6. Patterns of abundance and diversity in late Cenozoic bovids from the Turkana and Hadar Basins, Kenya and Ethiopia

R. BOBE
Department of Anthropology
The University of Georgia
Athens, GA 30602, USA
renebobe@uga.edu

A.K. BEHRENSMEYER
Department of Paleobiology and Evolution of Terrestrial Ecosystems Program
National Museum of Natural History
Smithsonian Institution
Washington, DC, USA
behrensa@si.edu

G.G. ECK
Department of Anthropology
University of Washington
Seattle, Washington, USA
ggeck@u.washington.edu

J.M. HARRIS
George C. Page Museum
5801 Wilshire Boulevard
Los Angeles, California 90036, USA
jharris@nhm.org

Keywords: East Africa, Omo, Pliocene, Pleistocene, Bovidae, paleoenvironments

Abstract

After decades of fieldwork spurred by the search for human ancestors, paleontologists in East Africa are compiling networks of databases to address questions of long-term evolutionary, environmental, and ecological change. Paleontological databases from the Turkana Basin of Kenya and Ethiopia (East Turkana, West Turkana, Kanapoi, Lothagam, and Omo) and the Hadar Basin of Ethiopia's Afar region consist of nearly 70,000 specimens of fossil vertebrates (mostly mammals) that date from the late Miocene to the Pleistocene. Here we focus on the most abundant family of fossil mammals, the Bovidae (N = 8213 specimens), and illustrate patterns of taxonomic abundance and diversity from about 7 Ma (million years ago) to about 1 Ma. The key questions we address are the following: How much variation in patterns of faunal change is there within different areas of a large sedimentary basin? How

R. Bobe, Z. Alemseged, and A.K. Behrensmeyer (eds.) Hominin Environments in the East African Pliocene: An Assessment of the Faunal Evidence, 129–157.

much variation is there between basins? How are these patterns related to broad signals of climatic change? What are the implications of the bovids for East African environments and for hominin evolution in the late Cenozoic? A correspondence analysis of bovid tribes indicates that important differences in taxonomic abundance existed among different areas of the Turkana Basin, and that some of these differences had environmental implications. The lower Omo Valley appears to have remained distinct from other parts of the Turkana Basin between 3 and 2 Ma, with consistently higher proportions of Tragelaphini and Aepycerotini, and at times of Reduncini and Bovini. These bovids are indicative of woodlands or forests (Aepycerotini and Tragelaphini) or of moist grasslands near wooded habitats (Reduncini and Bovini). An analysis of bovid tribes indicative of open and seasonally arid grasslands (Alcelaphini, Antilopini, and Hippotragini) shows relatively high proportions of these bovids in the West Turkana areas, but very low proportions in the Omo, especially prior to about 2 Ma. This indicates that the Omo remained wetter and more wooded than other parts of the Turkana Basin for much of the Plio-Pleistocene, while the West Turkana area appears to have been more open than other parts of the basin, and East Turkana had conditions intermediate between those at West Turkana and those in the Omo. Fossil bovids from the Hadar Basin suggest diverse environments including woodlands, wet grasslands, and drier savanna grasslands. An increase in the abundance of arid adapted bovids in the late Pliocene and early Pleistocene of the Turkana and Hadar Basins provides evidence that faunal changes in these different areas were driven by common factors consistent with the known record of climatic change. Analyses of species diversity among bovids show three peaks of richness in the Pliocene and Pleistocene. The first peak occurred at about 3.8–3.4 Ma, the second at 2.8–2.4 Ma, and the last from about 2.0 to 1.4 Ma. The last two of these peaks coincide with previously identified periods of high faunal turnover in East Africa. Although climate appears to have shaped major patterns in the evolution of bovids, the fact that different areas of a single sedimentary basin show distinct responses highlights the complexities involved in establishing causal links between paleoclimate and evolution.

Introduction

A key problem in paleoanthropology is the extent to which climate change has influenced the course of early human evolution (Vrba et al., 1989; Feibel, 1997; Potts, 1998; Wynn, 2004; Behrensmeyer, 2006). Patterns of hominin evolution through the Pliocene and Pleistocene are sometimes used as evidence of climatic forcing, with key diversification events said to coincide with significant climatic change. However, hominin fossils are rare, and the pattern of hominin diversification is still poorly known. Discoveries in recent years have highlighted how little we still know about the early stages of human evolution (Asfaw et al., 1999; Leakey et al., 2001; Senut et al., 2001; Brunet et al., 2002; Haile-Selassie et al., 2004). Among those mammals that are most frequently associated with fossil hominins in the late Cenozoic of Africa, bovids provide the most comprehensive record of evolutionary and environmental change over the last several million years (Vrba, 1974, 1980, 1995a; Gentry, 1978, 1985; Shipman and Harris, 1988). A detailed picture of evolutionary change in African bovids can help us understand how mammals respond to climatic changes as well as to local and regional alterations in habitat and can help us formulate hypotheses about how hominins may have responded to similar challenges. By focusing on the bovids, we aim to establish patterns that can be tested with other elements of the East African fauna.

Patterns of faunal change can be studied in a variety of ways, but here we focus on just two variables: relative abundance and taxonomic richness. We study these variables through time in scales of millions of years, and across geographical space including two distinct sedimentary basins in Kenya and Ethiopia. The key questions we seek to address are the following. What are the main patterns of faunal change in East Africa during the late Cenozoic? To what extent do different areas within the same sedimentary basin produce similar patterns of faunal change? To what extent do patterns of faunal change in one sedimentary basin resemble patterns in a different basin? Identifying significant patterns of faunal change must come before attempts to explain their causes. As suggested by Behrensmeyer and colleagues (2007), the null hypothesis is that local and regional tectonics and environmental processes control patterns of faunal change. However, if broad patterns of climate change are driving mammalian evolution in Africa (Vrba, 1995b; deMenocal, 2004), then we would expect to find similar patterns of faunal change across different regions.

To address these questions and hypotheses we provide an analysis of relative abundance and diversity in fossil bovids from the Turkana Basin of Kenya and Ethiopia, including the Shungura, Usno, Mursi, Nachukui, Koobi Fora, Kanapoi, and Nawata Formations, and from the Hadar Basin of Ethiopia's Afar region, including the Hadar and Busidima Formations. This chapter builds on the tremendous contribution of earlier research in the Turkana and Hadar areas to attempt a broad and integrative view of faunal change through time.

THE TURKANA BASIN

The Lake Turkana Basin and its northern extension, the lower Omo Valley, hold one of the most complete and well studied archives of late Cenozoic faunal and environmental change on earth (Figure 1). The main geological formations from this area provide a relatively continuous record from the late Miocene to the early Pleistocene, i.e., from about 8 Ma (million years ago) to about 1 Ma. Extensive paleontological work in the Turkana Basin over the last few decades has produced a wealth of knowledge about faunal evolution in Africa (Coppens et al., 1976; Leakey and Leakey, 1978; Harris, 1983, 1991; Eck et al., 1987; Howell et al., 1987; Harris et al., 1988; Wood, 1991; Harris and Leakey, 2003; Leakey and Harris, 2003). The importance of the Turkana Basin for our understanding of human evolution and its environmental context has long been recognized (Howell, 1968; Behrensmeyer, 1975; Coppens, 1975; Boaz, 1977), and its fossil record continues to provide crucial contextual evidence for new analytical studies (Leakey, 2001; Alemseged, 2003). The geologic framework of the Turkana Basin has been extensively studied, and strong stratigraphic correlations as well as chronometric dates have been established (Brown, 1969, 1994; de Heinzelin, 1983; McDougall, 1985; Feibel et al., 1989; McDougall and Feibel, 1999; Brown et al., 2006). A summary of dating and correlations is presented in Table 1.

HADAR

Another major area of research for human evolution in Africa has been the Hadar Basin in the Afar region of northern Ethiopia (Figure 1). Hadar provides a rich record of fossil vertebrates including early hominins, but it is more restricted than the Turkana Basin in both geographical extent and temporal depth. Nevertheless, Hadar has played a pivotal role in our understanding of early human evolution and its environmental context (Johanson and Taieb, 1976; Gray, 1980; Aronson and Taieb, 1981; White et al., 1981; Johanson et al., 1982; Kalb et al., 1982; Tiercelin, 1986; Bonnefille et al., 2004). The Hadar Formation deposits date from at least 3.4 Ma to about 2.9 Ma, and is divided into the Basal Member (>3.4 Ma), the Sidi Hakoma Member (3.4–3.22 Ma), the Denen Dora Member (3.22–3.18 Ma), and the Kada Hadar Member (3.18–2.9 Ma) (Aronson and Taieb, 1981; Walter and Aronson, 1993; Walter, 1994; Alemseged et al., 2005). A major unconformity separates the Hadar Formation from the overlying Busidima Formation as defined in the Gona area west of Hadar (Quade et al., 2004). A.L. 666 in the Maka'amitalu drainage, a locality that has yielded a maxilla attributed to early *Homo* and associated lithic artifacts (Kimbel et al., 1996), is considered here as part of the Busidima Formation, even though it has not been formally assigned to that

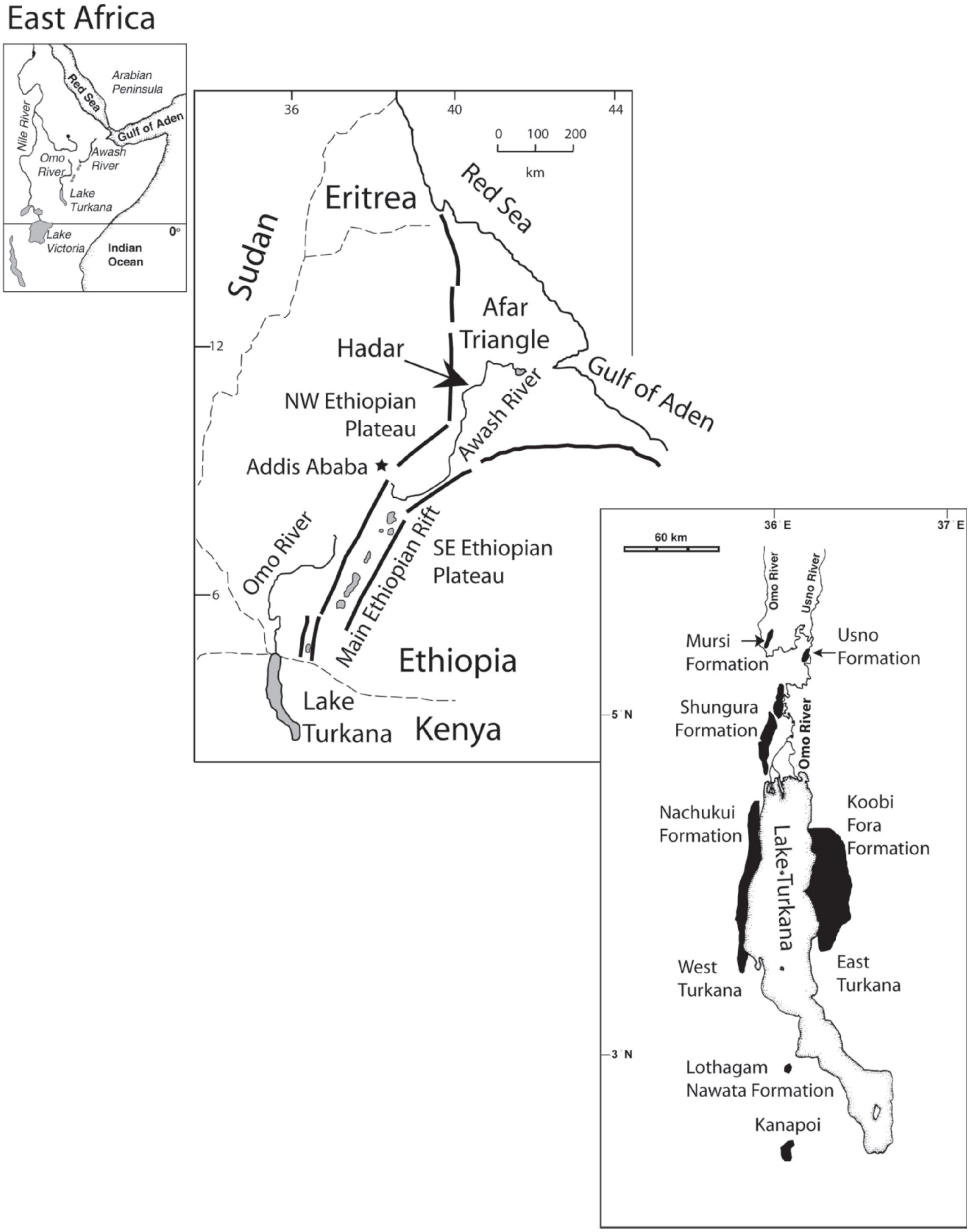

Figure 1. Map of East Africa showing the Turkana Basin and the Hadar area. Here we use the term "Turkana Basin" to refer to both the Lake Turkana area and the adjacent lower Omo Valley. The Nawata, Kanapoi, Nachukui, Koobi Fora, Shungura, Usno, and Mursi Formations from the Turkana Basin are considered in this study. The term "Hadar Basin" as used here refers to the Hadar Formation in Ethiopia's Afar region.

Table 1. Dating and correlations among formations in the Turkana Basin of Kenya and Ethiopia

Mbs	Omo	Mbs	West Turkana	Mbs	East Turkana	GPTS	Age (Ma)	+/−	Dated unit (Fm)	Method	Refs.
			Silbo Tuff		Silbo Tuff	■	0.74	0.01	Silbo Tuff (KF)	K-Ar, Ar-Ar	16, 24
							0.780			Matuyama/Brunhes	1, 10, 30
		Nariokotome	top Nariokotome Mb				0.980	0.05		Stratigraphic scaling	14
						■	0.990			GPTS Jaramillo top	1, 10
L	L9 (top)					■	1.05	0.12		Stratigraphic scaling	14
						■	1.070			GPTS Jaramillo base	1, 10
	L5/L6					■	1.12	0.02	L5/6 (Sh)	GPTS Cobb Mtn subchron (N)	10, 14, 19
					Gele Tuff		1.25	0.02	Gele Tuff (KF)	K-Ar	8
			L. Nariokotome Tuff				1.33	0.03	Nariokotome (Nk)	K-Ar	8, 16
	Tuff L-3		Naito Tuff								11, 18
	Tuff L		Chari Tuff		Chari Tuff		1.39	0.02	Chari Tuff (KF)	K-Ar, Ar-Ar	4, 24
K	Tuff K1				Koobi Fora Tuff						15
		Natoo			MFB		1.49	0.05	MFB (KF)	Stratigraphic scaling	14
	Tuff K (α)		Upper Okote Tuff	Okote	Upper Okote Tuff		1.53	0.03	Tuff K (Sh)	Stratigraphic scaling	7, 14
J	Tuff J7-1		Black Pumice Tuff		Black Pumice Tuff		1.55	0.03	BPT (KF)	Stratigraphic scaling	5, 14, 16
	Tuff J6-2		L. Koobi Fora Tuff		L. Koobi Fora Tuff		1.62	0.02	LKF Tuff (KF)	Interpolation	14
					Okote Tuff						6
		Kaitio		KBS	Lower Okote Tuff		1.62	0.02	L. Okote Tuff (KF)	Stratigraphic scaling	14
	Tuff J4		Morutot Tuff		Morutot Tuff		1.65	0.03	J4 (Sh)	K-Ar	14, 26
					A6		1.68	0.05	A6 (KF)	Stratigraphic scaling	6, 14
					White Tuff		1.70	0.03	WT (KF)	Stratigraphic scaling	5, 14
					C6		1.73	0.05	C6 (KF)	Stratigraphic scaling	6, 14
	Tuff J						1.74	0.03	Tuff J (Sh)	Stratigraphic scaling	14
	Unit H7					■	1.770		H7 (Sh)	GPTS Olduvai (top)	1, 10, 14
					A2	■	1.78	0.05	A2 (KF)	Stratigraphic scaling	6, 14
						■	1.796		Pliocene/Pleistocene boundary		1, 10, 31
	Unit H5				C4	■	1.86	0.05	C4 (KF)	Stratigraphic scaling	3, 6, 14
	Tuff H4		Malbe Tuff		Malbe Tuff	■	1.86	0.02	Malbe Tuff (KF)	K-Ar, Ar-Ar	24
	Tuff H2		KBS Tuff		KBS Tuff	■	1.88	0.02	KBS Tuff (KF)	K-Ar, Ar-Ar	4, 24
H	Tuff H					■	1.90	0.03	Tuff H (Sh)	Stratigraphic scaling	14
G					Lorenyang Tuff	■	1.90	0.05	Lorenyang (KF)	Stratigraphic scaling	14
	Unit G27					■	1.950		Unit G27 (Sh)	GPTS Olduvai base	1, 10, 14

(*Continued*)

Table 1. Dating and correlations among formations in the Turkana Basin of Kenya and Ethiopia—cont'd

F	Unit G14	Kalochoro		Burgi		■	2.09	0.04	Unit G14 (Sh)	GPTS Reunion II top	20, 27
	Unit G12					■	2.13	0.04	Unit G 12 (Sh)	GPTS Reunion II base	20, 27
	Unit G9					■	2.17	0.04	Unit G9 (Sh)	GPTS Reunion I top	20, 27
	Unit G4					■	2.25	0.04	Unit G4 (Sh)	GPTS Reunion I base	20, 27
	Tuff G						2.32	0.03	Tuff G (Sh)	K-Ar	8
	Units F3/4					■	2.37		Units F3/4 (Sh)	GPTS X(N) subchron	14
	Tuff F1		Ekalalei Tuff								14
	Tuff F		Kalochoro Tuff				2.34	0.05	Tuff F (Sh)	K-Ar	8, 14
E	Tuff E	Lok	Kokiselei Tuff				2.40	0.05	Tuff E (Sh)	Stratigraphic scaling	14
D	Tuff D		Lokalalei Tuff		Lokalalei Tuff		2.52	0.05	Tuff D (Sh)	K-Ar, Ar-Ar	8, 14, 16
C	Tuff C9	Lomekwi	Emekwi Tuff				2.581		Emekwi (Nk)	GPTS Gauss/Matuyama	11, 14, 10
	Unit C9				Basal Burgi Mb	■	2.581		Unit C9 (Sh)	GPTS Gauss/Matuyama	2, 14, 10
					Burgi Tuff	■	2.64	0.05	Burgi Tuff (KF)	K-Ar	14
	Tuff C4			Tulu Bor	Ingumwai Tuff	■	2.74	0.08	Tuff C4 (Sh)	Stratigraphic scaling	14
	Tuff C (α)				Hasuma Tuff	■	2.85	0.08	Tuff C (Sh)	Stratigraphic scaling	14
B	Tuff B10					■	2.95	0.05	Tuff B-10 (Sh)	K-Ar	8
							3.04			GPTS Kaena top	1, 10, 27
					Ninikaa Tuff		3.08	0.03	Ninikaa (KF)	K-Ar, Ar-Ar	24
							3.11			GPTS Kaena base	1, 10, 27
	U14				Karo	■	3.2		U14 (Us)		9
					Allia Tuff	■	3.22	0.05	Allia Tuff (KF)	Stratigraphic scaling	14
	Unit B2 (U12)						3.22		Unit B2 (Sh)	GPTS Mammoth top	2, 10, 27
	Unit B1 (U11-12)						3.33		Unit B1 (Sh)	GPTS Mammoth base	2, 10, 27
					Toroto Tuff	■	3.32	0.02	Toroto (KF)	K-Ar, Ar-Ar	24
	Tuff B-β (U10)		Tulu Bor Tuff (beta)		Tulu Bor Tuff (β)	■	3.40	0.03	SHT (Hadar)	Ar-Ar	2, 28, 32
		Kataboi	Burrowed bed			■	3.53			Interpolation	23
A	Tuff A (U6)		Lokochot Tuff	Lok	Lokochot Tuff		3.594		Tuff A (Sh)	GPTS Gilbert/Gauss	12, 14, 29
				Moi	Wargolo Tuff		3.77		VT-3 (Maka)		15, 33
	Usno 1		Moiti Tuff		Moiti Tuff		3.94	0.04	Moiti Tuff (Nk)	Ar-Ar	23, 24, 33

	Topernawi Tuff	Lonyumun	Topernawi Tuff	3.96	0.03	Topernawi Tuff (Nk)	Ar-Ar	14, 23
	Kataboi Basalt			4.05	0.06	Basalt (Nk)	K-Ar	8
	Kanapoi Tuff			4.07	0.02	KT (Kp)	Ar-Ar	21, 22
Usno Basalt				4.10	0.06	Basalt (Us)	K-Ar, Ar-Ar	8, 11, 17
Mursi Basalt				4.2	0.2	Basalt (Mu)	K-Ar	8, 14, 17
	Kanapoi upper pumiceous tuff			4.12	0.02	tuff (Kp)	Ar-Ar	21
	Kanapoi lower pumiceous tuff			4.17	0.03	tuff (Kp)	Ar-Ar	21
	Lothagam Basalt			4.20	0.03	Lothagam Basalt (Nw)	K-Ar, Ar-Ar	13, 17, 25
	Tuff in Apak Mb			4.22	0.03	Tuff in Apak Mb (Nk)	Ar-Ar	13, 25
			Karsa Basalt	4.35	0.05	Karsa Basalt (KF)	K-Ar	14, 17, 24
				5.3		Miocene/Pliocene boundary		1, 10
	Marker Tuff			6.54	0.04	Marker Tuff (Nw)	Ar-Ar	13
	Lower Markers			7.44	0.05	Lower Markers (Nw)		25

References:

1) Berggren et al., 1995; 2) Brown, 1983; 3) Brown, 1995; 4) Brown and Nash, 1976; 5) Brown and Feibel, 1985; 6) Brown and Feibel, 1986; 7) Brown and McDougall, 1993; 8) Brown et al., 1985; 9) Brown et al., 1992; 10) Cande and Kent, 1995; 11) de Heinzelin, 1983; 12) de Heinzelin and Haesaerts, 1983; 13) Feibel, 2003; 14) Feibel et al., 1989; 15) Haileab and Brown, 1992; 16) Haileab and Brown, 1994; 17) Haileab et al., 2004; 18) Harris et al., 1988; 19) Howell et al., 1987; 20) Lanphere et al., 2002; 21) Leakey et al., 1995; 22) Leakey et al., 1998; 23) Leakey et al., 2001; 24) McDougall, 1985; 25) McDougall and Feibel, 2003; 26) McDougall et al., 1985; 27) McDougall et al., 1992; 28) Sarna-Wojcicki et al., 1985; 29) Shackleton, 1995; 30) Tauxe et al., 1992; 31) Van Couvering, 1996; 32) Walter and Aronson, 1993; 33) White et al., 1993.

Key to Abbreviations: Sh = Shungura Formation, Nk = Nachukui Formation, KF = Koobi Fora Formation; GPTS = Global Polarity Time Scale; black indicates intervals of normal polarity and white indicates intervals of reversed polarity.

Note: Ages given of sub-members reflect the age at the base of the unit, unless noted otherwise. For the three major regions of the Turkana Basin, alternating gray shading and white are used to separate successive members within each formation. Gray bands on right side of the table highlight the major Epoch boundaries.

sequence. Thus, the specimens analyzed here derive from the well-studied Hadar deposits north of the Awash River and the A.L. 666 locality in the Maka'amitalu drainage.

PALEONTOLOGICAL DATABASES

One of the earliest efforts in East Africa to maintain an electronic catalogue of collected specimens was made in the 1960s and 1970s by the Omo Research Expedition (Eck, 2007). Researchers today routinely keep their paleontological records in electronic databases, but there is little standardization of fields or compatibility among the various formats that are used. Following the model of the Shungura Formation Catalogue of Fossil Specimens (compiled by G. Eck), we have developed a network of paleontological databases which, although independent of each other, maintain comparable fields of information about each fossil specimen and its geological context. The Shungura Formation American Catalogue has 22,335 records, most of which consist of fossil mammals. A separate catalogue documenting specimens from the French Shungura collection has nearly 27,000 records (Alemseged et al., 2007). There is also a Mursi Formation Catalogue, with 142 records and an Usno Formation Catalogue, with 2525 records (maintained by G. Eck and R. Bobe). For the rest of the Turkana Basin (Koobi Fora, Nachukui, Kanapoi, and Nawata Formations), we have compiled the Turkana Basin Paleontology Database, which has about 16,500 records of fossil mammals (and is maintained by R. Bobe, A.K. Behrensmeyer, E. Mbua, and M. Leakey). This database has been created by a collaborative project between the National Museums of Kenya and the Smithsonian Institution, and is scheduled to be posted online by these institutions. A separate database (created and maintained by G. Eck) archives records of fossil vertebrates from Hadar; the Catalogue of Hadar Fossil Specimens has 8131 records. This network of databases relies on FileMaker Pro software, but records can be easily exported to other formats. We use this network of databases to analyze patterns of relative abundance and diversity in bovids from the late Cenozoic of the Turkana and Hadar Basins. We exclude the French Shungura database because it is being separately analyzed by Alemseged and colleagues (2007).

Methods

In order to assess patterns of faunal change over intervals of several million years, we use the geological member as our basic "sampling unit" (Table 2) (Ludwig and Reynolds, 1988). A few members spanning long time intervals were subdivided as long as adequate sample size could be maintained (n >50 specimens). For example, the Lomekwi Member of the Nachukui Formation is divided into lower, middle, and upper sections; we combined the lower with the middle sections, and the upper section with the overlying Lokalalei Member. Member B of the Shungura Formation has a rich fossil record in the upper sections, but a very poor record in the lower ones. The rich record of the Usno Formation (U-12) correlates with lower Member B, and therefore we separate Member B into a lower section that includes Usno, here labeled as B(L), and an upper section, B(U). Shungura Member G is divided into a fluvio-deltaic lower section, G(L), and a largely lacustrine upper section, G(U). Analyses at finer levels of temporal resolution are possible given the rich fossil record of some sections of the Turkana and Hadar deposits (Bobe et al., 2002), but the goal here is to detect the major trends over long time intervals. Geological members with small numbers of bovid specimens (<50) were combined with adjacent members (e.g., Kataboi-Kaiyumung, Upper Lomekwi-Lokalalei, and Natoo-Nariokotome) so that

Table 2. Abundance of bovid tribes (number of specimens) across geological members from the Hadar, Busidima, Shungura, Usno, Koobi Fora, Nachukui, Kanapoi, and Nawata Formations

		BOVID TRIBES								
Formation	Member or unit	Aepycerotini	Alcelaphini	Antilopini	Boselaphini	Bovini	Hippotragini	Reduncini	Tragelaphini	Total
Nawata	L. Nawata	72	7	1	37	2	8	17	5	149
Nawata	U. Nawata	58	25	2	11	3	8	31	3	141
Nachukui	Apak Mb	20	9	3	2	6	3	6	13	62
Kanapoi	Kanapoi	18	23	2	0	4	4	8	52	111
Nachukui	Kataboi-Kaiyumung	14	10	4	0	7	2	8	13	58
Nachukui	Lomekwi (L-M)	79	102	42	0	10	17	61	36	347
Nachukui	Lomekwi(U)-Lokalalei	10	46	10	0	9	6	65	14	160
Nachukui	Kalochoro	10	27	14	0	5	5	40	9	110
Nachukui	Kaitio	9	23	3	0	10	4	14	30	93
Nachukui	Natoo-Nariokotome	9	50	16	0	8	3	43	11	140
Koobi Fora	Lokochot	16	9	4	0	4	0	10	24	67
Koobi Fora	Tulu Bor	4	14	7	0	25	0	96	39	185
Koobi Fora	Burgi(U)	36	59	47	0	12	5	194	65	418
Koobi Fora	KBS	78	172	81	0	66	14	318	121	850
Koobi Fora	Okote	6	35	7	0	15	0	71	33	167
Usno	B(L)	128	4	3	0	28	0	4	50	217
Shungura	B(U)	49	7	1	0	24	0	63	32	176
Shungura	C	94	5	3	0	73	3	74	178	430
Shungura	D	56	6	1	0	15	0	30	66	174
Shungura	E	91	9	0	0	13	1	56	117	287
Shungura	F	141	25	5	0	15	0	69	87	342
Shungura	G(L)	461	51	4	0	38	2	684	375	1615
Shungura	G(U)	24	13	9	0	2	0	29	2	79
Shungura	H	7	12	3	0	2	0	125	4	153
Shungura	J	6	8	0	0	1	0	39	0	54
Shungura	K	5	15	2	0	1	0	27	1	51
Shungura	L	4	11	1	0	2	0	42	2	62
Hadar	SH	146	94	16	0	83	12	53	92	496
Hadar	DD	132	127	5	0	77	7	298	103	749
Hadar	KH	28	46	46	0	24	7	15	33	199
Busidima	Maka'amitalu	2	11	11	0	14	5	10	18	71
	Total	1813	1055	353	50	598	116	2600	1628	8213

the total sample size per interval exceeds 50 specimens (Table 2). Thus we have tried to maximize resolution across geological formations while maintaining samples adequate for statistical analyses.

There are 12 bovid tribes represented in the late Cenozoic fossil record of the Turkana Basin: Aepycerotini, Alcelaphini, Antilopini, Boselaphini, Bovini, Caprini, Cephalophini, Hippotragini, Neotragini, Ovibovini, Reduncini, and Tragelaphini. Boselaphini are found only in the Nawata Formation and the lowermost Nachukui Formation (Apak Member) at Lothagam (Harris, 2003). Caprini, Cephalophini, Neotragini, and Ovibovini have a sparse fossil record and therefore are not used here in the analyses of abundance, but they are used in analyses of diversity. Our analyses of taxonomic abundance are based on numbers of fossil specimens, counting multiple catalogued specimens of the same individual as one. Because of taphonomic processes, these abundances likely are a biased representation of actual live abundances in the original ecosystems. However, these biases can be controlled by restricting the analysis to the most commonly collected and identifiable elements of the bovid skeleton, primarily horn cores and teeth. We assess relative abundances with two methods: correspondence analysis and changes in tribe-specific proportions through time. Correspondence analysis provides a visual assessment of contingency tables with cells containing frequency counts (Table 2). Correspondence analysis displays graphically the relationship between two nominal variables (e.g., geological members and bovid taxa). Categories that are similar to each other appear close together in the graphic display, and those that are different occur farther apart (Benzécri, 1992; Greenacre, 1993). The graphical output (Figure 2) shows each taxon pulled toward the geological members in which the taxon has high relative abundance. Thus we may obtain associations of taxa that have high abundances in particular members. Correspondence analysis also distributes members (sampling units) in relation to the taxa they contain. Interpretations of these graphs consist of examining the spread of taxa and sampling units across each axis in search of underlying ecological or environmental features that may explain the spread of points (Greenacre and Vrba, 1984). The correspondence analysis shown in Figure 2 excludes the Nawata Formation because the high abundance of Boselaphini in the late Miocene makes this sequence distinctly different from the later deposits in the Turkana and Hadar areas. Boselaphini became rare or absent from the East African fossil record after

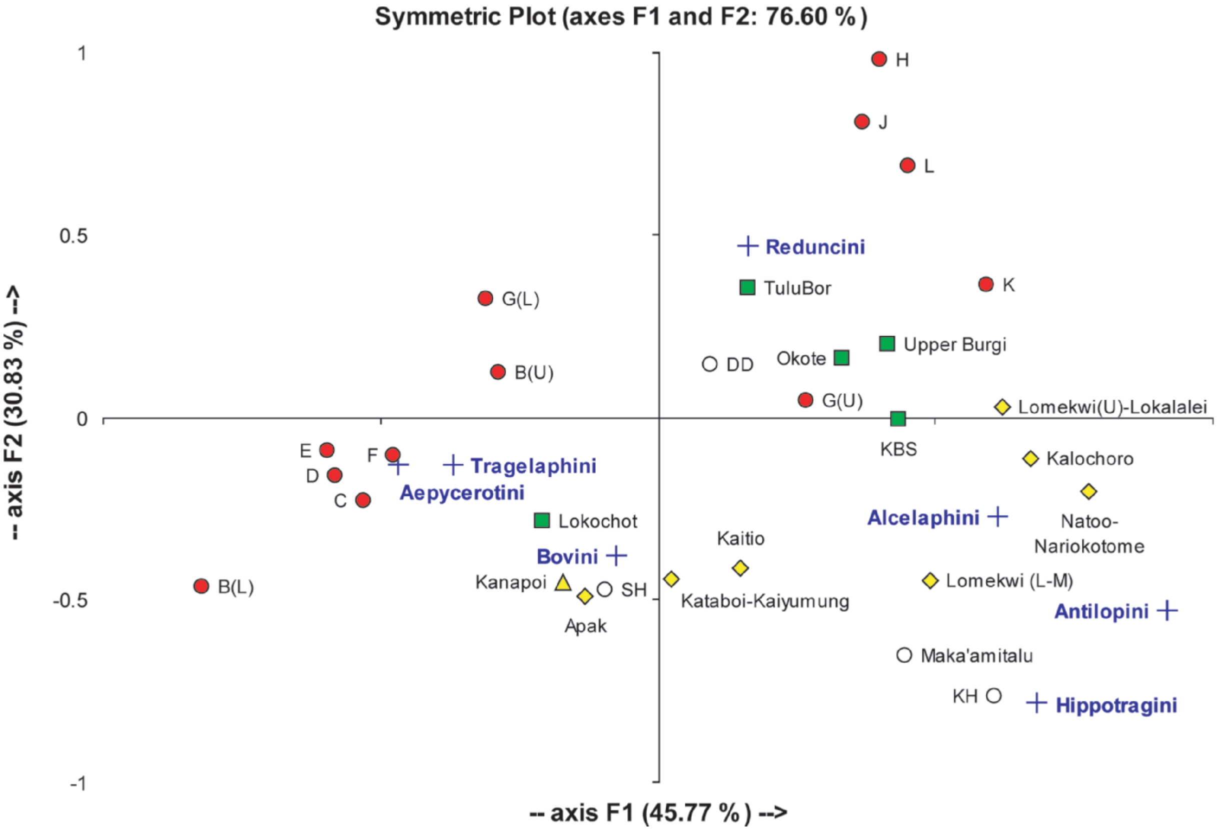

Figure 2. Correspondence analysis of bovid tribes in the Shungura, Usno, Koobi Fora, Nachukui, Kanapoi, Hadar, and Busidima Formations (Maka'amitalu drainage).

the Miocene/Pliocene boundary (Vrba, 1995a; Harris, 2003).

The correspondence analysis display (Figure 2) shows an association among Alcelaphini, Antilopini, and Hippotragini, and this association is confirmed by different methods with a cluster analysis (Figure 3). Modern Alcelaphini (wildebeests, hartebeests, and topi) are cursorial and hypsodont grazers that typically occur in open grasslands or wooded grasslands (Kingdon, 1982b; Gagnon and Chew, 2000), and their Plio-Pleistocene ancestors may have shared those habits (Kappelman et al., 1997; Spencer, 1997; Sponheimer et al., 1999). Antilopini are cursorial and hypsodont grazers or browsers in arid bushland–grasslands (Kingdon, 1982b). Although not all species of Antilopini are grazers (Sponheimer et al., 1999; Gagnon and Chew, 2000; Cerling et al., 2003), they tend to occur in arid grasslands or bushland, and even in deserts. Hippotragini are cursorial and hypsodont grazers that occur in wooded grasslands, grasslands, or semideserts (Kingdon, 1982b). The close association among these three tribes (Alcelaphini, Antilopini, and Hippotragini) in both the correspondence and the cluster analyses suggests that they may be combined and treated as a variable. Vrba (1980) has argued that the abundance of Alcelaphini and Antilopini as a proportion of the entire bovid fauna may be used as an indication of open and arid conditions. As noted above, Hippotragini (especially the genera *Oryx* and *Addax*) are likewise well adapted to open and arid conditions (Kingdon, 1982a). Thus we use the Alcelaphini–Antilopini–Hippotragini (AAH) criterion as a variation of Vrba's (1980) Alcelaphini–Antilopini criterion of open-dry environments, usually savanna grasslands, bushland or woodland–grassland mosaics. It should be noted that Reduncini and Bovini are also grazers, but these bovids consume fresh grasses in moist habitats, woodland clearings, or near waterlogged conditions (Kingdon, 1982b), and therefore are poor indicators of seasonally arid grasslands. AAH is measured as the combined proportion of Alcelaphini, Antilopini, and Hippotragini among all bovid specimens that can be identified to tribe. Confidence limits of AAH proportions are calculated with the methods of Buzas and Hayek (Buzas, 1990; Hayek and Buzas, 1997).

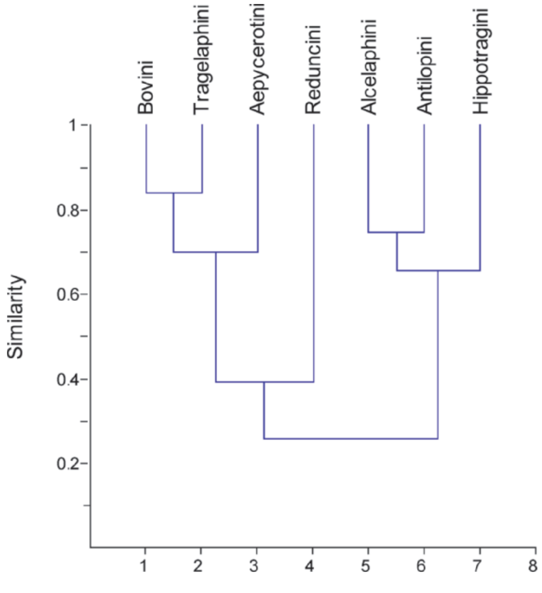

Figure 3. Cluster analysis of bovid tribes based on abundance data across geological members from the Turkana and Hadar areas. Paired groups using rho similarity measure with Past software.

There have been notable efforts to identify the feeding adaptations and habitat preferences of extinct bovids through analyses of ecomorphology (Plummer and Bishop, 1994; Kappelman et al., 1997; Spencer, 1997; Sponheimer et al., 1999; DeGusta and Vrba, 2003). These studies indicate that the habitat preferences of bovid tribes have remained relatively consistent over the last few million years, even if some taxa have changed their feeding behavior since the Pliocene. Alcelaphini and Antilopini in particular appear to have radiated into seasonally arid habitats early in their evolutionary history (Greenacre and Vrba, 1984; Vrba, 1987).

The AAH variable is not meant to provide a direct translation of habitat type at any one time. An AAH abundance of 50% does not necessarily mean that the environment from which these bovids derive was composed of grasslands over 50% of its area. Several biases influence this proportion. For example, most collections are probably biased against small bovids such as duikers or dik-diks, which may fragment more easily or be more difficult to see in surface surveys than larger bovids. But if taphonomic and collection biases are relatively constant among sampling units, then changes in this variable over time should convey important environmental information. Thus, we assume that a significant increase in AAH means an increase in the importance of seasonally arid environments in the landscape, even though we do not know exactly the proportions of different vegetation types on that landscape.

In analyses of relative abundance in the fossil record it is important to evaluate the taphonomic context of the specimens under consideration. In previous analyses of relative abundance we have done just that (Bobe and Eck, 2001; Bobe et al., 2002): we have considered the sedimentological context and used skeletal elements as a proxy measure of taphonomic conditions. After controlling for taphonomic and sedimentologic conditions, we have found that changes in taxonomic relative abundances can provide important environmental and ecological information. In this regard it is also critical to consider collection methods in the field that may bias the proportions of the taxa being analyzed. Eck (2007) provides an important analysis of collection effort in relation to the Shungura Formation. A detailed assessment of taphonomy, sedimentology, and collection biases in the Turkana and Hadar areas is beyond the scope of this paper, although efforts in this regard are in progress (Behrensmeyer et al., 2004; Campisano et al., 2004). Thus, we assume for the time being that these processes bias relative abundances more or less equally across geological members. The results presented here would not be significantly altered as long as these biases affect the sampling units to a similar degree. However, until further research can be done to assess how taphonomic and collection factors affected the catalogued fossil collections from the Turkana and Hadar Basins, our results should be considered as hypotheses and subjected to further testing.

In the analysis of diversity we have focused on species richness, i.e., the number of bovid taxa per time interval. In the assessment of species richness over time it is desirable to consider approximately equal time intervals. We have divided the time span from 4.2 to 1 Ma into intervals of 200 Kyr (thousand years) (Table 3). Finer levels of temporal resolution are possible for the Shungura record, which often contains information at the submember level, but resolution tends to be coarser elsewhere. Many of the fossils analyzed here derive from geological units that do not fall neatly into 200-Kyr categories. In these cases we have assigned specimens to the 200-Kyr intervals encompassed by the geological unit. For example, the Kaitio Member of the Nachukui Formation spans from 1.88 Ma to about 1.6 Ma, and we have assigned taxa that occur in that member to both the 2.0–1.8 Ma interval and the 1.8–1.6 Ma interval. This procedure undoubtedly introduces an error into the richness calculations, and highlights the need to assign fossil specimens to finer levels of stratigraphic resolution. Nevertheless, by using broad time intervals we have tried to match the scale of the analysis to the quality of the record.

Results

CORRESPONDENCE ANALYSIS

The correspondence analysis depicted in Figure 2 shows the distribution of bovid tribes with respect to their abundance across geological members in the Shungura, Usno, Nachukui,

Table 3. Turkana Basin Bovidae across time intervals in the late Cenozoic

Time in Ma	7.44–6.54	6.54–5.23	4.5–4.22	4.2–4.0	4.0–3.8	3.8–3.6	3.6–3.4	3.4–3.2	3.2–3.0	3.0–2.8	2.8–2.6	2.6–2.4	2.4–2.2	2.2–2.0	2.0–1.8	1.8–1.6	1.6–1.4	1.4–1.2	1.2–1.0	
Omo				Mursi			A	B2–3 -U12	B6–B9	B10–C2	C3–C9	D0–5	E-F–G8	G9–23	G24–H	J	K	L0–L4	L5–L9	
West Turkana	Nawata (L)	Nawata (U)	Apak	Kanapoi	Kataboi – Kaiyumung	Kataboi – Kaiyumung	Kataboi – Kaiyumung	L. Lomekwi	L. Lomekwi	M. Lomekwi LO10	M. Lomekwi LO9	U. Lomekwi – Lokalalei	Kalochoro	Kalochoro	Kalochoro – Kaitio	Kaitio	Natoo	Nariokotome	Nariokotome	
East Turkana				Lonyumun	Lonyumun – Moti	Moiti	Lokochot	L. Tulu Bor	L. Tulu Bor	U. Tulu Bor	U. Tulu Bor	L. Burgi	Unconformity	Unconformity	U. Burgi – KBS	KBS	Okote	Chari	Chari	Total
AEPYCEROTINI																				
Aepyceros premelampus	70	58	20	7	3	3	3	0	0	0	0	0	0	0	0	0	0	0	0	164
Aepyceros shungurae-melampus	0	0	0	0	0	3	20	176	10	50	95	60	408	290	97	55	14	5	2	1285
Aepyceros sp. Nov. A	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	6
Aepyceros sp. Nov. B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
ALCELAPHINI																				
Beatragus antiquus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	8	2	0	0	13
Beatragus hunteri	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Connochaetes aff. gentryi	0	0	0	0	0	0	7	3	0	0	0	0	0	0	0	0	0	0	0	10
Connochaetes gentryi	0	0	0	0	0	0	0	0	0	0	0	2	0	0	13	16	9	0	0	40
Damalacra sp. A	4	23	4	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	32
Damalacra sp. B	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
Damaliscus (Parmularius)	0	0	0	0	0	0	0	0	0	0	5	0	0	0	33	33	7	0	0	78
Damaliscus cf. niro	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	3
Damalops aff. palaeindicus	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Megalotragus isaaci	0	0	0	0	0	0	0	0	0	0	0	0	0	0	35	37	9	0	0	81

(*Continued*)

Table 3. Turkana Basin Bovidae across time intervals in the late Cenozoic—cont'd

Megalotragus kattwinkeli	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	5	1	0	7
Parmularius altidens	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	3
cf. Parmularius angusticornis	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	2
ANTILOPINI																				
Antidorcas recki	0	0	0	0	0	0	1	4	3	1	1	1	4	5	18	49	3	0	0	90
Antilope aff. subtorta	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	2
Gazella cf. granti	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	1	0	0	4
Gazella janenschi	0	0	0	1	0	0	0	2	1	0	1	0	0	0	4	4	2	0	0	15
Gazella praethomsoni	0	0	0	0	0	0	4	2	2	0	1	1	4	2	19	11	5	1	0	52
BOSELAPHINI																				
Tragoportax cf. cyrenaicus	7	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10
Tragoportax sp. A	4	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6
Tragoportax sp. B	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
BOVINI																				
Pelorovis oldowayensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	12	7	0	0	21
Pelorovis turkanensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	53	8	1	0	68
Simatherium cf. kohllarseni	0	0	1	0	1	1	2	14	0	11	0	0	0	0	0	0	0	0	0	30
Simatherium shungurense	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Syncerus acoelotus	0	0	0	0	0	0	0	0	0	0	13	0	4	3	1	0	0	2	0	23
Syncerus cf. caffer	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2
Ugandax sp. Nov.	0	0	0	0	0	0	0	3	2	2	1	1	1	1	0	0	0	0	0	11
CAPRINI																				
Caprini sp. 1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	2
Caprini sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	2
Caprini sp. B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
Caprini sp. C	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	2
CEPHALOPHINI																				
Cephalophus	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	2
HIPPOTRAGINI																				
Hippotragus sp.	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
Hippotragus gigas	0	0	0	0	0	0	0	0	0	0	1	0	0	0	3	3	1	0	0	8
Oryx sp.	0	0	0	0	0	0	0	0	0	0	1	1	0	0	2	12	0	0	0	16
Praedamalis sp.	2	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6
NEOTRAGINI																				
Madoqua	1	3	1	1	0	0	1	0	0	0	0	0	0	0	2	0	0	0	0	9
Raphicerus	1	1	2	1	1	1	0	0	0	0	0	0	2	0	1	5	0	0	0	15
OVIBOVINI																				
Makapania	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	3

REDUNCINI																			
Kobus ancystrocera	0	0	0	0	0	0	0	3	2	3	11	0	6	25	6	44	0	0	0	100
Kobus ellipsiprymnus	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	5	2	0	1	10
Kobus cf. kob	0	0	0	0	0	0	1	1	1	2	2	1	0	1	0	0	0	0	0	9
Kobus kob	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	29	65	6		100
Kobus laticornis	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10
Kobus aff. Leche	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	15	1	0	1	20
Kobus oricornus	0	0	0	0	0	2	6	11	12	7	14	2	0	0	0	0	0	0	0	54
Kobus presigmoidalis	5	13	4	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	23
Kobus sigmoidalis	0	0	0	0	0	2	2	6	6	1	8	11	204	40	108	81	4	0	0	473
Menelikia leakeyi	4	3	0	0	0	13	0	4	4	5	11	1	0	0	0	0	0	0	0	45
Menelikia lyrocera	0	0	0	0	0	1	0	1	1	0	1	2	94	45	51	84	3	0	0	283
Redunca	0	0	0	0	0	0	0	0	0	1	2	0	2	0	0	0	1	1	0	7
TRAGELAPHINI																				
Taurotragus arkelli-oryx	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	2
Tragelaphus gaudryi	0	0	0	0	0	0	0	0	0	0	0	0	162	39	2	0	0	0	0	203
Tragelaphus kyaloae	0	1	7	38	13	3	3	0	0	0	0	0	0	0	0	0	0	0	0	65
Tragelaphus nakuae	0	0	1	0	4	2	19	60	18	31	176	62	301	93	21	5	1	0	0	794
Tragelaphus pricei	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
Tragelaphus scriptus	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	3
Tragelaphus strepsiceros	0	0	0	0	0	0	0	0	0	0	0	0	0	3	38	105	21	2	1	170
Sample size	102	123	44	48	23	32	71	291	62	115	349	150	1203	549	470	673	174	20	11	4510
Number of taxa	12	13	9	5	5	11	14	15	12	12	21	17	18	14	24	26	23	9	9	

Koobi Fora, and Hadar Formations. It is noteworthy that bovid tribes in this analysis separate strongly into recognizable habitat categories. The bovid tribes Tragelaphini, Aepycerotini, and Bovini occur on the left side of the graph. These bovids are associated with woodlands or forests (Tragelaphini), woodland–grassland ecotones (Aepycerotini), or woodland–grasslands near water (Bovini). The tribes Alcelaphini, Antilopini, and Hippotragini cluster toward the right side of the graph. These bovids generally are hypsodont and cursorial grazers, although some species of recent Antilopini are browsers in semiarid bushland. Thus, the main axis of the correspondence analysis (horizontal axis in Figure 2, explaining 46% of the variation) may be interpreted as a gradient from closed and moist environments associated with the Tragelaphini–Aepycerotini–Bovini pole to dry and open environments associated with the Alcelaphini–Antilopini–Hippotragini pole. A third pole occupied by Reduncini on the upper part of the graph likely indicates wet grasslands or waterlogged conditions.

The distribution of geological units in Figure 2 shows that Omo Shungura Members B through lower G are pulled strongly toward the Tragelaphini–Aepycerotini–Bovini pole. These members are clearly separated from Shungura Members H through L, with upper Member G in an intermediate position. This separation into lower and upper members indicates a major shift in the bovid fauna through the sequence. The association of Members B through lower G with Tragelaphini–Aepycerotini–Bovini (and to some extent with Reduncini) indicates that these members were characterized by wooded and moist habitats. The later members of the Shungura Formation (H through L) have higher proportions of Alcelaphini, Antilopini, and Reduncini, and indicate a greater dominance of open grasslands during deposition of these members, even though moist grasslands and waterlogged conditions also occurred near the environments of deposition. Thus, the distribution of Shungura members depicted in this analysis provides evidence of environmental changes in the lower Omo Valley during the Plio-Pleistocene, with increasingly open environments dominating the landscape after about 2 Ma (the age of upper Member G).

The lower members of the Shungura Formation contrast not only with the upper members, but also with most of the geological members from the Nachukui, Koobi Fora, and Hadar Formations. Only the Lokochot Member of the Koobi Fora Formation, the Apak Member of the Nachukui Formation, the Sidi Hakoma Member of the Hadar Formation, and the Kanapoi sequence approach the lower Omo members in the distribution of bovid tribes (Figure 2). These members (Lokochot, Apak, Sidi Hakoma, and Kanapoi) are older than 3.4 Ma, and they all cluster toward the closed-wooded end members of the correspondence analysis figure.

Geological units most strongly pulled toward the Alcelaphini–Antilopini–Hippotragini pole are the Kada Hadar Member of the Hadar Formation, the Maka'amitalu site (A.L. 666 locality), and the Lomekwi, Lokalalei, Kalochoro, Natoo, and Nariokotome Members of the Nachukui Formation. Thus, most of the Nachukui Formation members occur toward the open-arid pole of the correspondence analysis graph, in contrast to Shungura members which occur either near the wet-closed pole or the wet-open pole (Reduncini).

The Hadar units are spread out in the graph: the Sidi Hakoma Member is pulled in the direction of Tragelaphini–Aepycerotini–Bovini, the Denen Dora Member in the direction of Reduncini, and the Kada Hadar Member with the Maka'amitalu locality toward the Alcelaphini–Antilopini–Hippotragini pole. This would indicate a prevalence of closed environments during Sidi Hakoma times, wet grasslands during Denen Dora times, and a shift to more open environments during Kada Hadar times.

The correspondence analysis of bovid tribes across geological units from the Turkana and

Hadar Basins suggests several noteworthy points. First, the lower Shungura Formation members (B through lower G) differ from most other geological units and were characterized by a high abundance of bovids indicative of closed, wet, and wooded environments. Second, the upper members of the Shungura Formation (H through L) clearly differ from earlier members and indicate that significant environmental changes occurred in the lower Omo Valley toward more open conditions beginning with the deposition of upper Member G, i.e., around 2 Ma. Third, most of the Nachukui Formation members are pulled toward the Alcelaphini–Antilopini–Hippotragini pole and suggest that environmental conditions in the western parts of the Turkana Basin were consistently more open and arid than in the lower Omo Valley during the Plio-Pleistocene. Fourth, Koobi Fora Formation members are separated into two groups: the Lokochot Member is pulled toward the Tragelaphini–Aepycerotini–Hippotragini pole while the Tulu Bor, Upper Burgi, KBS, and Okote members are pulled toward a Reduncini–Alcelaphini pole, a pattern that suggests a greater importance of grasslands (both moist and dry) in the eastern parts of the Turkana Basin after 3.4 Ma. Finally, the Hadar sampling units are well separated from each other in the correspondence analysis figure: the Sidi Hakoma Member is dominated by bovids characteristic of wet and wooded conditions; the Denen Dora Member is dominated by bovids characteristic of wet grasslands; while the Kada Hadar Member and the Maka'amitalu locality are dominated by bovids indicative of more open and arid habitats. This distribution of Hadar units indicates a shift to drier conditions after about 3.2 Ma.

CLUSTER ANALYSIS

The cluster analysis (rho similarity measure) presented in Figure 3 provides a grouping of bovid tribes similar to the pattern seen in the correspondence analysis figure. Correspondence analysis suggests a correlation, or covariation, of Tragelaphini and Aepycerotini which is confirmed in the cluster analysis of Figure 3. These two taxa also cluster with Bovini and Reduncini, but are distinctly separated from the cluster of Alcelaphini, Antilopini, and Hippotragini. The cluster formed by the "moist-grass grazers" (Reduncini) plus Bovini, Aepycerotini, and Tragelaphini likely represents vegetation types that depend on moister climatic or ground-water conditions with less severe dry seasons, while the cluster formed by Alcelaphini, Antilopini, and Hippotragini represents open or bushy vegetation that characterizes environments with marked dry seasons. Thus, this cluster analysis reinforces the associations of bovid tribes derived from correspondence analysis.

HABITAT INDICATORS

The proportions of Alcelaphini–Antilopini–Hippotragini (AAH) among bovids from the Turkana and Hadar Basins during the interval from about 7 to 1 Ma are shown in Figure 4A, while Figure 4B presents the same data focused on the Turkana Basin during the interval from 4 to 1 Ma. A noteworthy aspect of this analysis is that Omo Shungura members from 3.4 to about 2 Ma show consistently low proportions of AAH. As this proportion increases after 2 Ma, Shungura members approach the levels seen in other sequences. The persistently low proportion of AAH in Members B through lower G indicates a high degree of environmental stability in the lower Omo Valley during the interval from about 3.4 to 2 Ma. This is evidence for wooded environments in the Omo during the late Pliocene, even though other parts of the Turkana Basin and other regions of Africa had more open and perhaps more unstable environments. The idea of an Omo refugium during the Pliocene has

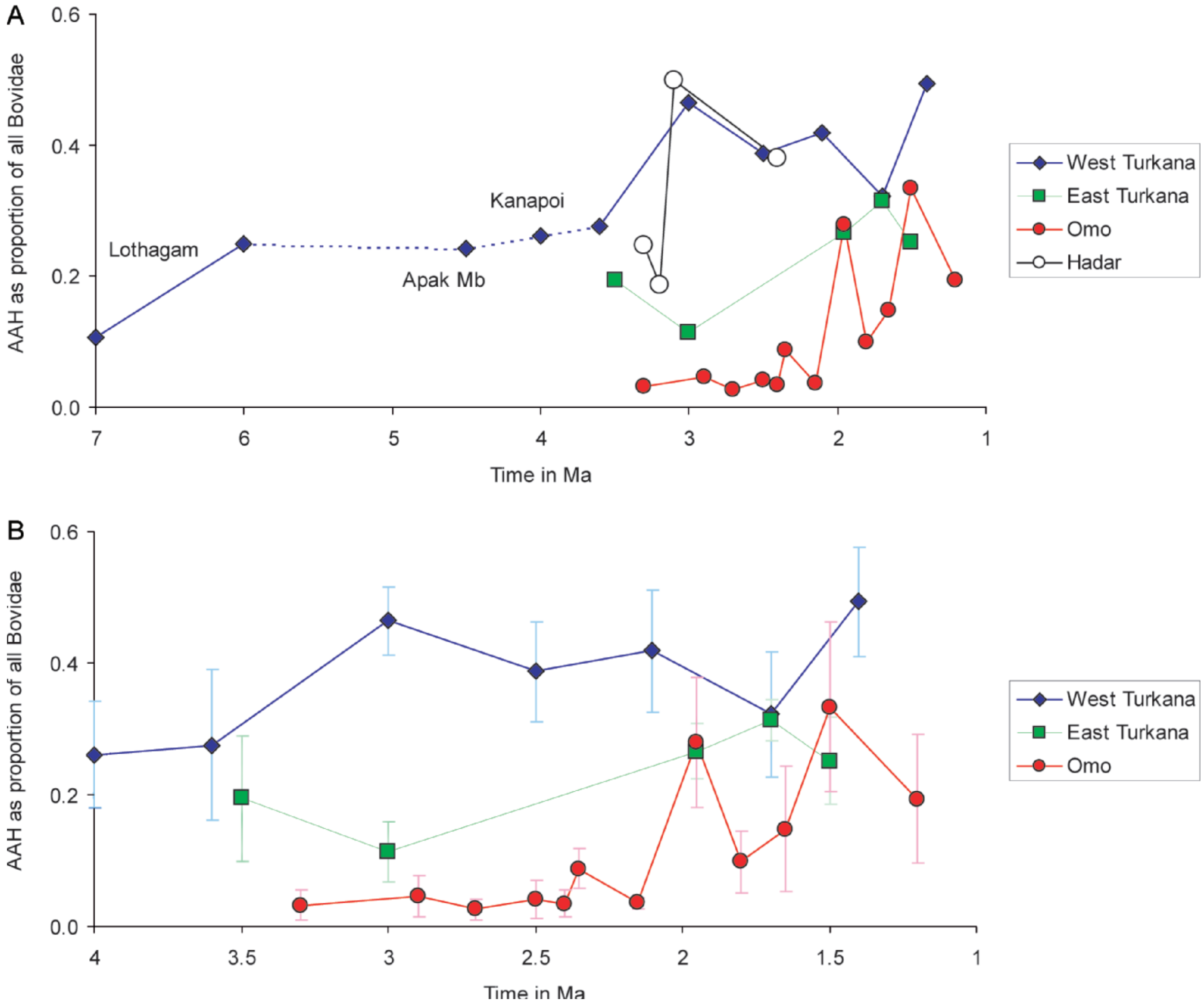

Figure 4. Abundance of Alcelaphini, Antilopini, and Hippotragini (AAH) as a proportion of all bovid specimens per geological interval.

been proposed by Vrba (1988) and is supported by this analysis.

The Nachukui Formation has significantly higher proportions of AAH than the Shungura Formation during the Plio-Pleistocene, but both sequences show a degree of convergence after 2 Ma. Although the lowest proportion of AAH in the Nachukui Formation occurs in the earliest interval (Apak Member), and the highest proportion occurs in the latest interval (Natoo-Nariokotome Members), the West Lake Turkana sequence does not show as strong a trend toward higher proportions of AAH over time as the Omo does. At East Turkana, the earliest intervals (Lokochot and Tulu Bor) show the lowest AAH proportions and the later intervals (Upper Burgi, KBS, and Okote) the highest. Thus at East Turkana, as in the Shungura and Nachukui Formations, the trend is toward increasing proportions of open country bovids toward the latest Pliocene and earliest Pleistocene. Nevertheless, the significant differences in AAH proportions among the three main Turkana Basin areas suggest that intra-basinal faunal differences existed through the Pliocene and Pleistocene. These differences are consistent with the idea that the Shungura Formation sampled the main axis of the Plio-Pleistocene Turkana Basin, close to the course of the paleo-Omo River, whereas the Nachukui Formation sampled more marginal habitats in the basin, as proposed by Feibel et al. (1991). In this view, the Koobi Fora Formation on the eastern margin of the basin presents a more complex picture that included axial and marginal habitats at different times. This is consistent with the structural configuration of the Turkana Basin half-graben, with the major fault on the west side and a hinged platform or "ramp" on the east. This configuration allowed the paleo-Omo river to avulse occasionally into the East Turkana area, and west-flowing tributaries from areas east of the basin also could have drained into the basin across the west-sloping rift margin.

The Sidi Hakoma and Denen Dora Members of the Hadar Formation have AAH proportions similar to those of contemporaneous members in the Koobi Fora Formation. The significant increase in AAH proportions in the Kada Hadar Member suggests environmental changes toward more open conditions in the Hadar area after 3.2 Ma, following upon a significant wet interval associated with the Denen Dora Member (Figure 2). The Maka'amitalu locality (A.L. 666) indicates that these open conditions persisted in the Hadar Basin at around 2.4–2.3 Ma, where both *Homo* and lithic artifacts occur in close association (Kimbel et al., 1996).

SPECIES RICHNESS

Given that there are differences among Turkana Basin areas in the proportions of the different bovid tribes, we now ask whether differences exist in species richness among the different areas under consideration. Richness is defined as the total number of species (or distinct taxa) in a sample. It is well known that taxonomic richness is dependent on sample size (Figure 5).

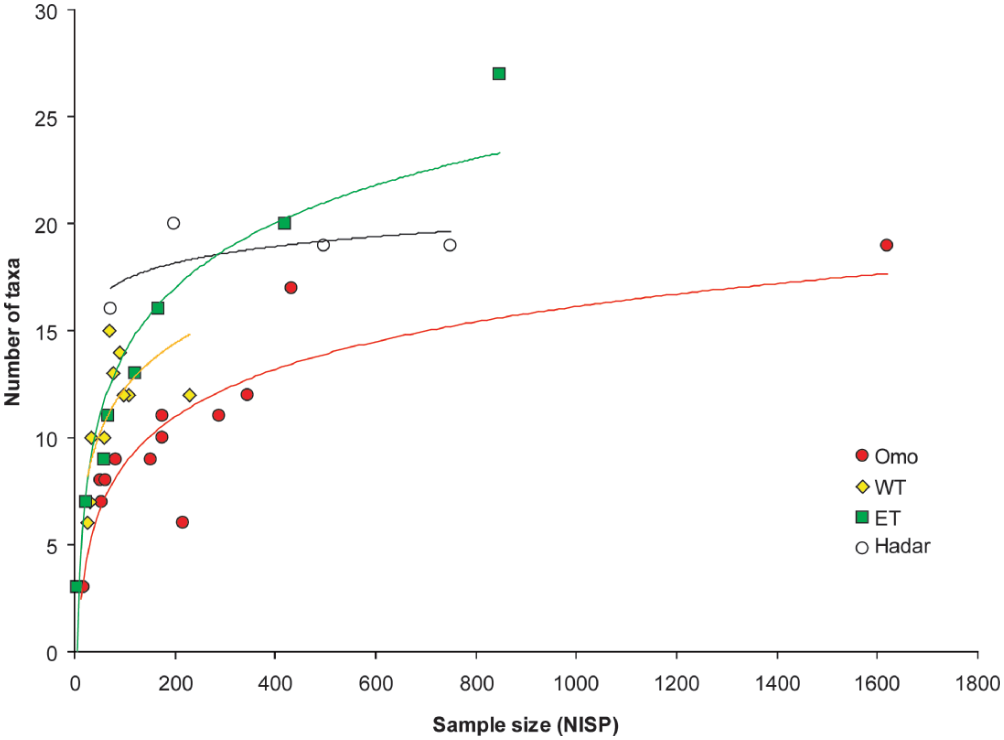

Figure 5. Bovid species richness vs. sample size, with logarithmic trend lines (rarefaction curves) highlighting the differences in this relationship for the different samples.

For a given sample size, the Shungura Formation tends to have lower richness than other parts of the Turkana Basin. The lower richness in the Shungura samples could be due to differences in taphonomic conditions, rather than to a lower number of species in the Shungura paleoecosystem. The Shungura collections include large numbers of isolated teeth, and specimens often show signs of rolling and abrasion that indicate reworking and deposition under relatively high energy fluvial conditions. The fragmentary nature of many Shungura specimens would thus tend to reduce the likelihood that these could be identified to genus or species. Better preservation in other parts of the basin would thus contribute to the greater species richness in samples from the Koobi Fora and Nachukui Formations. Two of the Hadar samples (Kada Hadar and Maka'amitalu) are richer in bovid species and a third (Sidi Hakoma) is similar in richness to samples of comparable size from the Turkana Basin. However, the largest of the Hadar samples (Denen Dora Member) appears to have low species richness, perhaps because it spans a comparatively short interval of time (40,000 years) and is strongly dominated by a single bovid tribe, the Reduncini.

As noted above, species richness is dependent on sample size, and sample size varies greatly across geological members in the Turkana Basin. Figure 6A shows the number of bovid taxa in the Turkana Basin during the 3.5 million-year interval from the Apak Member of the Nachukui Formation to the top of Member L of the Shungura Formation, and Figure 6B shows the abundance of the bovid fossil record during this time. This span of time in the Turkana Basin has a high concentration of fossils and a relatively continuous record that can be divided into roughly 200 thousand-year intervals. The dating and correlations among the different areas of the basin is based on the data provided in Table 1, and the distribution of bovid specimens identified below the tribal level is provided in Table 3.

There is a plethora of indices to measure species richness in relation to sample size (Ludwig and Reynolds, 1988; Magurran, 1988; Hayek and Buzas, 1997), but Fisher's α is recommended as a reliable measure when a single index is used (Hayek and Buzas, 1997). As measured by Fisher's α (Figure 7), bovid species richness in the Turkana Basin shows three major peaks in the time from about 4.5 to about 1 Ma. The first of these peaks occurred from 3.8 to 3.4 Ma, and includes the Moiti and Lokochot Members of the Koobi Fora Formation, the Kataboi Member of the Nachukui Formation, and Member A of the Shungura Formation. The second peak occurred from 2.8 to 2.4 Ma, including the upper Tulu Bor Member of the Koobi Fora Formation, the middle-upper Lomekwi and Lokalalei Members of the Nachukui Formation, and Members C and D of the Shungura Formation. A third and more sustained peak occurred from about 2 to 1.4 Ma, and includes the abundant record of the Upper Burgi, KBS, and Okote Members of the Koobi Fora Formation, the Kalochoro (part), Kaitio, and Natoo Members of the Nachukui Formation, and Members G (upper) to K of the Shungura Formation. These peaks of diversity in the Turkana Basin appear to come in cycles of about one million years, although the significance and causes of this pattern are not clear. The peak in diversity between 2.8 and 2.4 Ma occurred during the time of Vrba's (1995a) hypothesized turnover pulse in Africa. Elsewhere we have shown that significant faunal changes occurred at about 2.8 Ma: there is a peak of turnover at this time (although not as pronounced as a later Plio-Pleistocene peak) (Bobe and Behrensmeyer, 2004), and there are significant changes in the relative abundances of Omo bovids (Bobe and Eck, 2001). The third peak of taxonomic richness at 2.0–1.4 Ma coincides with another period of important faunal changes in the Turkana Basin. The time around the Pliocene–Pleistocene boundary (~1.8 Ma) is characterized by high rates of faunal turnover (Behrensmeyer et al., 1997)

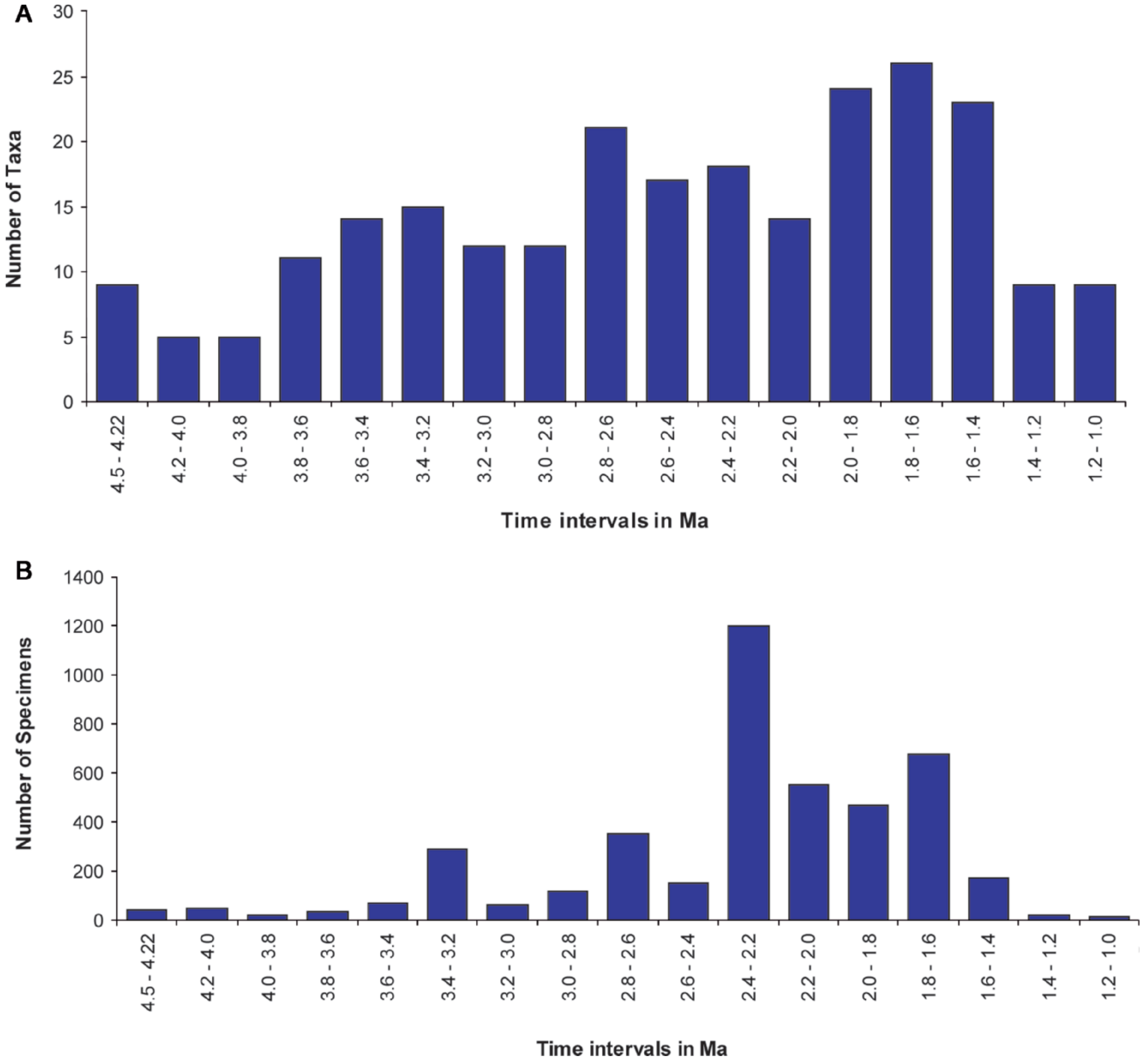

Figure 6. A) Number of bovid taxa per 200,000 year intervals in the Turkana Basin. B) Number of bovid specimens per 200,000 year intervals in the Turkana Basin.

and an increase in the importance of open grassland environments in the Turkana Basin (Bobe and Behrensmeyer, 2004).

The record of the Hadar Formation is not long enough to analyze patterns of species richness at 200-Kyr intervals. Such an analysis would include the Sidi Hakoma Member and half of the Denen Dora Member in the interval from 3.4 to 3.2 Ma, and the other half of the Denen Dora Member plus the Kada Hadar Member in the interval from 3.2 to 3.0 Ma. Such a partitioning of the Hadar record produces Fisher's α values of 4.8 and 5.4 for the earlier and later intervals respectively. Both values are higher than those of contemporaneous Turkana Basin intervals. Although sampling and taphonomic considerations remain to be assessed, these values confirm the results of Figure 5 that show taxonomic richness at Hadar within the upper part of the range of the Turkana Basin samples.

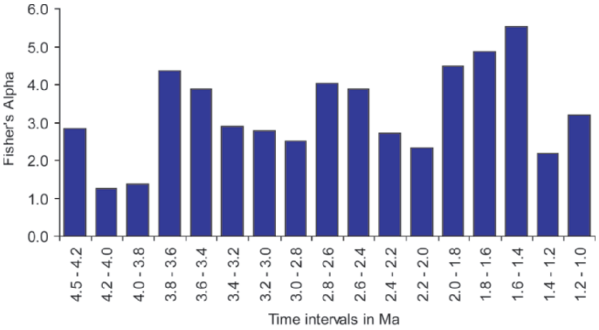

Figure 7. Fisher's α, a measure of taxonomic (species) richness relative to sample size, plotted by 200,000 year interval for the Turkana Basin bovid sample.

Discussion and Conclusion

This analysis has sought to identify significant trends in the abundance and diversity of bovids during the late Cenozoic of East Africa (Figure 1). A correspondence analysis of bovid tribes and geological members in the Turkana and Hadar Basins produces distribution of bovid tribes that can be interpreted in terms of environmental conditions (Figure 2). At one end of the principal (horizontal) axis, the tribes Aepycerotini, Tragelaphini, and Bovini indicate mostly closed and moist environments dominated by woodlands and fresh grasses. At the other end, the tribes Alcelaphini, Antilopini, and Hippotragini indicate more open and seasonally dry environments dominated by grasslands, wooded grasslands, or bushland. A third pole toward the position of the tribe Reduncini (high on the vertical axis) suggests open but moist-soil environments dominated by fresh or edaphic grasses. This distribution of bovid tribes parallels the associations indicated by cluster analysis (Figure 3).

The distribution of geological members in the correspondence analysis diagram (Figure 2) shows that the lower Omo Valley was characterized by closed and wet environments from about 3.4 to 2.0 Ma (Usno U-12 and Members B to lower G). These environmental characteristics contrast with those that predominated in the Omo after 2 Ma and elsewhere in the Turkana Basin for much of the late Pliocene and early Pleistocene. This marked difference between the lower and upper members of the Shungura Formation has been shown for the mammalian fauna as a whole (Geraads and Coppens, 1995). It is noteworthy that during this time interval the Nachukui Formation maintained consistently more open environments than the lower Omo Valley. East Turkana (Koobi Fora) paleoenvironments show intermediate conditions between those in the Omo and those in the West Turkana areas. The wide separation of Hadar Formation members in the correspondence analysis diagram (Figure 2) indicates that significant environmental changes occurred in the Hadar area from 3.4 to 3 Ma, as closed environments in the Sidi Hakoma Member gave way to extensive moist grasslands in the Denen Dora Member, followed by drier and more open environments in the Kada Hadar Member and the A.L. 666 locality. These results show that significant environmental changes occurred in the Turkana and Hadar Basins during the Pliocene, and that important environmental differences existed in different areas of the same sedimentary basin.

The use of Alcelaphini, Antilopini, and Hippotragini (AAH) as indicators of open and seasonally arid environments dominated by grasslands confirms that the lower Omo Valley remained significantly more wooded and moist than other parts of the Turkana Basin during the late Pliocene, from about 3.4 to 2.0 Ma (Figure 4). These results are consistent with the view that the Omo Shungura Formation sampled the axis of a sedimentary basin incised by a large meandering river, while the West Turkana deposits sampled more marginal habitats nearer the tectonic margins of the basin (Feibel et al., 1991). The Koobi Fora Formation on the east side of modern Lake Turkana sampled more complex or intermediate environments on the hinged side of a half-graben, while West Turkana sampled the fault-bounded side. The latter might be expected to subside more rapidly and be consistently wetter, but the uplifted rift shoulder to the west may have acted as a rain shadow and may have had limited runoff into the Turkana Basin (drainages on uplifted rift shoulders usually are directed away from the rift valley). In the latest Pliocene the Turkana Basin underwent significant tectonic changes; outflow of the paleo-Omo River to the Indian Ocean became blocked and this resulted in the expansion of a major lake at about 2.1 Ma. Subsequently the outflow of the river was diverted to the Nile drainage (Feibel et al., 1991). Thus, tectonism likely had a significant impact in the faunal changes that occurred in the Omo after 2 Ma.

In the Afar, the distribution of Hadar Formation samples indicates shifts from closed and wooded environments in the Sidi Hakoma Member (3.4–3.22 Ma) to moist substrate-waterlogged conditions in the Denen Dora Member (3.22–3.18 Ma), and seasonally arid grasslands in the Kada Hadar Member (3.18–3.0 Ma) and in the Maka'amitalu locality (~2.34 Ma) (Figures 2 and 4). Because of the short temporal spans of the Hadar faunal samples, the shift from woodland to moist grasslands to drier grasslands in could reflect either facies changes in the paleo-Awash drainage basin or short-term, basin-scale climate changes.

The relative abundance of Alcelaphini, Antilopini, and Hippotragini as a proportion of all bovid specimens increased in all areas toward the late Pliocene and the earliest Pleistocene, suggesting a common driving mechanism across basins (Figure 4). These bovid tribes are indicators of seasonally arid grasslands or bushland, and their increase in relative abundance during the late Cenozoic indicates an expansion of arid environments. The increase in aridity in East Africa is consistent with the known record of climatic change derived from marine sediments (deMenocal, 1995). Nevertheless, these aridity trends in the Turkana and Hadar areas show different responses at different times, evidence that local geography and tectonics played an important role in mediating environmental change.

The analysis of bovid diversity over time highlights three intervals of high species richness (Figure 7). The first one occurred from about 3.8 to 3.4 Ma, a time during which bovids such as *Kobus oricornus*, *Kobus sigmoidalis*, and *Aepyceros shungurae* first appear in the fossil record (Vrba, 1995a; Bobe and Behrensmeyer, 2004). The second interval of high species richness occurred from 2.8 to 2.4 Ma. Previous analyses have shown considerable changes in bovid relative abundances at 2.8 Ma (Bobe and Eck, 2001), a time that also corresponds to Vrba's hypothesized late Pliocene turnover event (Vrba, 1995a) and significant changes in African climate (deMenocal, 1995). The third interval of high species richness occurs across the Pliocene–Pleistocene boundary, from about 2 to 1.4 Ma. This was a time of expanding grasslands and diversification of grazing bovids, including the species *Pelorovis turkanensis*, *Pelorovis oldowayensis*, *Megalotragus isaaci*, and *Beatragus antiquus* (Vrba, 1995a; Bobe and Behrensmeyer, 2004). Previous analyses of bovid diversity using evenness and richness data have also identified the earliest Pleistocene as a time of high bovid diversity (Geraads, 1994). Bovid diversity seems to decrease significantly after 1.4 Ma, but samples are small.

Although hominins were relatively rare elements of the East African fauna during the late Pliocene, species of *Australopithecus* (*A. afarensis*), *Paranthropus*, and early *Homo* persisted through significant changes in local and regional landscapes (Bobe et al., 2002; Bonnefille et al., 2004). By the early Pleistocene, East African landscapes were becoming increasingly open and seasonal, and hominins were showing significant shifts in biological and cultural adaptations to these novel conditions (McHenry and Coffing, 2000).

Patterns of faunal change are dependent on the scale of analysis, and this analysis is meant to elucidate the main trends in bovid abundance and diversity over millions of years. Studies of the Omo fauna at finer levels of temporal resolution have shown that during the time between 3.4 and 2 Ma there were intervals of environmental stability and intervals of instability (Bobe et al., 2002). Also, different methods of assessing taxonomic abundance changes over time have shown that significant faunal shifts occurred in the Omo at about 2.8 Ma (Bobe and Eck, 2001). These patterns are obscured in the lower resolution analyses presented here, which focus on longer time intervals and broader geographic scales.

The diverse patterns of faunal abundance and richness documented above highlight the complexities involved in establishing correlations between climatic change and faunal evolution. Both within the Turkana Basin and between this basin and the Afar region there are similar but asynchronous trends that suggest increasing dry season stress on the vegetation and the faunas. This provides a measure of the capacity of local environmental "buffering" on larger-scale climatic trends. It is clear that during the critical period of human evolution between 4.0 and 2.0 Ma there were many different habitats in East Africa, but after 2.0 Ma the more vegetated and moist end of the habitat spectrum became more limited. This analysis highlights broad patterns of faunal change, but it is based on only one major group of mammals, the Bovidae. This provides a foundation for future testing with other mammals, as well as with geological, geochemical, and other types of paleontological evidence.

Acknowledgments

For insightful comments that greatly improved this paper, we are grateful to Meave Leakey, Louise Leakey, Denis Geraads, Chris Campisano, Zeresenay Alemseged, Eric Delson, and the anonymous reviewers. The Turkana Basin Paleontology Database is a collaborative Project between the National Museums of Kenya and the Smithsonian Institution. The database was created with support from the Smithsonian Institution's Evolution of Terrestrial Ecosystems Program and Scholarly Studies Program, and from the National Science Foundation (BSC0137235).

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