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The evolution of arid ecosystems in eastern Africa

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Abstract

The present aridity of Africa contrasts with the lush environments that existed over most of the continent in the early Cenozoic. The extinction of large terrestrial herbivores at the end of the Mesozoic, and relatively warm global climatic conditions in the early Cenozoic contributed to the spread of forests and woodlands in regions today occupied by grasslands and deserts. The increase in aridity after the Eocene climate optimum has been complex, characterized by multiple reversals and modulated by rifting in eastern Africa. The paleobotanical evidence indicates that ecological differentiation within the continent existed early in the Cenozoic, with some areas dominated by moist forests and others by drier *Acacia* woodlands. C4 grasslands began to spread during the Late Miocene, and became more prominent during the Pleistocene. In parallel to the spread of grassland mosaics during the Cenozoic there was an increase in the diversity of large herbivorous mammals (with body mass >350 kg). This diversity in megafauna peaked in the Pliocene. One of the key ecological roles of the megafauna was to create and maintain complex mosaics that included open habitats. Faunal evidence of paleoenvironments in the Turkana Basin of Kenya corroborates conclusions derived from other lines of evidence, but raises new questions. Hypsodont and cursorial bovids increased in abundance in the Late Miocene about 6 Ma, in the Pliocene after 3 Ma, and again in the Plio-Pleistocene after 2 Ma. But this faunal evidence also demonstrates that not all parts of the Turkana Basin responded in the same way to climatic changes. The lower Omo valley of Ethiopia, a northern extension of the Turkana Basin, remained significantly more forested than the areas near the western margins of the basin. Major river valleys like the Omo served as refuges and centers of endemism during intervals of significant climatic fluctuations. A similar role was played by the coastal and montane forests of eastern Africa, which were separated from the Central African forests by an arid corridor that stretched from northeast Africa to Namibia, and probably originated in the

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Miocene. The complex mosaic of environments in eastern Africa today continues to support an immensely diverse range of plants and animals, many of them found nowhere else on earth.

1. Introduction

Although Africa supports an astonishing diversity of environments, ranging from tropical rain forests to deserts, the continent as a whole is a relatively arid landmass. Excluding agricultural lands, 70% of Africa's surface is covered by desert, open grassland, or shrubland, i.e. arid or semi-arid landscapes (see Table 1 and Fig. 1) (Mayaux et al., 2004). In eastern Africa the proportion of arid and semi-arid environments is close to 83%. There is no doubt that people have played a key role in the patterning of modern landscapes (Foley et al., 2005), but Africa's arid and semi-arid ecosystems have roots that go deep in time.

The focus of this contribution is on the evolution of African environments that range from savanna to desert, tropical and subtropical regions that typically have less than 40% woodland or bushland cover, and receive less than 1000 mm of rainfall per year, with pronounced dry seasons (Jacobs, 2004). In terms of structure, savannas are considered open environments, and are taxonomically dominated by grasses. Strong seasonality in precipitation results in plant species that can tolerate aridity for several months each year. Annual fires play a critical role in the maintenance of open savanna habitats (Menaut, 1983; Gichohi et al., 1996). In this regard, wetter savannas with higher productivity, and thus greater fuel loads, may be more prone to fire than drier savannas with lower combustible loads. At the wetter end of the savanna spectrum wooded grasslands may be common. Wooded grasslands rich in wildlife characterize extensive areas of eastern Kenya and central Tanzania where precipitation ranges from about 300 to 900 mm per year, with two rainy seasons (Gichohi et al., 1996). At the drier end of the savanna spectrum, thorn scrublands become dominant and merge into semi-deserts (Menaut, 1983; Belsky, 1995;

Table 1
Major environment categories in Africa, in hectares (data adapted from Mayaux et al., 2004)

	Africa	%	% Excl. agric.	East Africa	%	% Excl. agric.
Forest	235,910	7.9	8.9	7205	1.2	1.5
Forest mosaic	127,916	4.3	4.8	15,119	2.4	3.1
Woodlands	411,582	13.7	15.5	55,152	8.9	11.3
Shrublands	402,750	13.4	15.2	86,315	13.9	17.7
Grasslands	460,064	15.4	17.4	160,059	25.9	32.9
Bare soil	993,852	33.2	37.5	158,872	25.7	32.6
Wetlands	17,009	0.6	0.6	4502	0.7	0.9
Agriculture	346,909	11.6		131,631	21.3	
Total	2,995,992	100.0		618,855	100.0	
Total excluding agriculture	2,649,083	88.4	100.0	487,224	78.7	100.0
Arid or semi-arid (%)		62.0	70.1		65.5	83.2
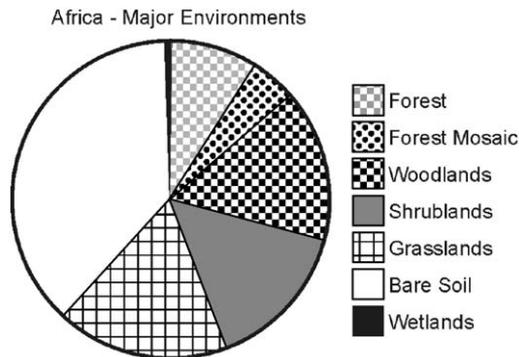
Fig. 1. Major environment types in Africa (adapted from Mayaux et al., 2004).

Swift et al., 1996). The Sahara Desert, which covers about one-third of the continent, encompasses most of the "bare soil" environments (Fig. 1); these consist of sands, dunes, and stony deserts (Mayaux et al., 2004). Major river systems originate in the East African highlands where precipitation is high (>1400 mm), and meander into arid and semi-arid landscapes, providing the main source of permanent water and allowing the penetration of forest vegetation deep into arid regions (Medley and Hughes, 1996).

Aridity has been difficult to quantify in the geological record, but various proxy records can be used (e.g. carbon isotopes, oxygen isotopes, eolian sedimentation, palynological and paleobotanical remains, etc.). There is much evidence to indicate that in the past Africa was a wetter continent than it is today, and that it was covered by extensive woodlands and forests (van Zinderen Bakker and Mercer, 1986). On broad temporal and spatial scales, the extinction of large herbivores at the end of the Mesozoic 65 Ma (million years ago) and the warming of the Earth in the early Cenozoic provided suitable conditions for the expansion of woody vegetation and closed environments (Wing and Sues, 1992). The warm temperatures of the Paleocene and Eocene were associated with high precipitation, while the disappearance of large Mesozoic herbivores temporarily eliminated a suite of animals that could open up forests by knocking down trees and consuming fresh growth (Wing and Sues, 1992). Warm ocean waters supplied abundant atmospheric moisture for precipitation on the continents (Zachos et al., 2001). After the Eocene peak in global temperatures some 50 Ma, declining global temperatures and lower precipitation in many parts of the planet promoted the expansion of more open habitats. Ever since the Eocene, the environmental history of Africa has involved the expansion of open habitats and arid-adapted vegetation, and the evolution of a fauna well adapted to coping with open and arid conditions. These environmental changes were characterized by multiple fluctuations, and a complex interplay of climatic, tectonic, and biotic factors (Potts and Behrensmeyer, 1992).

This contribution is divided into three parts. First, it presents a brief overview, based on a survey of the primary literature, of paleoenvironmental and paleoclimatic changes in Africa through the Cenozoic. Second, it provides an analysis of Cenozoic faunal change with a focus on the taxonomic richness of large terrestrial herbivorous mammals. Broad parallels seem to exist between the evolution of megafaunas and open environments; although large mammals can live in closed, forested environments, they typically contribute to the creation and maintenance of open or mosaic habitats and thrive in such conditions. The third part of this contribution presents a new analysis of changes in

the abundance of bovids indicative of seasonally arid environments from the Late Miocene to the Pleistocene of the Turkana Basin in Kenya.

2. Materials and methods

All animal species to some extent modify their environments, and this is particularly true for large herbivorous mammals. Large mammals are not necessarily indicative of open environments (Andrews and O'Brien, 2000), but their activities contribute to the creation and expansion of mosaic habitats that include open conditions (Owen-Smith, 1988; Belsky, 1995). In parts of Africa for example, elephants diversify forest ecosystems by browsing and destroying trees and saplings, thus facilitating the occurrence of fires and the expansion of grasslands into previously forested areas (Laws, 1970; Gichohi et al., 1996). Additionally, in modern ecosystems, closely related species or populations that inhabit both closed and open environments show significant differences in body size and diet between populations in the different kinds of habitats. For example, the modern forest elephant weighs some 3500 kg and is primarily a browser, whereas the bush elephant can weigh more than 6000 kg and often adds grass to its diet (Kingdon, 1997). Likewise, the forest buffalo tends to browse and graze and weighs about 300 kg, while the Cape buffalo can weigh nearly 1000 kg and typically relies on grasses for food. Among modern hippopotamids, the forest pygmy hippo relies mostly on browse, and can weigh up to 275 kg, whereas the common hippo is primarily a grazer weighing up to 3000 kg (Kingdon, 1997). Here I provide an analysis of taxonomic richness at the genus level of large terrestrial mammals through the African Cenozoic (Table 2 and Fig. 2). Large mammals were defined as those with estimated body mass of at least 350 kg. This body mass was chosen as a cut off point because many African mammals are described in terms of body weight classes ranging from 1 to 6, in which categories 4–6 are made up of animals weighing at least 350 kg (Bunn, 1982). There are numerous uncertainties associated with body mass estimates in extinct mammals (Damuth and MacFadden, 1990), but the categories used here are broad and include only those mammals that clearly fall in the large body size classes. The data derive from a survey of descriptions and faunal lists in the primary literature (as cited below).

Bovids are often used in African paleoecological environmental reconstructions (Vrba, 1975, 1980; Shipman and Harris, 1988; Reed, 1998). The bovid tribes Alcelaphini (wildebeests and hartebeests) and Antilopini (gazelles) are particularly good indicators of open and seasonally arid environments (Greenacre and Vrba, 1984). These antelopes are characterized by hypsodont dentition and cursorial limbs. The alcelaphines are almost entirely grazers in open environments, while the antilopines include some species better adapted to browsing rather than grazing (Sponheimer et al., 1999). However, antilopine browsers (e.g. gerenuk) tend to live in fairly arid environments in which the leaves of bushes constitute an important part of their diet. These browsers then would indicate bushland-grassland habitats rather than open grasslands. The tribe Hippotragini includes the modern roan and sable antelopes, oryx, and addax. This group of bovids occupies diverse habitats, ranging from grassy woodlands (sable antelope) to desert (addax), but all species are hypsodont grazers in seasonally arid environments (Dorst and Dandelot, 1970; Vrba, 1974, 1980, 1984; Gentry, 1978; Greenacre and Vrba, 1984). Thus, here I use the bovid tribes Alcelaphini, Antilopini, and Hippotragini (AAH) as indicators of relatively open and seasonally arid environments. Other grazing bovids (Reduncini and Bovini)

Table 2
Presence (= 1) or absence of large herbivorous mammals (>350 kg) through the African Cenozoic

Megafauna	Late Eocene	Early Oligocene	Oligocene: Chilga	Early Miocene	Middle Miocene	Late Miocene	Pliocene	Early Pleistocene	Middle Pleistocene	Late Pleistocene	Recent
Proboscidea											
Barytherium	1										
Palaeomastodontidae											
Palaeomastodon		1	1								
Phiomia		1	1								
Gomphotheriidae											
Gomphotherium			1	1	1	1					
Platybelodon				1							
Tetralophodon					1						
Anancus						1	1	1			
Elephantidae											
Stegotetrabelodon						1	1				
Stegodibelodon							1				
Primelephas						1	1				
Loxodonta							1	1	1	1	1
Elephas							1	1	1	1	
Mammuthus								1	1		
Mammutidae											
Zygolophodon							1				
Mammut				1							
Stegodon						1	1				
Deinotheriidae											
Gen. et sp. nov.			1								
Prodeinotherium				1	1	1					
Deinotherium							1	1			
Embrithopoda											
Arsinoitheriidae											
Arsinoitherium		1	1								
Perissodactyla											
Chalicotheriidae											
Chalicotherium				1							
Ancylotherium						1	1				
Rhinocerotidae							1	1			

	C1	C2	C3	C4	C5	C6	C7	C8	C9	C10	C11
Brachypotherium				1			1			1	1
Aceratherium				1			1			1	1
Dicerorhinus	1			1			1				
Chilotheridium	1			1	1						
Paradiceros	1			1	1						
Diceros						1	1	1	1	1	1
Ceratotherium						1	1	1	1	1	1
Equidae				1		1	1	1	1		
Eurygnatohippus						1	1	1	1	1	1
Equus					1	1	1	1	1	1	1
Artiodactyla											
Anthracotheriidae											
Masritherium				1		1					
Hippopotamidae											
Hexaprotodon						1	1	1	1		1
Hippopotamus						1	1	1	1	1	1
Suidae							1				
Notochoerus						1	1	1			
Kolpochoerus						1	1	1			
Metridiochoerus						1	1	1			
Camelidae						1	1	1			
Camelus								1			
Giraffidae											
Palaeotragus	1			1	1	1	1	1	1	1	1
Giraffa						1	1	1	1	1	1
Sivatherium				1		1	1	1	1		
Bovidae							1				
Taurotragus				1		1	1	1	1	1	1
Tragelaphus						1	1	1	1	1	1
Simatherium							1				
Syncerus								1	1	1	
Pelorovis						1		1	1	1	1
Megalotragus						1		1	1	1	1
Total	3	3	5	10	8	19	26	19	16	12	9

African megafauna

Fig. 2. Richness (number of genera) or large herbivorous mammals in the African Cenozoic.

usually occur close to waterlogged habitats or in woodlands, and therefore, even though they eat grasses, are not considered as indicators of aridity.

Bovid specimens used in this analysis derive from the west side of Lake Turkana in Kenya, and have been identified and described by John Harris and colleagues (Harris et al., 1988; Harris and Leakey, 1993, 2003; Leakey and Harris, 2003). These specimens have been studied and entered into the Turkana Basin Paleontology Database by the author. The database is a collaborative project between the Smithsonian Institution and the National Museums of Kenya, and is scheduled to be posted online by the Smithsonian Institution, and subsequently by the National Museums of Kenya. The database currently has about 16,300 entries representing specimens of fossil mammals from Lothagam, Kanapoi, West Turkana, and East Turkana. The western side of Lake Turkana was chosen for this analysis (Lothagam, Kanapoi, and West Turkana localities) because it preserves a relatively continuous record of fossil mammals spanning the last 8 million years, and samples the margins of a large sedimentary basin. The geological sections analysed here are the Nawata, Kanapoi, and Nachukui Formations, which have been well studied and well dated by several geologists over the last three decades (Brown et al., 1985; Feibel et al., 1989, 1991; Brown and McDougall, 1993; Feibel and Brown, 1993; Brown, 1994, 1995; Feibel, 2003a, b; McDougall and Feibel, 2003). The Koobi Fora Formation, on the east side of Lake Turkana, preserves a more discontinuous record (Brown and Feibel, 1991), and is not included in this analysis. Mammals from the Shungura Formation, in the lower Omo valley of Ethiopia, have been analysed previously by the author and colleagues (Bobe, 1997; Bobe and Eck, 2001; Bobe et al., 2002; Bobe and Behrensmeyer, 2004), and are discussed here for comparative purposes.

3. Cenozoic paleoenvironments in Africa

Terrestrial vegetation is influenced by precipitation, temperature, light, and nutrients (Wing and Sues, 1992). In tropical ecosystems, where light and temperature show comparatively little variation, precipitation (soil moisture) and edaphic conditions (soil characteristics and nutrients) are of primary importance in structuring plant communities (Belsky, 1995). However, over the long time intervals of the Cenozoic, changes in

temperature and precipitation have had profound effects on the biota. Most of our knowledge of paleoclimate derives from the marine record. Global temperatures as determined from marine foraminifera were relatively high in the early Cenozoic and reached a peak during the Early Eocene "climatic optimum" about 50 Ma (Zachos et al., 2001). There was a significant decline in marine temperatures during the Late Eocene, and an abrupt dip during the Eocene–Oligocene boundary, associated with the initial build up of Antarctic ice (Lear et al., 2000; Zachos et al., 2001; Coxall et al., 2005).

The early Cenozoic of Africa is poorly known, but it is thought that the extinction of large terrestrial vertebrates at the end of the Mesozoic facilitated the expansion of dense forests in many parts of the world (Wing and Sues, 1992). Thus, the early Cenozoic of Africa would have been characterized by a low diversity of vertebrate herbivores and fairly extensive woody vegetation (Potts and Behrensmeyer, 1992). Although extensive forests and woodlands were an important component of early Cenozoic vegetation, it appears that dry woodlands and even some grasslands occurred on the continent from the beginning of the Cenozoic (Adegoke et al., 1978; Jacobs et al., 1999). On the northern edge of the continent, Eocene paleobotanical localities in Egypt and Libya indicate that forests and woodlands dominated environments close to the Tethys seaway (Guinet et al., 1987; Maley, 1996). Farther south, an assemblage of fossil leaves from Mahenge, in Tanzania, provides the earliest record of *Acacia* in Africa, and shows that woodlands were dominant in parts of East Africa around 47 Ma (Herendeen and Jacobs, 2000). The Eocene–Oligocene Fayum deposits of Egypt show that mangrove forests occurred near the Tethys Sea (Bown et al., 1982). This evidence would suggest that northern Africa was warm and wet during the Eocene and Oligocene, but the interior of the continent (Tanzania) was showing indications of water-stressed plant communities (Jacobs, 2004). An interesting pollen record from Cameroon spanning the Late Eocene to the Early Miocene shows a decrease in the abundance of grass pollen through time, and an increase in the abundance of taxa indicative of rain forest (Salard-Cheboldaeff, 1981). This decrease in grass pollen coincides with warming marine conditions from the Oligocene into the Early Miocene (Zachos et al., 2001). Thus, the paleobotanical and paleoclimatic evidence from the Paleogene (Paleocene, Eocene, and Oligocene) indicates that environmental heterogeneity existed in Africa from early in the Cenozoic, and that even though moist forests and woodlands were dominant, grasses were present in parts of Africa.

Marine paleotemperature curves indicate that the Early Miocene was the warmest interval postdating the Early Eocene tropical expansion (Miller et al., 1987). The warming trend occurred in the Early Middle Miocene, from about 18 to 14 Ma, and was followed by marked global cooling, although reversals occurred during various intervals (Zachos et al., 2001). Localities dating to the Early and Middle Miocene of Ethiopia, Kenya, and Uganda provide paleobotanical evidence of forests and woodlands. Localities in Rusinga and Mfwangano islands in Lake Victoria date to about 18 Ma, and contain plant macrofossils of taxa associated with the wet forests of West and Central Africa (Chesters, 1957; Andrews and Van Couvering, 1975; Drake et al., 1988). Dating to about 14 Ma, the Fort Ternan locality in western Kenya provides evidence of heterogeneous environments that included woodlands (Shipman et al., 1981; Cerling et al., 1991) and some grasses (Retallack et al., 1990). The Middle Miocene locality of Kabarsero (about 12 Ma) in the Tugen Hills of Kenya reinforces the evidence of extensive forests during this time (Jacobs and Kabuye, 1987). Thus, woodlands and forests were common in eastern Africa during the Early and Middle Miocene, but grasslands contributed to the complexity and

heterogeneity of the landscape. The south-western part of the continent may have become increasingly arid in the mid-Miocene with the upwelling of cold waters associated with the Benguela current (Siesser, 1978; Segalen et al., 2004; Udeze and Oboh-Ikuenobe, 2005). This phenomenon probably marked the onset of desiccation in the Namib, and therefore the establishment of one of the main poles of aridity in Africa.

The Late Miocene decline in global temperatures (especially in high latitudes) resulted in marked temperature gradients from the poles to the equator, greater rainfall seasonality, and the spread of grassy vegetation in various parts of the world (Street, 1981; Traverse, 1982, 1988; Laporte and Zihlman, 1983; Wolfe, 1985). This cooling trend might be linked to the expansion of the East Antarctic ice sheet (Woodruff et al., 1981; van Zinderen Bakker and Mercer, 1986; Zachos et al., 2001). Evidence from both paleosol carbonates and dental enamel indicate that C4 grasslands expanded significantly in the Late Miocene (Cerling et al., 1993, 1997; Morley and Richards, 1993; Morgan et al., 1994). Grass pollen and charred grass cuticle increased in abundance during the Late Miocene of western Africa, as demonstrated by analyses of drilled sediments from the Niger Delta (Morley and Richards, 1993; Jacobs, 2004). The evidence of abundant charred grass cuticle indicates that fire, one of the key elements in the maintenance of open grasslands, was playing a significant role in savanna ecosystems going back to this time. Thus, by the Late Miocene grasslands were becoming a major component of African ecosystems, and one of the poles of aridity in the south-west of the continent was well established.

A reversal in the late Cenozoic cooling trend occurred in the Early Pliocene. Marine oxygen isotopes indicate that the Early Pliocene was the warmest period of the last 5 million years (Wara et al., 2005), and rainforests may have expanded into regions of eastern Africa (Williamson, 1985; Pickford et al., 2004). Temperatures gradually declined after 3.5 Ma. Cooler conditions intensified in high latitudes between 3 and 2 Ma, establishing the onset of northern hemisphere glaciations and the modern ice ages (Shackleton et al., 1984; Kennett, 1995). The intensification of aridity in Africa has been linked to the closing of the Indonesian Seaway, and cascading effects on the Indian Ocean and precipitation on land (Cane and Molnar, 2001). Alternative hypotheses emphasize the emergence of the Isthmus of Panama and changes in Atlantic Ocean circulation (Haug and Tiedemann, 1998; Haug et al., 2001). The marine record of terrigenous sediments suggests that African Pliocene and Pleistocene climate alternated between wet and dry conditions, but these alternations were punctuated by periods of increased aridity at 2.8, 1.7, and 1.0 Ma (deMenocal, 1995). Prior to 2.8 Ma, the marine record shows that African climate varied at periodicities of 19,000 and 23,000 years; after 2.8 Ma the dominant variation shifted to 41,000-year cycles, and after 1.0 Ma to 100,000-year cycles (deMenocal and Bloemendal, 1995). Pollen data provide evidence of increasing aridity in the Saharan region of the continent between 3 and 2 Ma (Dupont and Leroy, 1995). Carbon isotope records from paleosols in the Turkana Basin show significant increases in C4 vegetation and greater aridity at around 3.6, 2.5 Ma, and then again at about 1.8 Ma (Wynn, 2004). Plio-Pleistocene aridification events in East Africa may have resulted in more heterogeneous ecology and more diverse mosaic environments, with enhanced gradients from gallery forests to the grassy floodplains away from the rivers (Wynn, 2004). Although evidence of grasses can be traced as far back as the Paleocene, and grasslands became more prominent in the Late Miocene, it was during the latest Pliocene and early Pleistocene that a significant expansion of grass-dominated ecosystems occurred in many regions of East

Africa and resulted in landscapes that appear more similar to the modern ones (Cerling et al., 1988; Cerling, 1992; Kingston et al., 1994; Bobe and Behrensmeyer, 2004).

The expansion of grasslands beginning in the Miocene and becoming more pronounced in the Pleistocene was accompanied by several trends in the mammalian fauna (as identified by Potts and Behrensmeyer, 1992): (1) increase in hypsodonty; (2) development of cursoriality; (3) increase in body size among herbivores; (4) diversification of small herbivores (mostly rodents); and (5) diversification of carnivores to prey on diverse herbivores. The next section explores changes in taxonomic richness among large terrestrial herbivores through the African Cenozoic, and the subsequent section presents an analysis of abundance in hypsodont and cursorial bovids indicative of open and arid environments over the last 8 million years.

4. The evolution of large terrestrial mammals

Relative to other continents, Africa today preserves a disproportionate diversity of large herbivorous mammals. Until the Pleistocene this diversity was characteristic of most major land masses. With an abundance of elephant, hippopotamus, giant forest hog, giraffe, buffalo, eland, rhinoceros and large carnivores, Africa is sometimes described as having a pre-Pleistocene character (Bigalke, 1978). This diversity is a result of millions of years of evolutionary and environmental history. One of the major trends in mammalian evolution has been the increasing diversity of large mammals during the Cenozoic and their decline during the final stages of the Pleistocene. Table 2 presents a tabulation of African large herbivorous mammals, defined as genera whose maximum weight exceeds 350 kg, and Fig. 2 depicts the diversity (number of genera) of large mammals through the Cenozoic.

Most of the vertebrate fossil localities in the early Cenozoic of Africa occur in the northern part of the continent, and these yield mostly small body size mammals including primates, elephant shrews, hyracoids, and rodents (Gheerbrant, 1992, 1994; Rasmussen et al., 1992). Relatively small proboscideans also occur in the early Cenozoic of North Africa (Gheerbrant et al., 1996). Large mammals were rare during the Eocene and Early Oligocene (Fig. 2). Only a few large mammals are recorded from this time in the Fayum deposits of North Africa; these include *Arsinoitherium*, *Phiomia*, *Palaeomastodon*, and *Barytherium* (Rasmussen et al., 1992). However, later in the Oligocene the large mammalian fauna was beginning to diversify. The Chilga locality of Ethiopia, dated to about 27 Ma, has several proboscideans (*Palaeomastodon*, *Phiomia*, *Gomphotherium*, and *Chilgatherium*) and a new species of Embrithopoda (*Arsinoitherium giganteum*), and indicate that large mammals were beginning to increase in diversity during a time of African isolation from Eurasia (Kappelman et al., 2003; Sanders et al., 2004). By the Early Miocene, Africa's isolation was breaking down, and the increasing diversity of large mammals was due to the appearance of immigrants from Eurasia. Notable among these immigrants were several species of Perissodactyla, including rhinocerotids (*Brachypotherium*, *Aceratherium*, *Dicerorhinus*, and *Chilotheridium*) and chalicotheriids (*Chalicotherium*). Rhinocerotidae arrived from Eurasia in the Miocene. The modern genera *Ceratotherium* and *Diceros* have their origin in the Mio-Pliocene of Africa (Hooijer, 1978; Hooijer and Churcher, 1985). Modern *Ceratotherium* weighs up to 3600 kg, and *Diceros* up to 1400 kg (Kingdon, 1997). Toward the Late Miocene, the proboscideans continued to increase in diversity, and were joined by equids coming from Eurasia (*Eurygnathohippus*). The global transition from C3 to C4 vegetation during the Late Miocene appears to have had a

marked effect on the African fauna. Several lineages of large mammals began to diversify. Some of these took advantage of the expanding grasslands, while others remained committed to a diet of leafy vegetation. The expansion of grasslands in Africa occurred at different times in different places. Among African equids, the largest sizes were achieved by the lineage of *Equus numidicus*, *E. oldowayensis*, *E. capensis*, and *E. grevyi*. This lineage appeared in North Africa during the Pliocene, and its surviving member is Grevy's zebra, which can weigh up to 450 kg (Churcher and Richardson, 1978; Eisenmann, 1983, 1985; Hooijer and Churcher, 1985; Kingdon, 1997). The Anthracotheriidae occurred in Africa from the Eocene (Qasr el Sagha Formation, Fayum) to the Mio-Pliocene boundary. The largest anthracotheres, of genus *Masritherium*, approached the size of a hippopotamus during the Miocene (Black, 1978). Among several groups of mammals, some of the largest forms evolved in the early Pleistocene, and many persisted into the later Pleistocene prior to the megafaunal extinctions. Among bovids, large grazers such as *Megalotragus* and *Pelorovis* reached very large size in the Pleistocene. The main lineages of Mio-Pliocene African Suidae (*Nyanzachoerus-Notochoerus*, *Kolpochoerus*, and *Metridiochoerus*) incorporated C4 grasses in their diet (Harris and Cerling, 2002), but postcranial evidence indicates that they were not necessarily occupying open environments until later in the Pleistocene (Bishop, 1999). Among suids, species of *Notochoerus* and *Metridiochoerus* reached body masses approaching 400 kg (Turner and Antón, 2004). The largest known African primates appeared during the Pleistocene: *Theropithecus oswaldi*, *Megaladapis*, and possibly the modern gorilla (although gorillas lack a fossil record). These primates probably evolved in response to a coarse, high-bulk plant diet, but did not reach the body size of other lineages of large mammals (Potts and Behrensmeyer, 1992).

Thus, there was a significant increase in the diversity of African large mammals during the Late Miocene as grassland mosaics were becoming a prominent feature of the landscape. The abundance of large herbivorous mammals almost certainly contributed to the more open nature of Late Miocene vegetation, but the animals themselves were likely responding to predation pressures and to a high-bulk plant diet. The Pliocene shows an even higher richness of large mammals (Fig. 2). Many of the taxa that first appear in the Late Miocene continue into the Pliocene, and many of the large mammals that become common in the Pleistocene have their origin in the Middle and Late Pliocene. Thus, even though the African Early Pliocene may have been wetter and probably more wooded than the Late Miocene and Pleistocene, the pivotal role of the Pliocene encompasses the peak of megafaunal diversity shown in Fig. 2. It is noteworthy that as the landscape was becoming more clearly dominated by open grasslands in the Pleistocene, the diversity of large mammals declined. Many lineages of large mammals became extinct in the Middle Pleistocene. Among closely related taxa, it was often the larger and more specialized taxa that became extinct, while their smaller and more generalized relatives survived the climatic and environmental fluctuations of the last one million years (Potts, 1996).

5. Faunal indicators of open environments

The relative abundance of bovids indicative of open and seasonally arid conditions in three consecutive geological formations from the west side of Lake Turkana in Kenya is shown in Fig. 3. The Nawata, Kanapoi, and Nachukui Formations provide a relatively continuous record of fossil mammals from the Late Miocene to the Middle Pleistocene. AAH are rare in the Late Miocene Lower Nawata Formation (about 7.5–6.5 Ma) of the

Turkana Basin - West Side: Nawata, Kanapoi, Nachukui Fms
Alcelaphini, Antilopini, Hippotragini as % of Bovidae
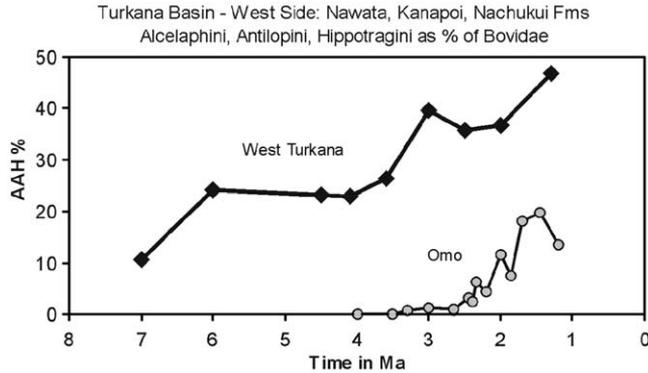
Fig. 3. Abundance of Alcelaphini, Antilopini, and Hippotragini (AAH) as a percentage of all bovids in the Nawata, Kanapoi, and Nachukui Formations, Turkana Basin, Kenya. The percentage of these tribes in the Omo (Ethiopia) is depicted for comparison (Bobe and Behrensmeyer, 2004). AAH% is used here as a proxy measure of relatively open and seasonally arid environments.

Turkana Basin, where they make up only about 10% of all bovids. Their abundance increases in the Upper Nawata Formation (6.5–5 Ma) to about 24% of the bovid fauna, and remains over 20% through the Kaiyumung and Kataboi Members (till about 3.4 Ma). Another step-like increase occurs in the Lomekwi Member of the Nachukui Formation, where these arid adapted bovids increase in abundance to nearly 40% of the bovid fauna, and remain at that level till the Kalochoro and Kaitio Members (till about 1.6 Ma). The last step-like increase in the abundance of AAH occurs in the Natoo and Nariokotome Members, dated from 1.6 Ma to around 1 Ma. At this time, these antelopes reach an abundance of about 47% of all bovids. It should be noted that the intervals of time analysed here are rather broad, and therefore this analysis is likely to mask finer variation and fluctuations in the abundance of arid adapted bovids. Instead, this analysis is meant to show the major trends in the abundance of aridity indicators over an interval of 7 million years.

Thus, as indicators of open, seasonally arid grasslands and bushland, AAH show three-step-like increases in abundance. The first step occurs at the end of the Miocene, about 6.5 Ma. The second occurs in the Middle to Late Pliocene, about 3 Ma, and the last occurs after 1.6 Ma. The Late Miocene shift may relate to the well-documented spread of C4 grasslands, and perhaps to some extent to the Messinian salinity crisis documented in the Mediterranean region (Cerling et al., 1997). The second shift at around 3 Ma may be an expression of a similar shift documented in the Omo region at about 2.8 Ma (Bobe and Eck, 2001; Bobe et al., 2002; Bobe and Behrensmeyer, 2004). However, a comparison with a similar analysis from the Omo region suggests that the changes in the west Turkana region occurred earlier, probably because of the stabilizing effects of the large riverine forest associated with the Omo valley deposits (Vrba, 1988). The third shift beginning about 1.6 Ma may document the beginning of more modern grassland environments in eastern Africa. Evidence from the Omo shows a significant increase in the abundance of open country bovids beginning at about 1.8 Ma (Bobe and Behrensmeyer, 2004). These results highlight the fact that environmental heterogeneity occurred in eastern Africa even within a single sedimentary basin. The Omo valley deposits are known to sample the axis

of a major river, and therefore provide evidence of fauna in the vicinity of large riverine forests. The west Turkana deposits are known to sample more marginal habitats within the Turkana Basin, and therefore provide evidence of fauna associated with the more open-vegetation margins of the basin (Feibel et al., 1991).

It is important to note that the relative abundances of bovid tribes shown here (Table 3 and Fig. 3) do not necessarily indicate the abundances of those tribes in the past. In other words, the fact that AAH make up about 47% of the bovid sample in the Natoo and Nariokotome Members of the Nachukui Formation (Table 3) does not mean that these bovid tribes made up 47% of the bovid fauna in the Early Pleistocene of the Turkana Basin. Multiple taphonomic and collection factors are likely to bias the proportions of these antelopes in the fossil record relative to the living communities from which they derived. Similarly, an AAH proportion of 47% does not necessarily mean that the paleo-Turkana landscape was made up of 47% open grasslands relative to other habitat categories. Instead, what is important here is the relative changes in this variable through time. The aim of this analysis is not to arrive at an environmental reconstruction (e.g. 47% grasslands, 53% woodlands), but to show the dynamics of faunal changes through time and their environmental and evolutionary implications. If the effects of taphonomic, sedimentologic, and collection factors are taken into account, the relative abundances of habitat-indicator faunas through time may provide insights into the ecological dynamics of past ecosystems (Bobe and Eck, 2001). Future research should focus on the taphonomic, sedimentologic, and collection biases involved in the collections from the west side of Lake Turkana. Also, finer levels of stratigraphic and temporal resolution might reveal intervals of high faunal variability through time, as has been found in the Shungura Formation of Ethiopia (Bobe et al., 2002). The focus on the behavior of ecological variables rather than on environmental reconstructions is a point that has been emphasized by Rick Potts in the context of Plio-Pleistocene archeological research (Potts, 1994).

6. Discussion and conclusions

There are many difficulties involved in the reconstruction of environmental and faunal histories through geologic time. Much of the information that we have about past climate derives from marine basins, where sedimentation tends to be relatively continuous. Continental records tend to be discontinuous in both the geographic and temporal dimensions, and the link between the marine and the terrestrial realms is not always clear. The early Cenozoic of Africa remains poorly known, and much work is still needed to document the evolution of Africa's fauna and environments. Exposed sediments like those in the Turkana Basin of Kenya and Ethiopia provide rich but limited windows into the past of the continent. Imperfect as they are, these geohistorical records remain a critical source of information for elucidating long-term ecological, environmental, and evolutionary changes. In this regard, it is crucial to assess independent lines of evidence whenever possible, and compare different regions from which contemporaneous records can be obtained.

Although substantial gaps remain in our knowledge of the African Cenozoic, a broad outline of the continent's history can be discerned. There has been a strong trend toward greater aridity, with consequent spread of grasslands, grassland–woodland mosaics, and deserts in the north and south-west of the continent. Africa was dominated by woodlands and forests during the early Cenozoic, although grasslands were present. The dominance of

Table 3
Abundance (number of specimens) of bovid tribes in the Nawata, Kanapoi, and Nachukui Formations, Turkana Basin, Kenya

| Age in Ma | | | | | | | | | |
| Midpoint | 8.0–6.5 | 6.5–5.0 | 5.0–4.2 | 4.2–3.9 | 3.9–3.4 | 3.4–2.7 | 2.7–2.36 | 2.36–1.60 | 1.60–1.0 | |
Geological formations west side of Lake Turkana	7.0 Lower Nawata Fm	6.0 Upper Nawata Fm	4.5 Apak Mb	4.1 Kanapoi Fm	3.6 Kaiyumung—Kataboi Mbs	3.0 Lomekwi (L–M)	2.5 Lomekwi (U)—Lokalalei	2.0 Kalochoro—Kaitio	1.3 Natoo—Nariokotome	Total
Aepycerotini	72	58	20	18	14	79	10	19	9	299
Alcelaphini	7	25	9	23	11	101	46	49	50	321
Antilopini	1	2	3	2	2	11	4	15	12	52
Boselaphini	37	11	2	0	0	0	0	0	0	50
Bovini	2	3	6	4	7	10	9	15	7	63
Caprini	0	0	0	1	0	2	0	0	4	7
Hippotragini	8	8	3	4	2	17	5	9	3	59
Neotragini	2	4	3	15	1	5	0	0	0	30
Reduncini	17	31	6	9	8	61	65	54	43	294
Tragelaphini	5	3	13	50	12	39	15	38	11	186
Total	151	145	65	126	57	325	154	199	139	1361
Percentage of Alcelaphini, Antilopini, and Hippotragini	10.6	24.1	23.1	23.0	26.3	39.7	35.7	36.7	46.8	31.7

closed vegetation was due in part to warm and wet climatic conditions, but the scarcity of large herbivorous vertebrates contributed to this pattern. Large mammals (such as species of Proboscidea and Embrithopoda) evolved in Africa during a period of isolation from Eurasia. As this isolation broke down in the Miocene several large mammals, including rhinocerotids and chalicotheriids, invaded from the north. Large herbivorous mammals likely contributed to the opening of vegetation mosaics that were driven primarily by climatic and tectonic changes. In this regard, the process of rifting would have created vegetational and climatic heterogeneity in eastern Africa as early as the Eocene (Partridge et al., 1995; Herendeen and Jacobs, 2000).

By the Late Miocene, with a well-established Eurasian connection, several immigrants arrived in Africa as C4 grasslands were expanding (e.g. *Anancus*, *Ancylotherium*, *Eurygnathohippus*). The spread of grasslands and grassland mosaics resulted in significant increases in the abundance of cursorial and hypsodont bovids in the Turkana Basin of Kenya. However, as open ecosystems were expanding, major river valleys served as refuges for forest and woodland vegetation, and for the fauna that depended on these closed habitats for survival. The abundance of open habitat indicators in the Turkana Basin increased significantly toward the latest Miocene, but their abundance in the lower Omo basin remained low until the Early Pleistocene (Bobe and Behrensmeyer, 2004). This suggests that corridors for forest and woodland mammals continued to exist in the Late Miocene as grasslands began to take a more dominant role in the landscape. Eurasian immigrants that may have made use of relatively moist and wooded corridors in the Late Miocene include species of Bovini, the ancestors of the modern buffalo.

The major river valleys provided biogeographical connections for forest and woodland fauna, and served as centers of endemism during the extremes of Pliocene and Pleistocene climatic oscillations. In the Omo Shungura Formation, for example, the Pliocene species *Tragelaphus pricei* shows connections between browsing antelopes in eastern and southern Africa. Other mammals seem to have been largely restricted to the Omo basin, and to areas connected to it in the Turkana Basin. The bovid *Tragelaphus nakuae*, for example, is abundant in the Pliocene of the Omo, but rare elsewhere in Africa. Among primates, *Theropithecus brumpti* was common in the Omo and elsewhere in the Turkana Basin, but also rare elsewhere. This emphasizes the idea that major rivers and their basins played important roles in the evolution of African mammals during the Plio-Pleistocene (Kingdon, 2003).

The forests of Kenya and Tanzania also provide important refuges. The history of East African highland and coastal forests remains poorly known, but modern faunal distributions indicate that, in addition to the river valley habitats just described, eastern forests remain important centers of endemism and diversity (Lovett and Wasser, 1993). The eastern forests would have been isolated from the more extensive Central African rainforests by an arid corridor stretching from the northeast of the continent to the coast of Namibia in the south-west. The Namibian center of aridity can be traced at least to the Miocene, and the arid corridor could well date to that epoch.

The various factors discussed here have contributed to the evolution of extremely varied and complex landscapes in Africa. The processes of rifting have created high peaks that capture moisture from the Indian Ocean, and low areas of extreme aridity. From time to time, volcanism would have covered the landscape with ash and transformed, at least temporarily, ecological conditions on regional scales. However, it appears that the effects of "mock aridity" as a result of volcanic activity (Harris and Van Couvering, 1995) were

relatively short lived (Behrensmeyer et al., 2003). Rifting has created a significant rain shadow along the western Rift Valley, where the highlands capture moisture from the Atlantic Ocean that cannot penetrate farther east. The Indian Ocean also provides consistent moisture along the coast for the existence of a network of coastal forests. The arid corridor separating East from Central African forests may have been one of the centers for the spread of C4 grasslands. It also appears that the spread of arid landscapes in the Late Miocene did not reach the extremes of the Pleistocene. The evidence discussed here indicates that major steps toward greater aridity occurred in the Late Miocene ($\sim$6 Ma), in the Pliocene ($\sim$3 Ma), and then again near the Pliocene–Pleistocene boundary ($<$2 Ma). There was no single episode of drastic environmental change, but several events followed by reversals, as well as changes in the periodicity and amplitude of climatic oscillations.

7. Summary

The major conclusions of this contribution are the following. First, a survey of the primary literature reveals a complex trend, accompanied by multiple reversals, of increasingly open and arid environments in Africa. This trend was modulated by the regional effects of rifting in the eastern parts of the continent. Second, the increase in the importance of open environments has a broad parallel in the increasing taxonomic diversity of large terrestrial herbivores. This diversity reached a peak in the Pliocene. Large mammals probably contributed to the opening of forest vegetation and to the formation of complex vegetational mosaics. Third, analyses of bovids as environmental indicators show increases in the importance of grasslands at about 6 Ma, 3 Ma, and after 2 Ma. However, these analyses and comparisons with previous work also show that areas within a single sedimentary basin responded differently to climatic fluctuations. The lower Omo valley, along the central axis of the Turkana Basin, shows a lower proportion of open country antelopes than the west Lake Turkana formations, which sample the margins of the Turkana Basin. Thus, major river basins such as the Omo would have provided a refuge to the woodland and forest biota of eastern Africa. These results show a complex history of environmental changes in eastern Africa, a region that even today supports a tremendously diverse array of plants and animals, many found nowhere else on earth.

Acknowledgements

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