2007). Northern parts of the basin, those along the lower Omo River, retained more C_3-dominated environments and riparian woodlands compared to the floodplains farther south where the Koobi Fora and Nachukui Formations were deposited. The floodplains downstream supported more C_4 grasses (Levin et al., 2011). Even as C_4 grasslands expanded, the Turkana Basin was characterized by heterogeneity, and this provided multiple niche opportunities for faunal evolution. Further aridification occurred after 1.6 Ma (Wynn, 2004), but pure C_4 grasslands did not emerge until 1.0 Ma (Cerling, 1992).

Faunal evidence.

Faunal studies reveal similarities to paleosol evidence with turnover events and multiple pulses throughout the late Pliocene and early Pleistocene. The greatest amount of change occurred after 2.0 to 1.8 Ma with significant increases in grazing and open-adapted fauna (Behrensmeyer et al., 1997; Reed, 1997; Spencer, 1997; Harris and Cerling, 2002; Fernandez and Vrba, 2006). In the fossil record, grazers can be identified by the isotopic signatures from their dental enamel and the degree of hypsodonty for their cheekteeth. The enrichment or depletion of $\delta^{13}C$ values in the enamel indicates whether the animal fed primarily on C_4 or C_3 vegetation, respectively. In tropical Africa today, all grasses, except those growing at higher altitudes, use a C_4 photosynthetic pathway. Therefore, a C_4 isotopic signature indicates that the animal fed in an environment with grasses (Cerling et al., 2003).

Hypsodont dentition is an adaptation to tooth wear during mastication. The causative agents of tooth wear include fibrous and tough vegetation and phytoliths in plant tissues. These are associated with grasslands or open environments, where animals feed on more abrasive vegetation close to the ground. Non-dietary abrasives such as grit and dirt can also be ingested in these settings, contributing to a high degree of hypsodonty (Damuth and Janis, 2011).

In the Turkana Basin, faunal diversity increased from 3.0 to 2.0 Ma because open habitats expanded and provided new niche opportunities but woodland habitats also persisted. Major faunistic turnover after 1.8 Ma was marked by a decline in faunal diversity as open habitats and grasslands became more extensive and woodlands receded. More taxa displayed hypsodonty, and hypsodont bovids, suids, and equids became dominant. *H. erectus* also appeared around 1.8 Ma in the Turkana Basin. The localized grassland expansion may have facilitated their migration into the basin, where they were able to exploit newly open environments (Behrensmeyer et al., 1997; Bobe and Behrensmeyer, 2004; Bobe and Leakey, 2009). As grazing mammals increased in abundance after 1.8 Ma, arboreal and frugivorous taxa declined and were restricted to closed environments in riparian zones (Reed, 1997).

Evolutionary history of the larger mammals present within the Turkana Basin: bovids, suids, equids, and cercopithecids.

Bovids, suids, equids, and cercopithecids have long evolutionary histories involving migrations, speciation, turnover, and extinction events. Each taxon exhibits significant evolution in East Africa, and specifically the Turkana Basin, during the late Pliocene and early Pleistocene, corresponding to aridification and grassland expansion. Bovids, suids, equids, and cercopithecids all contributed to the major faunal turnover after 1.8 Ma (Behrensmeyer et al., 1997).

Bovids immigrated into Africa from Eurasia by the early Miocene, around 18 Ma (Turner and Antón, 2004:166), and are fairly common in the African record by the mid-Miocene. Bovids increased in species richness by the mid-Pliocene. By the Plio-Pleistocene transition, bovids were the predominant artiodactyl family, and members of modern grazing bovid tribes had evolved (Janis, 2007). Alcelaphini and Antilopini are the two bovid tribes most closely associated with arid conditions and open grasslands because of hypsodont dentition and limbs showing cursorial adaptations. These provide evidence for grassland expansion throughout the Turkana Basin at 2.0 Ma (Bobe and Behrensmeyer, 2004; Bobe and Leakey, 2009).

Suids first evolved in Eurasia during the Eocene and dispersed throughout those continents during the Oligocene (Harris and Li-ping, 2007). Suids migrated into Africa around 17.5 Ma during the early Miocene. By the late Miocene and early Pliocene, the genera *Nyanzachoerus* and *Notochoerus* had replaced the earlier diversity of African suids (Turner and Antón, 2004:131). The *Nyanzachoerus-Notochoerus* lineage showed a temporal trend toward decreasing premolar size, progressively increasing size in third molars, and increasing hypsodonty until their last appearances around 1.8 Ma. These characteristics are observed in Koobi Fora specimens (Bishop, 2010). As *Nyanzachoerus* and *Notochoerus* declined, *Metridiochoerus* and *Kolpochoerus* become numerically dominant near the Plio-Pleistocene boundary, as seen in Shungura specimens (Harris and Li-Ping, 2007; Bobe and Leakey, 2009). *Metridiochoerus* species progressed from grass-dominated mixed feeding at their earliest dates of 3.4 Ma to obligate grazing at their last dates ca. 0.7 Ma. After 2.5 Ma, *Metridiochoerus* experienced greater speciation and increase in complexity and crown height of third molars while East African grasslands expanded (Bishop, 2010). Members of the genus *Metridiochoerus* are the best indications of arid grasslands in the suids because of their extremely hypsodont molars (Bobe and Behrensmeyer, 2004).

The earliest African equids, from the genus *Hipparion*, date to the late Miocene around 10 Ma until their extinction by the mid-Pleistocene (Turner and Antón, 2004:124-126). The genus of modern horses, *Equus*, first appeared in East Africa at 2.33 Ma as they migrated from Eurasia onto the increasing open savanna (Bernor et al., 2010). *Equus* had higher-crowned teeth than *Hipparion*. *Equus* was also more closely associated with open environments and grasslands, whereas *Hipparion*, while still a hypsodont grazer, was more closely associated with densely vegetated areas (Behrensmeyer, 1975). *Equus* first appears in the Omo record of the Turkana Basin around 2.3 Ma, when this genus comprises 30% of the equid specimens. After 1.8 Ma in the Omo, *Equus* increases to more than half of all equid specimens (Bobe and Leakey, 2009).

Cercopithecids increased in prevalance and diversity beginning in the early Pliocene, most likely after the decline in Miocene ape diversity provided new niche opportunities for monkeys to exploit. In the Turkana Basin, Colobinae and Cercopithecinae, the two subfamilies of extant cercopithecids, initially had a low diversity during the early Pliocene, but that diversity increased through time. It was during the early Pliocene that *Theropithecus* first appeared. The mid-Pliocene saw the dominance of *T. brumpti* and the success of large colobines occupying terrestrial environments and ecotonal woodland savannas (Jablonski and Leakey, 2008).

A major faunal turnover occurred with the extinction of large terrestrial colobine monkeys around the KBS-Okote Members boundary (1.6 Ma). Paleosol evidence indicates increased aridification after 1.6 Ma (Wynn, 2004), which may have contributed to this extinction event. This was followed by the dominance of a now-extinct gelada, *T. oswaldi*, and the evolution of modern monkeys. Terrestrial colobines, whose thinly-enameled molars were poorly adapted to abrasives in grasses, could not successfully compete with species such as *T. oswaldi* and ungulates that were better adapted to grazing in open environments (Jablonski and Leakey, 2008; Leakey et al., 2008).

Hominins in the Turkana Basin

The Turkana Basin provides some of the best evidence for hominin evolution. The Koobi Fora Formation in East Turkana, in particular, has yielded *Australopithecus*, *Paranthropus*, and *Homo* specimens in addition to Oldowan and Acheulean stone tools. The earliest evidence of fossil hominins from East Turkana are *Australopithecus anamensis* specimens from Kanapoi and Allia Bay, dated between 4.2 and 3.9 Ma. The paleoecology of these sites suggest woodland and bushland habitats, and the presence of monkeys suggests a wide gallery forest (Coffing et al., 1994; Leakey et al., 1995; Ward et al., 1999). *A. afarensis* discoveries are rare within the Turkana Basin, possibly because deposits associated with this taxon's time range are uncommon. A partial cranium of *A. afarensis*, dated to 3.3 Ma, was found in Koobi Fora (Kimbel, 1988), and fragmentary mandibles, maxillae, and teeth were found in West Turkana (Brown et al., 2001). *Paranthropus aethiopicus* specimens date to 2.7 Ma in the Shungura Formation (Suwa et al., 1996) and 2.5 Ma in the Nachukui Formation in West Turkana (Walker et al., 1986).

P. boisei and *Homo* remains are abundant. The first appearance of *P. boisei* comes from a cranium and partial mandible recovered from deposits dating to 2.5 Ma (Leakey and Walker, 1988). Additional *P. boisei* specimens are found in the Turkana Basin until 1.4 Ma (Grausz et al., 1988; Feibel et al., 1989; Wood, 1991:259-261; Suwa et al., 1996; Brown et al., 2001). The earliest *Homo* evidence is in the Shungura and Nachukui Formations and dates to 2.4 Ma. *H.*

habilis and *H. rudolfensis* are both early species found in the Turkana Basin (Suwa et al., 1996; Prat et al., 2005).

The earliest *H. erectus* in the Turkana Basin dates to 1.8 Ma, coinciding with C_4 vegetation expansion and major faunal turnovers (Feibel et al., 1989). *H. erectus* evolution is closely associated with open and arid or semiarid environments (Rightmire, 1995). Nasal morphology indicates that *H. erectus* had enhanced moisture retention during expiration and could use the retained moisture for humidifying the air on the next breath (Franciscus and Trinkaus, 1988). Enhanced moisture retention and humidification are adaptations for arid conditions. Based on nasal morphology and traits such as longer legs, modern body proportions, and better thermoregulation, *H. erectus* likely engaged in prolonged activity in arid environments (Franciscus and Trinkaus, 1988). Its morphologic adaptations to grasslands may have led to its migration into the Turkana region from an unknown source as the local environment became more arid. As *H. erectus* members evolved larger body sizes, they needed higher-quality diets. *H. erectus* members may have met this dietary need by incorporating more meat into their diets, expanding their range into more open habitats where primary productivity is lower but resources for carnivores are more abundant (Antón et al., 2002). Range expansion, stimulated by the search for high-quality food resources, may have attracted these hominins into the Turkana Basin.

P. boisei, *H. habilis*, *H. rudolfensis*, and *H. erectus* (Brown et al., 1985; Feibel et al., 1989; Wood, 1991:259-261; Brown et al., 2001; Spoor et al., 2007) all lived in Koobi Fora between 2.0 and 1.5 Ma as the basin experienced major topographic, hydrologic, seasonal, and vegetational changes. These events diversified the environment, likely provided multiple habitat and niche opportunities, and changed patterns of resource use by hominins (Rogers et al., 1994).

Joordens et al. (2011) found that the Turkana Basin, compared to other basins in the East African Rift System, remained well-watered between 2.0 and 1.8 Ma, even during periods of low summer monsoon intensity. Therefore, the Turkana Basin may have acted as an aridity refugium with its permanent water source, attracting and facilitating the presence of four different hominin species in addition to other water-dependent animals. In addition to a dependable water supply, the basin supplied hominins with many food resources, which included aquatic animals (Braun et al., 2010). After 1.7 Ma, when the lake was replaced by a fluvial system and aridity intensified, archaeological sites increase in number in the Turkana Basin, suggesting that the basin continued to be a favorable habitat to hominins and that hominins were able to persist during fluctuating conditions (Potts and Teague, 2010).

Expected results of research

As global and regional climates changed during the early Pleistocene, East African environments became more arid, open, and heterogeneous. Analysis of mammals from the Turkana Basin should find evidence for temporal change in species distribution with an increase in the number of specimens and relative abundance of species adapted to open environments from the Upper Burgi to the Okote Members. Fauna succession should also indicate a persistence of some closed environments as well. Faunal evidence should show trends toward grazing within each family, indicated by traits, such as hypsodonty and enlarged molars, which are favorable in open habitats. Alcelaphini and Antilopini, both inhabitants of arid environments, should increase through time along with *Metridiochoerus* and *Equus*. Both *Metridiochoerus* and *Equus* have extremely hypsodont molars, which indicates grass-dominated diets. Browsing species and arboreal cercopithecids should decline in abundance as grasslands and grazing animals increase. Taphonomic bias will also be expected because of differential fossilization of elements and bias during collection. The results should show mammals responding to environmental changes as C_4 plants and grasslands came to dominate the local vegetation between 2.0 and 1.5 Ma.

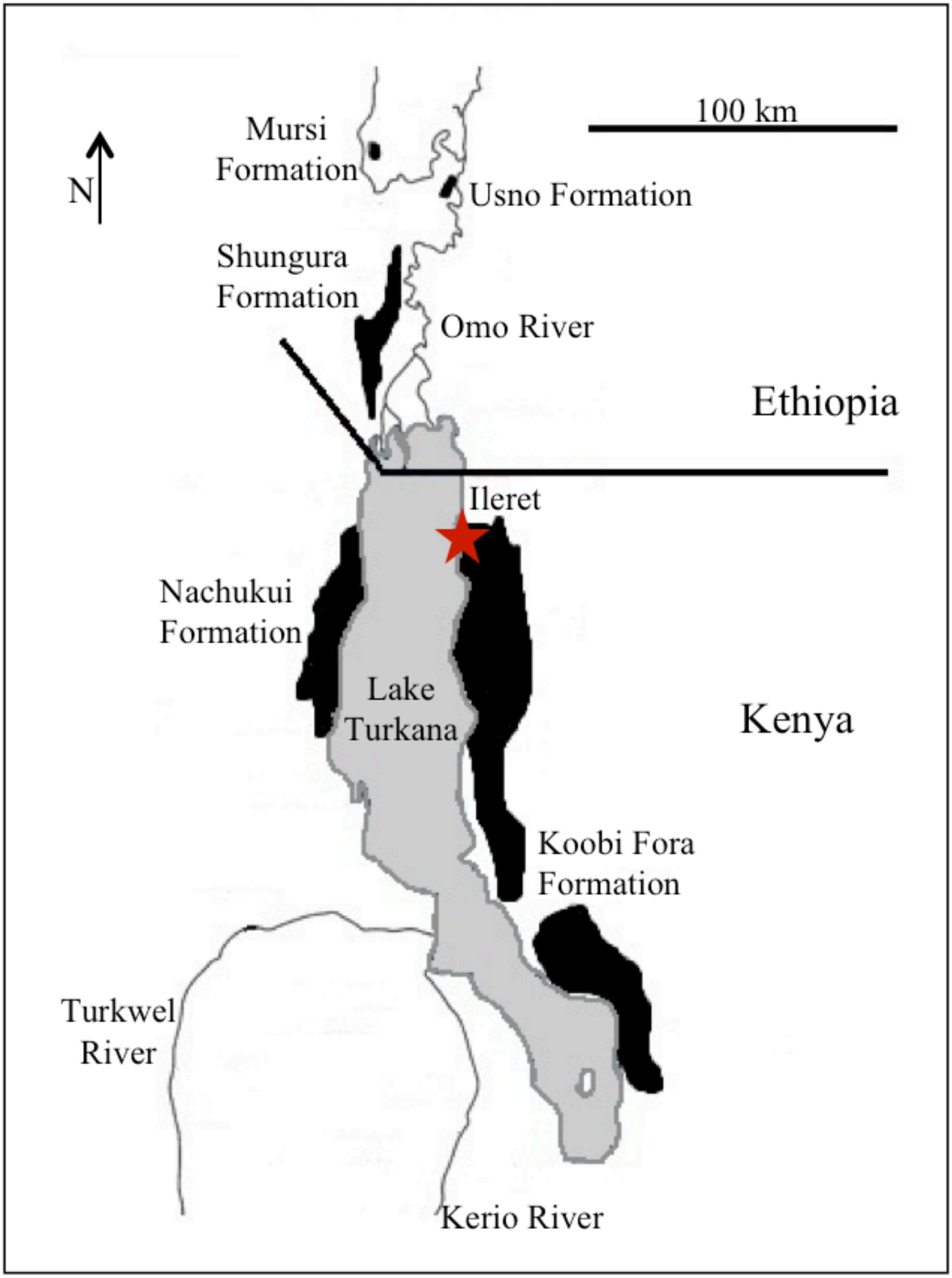


Fig. 1.1. Map of the Turkana Basin in Northwest Kenya; includes Lake Turkana and the Omo Group Deposits.

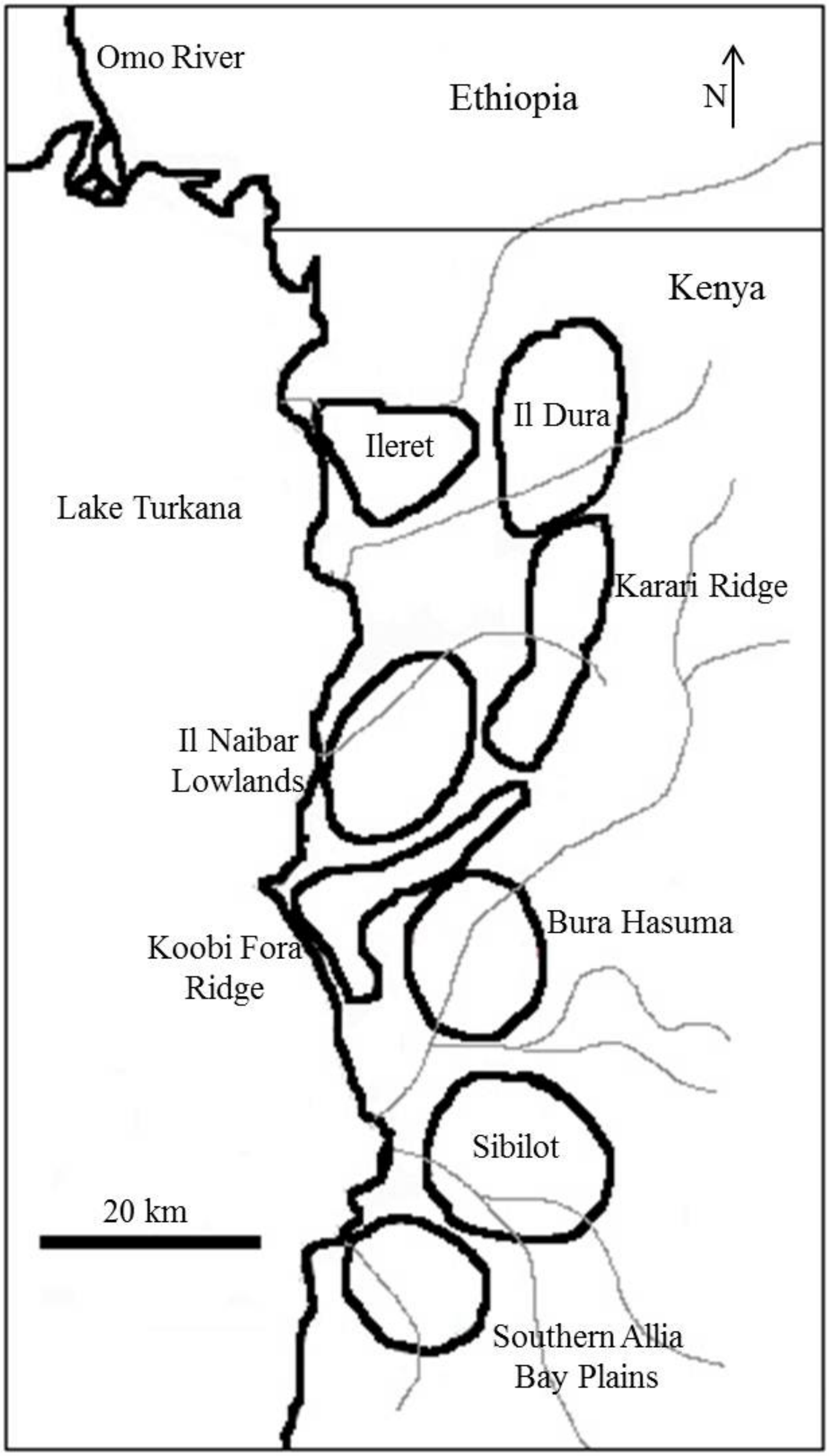


Fig. 1.2. Map of the major regions of the Koobi Fora Formation; areas 1, 1A, 6, and 8A are in the Ileret region.

TABLE 1.1. Major Plio-Pleistocene climatic and evolutionary events

Time (million years)	Event
2.8	Onset of Northern Hemisphere Glaciation
	First appearance of *Paranthropus*
2.5	First appearance of *Homo*
	Increase in C_4 vegetation in Turkana Basin
2.0	Initial development of Walker Circulation
	Presence of Lake Lorenyang in Turkana Basin
	Increase in faunal turnover in Turkana Basin
1.8	Glacial intensification
	Strong Walker Circulation and onset of ENSO
	Increased variability in East African seasonality
	Dominance of C_4 vegetation in Turkana Basin
	Appearance of *H. erectus* and faunal turnover in Turkana Basin
1.7	Evidence for Acheulean stone tools
	Disappearance of lake in Turkana Basin, replaced by fluvial system
1.6	Increased aridification in Turkana Basin

TABLE 1.2. Members of the Koobi Fora Formation[a]

Member	Time Period (Ma)
Lonyumun	4.35 – 4.0
Moiti	4.0 – 3.6
Lokochot	3.6 – 3.42
Tulu Bor	3.36 – 2.68
Burgi	Lower 2.68 – 2.0 Upper 2.0 – 1.88
KBS	1.88 – 1.6
Okote	1.6 – 1.39
Chari	1.39 – 0.7

[a] (Brown and Feibel, 1991; Brown and McDougall, 2011).

CHAPTER 2

MATERIALS AND METHODS

The Koobi Fora Formation on the eastern side of Lake Turkana is one of five Plio-Pleistocene formations within the Turkana Basin. Analysis was performed on specimens from the Koobi Fora Formation at two levels: on previously collected specimens catalogued in the Turkana Basin Paleontology Database and on data collected during recent fieldwork in the 2011 field season. This chapter reviews: (1) the excavation history of the Koobi Fora Formation, when specimens in the Turkana Basin Paleontology Database were collected, and (2) the materials and methods used in this study to analyze the database and the summer fieldwork results.

Fossil recovery and excavation date back to the early 1900s when a French expedition uncovered vertebrate fossils in the lower Omo Valley. Numerous expeditions continued during the early to mid 20th century, surveying the geology and hydrology of the basin, recovering vertebrate fossils, and studying the archaeology. Work on Plio-Pleistocene exposures of the Omo group began in 1967 by a joint French, American, and Kenyan expedition. Initial prospecting on the eastern side of Lake Turkana, then Lake Rudolf, began a year later, led by Richard Leakey. By 1970, the East Rudolf Research Project was established. Excavation continued over the next several years, focusing on paleontology and archaeology. In 1975, the lake was renamed Lake Turkana and the research project was known as the Koobi Fora Research Project thereafter. Research continued, especially focusing on biostratigraphic correlation and dating of volcanic tuffs (Harris et al., 2006). During the1980s, work by Frank Brown and Craig Feibel (1991) established the stratigraphy and a uniform chronology for the Koobi Fora Formation. Research continues today with teams of geologists, paleontologists, archaeologists, paleoecologists, and paleobotanists collaborating to discover new fossil evidence and reconstruct landscapes and hominin behavior (Harris et al., 2006).

The research presented in this study analyzed the temporal distribution of specified mammal taxa between the Upper Burgi, KBS, and Okote Members (Table 1.2). The Upper Burgi Member represents deposits from 2.0 to 1.88 Ma, the KBS spans from 1.88 to 1.6 Ma, and the Okote spans from 1.6 to 1.39 Ma (Brown and Feibel, 1991). The geographic regions of exposure that were targeted from the database were the Ileret (collecting areas 1 – 12), the Koobi Fora Ridge (collecting areas 100 – 104, 115, and 106), and the Karari Ridge (collecting areas 129, 130, 131, 118, and 105). Recent fieldwork presented here was conducted in the Okote Member of the Ileret region (collecting areas 1, 1A, 6, and 8A) (Fig. 1.2).

Database work

The Turkana Basin Paleontology Database created by René Bobe and Anna K. Behrensmeyer contains computerized data for over 16,000 specimens from the Lake Turkana Basin with over 11,000 specimens from the Koobi Fora Formation. The database uses FileMaker Pro software. Specimens recorded in the database were collected during multiple field seasons in the Turkana Basin following the 1970s. The majority of the specimens in the database are from the published record. All specimens recorded in the database are curated in the National Museums of Kenya, Nairobi, Kenya. The database fields include the locality/site, formation/member, taxonomy, element and description, taphonomic factors, and publication source for each specimen. Because of different sampling methods used by different collectors over time, considerable field collection bias exists. Much of the sampling was not designed specifically to enable environmental reconstructions.

This database was analyzed for temporal changes in mammal taxa among three members (Upper Burgi, KBS, and Okote Members). Specimen records with uncertain stratigraphic provenience were eliminated. Counts reflect the number of specimens, with one count per individual. The database indicates when two or more specimens are likely to represent one individual, so multiple counts can be eliminated. Temporal changes in relative abundances of taxa were evaluated with chi-square and correspondence analysis using PAST statistical software (Hammer et al., 2001). For chi-square analysis, significance of change was assessed by assuming no temporal change.

Data were analyzed at several different taxonomic levels. Cercopithecidae, Bovidae, Suidae, Equidae, Rhinocerotidae, Deinotheriidae, and Giraffidae were studied at the family level. Tribal level abundance analysis, based on number of specimens, was performed for Bovidae. Bovid tribes included in the tribal level analysis were Bovini, Reduncini, Tragelaphini, Alcelaphini, Antilopini, Aepycerotini, Neotragini, and Hippotragini. Genus and species level analyses were performed for Suidae, Equidae, and Cercopithecidae. Taphonomic factors were considered by comparing specimen count of bovid teeth to all recorded bovid specimens. Teeth were chosen because they are the most abundant element in the fossil record and are more likely to be preserved because of the high inorganic composition of enamel.

Fieldwork in Ileret, Koobi Fora Formation

The larger-scale analysis of the three members from throughout the Koobi Fora Formation in the Turkana Basin Paleontology Database was supplemented by finer-scale analysis of a relatively narrow time frame made possible by fieldwork in 2011. During the summer 2011 field season, surface surveys (bone walks) from localities within the Ileret Tuff Complex (1.53-1.51 Ma) of the Okote Member were conducted. These localities included areas 1, 1A, 6, and 8A. In designated survey areas, mammal, reptile, and fish specimens observed on the surface were recorded. Ancillary information including color, size, presence of matrix, and taphonomic condition was also recorded. Certain specimens, primarily teeth, limb elements, and phalanges, were collected for future analysis. The collected specimens are housed in the National Museums of Kenya, Nairobi, Kenya, and the associated data will be added to the Turkana Basin Paleontology Database in the future.

Mammals from 2011 field surveys are included in this research. The number of specimens in Cercopithecidae, Bovidae, Suidae, Equidae, Rhinocerotidae, Deinotheriidae, and Giraffidae were counted and compared to the specimen counts from the Upper Burgi, KBS, and Okote Members already recorded in the Turkana Basin Paleontology Database. Bovid tribal analysis, based on the number of specimens in each tribe, was also performed using the 2011 survey data and compared to the larger-scale results.

Conclusion

The methods used in this research are designed to study East Turkana paleoecology through a multi-faunal approach and to evaluate the Turkana Basin Paleontology Database's usefulness in paleoenvironmental reconstructions. These methods are used in subsequent chapters to reconstruct paleoecology and identify general environmental conditions, based on mammals present in the landscape, in the context of hominin environments. Results should show increases through time in taxa that are adapted to grassland environments.

CHAPTER 3

RESULTS OF THE PALEONTOLOGICAL ANALYSIS

Analyses of the mammal fossil record in the Turkana Basin Paleontology Database reveal changes in the number of specimens for families, genera, and species among the Upper Burgi, KBS, and Okote Members. The results provide inferences about the paleoenvironmental conditions in East Turkana during the early Pleistocene. Data from the 2011 fieldwork in Ileret supplement the larger-scale analysis to provide paleoenvironmental information for a more localized area in the northern part of the Koobi Fora Formation around 1.5 Ma.

Family level analysis

The total number of specimens in the family level analysis for the Upper Burgi, KBS, and Okote Member samples are 977, 1362, and 661 specimens, respectively (Table 3.1). The relative abundance of families, based on count, for each member is presented in Figure 3.1. During the earliest time period represented by the Upper Burgi Member, bovids account for 37% of the total number of specimens, and suids account for 30% of the total number of specimens. Cercopithecids are the third largest taxon. The other five taxa are rare.

The change in relative abundance between samples for the Upper Burgi and KBS Members is statistically significant (χ^2=210.44, $p<0.0001$). During the KBS Member, bovids account for 48% of the total number of specimens and suids for 24%. Unlike in the assemblage from the earlier period, equids are the third in abundance, cercopithecids are less abundant, and giraffids have increased. The other families contribute minimally to the collection.

During the latest stratigraphic layer, the Okote Member, bovids remain the most abundant taxon but have declined in relative abundance. Suids decline slightly. Cercopithecids, however, increase substantially and comprise a much greater percentage of the total number of specimens than in samples from either of the earlier members. The other families are minor components of the collection; deinotheres are absent altogether. The change in relative abundance between samples from the KBS and Okote Members is statistically significant ($\chi^2=468.51$, $p<0.0001$).

A correspondence analysis of families across the three members is shown in Figure 3.2. Along axis one the members do not follow chronological order. Along axis two the members follow the established chronological sequence, with a high abundance of suids towards the Upper Burgi and a high abundance of cercopithecids towards the Okote. While suids are pulled towards the Upper Burgi, they are also the family that is closest to the origin, indicating a more even distribution. Bovids, equids, and giraffids are pulled strongly in the direction of the KBS Member. Rhinocerotids and deinotheres are positioned in the periphery because of the low numbers of specimens for these families.

Bovid tribe analysis

For the bovid tribal level analysis, 358 specimens are recorded from the Upper Burgi Member, 653 specimens from the KBS Member, and 210 specimens from the Okote Member (Table 3.2). These number differ slightly from those recorded in Table 3.1 because the family level analysis included some indeterminate specimens that could not be attributed to a tribe. The relative abundance of bovid tribes is depicted in Figure 3.3. In the sample from the Upper Burgi interval, Reduncini are the most abundant tribe, followed by Tragelaphini and Alcelaphini. The other tribes are minor. In the sample from the KBS Member, Reduncini continue to be the most abundant tribe, and Alcelaphini increase in relative abundance to comprise 23% of the KBS sample. Tragelaphini rank third with 14%. The other tribes continue to make minor contributions. The change in relative abundance of bovid tribes between samples from the Upper Burgi and KBS Members is statistically significant (χ^2=107.79, p<0.0001). In the Okote Member sample, Reduncini increase significantly to 46% of the total sample. Alcelaphini remain second, and Tragelaphini remain third. All other tribes decline further from KBS levels, and Hippotragini are absent. The change in the relative abundance between samples from the KBS and Okote Members is statistically significant (χ^2=17.44, p=0.0078).

A correspondence analysis of bovid tribes across the three members is presented in Figure 3.4. The positions of the members follow a chronological succession along the first axis, with the highest abundance of Antilopini in the Upper Burgi and the highest abundance of Bovini in the KBS. Alcelaphini are pulled in the direction of the KBS Member while Reduncini and Tragelaphini are not pulled toward any one member but are positioned closer to the origin. This indicates their relatively even distribution among the three members. Aepycerotini are not pulled in any one direction but is positioned furthest from the Okote. Neotragini and Hippotragini lie in the periphery because of their low number of specimens.

Bovid taphonomic considerations.

For taphonomic considerations, bovid tribal level analysis is based only on teeth (Table 3.3), though comparison to bovid tribe results based on all specimens, including teeth, is presented in Figure 3.5. The total number of teeth specimens for the bovid tribes in consideration is 129 specimens for the Upper Burgi Member, 220 specimens for the KBS Member, and 70 specimens for the Okote Member. Reduncini teeth comprise 40% of the Upper Burgi teeth, followed by Alcelaphini (22% of the Upper Burgi teeth) and Antilopini (16% of the Upper Burgi teeth). The most abundant tribe in the KBS sample is Alcelaphini, and the second most abundant is Reduncini. Reduncini return as the most abundant tribe in the Okote Member sample. Alcelaphini and Tragelaphini are the second and third most abundant tribes. Neotragini and Hippotragini are absent or minor components in all members.

The relative abundances, based on counts of teeth, differ from the abundances based on counts for all specimens (Fig. 3.5). For samples including all specimens, Reduncini are dominant in samples from all three members, but for teeth samples, Alcelaphini are dominant during the KBS Member. The differences between relative abundance based on teeth and on all specimens in the Upper Burgi and KBS samples are statistically significant (Upper Burgi: $\chi^2=13.871$, $p=0.017$; KBS: $\chi^2=18.151$, $p=0.006$). The differences between these two categories in samples from the Okote Member are not statistically significant ($\chi^2=4.150$, $p=0.528$).

A correspondence analysis of bovid tribes based on teeth specimens across the three members is presented in Figure 3.6. Tragelaphini are strongly pulled in the direction of the Okote, Reduncini are pulled in the direction of the Upper Burgi, and Bovini and Alcelaphini are pulled in the direction of the KBS. Neotragini and Hippotragini are outliers; their positions fall outside the bounds of the graph. In comparison to the correspondence analysis of bovid tribes based on all specimens (Fig. 3.4), Reduncini and Tragelaphini show major differences in position. When considering teeth specimens, Tragelaphini and Reduncini are less evenly distributed and tend to have higher abundances in the Okote and Upper Burgi Members, respectively. Antilopini, Aepycerotini, Alcelaphini, and Bovini are in similar positions overall in relation to the member points.

Suid, equid, and cercopithecid analysis

Genus and species level analysis were performed for suids. The genera attributed to suid fossils in the upper members of the Koobi Fora Formation are *Kolpochoerus*, *Notochoerus*, and

Metridiochoerus (Table 3.4, Fig. 3.7). In the Upper Burgi sample, *Kolpochoerus* is the dominant genus, contributing 49% of the total number of specimens. *Notochoerus* and *Metridiochoerus* account for 31% and 20% of the total specimens in each respective sample. Relative abundance changes dramatically between the Upper Burgi and KBS. In the KBS interval, *Metridiochoerus* increases, and both *Kolpochoerus* and *Notochoerus* decline. In the Okote Member, *Metridiochoerus* is very abundant, and *Notochoerus* is absent.

Kolpochoerus limnetes and *Notochoerus scotti* are the only species in those genera recorded in the database for the three members. Four species of *Metridiochoerus* are found in East Turkana between 2.0 and 1.3 Ma. Relative abundance for suid species is presented in Table 3.5 and Figure 3.8. In the Upper Burgi sample, the dominant *Metridiochoerus* species is *M. andrewsi*. In the KBS Member, *M. andrewsi* abundance increases further. A new *Metridiochoerus* species, *M. compactus*, enters the area but remains in low abundance. Samples from the Okote Member record the rise of *M. compactus* to become the dominant suid species, and *M. andrewsi* declines. *M. modestus* and *M. hopwoodi* are minor components in samples from all three members.

A correspondence analysis of suids at the species level is depicted in Figure 3.9. From left to right, the members follow a chronological succession along the first axis, bounded by a high abundance of *N. scotti* at the Upper Burgi end and a high abundance of *M. compactus* at the Okote end. The analysis clearly shows a progression of dominance of *N. scotti* in the Upper Burgi to *M. andrewsi* in the KBS to *M. compactus* in the Okote. Each of these species is pulled strongly in the direction of its respective member. *K. limnetes* is pulled slightly towards the Upper Burgi but remains close to the origin and, therefore, is the most evenly distributed species.

All *Metridiochoerus* species are grouped in closer proximity to the KBS and Okote than to the Upper Burgi.

The two genera recorded in the equid family are *Equus* and *Hipparion* (Table 3.6). *Equus* is dominant throughout all three members. Its relative abundance progressively increases through time, coinciding with a decline in *Hipparion* relative abundance.

The cercopithecid genera present in Koobi Fora during the early Pleistocene included colobines (*Cercopithecoides, Rhinocolobus, Paracolobus,* and *Colobus*) and cercopithecines (*Parapapio, Cercopithecus, Cercocebus, Lophocebus,* and *Theropithecus*). The number of specimens and relative abundances are presented in Table 3.7 and Figure 3.10. In samples from all three members, *Theropithecus* is the most abundant genus, but its abundance decreases through time from 81% of the specimens in the Upper Burgi sample to 58% of the specimens in the Okote sample. Large-bodied colobines (*Cercopithecoides, Rhinocolobus,* and *Paracolobus*) are present in samples from the Upper Burgi, and their abundance declines through time with only a few specimens remaining in the Okote sample. Extant taxa (*Cercopithecus*, *Colobus*, and *Lophocebus*) appear in small numbers in the KBS sample and increase in the Okote sample.

A correspondence analysis of cercopithecids at the genus level shows a chronological transition from large-bodied colobines at one end to extant taxa at the other end (Fig. 3.11). The large-bodied colobines are clustered near each other and, as a group, are pulled towards the Upper Burgi Member. *Theropithecus* and *Parapapio* both have a fairly even distribution among the three members, as suggested by their close position to the origin. *Colobus* and *Cercocebus* occupy the same position on the graph and are located close to *Lophocebus*. These three genera are extant taxa and are pulled closest to the Okote Member. The small number of specimens of *Cercopithecus* results in its outlier position.

Summer fieldwork in Ileret

The total number of specimens collected during the summer fieldwork in Ileret for the selected families is 134 specimens (Table 3.8). Their relative abundance is shown in Figure 3.12. Bovids are the most abundant family, and suids are the second most abundant family. Specimens from the remaining families are minor contributions, and deinotheres are absent. Figure 3.13 compares the abundance of families from the Ileret survey data with database samples from the Upper Burgi, KBS, and Okote Members. In general, the curves show an overall similar pattern for all of the represented families. Bovids have the highest percentage, and suids and equids are comparable. Rhinocerotids, deinotheres, and giraffids are low in all four. Cercopithecids are the exception with very low percentages in the Ileret and the KBS and much higher percentages in the Upper Burgi and Okote.

Of the 91 bovid specimens, 80% are indeterminate (Table 3.9, Figure 3.14). The bovid tribes represented by the remaining specimens include Alcelaphini, Tragelaphini, Reduncini, Bovini, Neotragini, and Cephalophini. Reduncini is the most common tribe, and Alcelaphini is the second most abundant tribe, although, each tribe contributes minimally to the number of specimens. The remaining four tribes contribute small percentages of the total.

Conclusion

Overall, bovids are the most abundant family in both the larger-scale analysis from throughout Koobi Fora and the smaller-scale analysis from the 2011 summer fieldwork in Ileret. Among the bovids, reduncines are the most abundant tribe. Among the suids, *Metridiochoerus*, specifically *M. compactus*, is dominant in the sample from the Okote Member. Among the cercopithecids, *Theropithecus* is the dominant genus; however, its relative abundance declines in the Okote sample, reflecting the increase in modern taxa. These results are discussed in chapter

4 in relation to previous faunal and paleoenvironmental studies, the expansion of grasslands, and the presence of several hominin species in the basin.

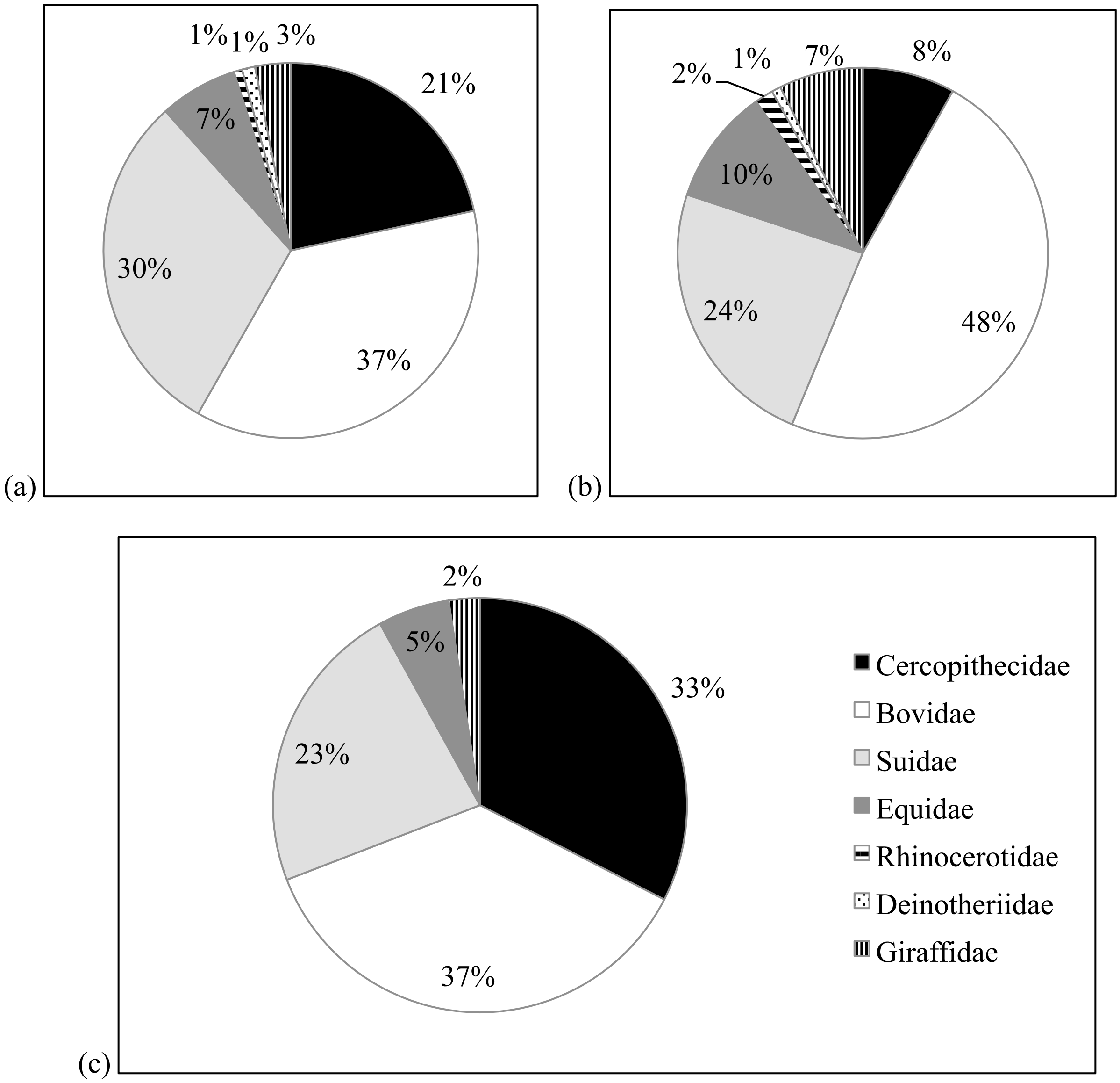


Fig. 3.1. Relative abundance of families based on count. (a) Upper Burgi Member, (b) KBS Member, (c) Okote Member.

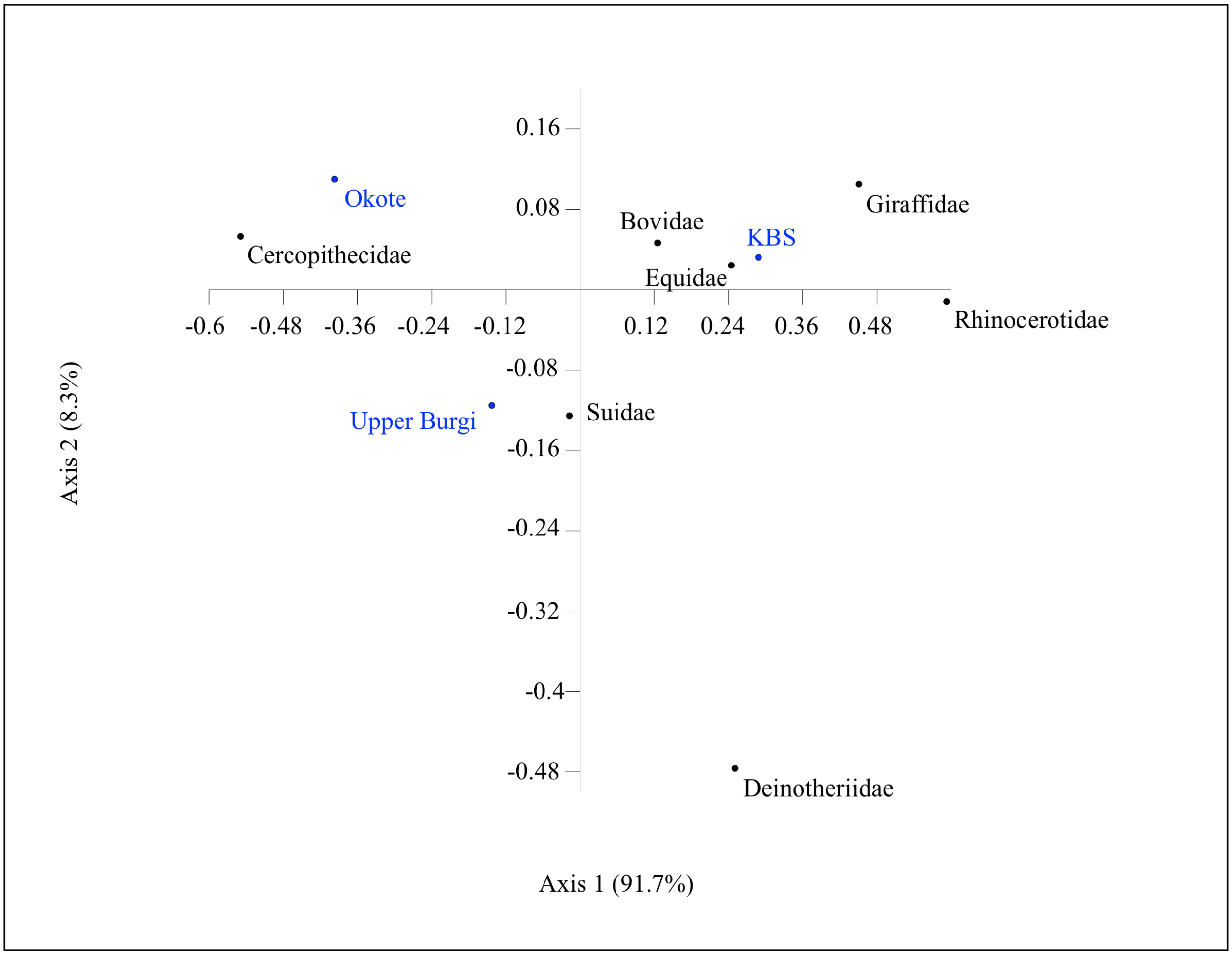


Fig. 3.2. Correspondence analysis of families in the Upper Burgi, KBS, and Okote Members; axis 1 explains 91.7% of the variation and axis 2 explains 8.3% of the variation when based on two dimensions.

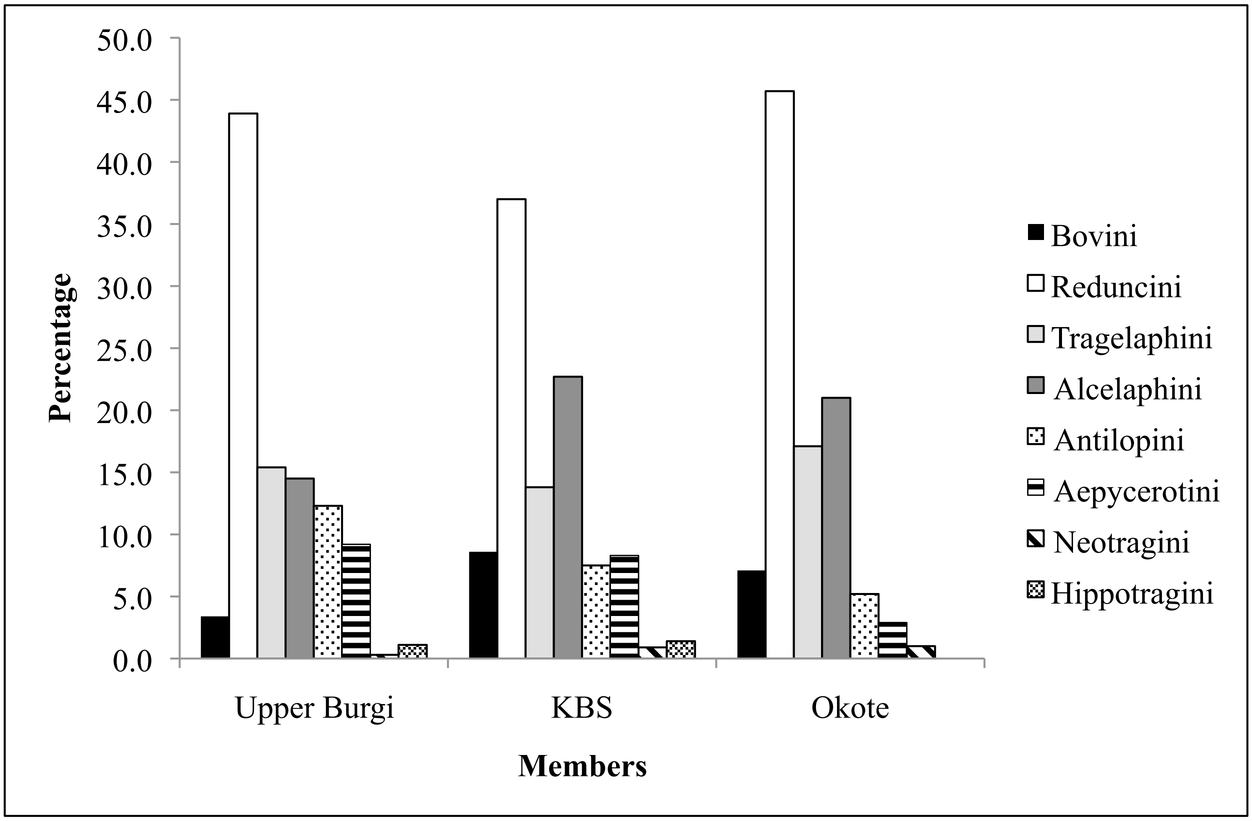


Fig. 3.3. Relative abundance of bovid tribes.

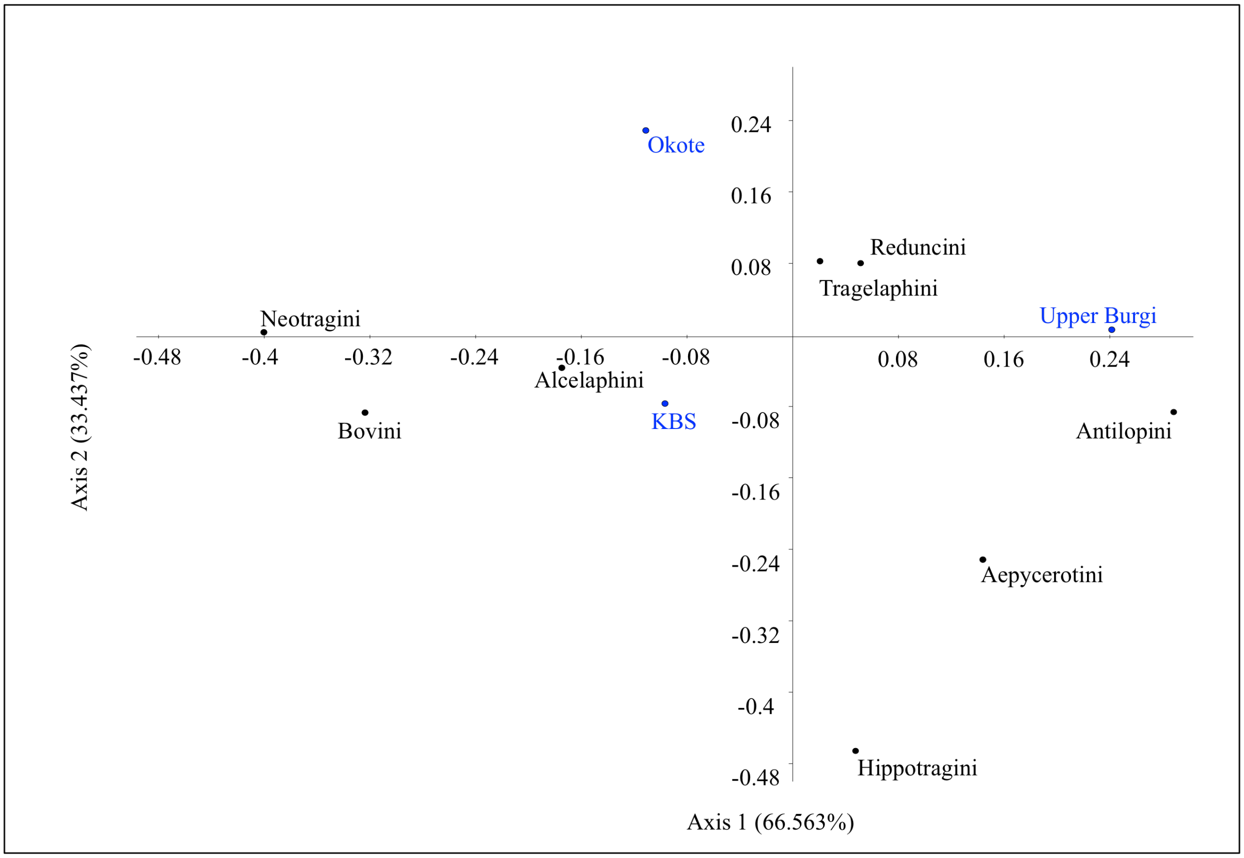
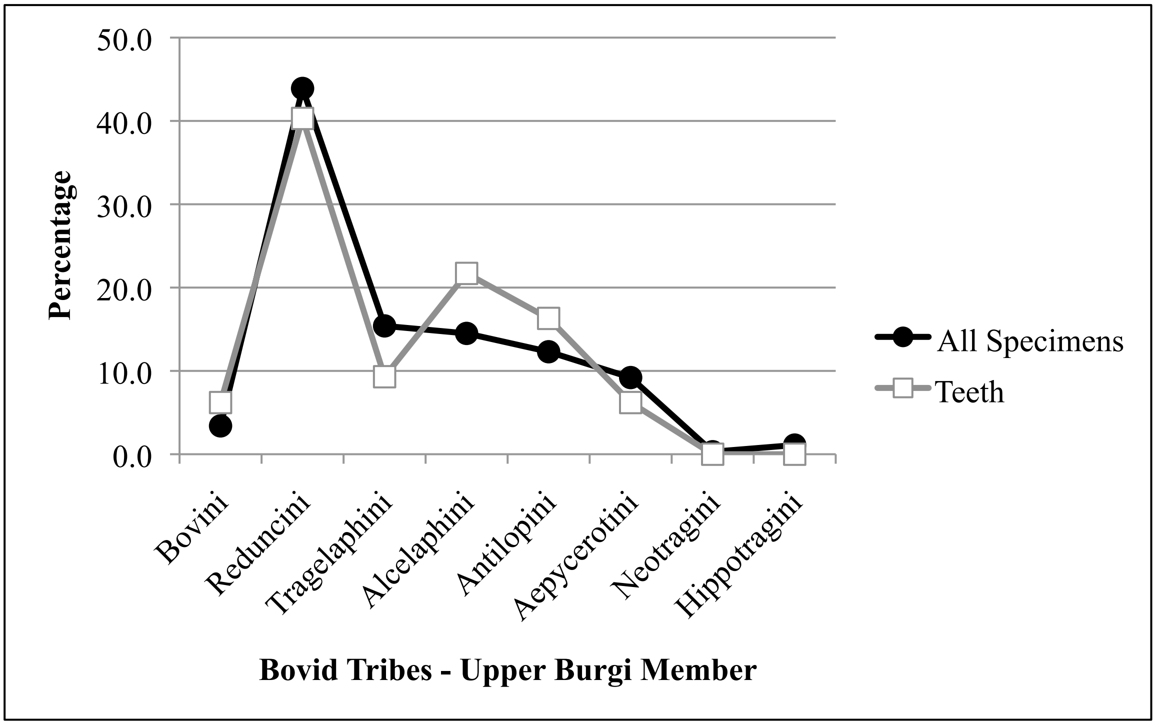
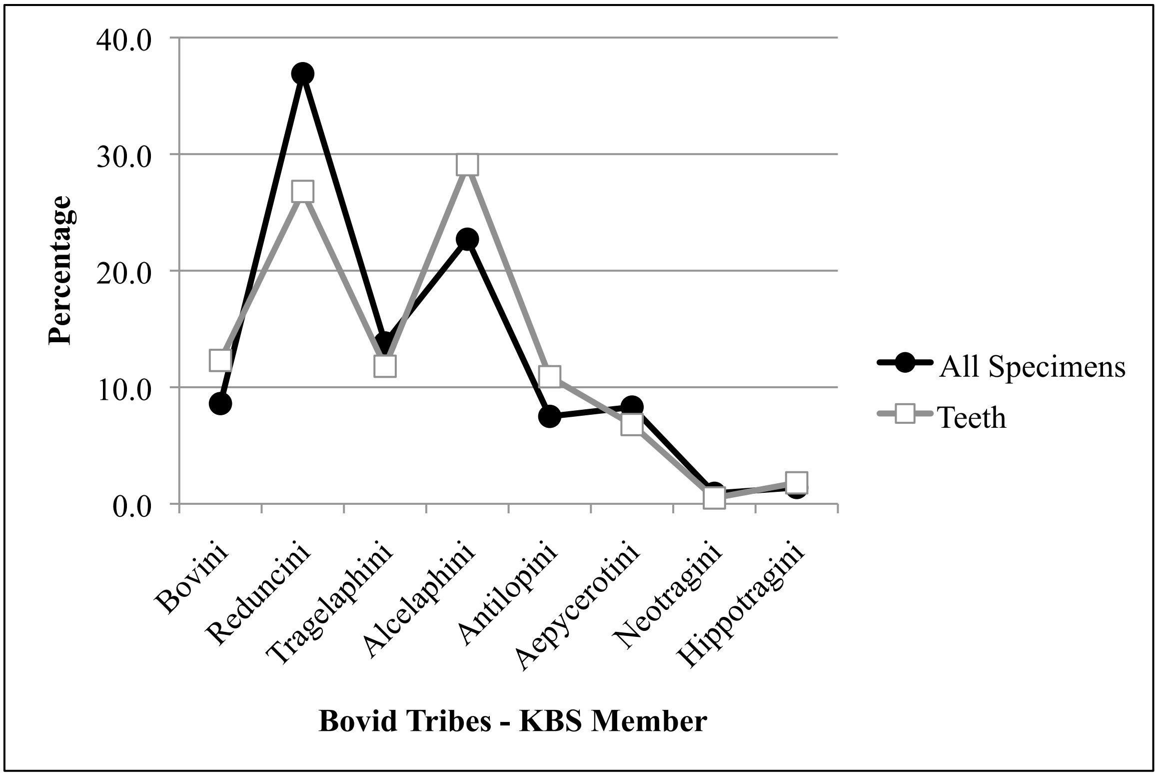


Fig. 3.4. Correspondence analysis of bovid tribes in the Upper Burgi, KBS, and Okote Members; axis 1 explains 66.563% of the variation and axis 2 explains 33.437% of the variation when based on two dimensions.



50.0
40.0
30.0
20.0
10.0
0.0
Percentage
Bovini
Reduncini
Tragelaphini
Alcelaphini
Antilopini
Aepycerotini
Neotragini
Hippotragini
Bovid Tribes - Upper Burgi Member
All Specimens
Teeth

(a)



40.0
30.0
20.0
10.0
0.0
Percentage
Bovini
Reduncini
Tragelaphini
Alcelaphini
Antilopini
Aepycerotini
Neotragini
Hippotragini
Bovid Tribes - KBS Member
All Specimens
Teeth

(b)

(c)

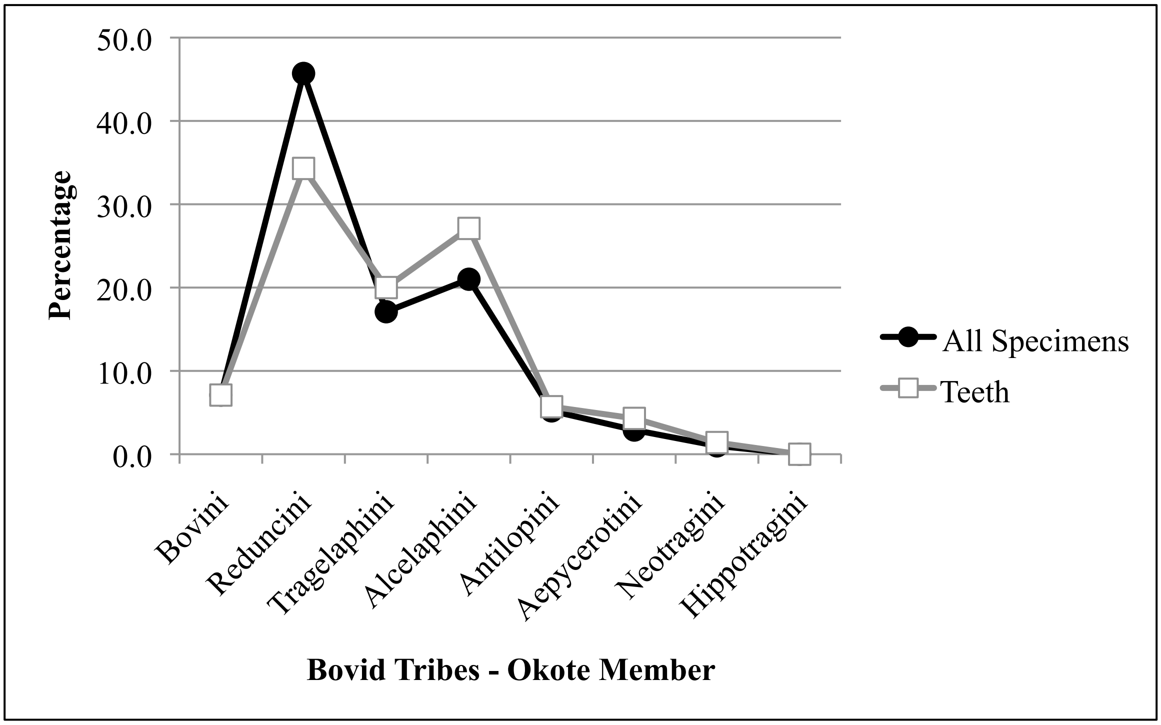


Fig. 3.5. Taphonomic analysis of bovid tribes. (a) Upper Burgi Member, (b) KBS Member, (c) Okote Member. The "All specimens" category includes teeth.

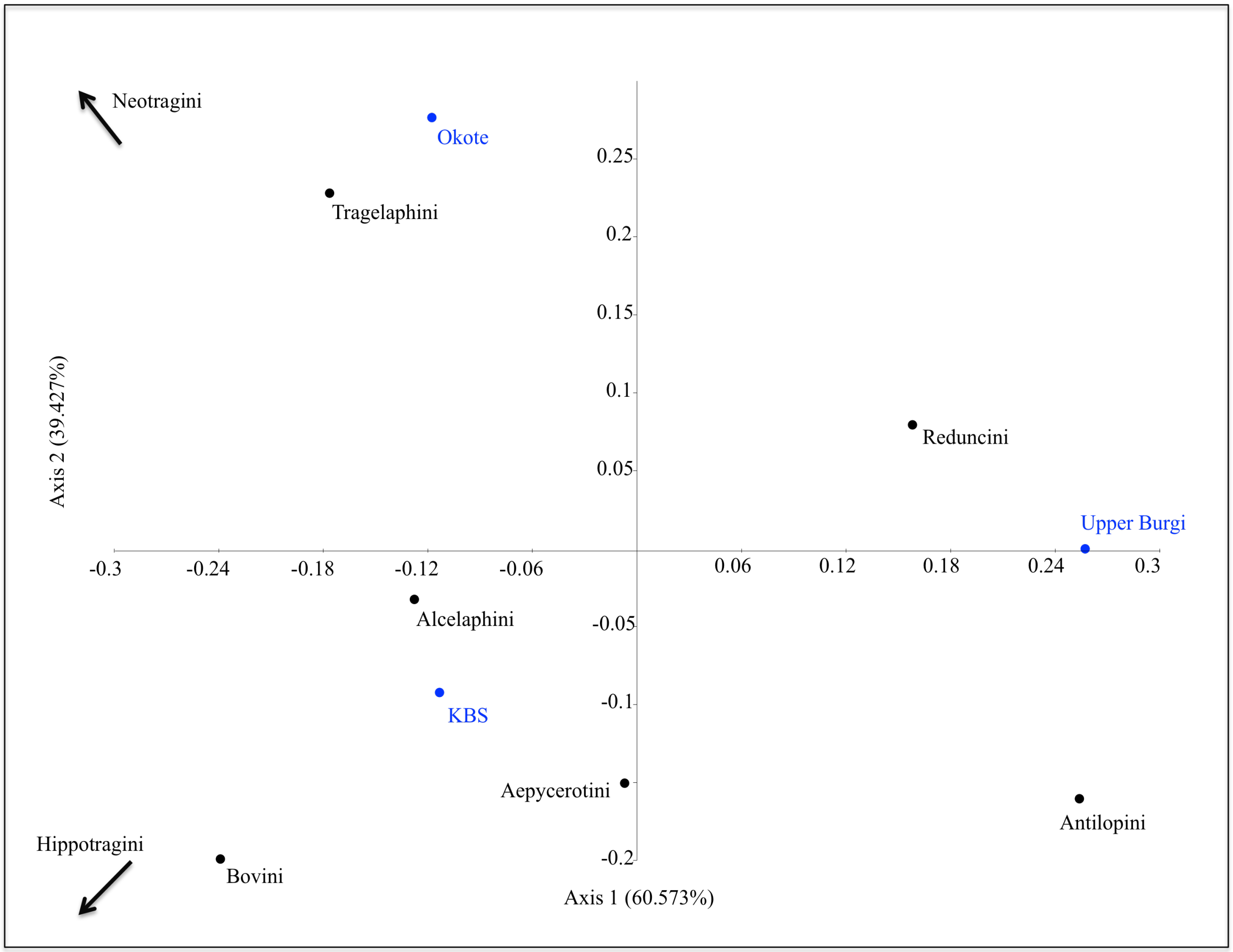


Fig. 3.6. Correspondence analysis of bovid tribes based on teeth specimens in the Upper Burgi, KBS, and Okote Members; axis 1 explains 60.573% of the variation and axis 2 explains 39.427% of the variation when based on two dimensions.

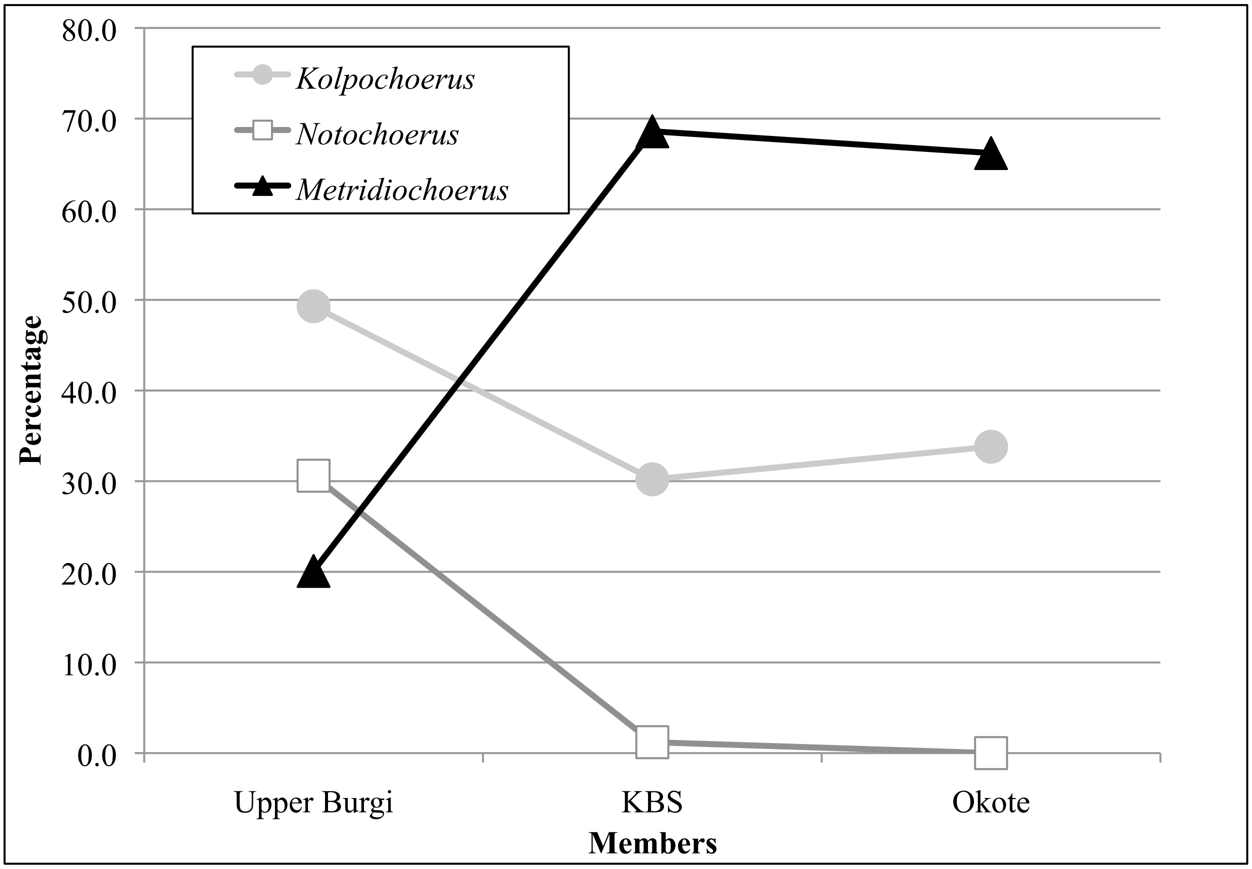


Fig. 3.7. Relative abundance of suid genera.

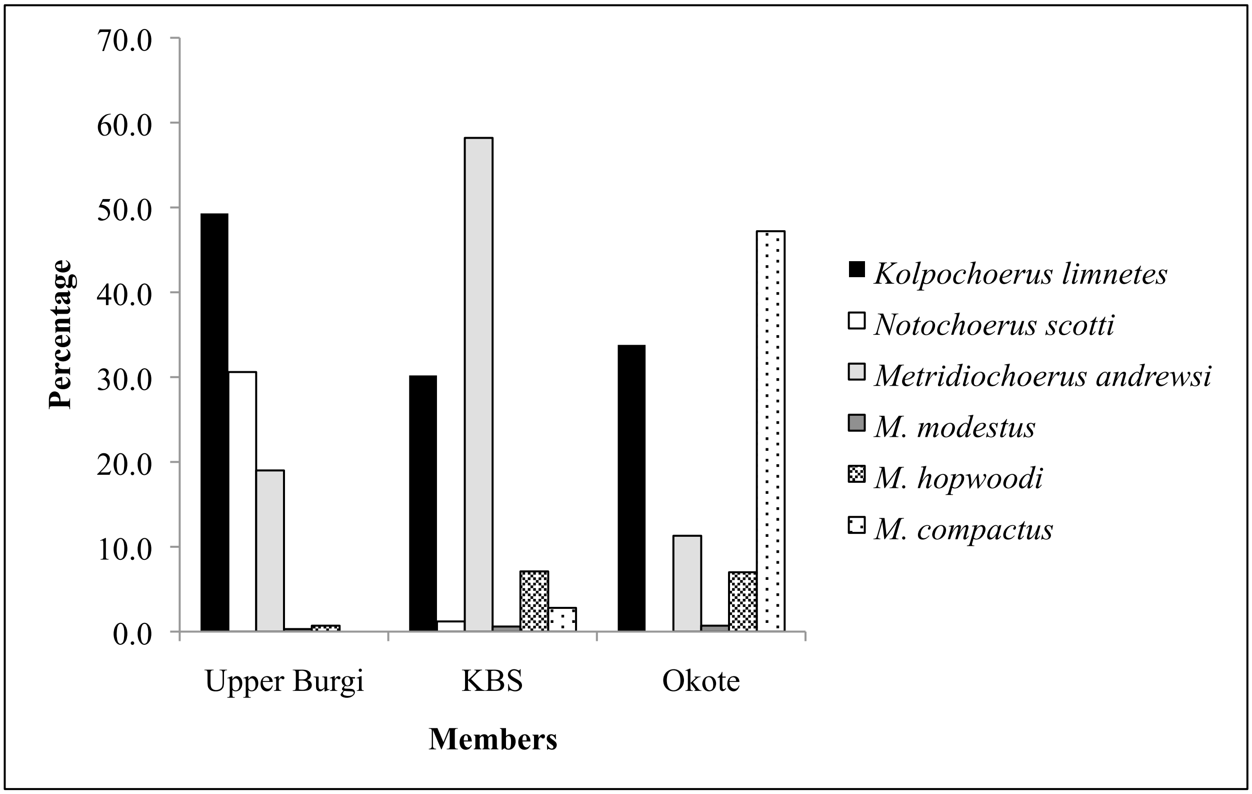


Fig. 3.8. Relative abundance of suid species.

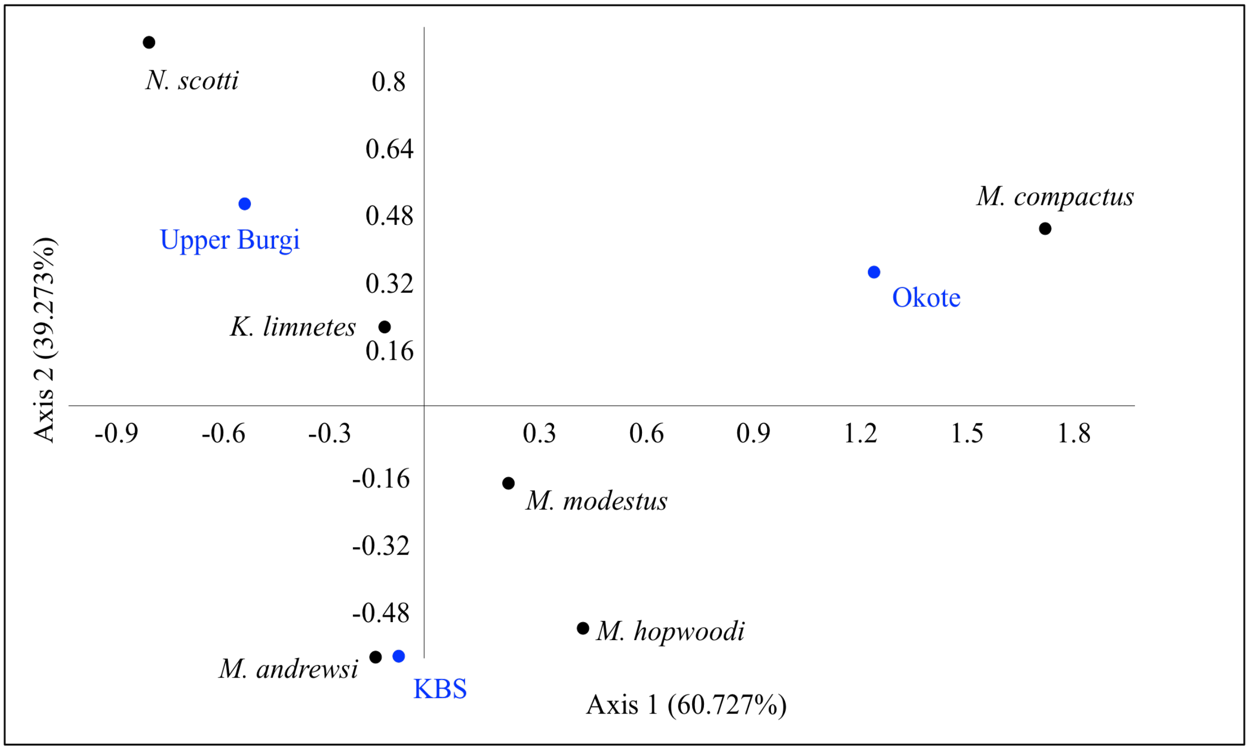


Fig. 3.9. Correspondence analysis of suid species in the Upper Burgi, KBS, and Okote Members; axis 1 explains 60.727% of the variation and axis 2 explains 39.273% of the variation when based on two dimensions.

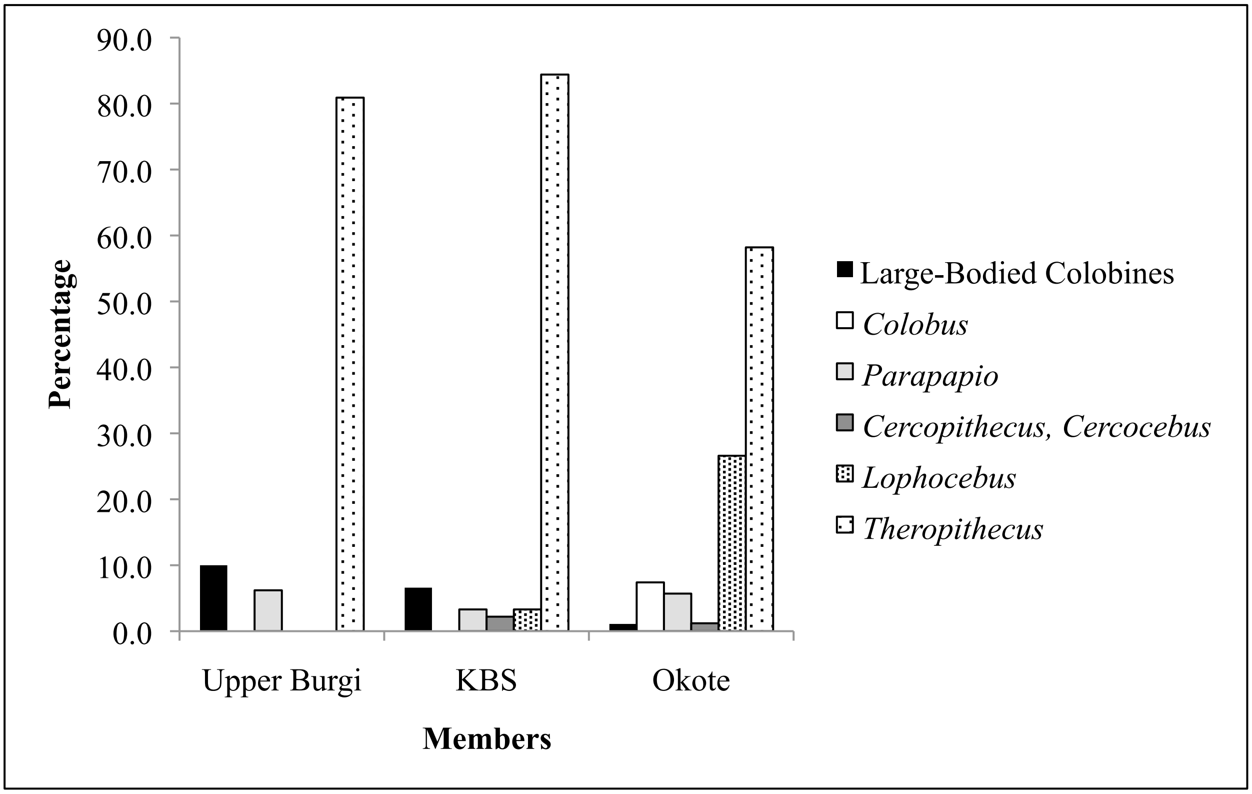


Fig. 3.10. Relative abundance of cercopithecids; "large-bodied colobines" combine *Cercopithecoides*, *Rhinocolobus*, and *Paracolobus*.

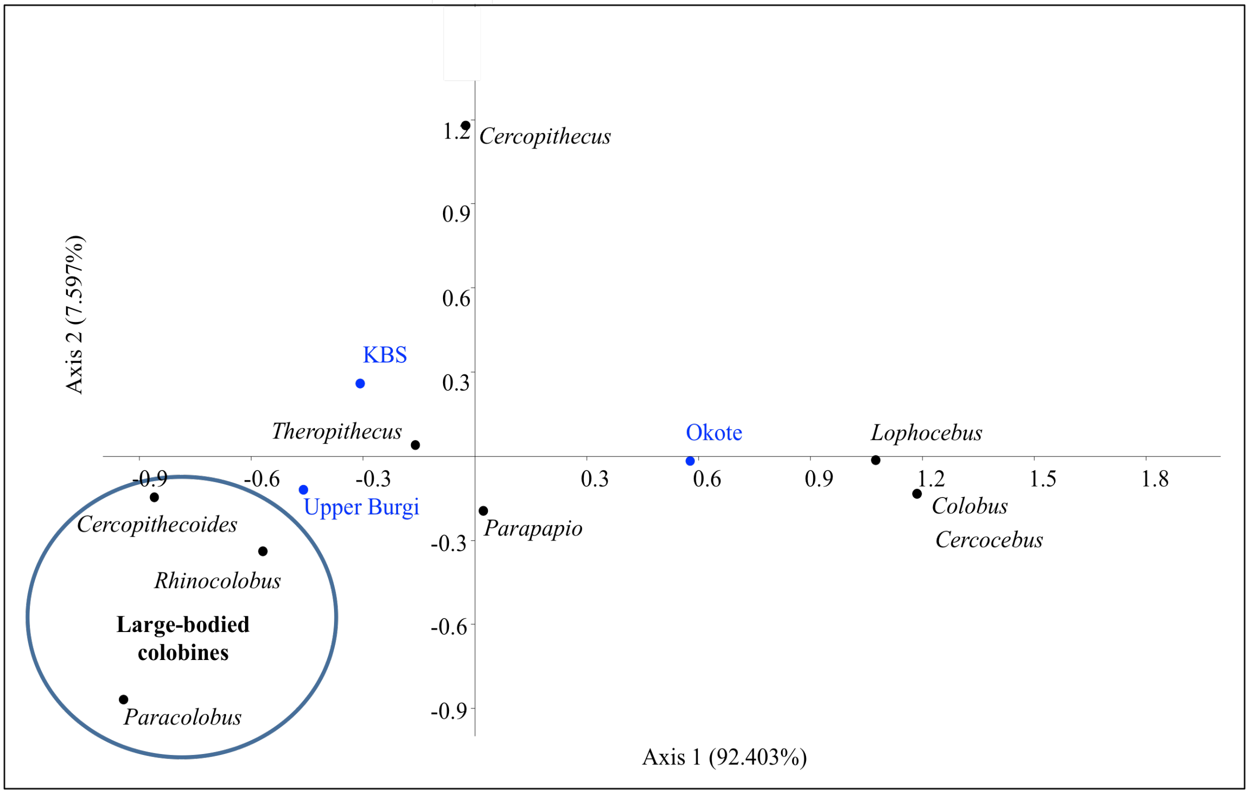


Fig. 3.11. Correspondence analysis of cercopithecid genera in the Upper Burgi, KBS, and Okote Members; axis 1 explains 92.403% of the variation and axis 2 explains 7.597% of the variation when based on two dimensions.

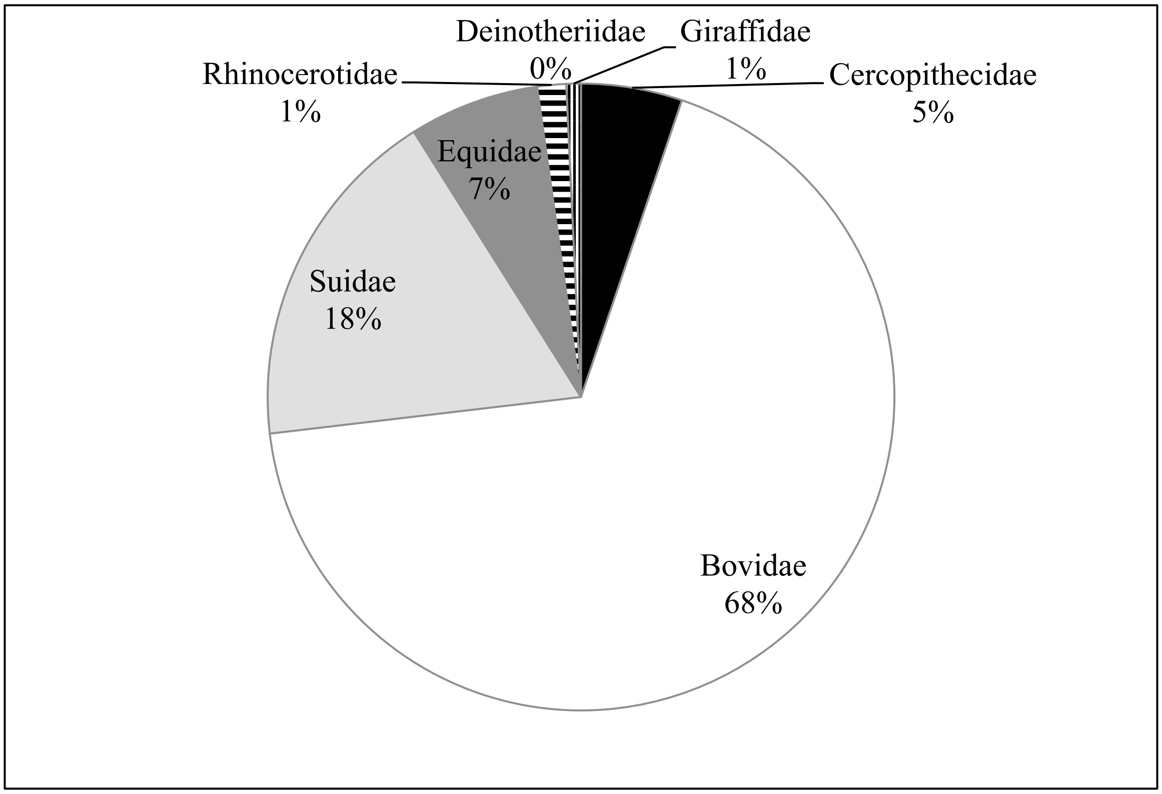


Fig. 3.12. Relative abundance of families for 2011 summer fieldwork survey results from the Okote Member in Ileret, Koobi Fora.

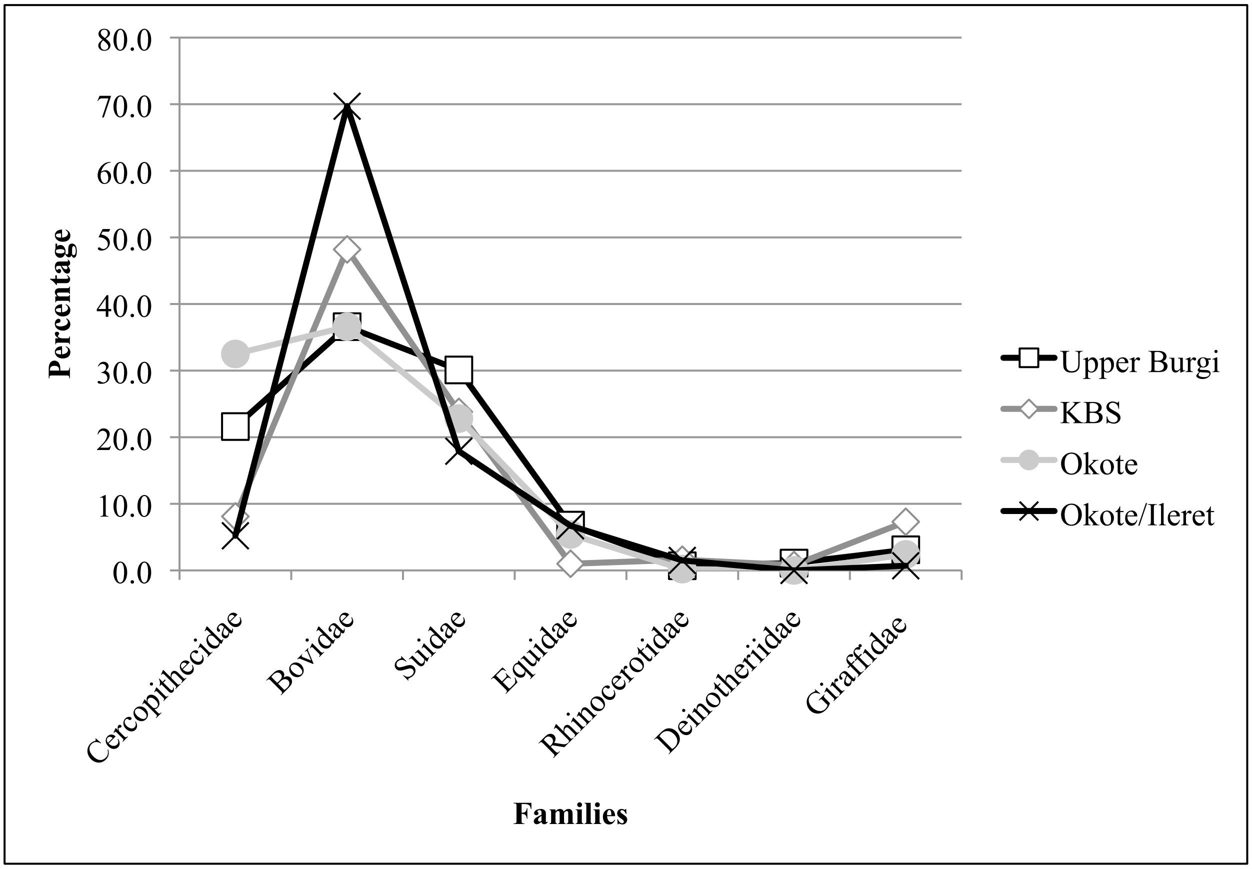


Fig. 3.13. Relative abundance of families from the Ileret fieldwork (Okote Tuff Complex) compared to the relative abundance of families from the Upper Burgi, KBS, and Okote Member samples.

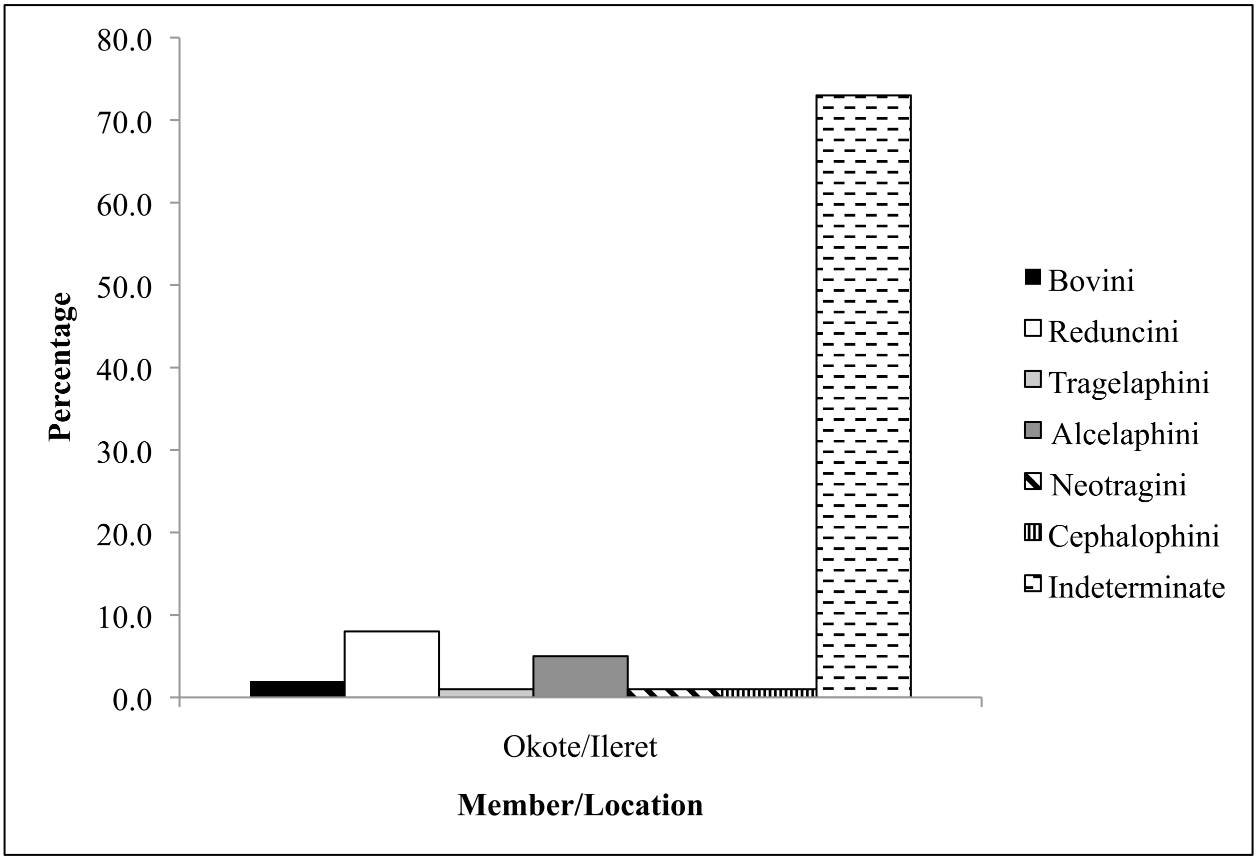


Fig. 3.14. Relative abundance of bovid tribes for 2011 summer fieldwork survey results from the Okote Member in Ileret, Koobi Fora.

TABLE 3.1. Number and relative abundance of specimens of families

	Upper Burgi	KBS	Okote
Number of Specimens			
Cercopithecidae	211	110	215
Bovidae	358	656	242
Suidae	294	325	151
Equidae	66	138	36
Rhinocerotidae	7	22	1
Deinotheriidae	11	11	0
Giraffidae	30	100	16
Total	977	1362	661
Relative Abundance			
Cercopithecidae	21.6	8.1	32.5
Bovidae	36.6	48.2	36.6
Suidae	30.1	23.9	22.8
Equidae	6.8	10.1	5.5
Rhinocerotidae	0.7	1.6	0.2
Deinotheriidae	1.1	0.8	0.0
Giraffidae	3.1	7.3	2.4
Total	100.0	100.0	100.0

TABLE 3.2. Number and relative abundance of specimens of bovid tribes

	Upper Burgi	KBS	Okote
Number of Specimens			
Bovini	12	56	15
Reduncini	157	241	96
Tragelaphini	55	90	36
Alcelaphini	52	148	44
Antilopini	44	49	11
Aepycerotini	33	54	6
Neotragini	1	6	2
Hippotragini	4	9	0
Total	358	653	210
Relative Abundance			
Bovini	3.4	8.6	7.1
Reduncini	43.9	36.9	4.57
Tragelaphini	15.4	13.8	17.1
Alcelaphini	14.5	22.7	21.0
Antilopini	12.3	7.5	5.2
Aepycerotini	9.2	8.3	2.9
Neotragini	0.3	0.9	1.0
Hippotragini	0.1	0.4	0.0
Total	100.0	100.0	100.0

TABLE 3.3. Number and relative abundance of specimens of isolated teeth of bovid tribes

	Upper Burgi	KBS	Okote
Number of Specimens			
Bovini	8	27	5
Reduncini	52	59	24
Tragelaphini	12	26	14
Alcelaphini	28	64	19
Antilopini	21	24	4
Aepycerotini	8	15	3
Neotragini	0	1	1
Hippotragini	0	4	0
Total	129	220	70
Relative Abundance			
Bovini	6.2	12.3	7.1
Reduncini	40.3	26.8	34.3
Tragelaphini	9.3	11.8	20.0
Alcelaphini	21.7	29.1	27.1
Antilopini	16.3	10.9	5.7
Aepycerotini	6.2	6.8	4.3
Neotragini	0.0	0.5	1.4
Hippotragini	0.0	1.8	0.0
Total	100.0	100.0	100.0

TABLE 3.4. Number and relative abundance of specimens of suid genera

	Upper Burgi	KBS	Okote
Number of Specimens			
Kolpochoerus	145	98	48
Notochoerus	90	4	0
Metridiochoerus	59	223	94
Total	294	325	142
Relative Abundance			
Kolpochoerus	49.3	30.2	33.8
Notochoerus	30.6	1.2	0.0
Metridiochoerus	20.1	68.6	66.2
Total	100.0	100.0	100.0

TABLE 3.5. Number and relative abundance of specimens of suid species

	Upper Burgi	KBS	Okote
Number of Specimens			
Kolpochoerus limnetes	145	98	48
Notochoerus scotti	90	4	0
Metridiochoerus andrewsi	56	189	16
M. modestus	1	2	1
M. hopwoodi	2	23	10
M. compactus	0	9	67
Total	294	325	142
Relative Abundance			
Kolpochoerus limnetes	49.3	30.2	33.8
Notochoerus scotti	30.6	1.2	0.0
Metridiochoerus andrewsi	19.0	58.2	11.3
M. modestus	0.3	0.6	0.7
M. hopwoodi	0.7	7.1	7.0
M. compactus	0.0	2.8	47.2
Total	100.0	100.0	100.0

TABLE 3.6. Number and relative abundance of specimens of equid genera

	Upper Burgi	KBS	Okote
Number of Specimens			
Equus	44	103	26
Hipparion	20	34	7
Total	64	137	33
Relative Abundance			
Equus	68.8	75.2	78.8
Hipparion	31.2	24.8	21.2
Total	100.0	100.0	100.0

TABLE 3.7. Number and relative abundance of specimens of cercopithecid genera

	Upper Burgi	KBS	Okote
Number of Specimens			
Cercopithecoides	11	4	0
Rhinocolobus	9	2	2
Paracolobus	1	0	0
Colobus	0	0	13
Parapapio	10	3	10
Cercopithecus	0	2	1
Cercocebus	0	0	1
Lophocebus	0	3	47
Theropithecus	131	76	103
Total	162	90	177
Relative Abundance			
Cercopithecoides	6.7	4.5	0.0
Rhinocolobus	5.6	2.2	1.1
Paracolobus	0.6	0.0	0.0
Colobus	0.0	0.0	7.3
Parapapio	6.2	3.3	5.7
Cercopithecus	0.0	2.2	0.6
Cercocebus	0.0	0.0	0.6
Lophocebus	0.0	3.3	26.5
Theropithecus	80.9	84.5	58.2
Total	100.0	100.0	100.0

TABLE 3.8. Number of specimens of selected families from 2011 field survey in Ileret

Area	1	1A	6	8A	Total
Cercopithecidae	0	7	0	0	7
Bovidae	22	58	5	6	91
Suidae	1	22	1	0	24
Equidae	2	7	0	0	9
Rhinocerotidae	0	2	0	0	2
Deinotheriidae	0	0	0	0	0
Giraffidae	0	1	0	0	1
Total	25	97	6	6	134

TABLE 3.9. Number of specimens of bovid tribes from 2011 field survey in Ileret

Area	1	1A	6	8A	Total
Alcelaphini	0	4	1	0	5
Tragelaphini	0	0	0	1	1
Reduncini	4	3	1	0	8
Bovini	0	2	0	0	2
Neotragini	0	1	0	0	1
Cephalophini	0	1	0	0	1
Indeterminate	18	47	3	5	73
Total	22	58	5	6	91

CHAPTER 4

DISCUSSION

This chapter discusses each taxon's change in relative abundance through time and the environmental changes suggested by the taxon's shift. Specimens are used as proxies for taxa, and environments are reconstructed using ecological analogy. Bovids, suids, equids, and cercopithecids respond differently to environmental changes, but overall trends show an increase in relative abundance of taxa adapted to grasslands and abrasive diets and that consume C_4 grasses. These findings contribute to our understanding of hominin environments and evolution by indirectly suggesting the presence of multiple habitat types that could support evolving hominins. The chapter concludes with a summary, major limitations, and areas for further research.

Mammals and Koobi Fora environments

Bovids are the most abundant taxon in samples for all there members. Bovids have been the predominant artiodactyl family in Africa since the mid-Pliocene (Janis, 2007) and are also abundant throughout the African fossil record compared to other mammalian taxa. The most abundant bovids in the database samples are members of tribes able to flourish in both open and closed environments and under dry and wet conditions, indicating the flexibility of these tribes and the mosaic quality of the environment. Some taxa, such as suids, show major changes within the family, with *Kolpochoerus* dominant in the Upper Burgi sample and *Metridiochoerus* dominant among the suids in the KBS and Okote samples. Equids show a steady increase in the grassland-adapted genus *Equus* between the Upper Burgi, KBS, and Okote Members while cercopithecid speciation indicates the continued presence of gallery forests in an expanding grassland environment.

Bovids and mosaic environments.

The distribution of bovid tribes illustrates the mosaic nature of the East Turkana environment and the flexibility of some family members. Bovids are a large group and members exhibit a variety of habitat preferences (Table 4.1); therefore, they can provide information about the range of environmental conditions present within a certain area. Many of bovid habitat preferences are inferred from observations of modern taxa, which may not be valid for earlier time periods or taxa.

The three most abundant bovid tribes, Reduncini, Alcelaphini, and Tragelaphini, are the most abundant tribes in samples from all three members, and all three tribes differ in their habitat preferences (Table 4.1). Even though grasslands expanded in size and dominance over the study period, based on paleosol evidence (Cerling et al., 1988; Cerling, 1992), the East Turkana environment consisted of a variety of habitat types that would support bovids with different habitat preferences. Bovids adapted to open and wet habitats (Reduncini) are consistently the most abundant taxa in this study (Fig. 4.1). Reduncines are commonly associated with edaphic grasslands so this type of habitat probably was widespread in East Turkana during the time periods associated with all three members. Alcelaphini are adapted to open and dry habitats, and, along with Antilopini, are the best indicators of open grasslands (Bobe and Eck, 2001; Bobe and Behrensmeyer, 2004). Their rank among the bovid tribes in samples from all three members indicates the presence of open/dry habitats in the basin as well. Tragelaphines are adapted to closed and dry environments ranging from woodlands/bushlands to forests (Bobe and Eck, 2001). These affiliations indicate that closed and open environments as well as wet and dry conditions were all present in the landscape. As the region became more arid, the closed environments would have survived in riparian zones, either along the large lake that existed from 2.0 to 1.8 Ma or along the fluvial system after 1.7 Ma.

Bovid distributions show slight shifts between samples from the Upper Burgi and KBS Members, but no major turnovers occurred. Specimens from tribes adapted to closed and dry conditions, such as Tragelaphini and Aepycerotini, decreased in relative abundance between the Upper Burgi and KBS samples while Alcelaphini, which are adapted to open, dry areas, increased in relative abundance. The increase in Alcelaphini abundance likely reflects the expansion of C_4 grasslands after 1.8 Ma. Heavily vegetated areas with thick cover, such as gallery forests, are still present on the landscape, as evidenced by the relative increase in Bovini. In the Okote Member sample, specimens from bovids adapted to open and wet areas are the most abundant while specimens from bovids adapted to closed and wet areas are the least abundant. However, specimens from bovids adapted to each of these habitat types remained fairly constant from 2.0 to 1.5 Ma (Fig. 4.1).

The environment in northern Ileret around 1.5 Ma supported an abundance of bovids compared to other families. Although most of the specimens are indeterminate, those of Reduncini are the most abundant among the specimens that could be identified, followed by Alcelaphini and Bovini. Reduncini abundance from the 2011 field work shows similarity to the database samples from the Upper Burgi, KBS, and Okote Members of Koobi Fora. Edaphic and open habitats likely formed a substantial part of the Ileret environment for Reduncini and Alcelaphini to be supported. Despite the continued aridification throughout the basin, this area was well-watered. Additionally, other habitat types were present, including areas with thicker cover and woodlands. The 2011 Ileret data provide a snapshot for a specific time and location. Since other evidence shows that climate exhibited increasing variability and seasonal extremes through time (de Menocal, 1995; Potts, 1998), this snapshot may represent a wetter period for the environment within the fluctuating wet-dry cycle as suggested by reduncine prevalence.

Suids: the dominance of Metridiochoerus.

Suid relative abundance decreases from the time represented by the Upper Burgi Member to the time period represented by the Okote Member, but the family persists as one of the top three families (Fig. 3.1). Suid relative abundance declines steadily while bovid and cercopithecid relative abundance is more variable over time. Suid abundance does not show the same variation, perhaps because all suid species were already adapted to grass diets. Their continued decline in relative abundance may simply reflect another taxon's increase or may relate to suid fidelity to grassland environments, whereas both bovids and cercopithecids had members adapted to grasslands as well as forested areas. The species documented from the Koobi Fora Formation in the Upper Burgi, KBS, and Okote Members, *N. scotti*, *K. limnetes*, and *Metridiochoerus* spp. (Fig. 3.8), are among the suids that consume the greatest amount of grassy vegetation, and their adaptations to eating abrasive vegetation increased through time as evidenced by increased hypsodonty (Behrensmeyer, 1975; Bobe and Behrensmeyer, 2004). The decline in suid relative abundance masks a transition in suids at the genus level, specifically the replacement of two genera, *Notochoerus* and *Kolpochoerus*, by one, *Metridiochoerus*, a taxon even more markedly adapted to grasslands.

N. scotti is relatively abundant in the Upper Burgi sample, but this species, which was more common during the Pliocene, was already on the decline. In the Okote, *N. scotti* is absent from Koobi Fora. Isotopic analysis and hypsodonty indicate that the species fed primarily on C_4

graze. Their third molars displayed greater elongation and hypsodonty compared to earlier members of the genus (Harris and Cerling, 2002; Bishop, 2010). *N. scotti* is the most advanced and one of the last species in the *Notochoerus* lineage (Bishop, 2010). Their evolving hypsodont dentition enabled them to remain successful during the time period represented by the Upper Burgi Member. However, as grasslands expanded and became dominant between 1.88 to 1.6 Ma, *Notochoerus* may have been less successful in competition with *Kolpochoerus* and *Metridiochoerus*, and they eventually went extinct after 1.6 Ma.

As with *N. scotti*, *K. limnetes* declines between the Upper Burgi and KBS, likely a result of competition with *Metridiochoerus*, which were better adapted to eating abrasive foods. Through time, the length, height, and number of pillars on *Kolpochoerus* third molars increased, becoming more hypsodont. However, *Kolpochoerus* teeth were never as hypsodont as those of *Metridiochoerus*, and in all three members, isotopic analysis of *Kolpochoerus* reveals that they were dedicated C_4 grazers (Harris and Cerling, 2002). The percentage of *K. limnetes* specimens is relatively constant between the KBS and Okote, perhaps because they were C_4 grazers.

Metridiochoerus is the least abundant suid genus in the Upper Burgi sample but experiences a large increase in the KBS sample, when it comprises nearly 70% of the suid specimens (Fig. 3.7). This increase coincides with the major increase in C_4 plants after 1.8 Ma (Cerling et al., 1988). All *Metridiochoerus* species are dedicated C_4 grazers, as evidenced by carbon isotope analysis (Harris and Cerling, 2002). The increase in *Metridiochoerus* relative abundance indicates that grassland habitats were abundant (Bobe and Behrensmeyer, 2004). *Metridiochoerus* abundance remains high in the Okote, indicating grassland habitats continued to be an overwhelming part of the basin after 1.6 Ma.

Within the *Metridiochoerus* genus, *M. andrewsi* is prolific and *M. compactus* has a low relative abundance in the KBS sample. The two species switch positions in the Okote sample as *M. compactus* becomes dominant. The earliest evidence for *M. andrewsi* is from the Usno Formation at 3.4 Ma. During the early time range, the species had a grass-dominated, mixed diet. The species became increasingly dependent on grasses through time, and by the time represented by the KBS Member, the species was completely dependent on tropical C_4 grasses based on carbon isotopes (Bishop, 2010). *M. compactus* is the largest and most advanced *Metridiochoerus*. Because root fusion is very delayed in their third molars, the teeth are extremely hypsodont (Bishop, 2010). When aridification in the Turkana Basin intensified around 1.6 Ma (Wynn, 2004), the extremely hypsodont dentition of *M. compactus* enabled this species to dominate over other *Metridiochoerus* species.

Equids: the increase of Equus.

Overall, equids are much less abundant than bovids, suids, and cercopithecids. A major difference between equids and bovids is their method of digesting plant materials. Equids digest cellulose through hindgut fermentation and are able to process large quantities of low- quality foods. In contrast, the bovid digestive system uses foregut rumination, an adaptation to smaller quantities of higher-quality foods. Increasing seasonal extremes between 2.0 and 1.5 Ma likely favored bovids over equids because, in general, seasonal habitats produce lower quantities of higher quality vegetation (Janis, 2007).

Among the Upper Burgi, KBS, and Okote samples, the proportions of equids only fluctuate slightly, from 6.8% to 10% to 5.5%. The increase in the KBS may relate to the increase of *Equus*. Through time *Equus* specimens show a steady increase with a corresponding decrease in *Hipparion* specimens. The steady increase in *Equus* suggests the expansion of open habitats and grasslands. Their extremely hypsodont teeth enabled them to sustain wear from grit and dirt in open environments and to withstand abrasion from tough and fibrous graze. Because *Hipparion* species lived in densely vegetated habitats (Behrensmeyer, 1975), their persistence into the time period represented by the Okote Member indicates some areas within Koobi Fora had heavier cover sufficient to support small populations of *Hipparion* even as grasslands expanded. These more heavily covered areas likely occurred in riparian zones. The presence of both *Equus* and *Hipparion* reinforces interpretations of East Turkana as a mosaic landscape during the early Pleistocene, but the high abundance of *Equus* indicates the increasing dominance of grasslands.

Cercopithecid turnover and evolution.

Monkeys are sensitive indicators of environmental change because they require high quality foods compared to other mammals of similar body size. They are usually among the first animals to respond to climatic deterioration (Jablonski and Leakey, 2008). Therefore, distributional changes in cercopithecids are strong indicators of small-scale environmental changes. The fossil record of monkeys in the Koobi Fora Formation from the Upper Burgi to the Okote Member provides a record of extinction, turnover, and speciation.

Cercopithecids experience major change in overall relative abundance between the Upper Burgi and KBS Members and again between the KBS and Okote Members (Fig. 3.1). The major decline in cercopithecid abundance from 21% to only 8% of the specimens likely reflects the spread of grasslands after 1.8 Ma. This led to the extinction of the large-bodied terrestrial colobine species: *Cercopithecoides*, *Rhinocolobus*, and *Paracolobus*. These species were more successful between 2.0 and 1.88 Ma before seasonal extremes widened and when woodlands occupied a larger area within the Turkana Basin. Because large-bodied colobines were less able to eat abrasive food, their decline suggests that grasslands expanded between 1.88 and 1.6 Ma, represented by the KBS Member. They were unable to compete with ungulates in grasslands and were rare after 1.6 Ma except for a few *Rhinocolobus*.

Between the KBS and Okote samples, cercopithecid relative abundance increased from 8% to 32%. The large increase in abundance may relate to the appearance of modern taxa that took advantage of riparian woodlands and forests along the proto-Omo River (Jablonski and Leakey, 2008). The return of a fluvial system to the basin around 1.7 Ma (Brown and Feibel, 1991) may have led to the expansion of gallery forests compared to earlier times when the Upper Burgi Lake was present. The modern genera include *Lophocebus*, *Colobus*, *Cercopithecus*, and *Cercocebus*, taxa more abundant in the Okote Member than in either the Upper Burgi or KBS Members. Cercopithecids were clearly successful during the time period marked by Okote deposits, despite increases in aridity and seasonality in the basin (Wynn, 2004), and this may have resulted in part from riparian zones buffering these modern taxa from environmental changes.

The cercopithecid genus that is dominant in all three members is *Theropithecus*. Their numbers are the most consistent through time when compared to other genera. *Theropithecus*, and specifically *T. oswaldi*, was more successful than other monkeys at competing with ungulates and suids for grazing niches. Their adaptations to grasslands, such as wear-resistant thick enamel and bulk feeding on the highest quality grasses, enabled *T. oswaldi* to dominate over other cercopithecids as grasslands expanded (Jablonski and Leakey, 2008). While *Theropithecus* remains the most abundant in the Okote sample, their numbers decline as modern species, especially *Lophocebus*, increase in number. Their initial decline could also be attributed to further aridification and intensified seasonality in the Turkana Basin after 1.6 Ma when they were outcompeted by ungulates that were able to migrate in response to the seasonal availability of resources (Jablonski and Leakey, 2008).

Deinotheres, rhinocerotids, and giraffids.

The families that are the least abundant in the Turkana Basin Paleontology Database are the deinotheres, rhinocerotids, and giraffids. Skeletal and dental elements of members of these families are very large. The low number of specimens recorded for them compared to bovids, cercopithecids, suids, and equids, therefore, may reflect collecting bias if larger specimens were left in the field because of transportation and storage difficulties. Deinotheres are extinct proboscideans highly specialized for a browsing diet with bilophodont, low-crowned cheekteeth. Their dietary adaptation restricted their habitat range to densely vegetated forests (Sanders et al., 2010). Deinothere decline in abundance from 1% of the Upper Burgi and KBS samples to none in the Okote sample. Other evidence documents that deinotheres went extinct as closed environments with heavy vegetation cover disappeared (Sanders et al., 2010). Deinotheres were able to survive into the time period represented by the KBS Member by occupying gallery forests and other areas with dense vegetation, but their severe decline in numbers indicates increased aridification and expansion of open environments in the Okote. Their teeth were poorly adapted for a grazing diet, and competition with hypsodont bovids, suids, and equids may have pushed this family to extinction. The absence of deinotheres in the 2011 Ileret field surveys reflects their extinction by 1.53 to 1.51 Ma.

Both the white rhino (*Ceratotherium simum*) and black rhino (*Diceros bicornis*) are recorded in the Turkana Basin Paleontology Database in the Upper Burgi, KBS, and Okote Members. The white rhino is associated with an increasingly grazing diet, based on changes in tooth morphology, while the black rhino feeds on browse in ecotonal woodland areas (Turner and Antón, 2004:120; Geraads, 2010). The presence of both species supports the argument that the environment contained both grasslands and woodlands. Similar to equids, the low relative abundance of rhinocerotids, compared to other families, may relate to their digestive physiology and the lower quantities of food available in increasingly seasonal habitats, in addition to sampling and collecting bias associated with large-sized specimens.

Of the largest mammals considered in this study, including the deinotheres, rhinocerotids, and giraffids, giraffids are the most abundant in samples for all of the members. The most common genus of giraffids in the Turkana Basin Paleontology Database is *Giraffa*. A few specimens are attributed to *Sivatherium*. Carbon isotopes indicate that members of *Giraffa* were browsers. This may explain their lower abundance compared to families consisting of dedicated grazers (Harris et al., 2010). By the start of Okote deposition, deinotheres were near extinction, and giraffids, a ruminant artiodactyl, may have held a slight advantage over rhinocerotids.

The 2011 Ileret fieldwork, during which all rhinocerotid and giraffid specimens were consistently and routinely recorded, reveals a low abundance of these large mammals and shows similar trends to samples from the Upper Burgi, KBS, and Okote Members in which collection of these specimens was likely not consistent. Despite biases against large mammals in the database, the low abundance of these large mammals in the database may be more accurate than originally thought, based on similarities to the recent fieldwork where this bias was controlled.

Hominin environments in the Turkana Basin

Based on the faunal analysis, increases in the relative abundance of grassland-adapted taxa occurred between the Upper Burgi and KBS and continued between the KBS and Okote. The first increase likely corresponded to intensification of Northern Hemisphere glaciation, aridification in East Africa, and expansion of C_4 grasslands. The second increase corresponded to further intensification of aridity in East Africa. As grasslands expanded, however, some areas with thicker vegetative cover, such as woodlands and forests in riparian settings, persisted, as evidenced by bovids and cercopithecids. The region also experienced increasing seasonal extremes and variability in amplitude between wet and dry cycles, possibly caused by the development of the Walker circulation in the Pacific and the onset of ENSO.

All of these events impacted hominins living in the Turkana Basin. At least four species coexisted: *P. boisei*, *H. habilis*, *H. rudolfensis*, and *H. erectus*. Some of the primary factors associated with hominin distribution are the presence of vegetation, food, and water (Holmes, 2007). The Turkana Basin apparently provided resources sufficient to support multiple hominin populations. The high frequency of Reduncini in all three members indicates a well-watered environment prevailed, especially edaphic grasslands. *Metridiochoerus* is also considered to be a relatively water-dependent genus (Bobe and Behrensmeyer, 2004), and this genus dominates the suids after 1.8 Ma even as East African aridity intensifies. The basin may have been wetter than other East African basins during the Plio-Pleistocene period and, therefore, acted as a refugium during the seasonally dry and arid phases (Joordens et al., 2011). The wetter conditions would have attracted hominins and other animals from surrounding areas. Terrestrial animals and aquatic resources both could have supplied hominins, especially *H. erectus*, with food choices. The well-watered environment of the Turkana Basin may have also buffered intense seasonal extremes seen in other East African areas, further supporting diverse hominin taxa.

The mosaic quality of the environment in the Turkana Basin likely provided each hominin species a different habitat to occupy. Dental evidence suggests that each hominin species had a slightly different dietary preference and adaptation, and, therefore, each species may have depended on a different set of resources. Carbon isotopes, morphology, and microwear have been used to study the diet of hominin species living in the Turkana Basin during the early Pleistocene. Morphology examines phylogenetic adaptations to chewing and ingesting food while carbon isotopes and microwear are proxies for the actual foods consumed. For example, microwear analysis examines the percentages of pits and scratches on teeth surface to infer properties of food in the diet. Greater percentages of pitting represent greater consumption of brittle, hard foods, while greater percentages of scratches represent greater amounts of tough foods in the diet (Ungar et al., 2006b).

P. boisei did not specialize in particularly hard foods, as conventionally thought. Its morphological specializations, such as large cheekteeth, robust jaws, and thick enamel, indicate that the species consumed foods ranging from hard and brittle to soft (Ungar et al., 2008). These adaptations also may have allowed *P. boisei* to process large amounts of low-quality vegetation. Carbon isotopes indicate that this species' diet was dominated by C_4 vegetation and included much larger amounts of C_4 grasses than did the diet of early *Homo* (van der Merwe et al., 2008; Cerling et al., 2011).

Early *Homo* did consume some C_4 foods, but, nonetheless, they had a diet dominated by more than 50% of C_3 vegetation based on isotopic analysis (van der Merwe et al., 2008; Ungar and Sponheimer, 2011). Additionally, early *Homo* had a versatile subsistence strategy, and microwear studies suggest that they did not specialize in hard, brittle, or tough foods; members of this genus would have been able to consume a broader range of resources (Ungar et al., 2006a; Ungar and Scott, 2009; Ungar and Sponheimer, 2011). *H. erectus* relied on a slightly different diet with its ability to fallback on higher amounts of tough or hard and brittle foods than earlier *Homo* species, as indicated by microwear analysis (Ungar et al., 2006b; Ungar and Scott, 2009).

This evidence suggests that the diet of *P. boisei* and contemporaneous early *Homo* species were sufficiently different that these hominins did not directly compete with each other (Cerling et al., 2011). *P. boisei* may have exclusively occupied a grassland habitat, which was abundant in Koobi Fora during the KBS and Okote as evidenced by the increase of *Equus* and the dominance of the *Metridiochoerus* genus and especially *M. compactus* after 1.6 Ma. *H. habilis* and *H. rudolfensis* may have shared woodland areas with extant cercopithecids and closed-environment adapted bovids more frequently than did later members of the *Homo* genus. *H. habilis* and *H. rudolfensis* occasionally used grasslands since their diet included some C_4 foods. *H. erectus* was a grassland species with expanded tool use. The presence of large concentrations of stone tools and modified bones at Koobi Fora coincides with first appearances of *H. erectus* (Ungar et al., 2006a). Increased use of tools and the development of Acheulean tools, which likely provided *H. erectus* with an expanded toolkit, enabled them to access a new range of resources inaccessible to other members of the genus *Homo* and *P. boisei*. This included greater consumption of meat (Ungar et al., 2006a). Accessing new resources may have reduced competition and enabled feeding niche differentiation between the different species. Although, the combination of an expanded toolkit and morphological change, which increased the dietary flexibility of *H. erectus*, likely contributed to its eventual success over *H. habilis*, *H. rudolfensis*, and *P. boisei*.

Different adaptations enabled these four hominin species to coexist in a mosaic environment, and their adaptive flexibility enabled them to contend with environmental change. With the mosaic environment and well-watered habitats available, hominin species may have been able to coexist without heavy competition for resources while maintaining different feeding niches.

Summary, limitations, and areas for further research

Faunal analysis using the Turkana Basin Paleontology Database supports the interpretation of a mosaic landscape where woodlands declined and grasslands expanded from 2.0 to 1.5 Ma. Different species of hominins likely exploited different parts of the basin's well-watered and resource-rich environment. This research demonstrates the value of further work with this application database and provides a baseline for future mammalian studies in the Turkana region. The database work provides a broad scale analysis but identifies several areas for future paleoenvironmental field surveys.

Analysis of the Turkana Basin Paleontology Database provides a good general representation of what is present in the fossil record and of environmental conditions, comparable to previously published paleoenvironmental material. Although the number of bovid teeth compared with the number of all bovid specimens is significantly different over time, results show the same general trends. Use of the database for faunal analysis presents several limitations, however. Inconsistent collection methods and bias against collecting large specimens, due to physical constraints of transportation and storage, are major biases. Sampling techniques, collection of specimens, and records in the database have largely focused on mammals. Incorporating vertebrates other than mammals as well as invertebrates can significantly contribute to paleoenvironmental studies. During the 2011 summer fieldwork in Ileret, the most abundant specimens, based on general observation, were crocodile teeth and fish elements. The abundance of crocodile and fish elements lends further support to the presence of large amounts of water in the basin. Despite efforts to record all specimens during the 2011 bone walks, many of the small-sized specimens, such as primate teeth, may have gone unnoticed. This may explain why cercopithecid relative abundance from the 2011 summer fieldwork in

Ileret is much lower than from the database samples for the Upper Burgi, KBS, and Okote Members.

An additional limitation to this study is that the percentages of taxa cannot be exactly translated into the percentage of grasslands or woodlands present. This study can only make inferences about the presence, not percentage, of prevailing environmental conditions. Time-averaging for members also limits interpretations.

Database work combined with larger-scale fieldwork will likely produce more robust results. The continued addition of specimens to the database as they are collected, brought to the National Museums of Kenya, and published will further improve results. In future studies, use of the Turkana Basin Paleontology Database for paleoecology can be enhanced with sampling techniques designed for paleoenvironmental reconstructions. Multiproxy approaches using stable isotopes as well as dental and ecomorphological analysis of the full range of fossil specimens recorded in the database will provide more accurate interpretations of habitat preference and environmental reconstructions, compared to analysis derived from diet and habitats of modern taxa.

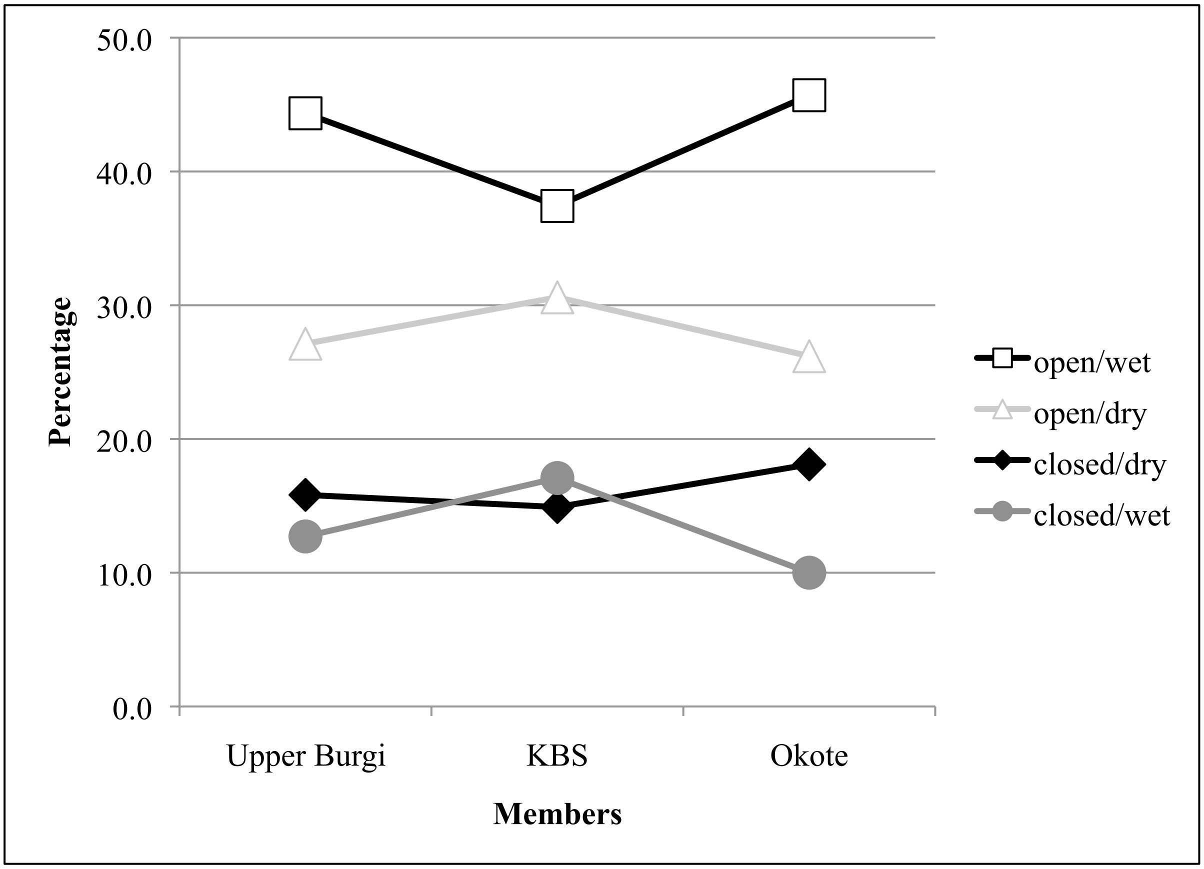


Fig. 4.1. Change in relative abundance of bovids based on habitat preference; open/wet includes Reduncini, open/dry include Alcelaphini and Antilopini, closed/dry include Tragelaphini and Neotragini, and closed/wet include Bovini and Aepycerotini.

TABLE 4.1. Bovid tribe habitat preferences and diet

	Habitat Preference[a]		Diet
	Habitat type	Wet/dry preference	Based on $\delta^{13}C$ values in extant bovids[b]
Bovini	riverine forests, thick cover	moist habitats	grazer
Reduncini	edaphic grasslands	grazing near water	grazer
Tragelaphini	woodlands/bushland, forests	drier habitats	browser
Alcelaphini	open habitats	dry habitats	hypergrazer
Antilopini	semiarid/arid open areas	dry habitats	browser
Aepycerotini	woodlands/bushland	close to water	mixed feeder
Neotragini	bushland	dry habitats	browser
Hippotragini	woodlands/bushlands/grasslands	dry habitats	grazer

[a] (Harris, 1991; Bobe and Eck, 2001).

[b] (Cerling, 1992).

CHAPTER 5

SUMMARY AND CONCLUSIONS

The Plio-Pleistocene between 2.0 and 1.5 Ma is a period when significant changes occurred in East Africa and, specifically, in the Lake Turkana Basin. This is an interesting time and place for paleoenvironmental studies due to climatic intensification, faunal turnover, and the coexistence of four hominin species (*P. boisei*, *H. habilis*, *H. rudolfensis*, and *H. erectus*). The onset of Northern Hemisphere glaciation led to global cooling and aridification. Uplift in the African Rift Valley and closure of the Indonesian seaway contributed to further aridification in East Africa. Aridification in the Turkana Basin was marked by expansion of grasslands and C_4 vegetation. Increasing seasonal variability and increase in amplitude between wet and dry cycles in East Africa coincided with overall aridification.

This study investigated change in relative abundance for larger mammals in the Koobi Fora Formation during a period of high climatic and environmental activity and recorded in the Turkana Basin Paleontology Database. The Upper Burgi, KBS, and Okote Members represent the younger deposits in the Koobi Fora Formation and highlight the depositional period from 2.0 to 1.5 Ma. The start of the KBS roughly corresponds to significant expansion of C_4 grasslands, and the start of the Okote corresponds to intensified aridification in the Turkana Basin (Cerling et al., 1988; Wynn, 2004). Taxa in the database responded differently to these environmental changes but the overall trend is for the relative abundance of grassland-adapted species to increase. Major changes in relative abundance of taxa can be seen between samples from the Upper Burgi and KBS Members and between samples from the KBS and Okote Members.

Suids experience major change between the Upper Burgi and KBS with the increase of *Metridiochoerus* whereas cercopithecids experience major change between the KBS and Okote with the evolution of modern monkeys. Equids show a steady increase through time in the hypsodont genus *Equus* and a corresponding decline in *Hipparion*. Bovids show more stability through time with Reduncini, Alcelaphini, and Tragelaphini persisting as the three most abundant tribes in samples from all three members. Reduncini has the highest frequency for the entire study period, and, because of its adaptation to edaphic grasslands, East Turkana must have remained a well-watered environment despite regional aridification. Woodlands and some forests likely remained part of a mosaic environment, especially along riparian zones, as indicated by the steady abundance of Tragelaphini and Bovini and the presence of arboreal monkeys.

Despite limitations related to field collection and sampling, the Turkana Basin Paleontology Database confirms trends proposed on the basis of other data. Using the database for faunal analysis supports the interpretation that the environment was heterogeneous. The data from the 2011 summer fieldwork in Ileret also supports this interpretation and additionally narrows the impact of time-averaging. Heterogeneity characterized the environment between 1.53 to 1.51 Ma in areas of the Ileret subregion. Because East Turkana was a well-watered mosaic environment, different species of hominins were able to coexist by partitioning resources and avoiding direct competition. Dental evidence supports the interpretation that *P. boisei*, early *Homo*, and *H. erectus* had diets that were sufficiently different that each species exploited different niches. All species likely exploited different aspects of the grassland environments, but around 2.0 Ma early *Homo* also may have supplemented or lived concurrently in woodland areas. The heavy C_4 component in the diet of *P. boisei* suggests that this species, at least, foraged almost exclusively in C_4 grasslands. *H. erectus* exploited grasslands, but its morphological and behavioral adaptations provided adaptive flexibility that enabled it to inhabit other habitats in the Turkana Basin, especially important during times of increased seasonality and variability. Faunal analysis in this study supports previous paleosol and faunal studies that grasslands were a heavy component of the landscape after 1.8 Ma and that they continued to constitute large parts of the environment after 1.6 Ma, as represented in the Okote Member.

The database work presented in this paper provided useful insights for paleoenvironmental reconstructions despite flaws in recovery, small individual samples, and incomplete records. Many of the interpretations concluded from this study are supported by available proxy evidence and likely new proxies can elaborate on similar studies. Database work will likely have increasing importance for future paleoecological research through storing and recording data on large numbers of collected specimens and facilitating multi-faunal analysis for interpreting paleoenvironments.

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