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The expansion of grassland ecosystems in Africa in relation to mammalian evolution and the origin of the genus *Homo*

René Bobe*, Anna K. Behrensmeyer

Department of Paleobiology, Smithsonian Institution, PO Box 37012, NHB MRC 121, Washington, DC 20013-7012, USA

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Abstract

The relationship between climatic change and human evolution can be framed in terms of three major hypotheses. A modern version of the long-held savanna hypothesis posits that the expansion of grassland ecosystems in Africa was driven by global climatic change and led to the divergence of hominins from the apes and to the origin of the *Homo* clade. A related idea suggests that hominins originated in the late Miocene, and *Homo* in the late Pliocene, as constituents of broader pulses of faunal turnover synchronized by episodes of global climatic change. A more recent concept, the variability selection hypothesis, emphasizes the importance of fluctuating climates and environments, rather than any single trend, in shaping human adaptation and evolution. Here we evaluate these ideas for the Plio-Pleistocene in light of new analyses of fossil mammals from the Turkana Basin of Kenya and Ethiopia. Our results show that between 4 and 1 Ma (million years ago), there were profound faunal changes in the Turkana Basin. The most important of these changes include significant shifts in the abundance of the common families of mammals, episodes of high faunal turnover, and an increase in the number and abundance of species that show adaptations to grassland ecosystems. Episodes of relatively high faunal turnover occurred in the intervals 3.4–3.2, 2.8–2.6, 2.4–2.2, and 2.0–1.8 Ma. *Paranthropus* and *Homo* appear in the Turkana Basin during successive intervals of high turnover at 2.8–2.6 and at 2.4–2.2 Ma, while the appearance of *Homo erectus* is coupled to a major episode of turnover and grassland expansion after 2 Ma. Thus, there was not a single turnover pulse of relevance to late Pliocene hominins, but multiple events that successively led to the appearance of *Paranthropus*, early *Homo*, and *H. erectus*. Our results also show evidence of large-scale, 100 ky-periodicity shifts in the fauna beginning at 2.5 Ma, during the time that *Homo* and lithic artifacts first appear in the Turkana Basin, lending support to the variability selection hypothesis [Science 273 (1996) 922; Potts R., 1996b. *Humanity's Descent: The Consequences of Ecological Instability*. Avon Books, New York.] during the latest Pliocene. The savanna hypothesis may not explain the divergence of hominins from other apes, but it could be correct in stressing the importance of grasslands to the early evolution of *Homo*. The fundamental importance of grasslands may lie in the complexity and heterogeneity they added to the range of habitats available to the early species of the genus *Homo*. The turnover pulse hypothesis [Vrba, E.S., 1988. Late Pliocene climatic events and hominid evolution. In: Grine, F.E. (Ed.). *Evolutionary History of the "Robust" Australopithecines*. Aldine, New York, pp. 405–426; Vrba, E.S., 1995. The fossil record of African antelopes (Mammalia, Bovidae) in relation to human evolution and paleoclimate. In: Vrba, E.S., Denton, G.H., Partridge, T.C., Burckle, L.H. (Eds.). *Paleoclimate and Evolution, with Emphasis on Human Origins*. Yale Univ. Press, New Haven, pp. 385–424.] may be correct in linking critical events in human evolution to broader pulses of faunal change ultimately driven by climate, but our

* Corresponding author.

E-mail addresses: bobe.rene@nmnh.si.edu (R. Bobe), behrensmeyer.kay@nmnh.si.edu (A.K. Behrensmeyer).

results show that any such link is complex, with at least four rather than one pulse of change during the Pliocene and early Pleistocene of the Turkana Basin.

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1. Introduction

The expansion of grasslands in Africa has been linked to several key events in human evolution. A broad set of ideas, generally referred to as the savanna hypothesis, indicates that humans emerged as a consequence of the spread of savanna grasslands in Africa. According to this long-held hypothesis, adaptation to the open savanna led to the divergence of humans from our nearest living relatives, the apes, who remained tied to the dense forests of central Africa (e.g., Dart, 1925; Robinson, 1954; Jolly, 1970; Klein and Edgar, 2002). In Dart's (1925) words, it was the "vast open country with occasional wooded belts and a relative scarcity of water, together with a fierce and bitter mammalian competition" that provided the ecological context for the divergence of humans from the apes. Variations on this theme abound in anthropology textbooks (e.g., Boyd and Silk, 1997). However, in the last decade or so, new evidence and interpretations show that early hominins may have inhabited rather closed, forested environments (Andrews, 1989, 1995; Rayner et al., 1993; WoldeGabriel et al., 1994; Clarke and Tobias, 1995; Berger and Tobias, 1996). This evidence also suggests that although grasslands may have been present in Africa since earlier times, they did not become a prominent element of the landscape until the late Pliocene or early Pleistocene.

An idea related to the savanna hypothesis posits that the expansion of savanna grasslands is tied not only to important events in human evolution, but also to major pulses of faunal turnover in many mammal taxa over wide geographical scales. This idea, postulated by Vrba (1985, 1988, 1995) links global climatic change to faunal turnover and the emergence of the hominin genera *Homo* and *Paranthropus*. There is much evidence that supports the hypothesis of broad climatic changes in the late Pliocene (e.g., Shackleton et al., 1984; Kennett, 1995), with these changes expressed by increasing aridity in Africa (e.g.,

Burckle, 1995; deMenocal, 1995; Dupont and Leroy, 1995). The emergence of the genus *Homo* in the Pliocene of East Africa does appear to be broadly correlated in time with the advent of major global and regional climatic changes (Brain, 1981; Vrba, 1985, 1988; Stanley, 1992), but the turnover pulse hypothesis in relation to human evolution remains controversial (Hill, 1987; Kimbel, 1995; White, 1995; Behrensmeyer et al., 1997; Feibel, 1997, 1999).

An altogether different idea about the influence of climate on human evolution posits that it was the increasing *variability* of Plio-Pleistocene climates and environments that selected for the adaptations that characterize the hominin clade. This increasing variability, rather than the trend toward more open (i.e., grassland) and arid conditions in Africa, caused selection pressures that led to new coping mechanisms for hominins, including the reliance on technology and culture (Potts, 1996a,b, 1998a,b). In this study, we consider these hypotheses in light of a new analysis of fossil mammals from the northern Turkana Basin of Kenya and Ethiopia (Fig. 1). Thus, we provide new analyses of turnover, grassland-adapted taxa, and faunal variability through the Plio-Pleistocene, but first, we briefly review the evidence of grassland expansion in East Africa.

What is the evidence for the earliest savanna grasslands in East Africa? Here we use the term grassland, or savanna grassland, for tropical ecosystems dominated by C₄ grasses (Sarmiento, 1984; Cerling, 1992), not edaphic, or wet grasslands characterized by waterlogged conditions. Grasslands may have been present in Africa since Miocene times, but the extent and distribution of grassland ecosystems during that epoch remain unclear. Analysis of paleosol micromorphology and fossil pollen from the Middle Miocene site of Fort Ternan in Kenya indicates that grassy areas, and perhaps more widespread grasslands, occurred in East Africa as far back as 14 Ma (Bonnefille, 1984; Retallack et al., 1990; Retallack, 1992). If so, these were probably cool growing season (C₃) grasses, because

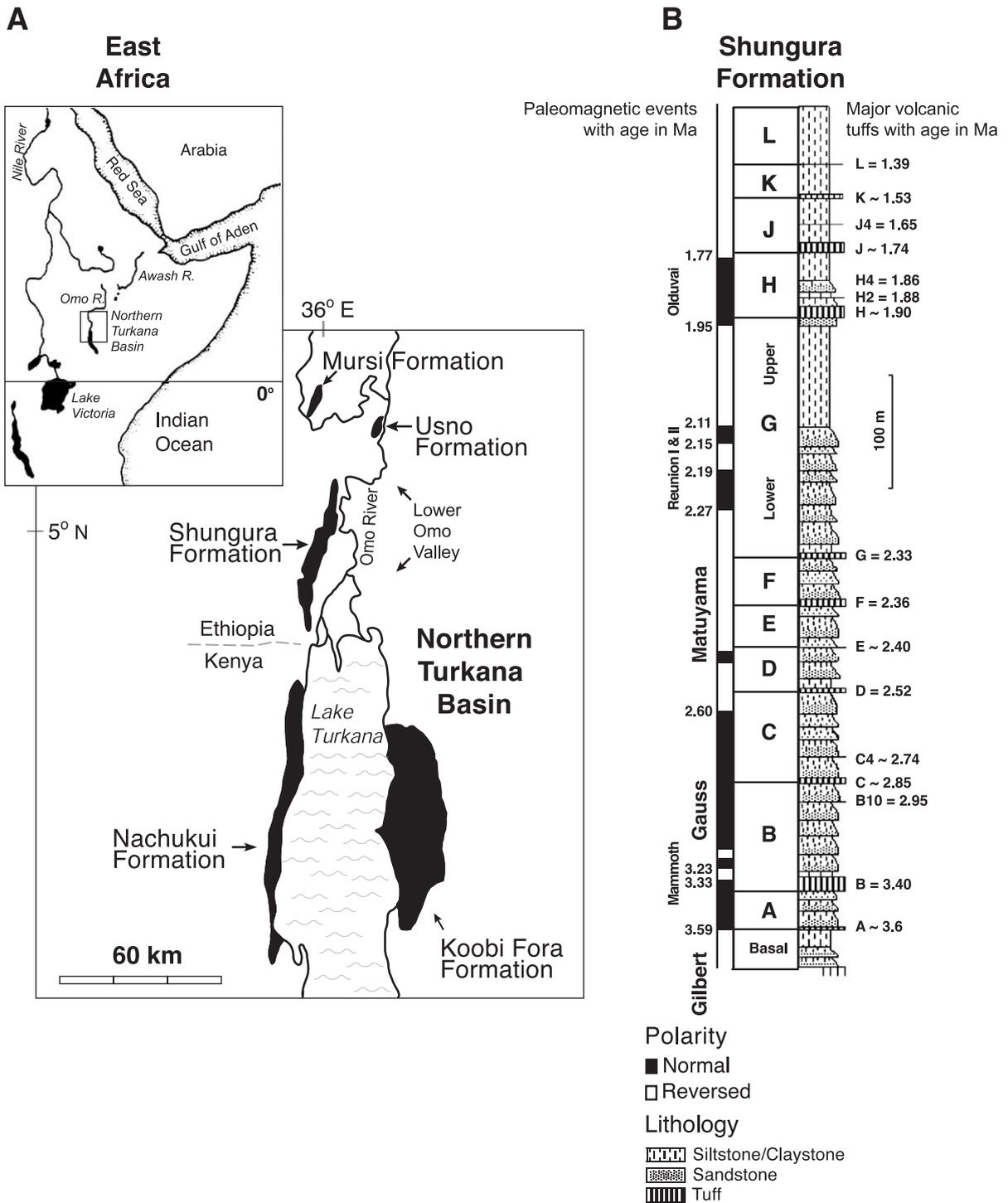


Fig. 1. (A) The Turkana Basin of northern Kenya and southern Ethiopia, including the lower Omo valley, showing the geographical distribution of the Koobi Fora, Nachukui, Shungura, Usno, and Mursi Formations, the sources for the faunal data used in this study. (B) Stratigraphic section of the Shungura Formation depicting age determinations based on radiometric dating and paleomagnetism.

paleosol and dental enamel carbon isotopes from the same locality document a dominantly C_3 ecosystem (Cerling et al., 1991). Paleosol carbonates from the Baringo Basin of Kenya show little evidence of strong trends toward C_4 -dominated ecosystems during the Miocene to Pleistocene (Kingston et al., 1994). Instead, the Baringo Basin pedogenic carbonate analyses support a view of a persistent mosaic of habitats that included grasslands and wooded or bushy vegetation. Macrobotanical remains from 12.6 Ma Ngorora Formation deposits, also in the Baringo Basin, show that tropical rainforests with West African affinities were, at least at times, an important component of East African ecosystems (Jacobs and Kabuye, 1987). Thus, it appears that C_4 grasslands existed in the East African Miocene, but the available evidence indicates that closed, wooded, bush-dominated, or forested environments with some C_3 grasslands were dominant throughout this time interval.

In the Pliocene and Pleistocene, soil carbonate evidence from the Turkana Basin indicates that the interval from 4 to 1.8 Ma was dominated by C_3 plants with some C_4 components, and that C_4 plants began to dominate the landscape at 1.8 Ma (Cerling et al., 1988). New evidence from the Gona deposits in the lower Afar Depression of Ethiopia shows a shift from woodlands and grassy woodlands in the early Pliocene to more open environments by the late Pliocene (Levin, 2002). This indicates regional variability between different parts of the East African Rift System in the extent of open grasslands by the late Pliocene. Paleosol carbonates from the Turkana and Olduvai–Laetoli (Tanzania) areas show a peak of C_4 -dominated vegetation at about 1.7 Ma, followed by lower values between 1.6 and 1.4 Ma, and another peak at about 1.2 Ma (Cerling, 1992). Thus, the paleosol carbonate record indicates that Pliocene ecosystems in East Africa were dominated by C_3 vegetation, and that the Pleistocene spread of C_4 grasslands occurred at different times in different regions.

Palynological records from the East African Pliocene are discontinuous and subject to significant taphonomic biases but provide a broad picture of environmental change in the region. Records from the Turkana Basin indicate closed and humid environments at about 4 Ma, and again at about 3.4 Ma, followed by an increase in grasslands at about 2.5 Ma (Bonnefille and Letouzey, 1976; Bonnefille and

Dechamps, 1983; Bonnefille, 1995). An analysis of nine pollen samples from Olduvai Bed I and lower Bed II (between 1.9 and 1.7 Ma) shows that there was a trend toward increasing aridity culminating at 1.77 Ma, but oscillating conditions thereafter (Bonnefille, 1995).

Against this background, we examine another line of paleoenvironmental evidence derived from the mammalian fauna of East Africa. One of the most complete records of mammalian evolution in Africa comes from the Turkana Basin of northern Kenya and southern Ethiopia (Fig. 1A). The well-dated sediments of the Omo Group deposits of this area span much of the Pliocene and early Pleistocene, and provide a unique window into environmental and faunal changes during a time when key events in human evolution were taking place (Butzer, 1976; de Heinzelin, 1983; Howell et al., 1987; Harris et al., 1988; Feibel et al., 1989; 1991; Brown and Feibel, 1991; Brown, 1994, 1995).

2. Materials and methods

Our analysis takes a multi-layered approach to faunal change in the East African Plio-Pleistocene: it ranges from a broad view of faunal turnover in the Turkana Basin to finely resolved, locality-based analysis of faunal associations in the lower Omo valley. The analysis of faunal turnover, i.e., first and last appearance data (FADs and LADs), presented here is based on the Mursi, Usno, Shungura, Koobi Fora, and Nachukui Formations, all situated in the northern Turkana Basin. Data from the Mursi, Usno, and Shungura Formations derive from the Omo Faunal Database (see below). The Koobi Fora and Nachukui Formations data derive from the Evolution of Terrestrial Ecosystems database (see Behrensmeyer et al., 1997; also <http://www.nmnh.si.edu/ete/> and <http://www.paleodb.org/>), and from a new database that aims to document all fossil occurrences from the Turkana Basin (the Turkana Basin Paleontology Database, currently being developed by the authors in collaboration with the National Museums of Kenya).

The main source of data in this study derives from the Omo Faunal Catalog, a database of fossils collected from the lower Omo valley formations during

the late 1960s and early 1970s (Fig. 1). These specimens were collected by the American contingent of the International Omo Research Expedition led by F. Clark Howell (Howell, 1968, 1978a). The Omo database contains about 18,000 specimens of fossil mammals (Table 1) taxonomically identified and described by many specialists (e.g., Cooke, 1976; Coppens and Howell, 1976; Eisenmann, 1976, 1985; Howell and Coppens, 1976; Gentry, 1985; Hooijer and Churcher, 1985; Eck et al., 1987; Suwa et al., 1996). A separate database of specimens collected by the French contingent of the Omo expeditions also exists (see Coppens, 1975; Geraads and Coppens, 1995; Alemseged, 1998), but is not considered in this study. The French Omo data is being analyzed by Zeresenay Alemseged, and in-depth comparisons between the French and American data are in progress. Preliminary analyses show that the French and American databases yield similar patterns of taxonomic relative abundance, but further work is needed to evaluate these results (Alemseged et al., 2003). We analyze relative abundance changes through time in the most common families of medium-size mammals from the lower Omo valley: Bovidae, Suidae, Equidae, Cercopithecidae, and Hominidae. We exclude micromammals (Rodentia, Lagomorpha, Chiroptera, Insectivora), very large mammals (Proboscidea, Hippopotamidae, Giraffidae, Rhinocerotidae), and the more rare medium-size mammals (Felidae, Hyaenidae). Bovids, suids,

equids, cercopithecids, and hominids combined make up about 71% of all mammals collected from the Omo (Table 2). Among these families, we focus on the taxa that provide the clearest indication of grassland habitats (Table 3). Our previous work (Bobe et al., 2002) reported changes in the abundances of bovids, suids, and primates between 4 and 2 Ma. Here we extend the total time interval from 2 Ma up to 1 Ma and also include equids, which were not analyzed previously. It is important to note that our assessment of taxonomic relative abundance is not meant to provide a reconstruction of mammalian abundances at any given time in the past. Instead, we argue that with consistent collection methods and comparable taphonomic conditions, relative taxonomic abundances can be treated as variables through time. Changes in the value of these variables through time provide the most useful information relating to environmental change. The focus on the dynamics of variables rather than environmental reconstruction has been emphasized by Potts in a different context (Potts, 1994).

Documentation of species turnover patterns depends on accurate information on true (as opposed to apparent) dates of a species' first appearance (FAD) and last appearance (LAD) in the stratigraphic record. To determine the most probable dates for first and last occurrences of mammals in the Turkana Basin, we place confidence limits on each event using a method described by Koch (1987) and Barry et al. (2002). In

Table 1

Number and relative abundance of specimens of isolated teeth, various skull parts, and postcranial elements of fossil mammals from the Mursi, Usno, and Shungura Formations, lower Omo valley, Ethiopia^a

	Omo sequence														Total
	Mursi	A	U12	B	C	D	E	F	G(L)	GU	H	J	K	L	
Age of interval midpoint															
	>4	3.5	3.3	3.0	2.65	2.45	2.4	2.35	2.2	2.0	1.85	1.7	1.45	1.2	
Isolated teeth	103	30	1648	1359	1798	608	1094	1594	2389	107	229	105	145	128	11,337
Other skull parts	25	4	164	151	469	152	295	319	1293	45	82	31	34	56	3120
Postcrania	2	6	153	412	877	135	317	439	716	192	147	0	62	90	3548
Total	130	40	1965	1922	3144	895	1706	2352	4398	344	458	136	241	274	18,005
Proportions per interval															
Isolated teeth	0.79	0.75	0.84	0.71	0.57	0.68	0.64	0.68	0.54	0.31	0.50	0.77	0.60	0.47	0.63
Other skull parts	0.19	0.10	0.08	0.08	0.15	0.17	0.17	0.14	0.29	0.13	0.18	0.23	0.14	0.20	0.17
Postcrania	0.02	0.15	0.08	0.21	0.28	0.15	0.19	0.19	0.16	0.56	0.32	0.00	0.26	0.33	0.20

^a Usno unit U12 includes Shungura B2–B3, and Shungura Member B refers to units above B3.

Table 2

Number of specimens of the most abundant families of medium-size mammals in the Omo sequence^a

	Omo sequence														Total
	Mursi	A	U12	B	C	D	E	F	G(L)	GU	H	J	K	L	
	Age of interval midpoint														
	4	3.5	3.3	3.0	2.65	2.45	2.4	2.35	2.2	2.0	1.85	1.7	1.45	1.2	
Bovidae	20	5	332	332	797	261	585	826	2362	220	296	101	91	134	6362
Suidae	64	18	541	158	219	101	214	220	448	34	49	45	60	50	2221
Equidae	1	0	15	27	31	14	17	37	80	17	11	5	18	10	283
Cercopithecidae	0	7	518	353	1157	256	330	515	614	18	13	9	12	14	3816
Hominidae	0	0	21	8	22	16	13	34	17	1	1	0	2	0	135
Total	85	30	1427	878	2226	648	1159	1632	3521	290	370	160	183	208	12,817

Mursi data from Mursi Analytic database. Mb A–L data from MammaliaMNI. U12 includes Shungura B2–B3. Mb B refers to units above B3.

^a Usno unit U12 includes Shungura B2–B3, and Shungura Member B refers to units above B3.

this method, first and last occurrence events are given a probability of occurring in a given interval depending on the abundance of any particular species through its entire time range and the total number of all mammal specimens over that range. Thus, we estimate the probability P_i that a species appeared in (or disappeared from) the Turkana Basin when it was first (or last) observed by

$$P_i = 1 - (1 - n/m)^r$$

where n is the abundance of the taxon over its range (number of specimens); m is the total number of fossils in the faunal collection over the same range, and r is the number of specimens in successive intervals adjacent to the first (or last) occurrence of the taxon under consideration. Following Barry et al.

(2002), we use a P_i value of at least 0.8 to determine the most likely interval of appearance or disappearance of the species. Here we base our analysis of turnover only on taxa whose inferred first and last occurrences have a 0.8 probability of occurring in the observed interval (observed FAD=inferred FAD, and observed LAD=inferred LAD). Thus, the analysis eliminates taxa with first or last occurrences that cannot be confidently established in terms of congruence between the observed event (actual first or last occurrence) and the inferred event. In evolving lineages, only the first and last occurrences of the lineage are counted as speciation and extinction events. Thus, in the analysis to follow, the first occurrence of *Paranthropus aethiopicus* is considered a FAD, and the last occurrence of *Paranthropus boisei* is considered a LAD, but the origin of *P. boisei*, regarded as an

Table 3

Number of specimens of mammalian taxa indicative of savanna grasslands in the Omo sequence^a

	Omo sequence														Total
	Mursi	A	U12	B	C	D	E	F	G(L)	GU	H	J	K	L	
	Age of interval at midpoint														
	4	3.5	3.3	3.0	2.65	2.45	2.4	2.35	2.2	2.0	1.85	1.7	1.45	1.2	
Alcelaphini	0	0	5	6	6	6	9	72	55	13	12	8	15	11	218
Antilopini	0	0	2	1	3	1	0	5	4	9	3	0	2	1	31
<i>Metridiochoerus</i>	0	0	3	4	13	13	16	17	63	5	3	15	9	7	168
<i>Equus</i>	0	0	0	0	0	0	0	0	23	5	3	3	9	8	51
<i>Theropithecus oswaldi</i>	0	0	0	0	0	0	2	9	10	2	7	3	1	1	35
Total	0	0	10	11	22	20	27	103	155	34	28	29	36	28	503

Mursi data from Mursi Analytic database. Mb A–L data from MammaliaMNI. U12 includes Shungura B2–B3. Mb B refers to units above B3.

Equus in F is from French database. In Mb H–L, all *Theropithecus* are assumed to be *T. oswaldi*.^a Usno unit U12 includes Shungura B2–B3, and Shungura Member B refers to units above B3.

anagenetic speciation event from *P. aethiopicus*, is not a FAD. We divide the Turkana Basin sequence into 200-ka intervals, based on radiometric and paleomagnetic calibration of strata in the different regions, and we limit the analysis to mammalian taxa that occur in the basin, regardless of their first or last occurrences elsewhere in Africa (Table 4). Table 4 excludes taxa with FADs or LADs that cannot be confidently determined based on the method outlined above.

In previous analyses (Bobe, 1997; Bobe and Eck, 2001; Bobe et al., 2002), we have used a restricted subset of the Omo database, a subset collected under rigorous procedures from localities spanning the interval from Members B to G of the Shungura Formation and contemporaneous horizons from the Usno Formation (details in Bobe and Eck, 2001). Here we use this restricted data set in the analysis of faunal associations between hominins and other mammals (Table 5), but to establish broad faunal trends, we use a less restricted data set that incorporates localities from Members H to L of the Shungura Formation and excavated specimens from other horizons in the sequence. The collection procedures used in localities from Members H to L have not been explicitly described, but we analyze the proportions of skeletal elements from these horizons against depositional environments to assess potential taphonomic and collection biases. In particular, we use the relative abundance of isolated teeth, the most common elements recovered from the Omo deposits, as a measure of variation in taphonomic conditions through the sequence that could affect the record of species' FADs, LADs, and relative abundance.

The associations of early hominins with other mammalian taxa may provide insights into the ecological context of the hominins. This claim is based on the assumption that, in a large sample of localities, taxa that co-occur as fossils are more likely to have been associated in the same habitats in life than taxa that do not co-occur in fossil assemblages. This assumption could be affected by a number of different taphonomic processes, e.g., relatively high durability of teeth or other identifiable body parts leading to associations of taxa in the fossil deposit that were not associated in life. This would certainly be expected in the reworked, fluvially concentrated assemblages typical of the Omo. However, given the taphonomic

equivalence of the Omo sequence's tooth-dominated fossil assemblages (see discussion below), we argue that any such biases should be constant through time and from locality to locality. Thus, associations of taxa that are significantly different from random suggest (though they cannot prove) an ecological signal that has not been completely overprinted by the taphonomic processes responsible for assemblage formation. In this analysis, chi-square tests are computed to determine if hominin taxa are significantly associated with other mammalian taxa across Omo localities (Table 5). The strength of significant associations is computed with the Ochiai index (formulae in Ludwig and Reynolds, 1988). The chi-square test in this context is meant to test one association at a time, and numerous tests (as performed here) increase the probability of "significant" results due to chance alone (Ludwig and Reynolds, 1988). To compensate for this problem, we use a more conservative level of significance, at $p < 0.01$ instead of the usual $p < 0.05$. In the study of faunal associations, only localities with a minimum of 10 specimens are used in the analysis. Sample size among Omo localities varies greatly, with some localities having just a few specimens, and others having thousands.

The hominin specimens analyzed here have been identified in the Omo Faunal Catalog and in the published literature primarily by F.C. Howell, T.D. White, and G. Suwa (Howell and Coppens, 1976; Howell, 1978b; White, 1988; Suwa, 1990; Suwa et al., 1996). In the analysis of associations between hominins and other mammals, the Omo sequence is divided into three intervals. In the first interval, comprised of Usno Formation Unit U-12 and Shungura Member B, the only hominin present is *Australopithecus*. Most specimens are isolated teeth and are not identified to the species level. There are only eight localities in this interval with sample size greater than 10 specimens, and these span the time interval from 3.3 to 2.9 Ma. The second interval spans from 2.85 to 2.4 Ma, and includes Members C and D, an interval during which *Australopithecus* continues to occur but is joined by *P. aethiopicus*. There are 58 localities from these members in the analysis. In the third interval, which includes 55 localities, *Australopithecus* is extinct, and *Paranthropus* is joined by *Homo*. The taxonomy of early *Homo* has been problematic, and there is no consensus about how many species of

Table 4

First and last appearance data (FADs and LADs) of mammals (Bovidae, Suidae, Cercopithecidae, and Hominidae) from the northern Turkana Basin between 4 and 1 Ma^a

Time interval	FAD	LAD
1.2–1.0		
1.4–1.2	<i>Syncerus</i> cf. <i>caffer</i>	<i>Paranthropus boisei</i>
1.6–1.4		
1.8–1.6		<i>Syncerus acoelotus</i> <i>Tragelaphus gaudryi</i> <i>Notochoerus scotti</i>
2.0–1.8	<i>Homo erectus</i> (sensu lato) <i>Beatragus antiquus</i>	<i>Paracolobus mutiwa</i> <i>Rhinocolobus turkanaensis</i>
	<i>Damaliscus eppsi</i> <i>Kobus</i> cf. <i>leche</i>	<i>Ugandax</i> sp. <i>Cercopithecoides williamsi</i>
	<i>Megalotragus isaaci</i> <i>Pelorovis oldowayensis</i> <i>Pelorovis turkanensis</i> <i>Cercopithecoides williamsi</i> <i>Metridiochoerus hopwoodi</i> <i>Metridiochoerus modestus</i>	<i>Kolpochoerus afarensis</i>
2.2–2.0		<i>Notochoerus euilus</i> <i>Theropithecus brumpti</i>
2.4–2.2	<i>Homo</i> sp. (<i>Paranthropus boisei</i>)	<i>Kobus oricornus</i> (<i>Paranthropus aethiopicus</i>)
	<i>Theropithecus oswaldi</i> <i>Tragelaphus strepsiceros</i> <i>Metridiochoerus compactus</i> <i>Parmularius altidens</i>	
2.6–2.4		<i>Tragelaphus pricei</i> <i>Gazella granti</i> <i>Australopithecus</i> sp.
2.8–2.6	<i>Paranthropus aethiopicus</i> <i>Tragelaphus pricei</i> <i>Antilope sub torta</i> <i>Oryx</i> sp.	<i>Menelikia leakeyi</i> <i>Simatherium kohllarseni</i> <i>Antilope sub torta</i> <i>Nyanzachoerus kanamensis</i>
3.0–2.8	<i>Antidorcas recki</i> <i>Kobus ancystrocera</i> <i>Notochoerus scotti</i>	
3.2–3.0		<i>Tragelaphus kyaloae</i>
3.4–3.2	<i>Theropithecus brumpti</i>	<i>Nyanzachoerus jaegeri</i>
	<i>Kolpochoerus limnetes</i> <i>Metridiochoerus andrewsi</i> <i>Menelikia lyrocera</i>	
3.6–3.4		
3.8–3.6		
4.0–3.8	<i>Nyanzachoerus kanamensis</i> <i>Notochoerus euilus</i> <i>Australopithecus anamensis</i> (>4 Ma)	

Homo occurred in the late Pliocene (Wood, 1992; Wood and Collard, 1999). Here it should be noted that specimens identified as *Homo* in the Shungura collections are recognized primarily in relation to dental characters, not in terms of other characteristics associated with our genus, such as large cranial capacity. Thus most Pliocene specimens of early *Homo* from the Shungura Formation are identified only to the genus level (Suwa et al., 1996). *Paranthropus* and early *Homo* co-occur in the Omo sequence in Members E, F, and in the lower units of Member G (up to Unit G-5), from about 2.4 to 2.3 Ma. The species *P. boisei* is recognized in lower Member G and above, beginning at about 2.3 Ma (Suwa et al., 1996). The species *H. erectus* (sensu lato) appears in the Turkana Basin at about 1.8 Ma (Feibel et al., 1989). There are too few specimens of *P. boisei* and *H. erectus* in the Omo to perform association analyses of these taxa in the intervals above Shungura G-5.

3. Grassland indicators

As a proxy for the extent of grassland environments in the paleo-Omo ecosystem, we use the abundance of individuals belonging to mammalian species or clades that show clear adaptations to grassland environments. Grassland adaptation has been determined both through direct functional analysis of teeth (hypsodonty) and skeletal morphology (cursorial adaptation) as well as known adaptations to grassland habitats among members of a clade with modern representatives, such as the tribe Alcelaphini (Vrba, 1980, 1984). Abundance is calculated as the total number of specimens belonging to each taxon divided by the total number of mammals at each interval. Each estimate of abundance is accompanied by an error bar representing the 95% confidence interval based on the methods of Buzas (1990) and Hayek and Buzas (1997).

Note to Table 4:

This table includes taxa for which the observed event (FAD or LAD) has a high probability of corresponding to the true (inferred) speciation or extinction event (method derived from Barry et al., 2002). Species in parentheses (e.g., *P. boisei*) represent anagenetic speciation events and are not counted in the turnover analysis.

Table 5
Associations of *Homo* and *Paranthropus* fossils with other mammals from the Omo sequence between 2.4 and 2.3 Ma^a

	<i>Homo</i>		<i>Paranthropus</i>	
	Chi-square	Ochiai index	Chi-square	Ochiai index
<i>Tragelaphus nakuae</i>	2.53	0.39	2.48	0.55
<i>Tragelaphus gaudryi</i>	7.51	0.48	0.73	0.44
<i>Aepyceros</i>	1.88	0.37	0.12	0.50
<i>Alcelaphini</i>	4.77	0.43	0.03	0.36
<i>Antilopini</i>	0.00	0.00	0.00	0.11
<i>Bovini</i>	4.32	0.42	0.37	0.41
<i>Kobus sigmoidalis</i>	0.00	0.24	1.21	0.29
<i>Menelikia</i>	4.03	0.40	0.46	0.36
<i>Notochoerus scotti</i>	1.02	0.32	0.07	0.39
<i>Kolpochoerus limnetes</i>	2.25	0.37	1.06	0.32
<i>Metridiochoerus andrewsi</i>	4.61	0.41	4.78	0.50
<i>Colobinae</i>	2.24	0.33	0.25	0.32
<i>Paracolobus</i>	0.00	0.00	2.26	0.00
<i>Papio</i>	9.61	0.51	2.35	0.44
<i>Theropithecus oswaldi</i>	0.12	0.15	6.97	0.47
<i>Theropithecus brumpti</i>	0.21	0.14	0.32	0.27
<i>Paranthropus</i>	9.61	0.51		
<i>Homo</i>			9.61	0.51

^a The interval from 2.4 to 2.3 Ma includes Members E, F, and lower G (up to Submember G-5). There are 55 localities in this interval with sample size of at least 10 specimens. Associations are considered significant if chi-square >6.635, or $p < 0.01$ (highlighted as bold numbers). The strength of the association is measured by the Ochiai Index.

Among bovids, we use the tribes Alcelaphini and Antilopini as the best indicators of open grassland ecosystems (Vrba, 1980, 1984, 1985; Greenacre and Vrba, 1984; Gentry, 1985; Shipman and Harris, 1988; Harris, 1991). These antelopes show consistently hypsodont dentition and cursorial limbs. Alcelaphines in the Omo are represented by the genera *Damalops*, *Parmularius*, *Megalotragus*, and *Connochaetes*, but most specimens are hypsodont teeth identified only to the tribal level. It should be noted that the tribe Antilopini (represented in the Omo by *Gazella*, *Antidorcas*, and *Antilope*) might include species that rely strongly on browsing rather than grazing (Sponheimer

et al., 1999). However, antilopine browsers tend to live in fairly arid environments in which the leaves of bushes constitute an important part of their diet. These browsers then would indicate bushland–grassland habitats rather than grasslands per se. Antilopini are almost always very rare in the Omo, making up little more than 2% or 3% of the mammalian fauna. Other bovids indicative of open savanna grasslands include *Oryx*, which is present in the Omo but represented by a single specimen from Member C.

The family Suidae has been difficult to interpret in terms of Pliocene and Pleistocene habitat preferences. Based on functional dental morphology, Kullmer (1999) regarded *Nyanzachoerus* and *Notochoerus euilus* as generalized omnivores inhabiting closed, often forested environments. The work of Bishop (1999) indicates that the species *Nyanzachoerus kanaanensis*, *N. euilus*, and *Metridiochoerus modestus* occupied closed or intermediate habitats. However, analysis of carbon isotopes from suid dental enamel provides strong evidence that C₄ grasses were an important component of their diets during the Pliocene and Pleistocene (Harris and Cerling, 2002). Among species of Pliocene and Pleistocene suids, *N. euilus*, *Notochoerus scotti*, *Kolpochoerus limnetes* and species of *Metridiochoerus* consumed the highest proportion of grassy vegetation. Among these, species of *Metridiochoerus* were also found to be relatively water-independent (Harris and Cerling, 2002). Also, during the late Pliocene and early Pleistocene, *Metridiochoerus* developed extremely hypsodont molars (Cooke, 1976; Harris and White, 1979). Thus, among suids, we use *Metridiochoerus* as the taxon providing the clearest indication of seasonally arid grassland habitats.

Equids have generally been associated with open habitats, at least since their diversification in the middle Miocene (Simpson, 1951; Churcher and Richardson, 1978; Cerling et al., 1997). Not all species of equids, even if moderately hypsodont, can be regarded as adapted to open habitats and a diet of grassy vegetation (Bernor et al., 1996; MacFadden et al., 1999). However, there is little doubt that the genus *Equus* spread from Eurasia into Africa by taking advantage of the open savanna grasslands available on both land masses (Azzaroli et al., 1988; Agustí et al., 2001). Thus, we use *Equus* as the main indicator among equids of open grasslands. The earliest appearance of *Equus* on the

African continent is recorded in lower Member G of the Shungura Formation, at about 2.3 Ma (Lindsay et al., 1980; Eisenmann, 1985; Hooijer and Churcher, 1985).

Because of the strong association of primates with trees for food and protection, cercopithecids are generally indicative of closed environments, woodlands or forests. There are, however, a few species of primates that have lost the clade's strong dependence on trees. Among these, the gelada baboon, *Theropithecus gelada*, provides a notable modern example. Although *Theropithecus* is restricted today to rocky outcrops in the Ethiopian highlands, where these monkeys feed on grasses and their seeds, the genus was widespread and abundant during the Plio-Pleistocene (Foley, 1993; Iwamoto, 1993). The main lineage of Plio-Pleistocene *Theropithecus*, composed of *T. darti* and *T. oswaldi*, occupied open environments and became increasingly graminivorous through time (Jablonski, 1993; Leakey, 1993). However, at least one species of late Pliocene *Theropithecus*, *Theropithecus brumpti*, is considered a semi-arboreal frugivore that lived in gallery forests (Eck et al., 1987; Krentz, 1993). *T. brumpti* was the most common primate in Shungura Members B to lower G, but the species was extinct by 2 Ma (in upper Member G). Here we regard specimens of *T. oswaldi* to be indicative of open grasslands. Specimens from the Omo identified only to the genus *Theropithecus* after the extinction of *T. brumpti* are regarded as belonging to *T. oswaldi*.

4. Results and analyses

The interval from 4 to 1 Ma shows major shifts in the abundance of the main families of mammals from the Omo sequence (Table 2 and Fig. 2A–B). Fig. 2A shows that suids underwent a significant decline in abundance between the middle and late Pliocene but had a resurgence in the early Pleistocene beginning at about 1.75 Ma. Bovids, the most common family of fossil mammals at most Plio-Pleistocene African localities, experienced an increase in abundance during the late Pliocene, especially between 2.5 and 1.8 Ma. It is noteworthy that equids were a consistently minor component of the Omo fauna during the Pliocene and Pleistocene, even though their abundance in other

parts of Africa (e.g., the Hadar area in the Pliocene or Olduvai in the Pleistocene) was significantly greater than in the Omo (e.g., see Gray, 1980). Fig. 2B shows that cercopithecids reached a peak of abundance between 3.0 and 2.5 Ma, but then declined and remained a relatively small component of the mammalian fauna after 2.0 Ma. Pliocene hominins in the Omo reached their highest abundance between 2.5 and 2.3 Ma, yet they made up no more than 2% of the mammalian fauna during this time. In the analysis of relative abundance shown in Fig. 2A–B, it is important to note that the abundance of a fossil taxon in any given interval can be taken as only a rough estimate of its abundance in the paleocommunity. Many taphonomic and collection factors, some already mentioned here, influence the number of specimens recovered. The important point is that, under consistent taphonomic conditions and methodical collection procedures, it is the changes in relative abundance through time that are meaningful. Thus, the abundance of suids as a proportion of all mammals may be read as a variable that changed through time, even though the actual abundance of suids in the paleocommunity may not be known with certainty.

The Omo collections of fossil mammals are characterized by a high proportion of isolated teeth (Table 1, Fig. 2C), which is consistent with the fluvial channel depositional environments that predominate in the lower Omo valley deposits (de Heinzelin, 1983). Fluvial deposition in the Omo is interrupted in upper Member G, and in the uppermost units of Member L, during times of lake transgression. The abundance of isolated teeth as a proportion of all fossils in the Omo can be used as a proxy of taphonomic conditions. Fig. 2C shows that as the abundance of mammalian families in the Omo was undergoing major changes, taphonomic conditions in the basin were relatively stable, with the exception of the interval around 2 Ma when a major lake occupied most of the Turkana Basin (Brown and Feibel, 1991), and the relative abundance of isolated teeth decreased in relation to other skeletal elements (crania and postcranial elements). Another major lake occupied the basin near the top of Member L, an interval also characterized by a low proportion of isolated teeth. Fig. 2C shows that, with the exception of upper Member G and Member L, isolated teeth constitute at least 50% of the Omo specimens throughout the

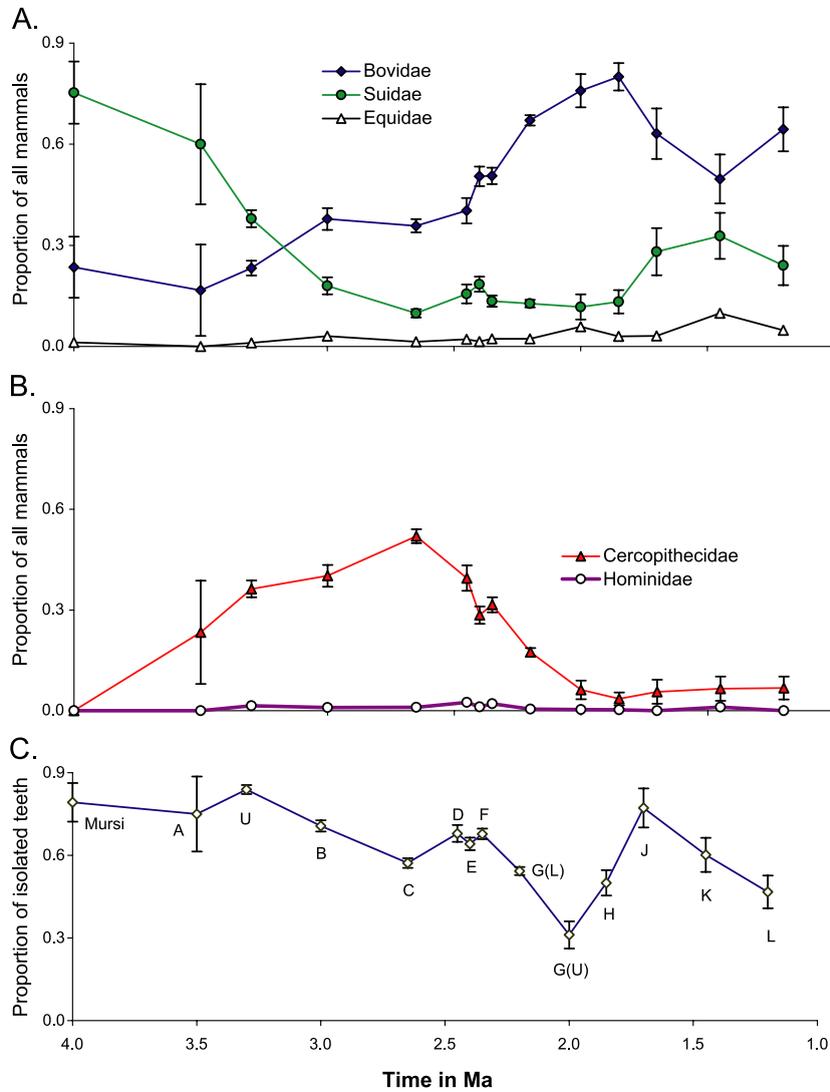


Fig. 2. (A)–(B) Relative abundance of the main families of medium-size mammals in the Omo sequence as a proportion of all mammals per interval, showing significant shifts in the major mammalian families. Suids are most abundant in the early part of the sequence, and bovids in the later part of the sequence, while the highest abundance of cercopithecids occurs in between the suid and bovid peaks. The overall abundance of equids in the Omo is lower than in other, contemporaneous Plio-Pleistocene sites in Africa. Hominids are rare, but their highest abundance occurs between 2.5 and 2.3 Ma. (C) Relative abundance of isolated teeth (as a proportion of all specimens per interval) in the lower Omo valley collections. Isolated teeth are the most abundant element in the fluvial sediments of the Omo sequence. The lowest abundance of isolated teeth occurs in the lacustrine depositional environments of upper Member G, between about 2.1 and 1.9 Ma and at the top of Member L, at about 1.2 Ma. Error bars denote 95% confidence intervals (For color see online version).

sequence. This consistently high proportion of isolated teeth, reflecting the predominance of fluvial channel deposition, gives the Omo assemblages a more-or-less consistent degree of taphonomic equivalence from one interval to the next (Bobe et al., 2002).

Additionally, collection methods in the Omo (Bobe and Eck, 2001) increase the likelihood that perceived changes in the fauna reflect factors other than taphonomic or collection biases, i.e., real biological processes.

The analysis of faunal turnover in the northern Turkana Basin between 4 and 1 Ma shows four intervals with higher than average turnover: 3.4 to 3.2, 2.8 to 2.6, 2.4 to 2.2, and 2.0 to 1.8 Ma (Fig. 3A). Notable among these is the peak of first and last occurrences in the interval between 2.8 and 2.6 Ma, and the more pronounced peak between 2.0 and 1.8 Ma. Taxa that first occur in the 2.8- to 2.6-Ma interval are *P. aethio-*

picus, *Oryx*, *Tragelaphus pricei*, and *Antelope subtorata* (its only occurrence in Africa), while those that have their last occurrence in this interval include *N. kana-*
mensis, *Simatherium kohllarseni*, and *Menelikia leakeyi*. Thus, among the first occurrences we have a clear indicator of grassland habitats (*Oryx*) while the last occurrence taxa appear more closely associated with closed and wet environments. The *Homo* lineage made

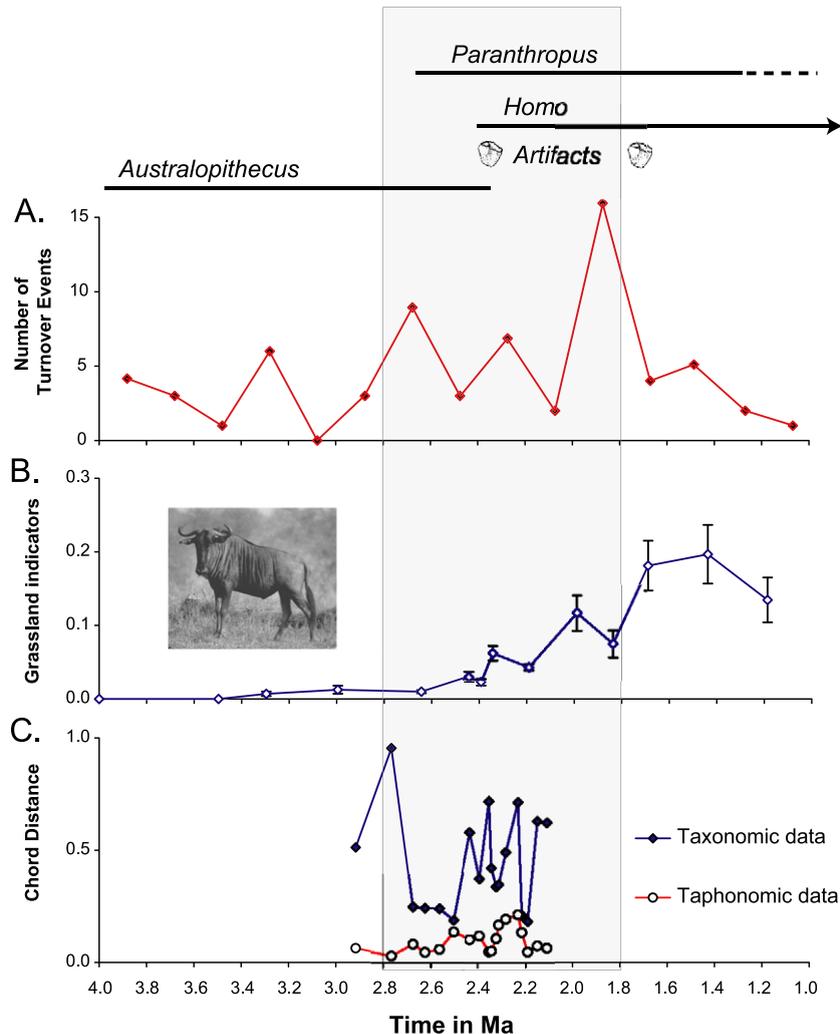


Fig. 3. (A) Turnover in species of Bovidae, Suidae, Cercopithecidae, and Hominidae in the northern Turkana Basin: Shungura, Usno, Mursi, Koobi Fora, and Nachukui Formations. First appearance and last appearance data (FAD and LAD) used here derive only from taxa in which there is high probability that the turnover event occurred during the interval it is observed (method derived from Barry et al., 2002). (B) Abundance (number of specimens) of taxa indicative of grassland ecosystems in the lower Omo sequence. (C) Chord distance, a measure of faunal similarity, compares adjacent units. This graph shows a peak of faunal change (large faunal distance between two adjacent units) at about 2.8 Ma, followed by an interval of faunal stability (low values of chord distance) and then variability (high and low values) after 2.5 Ma. C has been modified from Bobe et al. (2002), which should be consulted for more details (For color see online version).

its first appearance in the Turkana Basin, and in the African record, during a period of moderate turnover (2.4 to 2.2 Ma) that also saw the appearance of grassland-adapted taxa such as the hypsodont alcelaphine bovid *Parmularius altidens*, a hypsodont suid *Metridiochoerus compactus*, and the grazing cercopithecoid *Theropithecus oswaldi*. The turnover peak between 2.0 and 1.8 Ma marks the appearance of *H. erectus* (sensu lato) and an increase in the number of FADs of species associated with grassland habitats (Table 4). These taxa include the highly hypsodont suids, *Metridiochoerus hopwoodi* and *M. modestus*, and hypsodont alcelaphines, *Megalotragus isaaci*, *Damaliscus epsi*, and *Beatragus antiquus*. *Pelorovis oldowayensis* and *P. turkanensis* are also present, and are characterized as open-habitat species, in contrast to the closely related genera *Syncerus* and *Ugandax* (Harris, 1991). Taxa that become extinct between 2.0 and 1.8 Ma show adaptations to arboreal or closed settings, i.e., the colobine monkeys *Paracolobus mutiwa* and *Rhinocolobus turkanaensis*, the bovine *Ugandax*, and the suid *Kolpochoerus afarensis*.

Fig. 3B tracks the abundance of grassland indicators through the Omo sequence. Some of these taxa did not appear in the African record until the later Pliocene (*Metridiochoerus*, *Equus*, *T. oswaldi*), but Alcelaphini and Antilopini were present in Africa since Miocene times. Grassland-adapted taxa were uncommon in the early part of the Omo sequence (Mursi to Member C), where they constitute less than 2% of the fossil fauna. The low abundance of Alcelaphini and Antilopini in the lower part of the Omo sequence is in stark contrast to the much higher abundance of these bovids in contemporaneous sites elsewhere in Africa (e.g., at Hadar, data from Gray, 1980). Only after 2.5 Ma do grassland indicators begin to show major and significant increases in abundance in the Omo. There is a peak in Member F (2.35 Ma), composed largely of Alcelaphini, a peak in upper Member G (at about 2 Ma), in which Antilopini make an important contribution, and another peak in Members J and K (1.75 to 1.4 Ma), with significant contributions from Alcelaphini, *Metridiochoerus*, and *Equus*.

Fig. 3C presents previously reported results in which faunal (chord) distance between adjacent units is computed for the interval with the highest density of fossil mammals (Bobe et al., 2002). This figure shows that there is a peak of faunal change at about 2.8 Ma,

followed by an interval of stability, and then a period of high faunal variability beginning at 2.5 Ma. The low chord distance values of the taphonomic data (specimens grouped into skeletal element categories) imply that taphonomic conditions were relatively stable during the interval between 3 and 2 Ma. The time ranges of hominin genera and the appearance of lithic artifacts in the Omo are also noted in Fig. 3.

Hominins form a relatively small proportion of the Omo fauna (Table 2). Specimens attributable to a gracile *Australopithecus* occur in Usno U-12, and Shungura Members B to D, up to about 2.4 Ma. Specimens of the genus *Paranthropus* first appear in the Omo (and in Africa) in Member C, at about 2.7 Ma, and *Homo* first appears in Member E, at about 2.4 Ma (Fig. 3). Most of the hominin specimens in the Omo consist of isolated teeth and mandibular fragments, and their taxonomic attribution is based on dental characters (Suwa et al., 1996). Very few hominins occur in the Omo above lower Member G. During the time that *Australopithecus* is the only recognized taxon in the Omo (Usno and Member B), there are only eight localities that have large samples of fossil mammals. Eight occurrences are a small number with which to identify significant associations of *Australopithecus* with other mammalian taxa. Thus, there are no significant associations at the 0.01 confidence level. However, at the 0.05 confidence level, *Australopithecus* is significantly associated with the suid *K. limnetes* (Fig. 4). The association between fossils of these two taxa in Usno and Member B is perfect: both taxa co-occur in four of the eight localities, and both are absent from the other four. It is difficult to interpret the ecological meaning of this association. Early *Kolpochoerus* has been considered a relatively generalized suid, probably omnivorous and inhabiting closed habitats, perhaps analogous to those inhabited by the bushpig, *Potamochoerus porcus*, a close relative of the Pliocene species (Cooke, 1976). However, Harris and Cerling (2002) show that early *Kolpochoerus* was a dedicated grazer, a surprising result given its bunodont and brachyodont dentition.

Australopithecus persists through the Omo sequence between 2.8 and 2.5 Ma and is contemporaneous with the newly arrived robust hominin *Paranthropus* in Members C and D. During this interval, *Australopithecus* occurs in six of the localities with large samples. Its only strong asso-

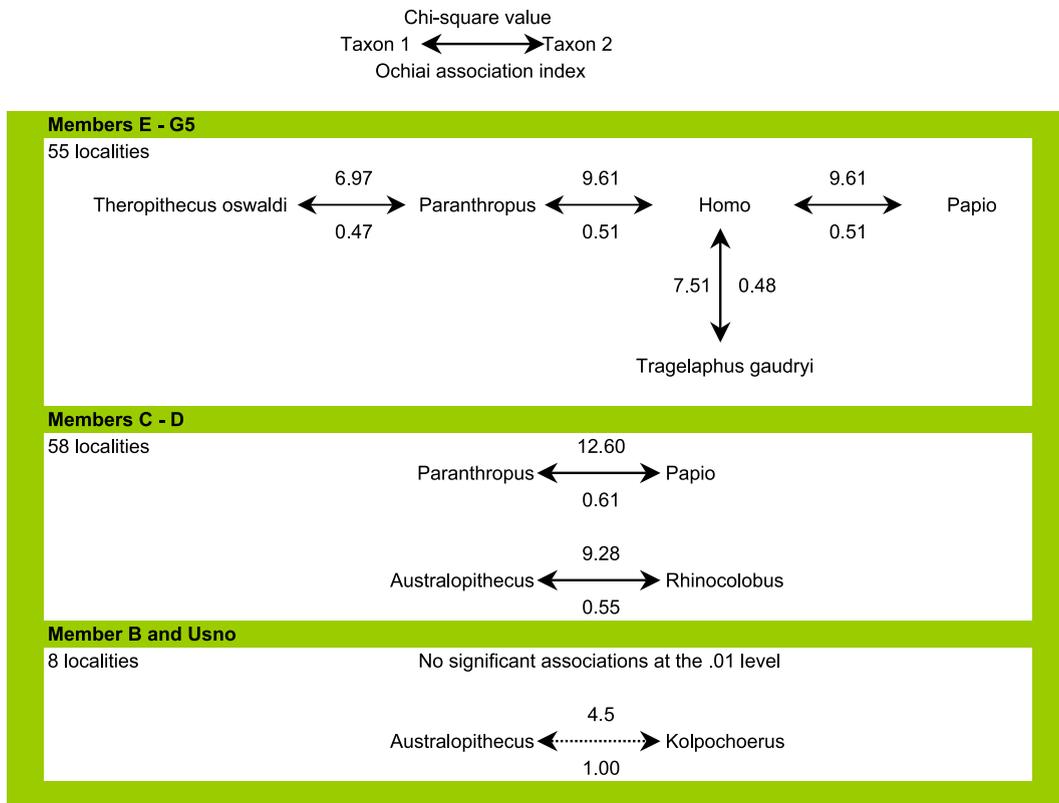


Fig. 4. Association of hominin taxa with other mammals (Primates, Bovidae, Suidae) for which a chi-square test yields significant results at $p < 0.01$, except for the first interval (Member B and Usno), with only eight localities, where the association is significant at the $p < 0.05$ level. Only taxa with a minimum of four occurrences per interval were used in this analysis. The Omo sequence is divided into three intervals: the first one in which only *Australopithecus* is present (Member B, Usno U-12, with 8 localities having at least 10 specimens), the second one in which *Australopithecus* and *Paranthropus* co-occur (Members C and D, with 58 localities having at least 10 specimens), and the third one in which *Paranthropus* co-occurs with *Homo* (Members E, F, and lower G, with 55 localities having at least 10 specimens). Key at top shows that the Chi-square value is given above the arrow and the Ochiai index below the arrow (For color see online version).

ciation is with the colobine primate *R. turkanaensis* (Fig. 4). In the same part of the sequence, the only recognized species of *Paranthropus* is *P. aethiopicus*, which shows associations with *Papio*. Thus, fossils of the two species of hominin between 2.8 and 2.4 Ma show strong patterns of co-occurrence with those of other primates, *Australopithecus* with the arboreal and folivorous *Rhinocolobus*, and *Paranthropus* with the more terrestrial and omnivorous *Papio*. *Homo* and *Paranthropus* co-occur in the Omo sequence in strata above Member D. There are 55 localities (with samples >10 specimens) in the interval from Tuff E to Submember G-5 in which *Homo* and *Paranthropus* are broadly associated. Hominins are rare in the Omo in the units above G-5. Thus,

between Shungura G-5 and Member L, a span of more than 1 million years, there are only four hominin specimens: a fragmentary cranium of *P. boisei* (Omo-323-1976-896) in the French collection from G-8 (Alemseged et al., 2002), a fragmentary cranium of *Homo habilis* (L894) in G-28 (Boaz and Howell, 1977), a specimen of *H. erectus* in K-3 (P996-17), and another *P. boisei* in K-4 (P204-1). In contrast with the small number of hominins above G-5, there are 64 hominins in the interval from Tuff E to G-5 (a time span of about 100 kyr). In this interval, *Paranthropus* is associated with *T. oswaldi* and with *Homo*, while *Homo* shows associations also with *Papio* and *Tragelaphus gaudryi* (Fig. 4). It is perhaps surprising that fossils of both hominin genera should be associated with each

other if these species had, as is often suggested, different ecological niches. *Homo* occurs in six localities during this interval, and in five of them it co-occurs with *Paranthropus*. However, *Paranthropus*'s other association is with a grazing primate, *T. oswaldi*, while *Homo*'s is with a generalized primate, *Papio*, and with a kudu-like antelope, *T. gaudryi*, thought to occupy bushy habitats.

5. Discussion

Our analysis has shown that in the interval from 4 to 1 Ma there were profound faunal changes in the Turkana Basin. The most important of these changes include significant shifts in the abundance of the most common families of mammals, episodes of high faunal turnover, and an increase in the number and abundance of species that show adaptations to grassland ecosystems. Hominins, an integral element of Plio-Pleistocene East African faunas, fit into these patterns of change in complex ways that may shed light on the origin and evolution of key human characteristics.

The record of the lower Omo valley indicates that during the 4–1-Ma interval, there were important changes in the relative abundances of the main families of mammals. Suid abundance was high in the early part of the Omo sequence, but declined to relatively low levels between 3 and 1.8 Ma (Table 2, Fig. 2A). The high abundance of suids in the mid to late Pliocene was not matched by high species richness. In Shungura Member A and Usno U-12, for example, there were only three suid species, *Nyanzachoerus kanamensis*, *Notochoerus euilus*, and *K. limnetes*, and one of these (*N. euilus*) was particularly abundant. In the same intervals, there were at least twice as many species of bovids as of suids, but their fossils were less abundant. After their late Pliocene decline in abundance, suids increased again during the early Pleistocene, as various species, especially of the genus *Metridiochoerus*, became more hypsodont. It is conceivable that the specialization of suid molars for coping with expanding grasslands in the early Pleistocene may have provided a competitive edge to this family that resulted in higher relative abundance in the mammalian fauna, but this assertion would require further testing. Bovid abundance increased through the late Pliocene to reach its highest levels at the close

of the Pliocene 1.8 Ma. It is noteworthy that equids in the Shungura Formation never reached the high abundance of Equidae in other Pliocene and Pleistocene sites (e.g., Hadar, Olduvai), even though equids, like suids, were well equipped to cope with grassy vegetation. Monkeys were rare in the earliest samples from the lower Omo valley but reached very high relative abundance between about 3.3 and 2.3 Ma (from Usno U-12 to Member F). Most monkey specimens from the Omo are attributed to *Theropithecus* (Eck et al., 1987), a genus that declined considerably in abundance after 2.1 Ma (Fig. 2B). Hominins were rare throughout this time; their highest relative abundance is about 2% in Shungura Members D and F. Thus, the Omo fauna shows major shifts in the abundance of mammalian families between about 4 and 1 Ma, and demonstrates that taxonomic abundance in terms of numbers of individuals (e.g., high abundance of suids during some intervals) is not necessarily associated with taxonomic richness (fewer suid species in relation to bovid species at any one time). Other sites in Africa (e.g., Olororgesailie) document continued shifts in the abundance of common mammalian families after 1 Ma, with equids, cercopithecids, and suids alternating in the position of highest abundance (Potts, 1996b). It remains to be seen whether the patterns of abundance seen in the Omo are restricted to the northern Turkana Basin or form part of larger regional trends. However, these shifts indicate major changes in at least some of the environments occupied by Pliocene and early Pleistocene hominins.

Our analysis of first and last appearances of mammalian species in the Turkana Basin shows that there was significant turnover in the interval from 4 to 1 Ma. The method used here incorporates abundance and sample size information to arrive at first and last occurrence events that are known with a high degree of confidence. Intervals of higher than average turnover occurred between 3.4 and 3.2, 2.8 and 2.6, 2.4 and 2.2 Ma, and especially between 2.0 and 1.8 Ma (Fig. 3A). The turnover peak between 2.8 and 2.6 Ma coincides with the beginning of previously documented climatic and faunal changes in Africa (deMenocal, 1995; Dupont and Leroy, 1995; Vrba, 1995). The hominin species *P. aethiopicus* first appears in the basin during this interval of faunal turnover: the earliest record of *Paranthropus* in Africa is that from Shungura Member C, at about 2.7 Ma (Suwa et al.,

1996). The FAD for *Paranthropus* was accompanied by the only occurrences of the bovids *Oryx*, *A. subtorta*, and *T. pricei* in the Omo record. The appearance of *Oryx* indicates that vegetation in the Omo may have been more open in the interval between 2.8 and 2.6 Ma than in earlier intervals, but *Oryx* is represented by a single specimen, and other grassland-adapted taxa in the Omo remained rare during this time. *Antelope* provides evidence of biogeographical connections between East Africa and Asia, while *T. pricei* shows links between the Turkana Basin and southern African faunas. Although these three bovid taxa occur in low abundance in the Omo record, they support earlier work showing that the interval from 2.8 to 2.6 Ma was one during which important biotic changes were taking place in Africa (Wesselman, 1984; Dupont and Leroy, 1995; Vrba, 1995). Environmental changes in the Omo during this time are marked by decreases in humid forests and woodlands and increases in seasonal woodlands (Bobe, 1997; Bobe and Eck, 2001). The data suggest that *Paranthropus* originated (or immigrated) before any significant increase in the prevalence of grassland environments in the Omo (Fig. 3B). The local appearance of *Paranthropus* preceded that of *Homo* by about 300,000 years. However, it is not clear whether the earlier appearance of *Paranthropus* is due to an earlier origin or to our ability to recognize the specialized dentition of *Paranthropus* more easily than that of *Homo*. It is conceivable that specimens from Shungura Member C that are diagnostically neither *P. aethiopicus* nor *Australopithecus afarensis* could represent the earliest record of the *Homo* clade (Suwa, 1990), but further work and more complete specimens are needed to substantiate this possibility.

The origin of the genus *Homo* remains poorly understood. Definitions of *Homo* have changed through time, but usually have emphasized large cranial capacity, relatively small dentition, obligate bipedality, and the ability to make tools (e.g., Leakey et al., 1964; Wood, 1992; Kimbel et al., 1997; Wood and Collard, 1999). The *Homo* clade first appears in the Turkana Basin at about 2.4 Ma, in Shungura Member E, very close to its earliest global first occurrence at 2.4 Ma in the Baringo area of Kenya (Hill et al., 1994). This is also very close to the time of the earliest lithic artifacts in the Omo and elsewhere in the Turkana Basin (Howell et al., 1987; Roche et al., 1999), even

though stone tools occur earlier elsewhere in Africa (Semaw et al., 1997). The first appearance of *Homo* in the Turkana Basin is accompanied by the appearance of taxa with adaptations to grasslands (*T. oswaldi*, *P. altidens*, and *M. compactus*), and by an increase in the individual abundance of grassland-adapted taxa like the Alcelaphini (Fig. 3B). This increase in grassland indicators, however, is variable and irregular, even at the coarse level of temporal resolution used in this analysis.

In previous work (Bobe et al., 2002), we have shown that *Homo* first appeared in the lower Omo valley during an interval of high faunal and environmental variability (Fig. 3C). This high variability is masked at the broader scales of resolution used in this analysis. Thus, *Homo* first appears in the Turkana Basin at a time when grasslands are just beginning to expand in the northern portion of the basin. The Omo fauna suggests that this expansion of grasslands was not a monotonic progression, but an irregular, probably regionally variable phenomenon. The expansion of grasslands beginning at about 2.5 Ma added an element of environmental complexity and heterogeneity that may have been well suited to the dispersal of *Homo* into the basin.

The timing of the appearance of *Homo* and lithic artifacts in the Omo, both at 2.4 Ma (Fig. 3), suggests that *Homo* may have been responsible for producing the lithic artifacts. In the Hadar Formation of Ethiopia, there is also a close correspondence between the appearance of *Homo* and lithic artifacts at 2.35 Ma (Kimbel et al., 1996). It is not yet possible unequivocally to attribute stone tool making to any hominin taxon to the exclusion of others. Nevertheless, stone tools appear in the Omo at a time of increasingly open and variable environments. In this ecological context, tools could have supported increased resource acquisition in open habitats and buffered the effects of ecological instability (Potts, 1996b).

The patterns of faunal change discussed thus far provide the general context of environmental and faunal change, but the specific ecological preferences of early hominins may be inferred from the species that were most closely associated with the hominins. Patterns of faunal association, even when significant at the $p < 0.01$ level, undoubtedly combine both taphonomic and paleoecological signals (Behrensmeyer, 1982, 1991) and need further testing as well as

additional field work before their ecological significance can be firmly established. However, with this caveat in mind, our preliminary analysis shows that fossils of *Australopithecus* co-occur most commonly with the generalized suid *Kolpochoerus* in the interval from 3.4 to 2.8 Ma, and with the arboreal primate *Rhinocolobus* after 2.8 Ma (Fig. 4). Although *Kolpochoerus* was a grazer (Harris and Cerling, 2002), it appears to have frequented somewhat closed, perhaps densely thicketed environments (Bishop, 1999), and by association, *Australopithecus* may have occupied such habitats as well. The association of *Australopithecus* with *Rhinocolobus* after 2.8 Ma supports this inference. Although the faunal associations of *Australopithecus* do not provide direct evidence of hominin locomotion, they indicate that *Australopithecus* was more likely to occur in closed and wooded environments rather than in open savannas. More direct evidence for *Australopithecus* locomotion must come from studies of functional morphology (e.g., Stern and Susman, 1983; Lovejoy, 1988).

Fossils of *Paranthropus* are first associated with those of *Papio* and then with *T. oswaldi* and *Homo* (Fig. 4). The pattern of successive associations with *Papio* and then with *T. oswaldi* may indicate a shift in the environmental preferences of *Paranthropus*, a shift in the direction of more open grassland habitats, such as those inferred for *T. oswaldi*. Thus, in the interval from 2.8 to 2.4 Ma, *Paranthropus* may have preferred more open environments than those occupied by contemporaneous *Australopithecus*, but by 2.4 Ma *Paranthropus* was shifting toward even more open grassland habitats. The highly specialized, megadont dentition of *P. boisei* may indicate an adaptive response to this shift toward open environments, with concomitant changes in dietary preferences. The hypermasticatory apparatus already evident in *P. aethiopicus* became even more exaggerated with the appearance of *P. boisei* at 2.3 Ma (Wood, 1995; Suwa et al., 1996).

In the interval from 2.4 to 2.3 Ma, *Homo* fossils are associated with those of *Paranthropus*, *Papio*, and *T. gaudryi* (Table 5, Fig. 4). These associations may indicate that early *Homo* occupied a complex mosaic of environments, ranging from wooded grasslands to drier, bushy habitats. The appearance of the genus *Homo* occurred during a moderate shift toward grassland dominance, but *Homo* was probably not tied to

the expanding grasslands per se, because it does not show strong associations with hypsodont bovids or grazing suids. The appearance of *Homo* is associated in time with a transition toward a complex mosaic of habitats that included savanna grasslands, and also a range of woodlands and bushland habitats (Bobe and Eck, 2001). These vegetational mosaics also changed through time, providing late Pliocene hominins with a spatially and temporally variable environment before the increased dominance (and perhaps decreased habitat diversity) of grasslands in the early Pleistocene.

Although both *Paranthropus* and *Homo* originated in the Omo sequence along with taxa adapted to grassland ecosystems, the major pulse (appearances) of grassland-adapted mammals occurs in the 2.0–1.8-Ma interval, and the highest abundance of grassland-adapted fauna in the Omo occurs in the interval from 1.75 to 1.4 Ma (in Members J and K, Fig. 3). Thus, the Omo environments after 2 Ma became markedly more open. The species *H. erectus* was part of the pulse of first appearances between 2.0 and 1.8 Ma. Analysis of *H. erectus* postcrania reveals that this species had a large but narrow body with long legs, i.e., body proportions similar to those of modern people in arid tropical savanna grasslands (Ruff, 1991; Ruff and Walker, 1993). Thus, the anatomical adaptations of *H. erectus* to open, hot, and dry environments fit well with the proxy data presented here of expanding grassland ecosystems after 2 Ma.

Other proxies of environmental change in the Omo could test the paleoecological patterns obtained here. For example, it would be particularly interesting to obtain data from pedogenic carbonates and phytoliths in the Omo and juxtapose the environmental signal obtained from those data with the palynological and paleontological record. Further studies of ecomorphology (e.g., Plummer and Bishop, 1994) would also enrich the paleoenvironmental picture and test previous interpretations. It will also be important to determine if the patterns seen in the paleo-Omo ecosystem occur elsewhere in East Africa as well as more broadly across the continent as a whole.

6. Conclusions

Our results show that there were profound faunal and environmental changes in the Turkana Basin dur-

ing the interval from 4 to 1 Ma. The most important of these changes include significant shifts in the abundance of the most common families of mammals, episodes of high faunal turnover, and an increase in the number and abundance of species that show adaptations to grassland ecosystems. The *Paranthropus* clade originated at about 2.7 Ma, following an episode of major faunal change in the Omo at 2.8 Ma. The *Homo* clade appeared in the Turkana Basin at 2.4 Ma, during an interval of high faunal variability and turnover. The genus *Homo* and the earliest record of lithic technology coincide with a moderate expansion of savanna grasslands that added heterogeneity and complexity to the range of habitats available in the basin. This range of habitats was also subject to repeated fluctuations between 2.5 and 2.0 Ma, reflected in peaks of faunal change at intervals of 100 ky. The major pulse of faunal turnover and most significant expansion of grassland habitats in the Omo occurred after 2 Ma, during the time that *H. erectus* (sensu lato) appeared in East Africa.

These results indicate that climatic and environmental change in Africa influenced human evolution in complex ways. Each of the three hypotheses of human evolution outlined in the Introduction could explain different elements of the picture presented here. The savanna hypothesis fails to explain the divergence of hominins from the apes, but it could be partly correct in stressing the importance of grasslands in the early evolution of *Homo*. The more fundamental importance of grasslands may lie in the complexity and heterogeneity they added to the range of habitats available to the early species of the genus *Homo*. The turnover pulse hypothesis (Vrba, 1988, 1995) may be correct in linking critical events in human evolution to broader pulses of faunal change driven ultimately by climate, but our results show that this link is complex, with a number of events that are not precisely correlated in time with specific episodes of faunal turnover or global climate change. *Paranthropus* and *Homo* appear to have originated in the Turkana Basin in separate immigration events associated with episodes of high turnover at 2.8–2.6 and at 2.4–2.2 Ma, while the appearance of *H. erectus* is coupled with a major episode of turnover and grassland expansion after 2 Ma. Thus, there were multiple events that successively led to the appearance of *Paranthropus*, early *Homo*, and *H. erectus*. Our re-

sults show evidence of large-scale shifts in the fauna beginning at 2.5 Ma, during the time that *Homo* and lithic artifacts first appear in the Turkana Basin, lending support to the variability selection hypothesis (Potts, 1996a, 1998a), which emphasizes large-scale shifts (variability) in climate and environments occupied by early hominins rather than overall change toward drier and more open habitats. Testing predictions of the variability selection hypothesis in other parts of the Turkana Basin sequence as well as more broadly in Africa are a goal for future research.

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