



Plio-Pleistocene climatic change in the Turkana Basin (East Africa): Evidence from large mammal faunas

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Abstract

We investigated palaeoclimatic change in the Turkana Basin during the Pliocene climatic shift toward increased aridity in Africa. We analyzed the palaeoecology of this area using mammal faunas as environmental indicators. Twenty Plio-Pleistocene fossil assemblages and a comparative dataset of 16 modern localities covering a wide range of climatic and ecological conditions across Africa were analyzed. We constructed community profiles using taxonomic variables which reflect ecological information. Principal component analysis and bivariate correlation were used to study changes in the community structure of these mammalian faunas and to draw palaeoenvironmental inferences. Subsequently, least-squares regressions yielded climatic estimates (annual rainfall and drought length) for the studied period. An additional set of 8 modern faunas was used to validate these regression models. The climatic estimates showed a drying trend throughout the sequence. The biomes in the Turkana Basin changed from semi-evergreen rain forest to deciduous woodland and savanna during the middle-late Pliocene. This was the most important climatic shift detected in our study. Evidence suggests a continuous presence of savannas from 2.5 million years ago onwards. This pattern of climatic change is consistent with isotopic evidence on global climate, and with independently derived regional palaeoenvironmental evidence (i.e., micromammals, palaeovegetation, soil carbonates and palaeosols).

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Introduction

Over the last several decades palaeoclimatology has developed into a distinct research field. Uncertainty about future climatic change is one of the most serious global environmental concerns and the past climatic history offers analogies and comparisons for present and future climatic states (Hay et al., 1997; IPCC, 2001). Beyond that, and apart from the intrinsic scientific interest of palaeoclimate, climatic change has

had an important influence on evolution and community change in mammals in general and in hominids in particular (see e.g. Coppens, 1975; Vrba, 1985a, 2000, in press; Vrba et al., 1995; Agustí et al., 1999; Bromage and Schrenk, 1999).

Plio-Pleistocene global climate change is believed to have had an important influence on local habitats and early human evolution in Africa. During the Pliocene there was an important transition from a relatively warm climate, with low ice volume in the Northern Hemisphere, to a generally colder climate in the Pleistocene, with prominent glacial-interglacial cycles accompanied by periodic increase and decrease of polar ice volume (Shackleton, 1995). Within the African context, warm and humid conditions were extensive during the Miocene and early Pliocene (Vrba, 1985b; Yemane et al., 1985; Andrews, 1989; Wolde Gabriel et al., 1994; Burckle, 1995;

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Hill, 1995). African environments became cooler, drier and more seasonal during the late Pliocene and Pleistocene, which triggered the spread of savannas and deserts in northern (Dupont and Leroy, 1995), eastern (Coppens, 1975; Kappelman, 1984; Feibel et al., 1991; Cerling, 1992; Bonnefille, 1995; deMenocal, 1995; deMenocal and Bloemendal, 1995; Wesselman, 1995; Potts, 1998; Bobe and Eck, 2001; Bobe et al., 2002; Kovarovic et al., 2002; Bobe and Behrensmeyer, 2004; Suwa et al., 2003; Vrba, 2005, in press) and southern Africa (Vrba, 1974, 1975; Avery, 1995; deMenocal, 1995; deMenocal and Bloemendal, 1995; Potts, 1998). The purpose of this study is to assess the climatic change of the East African Plio-Pleistocene and the development of the savanna environment in this area of the continent.

Although the relatively continuous marine isotopic record during the Plio-Pleistocene supplies a general climatic background, it does not give direct evidence on continental palaeoenvironments (Bobe and Eck, 2001). Evidence on continental palaeoclimate usually includes data from lake levels, isotope records and palynology. Nevertheless, the continental record is quite discontinuous and these data are seldom available for particular periods or regions. On the other hand, mammalian fossil assemblages have traditionally been considered to be a suitable proxy for climatic or environmental reconstructions (for qualitative inference see e.g. van de Weerd and Daams, 1978; Andrews et al., 1979; Legendre, 1986; de Bonis et al., 1992a; Kovarovic et al., 2002; Hernández Fernández and Peláez-Campomanes, 2003; for semi-quantitative reconstructions see e.g. van der Meulen and Daams, 1992; Reed, 1998; van Dam and Weltje, 1999; Bobe et al., 2002; Fortelius et al., 2002; Hernández Fernández et al., 2003; for quantitative inferences see e.g. Hokr, 1951; Thackeray, 1987; Avery, 1992, 2001; Kay and Madden, 1997; Montuire et al., 1997; Jeannot and Cartonnet, 2000; Hernández Fernández and Peláez-Campomanes, 2005). Mammal species are highly responsive to climatic changes and they are abundant in a wide range of continental sedimentary settings, thus allowing a high temporal and spatial resolution as well as a relatively continuous record of climatic reconstructions. Therefore, among the numerous proxy indicators preserved in continental sediments, fossil remains of mammal communities are established as a promising source of information for quantifying past changes in climate.

In this study, we analysed a specific sequence of large mammal assemblages in the Turkana Basin covering more than 3 million years during the Plio-Pleistocene and compared them with a set of modern African faunas of known environment and climate. Although evolutionary and ecological analyses of different sequences from the Turkana Basin have been reported (Behrensmeyer et al., 1997; Reed, 1997; Bobe and Eck, 2001; Bobe et al., 2002; Alemseged, 2003; Bobe and Behrensmeyer, 2004; Vrba, 2005), our main objective here is to produce a quantitative climatic reconstruction, which allows for a precise interpretation of the environmental changes in the area. Following Hernández Fernández and Peláez-Campomanes (2005), here we define quantitative climatic reconstruction as the inference of numerical estimates for

a set of climatic variables in a series of fossil sites. The method used in this work is based on multivariate analysis of the taxonomic structure of communities of large non-carnivoran mammals. Our results were tested by comparisons with independent data-sets (i.e., oxygen isotope record, rodent faunas, palaeobotany).

Material and methods

Plio-Pleistocene mammal faunas from the Turkana Basin

Species sampling problems are usually recognized to constitute a significant obstacle in palaeoecological studies of ancient mammalian communities. In particular, it has been shown that the number of species recorded at any fossil locality is sensitive to the number of specimens recovered (van de Weerd and Daams, 1978; Daams et al., 1999). Therefore, fossil assemblages with a number of identified specimens lower than 100 were discarded. We consider that this number is a suitable compromise between the need for a representative fossil species number from the virtual total number obtainable with a higher sample size and the need for sufficient localities to arrive at palaeoclimatic conclusions. In order to avoid potential sampling and taphonomic biases, small mammals and carnivores were excluded from the analysis. Small mammals have been excluded from the analysis because the sampling techniques for small and large fossil mammals are very different and the former have not been as intensively sampled as the latter in most of the assemblages studied here. Carnivores are usually a minor component of fossil assemblages, which would have affected the results of our analysis when comparing with modern faunas that include a complete sample of this group.

Thus, the data set studied here includes all the species in the orders Artiodactyla, Perissodactyla, Primates, Proboscidea, Hyracoidea, Tubulidentata and Pholidota. The final data set consisted of 20 species lists for large mammal assemblages from the Plio-Pleistocene of Lothagam, Kanapoi, Usno, Shungura, Nachukui and Koobi Fora Formations (Appendix 1), which outcrop around the Lake Turkana in southern Ethiopia and northern Kenya (Fig. 1A). In spite of its smaller sample size, we included Kanapoi because of its relevance. The data were compiled from Harris et al. (1988), Feibel et al. (1991), Leakey et al. (1995), Bobe (1997), Turner et al. (1999), Alemseged (2003), Brugal et al. (2003) and Leakey and Harris (2003), with corrections by authorities on various groups (Raymond Bernor for Equidae; Eric Delson for Cercopithecidae; Alan W. Gentry and Elisabeth S. Vrba for Bovidae; John M. Harris for Giraffidae and Proboscidea; Tim D. White for Suidae and Hominidae). The geological context of these formations was described by Brown and de Heinzelin (1983), de Heinzelin and Haesaerts (1983a,b), Harris et al. (1988), Leakey et al. (1995), Brown and Feibel (1991) and Feibel (2003).

This data set is particularly useful for five reasons. First, extensive geochronometric analyses have been performed on each formation and many of the numerous volcanic tuffs in

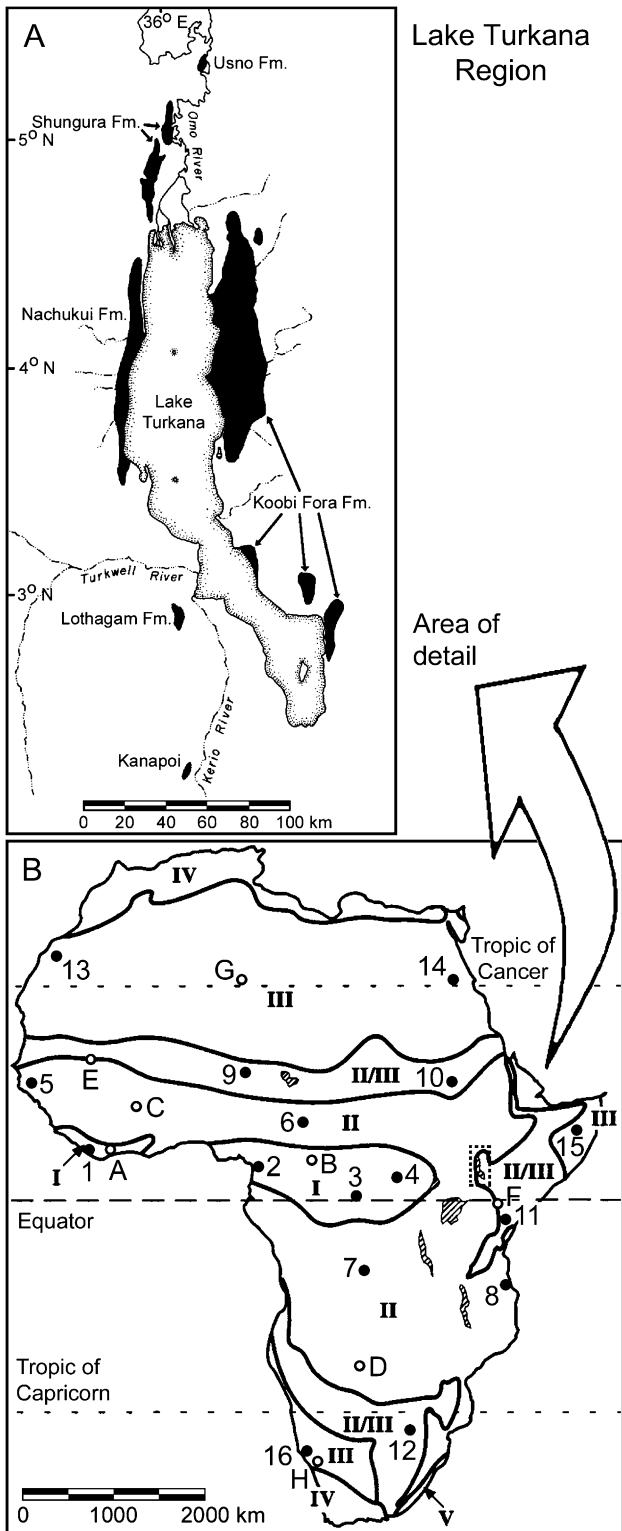


Fig. 1. A, Map of the Turkana Basin, showing the outcrop areas of the sedimentary formations used in this work (modified from Brown and Feibel, 1991 and Wesselman, 1995). B, Distribution of the modern mammal faunas used in the analysis. Numbers and letters as in Tables 2 and 5 respectively. Biomes, after Walter's (1970) climatic typology, are also shown (modified from Hernández Fernández and Vrba, 2005): I, evergreen tropical rain forest; II, tropical deciduous woodland; II/III, savanna; III, subtropical desert; IV, sclerophyllous woodland-scrubland; V, temperate evergreen forest.

the three long-ranging formations have been geochemically correlated, firmly tying the local sequence to an absolute time scale (Table 1). Second, each of the three main formations spans comparable time intervals (Cooke, 1997). Third, the whole data set is a rich and fairly continuous sequence of assemblages spanning more than 3.0 my, from 4.6 to 1.5 Ma. This interval is long enough and allows us to capture the most significant climatic changes that occurred during the Plio-Pleistocene. Fourth, potential links with palaeoclimatic data in deep-sea cores have been established (Brown, 1995). Finally, for the time period considered here, the Turkana Basin is an area of great significance to early hominid evolution. Hominid remains discovered in several of the localities studied in this work include *Australopithecus* (*A. anamensis* and *A. afarensis*), *Paranthropus* (*P. aethiopicus* and *P. boisei*) and *Homo* (*H. rudolfensis*, *H. habilis*, *H. ergaster* and *H. erectus*). Additionally, *Kenyanthropus platyops* has been recently described on the western shore of Lake Turkana, in deposits dated to between 3.5 and 3.2 Ma (Leakey et al., 2001; but criticized by White, 2003).

A major obstacle in palaeoecological studies is that fossil associations may reflect the original communities from which they were derived to a varying degree, depending on the proportion of preserved taxa from the total community. Nevertheless, modern mammal communities show a high degree of functional redundancy and thus we assume that the structure shown by the fossil assemblages is likely to afford a broadly reliable representation of the extinct community (Hernández Fernández et al., in press). Additionally, although the different taphonomic processes involved in the fossilization of

Table 1

Fossil assemblages studied in this work and their minimum, maximum and mean ages (Leakey et al., 1995; Behrensmeyer et al., 1997; Bobe, 1997; Bobe and Eck, 2001; McDougall and Feibel, 2003)

Abbr.	Formation	Member	Maximum age (ma)	Minimum age (ma)	Mean age (ma)
NAT	Nachukui	Natoo	1.60	1.33	1.47
OKT	Koobi Fooraa	Okote	1.64	1.39	1.52
KAI	Nachukui	Kaitio	1.88	1.60	1.74
KBS	Koobi Fooraa	KBS	1.88	1.64	1.76
UBU	Koobi Fooraa	upper Burgi	2.00	1.88	1.94
LG	Shungura	lower G	2.33	2.11	2.22
F	Shungura	F	2.36	2.33	2.35
E	Shungura	E	2.40	2.36	2.38
D	Shungura	D	2.52	2.40	2.46
UC	Shungura	upper C	2.75	2.52	2.64
ULM	Nachukui	upper Lomekwi + Lokalalei	2.94	2.35	2.65
UTB	Koobi Fooraa	upper Tulu Bor	2.90	2.68	2.79
LC	Shungura	lower C	2.85	2.75	2.80
B	Shungura	B	3.36	2.85	3.11
LTB	Koobi Fooraa	lower Tulu Bor	3.36	2.90	3.13
LLM	Nachukui	lower and middle Lomekwi	3.36	2.94	3.15
U-12	Usno	U-12	3.20	3.20	3.20
LOK	Koobi Fooraa	Lokochot	3.50	3.36	3.43
KAN	Kanapoi	Kanapoi	4.10	4.10	4.10
APK	Lothagam	Apak	5.00	4.22	4.61

See Appendix 1 for the faunal lists.

a mammalian assemblage are usually identifiable, we do not know whether the resulting structure exhibited by the fossil assemblages is more dependent on these processes or on the original mammal community, in which the relative abundances of the constituent taxa may strongly determine the observed structure. In fact, the question of whether taphonomic processes appreciably distort the community structure of fossil assemblages, to the point that any palaeoecological analysis based on community composition would be insignificant, remains uncertain (Damuth, 1982; Maas, 1994; Soligo, 2002). Finally, although it cannot be completely eliminated, the potential influence of taphonomic processes on our palaeoenvironmental analysis was reduced because, instead of abundance of taxa, only presence/absence data were used (see Behrensmeyer, 1991).

Modern faunas for comparison

In order to interpret and evaluate the magnitude of the climatic changes inferred from the Plio-Pleistocene palaeocommunities, these were compared with a data set of 16 modern African mammalian communities, which was collected from the literature (Table 2, Appendix 2, Fig. 1B). The faunal list of each locality has been obtained from Kingdon (1971, 1979, 1982a,b, 1997), Dorst and Dandelot (1973), Corbet (1978) and Nowak (1991). For these modern faunas, taxonomic allocations follow Wilson and Reeder (1993). The area of study was restricted to the African continent in order to avoid extreme differences among the recent faunas due to the influence of different historical factors. The recent localities were selected in order to obtain a distribution as widely scattered as possible all over Africa. Nevertheless, they were taken from four major habitat types corresponding to biomes (evergreen tropical rainforest, tropical deciduous woodland, savanna, and subtropical desert), and four localities containing both faunal and climatic information were selected from each biome in order to have comparable data for all the four biomes. Sampling areas of these faunas represent a wide climatic diversity. Finally, in order to avoid high climatic variations imposed by differences in topography, the selected localities are below 1000 m above sea level.

Clearly, the ecological classification of African habitats is subtle and complex. Our reduction of the environmental variability into a few biome definitions risks oversimplification. However, this risk may be balanced by recognizing the limits of resolution of our approach. We categorized localities into biomes rather than specific habitats because the purpose of this study is to provide palaeoclimatic reconstructions. Fossil assemblages are more likely to represent these broadly defined vegetation types, due to possible time and space averaging of animals in fossil assemblages. Thus, biomes are broad enough to be discerned reliably in the fossil record, while they are still specific enough to show climatic and environmental change. Therefore, it must be kept in mind that the vegetational definitions above are based on the concept of biome. This includes not only the climatic community that constitutes the key for its recognition (Simmons, 1979) and is mainly determined by

Table 2
Modern faunas used in this work and values in these localities for each studied climatic variable

N	Biome	Locality	Country	Latitude	Longitude	Altitude (m)	T (°C)	Tmin (°C)	Mta (°C)	P (mm)	D (months)	Climate references
1	I	Greenville	Liberia	5° 04' N	9° 04' W	10	26.3	25.3	2.0	4615.0	0.0	Meteorological Office, 1967
2	I	Kribi	Cameroon	2° 57' N	9° 54' E	624	25.8	24.5	2.5	3028.0	0.0	Bultot and Griffiths, 1972
3	I	Boende	Democratic Republic of Congo	0° 13' S	20° 51' E	351	25.5	24.7	1.3	2109.0	0.0	Meteorological Office, 1983
4	I	Yangambi	Democratic Republic of Congo	0° 49' N	24° 29' E	487	24.7	24.0	1.5	1828.0	0.0	Bultot and Griffiths, 1972
5	II	Ziguinchor	Senegal	12° 35' N	16° 16' W	10	26.8	24.0	4.5	1626.0	6.7	Griffiths, 1972a
6	II	Moundou	Chad	8° 37' N	16° 04' E	420	27.0	24.5	6.0	1232.0	5.8	Griffiths, 1972a
7	II	Dundo	Angola	7° 24' S	20° 49' E	775	24.4	23.8	1.0	1653.0	3.3	Meteorological Office, 1983
8	II	Mtwara	Tanzania	10° 16' S	40° 16' E	113	25.9	24.0	3.0	1159.0	5.5	Griffiths, 1972b
9	II/III	Zinder	Niger	13° 48' N	8° 59' E	510	28.3	22.5	10.5	530.5	8.9	Griffiths, 1972a
10	II/III	Sennar	Sudan	13° 33' N	33° 37' E	419	28.6	24.9	7.8	489.5	9.0	Meteorological Office, 1983
11	II/III	Voi	Kenya	3° 24' S	38° 34' E	560	24.9	22.5	4.5	538.0	7.4	Griffiths, 1972b
12	II/III	Gaberone	Botswana	24° 41' S	25° 55' W	983	20.2	12.6	13.0	497.0	5.5	Meteorological Office, 1983
13	III	Smara	W Sahara	26° 44' N	11° 26' W	140	21.7	14.8	12.9	35.8	12.0	Font Tullot, 1955
14	III	Assuan	Egypt	23° 58' N	33° 40' E	194	26.5	16.1	18.0	2.0	12.0	Estienne & Godard, 1970
15	III	Galcaio	Somalia	6° 46' N	47° 26' E	240	27.2	25.1	3.7	101.4	12.0	Meteorological Office, 1983
16	III	Lüderitz Bay	Namibia	26° 38' S	15° 06' E	23	15.9	13.5	4.5	18.0	12.0	Schulze, 1972

See Appendix 2 for the faunal lists.

T, mean annual temperature; Tmin, mean temperature of the coldest month; Mta, mean annual thermal amplitude; P, annual total precipitation; D, drought length; N, as in Fig. 1B. Biome after Walter's (1970) climatic typology: I, evergreen tropical rainforest; II, tropical deciduous woodland; III, savanna; III, subtropical desert.

climate, but also all the edaphic vegetation types and successional stages, which in many cases are dominated by other plant life forms. For example, in tropical areas the forest communities are shaped by a natural cycle of fire, which promotes the temporary development of grasslands in areas where the climax vegetation is forest or woodland. Processes that promote vegetational heterogeneity operate in each biome to generate a patchy and dynamic environment that may be essential for the survival of many of its constituent species. Consequently, all the habitats in a particular climate zone, whether or not they represent the climax community, are natural parts of that biome (Odum, 1971). In summary, successional processes at the landscape scale generate numerous different environments in each biome. This is specially so in the tropical deciduous woodland biome, where three types of vegetation are characteristic: woodlands, grasslands and parklands (Breckle, 2002). Their distribution depends on topography and the allocation and extension of edaphic types, flooded areas and the relatively frequent fires, which make the vegetation of this biome very dynamic and heterogeneous. Finally, our classification benefits from a biome typology based on climatic definitions (Walter, 1970), which allows comparability across different habitat classifications.

As a final remark, the comparability of modern and fossil communities might be rendered difficult due to differences between the areas of origin of the sampled individuals. While our modern faunas represent regional faunas from areas of approximately 10,000 Km² (Hernández Fernández, 2001), the fossil locality data usually come from much smaller areas. Nevertheless, since there is heterogeneity and dynamism in the landscape and time and space averaging in the accumulation of fossils, we believe that there is substantial comparability between the two data sets.

Multivariate analysis of mammalian faunas

Community structure can be defined as the entire set of occupied niches in a particular community (Andrews, 1996), and one of its most important factors is the frequency of the different types of niches. It is generally assumed that past macroclimatic factors and landscape features may be recognized by the study of the community structure of fossil mammal assemblages (van de Weerd and Daams, 1978; Artemiou, 1984; Andrews, 1995; Hernández Fernández, 2001; Nieto and Rodríguez, 2003). Palaeoecological methods describe this structure using variables defining the different niches, and use these data to compare the fossil assemblages with recent communities in order to infer palaeoenvironmental features. Underlying these methods is the concept of community convergence, according to which communities developing under similar environmental conditions have similar community structures (Cody and Mooney, 1978; Crowder, 1980; Samuels and Drake, 1997).

Several methods have been developed in order to describe the structure of mammalian communities, to compare recent and past assemblages, and to reconstruct the palaeoenvironments of the latter. Here we used principal component analysis

(PCA) to study the taxonomic structure of the mammal faunas, which is generally considered to be informative on ecology (Andrews et al., 1979; Greenacre and Vrba, 1984; de Bonis et al., 1992a,b, 1999; Reed, 1998; Hernández Fernández et al., 2003). Taxonomic analyses (*sensu* Andrews, 1996) assume that taxa are to some extent restricted to specific adaptive zones due to shared inheritance of aspects of habitat-specificity and, thus, that ecological information from living forms may be transferred to extinct relatives within the same clade (Vrba, 1975, 1985c; Dood and Stanton, 1981; Greenacre and Vrba, 1984; Shipman and Harris, 1988; Bobe and Eck, 2001). Under this assumption, the proportions of species in higher taxonomic units (Table 3) may indicate which adaptive zones are the most prevalent in a determined environment. Nevertheless, two of the studied taxonomic categories may be judged as problematic when applied to the African modern faunas: Camelidae and Hominoidea. The modern distribution of *Camelus dromedarius* in Africa (Köhler-Rollefson, 1991) was influenced by recent human activity and domestication.

Table 3

Taxonomic categories used as variables in the multivariate analyses and genera included in each of them

1	% Phacochoerini	<i>Metridiochoerus</i> , <i>Phacochoerus</i> , <i>Stylochoerus</i>
2	% Potamochoerini	<i>Hylochoerus</i> , <i>Kolpochoerus</i> , <i>Potamochoerus</i>
3	% Hippopotamidae	<i>Hexaprotodon</i> , <i>Hippopotamus</i>
4	% Camelidae	<i>Camelus</i>
5	% Tragulidae	<i>Hyemoschus</i>
6	% Giraffidae	<i>Giraffa</i> , <i>Okapia</i> , <i>Sivatherium</i>
7	% Bovinae	<i>Pelorovis</i> , <i>Simatherium</i> , <i>Syncerus</i> , <i>Taurotragus</i> , <i>Tragelaphus</i> , <i>Tragoptax</i> , <i>Ugandax</i>
8	% Neotragini	<i>Madoqua</i> , <i>Neotragus</i> , <i>Oreotragus</i> , <i>Ourebia</i> , <i>Raphicerus</i>
9	% Antilopini	<i>Ammodorcas</i> , <i>Antidorcas</i> , <i>Antilope</i> , <i>Gazella</i> , <i>Litocranius</i>
10	% Reduncinae	<i>Dorcadoxa</i> , <i>Kobus</i> , <i>Menelikia</i> , <i>Redunca</i>
11	% Cephalophinae	<i>Cephalophus</i> , <i>Sylvicapra</i>
12	% Orygini	<i>Addax</i> , <i>Oryx</i>
13	% Hippotragini	<i>Hippotragus</i>
14	% Alcelaphinae	<i>Alcelaphus</i> , <i>Beatragus</i> , <i>Connochaetes</i> , <i>Damalacra</i> , <i>Damaliscus</i> , <i>Damalops</i> , <i>Megalotragus</i> , <i>Parmularius</i> , <i>Sigmoceros</i>
15	% Caprinae	<i>Ammotragus</i> , <i>Capra</i>
16	% Other Bovidae	<i>Aepyceros</i> , <i>Pelea</i>
17	% Rhinocerotidae	<i>Brachypotherium</i> , <i>Ceratotherium</i> , <i>Diceros</i>
18	% Equidae	<i>Equus</i> , <i>Eurygnathohippus</i> , 'Hipparion'
19	% Proboscidea	<i>Anancus</i> , <i>Deinotherium</i> , <i>Elephas</i> , <i>Loxodonta</i> , <i>Stegodon</i> , <i>Stegotetrabelodon</i>
20	% Hominoidea	<i>Australopithecus</i> , <i>Gorilla</i> , <i>Homo</i> , <i>Pan</i> , <i>Paranthropus</i>
21	% Cercopithecinae	<i>Allenopithecus</i> , <i>Arctocebus</i> , <i>Cercocebus</i> , <i>Cercopithecoides</i> , <i>Cercopithecus</i> , <i>Chlorocebus</i> , <i>Erythrocebus</i> , <i>Lophocebus</i> , <i>Mandrillus</i> , <i>Papio</i> , <i>Parapapio</i> , <i>Theropithecus</i>
22	% Colobinae	<i>Colobus</i> , <i>Paracolobus</i> , <i>Procolobus</i> , <i>Rhinocolobus</i>
23	% Other Primates	<i>Euoticus</i> , <i>Galago</i> , <i>Galagoides</i> , <i>Otolemur</i> , <i>Perodicticus</i>
24	% Other large non-carnivorans	<i>Notochoerus</i> , <i>Nyanzachoerus</i> , <i>Dendrohyrax</i> , <i>Gigantohyrax</i> , <i>Heterohyrax</i> , <i>Procavia</i> , <i>Ancylotherium</i> , <i>Manis</i> , <i>Orycteropus</i>

Yet, we believe that it reflects accurately the environmental requirements of the species. Additionally, evidence of the presence in Africa of the ancestor of domestic camels (*Camelus thomasi*) is well established (Peters, 1998; Churcher et al., 1999). Therefore, it is a sound inference that camels were present in arid areas at least in northern and eastern Africa before domestication. Finally, in our opinion, the exclusion of camels from the modern faunas would result in greater uncertainty in the results of the analysis of fossil faunas than would its inclusion. In the same way, to eliminate *Homo sapiens* from the modern faunas in the analysis would reduce the Hominoidea to the inhabitants of the rainforest in central Africa (*Pan* and *Gorilla*). This would mean that the presence of fossil hominids would imply automatically the presence of rainforest in the fossil site (at least according to this variable). Since we know that hominid species were variously associated with habitats other than rainforest, we included modern *Homo sapiens* in the modern faunas to represent this fact. Additionally, from a philosophical point of view, we consider the inclusion of *Homo sapiens* in the modern faunas to be important because this mammalian species has been the product of evolution in Africa, just like the other species in our data base. Nevertheless, somebody may argue that a cosmopolitan species is not useful as an indicator of ecology. However, we consider that the degree of biome-specificity of species should not influence their inclusion in the study. That is, if species are present, they should be included. It should be noted that the analyses were rerun without *Homo sapiens* in order to reassure their robustness. Although the results are not shown, we can report that, while the precipitation and aridity values changed, the results without *Homo* maintained the same general trends in those which included *Homo*.

In order to avoid the potential influence of species richness on the results, we used species percentages in each taxonomic unit instead of numbers of species. Since percentages generate a closed system, they give rise to the so called ‘closure problem’ (Butler, 1981). The use of percentages imposes the constant-sum constraint (i.e., as the relative percentage of one taxonomic variable increases, one or more other variables must decrease in the total count, which is always 100%). Thus, because of closure and the implicit dependency of the variables on one another, the variables lack statistical independence (Jackson, 1997). Nevertheless, the magnitude of this bias depends on the number of variables used in the analysis. It is most pronounced with few variables and decreases in magnitude as the number of variables is increased (Grayson, 1984; Jackson, 1997). Our analysis incorporated 24 taxonomic variables and, therefore, the large number of implied degrees of freedom minimizes this problem (Bobe et al., 2002).

The matrix including the taxonomic data calculated for both modern and Plio-Pleistocene mammalian faunas is presented in Table 4. We used three different versions of PCA to analyse these data.

PCA A, including both modern and fossil faunas

Conventionally, both modern and fossil faunas have been included in the same multivariate analysis (de Bonis et al.,

1992a,b; Sen et al., 1998; Hernández Fernández et al., 2003, in press). Hernández Fernández et al. (in press) consider that the inclusion of fossil faunas in the PCA allows the extraction of differences in community structure between modern and fossil faunas, which are generally associated with the first PCA factor. The remaining PCA factors are interpreted as ecological gradients and the positions of the fossil assemblages within these gradients can be directly obtained from their scores in each of the PCA factors. These scores represent the values for the studied localities in the factors, and thus indicate the relative placement of each locality in the “eco-space” defined by the PCA factors.

PCA B, including only modern faunas

Recently, Rodríguez (2004) expressed concerns about the influence of the fossil faunas on the PCA because “they may distort the analyses if their composition is very different to that of the recent communities”. For example, there are numerous species of hippopotamids and suids in the Plio-Pleistocene localities of the Turkana Basin, whereas these taxa are not so speciose in modern African faunas. In order to solve this problem, Rodríguez (2004) proposed that the PCA should be performed using only modern faunas, followed by computation of the position of the fossil assemblages in the “eco-space” defined by the PCA factors using the factor loadings of the PCA.

PCA C, including only fossil faunas

Based on a similar philosophy, de Bonis et al. (1994, 1999) proposed a third possibility, which is to compute a PCA that includes only fossil assemblages.

Ecological interpretation of the PCAs

We compiled the values of several climatic variables for the modern localities: mean annual temperature (T, in °C), mean temperature of the coldest month (Tmin, in °C), mean annual thermal amplitude (Mta, in °C; range between the average temperatures of the warmest and coldest months of the year), annual precipitation (P, in mm) and drought length (D, in months; number of months in which precipitation is less than twice the temperature, Walter, 1970). Data on these climatic variables for each modern fauna are presented in Table 2.

In order to detect which PCA factors and climatic variables are significantly related, in the case of PCA A and PCA B, we calculated the correlations between the scores of each modern fauna for each PCA factor and the values for the climatic variables in their localities. In the case of PCA C, since the modern localities are not used in the analysis, the ecological interpretation of the different PCA factors is more complicated. We utilized two different approaches. First, we analyzed the correlations between the PCA factors and the original taxonomic variables (component matrix) and compared these correlations with the ones in the PCA including only modern localities (PCA B). This was done by correlation analysis between the factors in the component matrices of PCAs B

Table 5
Protected natural areas used in this work for the validation of the regression models and values for the studied climatic variables in localities close to these protected natural areas (Bultot and Griffiths, 1972; Meteorological Office, 1983)

N	Biome	Protected Natural Area	Country	Locality	Latitude	Longitude	Altitude (m)	T (°C)	Tmin (°C)	Mta (°C)	P (mm)	D (months)
A	I	Tai	Ivory Coast	Tabou	4° 55' N	7° 22' W	4	26.0	24.0	3.5	2383.0	0.3
B	I	Nouabale-Ndoki	Republic of Congo	Ouesso	1° 37' N	16° 03' E	340	25.4	24.5	1.9	1705.0	0.0
C	II	Mare aux Hippopotames	Burkina Faso	Bobo Dioulasso	11° 10' N	4° 18' W	432	27.0	25.2	4.7	1215.0	5.9
D	II	Mamili	Namibia	Sesheke	17° 28' S	24° 18' E	946	21.3	14.6	11.2	756.0	6.6
E	II/III	Boucle du Baoule	Mali	Kayes	14° 26' N	11° 26' W	46	29.3	25.3	9.7	750.0	7.7
F	II/III	Amboseli	Kenya	Makindu	2° 17' S	37° 50' E	993	22.6	20.0	4.6	584.0	7.0
G	III	Tassili N' Ajjer	Algeria	Djanet	24° 33' N	9° 28' E	1054	23.4	12.8	18.4	24.0	12.0
H	III	Richtersveld	South Africa	Port Nolloth	29° 14' S	16° 52' E	4	14.3	12.4	3.5	61.0	12.0

See Appendix 3 for the faunal lists. Legend as in Table 2.

not analysed in the PCAs, we computed the position of the fossil assemblages in each PCA factor with climatic interest using the factor loadings of the corresponding PCA.

To test the accuracy of the regression models we followed the methodology of Hernández Fernández and Peláez-Campomanes (2005). In each case a coefficient of determination between the observed and predicted values for the climatic values in the new localities was calculated (r_p^2). These r_p^2 were compared to the coefficient of determination of the corresponding calculated regression (r_r^2) in order to determine the degree of decrease in goodness of fit. Due to sample chance, small decreases are expected even within accurate models. Hernández Fernández and Peláez-Campomanes (2005) consider a decrease in goodness of fit of 10% as the threshold for accepting a model as inaccurate. Thus, if $r_r^2 - r_p^2$ was larger than $r_r^2/10$ the model was considered inaccurate. Finally, if $r_r^2 - r_p^2$ was between $r_r^2/10$ and $r_r^2/20$ the model was considered to be accurate and, if it was lower than $r_r^2/20$, very accurate (Hernández Fernández and Peláez-Campomanes, 2005).

Finally, the models that we considered accurate were applied to the fossil faunas in order to obtain climatic values for these localities during the Plio-Pleistocene.

Results

The three PCA component matrices are given in Appendices 4–6. In the PCAs A, B and C respectively, seven, six, and eight significant components were retained because their eigenvalues are larger than 1. These components account for about 80% of the variance in the original data for the analyses including fossil faunas (PCAs A and C), and 90% in the analysis including only modern faunas (PCA B).

The modern mammalian communities from different biomes are clearly separated regardless of the methodological approach used (Fig. 2), which indicates the existence of a strong relationship between community structure on the one hand and climate or biome type on the other hand (Porter et al., 2000; Mendoza et al., 2004). Similar results have been observed by other authors who have analyzed the relationship between different components of the ecological structure of mammalian communities and ecosystem or biome type in various areas of the world (de Bonis et al., 1992a,b, 1999; Sen et al., 1998; Shepherd, 1998; Williams and Marsh, 1998; Hernández Fernández et al., 2003, in press; Mendoza et al., 2004; Rodríguez, 2004).

Table 7 shows the correlations between the PCA factors of each data-set and the values of mean annual temperature (T), mean temperature of the coldest month (Tmin), mean annual thermal amplitude (Mta), annual precipitation (P) and drought length (D) of the modern communities.

PCA A, including both modern and fossil faunas

The first component of PCA A separates fossil assemblages and modern faunas (Fig. 2A) and is correlated with annual precipitation (P) and drought length (D). Of all the PCA A components, the one with the highest levels of correlation is factor

Table 6

Statistics related to the taxonomic structure (see Table 3) of the modern African mammal faunas from protected natural areas used in order to validate the regression models for palaeoclimatic inference

N	Biome	Locality	Sp.																									
				% Phacochoerini	% Potamochoerini	% Hippopotamidae	% Camelidae	% Tragulidae	% Giraffidae	% Bovinae	% Neotragini	% Antilopini	% Reduncinae	% Cephalophinae	% Orygini	% Hippotragini	% Alcelaphinae	% Caprinae	% Other Bovidae	% Rhinocerotidae	% Equidae	% Proboscidea	% Hominoidea	% Cercopitheciae	% Colobinae	% Other Primates	% Other large non-carnivores	
A	I	Tai	32	0.00	6.25	3.13	0.00	3.13	0.00	9.38	3.13	0.00	0.00	25.00	0.00	0.00	0.00	0.00	0.00	0.00	3.13	6.25	18.75	3.13	6.25	12.50		
B	I	Nouabale-Ndoki	34	0.00	5.88	2.94	0.00	2.94	0.00	8.82	0.00	0.00	0.00	17.65	0.00	0.00	0.00	0.00	0.00	0.00	2.94	8.82	20.59	5.88	8.82	14.71		
C	II	Mare aux Hippopotames	16	6.25	0.00	6.25	0.00	0.00	0.00	6.25	0.00	0.00	12.50	25.00	0.00	6.25	6.25	0.00	0.00	0.00	6.25	6.25	12.50	0.00	0.00	6.25		
D	II	Mamili	32	3.13	3.13	3.13	0.00	0.00	3.13	15.63	6.25	0.00	12.50	3.13	3.13	3.13	9.38	0.00	3.13	6.25	3.13	3.13	3.13	6.25	0.00	3.13	6.25	
E	II/III	Boucle du Baoule	13	7.69	0.00	7.69	0.00	0.00	7.69	15.38	7.69	0.00	7.69	0.00	0.00	7.69	7.69	0.00	0.00	0.00	7.69	7.69	15.38	0.00	0.00	0.00		
F	II/III	Amboseli	32	3.13	0.00	3.13	0.00	0.00	3.13	12.50	9.38	9.38	6.25	6.25	3.13	0.00	6.25	0.00	3.13	3.13	3.13	3.13	3.13	9.38	0.00	3.13	9.38	
G	III	Tassili N'Ajjer	7	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	14.29	0.00	0.00	28.57	14.29	0.00	14.29	0.00	0.00	0.00	14.29	0.00	0.00	0.00	14.29		
H	III	Richtersveld	9	0.00	0.00	0.00	0.00	0.00	0.00	0.00	22.22	0.00	0.00	11.11	0.00	0.00	0.00	0.00	0.00	11.11	0.00	11.11	0.00	11.11	22.22	0.00	0.00	11.11

N, as in Fig. 1B. Sp, number of species.

2, which is highly correlated to all the environmental factors, except mean annual temperature (Table 7). The fact that one factor is correlated with most of the climatic variables is evidently related to the strong collinearity among the studied climatic variables in the African continent (Hernández Fernández and Vrba, 2005).

In summary, although there is clear evidence that the Plio-Pleistocene mammal faunas have a different ecological structure from the modern ones (Reed, 1998; Bobe et al., 2002; Rodríguez, 2004; Rodríguez et al., 2004), our results support the suggestion by Hernández Fernández et al. (in press) that the PCA factor 1 in this kind of analysis (including modern and fossil assemblages) seems to absorb the chief differences in community structure between fossil and modern faunas, allowing the ecological interpretation of the remaining components (or at least some of them). According to Appendix 4, the most important differences between fossil and modern assemblages are due to the proportions in taxonomic categories (see Table 3) Other Primates, Cephalophinae, Tragulidae, Reduncinae, Alcelaphinae, and Other Bovidae, which are the main variables responsible for the scores of PCA A factor 1.

PCA B, including only modern faunas

Again the modern and fossil assemblages are separated as a function of their scores for factor 1, and also factor 2 (Fig. 2B). In this case the variables responsible for these factors are the percentages of Hominoidea, Camelidae, Cephalophinae and Bovinae -factor 1-, and Colobinae, Tragulidae, Phacochoerini and Alcelaphinae -factor 2- (Appendix 5). PCA B 1 is also the main ecological factor, which highly correlates with all the environmental factors except mean annual temperature (Table 7). Additionally, PCA B 2 correlates with annual total precipitation (P) and PCA B 4 correlates with mean annual temperature (T).

PCA C, including only fossil faunas

There are no significant correlations between the factors in the component matrices of PCAs B and C (Table 8). Nevertheless, PCA C factor 4 correlates marginally with PCA B factor 3, which indicates that this factor may relate to most of the climatic variables studied. PCA C 6 correlates marginally with PCA B 2. On the other hand, according to the correlations between the scores in each PCA C factor and the values for the climatic variables in each modern locality, it appears that there are numerous PCA factors that could be termed climatic factors (Table 7). The main climatic factor is the PCA factor 4, which has highly significant correlations with all the variables, except for mean annual temperature (T). PCA factors 2, 6 and 7 are also correlated with most of the climatic variables, although their coefficients are generally lower than those of the PCA factor 5. Additionally, PCA factor 1 is correlated with mean temperature of the coldest month (Tmin) and mean annual thermal amplitude (Mta), whereas PCA factor 8 correlates with mean annual thermal amplitude (Mta), annual precipitation (P) and drought length (D).

In this analysis, according to the scores for the main climatic factor (PCA C 4) the modern faunas cluster with the fossil assemblages, although the latter are still somewhat isolated due to their scores for the remaining factors (Fig. 2C).

Quantitative inference of climatic variables

Table 9 shows that, of all the potentially climatic factors, only PCA A 1, PCA A 2, PCA B 4 and PCA C 1 are significantly correlated with the marine isotopic record. In order to infer climatic values for the Plio-Pleistocene assemblages we computed regressions using these PCA factors as the independent variable and the climatic variables as the dependent one (Table 10). Although several of these regressions were significant, only PCA A 2 explained more than 75% of the

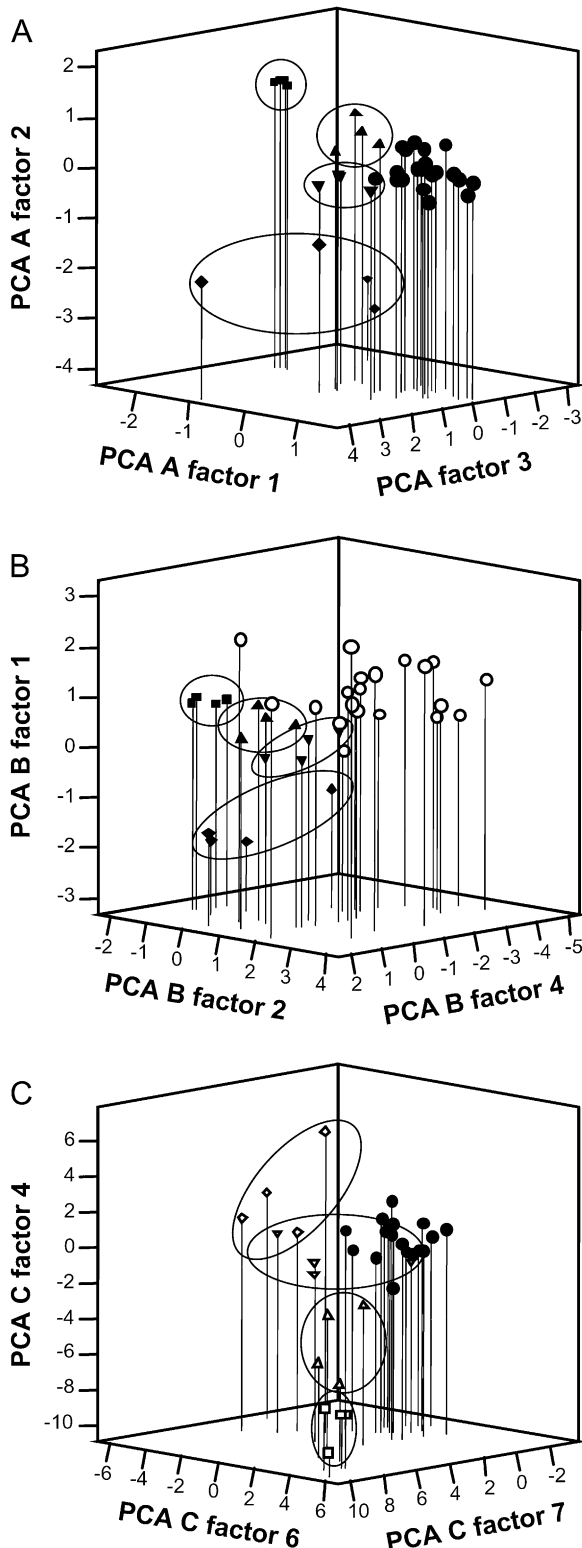


Fig. 2. Projection of the fossil (circles) and modern African mammalian communities (squares, rainforest; upright triangles, tropical woodland; inverse triangles, savanna; diamonds, desert) on the eco-space defined by three factors of the PCAs including both fossil and modern faunas (A), only modern faunas (B) and only fossil faunas (C). Black symbols identify the faunas included in the analysis; white symbols indicate faunas included a posteriori in the scatterplot, after computing their scores in each PCA factor using the factor loadings of each analysis. The vertical axis represents the main environmental factor.

variability in the original data, and only in the regressions for precipitation and drought length. This indicates that PCA A 2 is a better climatic indicator than the factors in PCAs B and C, suggesting that the separate analyses of fossil and recent data, for some reason, do not reflect the palaeoecological information in a directly interpretable form.

The best fit for our data was obtained in the exponential regression for precipitation and the quadratic regression for drought length (Fig. 3). Thus, these are the models we used to infer climatic variables for the studied Plio-Pleistocene faunas (Table 11).

Validation of the regression models

The results obtained from comparing the coefficient of determination of the regression model (r_r^2) and the determination coefficient of the regression between the observed and predicted values (r_p^2) indicate that both regression models, for precipitation and for drought length, are very accurate ($r_r^2 - r_p^2 < r_r^2/20$; respectively, $0.884 - 0.913 = -0.029$ and $0.944 - 0.904 = 0.040$). The placement of the 8 new localities used for the validation in Fig. 3 also indicates the accuracy of these regression models. Nevertheless, the confidence intervals for the predictions are ample (Fig. 3) and this must be kept in mind when interpreting the results obtained for the Plio-Pleistocene assemblages.

Environmental change in the Plio-Pleistocene of the Turkana Basin

Figure 4 shows the changes in precipitation during the Plio-Pleistocene in the Turkana area and the inferred biome for each assemblage, which is a function of the interaction between annual total precipitation and drought length (Figure 99 in Breckle, 2002). While values of these climatic variables cannot be inferred in temporal gaps, it is probable that the fossil localities included in this work represent the trends we discuss. The only major gaps present in our analysis are the ones between the Apak Member of Lothagam (4.6 Ma), Kanapoi (4.1 Ma) and the Lokochot Member of the Koobi Fora Formation (3.4 Ma).

The first two fossil assemblages of the sequence indicate the presence of climatic savannas (II/III), which are determined exclusively by climatic factors. Without special edaphic circumstances the vegetation reaches equilibrium between grasses and trees when the annual rainfall is around 400 mm (Walter, 1970). Nevertheless, as our analysis includes large gaps in this period, we cannot determine whether these were the distinctive conditions during the East African early Pliocene or whether they represent brief dry moments within an overall more humid period. A comparison with the Spanish climatic record for the Plio-Pleistocene (Hernández Fernández, 2005) suggests that the latter might by a more accurate interpretation. The Iberian rodent faunas indicate, for the early Pliocene, a general context of warm and humid

Table 7

Coefficients and their significance for the correlations between the climatic variables and the PCA factors derived from the analyses of African mammal faunas

	T ^a		Tmin ^a		Mta ^a		P ^a		D ^a	
	r ^b	p ^c	r ^b	p ^c	r ^b	p ^c	r ^b	p ^c	r ^b	p ^c
PCA A 1	-0.028	0.917	-0.174	0.520	0.255	0.340	-0.522	0.038	0.413	0.112
PCA A 2	0.366	0.163	0.706	0.002	-0.711	0.002	0.766	0.001	-0.904	< 0.001
PCA A 3	-0.469	0.067	-0.126	0.643	-0.333	0.207	-0.197	0.464	0.143	0.596
PCA A 4	0.350	0.184	0.362	0.168	-0.150	0.579	0.231	0.388	-0.147	0.586
PCA A 5	0.348	0.187	0.024	0.931	0.336	0.204	-0.158	0.559	0.104	0.701
PCA A 6	-0.314	0.236	-0.174	0.518	-0.130	0.631	0.409	0.116	-0.318	0.230
PCA A 7	-0.157	0.562	-0.317	0.231	0.286	0.283	-0.143	0.597	0.028	0.919
PCA B 1	0.431	0.095	0.721	0.002	-0.655	0.006	0.708	0.002	-0.841	< 0.001
PCA B 2	-0.003	0.990	-0.151	0.576	0.252	0.347	-0.553	0.026	0.440	0.088
PCA B 3	-0.447	0.082	-0.074	0.784	-0.400	0.125	-0.018	0.947	-0.025	0.926
PCA B 4	-0.511	0.043	-0.363	0.168	-0.042	0.877	0.142	0.600	-0.143	0.598
PCA B 5	0.288	0.279	0.027	0.921	0.249	0.353	-0.052	0.848	-0.024	0.929
PCA B 6	-0.222	0.409	-0.433	0.094	0.433	0.094	0.064	0.813	-0.204	0.448
PCA C 1 ^d	0.133	0.624	0.557	0.025	-0.732	0.001	0.496	0.051	-0.267	0.318
PCA C 2 ^d	-0.173	0.522	-0.596	0.015	0.767	0.001	-0.665	0.005	0.790	< 0.001
PCA C 3 ^d	-0.263	0.325	-0.446	0.083	0.418	0.108	-0.122	0.654	0.303	0.254
PCA C 4 ^d	-0.199	0.460	-0.629	0.009	0.785	< 0.001	-0.871	< 0.001	0.928	< 0.001
PCA C 5 ^d	-0.191	0.479	-0.182	0.501	0.090	0.741	-0.646	0.007	0.628	0.009
PCA C 6 ^d	0.341	0.196	0.566	0.022	-0.538	0.032	0.855	< 0.001	-0.948	< 0.001
PCA C 7 ^d	0.356	0.176	0.659	0.005	-0.650	0.006	0.854	< 0.001	-0.760	0.001
PCA C 8 ^d	-0.026	0.923	0.378	0.149	-0.670	0.005	0.713	0.002	-0.806	< 0.001

^a T, mean annual temperature; Tmin, mean temperature of the coldest month; Mta, mean annual thermal amplitude; P, annual total precipitation; D, drought length.

^b N = 16 modern assemblages.

^c Bold, significant correlations.

^d In PCA C the scores of each modern mammal fauna were calculated using the factor loadings of a PCA performed exclusively with fossil faunas (see text).

climate within which there are two drier and cooler periods coincident with the faunas from Apak and Kanapoi (Hernández Fernández et al., 2004; Hernández Fernández, 2005). Additionally, Kanapoi could be correlated with the isotopic stages Gi 16–18, which represent a relative maximum in the proportion of $\delta^{18}\text{O}$ (Tiedemann et al., 1994; Shackleton et al., 1995).

During the middle Pliocene there was a predominance of semi-evergreen tropical rain forest in the Turkana Basin. This kind of vegetation is located at the ecotone between the evergreen rain forest biome (I in Fig. 1B) and the tropical deciduous woodland biome (II). It is a transitional zone with

a mixture of both types of vegetation, whose species are adapted to the climatic seasonality imposed by a short dry period. The upper tree storey is deciduous, whereas the lower storeys are evergreen (Walter, 1970; Breckle, 2002).

As shown in Fig. 4B, there is a general drying trend during the late Pliocene. A decrease in rainfall and a lengthening of the dry season forced a change from semi-evergreen tropical rain forest towards the tropical deciduous woodland biome (II), where all the tree species are deciduous and the forest is bare for shorter or longer periods of time (moist or dry monsoon forests). Cane and Molnar (2001) linked the triggering of this drying trend in East Africa to the

Table 8

Coefficients and their significance for the correlations between the PCA factors of the analysis including only modern faunas (PCA B) and the one including only fossil faunas (PCA C)^a

	PCA B 1		PCA B 2		PCA B 3		PCA B 4		PCA B 5		PCA B 6	
	r ^b	p ^c	r ^b	p ^c	r ^b	p ^c	r ^b	p ^c	r ^b	p ^c	r ^b	p ^c
PCA C 1	-0.178	0.417	0.346	0.106	-0.103	0.640	0.182	0.405	-0.349	0.103	-0.122	0.579
PCA C 2	-0.033	0.880	0.019	0.931	-0.308	0.153	0.002	0.993	-0.159	0.468	0.222	0.308
PCA C 3	-0.361	<i>0.091</i>	-0.175	0.425	0.002	0.993	0.119	0.588	-0.148	0.499	-0.068	0.759
PCA C 4	-0.184	0.401	0.013	0.953	-0.224	0.304	0.251	0.249	0.205	0.349	0.111	0.613
PCA C 5	0.156	0.477	-0.141	0.522	0.252	0.246	-0.159	0.469	0.021	0.924	-0.183	0.404
PCA C 6	0.132	0.550	-0.382	<i>0.072</i>	-0.048	0.829	0.015	0.945	0.096	0.664	0.152	0.488
PCA C 7	0.125	0.570	-0.112	0.611	-0.058	0.793	0.067	0.762	-0.154	0.483	-0.175	0.424
PCA C 8	-0.138	0.529	-0.139	0.526	0.258	0.235	0.330	0.124	0.251	0.249	-0.230	0.291

^a % Tragulidae was not included in PCA C because there are no tragulids in the Plio-Pleistocene fossil record of eastern Africa.

^b N = 18 taxonomic variables.

^c Italics, marginally significant correlations.

Table 9

Coefficients and their significance for the correlations between the ecological PCA factors derived from the analyses of African mammal faunas and the $\delta^{18}\text{O}$ values from the 846 site of the Ocean Drilling Program

	$\delta^{18}\text{O}$	
	r^a	p^b
PCA A 1	0.560	0.010
PCA A 2	−0.482	0.032
PCA B 1	0.277	0.238
PCA B 2	0.147	0.537
PCA B 4	0.775	< 0.001
PCA C 1	0.647	0.002
PCA C 2	0.397	0.083
PCA C 4	0.195	0.411
PCA C 5	−0.009	0.968
PCA C 6	0.060	0.800
PCA C 7	−0.312	0.180
PCA C 8	0.028	0.907

^a N = 20 fossil assemblages.

^b Bold, significant correlations.

northward motion of New Guinea and Australia. This induced a decrease of temperature of the incoming water into the Indian Ocean across the Indonesian archipelago because the area of origin in the Pacific Ocean shifted from warm to cooler areas. This cooling was especially marked in the eastern coast of Africa and probably provoked a reduction of precipitation over East Africa (Cane and Molnar, 2001). Additionally, Partridge et al. (1995) and deMenocal and Bloemendal (1995) suggested that the variations in high-latitude ice cover and the regional uplift in Africa also influenced the aridity trend in East Africa.

Our results show an interesting pattern from the late Pliocene onwards. Fossil sites from the Nachukui Formation show consistently higher precipitation values than sites with

similar estimated ages from the Koobi Fora Formation (lower-middle Lomekwi and lower Tulu Bor, 3.1 Ma; Kaitio and KBS, 1.7 Ma; Natoo and Okote, 1.5 Ma). This result is probably due to the fact that these two formations come from different shores of Lake Turkana, which may show climatic differences as they do today; the western shore is more humid than the eastern one (Fig. 1).

Although with frequent oscillations in the precipitation values (e.g., upper Member C represents a moment of dry tropical deciduous woodland), from about 2.8 Ma onwards there is a general establishment of the savanna biome (II/III), which coincides with the isotopic stage G6 (Tiedemann et al., 1994; Shackleton et al., 1995). Finally, the drying trend established during the late Pliocene continued across the Plio-Pleistocene boundary, when the driest assemblage in our data set is observed, the KBS Member of the Koobi Fora Formation (1.8 Ma).

To provide a broader geographical context for the recorded climatic changes, we should consider that the Turkana Basin, which had riverine and rift-margin associated deltaic and lake environments throughout the time in question, was most likely a refugium (Vrba, 1988, 2005). This term is used here in the broad sense of a biome refugium (e.g., a forest surrounded by more open vegetation may preserve the characteristic forest vegetation physiognomy, although its detailed taxonomic composition differs from that of the more widespread parent community). A modern African analogue is provided by the Okavango delta, which preserves a species-rich, riverine-deltaic ecosystem within the Kalahari semi-arid region of Botswana. The ecological idiosyncrasy of these regions arises from the microclimate created by extensive flooded areas. Although the bodies of water do not provoke a prolongation of the rains beyond the season, they cause an increased thunderstorm activity around their peripheries (Schulze, 1972; Leroux, 2001). Water surfaces do not control precipitation

Table 10

Coefficients and their significance for the regressions using the ecological PCA factors derived from the analyses of African mammal faunas^a as the independent variable and the climatic variables as the dependent one

		T		Tmin		Mta		P		D	
		r^{2b}	p^c	r^{2b}	p^c	r^{2b}	p^c	r^{2b}	p^c	r^{2b}	p^c
Linear regression	PCA A 1	0.001	0.917	0.030	0.520	0.065	0.340	0.272	0.038	0.170	0.112
	PCA A 2	0.134	0.163	0.498	0.002	0.506	0.002	0.588	0.001	0.817	< 0.001
	PCA B 4	0.261	0.043	0.131	0.168	0.002	0.877	0.020	0.600	0.020	0.598
	PCA C 1	0.018	0.624	0.310	0.025	0.535	0.001	0.246	0.051	0.071	0.318
Quadratic regression	PCA A 1	0.004	0.977	0.034	0.799	0.066	0.642	0.441	0.023	0.524	0.008
	PCA A 2	0.143	0.367	0.500	0.011	0.508	0.010	0.791	< 0.001	0.944	< 0.001
	PCA B 4	0.307	0.092	0.138	0.380	0.013	0.921	0.162	0.317	0.253	0.150
	PCA C 1	0.023	0.858	0.357	0.057	0.573	0.004	0.356	0.057	0.080	0.583
Exponential regression	PCA A 1	0.001	0.888	0.033	0.502	0.182	0.099	0.000	0.959	n.a.	n.a.
	PCA A 2	0.146	0.145	0.470	0.003	0.508	0.002	0.884	< 0.001	n.a.	n.a.
	PCA B 4	0.250	0.049	0.124	0.180	0.005	0.794	0.003	0.836	n.a.	n.a.
	PCA C 1	0.014	0.663	0.310	0.025	0.373	0.012	0.230	0.060	n.a.	n.a.

n.a., not available.

^a Only those ecological PCA factors that have correlations with the $\delta^{18}\text{O}$ variation (see Table 6).

^b N = 16 modern assemblages.

^c Bold, significant regressions.

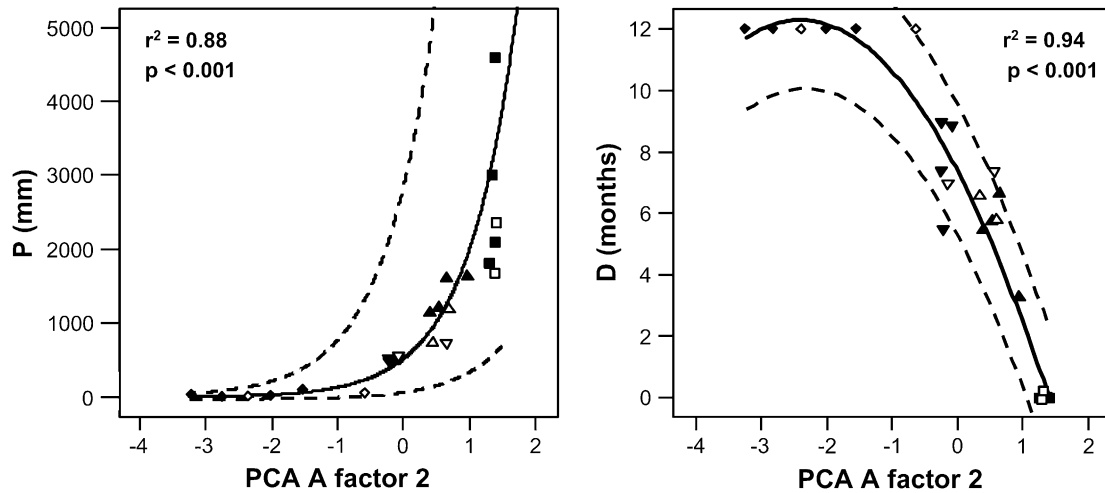


Fig. 3. Relation between PCA A 2 and annual total precipitation (A) and drought length (B). The exponential (A) and quadratic (B) regressions curves (solid line), their 95% confident intervals for the estimates (dashed line), coefficients and significance levels are shown. Symbols as in Fig. 2.

directly, but rather supply additional rainfall potential and meteoric water (Leroux, 2001).

Refugia are characterised by relatively stable communities with less variable dynamics than the surrounding areas. Vrba (1988) argued that climatic change in the larger region is recorded in a refugium only close to its ecotonal limits, by the new appearances (or disappearances) of taxa that represent occasional intrusive elements from the peripheral biome. Therefore, since sensitivity to climate change is reduced in refugia, the climatic changes that our analysis has detected should be very significant, and the incidence of such changes

in the larger adjacent areas was probably even more pronounced.

Comparison with previous evidence in the Turkana Basin

Our results compare well with other analyses of the East African Plio-Pleistocene large mammal faunas. Reed’s (1997) palaeoecological analysis, which is based on the ecological diversity method of Andrews et al. (1979), indicates that percentages of frugivores in East African communities fluctuated within ranges for woodland until the second half of the Late Pliocene when they drop to ranges for shrubland and grassland. On the contrary, the relative abundances of grazing mammalian species fluctuated in East African localities from around a mean of 20% until the Early Pleistocene when they rise to close to 50%, indicating the expansion of grasslands (Fig. 4). Additionally, during the Late Pliocene the percentage of arboreal mammals in East Africa fluctuated between the range for closed and open woodland until the Pleistocene when they drop to ranges for shrubland and grassland (Reed, 1997). In their study of the proportions of bovid tribes, Shipman and Harris (1988) concluded that Turkana habitats were mainly wooded during most of the sequence, which basically coincides with the results of Bobe and Eck (2001). Bobe et al. (2002) and Bobe and Behrensmeyer (2004) have studied the proportion of grassland taxa among the large mammal faunas of the Shungura Formation, indicating that grassland species remained a relatively minor component of the fauna in terms of overall abundance, and the dominant habitats on the Omo floodplain were riparian woodlands and seasonally wet grasslands until the Pleistocene. Nevertheless, Alemseged (2003) indicated that grasslands were becoming a much more important part of the palaeolandscape of the Shungura sequence in lower Member G, which is the driest member of that formation according to our analysis. Although savanna

Table 11
Values for annual total precipitation (P) and drought length (D) estimated by applying quadratic regression to the scores of PCA A 2 (Fig. 3) in each Plio-Pleistocene mammalian assemblage of the Turkana area

Abbr.	Formation	Member	P (mm)	D (months)
NAT	Nachukui	Natoo	514	7.6
OKT	Koobi Fora	Okote	357	8.6
KAI	Nachukui	Kaitio	563	7.3
KBS	Koobi Fora	KBS	292	9.1
UBU	Koobi Fora	upper Burgi	407	8.2
LG	Shungura	lower G	463	7.9
F	Shungura	F	606	7.0
E	Shungura	E	516	7.5
D	Shungura	D	517	7.5
UC	Shungura	upper C	691	6.6
ULM	Nachukui	upper Lomekwi + Lokalalei	495	7.7
UTB	Koobi Fora	upper Tulu Bor	585	7.2
LC	Shungura	lower C	982	5.4
B	Shungura	B	936	5.6
LTB	Koobi Fora	lower Tulu Bor	566	7.3
LLM	Nachukui	lower and middle Lomekwi	1076	5.1
U-12	Usno	U-12	1134	4.9
LOK	Koobi Fora	Lokocho	1083	5.1
KAN	Kanapoi	Kanapoi	481	7.8
APK	Lothagam	Apak	527	7.5

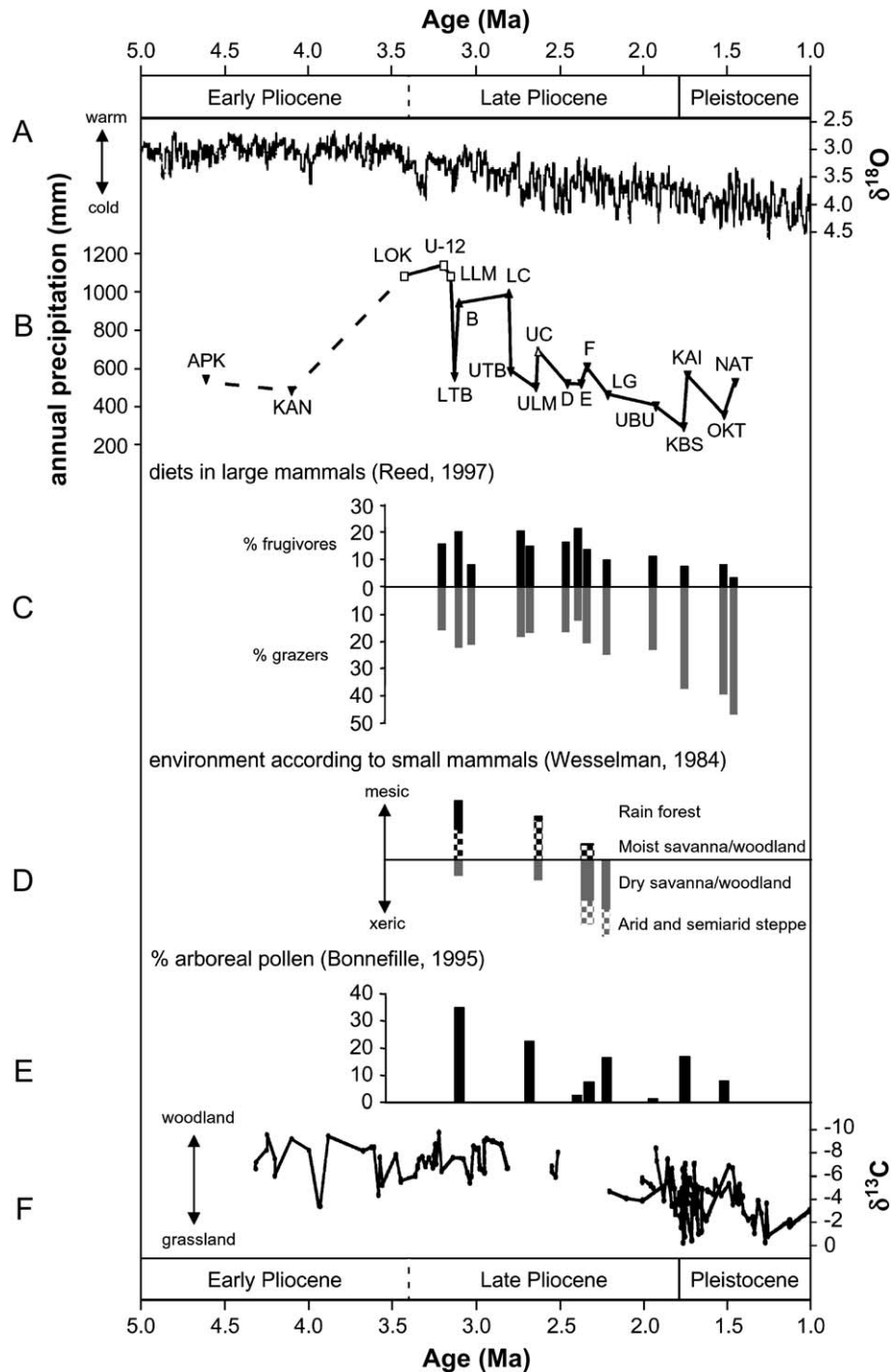


Fig. 4. Chronology and palaeoclimatic reconstruction of the East African Plio-Pleistocene. Different lines of palaeoenvironmental evidence are juxtaposed for comparison. (A) Oxygen isotope record for benthic foraminifera from ODP site 846 (Mix et al., 1995; Shackleton et al., 1995). (B) Evolution of the annual total precipitation during the African Plio-Pleistocene in the Turkana Basin, based on the taxonomical analysis of their macromammalian faunas. The inferred biomes according to the interaction between annual total precipitation and drought length are shown: white squares, semievergreen tropical rainforest (ecotone between biomes I and II); black upright triangles, moist tropical woodland (II humid); white upright triangles, dry tropical woodland (II dry); inverse triangles, savanna (II/III). Abbreviations as in Table 1. For data on precipitation and drought length in each fossil assemblage see Table 11. (C) Frugivory and grazing percentages in macromammalian faunas (Reed, 1997). (D) Micromammalian evidence (Wesselman, 1984). (E) Palaeobotanical evidence (Bonnefille, 1995). (F) East African soil carbonate data (Cerling and Hay, 1986; Cerling, 1992; deMenocal and Bloemendal, 1995; Wynn, 2000).

ecosystems were present regularly since the second half of the Late Pliocene, they would have had significant tree cover until the end of the Pliocene when precipitations lower than 400 mm became usual.

Also in agreement with our results are those for micromammalian faunas collected in the Shungura Formation (Wesselman, 1984, 1995), which show a progressive drying trend. This is suggested by the increasing percentage of

more xeric micromammals from Member B to lower Member G (Fig. 4). Although they are not as diverse as those from the Shungura Formation, samples of micromammals collected in the KBS and Okote members of the Koobi Fora Formation are similar to those from the Members F and G (Black and Krishtalka, 1986; Denys, 1999). Our results indicate that these members had similar semi-arid conditions.

In general, even if it is not complete, the palynological record supplies a feasible signal concerning the ecological change in the Plio-Pleistocene of East Africa (Bonnefille, 1995). Records from the Turkana Basin indicate closed and humid environments at the beginning of the Late Pliocene followed by oscillating conditions thereafter (Fig. 4), which coincides with our results. Grasslands did not develop into a major component of the African landscape until the Late Pliocene, although they were already present in Africa during the Miocene (Bonnefille, 1984, 1995).

In addition to pollen, the Shungura sequence has yielded several samples of macrobotanical remains (Bonnefille and Dechamps, 1983). *Antrocaryon*, which occurs today primarily in the western and central African rain forests, has been found in Unit U-12 of the Usno formation. On the other hand, members D, F and G contain taxa associated with savanna, although the persistence of forest, probably associated with riverine/deltaic areas, is indicated by *Ficus* and *Garcinia*.

The soil carbonate data from several hominid bearing sequences in East Africa (Cerling and Hay, 1986; Cerling et al., 1988; Cerling, 1992; Wynn, 2000) reflect vegetational fluctuations during the Plio-Pleistocene and also the continuous net trend towards more open landscapes (Fig. 4). Although the proportion of C₄ vegetation increased since the Late Miocene to the Pliocene, the landscapes were usually dominated by C₃ plants, mostly trees. There is no evidence for the development of relatively pure C₄ grasslands until the Pleistocene (Cerling, 1992), when our analysis shows the maximum of aridity.

Paleosols in the Kanapoi sequence (Wynn, 2000) indicate seasonal moisture (250–1000 mm/yr) and at least one annual dry season longer than four months. This is consistent with our results in showing an environment drier than that of other early and middle Pliocene fossil assemblages. In the same way, the overall pattern shown by the palaeosol record of the Shungura Formation indicates relatively arid climatic conditions from upper Member C upward, in contrast with more humid conditions in Member B (de Heinzelin et al., 1976; Haesaerts et al., 1983).

Concluding remarks

Our results based on the taxonomic structure of mammal assemblages show that communities from the same type of biome share a common pattern of community structure. Therefore, given that habitats grade into one another, that

many areas include a variety of different microhabitats, and that ecological preferences of mammal species may be somewhat flexible, our results suggest that the taxonomic analysis we used provides a robust and reliable method of evaluating past environmental conditions from mammalian fossil assemblages.

Our study combines modern and fossil assemblages together with climatic information in a single multivariate analysis. This approach avoids some of the drawbacks inherent in the fact that modern and fossil faunas differ in community structure, and produces a rich and complex picture of the Plio-Pleistocene environmental evolution in the Turkana Basin. Using an independent method for estimating palaeoclimatic and palaeoecological conditions, our results confirm the general trends shown by previous studies based on other lines of evidence from East Africa and the global context of climatic change. In general, the trend toward increased aridity suggested by mammal assemblages coincides with global records indicating the initiation near 2.7 Ma, and subsequent intensification, of glacial cycles in the northern latitudes and drier climate in the tropics of Africa.

Our study is too limited in geographic scope to inform on the specific ecological preferences of early hominids. Yet it offers some preliminary and general assessments on the biomes they inhabited in the Turkana area. The mammalian faunas indicate that there were profound environmental changes in the Turkana Basin during the interval from 4.5 to 1 Ma. The most important of these changes include a significant shift in the late Pliocene from forests and woodlands toward savannas. This drying trend intensified in the Plio-Pleistocene boundary, when there is a gradual transition to increasingly arid and seasonal environments.

These results demonstrate the complexity in the palaeoecological information that can be potentially obtained from mammal faunas. They also highlight the importance of carefully controlled modern comparative data sets in order to provide accurate palaeoclimatic data.

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4	<i>Camelus</i> sp.							1		1		1		1					
6	<i>Giraffa gracilis</i>			1				1	1			1	1	1	1	1	1		
6	<i>Giraffa jumae</i>		1	1	1			1	1			1	1	1	1	1	1		1
6	<i>Giraffa pygmaea</i>			1				1				1	1	1	1	1	1		1
6	<i>Giraffa</i> sp.					1													1
6	<i>Giraffa stillei</i>	1	1	1				1											
6	<i>Sivatherium maurusium</i>			1				1		1		1	1	1	1	1	1		1
7	Bovini indet.		1		1					1									
7	<i>Pelorovis</i> sp.													1	1				1
7	<i>Pelorovis</i> sp. nov.														1				1
7	<i>Pelorovis turkanensis</i>												1		1	1	1		1
7	<i>Simatherium kohllarseni</i>	1		1						1									
7	<i>Syncerus acoelotus</i>											1			1				
7	<i>Syncerus</i> sp.											1							
7	<i>Tragelaphus gaudryi</i>											1	1	1	1	1			
7	<i>Tragelaphus kyaloe</i>	1	1	1				1											
7	<i>Tragelaphus nakuae</i>			1	1	1	1	1	1	1	1	1	1	1	1	1	1		
7	<i>Tragelaphus pricei</i>											1							
7	<i>Tragelaphus scriptus</i>					1				1									1
7	<i>Tragelaphus strepsiceros</i>									1			1	1	1	1	1	1	1
7	<i>Tragoportax cyrenaicus</i>	1																	
7	<i>Ugandax</i> sp.					1				1									
8	<i>Madoqua</i> sp.	1	1																1
8	<i>Raphicerus</i> sp.	1	1											1	1	1	1		
9	<i>Antidorcas recki</i>													1	1	1	1	1	1
9	<i>Antilope</i> aff. <i>subtorta</i>											1							
9	<i>Antilopini</i> sp.				1														1
9	<i>Gazella janenschi</i>					1				1						1	1	1	1
9	<i>Gazella praethomsoni</i>				1								1	1	1	1			1
9	<i>Gazella</i> sp.	1	1																

T	Species	APK	KAN	LOK	U-12	LLM	LTB	B	LC	UTB	ULM	UC	D	E	F	LG	UBU	KBS	KAI	OKT	NAT
		Apak	Kanapoi	Lokochot	Usno	Lower and middle Lomekwi	Lower Tulu Bor	B	Lower C	Upper Tulu Bor	Upper Lomekwi + Lokalei	Upper C	D	E	F	Lower G	Upper Burgi	KBS	Kaitio	Okote	Natoo
10	<i>Dorcadoxa prorrepticornis</i>			1																	
10	<i>Kobus leche</i>																1	1			
10	<i>Kobus ancystrocera</i>						1	1		1		1		1		1	1	1			
10	<i>Kobus ellipsiprymnus</i>															1		1			
10	<i>Kobus kob</i>							1					1			1	1	1		1	1
10	<i>Kobus sp. nov.</i>						1									1	1	1		1	1
10	<i>Kobus oricornis</i>			1		1	1	1		1											
10	<i>Kobus presigmoidalis</i>	1																			
10	<i>Kobus sigmoidalis</i>									1	1	1	1	1	1	1	1	1		1	1
10	<i>Kobus sp.</i>		1							1											
10	<i>Menelikia lyrocera</i>										1	1		1	1	1	1	1		1	1
10	<i>Menelikia sp. nov.</i>										1										
10	<i>Menelikia sp. nov.</i>			1			1			1		1	1								
10	<i>Redunca sp.</i>														1						
10	<i>Reduncini indet.</i>				1				1										1		
11	<i>Cephalophus sp.</i>						1												1		
12	<i>Oryx sp.</i>										1	1				1	1	1			
13	<i>Hippotragini indet.</i>		1			1															
13	<i>Hippotragus gigas</i>											1					1	1	1		1
13	<i>Hippotragus sp.</i>	1														1					
14	<i>Alcelaphini indet. (large)</i>					1															
14	<i>Alcelaphini indet. (medium)</i>					1															
14	<i>Alcelaphini indet. (small)</i>						1														
14	<i>Alcelaphini indet.</i>		1		1																
14	<i>Beatragus antiquus</i>															1	1	1		1	
14	<i>Connochaetes gentryi</i>										1						1	1	1	1	1
14	<i>Damalacra sp. A</i>	1																			
14	<i>Damalacra sp. B</i>	1																			
14	<i>Damaliscus niro</i>																		1		
14	<i>Damaliscus eppsi</i>																		1		
14	<i>Damaliscus sp.</i>					1					1								1		1

14	<i>Damalops palaeindicus</i>							1												
14	<i>Damalops denendorai</i>								1											1
14	<i>Damalops sidihakomai</i>																			1
14	<i>Megalotragus isaaci</i>																			1
14	<i>Megalotragus katwinke</i>																			1
14	<i>Megalotragus sp.</i>																			1
14	<i>Parmularius eppi</i>																			1
14	<i>Parmularius sp. nov.</i>																			1
14	<i>Parmularius altidens</i>																			1
14	<i>Parmularius braini</i>																			1
14	<i>Parmularius angusticornis</i>																			1
14	<i>Parmularius sp.</i>																			1
15	Caprini indet. A																			1
15	Caprini indet. B																			1
15	Caprini indet. C																			1
15	Caprini indet. D																			1
16	<i>Aepyceros melampus</i>																			1
16	<i>Aepyceros premelampus</i>																			1
16	<i>Aepyceros shungurae</i>																			1
16	<i>Aepyceros sp.</i>																			1
16	<i>Aepyceros sp. nov.</i>																			1
16	Ovibovini indet.																			1
17	<i>Brachypotherium lewisi</i>																			1
17	<i>Ceratotherium praecox</i>																			1
17	<i>Ceratotherium simum</i>																			1
17	<i>Diceros bicornis</i>																			1
18	Equidae indet.																			1
18	<i>Equus burchelli</i>																			1
18	<i>Equus grevyi</i>																			1
18	<i>Equus koobiforensis</i>																			1
18	<i>Equus oldowayensis</i>																			1

T	Species	APK	KAN	LOK	U-12	LLM	LTB	B	LC	UTB	ULM	UC	D	E	F	LG	UBU	KBS	KAI	OKT	NAT
		Apak	Kanapoi	Lokochot	Usno	Lower and middle Lomekwi	Lower Tulu Bor	B	Lower C	Upper Tulu Bor	Upper Lomekwi + Lokalalei	Upper C	D	E	F	Lower G	Upper Burgi	KBS	Kaitio	Okote	Natoo
18	<i>Equus</i> sp.																				1
18	<i>Eurygnathohippus cornelianus</i>																1				
18	<i>Eurygnathohippus ethiopicus</i>														1		1				1
18	<i>Eurygnathohippus hasumense</i>					1				1											
18	<i>Eurygnathohippus lybicum</i>														1						
18	<i>Eurygnathohippus sitifense</i>							1				1			1	1					
18	<i>Eurygnathohippus</i> sp. (large)	1																			
18	<i>Eurygnathohippus</i> sp. (small)	1																			
18	<i>Eurygnathohippus</i> sp. A						1			1							1		1		
18	<i>Eurygnathohippus</i> sp. B.																1		1		
18	' <i>Hipparion</i> ' sp. (may include <i>Hippotherium</i>)		1						1							1					
19	<i>Anancus kenyensis</i>	1	1																		
19	<i>Deinotherium bozasi</i>	1	1		1	1	1	1		1		1	1	1	1	1	1	1	1		1
19	<i>Stegodon kaisensis</i>							1													
19	Elephantidae indet. A	1																			
19	Elephantidae indet. B	1																			
19	<i>Elephas ekorensis</i>	1	1		1																
19	<i>Elephas recki</i>					1	1	1		1		1	1	1	1	1	1	1	1		1
19	<i>Loxodonta adaurora</i>		1		1	1											1				
19	<i>Loxodonta atlantica</i>													1							
19	<i>Loxodonta exoptata</i>	1				1				1											
19	<i>Loxodonta</i> sp.																				1
19	<i>Stegotrabelodon orbus</i>	1																			
20	<i>Australopithecus afarensis</i>							1		1											

20	<i>Australopithecus anamensis</i>		1																
20	<i>Australopithecus</i> sp.				1				1			1			1				
20	Hominidae indet.	1		1				1											
20	<i>Homo</i> sp.?										1		1	1					
20	<i>Homo erectus</i>																		1
20	<i>Homo ergaster</i>																	1	
20	<i>Homo habilis</i>								1						1	1			
20	<i>Homo rudolfensis</i>														1	1			1
20	<i>Paranthropus aethiopicus</i>								1	1		1	1	1		1			
20	<i>Paranthropus boisei</i>											1	1		1	1	1		1
21	<i>Cercocebus</i> sp.															1			1
21	<i>Cercopithecoides keryoensis</i>	1																	
21	<i>Cercopithecoides kimeui</i>			1				1							1	1			
21	<i>Cercopithecoides williamsi</i>															1			
21	<i>Cercopithecus</i> sp.					1			1										1
21	<i>Papio quadratiostris</i>				1				1				1	1					
21	<i>Papio</i> sp.																		1
21	<i>Parapapio ado</i>		1																1
21	<i>Parapapio whitei</i>																		1
21	<i>Parapapio</i> sp.	1				1			1				1	1	1				1
21	<i>Theropithecus brumpti</i>			1		1		1	1				1	1	1				1
21	<i>Theropithecus oswaldi</i>													1	1		1	1	1
22	Colobinae indet. A													1					
22	Colobinae indet. C	1																	
22	Colobinae sp. nov.		1																
22	<i>Paracolobus mutiwa</i>					1			1		1		1	1	1			1	1
22	<i>Rhinocolobus turkanaensis</i>					1				1		1						1	1
23	<i>Galagooides demidoff</i>																		1
23	<i>Galago howelli</i>																		1
23	<i>Galago senegalensis</i>		1																1
24	<i>Notochoerus capensis</i>		1																
24	<i>Notochoerus eulius</i>	1	1		1			1						1		1			

Appendix 1 (continued)

T	Species	APK	KAN	LOK	U-12	LLM	LTB	B	LC	UTB	ULM	UC	D	E	F	LG	UBU	KBS	KAI	OKT	NAT
		Apak	Kanapoi	Lokochot	Usno	Lower and middle Lomekwi	Lower Tulu Bor	B	Lower C	Upper Tulu Bor	Upper Lomekwi + Lokalelei	Upper C	D	E	F	Lower G	Upper Burgi	KBS	Kaitio	Okote	Natoo
24	<i>Notochoerus scotti</i>										1	1	1	1	1	1	1	1	1		
24	<i>Notochoerus</i> sp.								1												
24	<i>Notochoerus</i> sp. nov.															1					
24	<i>Nyanzachoerus australis</i>	1																			
24	<i>Nyanzachoerus jaegeri</i>	1	1																		
24	<i>Nyanzachoerus kanamensis</i>		1		1	1	1						1								
24	<i>Nyanzachoerus pattersoni</i>													1							
24	<i>Nyanzachoerus syrticus</i>	1																			
24	<i>Gigantohyrax maguirei</i>							1	1	1											
24	<i>Heterohyrax brucei</i>							1													
24	<i>Ancylotherium hennigi</i>												1			1					
24	<i>Orycteropus afer</i>													1							

Appendix 2

Modern large mammal faunas used in PCAs and for the development of regression models for climatic inference. The faunal list of each locality has been obtained from Kingdon (1971, 1979, 1982a,b, 1997), Dorst and Dandelot (1973), Corbet (1978) and Nowak (1991). T, taxonomic categories (see Table 3).

T	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
		Greenville	Kribi	Boende	Yangambi	Ziguinchor	Moundou	Dundo	Mtwara	Zinder	Sennar	Voi	Gaberone	Smara	Assuan	Galcaio	Lüderitz Bay
1	<i>Phacochoerus africanus</i>					1	1	1	1	1		1	1				
2	<i>Hylochoerus meinertzhageni</i>	1	1		1												
2	<i>Potamochoerus larvatus</i>							1	1								
2	<i>Potamochoerus porcus</i>	1	1	1	1	1						1					
3	<i>Hexaprotodon liberiensis</i>	1															
3	<i>Hippopotamus amphibius</i>	1	1	1	1	1	1	1	1	1	1	1	1				
4	<i>Camelus dromedarius</i>										1			1	1	1	
5	<i>Hyemoschus aquaticus</i>	1	1	1	1												
6	<i>Giraffa camelopardalis</i>					1	1	1		1	1	1	1				1
6	<i>Okapia johnstoni</i>			1	1												
7	<i>Syncerus caffer</i>	1	1	1	1	1	1	1	1	1	1	1					
7	<i>Taurotragus derbianus</i>					1	1			1							
7	<i>Taurotragus oryx</i>							1	1			1	1				
7	<i>Tragelaphus euryceros</i>	1	1		1												
7	<i>Tragelaphus imberbis</i>											1					1
7	<i>Tragelaphus scriptus</i>	1	1	1	1	1	1	1	1	1	1		1				
7	<i>Tragelaphus spekii</i>		1	1	1	1	1	1									
7	<i>Tragelaphus strepsiceros</i>								1			1	1				
8	<i>Madoqua guentheri</i>											1					1
8	<i>Madoqua kirkii</i>											1					
8	<i>Neotragus batesi</i>		1		1												
8	<i>Neotragus moschatus</i>								1			1					
8	<i>Neotragus pygmaeus</i>	1															
8	<i>Oreotragus oreotragus</i>								1			1	1				1
8	<i>Ourebia ourebi</i>					1	1		1	1	1						
8	<i>Raphicerus campestris</i>											1	1				1
8	<i>Raphicerus sharpei</i>								1								
9	<i>Ammodorcas clarkei</i>															1	
9	<i>Antidorcas marsupialis</i>												1				1
9	<i>Gazella dama</i>									1							
9	<i>Gazella dorcas</i>									1				1			

(continued on next page)

T	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
		Greenville	Kribi	Boende	Yangambi	Ziguinchor	Moundou	Dundo	Mtwara	Zinder	Sennar	Voi	Gaberone	Smara	Assuan	Galcaio	Lüderitz Bay
9	<i>Gazella granti</i>											1					
9	<i>Gazella rufifrons</i>					1				1	1						
9	<i>Gazella soemmerringi</i>										1					1	
9	<i>Gazella spekei</i>															1	
9	<i>Gazella thompsoni</i>											1					
9	<i>Litocranius walleri</i>											1				1	
10	<i>Kobus ellipsiprymnus</i>					1	1	1	1			1					
10	<i>Kobus kob</i>					1	1										
10	<i>Redunca arundinum</i>							1	1								
10	<i>Redunca fulvorufula</i>												1				
10	<i>Redunca redunca</i>					1	1		1	1		1					
11	<i>Cephalophus callipygus</i>		1	1	1												
11	<i>Cephalophus dorsalis</i>	1	1	1	1												
11	<i>Cephalophus harveyi</i>											1					
11	<i>Cephalophus jentinki</i>	1															
11	<i>Cephalophus leucogaster</i>		1		1												
11	<i>Cephalophus maxwelli</i>	1				1											
11	<i>Cephalophus monticola</i>		1	1	1			1	1								
11	<i>Cephalophus natalensis</i>								1								
11	<i>Cephalophus niger</i>	1															
11	<i>Cephalophus nigrifrons</i>		1	1	1			1									
11	<i>Cephalophus ogilbyi</i>	1															
11	<i>Cephalophus rufilatus</i>					1	1										
11	<i>Cephalophus silvicultor</i>	1	1	1	1	1		1									
11	<i>Cephalophus zebra</i>	1															
11	<i>Sylvicapra grimmia</i>					1	1	1	1	1		1	1				
12	<i>Oryx dammah</i>									1							
12	<i>Oryx gazella</i>											1	1				1
13	<i>Hippotragus equinus</i>					1	1	1									
13	<i>Hippotragus niger</i>								1								
14	<i>Alcelaphus buselaphus</i>					1	1					1	1				
14	<i>Connochaetes taurinus</i>								1			1					
14	<i>Damaliscus lunatus</i>					1	1	1		1	1						
14	<i>Sigmoceros lichtensteini</i>								1								
15	<i>Capra nubiana</i>														1		
16	<i>Aepyceros melampus</i>								1			1	1				
16	<i>Pelea capreolus</i>												1				
17	<i>Ceratotherium simum</i>						1						1				
17	<i>Diceros bicornis</i>						1		1	1		1	1				
18	<i>Equus asinus</i>															1	
18	<i>Equus burchellii</i>								1			1	1				
18	<i>Equus grevy</i>											1				1	
18	<i>Equus zebra</i>																1
19	<i>Loxodonta africana</i>	1	1	1	1	1	1	1	1	1	1	1	1			1	
20	<i>Gorilla gorilla</i>		1														
20	<i>Homo sapiens</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

20	<i>Pan paniscus</i>			1			1									
20	<i>Pan troglodytes</i>	1	1			1										
21	<i>Allenopithecus nigroviridis</i>		1													
21	<i>Arctocebus aureus</i>		1													
21	<i>Cercocebus agilis</i>			1		1										
21	<i>Cercocebus torquatus</i>	1	1													
21	<i>Cercopithecus ascanius</i>			1		1					1					
21	<i>Cercopithecus campbelli</i>	1														
21	<i>Cercopithecus cephus</i>		1													
21	<i>Cercopithecus diana</i>	1														
21	<i>Cercopithecus dryas</i>			1												
21	<i>Cercopithecus mitis</i>					1				1				1		
21	<i>Cercopithecus mona</i>		1													
21	<i>Cercopithecus neglectus</i>			1		1					1					
21	<i>Cercopithecus nictitans</i>	1	1													
21	<i>Cercopithecus petaurista</i>	1														
21	<i>Cercopithecus wolffi</i>			1		1										
21	<i>Chlorocebus aethiops</i>						1	1	1	1	1	1	1	1	1	1
21	<i>Erythrocebus patas</i>						1	1			1					
21	<i>Lophocebus albigena</i>			1		1										
21	<i>Mandrillus leucophaeus</i>		1													
21	<i>Mandrillus sphinx</i>		1													
21	<i>Papio hamadryas</i>						1	1	1	1	1	1	1	1	1	1
22	<i>Colobus angolensis</i>			1		1			1							
22	<i>Colobus guereza</i>		1			1										
22	<i>Colobus pennanti</i>		1			1										
22	<i>Colobus polykomos</i>	1														
22	<i>Colobus satanas</i>		1													
22	<i>Procolobus badius</i>	1					1									
22	<i>Procolobus pennantii</i>			1												
22	<i>Procolobus verus</i>	1														
23	<i>Euoticus elegantulus</i>		1													
23	<i>Galago alleni</i>		1													
23	<i>Galago senegalensis</i>						1	1		1	1	1	1			
23	<i>Galagoides demidoff</i>	1	1	1		1										
23	<i>Galagoides thomasi</i>	1		1												
23	<i>Galagoides zanzibaricus</i>								1							
23	<i>Otolemur crassicaudatus</i>							1	1				1			
23	<i>Perodicticus potto</i>	1	1	1		1		1								
24	<i>Dendrohyrax arboreus</i>								1					1		
24	<i>Dendrohyrax dorsalis</i>	1	1	1		1										
24	<i>Heterohyrax brucei</i>								1				1			1
24	<i>Procavia capensis</i>						1	1			1	1	1	1		
24	<i>Manis gigantea</i>	1	1	1		1					1		1			1
24	<i>Manis temmincki</i>							1		1			1	1		
24	<i>Manis tetradactyla</i>	1	1	1		1										
24	<i>Manis tricuspis</i>	1	1	1		1				1						
24	<i>Orycteropus afer</i>			1		1	1	1	1	1	1	1	1	1		1

Appendix 3

Modern large mammal faunas used for the validation of the regression models developed for climatic inference. The faunal list of each locality has been downloaded from the project on Biological Inventories of World Protected Areas of the Information Center for the Environment (<http://www.ice.ucdavis.edu/bioinventory/bioinventory.html>). T, taxonomic categories (see Table 3).

T	Species	A		B		C		D		E		F		G		H	
		Tai	Nouabale-Ndoki	Mare aux Hippopotames	Mamili	Boucle du Baoule	Amboseli	Tassili N'Ajjer	Richtersveld								
1	<i>Phacochoerus aethiopicus</i>			1						1		1					
1	<i>Phacochoerus africanus</i>							1									
2	<i>Hylochoerus meinertzhageni</i>	1	1														
2	<i>Potamochoerus larvatus</i>							1									
2	<i>Potamochoerus porcus</i>	1	1														
3	<i>Hippopotamus amphibius</i>	1	1	1				1		1		1					
5	<i>Hyemoschus aquaticus</i>	1	1														
6	<i>Giraffa camelopardalis</i>							1		1		1					
7	<i>Syncerus caffer</i>	1	1					1				1					
7	<i>Taurotragus derbianus</i>									1							
7	<i>Taurotragus oryx</i>							1		1		1					
7	<i>Tragelaphus eurycerus</i>	1	1														
7	<i>Tragelaphus imberbis</i>												1				
7	<i>Tragelaphus scriptus</i>	1		1				1				1					
7	<i>Tragelaphus spekii</i>		1					1									
7	<i>Tragelaphus strepsiceros</i>							1									
8	<i>Madoqua kirkii</i>											1					
8	<i>Neotragus pygmaeus</i>	1															
8	<i>Oreotragus oreotragus</i>											1					1
8	<i>Ourebia ourebi</i>							1		1							
8	<i>Raphicerus campestris</i>							1				1					1
9	<i>Gazella dorcas</i>													1			
9	<i>Gazella granti</i>											1					
9	<i>Gazella thomsonii</i>											1					
9	<i>Litocranius walleri</i>											1					
10	<i>Kobus ellipsiprymnus</i>			1				1		1		1					
10	<i>Kobus kob</i>			1													
10	<i>Kobus leche</i>							1									
10	<i>Kobus vardonii</i>							1									
10	<i>Redunca arundinum</i>							1									
10	<i>Redunca redunca</i>											1					
11	<i>Cephalophus callipygus</i>		1														
11	<i>Cephalophus dorsalis</i>	1	1														
11	<i>Cephalophus harveyi</i>											1					
11	<i>Cephalophus jentinki</i>	1															
11	<i>Cephalophus leucogaster</i>		1														
11	<i>Cephalophus maxwellii</i>	1		1													
11	<i>Cephalophus monticola</i>	1	1														
11	<i>Cephalophus niger</i>	1															
11	<i>Cephalophus nigrifrons</i>		1														
11	<i>Cephalophus ogilbyi</i>	1															
11	<i>Cephalophus rufilatus</i>			1													
11	<i>Cephalophus silvicultor</i>	1	1	1													
11	<i>Cephalophus zebra</i>	1															
11	<i>Sylvicapra grimmia</i>			1				1				1					1
12	<i>Addax nasomaculatus</i>														1		
12	<i>Oryx dammah</i>														1		
12	<i>Oryx gazella</i>							1				1					
13	<i>Hippotragus equinus</i>			1						1				1			
13	<i>Hippotragus niger</i>							1									
14	<i>Alcelaphus buselaphus</i>			1				1		1		1					
14	<i>Connochaetes taurinus</i>							1				1					
14	<i>Damaliscus lunatus</i>							1									
15	<i>Ammotragus lervia</i>														1		
16	<i>Aepyceros melampus</i>							1				1					
16	<i>Pelea capreolus</i>																1
17	<i>Ceratotherium simum</i>							1									
17	<i>Diceros bicornis</i>							1				1					
18	<i>Equus burchellii</i>							1				1					

Appendix 3 (continued)

T	Species	A		B		C		D		E		F		G		H	
		Tai	Nouabale-Ndoki	Mare aux Hippopotames	Mamili	Boucle du Baoule	Amboseli	Tassili N'Ajjer	Richtersveld								
18	<i>Equus zebra</i>																1
19	<i>Loxodonta africana</i>	1	1	1		1		1		1		1					
20	<i>Gorilla gorilla</i>		1														
20	<i>Homo sapiens</i>	1	1	1		1		1		1		1		1			1
20	<i>Pan troglodytes</i>	1	1														
21	<i>Allenopithecus nigroviridis</i>		1														
21	<i>Arctocebus aureus</i>		1														
21	<i>Cercocebus agilis</i>		1														
21	<i>Cercocebus torquatus</i>	1															
21	<i>Cercopithecus cephus</i>		1														
21	<i>Cercopithecus diana</i>	1															
21	<i>Cercopithecus mitis</i>										1						
21	<i>Cercopithecus mona</i>	1															
21	<i>Cercopithecus neglectus</i>	1	1														
21	<i>Cercopithecus nictitans</i>	1	1														
21	<i>Cercopithecus petaurista</i>	1															
21	<i>Cercopithecus pogonias</i>		1														
21	<i>Chlorocebus aethiops</i>			1		1		1		1		1					1
21	<i>Erythrocebus patas</i>			1				1		1							
21	<i>Lophocebus albigena</i>		1														
21	<i>Papio hamadryas</i>					1					1						1
22	<i>Colobus guereza</i>		1														
22	<i>Colobus polykomos</i>	1															
22	<i>Procolobus pennantii</i>		1														
23	<i>Galago moholi</i>					1											
23	<i>Galago senegalensis</i>										1						
23	<i>Galagoides demidoff</i>	1	1														
23	<i>Perodicticus potto</i>	1	1														
24	<i>Dendrohyrax arboreus</i>	1									1						
24	<i>Dendrohyrax dorsalis</i>		1														
24	<i>Heterohyrax brucei</i>										1						
24	<i>Procavia capensis</i>											1					1
24	<i>Manis gigantea</i>	1	1														
24	<i>Manis temminckii</i>							1									
24	<i>Manis tetradactyla</i>	1	1														
24	<i>Manis tricuspis</i>	1	1														
24	<i>Orycteropus afer</i>		1			1		1			1						

Appendix 4

Results of the PCA including both modern and fossil mammalian assemblages (PCA A). The component matrix shows the correlations between every variable and each of the PCA factors.

	PCA A factor						
	1	2	3	4	5	6	7
Eigenvalue	5.749	4.715	2.425	1.969	1.547	1.269	1.146
% of total variance explained	24.0	19.6	10.1	8.2	6.4	5.3	4.8
Cumulative %	24.0	43.6	53.7	61.9	68.4	73.6	78.4
Variable	Component matrix						
% Phacochoerini	0.552	0.059	-0.006	0.358	-0.162	0.383	0.211
% Potamochoerini	0.059	0.531	-0.273	-0.178	-0.155	0.290	-0.034
% Hippopotamidae	0.561	0.360	-0.094	0.411	-0.103	0.158	-0.113
% Camelidae	-0.316	-0.762	-0.505	0.043	0.016	-0.124	-0.095
% Tragulidae	-0.701	0.488	-0.090	0.033	-0.183	0.259	-0.107
% Giraffidae	0.573	0.166	-0.192	-0.458	-0.318	-0.136	0.131
% Bovinae	0.122	0.711	0.019	0.139	0.114	-0.483	0.183
% Neotragini	-0.234	-0.267	0.881	0.029	0.102	-0.035	0.091
% Antilopini	-0.061	-0.683	0.107	0.131	-0.400	-0.266	-0.412
% Reduncinae	0.671	0.181	-0.172	-0.041	-0.149	-0.253	0.325

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Appendix 4 (continued)

Variable	Component matrix						
% Cephalophinae	-0.686	0.569	0.007	0.293	-0.038	0.040	0.028
% Orygini	-0.051	-0.333	0.729	-0.049	-0.205	0.132	0.358
% Hippotragini	0.337	0.185	0.071	0.579	0.447	-0.012	-0.147
% Alcelaphinae	0.685	0.093	-0.003	0.535	0.032	-0.009	-0.038
% Caprinae	-0.146	-0.449	-0.448	0.016	0.439	0.304	0.464
% Other Bovidae	0.694	0.122	-0.049	-0.383	0.051	-0.056	0.173
% Rhinocerotidae	0.641	0.106	0.089	-0.178	0.291	0.126	-0.134
% Equidae	0.513	-0.309	0.464	-0.110	-0.136	0.435	-0.191
% Proboscidea	0.407	0.213	0.009	-0.460	0.419	-0.024	-0.505
% Hominoidea	-0.374	-0.751	-0.399	0.058	-0.174	0.027	0.021
% Cercopithecinae	-0.427	0.671	0.187	-0.273	-0.229	-0.143	0.063
% Colobinae	-0.338	0.489	-0.181	-0.227	-0.129	0.443	-0.104
% Other Primates	-0.685	0.519	0.070	0.256	0.033	-0.074	-0.047
% Other large non-carnivorans	-0.614	-0.090	0.175	-0.285	0.572	0.020	0.095

Appendix 5

Results of the PCA including only modern mammalian assemblages (PCA B). The component matrix shows the correlations between every variable and each of the PCA factors.

Variable	PCA B factor					
	1	2	3	4	5	6
Eigenvalue	7.576	5.905	2.981	2.189	1.819	1.292
% of total variance explained	31.6	24.6	12.4	9.1	7.6	5.4
Cumulative %	31.6	56.2	68.6	77.7	85.3	90.7
Variable	Component matrix					
% Phacochoerini	0.378	0.789	-0.208	0.252	-0.041	0.099
% Potamochoerini	0.661	-0.618	0.017	0.231	-0.053	-0.057
% Hippopotamidae	0.787	0.141	-0.032	-0.207	0.009	0.271
% Camelidae	-0.772	-0.215	-0.550	-0.149	-0.105	0.122
% Tragulidae	0.470	-0.810	0.174	-0.020	0.044	0.194
% Giraffidae	0.256	0.493	0.129	-0.755	0.129	-0.103
% Bovinae	0.900	0.378	-0.080	-0.148	0.021	0.019
% Neotragini	-0.264	0.338	0.749	0.386	-0.062	-0.131
% Antilopini	-0.666	0.134	0.083	-0.471	-0.524	0.017
% Reduncinae	0.421	0.695	-0.346	0.356	-0.070	-0.250
% Cephalophinae	0.801	-0.502	-0.060	0.213	-0.053	-0.014
% Orygini	-0.361	0.236	0.694	0.389	-0.126	0.042
% Hippotragini	0.414	0.443	-0.440	0.319	-0.125	-0.490
% Alcelaphinae	0.398	0.806	-0.240	0.027	-0.018	-0.104
% Caprinae	-0.491	-0.203	-0.425	0.154	0.682	-0.052
% Other Bovidae	0.038	0.487	0.170	0.220	0.208	0.661
% Rhinocerotidae	0.177	0.726	-0.025	0.173	0.139	0.485
% Equidae	-0.468	0.235	0.734	0.013	0.038	-0.263
% Proboscidea	0.520	0.369	0.170	-0.710	0.130	-0.063
% Hominoidea	-0.786	-0.357	-0.420	0.041	-0.202	0.110
% Cercopithecinae	0.755	-0.316	0.412	-0.048	-0.069	-0.055
% Colobinae	0.582	-0.773	0.061	0.048	-0.026	0.045
% Other Primates	0.755	-0.433	-0.001	0.056	-0.078	-0.014
% Other large non-carnivorans	-0.182	-0.123	0.167	-0.064	0.931	-0.208

Appendix 6

Results of the PCA including only fossil mammalian assemblages (PCA C). The component matrix shows the correlations between every variable and each of the PCA factors. % Tragulidae was not included in the analysis because there are no tragulids in the Plio-Pleistocene faunas studied.

	PCA C factor							
	1	2	3	4	5	6	7	8
Eigenvalue	4.769	3.747	2.639	2.285	1.798	1.617	1.466	1.211
% of total variance explained	20.7	16.3	11.5	9.9	7.8	7.0	6.4	5.3
Cumulative %	20.7	37.0	48.5	58.4	66.3	73.3	79.7	84.9
Variable	Component matrix							
% Phacochoerini	0.581	0.136	0.363	0.164	0.146	0.254	-0.452	0.009
% Potamochoerini	-0.142	0.259	-0.483	-0.012	0.283	0.695	0.151	0.177
% Hippopotamidae	0.751	0.092	-0.365	-0.107	-0.062	-0.112	-0.233	-0.282
% Camelidae	-0.343	0.228	0.201	0.434	-0.710	0.096	0.090	-0.193
% Tragulidae	—	—	—	—	—	—	—	—
% Giraffidae	-0.335	0.423	0.402	-0.468	0.414	-0.060	0.276	-0.124
% Bovinae	-0.278	0.459	-0.387	0.469	0.324	-0.314	-0.035	-0.048
% Neotragini	0.013	-0.723	0.151	-0.036	0.031	-0.556	0.061	0.186
% Antilopini	0.743	0.057	-0.079	-0.142	0.355	-0.001	0.340	-0.299
% Reduncinae	-0.026	0.614	0.167	-0.227	-0.558	-0.251	0.237	-0.110
% Cephalophinae	0.156	-0.013	0.005	-0.613	-0.257	0.212	0.435	0.526
% Orygini	0.215	0.256	0.485	0.473	0.089	-0.073	0.267	0.446
% Hippotragini	0.524	-0.479	-0.263	0.361	0.213	-0.273	0.188	0.071
% Alcelaphinae	0.770	0.061	-0.215	-0.071	-0.101	-0.122	0.174	-0.034
% Caprinae	0.277	0.337	0.033	0.728	-0.005	0.229	0.077	0.219
% Other Bovidae	-0.388	0.530	-0.556	0.139	-0.120	-0.179	-0.016	0.086
% Rhinocerotidae	0.034	-0.617	0.133	0.105	-0.253	0.381	0.023	-0.302
% Equidae	0.707	-0.268	0.029	-0.216	-0.169	0.251	-0.315	0.137
% Proboscidea	-0.457	-0.609	-0.388	0.051	-0.310	-0.029	-0.190	0.209
% Hominoidea	0.050	0.384	0.616	-0.201	0.034	-0.263	-0.463	0.131
% Cercopitheciniae	-0.720	0.253	-0.123	-0.246	0.194	0.153	-0.259	-0.124
% Colobinae	-0.286	-0.292	0.693	0.287	0.203	0.205	0.076	-0.087
% Other Primates	-0.285	-0.402	0.149	0.123	0.013	0.041	0.402	-0.386
% Other large non-carnivorans	-0.656	-0.579	-0.067	-0.061	0.250	-0.060	-0.074	0.168

References

- Agustí, J., Rook, L., Andrews, P., 1999. The evolution of Neogene terrestrial ecosystems in Europe. In: *Hominid Evolution and Climatic Change in Europe*, vol. 1. Cambridge University Press, Cambridge.
- Alemseged, Z., 2003. An integrated approach to taphonomy and faunal change in the Shungura Formation (Ethiopia) and its implication for hominid evolution. *J. Hum. Evol.* 44, 451–478.
- Andrews, P.J., 1989. Paleoeology of Laetoli. *J. Hum. Evol.* 18, 173–181.
- Andrews, P., 1995. Mammals as palaeoecological indicators. *Acta Zool. Cracov.* 38, 59–72.
- Andrews, P., 1996. Palaeoecology and hominoid palaeoenvironments. *Biol. Rev.* 71, 257–300.
- Andrews, P., Lord, J.M., Evans, E.M.N., 1979. Patterns of ecological diversity in fossil and modern mammalian faunas. *Biol. J. Linn. Soc.* 11, 177–205.
- Artemiou, C., 1984. Mammalian community palaeoecology: a review of recent methods with special reference to Miocene mammalian faunas of Europe. *Paléobiologie Continentale* 14, 91–109.
- Avery, D.M., 1992. The environment of early modern humans at Border Cave, South Africa: micromammalian evidence. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 91, 71–87.
- Avery, D.M., 1995. Southern savannas and Pleistocene hominid adaptations: the micromammalian perspective. In: Vrba, E.S., Denton, G.H., Partridge, T.C., Burckle, L.H. (Eds.), *Paleoclimate and Evolution: with Emphasis on Human Origins*. Yale University Press, New Haven, pp. 459–478.
- Avery, D.M., 2001. The Plio-Pleistocene vegetation and climate of Sterkfontein and Swartkrans, South Africa, based on micromammals. *J. Hum. Evol.* 41, 113–132.
- Behrensmeyer, A.K., 1991. Terrestrial vertebrate accumulations. In: Allison, P.A., Briggs, D.E.G. (Eds.), *Taphonomy: Releasing the Data Locked in the Fossil Record*. Plenum Press, New York, pp. 291–335.
- Behrensmeyer, A.K., Todd, N.E., Potts, R., McBrinn, G.E., 1997. Late Pliocene faunal turnover in the Turkana Basin, Kenya and Ethiopia. *Science* 278, 1589–1594.
- Black, C.G., Krishtalka, L., 1986. Rodents, bats, and insectivores from the Plio-Pleistocene sediments to the East of Lake Turkana, Kenya. *Contrib. Sci.* 372, 1–15.
- Bobe, R., 1997. Hominid environments in the Pliocene: an analysis of fossil mammals from the lower Omo valley, Ethiopia. Ph.D. Dissertation, University of Washington, Seattle.
- Bobe, R., Behrensmeyer, A.K., 2004. The expansion of grassland ecosystems in Africa in relation to mammalian evolution and the origin of the genus *Homo*. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 207, 399–420.
- Bobe, R., Behrensmeyer, A.K., Chapman, R.E., 2002. Faunal change, environmental variability and late Pliocene hominin evolution. *J. Hum. Evol.* 42, 475–497.
- Bobe, R., Eck, G.G., 2001. Responses of African bovines to Pliocene climatic change. *Paleobiology* 27 (Suppl.), 1–47.
- de Bonis, L., Bouvrain, G., Geraads, D., Koufos, G., 1992a. Multivariate study of late Cenozoic mammalian faunal compositions and paleoecology. *Paleontologia i Evolució* 24–25, 93–101.

- de Bonis, L., Bouvrain, G., Geraads, D., Koufos, G., 1992b. Diversity and palaeoecology of Greek late Miocene mammalian faunas. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 91, 99–122.
- de Bonis, L., Bouvrain, G., Geraads, D., Koufos, G.D., Sen, S., Tassy, P., 1994. Les gisements de mammifères du Miocène supérieur de Kemiklitepe, Turquie: 11. Biochronologie, paléocologie et relations paléobiogéographiques. *Bull. Mus. Hist. Nat., Paris (4e série)* 16c, 225–240.
- de Bonis, L., Bouvrain, G., Koufos, G., 1999. Palaeoenvironments of late Miocene primate localities in Macedonia, Greece. In: Agustí, J., Rook, L., Andrews, P. (Eds.), *The Evolution of Neogene Terrestrial Ecosystems in Europe. Hominid Evolution and Climatic Change in Europe*, vol. 1. Cambridge University Press, Cambridge, pp. 413–435.
- Bonnefille, R., 1984. Cenozoic vegetation and environments of early hominids in East Africa. In: White, R.O. (Ed.), *The Evolution of the East Asian Environment*, vol. II. University of Hong Kong, Hong Kong, pp. 579–612.
- Bonnefille, R., 1995. A reassessment of the Plio-Pleistocene pollen record of East Africa. In: Vrba, E.S., Denton, G.H., Partridge, T.C., Burckle, L.H. (Eds.), *Paleoclimate and Evolution: with Emphasis on Human Origins*. Yale University Press, New Haven, pp. 299–310.
- Bonnefille, R., Dechamps, R., 1983. Data on fossil flora. In: de Heinzelin, J. (Ed.), *The Omo Group: Archives of the International Omo Research Expedition*. Musée Royal de l'Afrique Centrale, Tervuren, pp. 191–207.
- Breckle, W.H., 2002. *Walter's Vegetation of the Earth. The Ecological Systems of the Geo-Biosphere*. fourth ed., Springer-Verlag, Berlin.
- Bromage, T.G., Schrenk, F., 1999. *African Biogeography, Climate Change, and Human Evolution*. Oxford University Press, Oxford.
- Brown, F.H., 1995. The potential of the Turkana Basin for paleoclimatic reconstruction in East Africa. In: Vrba, E.S., Denton, G.H., Partridge, T.C., Burckle, L.H. (Eds.), *Paleoclimate and Evolution: with emphasis on human origins*. Yale University Press, New Haven, pp. 319–330.
- Brown, F.H., Feibel, C.S., 1991. Stratigraphy, depositional environments, and palaeogeography of the Koobi Fora formation. In: Harris, J.M. (Ed.), *The Fossil Ungulates: Geology Fossil Artiodactyls, and Palaeoenvironments*. Koobi Fora Research Project, vol. 3. Clarendon Press, Oxford, pp. 1–30.
- Brown, F.H., de Heinzelin, J., 1983. The lower Omo Basin. In: de Heinzelin, J. (Ed.), *The Omo Group: Archives of the International Omo Research Expedition*. Musée Royal de l'Afrique Centrale, Tervuren, pp. 7–24.
- Brugal, J.-P., Roche, H., Kibunjia, M., 2003. Faunes et palaeoenvironnements des principaux sites archéologiques Plio-Pléistocènes de la formation de Nachukui. *C. R. Palevol.* 2, 675–684.
- Bultot, F., Griffiths, J.F., 1972. The equatorial wet zone. In: Griffiths, J.F. (Ed.), *Climates of Africa*. World Survey of Climatology, vol. 10. Elsevier, Amsterdam, pp. 259–312.
- Burckle, L.H., 1995. Current issues in Pliocene paleoclimatology. In: Vrba, E.S., Denton, G.H., Partridge, T.C., Burckle, L.H. (Eds.), *Paleoclimate and Evolution: with Emphasis on Human Origins*. Yale University Press, New Haven, pp. 3–7.
- Butler, J.C., 1981. Effects of various transformations on the analysis of percentage data. *J. Math. Geol.* 13, 53–68.
- Cane, M.A., Molnar, P., 2001. Closing the Indonesian seaway as a precursor to east African aridification around 3–4 million years ago. *Nature* 411, 157–162.
- Cerling, T.E., 1992. Development of grasslands and savannas in East Africa during the Neogene. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 97, 241–248.
- Cerling, T.E., Bowman, J.R., O'Neil, J.R., 1988. An isotopic study of a fluvial-lacustrine sequence: the Plio-Pleistocene Koobi Fora sequence, East Africa. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 63, 335–356.
- Cerling, T.E., Hay, R.L., 1986. An isotopic study of paleosol carbonates from Olduvai Gorge. *Quatern. Res.* 25, 63–78.
- Churcher, C.S., Kleindienst, M.R., Schwarcz, H.P., 1999. Faunal remains from a Middle Pleistocene lacustrine marl in Dakhleh Oasis, Egypt: palaeoenvironmental reconstructions. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 154, 301–312.
- Cody, M.L., Mooney, H.A., 1978. Convergence versus non-convergence in mediterranean climate ecosystems. *Annu. Rev. Ecol. Syst.* 9, 265–321.
- Cooke, H.B.S., 1997. Plio-Pleistocene deposits and the Quaternary boundary in sub-Saharan Africa. In: Van Couvering, J.A. (Ed.), *The Pleistocene Boundary and the Beginning of the Quaternary*. Cambridge University Press, Cambridge, pp. 254–263.
- Coppens, Y., 1975. Evolution des Hominidés et de leur environnement au cours du Plio-Pléistocène dans la basse vallée de l'Omo en Ethiopie. *C. R. Acad. Sci. Paris Série II* 281, 1693–1696.
- Corbet, G.B., 1978. *The Mammals of the Palaearctic Region: a Taxonomic Review*. Cornell University Press, London.
- Crowder, L.B., 1980. Ecological convergence of community structure: a neutral model analysis. *Ecology* 61, 194–204.
- Daams, R., van der Meulen, A.J., Peláez-Campomanes, P., Álvarez Sierra, M.A., 1999. Trends in rodent assemblages from the Aragonian (early-middle Miocene) of the Calatayud-Daroca Basin, Aragon, Spain. In: Agustí, J., Rook, L., Andrews, P. (Eds.), *The Evolution of Neogene Terrestrial Ecosystems in Europe. Hominid Evolution and Climatic Change in Europe*, vol. 1. Cambridge University Press, Cambridge, pp. 127–139.
- van Dam, J.A., Weltje, G.J., 1999. Reconstruction of the Late Miocene climate of Spain using rodent palaeocommunity successions: an application of end-member modelling. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 151, 267–305.
- Damuth, J., 1982. Analysis of the preservation of community structure in assemblages of fossil mammals. *Paleobiology* 8, 434–446.
- deMenocal, P.B., 1995. Plio-Pleistocene African climate. *Science* 270, 53–59.
- deMenocal, P.B., Bloemendal, J., 1995. Plio-Pleistocene climatic variability in Subtropical Africa and the palaeoenvironment of hominid evolution: a combined data-model approach. In: Vrba, E.S., Denton, G.H., Partridge, T.C., Burckle, L.H. (Eds.), *Paleoclimate and Evolution: with Emphasis on Human Origins*. Yale University Press, New Haven, pp. 262–288.
- Denys, C., 1999. Of mice and men: evolution in East and South Africa during Plio-Pleistocene times. In: Bromage, T.G., Schrenk, F. (Eds.), *African Biogeography, Climate Change, and Human Evolution*. Oxford University Press, Oxford, pp. 226–252.
- Dood, J.R., Stanton, R.J., 1981. *Paleoecology, Concepts and Applications*. John Wiley and Sons, New York.
- Dorst, J., Dandelot, P., 1973. *A Field Guide to the Larger Mammals of Africa*. Collins, London.
- Dupont, L.M., Leroy, S.A.G., 1995. Steps toward drier climatic conditions in Northwestern Africa during the Upper Pliocene. In: Vrba, E.S., Denton, G.H., Partridge, T.C., Burckle, L.H. (Eds.), *Paleoclimate and Evolution: with Emphasis on Human Origins*. Yale University Press, New Haven, pp. 289–298.
- Estienne, P., Godard, A., 1970. *Climatologie*. Librairie Armand Colin, Paris.
- Feibel, C.S., 2003. Stratigraphy and depositional history of the Lothagam sequence. In: Leakey, M.G., Harris, J.M. (Eds.), *Lothagam: the Dawn of Humanity in Eastern Africa*. Columbia University Press, New York, pp. 17–29.
- Feibel, C.S., Harris, J.M., Brown, F.H., 1991. Palaeoenvironmental context for the late Neogene of the Turkana Basin. In: Harris, J.M. (Ed.), *The Fossil Ungulates: Geology, Fossil Artiodactyls, and Palaeoenvironments*. Koobi Fora Research Project, vol. 3. Clarendon Press, Oxford, pp. 321–370.
- Font Tullot, Y., 1955. *El clima del Sáhara (con especial referencia a la zona española)*. Consejo Superior de Investigaciones Científicas, Madrid.
- Fortelius, M., Eronen, J., Jernvall, J., Liu, L., Pushkina, D., Rinne, J., Tesakov, A., Vislobokova, I., Zhang, Z., Zhou, L., 2002. Fossil mammals resolve regional patterns of Eurasian climate change over 20 million years. *Evol. Ecol. Res.* 4, 1005–1016.
- Grayson, D.K., 1984. *Quantitative Zooarchaeology*. Academic Press, Orlando.
- Greenacre, M.J., Vrba, E.S., 1984. Graphical display and interpretation of antelope census data in African wildlife areas, using correspondence analysis. *Ecology* 65, 984–997.
- Griffiths, J.F., 1972a. Semi-arid zones. In: Griffiths, J.F. (Ed.), *Climates of Africa*. World Survey of Climatology, vol. 10. Elsevier, Amsterdam, pp. 193–220.
- Griffiths, J.F., 1972b. Eastern Africa. In: Griffiths, J.F. (Ed.), *Climates of Africa*. World Survey of Climatology, vol. 10. Elsevier, Amsterdam, pp. 313–348.
- Haesaerts, P., Stoops, G., Vliet-Lanoë, 1983. Data on sediments and fossil soils. In: de Heinzelin, J. (Ed.), *The Omo Group: Archives of the*

- International Omo Research Expedition. Musée Royal de l'Afrique Centrale, Tervuren, pp. 25–127.
- Harris, J.M., Brown, F.H., Leakey, M.G., 1988. Stratigraphy and paleontology of Pliocene and Pleistocene localities west of Lake Turkana, Kenya. *Contrib. Sci.* 399, 1–128.
- Hay, W.W., DeConto, R.M., Wold, C.N., 1997. Climate: is the past the key to the future? *Geol. Rundsch.* 86, 471–491.
- de Heinzelin, J., Haesaerts, P., 1983a. The Shungura formation. In: de Heinzelin, J. (Ed.), *The Omo Group: Archives of the International Omo Research Expedition*. Musée Royal de l'Afrique Centrale, Tervuren, pp. 25–127.
- de Heinzelin, J., Haesaerts, P., 1983b. The Usno formation. In: de Heinzelin, J. (Ed.), *The Omo Group: Archives of the International Omo Research Expedition*. Musée Royal de l'Afrique Centrale, Tervuren, pp. 129–139.
- de Heinzelin, J., Haesaerts, P., Howell, F.C., 1976. Plio-Pleistocene formations of the lower Omo basin with particular reference to the Shungura Formation. In: Coppens, Y., Howell, F.C., Isaac, G.L., Leakey, R.E.F. (Eds.), *Earliest Man and Environments in the Lake Rudolf Basin: Stratigraphy, Palaeoecology and Evolution*. University of Chicago Press, Chicago, pp. 29–49.
- Hernández Fernández, M., 2001. Bioclimatic discriminant capacity of terrestrial mammal faunas. *Glob. Ecol. Biogeogr.* 10, 189–204.
- Hernández Fernández, M., 2005. Análisis paleoecológico y paleoclimático de las sucesiones de mamíferos del Plio-Pleistoceno ibérico. Editorial Complutense, Madrid.
- Hernández Fernández, M., Azanza, B., Álvarez Sierra, M.A., 2004. Iberian Plio-Pleistocene biochronology: micromammalian evidence for MNs and ELMAs calibration in southwestern Europe. *J. Quatern. Sci.* 19, 605–616.
- Hernández Fernández, M., Alberdi, M., Azanza, B., Montoya, P., Morales, J., Nieto, M., Peláez-Campomanes, P. Identification problems of arid environments in the Neogene-Quaternary mammal record of Spain. *J. Arid Environ.*, in press.
- Hernández Fernández, M., Peláez-Campomanes, P., 2003. The bioclimatic model: a method of palaeoclimatic qualitative inference based on mammal associations. *Glob. Ecol. Biogeogr.* 12, 507–517.
- Hernández Fernández, M., Peláez-Campomanes, P., 2005. Quantitative palaeoclimatic inference based on mammal faunas. *Glob. Ecol. Biogeogr.* 14, 39–56.
- Hernández Fernández, M., Salesa, M.J., Sánchez, I.M., Morales, J., 2003. Paleología del género *Anchitherium* von Meyer, 1834 (Equidae, Perissodactyla, Mammalia) en España: evidencias a partir de las faunas de macromamíferos. In: López-Martínez, N., Peláez-Campomanes, P., Hernández Fernández, M. (Eds.), *En torno a fósiles de mamíferos: datación, evolución y paleoambiente*. Editorial Complutense, Madrid, pp. 253–280.
- Hernández Fernández, M., Vrba, E.S., 2005. Rapoport effect and biomic specialization in African mammals: revisiting the climatic variability hypothesis. *J. Biogeogr.* 32, 903–918.
- Hill, A., 1995. Faunal and environmental change in the Neogene of East Africa: evidence from the Tugen Hills sequence, Baringo District, Kenya. In: Vrba, E.S., Denton, G.H., Partridge, T.C., Burckle, L.H. (Eds.), *Paleoclimate and Evolution: with Emphasis on Human Origins*. Yale University Press, New Haven, pp. 178–193.
- Hokr, Z., 1951. Methoda kvantitativního stanovení klimatuve čtvrtohorach podle ssavčích společenstv. *Vestník Ústředního Ústavu Geologického* 18, 209–219.
- IPCC, 2001. *Climate Change 2001: The Scientific Basis*. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge.
- Jackson, D.A., 1997. Compositional data in community ecology: the paradigm or peril of proportions? *Ecology* 78, 929–940.
- Jeannot, M., Cartonnet, M., 2000. La microfaune de la Chênélaz (Hostias, Ain). L'environnement et son influence sur la biométrie dentaire chez *Arvicola terrestris* (Rodentia, Mammalia). *Revue de Paléobiologie* 19, 475–492.
- Kappelman, J., 1984. Plio-Pleistocene environments of Bed-I and lower Bed-II, Olduvai Gorge, Tanzania. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 48, 171–196.
- Kay, R.F., Madden, R.H., 1997. Mammals and rainfall: paleoecology of the middle Miocene at La Venta (Colombia, South America). *J. Hum. Evol.* 32, 166–199.
- Leakey, M.G., Feibel, C.S., McDougall, I., Walker, A., 1995. New four-million-years-old hominid species from Kanapoi and Allia Bay, Kenya. *Nature* 376, 565–571.
- Kingdon, J., 1971. In: *East African Mammals. An Atlas of Evolution in Africa*, vol. I. Academic Press, London.
- Kingdon, J., 1979. In: *East African Mammals. An Atlas of Evolution in Africa*, Part B (Large Mammals), vol. III. Academic Press, London.
- Kingdon, J., 1982a. In: *East African Mammals. An Atlas of Evolution in Africa*, Part C (Bovids), vol. III. Academic Press, London.
- Kingdon, J., 1982b. In: *East African Mammals. An Atlas of Evolution in Africa*, Part D (Bovids), vol. III. Academic Press, London.
- Kingdon, J., 1997. *The Kingdon Field Guide to African Mammals*. Academic Press, London.
- Köhler-Rollefson, I.U., 1991. *Camelus dromedarius*. *Mammalian Species* 375, 1–8.
- Kovarovic, K., Andrews, P., Aiello, L., 2002. The palaeoecology of the Upper Ndolanya Beds at Laetoli, Tanzania. *J. Hum. Evol.* 43, 395–418.
- Leakey, M.G., Harris, J.M., 2003. Lothagam: its significance and contributions. In: Leakey, M.G., Harris, J.M. (Eds.), *Lothagam: the Dawn of Humanity in Eastern Africa*. Columbia University Press, New York, pp. 625–660.
- Leakey, M.G., Spoor, F., Brown, F.H., Gathogo, P.N., Kiarie, C., Leakey, L.N., McDougall, I., 2001. New hominin genus from eastern Africa shows diverse middle Pliocene lineages. *Nature* 410, 433–440.
- Legendre, S., 1986. Análisis de mammalian communities from the Late Eocene and Oligocene of Southern France. *Palaeovertebrata* 16, 191–212.
- Leroux, M., 2001. *The Meteorology and Climate of Tropical Africa*. Springer, Berlin.
- Maas, M.C., 1994. Paleocology in primate evolution. *Evol. Anthropol.* 3, 6–8.
- McDougall, I., Feibel, C.S., 2003. Numerical age control for the Miocene-Pliocene succession at Lothagam, a hominoid-bearing sequence in the Northern Kenya Rift. In: Leakey, M.G., Harris, J.M. (Eds.), *Lothagam: the Dawn of Humanity in Eastern Africa*. Columbia University Press, New York, pp. 43–64.
- Mendoza, M., Goodwin, B., Criado, C., 2004. Emergence of community structure in terrestrial mammal-dominated ecosystems. *J. Theoret. Biol.* 230, 203–214.
- Meteorological Office, 1967. *Tables of Temperature, Relative Humidity, Precipitation and Sunshine for the World. Part IV. Africa, the Atlantic Ocean South of 35° N and the Indian Ocean*. Her Majesty's Stationery Office, London.
- Meteorological Office, 1983. *Tables of Temperature, Relative Humidity, Precipitation and Sunshine for the World. Part IV. Africa, the Atlantic Ocean South of 35° N and the Indian Ocean*. Her Majesty's Stationery Office, London.
- van der Meulen, A.J., Daams, R., 1992. Evolution of Early-Middle Miocene rodent faunas in relation to long-term palaeoenvironmental changes. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 93, 227–253.
- Mix, A.C., Le, J., Shackleton, N.J., 1995. Benthic foraminiferal stable isotope stratigraphy of site 846: 0–1.8 ma. *Proc. Ocean Drilling Program Sci. Results* 138, 839–854.
- Montuire, S., Michaux, J., Legendre, S., Aguilar, J.-P., 1997. Rodents and climate. 1. A model for estimating past temperatures using arvicolid (Mammalia: Rodentia). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 128, 373–379.
- Nieto, M., Rodríguez, J., 2003. Inferencia paleoecológica en mamíferos cenozoicos: limitaciones metodológicas. In: López-Martínez, N., Peláez-Campomanes, P., Hernández Fernández, M. (Eds.), *En torno a fósiles de mamíferos: datación, evolución y paleoambiente*. Editorial Complutense, Madrid, pp. 459–474.
- Nowak, R.M., 1991. In: *Walker's Mammals of the World*, vols. I–II. Johns Hopkins University Press, Baltimore.
- Odum, E.P., 1971. *Fundamentals of Ecology*. Saunders Company, Philadelphia.
- Partridge, T.C., Wood, B.A., deMenocal, P.B., 1995. The influence of global climate change and regional uplift on large-mammalian evolution in East

- and Southern Africa. In: Vrba, E.S., Denton, G.H., Partridge, T.C., Burckle, L.H. (Eds.), *Paleoclimate and Evolution: with Emphasis on Human Origins*. Yale University Press, New Haven, pp. 331–355.
- Peters, J., 1998. Camelus thomasi Pomel, 1893, a possible ancestor of the one-humped camel? *Z. Säugetierkd. Int. J. Mammal. Biol.* 63, 372–376.
- Porter, W.P., Budaraju, S., Stewart, W.E., Ramankutty, N., 2000. Calculating climate effects on birds and mammals: impacts on biodiversity, conservation, population parameters, and global community structure. *Am. Zool.* 40, 597–630.
- Potts, R., 1998. Environmental hypotheses of human evolution. *Yearb. Phys. Anthropol.* 41, 93–136.
- Reed, K.E., 1997. Early hominid evolution and ecological change through the African Plio-Pleistocene. *J. Hum. Evol.* 32, 289–322.
- Reed, K.E., 1998. Using large mammal communities to examine ecological and taxonomic structure and predict vegetation in extinct assemblages. *Paleobiology* 24, 384–408.
- Rodríguez, J., 2004. Stability in Pleistocene Mediterranean mammalian communities. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 207, 1–22.
- Rodríguez, J., Alberdi, M.T., Azanza, B., Prado, J.L., 2004. Body size structure in north-western Mediterranean Plio-Pleistocene mammalian faunas. *Glob. Ecol. Biogeogr.* 13, 163–176.
- Samuels, C.L., Drake, J.A., 1997. Divergent perspectives on community convergence. *Trends Ecol. Evol.* 12, 427–432.
- Schulze, B.R., 1972. South Africa. In: Griffiths, J.F. (Ed.), *Climates of Africa. World Survey of Climatology*, vol. 10. Elsevier, Amsterdam, pp. 501–586.
- Sen, S., Bouvrain, G., Geraads, D., 1998. Pliocene vertebrate locality of Çalta, Ankara, Turkey. 12. *Paleoecology, biogeography and biochronology. Geodiversitas* 20, 497–510.
- Shackleton, N.J., 1995. New data on the evolution of Pliocene climatic variability. In: Vrba, E.S., Denton, G.H., Partridge, T.C., Burckle, L.H. (Eds.), *Paleoclimate and Evolution: with Emphasis on Human Origins*. Yale University Press, New Haven, pp. 242–248.
- Shackleton, N.J., Hall, M.A., Pate, D., 1995. Pliocene stable isotope stratigraphy of site 846. *Proc. Ocean Drilling Program, Sci. Results* 138, 337–355.
- Shepherd, U.L., 1998. A comparison of species diversity and morphological diversity across the North American latitudinal gradient. *J. Biogeogr.* 25, 19–29.
- Shipman, P., Harris, J., 1988. Habitat preference and palaeoecology of *Australopithecus boisei* in Eastern Africa. In: Grine, F.E. (Ed.), *Evolutionary History of the “Robust” Australopithecines*. Aldine Publishing Company, New York, pp. 343–381.
- Simmons, I.G., 1979. *Biogeography. Natural and Cultural*. Edward Arnold Publishers Ltd., London.
- Soligo, C., 2002. Primatology, Paleoecology, and a new method for assessing taphonomic bias in fossil assemblages. *Evol. Anthropol. Suppl.* 1, 24–27.
- Suwa, G., Nakaya, H., Asfaw, B., Saegusa, H., Amzaye, A., Kono, R.T., Beyene, Y., Katoh, S., 2003. Plio-Pleistocene terrestrial mammal assemblage from Konso, southern Ethiopia. *J. Vertebr. Paleontol.* 23, 901–916.
- Thackeray, J.F., 1987. Late Quaternary environmental changes inferred from small mammalian fauna, southern Africa. *Climatic Change* 10, 285–305.
- Tiedemann, R., Sarnthein, M., Shackleton, N.J., 1994. Astronomic timescale for the Pliocene Atlantic $\delta^{18}\text{O}$ and dust flux records of Ocean Drilling Program site 659. *Paleoceanography* 9, 619–638.
- Turner, A., Bishop, L.C., Denys, C., McKee, J.K., 1999. A locality-based listing of African Plio-Pleistocene mammals. In: Bromage, T.G., Schrenk, F. (Eds.), *African Biogeography, Climate Change, and Human Evolution*. Oxford University Press, Oxford, pp. 369–399.
- Vrba, E.S., 1974. Chronological and ecological implications of the fossil Bovidae at the Sterkfontein australopithecine site. *Nature* 250, 19–23.
- Vrba, E.S., 1975. Some evidence of chronology and palaeoecology of Sterkfontein, Swartkrans, and Krom-draai from the fossil Bovidae. *Nature* 254, 301–304.
- Vrba, E.S., 1985a. Environment and evolution: alternative causes of the temporal distribution of evolutionary events. *S. Afr. J. Sci.* 81 (5), 229–236.
- Vrba, E.S., 1985b. African Bovidae: Evolutionary events since the Miocene. *S. Afr. J. Sci.* 81, 263–266.
- Vrba, E.S., 1985c. Paleoecology of early hominidae, with special reference to Sterkfontein, Swartkrans and Kromdraai. In: Beden, M., Gèze, R., Guérin, C., Harris, J., Koeniguer, J., Letouzey, F., Petter, G., Vincens, A., Vrba, E. (Eds.), *L’environnement des hominidés au Pliocène*. Masson, Paris, pp. 345–369.
- Vrba, E.S., 1988. Late Pliocene climatic events and hominid evolution. In: Grine, F.E. (Ed.), *The Evolutionary History of the “Robust” Australopithecines*. Aldine Publishing Company, New York, pp. 405–426.
- Vrba, E.S., 2000. Major features of Neogene Mammalian Evolution in Africa. In: Partridge, T.C., Maud, R. (Eds.), *Cenozoic Geology of Southern Africa*. Oxford University Press, Oxford, pp. 277–304.
- Vrba, E.S., 2005. Mass turnover and heterochrony events in response to physical change. *Paleobiology* 31 (2), 157–174.
- Vrba, E.S. Role of Environmental Stimuli in Hominid Origins. In: Henke, W., Rothe, H., Tattersall, I. (Eds.), *Handbook of Palaeoanthropology*, vol. 3. Phylogeny of Hominines. Springer-Verlag, New York, in press.
- Vrba, E.S., Denton, G.H., Partridge, T.C., Burckle, L.H., 1995. *Paleoclimate and Evolution: with Emphasis on Human Origins*. Yale University Press, New Haven.
- Walter, H., 1970. *Vegetationszonen und Klima*. Eugen Ulmer, Stuttgart.
- van de Weerd, A., Daams, R., 1978. Quantitative composition of rodent faunas in the Spanish Neogene and paleoecological implications. *Proceedings of the Koninklijke Nederlandse Akademie Van Wetenschappen Series B* 81, 448–473.
- Wesselman, H.B., 1984. The Omo micromammals. *Contrib. Vertebr. Evol.* 7, 1–219.
- Wesselman, H.B., 1995. Of mice and almost-men: regional paleoecology and human evolution in the Turkana Basin. In: Vrba, E.S., Denton, G.H., Partridge, T.C., Burckle, L.H. (Eds.), *Paleoclimate and Evolution: with Emphasis on Human Origins*. Yale University Press, New Haven, pp. 356–368.
- White, T., 2003. Early hominids – Diversity or distortion? *Science* 299, 1994–1997.
- Williams, S.E., Marsh, H., 1998. Changes in small mammal assemblage structure across a rain forest/open forest ecotone. *J. Trop. Ecol.* 14, 187–198.
- Wilson, D.E., Reeder, D.M., 1993. *Mammal Species of the World: a Taxonomic and Geographic Reference*. Smithsonian Institution Press, Washington.
- Wolde Gabriel, G., White, T.D., Suwa, G., Renne, P., de Heinzelin, J., Hart, W.K., Heiken, G., 1994. Ecological and temporal placement of early Pliocene hominids at Aramis, Ethiopia. *Nature* 371, 330–333.
- Wynn, J.G., 2000. Paleosols, stable carbon isotopes, and paleoenvironmental interpretation of Kanapoi, Northern Kenya. *J. Hum. Evol.* 39, 411–432.
- Yemane, K., Bonnefille, R., Faure, H., 1985. Paleoclimatic and tectonic implications of Neogene microflora from the north-western Ethiopian Highlands. *Nature* 318, 653–656.