Responses of African bovids to Pliocene climatic change

René Bobe and Gerald G. Eck

Abstract.—The record of fossil mammals from the Shungura Formation, lower Omo Valley of southern Ethiopia, represents one of the largest and most carefully controlled samples for deciphering the responses of land faunas to global-scale climatic change. We use the abundant and continuous fossil record of the family Bovidae to analyze the effects of a late Pliocene climatic shift toward increased aridity in Africa beginning at 2.8 Ma and intensifying at about 2.4 Ma. A database consisting of 4233 specimen-based records collected under well-defined procedures is used to define patterns through time in bovid abundances while also controlling for taphonomic and other potential biases. Univariate and multidimensional (correspondence analysis) methods are used to study changes in bovid abundances through time. Our results indicate that bovids experienced an increase in species richness and a rapid episode of change in taxonomic abundances at 2.8 ± 0.1 Ma (between Members B and C), and that this shift was followed by gradual and prolonged changes in abundance between 2.8 and 2.0 Ma (between Member C and upper Member G). An analysis of skeletal-element abundances through the Shungura sequence shows that only moderate changes in taphonomic conditions occurred between 3.0 and 2.1 Ma, when the lower Omo Valley was dominated by a large, meandering river, but that significant changes in the mode of preservation accompanied the onset of lacustrine depositional environments at 2.1 Ma (between lower and upper Member G). A juxtaposition of taxonomic with taphonomic patterns shows that the shift in taxonomic abundances at 2.8 Ma occurred in the absence of significant changes in taphonomic conditions. The main changes in bovid relative abundances and diversity appear to have been driven by broad environmental and climatic changes in Africa. As environmental indicators, bovids show a transition in the Omo at about 2.8 Ma from closed and wet environments in Member B to closed but dry environments in Member C. This drying trend intensified in Members D, E, and F, between about 2.5 and 2.3 Ma. In lower Member G, between 2.3 and 2.1 Ma, there was an increase in bovid abundance and diversity, which may be a result of greater environmental heterogeneity. The pattern of environmental change depicted by Shungura bovids is consistent with independently derived evidence of Omo paleoenvironments (from paleosols, paleoflora, and micromammals), and with regional and global evidence of climatic changes, especially acute between 2.8 and 2.3 Ma, that caused the initiation of glacial cycles in the north and drier climate in the tropics of Africa. Even though the Omo bovids showed distinct responses to large-scale climatic and environmental change, the Omo bovid community also had important attributes of long-term stability: two species, *Aepyceros shungurae* and *Tragelaphus nakuae*, dominated the community for nearly one million years. This study highlights the importance of carefully controlled collection procedures of fossil vertebrates and provides an important demonstration of the potential complexity in mode and rate of responses of land faunas to climatic change.

René Bobe. Evolution of Terrestrial Ecosystems Program, Department of Paleobiology, NHB MRC 121, Smithsonian Institution, Washington, D.C. 20560. E-mail: Bobe.Rene@nmnh.si.edu
Gerald G. Eck. Department of Anthropology, Box 353100, University of Washington, Seattle, Washington 98195. E-mail: ggeck@u.washington.edu

Accepted: 5 December 2000

Introduction

The Pliocene is considered an epoch of climatic contrasts, a time of transition between the relatively warm Miocene and the ice ages of the Pleistocene (Burckle 1995), but the effects of this climatic transition on African mammals remain poorly understood. So far, the evidence from the African continent has produced a complex, sometimes contradictory picture of late Pliocene faunal change. An analysis of fossil mammals from the Turkana Basin of East Africa suggests that East African faunas may have undergone gradual turnover from about 3 Ma (million years) to 2 Ma (Behrensmeyer et al. 1997). Other studies suggest that major faunal changes in East Africa occurred at about 2 Ma (Harris et al. 1988; Feibel et al. 1991). A different view is held by Vrba (1985a, 1988), who has argued that rapid global climatic change resulted in a turnover pulse of evolution in many groups of African mammals about 2.5 Ma, a pulse that included major speciation events in human evolution. The most recent version of the turnover pulse hy-

 0094-8373/01/2703-0001/$1.00

pothesis with respect to African Bovidae broadens the evolutionary pulse to the interval between 2.8 and 2.5 Ma (Vrba 1995). It seems clear that East African environments became increasingly arid, open, and seasonal after 2 Ma (Cooke 1978, 1985; Feibel et al. 1991; Cerling 1992; Bonnefille 1995), but there is still much disagreement about the nature and timing of faunal responses to late Pliocene climatic change in Africa.

Indirect evidence of African climate comes from extensive and continuous deep-ocean records containing calcareous foraminifera and terrigenous sediments. Oxygen isotopes indicate that the early Pliocene was the warmest period of the last 5 million years, but temperatures gradually declined after 3.5 Ma. In high latitudes, cooler and drier conditions intensified between 2.5 and 2.3 Ma (Shackleton et al. 1984; Kennett 1995). The marine record of terrigenous sediments suggests that African Pliocene and Pleistocene climate alternated between wet and dry conditions, but these alternations were punctuated by periods of increased aridity at 2.8, 1.7, and 1.0 Ma (deMenocal 1995). Prior to 2.8 Ma, the marine record shows that African climate varied at periodicities of 19,000 and 23,000 yr; after 2.8 Ma the variation shifted to 41,000-yr cycles, and after 1.0 Ma to 100,000-yr cycles (deMenocal 1995; deMenocal and Bloemendal 1995).

The marine record provides a general climatic background against which to study the evolution of terrestrial faunas, but it does not provide direct evidence about actual environments in Africa, nor does it tell us how terrestrial faunas responded to climatic changes. Correlations between global climate and evolutionary events on the African continent remain speculative, partly because of limitations in defining the exact timing of such events imposed by sampling, radiometric age determinations, and biostratigraphy.

An appropriate record to test hypotheses linking Pliocene climatic change to evolutionary responses in African mammals must fulfill several requirements. First, the record should be a continuous sequence of fossils spanning the period of interest. Second, samples need to be large enough to permit quantitative analysis. Third, specimens should be tightly controlled stratigraphically and chronologically. Finally, depositional, taphonomic, and sampling factors should be well understood and controlled. In Africa, the Shungura Formation, in the lower Omo Valley of southern Ethiopia (Figs. 1, 2), comes closest to fulfilling these requirements. As Vrba (1988: p. 411) has noted in regard to the turnover pulse idea, "the most useful data set for testing this hypothesis is currently that from the Shungura Formation, Ethiopia."

The Shungura Formation

The fossiliferous deposits of the Shungura Formation provide a rich, continuous, and well-dated sequence of fossil mammals spanning the Plio-Pleistocene. The first large-scale survey of Plio-Pleistocene deposits in the lower Omo Valley was carried out by Arambourg (1947), but most of the record from the Shungura Formation is the result of extensive geological and paleontological work carried out in the 1960s and 1970s by an international team of scientists constituting the Omo Research Expedition. Under the direction of Clark Howell, leader of the American contingent of the expedition, and Yves Coppens, leader of the French contingent, the Omo Research Expedition produced a large collection of fossil mammals, described and analyzed by numerous researchers (e.g., Beden 1976, 1987; Cooke 1976; Coppens and Howell 1976; Coryndon 1976; Eck 1976; Eck et al. 1987; Eisenmann 1976, 1985; Gentry 1976, 1985; Grattard et al. 1976; Guérin 1976, 1985; Howell and Coppens 1976; Howell and Petter 1976; Wesselman 1984; Hooijer and Churcher 1985; Suwa et al. 1996).

The Geological Setting.—The Plio-Pleistocene deposits of the lower Omo Valley are divided into three geological formations: the Shungura, Usno, and Mursi Formations (Fig. 1). The richest and most continuous record of Omo mammals derives from the Shungura Formation, which consists of 766 m of deposits divided into 12 members (Figs. 2, 3A). The lowermost sediments constitute the Basal Member. The other members are named Member A to Member L, based on widespread volcanic tuffs that underlie each member: Mem-

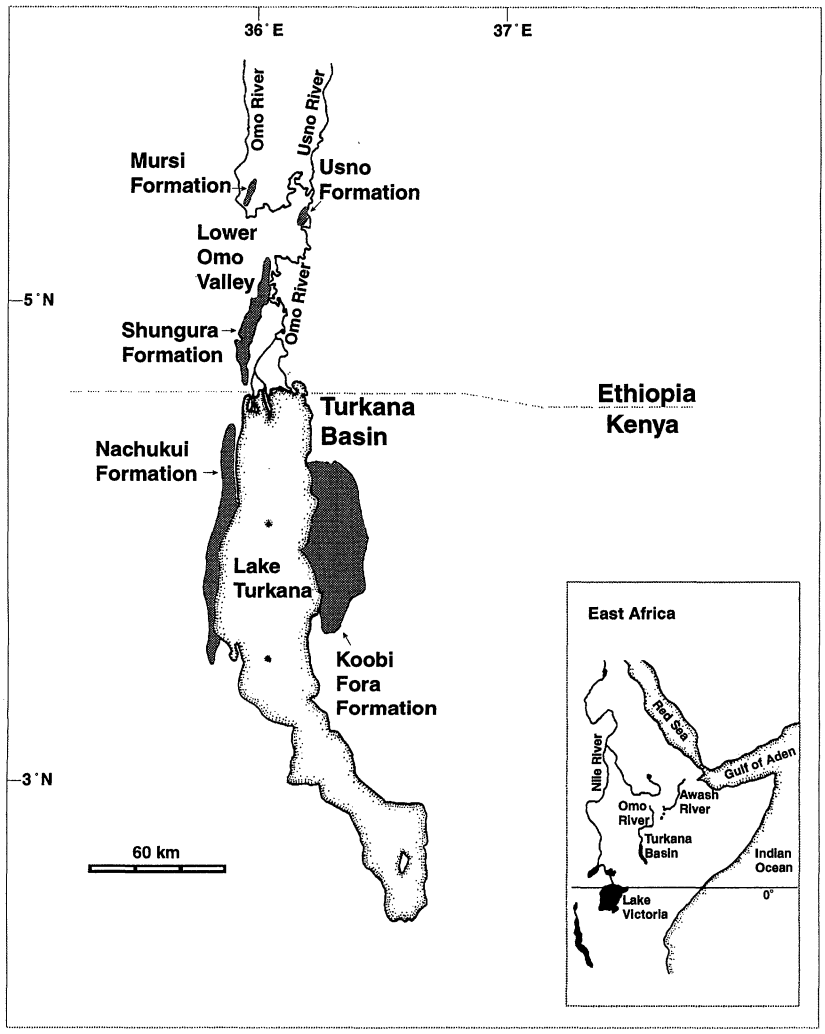

FIGURE 1. Map of the Turkana Basin, including Lake Turkana in Kenya and the lower Omo Valley in Ethiopia. Plio-Pleistocene formations discussed in the text are shown.

ber A is underlain by Tuff A, Member B by Tuff B, and so on through Member L. There is neither a member nor tuff "I" in the sequence. Each member is composed of several lithologic units, or submembers. Units are numbered above each major tuff from the bottom to the top of each member. Thus, for example, the second unit above Tuff A is called Unit A-2. Sedimentary units in the Shungura Formation vary in thickness from 2 m to 20 m but average about 7 m. Member A has 4 units, Member B has 12, Member C has 9, Members D, E, and F have 5 each, Member G has 29, Members H and J have 7 each, Member K has 4, and Member L has 9 units (de Heinzelin and Haesaerts 1983).

Five major phases of deposition have been identified in the Shungura Formation (Fig. 3B). The first phase is lacustrine and occurs only in the first unit of the Basal Member (Haesaerts et al. 1983). The second phase of deposition is fluvial and occurs between the second unit of the Basal Member and Unit G-13, although Units G-11 to G-13 show a transition toward deltaic fringe conditions. The third depositional phase, from Units G-14 to G-27, is lacustrine and includes littoral and lagoonal deposits. The fourth phase shows flu-

FIGURE 2. Photograph of the Shungura Formation exposures (photo by K. Behrensmeyer).

vial conditions from G-28 to L-6, although Units G-28 to H-7 are deltaic in character. Fluvial deposits beginning in Member K are distinct from earlier ones in the greater importance of eolian and colluvial deposition, with evidence of ephemeral streams. The last phase, from L-7 to L-9, is lacustrine (Haesaerts et al. 1983). Because of the fundamental differences in depositional conditions between lower Member G (fluvial environments up to Unit G-13) and upper Member G (lacustrine conditions in Units G-14 to G-27), in this study lower Member G and upper Member G are treated as separate members.

Although depositional conditions were relatively constant—essentially fluvial—from just above the base of the Shungura Formation to Unit G-13, there is some variation in the nature of these fluvial deposits (Fig. 3B). First, there is large-scale channeling in unit B-10 and in Member D (de Heinzelin et al. 1976). Massive channeling signals the presence of a large river eroding into older sediments and possibly mixing fossils from different strata. Second, there is a replacement of the large meandering river by a braided river in Unit F-1 and in Units G-3 to G-5 (de Heinzelin et al. 1976).

The Shungura fluvial deposits are characterized by a series of repetitive sedimentary cycles, and each cycle is defined as a formal unit. These cycles are typically composed of coarse sands at the bottom followed by finer silts and clays at the top. The coarse sands at the bottom of a unit represent sediments accumulated in the channel and point bars of a river, that is, in relatively high-energy environments. Most of the Shungura mammals derive from these coarse sands. Fossils from these coarse sands tend to be channel lag deposits dominated by isolated teeth (Dechant Boaz 1994). Medium and fine sands accumulated on the point bars of a river, while the finer silts and clays accumulated as levee and floodplain deposits in relatively low-energy environments. These repetitive sedimentary cycles are interpreted as superposed channels and floodplains of a large meandering river (de Heinzelin and Haesaerts 1983). The repetitive lithologic units show extensive lateral

continuity, indicating that the Plio-Pleistocene Omo river was depositing its load on a floodplain of very low gradient. The basin was subsiding at a rate nearly equal to the rate of deposition. Thus, the river could migrate back and forth across the floodplain without completely removing previously deposited sediments. Deposition of the Shungura Formation took place with little evidence of intraformational tectonics: visible deformations of the lower Omo Valley deposits postdate the Shungura Formation (Brown and de Heinzelin 1983).

The span of sedimentary units and the nature of the fluvial deposits themselves place limits on the level of temporal and spatial resolution attainable in the Shungura Formation. Bones entering a river system are typically transported some distance and then deposited in areas of accretion such as point bars. The transport of skeletal elements that enter the fluvial channel depends on the shape and density of the bones and the velocity of flow. As large meandering rivers migrate through the floodplain, previously buried bones may be exposed and transported along with the newer elements until reburial (Behrensmeyer 1982, 1988). The majority of fossil mammals from the Shungura Formation were collected from fluvial deposits consisting of small-pebble gravels and cross-bedded sands. The most common elements found in these deposits were isolated teeth. Such specimens are likely to have experienced fluvial transport and reworking under relatively high-energy conditions (de Heinzelin et al. 1976). Also, tributary streams from habitats that occupied a peripheral position in the basin may have contributed specimens to the Omo sample. Consequently, fossil assemblages from fluvial deposits may not be meaningful in terms of very short timescales or very localized environmental conditions, yet they may damp out short-term fluctuations to reveal long-term trends.

The chronological and stratigraphic framework of the lower Omo Valley was developed in the context of the Omo Group deposits (Fig. 1). In addition to the Shungura, Usno, and Mursi Formations of Ethiopia, the Omo Group includes the Koobi Fora and Nachukui Formations in the Turkana Basin of Kenya (de Heinzelin 1983; Brown 1994, 1995). Large-scale correlations have been established between the Turkana Basin formations and other East African sites, and between these and marine deposits off the coast of Africa (Brown 1995).

Chronological control of the Shungura Formation is provided by the following radiometric and paleomagnetic age determinations (Table 1, Fig. 3A). The Gilbert-Gauss Chron boundary, dated to 3.59 Ma (Shackleton 1995), occurs in Tuff A (de Heinzelin and Haesaerts 1983). Tuff B is part of a widely distributed ash layer, represented by Tuff U-10 in the Usno Formation, the Tulu Bor Tuff in the Koobi Fora and Nachukui Formations, and the Sidi Hakoma Tuff in the Hadar Formation in northern Ethiopia (Brown 1982). On the basis of its correlation with the Sidi Hakoma Tuff at Hadar, Tuff B is dated to 3.40 $\pm$ 0.03 Ma (Walter and Aronson 1993). Unit B-3 records the younger limit of the Mammoth Subchron (Feibel et al. 1989), which is dated to 3.23 Ma (Shackleton 1995). Tuff B-10, found near the top of Member B, has a K/Ar date of 2.95 $\pm$ 0.05 Ma (Feibel et al. 1989). Tuff C is dated by interpolation to about 2.85 Ma. Tuff C-4 is correlative to the Ingumwai Tuff at Koobi Fora, with an estimated age of 2.74 Ma. The Gauss-Matuyama Chron boundary occurs near the top of Member C, in Unit C-9 (Feibel et al. 1989). This paleomagnetic boundary is dated at 2.60 Ma (Shackleton 1995). Tuff D has a K/Ar date of 2.52 $\pm$ 0.05 Ma (Brown et al. 1985). The estimated age for the base of Member E is 2.40 Ma. Tuff F has a K/Ar date of 2.36 $\pm$ 0.05 Ma, and Tuff G has a K/Ar date of 2.33 $\pm$ 0.03 Ma (Brown 1994). The onset of lacustrine conditions in Unit G-14 dates to about 2.11 Ma (Brown 1995). Tuff H is estimated to be 1.90 Ma. In Member H, Tuffs H-2 and H-4 correlate with Koobi Fora's KBS and Malbe Tuffs, radiometrically dated to 1.88 $\pm$ 0.02 and 1.86 $\pm$ 0.02 Ma, respectively. The base of the Olduvai Subchron occurs in Unit G-27 and the top occurs in Unit H-7 (Feibel et al. 1989), an interval dating from 1.95 to 1.77 Ma (Shackleton 1995). The estimated age of Tuff J is 1.74 Ma, and Tuff J-4 has a K/Ar date of 1.65 $\pm$ 0.03 Ma. Tuff K has an estimated age of 1.53 Ma. Tuff

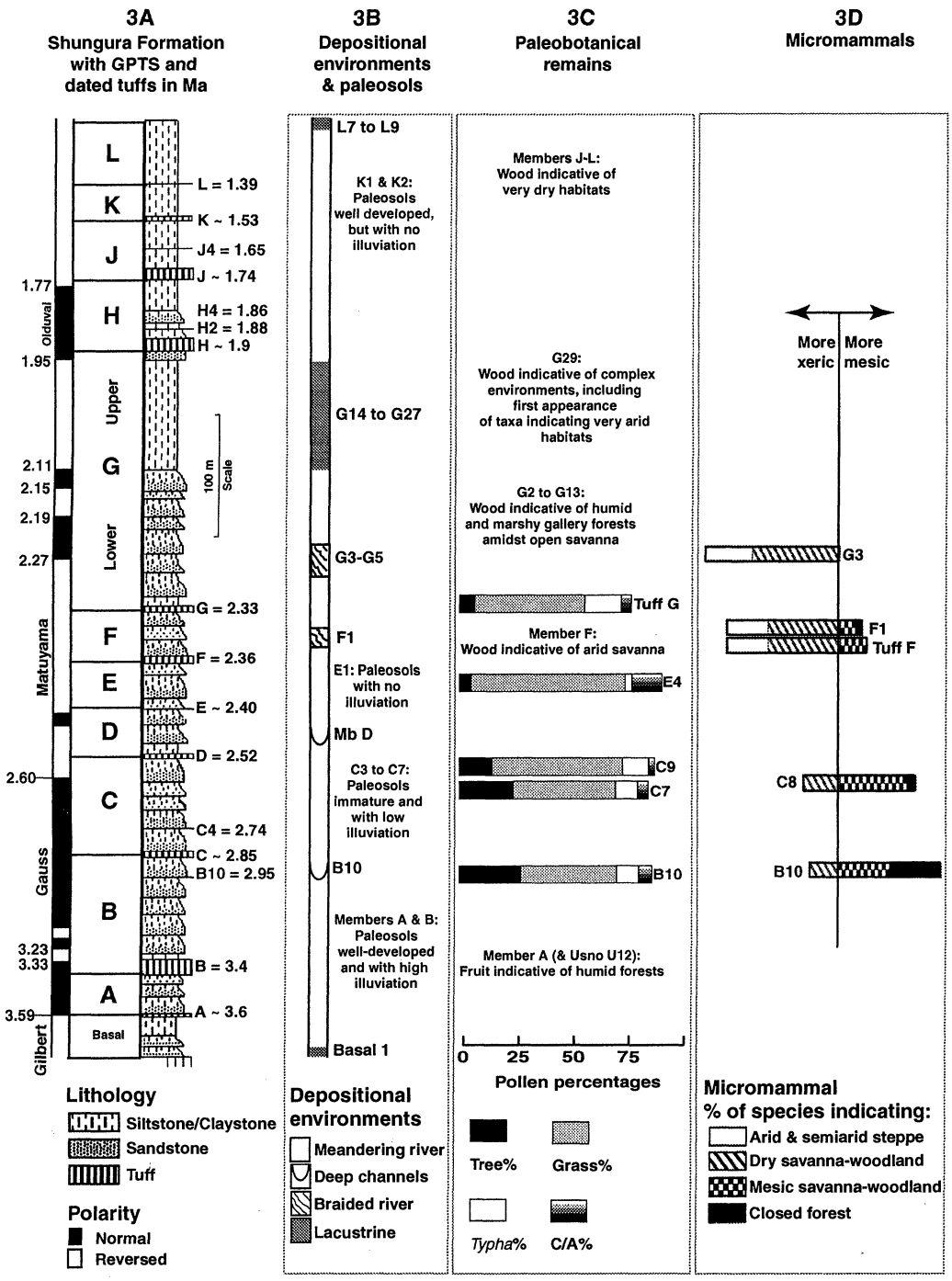

FIGURE 3. Chronology, stratigraphy, and paleoenvironmental reconstructions of the Shungura Formation. Different lines of paleoenvironmental evidence are juxtaposed for comparison. A, Chronology and schematic stratigraphic section of the Shungura Formation. See text for references. B, Depositional environments and paleosols from Haesaerts et al. 1983. C, Paleobotanical evidence from Bonnefille and Dechamps 1983. D, Micromammals from Wesselman 1984. E, Taphonomic patterns based on Figure 13 of this study. F, Taxonomic patterns based on Figure 19 of this study. G, Shungura environments based on bovid abundances (see text for discussion).

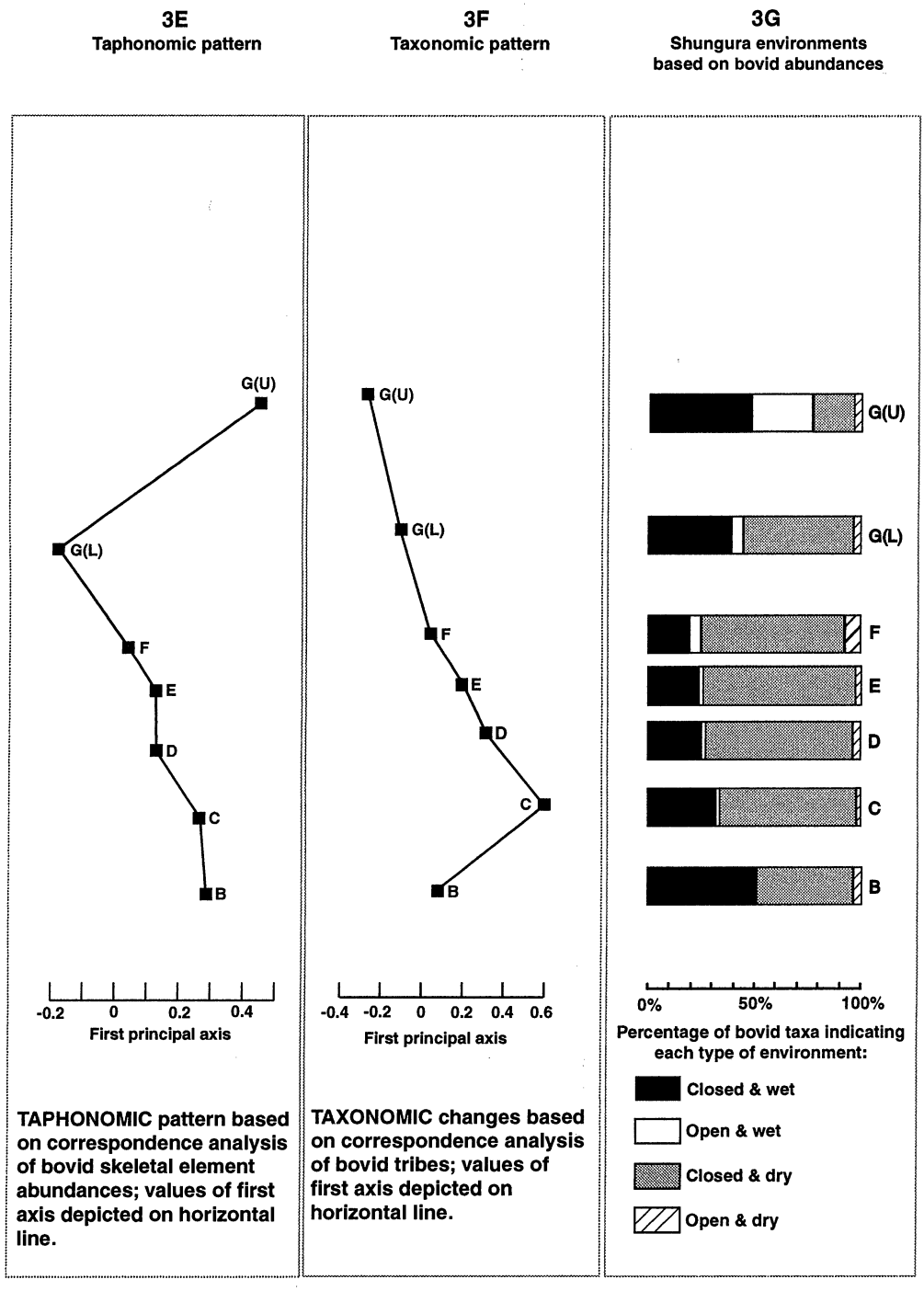

FIGURE 3. Continued.

L has a K/Ar date of 1.39 ± 0.01 Ma. Sediments at the top of the Shungura Formation are estimated to be about 1 Ma (Feibel et al. 1989). Thus, the Shungura Formation extends from about 3.6 to 1.0 Ma, but the majority of fossils derive from sediments dating from about 3 to 2 Ma, a critical period in the evolution of various groups of African mammals.

TABLE 1. Dating and correlations of Omo Group deposits in the Turkana Basin, Kenya and Ethiopia. Only the most recently published estimate for each unit is given.

Shungura (Sh)	Usno	Nachukui (Na)	Koobi Fora (KF)	Age (Ma)	Error	Method	Unit dated	Reference
			Silbo tuff	0.74	0.01	K-Ar, Ar-Ar	Silbo tuff at KF	McDougall 1985
				0.780		Brunhes/Matuyama		Shackleton 1995
			Gele Tuff	1.25	0.02	K-Ar, Ar-Ar	Gele Tuff at KF	Brown et al. 1985
		L. Nariokotome Tuff		1.33	0.02	K-Ar, Ar-Ar	Nariokotome at Na	Brown et al. 1985
Tuff L		Chari Tuff	Chari Tuff	1.39	0.02	K-Ar, Ar-Ar	Chari Tuff at KF	McDougall 1985
Tuff K				1.53	0.03	Interpolation	Tuff K at Sh	Feibel et al. 1989
Tuff J7			Black Pumice Tuff	1.55	0.03	Interpolation	BPT at KF	Feibel et al. 1989
			L. Okote Tuff	1.62	0.02	Interpolation	LOT at KF	Feibel et al. 1989
Tuff J4		Morutot Tuff		1.65	0.05	K-Ar, Ar-Ar	Morutot Tuff at Na	McDougall et al. 1985
			A6	1.68		Interpolation	A6 at KF	Feibel et al. 1989
			White Tuff	1.70	0.03	Interpolation	WT at KF	Feibel et al. 1989
			C6	1.72		Interpolation	C6 at KF	Feibel et al. 1989
Tuff J				1.74	0.03	Interpolation	Tuff J at Sh	Feibel et al. 1989
Unit H7				1.770		Olduvai (top)	H7 at Sh	Feibel et al. 1989; Shackleton 1995
			A2	1.78		Interpolation	A2 at Kf	Feibel et al. 1989
			C4	1.86		Interpolation	C4 at KF	Brown and Feibel 1986
Tuff H4			Malbe Tuff	1.86	0.02	K-Ar, Ar-Ar	Malbe Tuff at KF	McDougall 1985
Tuff H2			KBS Tuff	1.88	0.02	K-Ar, Ar-Ar	KBS Tuff at KF	McDougall 1985
Tuff H				1.90	0.03	Interpolation	Tuff H	Feibel et al. 1989
Unit G27				1.950		Olduvai (bot)	Unit G27 at Sh	Feibel et al. 1989; Shackleton 1995
Unit G14				2.11	0.04	Reunion II (top)	Unit G14 at Sh	McDougall et al. 1992
Unit G12				2.15	0.04	Reunion II (bot)	Unit G 12 at Sh	McDougall et al. 1992
Unit G9				2.19	0.04	Reunion I (top)	Unit G9 at Sh	McDougall et al. 1992
Unit G4				2.27	0.04	Reunion I (bot)	Unit G4 at Sh	McDougall et al. 1992
Tuff G				2.33	0.03	K-Ar, Ar-Ar	Tuff G at Sh	Brown et al. 1985
Tuff F		Kalochoro Tuff		2.36	0.05	K-Ar, Ar-Ar	Tuff F at Sh	Brown et al. 1985
Tuff E		Kokiselei Tuff		2.40	0.05	Interpolation	Tuff E	Feibel et al. 1989
Tuff D		Lokalalei Tuff	Lokalalei Tuff	2.52	0.05	K-Ar, Ar-Ar	Tuff D at Sh	Brown et al. 1985
Unit C9				2.600		Matuyama/Gauss	Unit C9 at Sh	Feibel et al. 1989; Shackleton 1995
			Burgi Tuff	2.68	0.06	K-Ar	Burgi Tuff at KF	Feibel et al. 1989
Tuff C4			Ingumwai Tuff	2.74	0.08	Interpolation	Tuff C4	Feibel et al. 1989
Tuff C			Hasuma Tuff	2.85	0.08	Interpolation	Tuff C	Feibel et al. 1989
Tuff B10				2.95	0.05	K-Ar, Ar-Ar	Tuff B-10 at Sh	Brown et al. 1985
				3.046		Kaena (top)		Shackleton 1995
			Ninikaa Tuff	3.06	0.03	K-Ar, Ar-Ar	Ninikaa at KF	McDougall 1985
				3.131		Kaena (bot)		Shackleton 1995
			Toroto Tuff	3.32	0.02	K-Ar, Ar-Ar	Toroto at KF	Brown 1994
Unit B3				3.233		Mammoth (top)	Unit B3 at Sh	Feibel et al. 1989; Shackleton 1995
Unit B2	U12			3.331		Mammoth (bot)	Unit B2 at Sh	Shackleton 1995
Tuff B	Tuff U10	Tulu Bor Tuff	Tulu Bor Tuff	3.4	0.02	K-Ar	SHT at Hadar	Walter and Aronson 1993
Tuff A	Tuff U6	Lokochot Tuff	Lokochot Tuff	3.594		Gilbert/Gauss	Tuff A	Feibel et al. 1989; Shackleton 1995

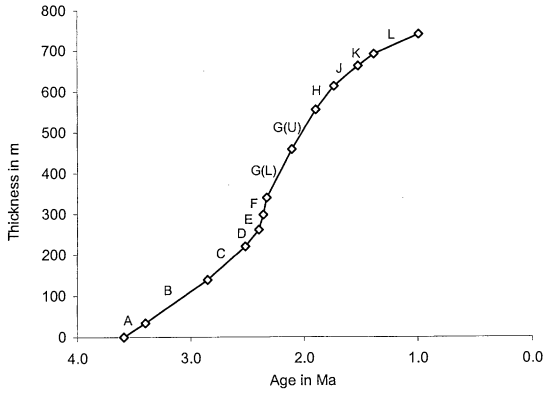

FIGURE 4. Rate of sedimentation in the Shungura Formation. Dates for member boundaries as in Figure 3. Thickness of Shungura members derived from de Heinzelin 1983.

The reconstruction of past environments, especially in relation to human evolution, has been one of the central goals of the Omo Research Expedition (Howell 1968, 1978; Howell et al. 1987; Coppens 1975, 1978, 1994). The following sections provide a brief synthesis of the most relevant paleoenvironmental framework, based on studies of paleosols (de Heinzelin et al. 1976; Haesaerts et al. 1983), paleobotanical remains (Bonnefille and Dechamps 1983), and micromammals (Wesselman 1984).

Paleosols.—Paleosol development is a function of climate and time, and the latter reflects land-surface stability. In an aggrading fluvial setting, soils under constant climatic conditions may be more or less developed depending on changes in rates of sediment accumulation. Therefore, if paleosol evidence is to be used in inferring climate, it is important to factor out possible effects of changing aggradation rates. Well-developed and highly illuviated soils reflecting high precipitation and equable climatic conditions occur in Members A and B (Fig. 3B), while soils in C-3 to C-7 are less evolved and less illuviated, suggesting reduced precipitation (de Heinzelin et al. 1976; Haesaerts et al. 1983). Lack of significant change in aggradation rates across Members A, B, and C (Fig. 4) supports climate as the major cause of this shift in pedogenesis. Member D has only a few incipient soils; E-1 soils show pedogenic structure but no illuviation, and Member G also has only weak soil development. Fully developed soils in K-1 and K-2 show no illuviation and indicate dry conditions (de Heinzelin et al. 1976). Although aggradation rates across all of these members are changing, the overall pattern is consistent with more arid climatic conditions from C-3 upward, in contrast with wetter conditions in Members A and B.

Vegetation and Paleobotanical Remains.—The major types of East African vegetation discussed here are defined as follows. Forests are characterized by columnar trees often reaching 50 m in height with crowns forming a continuous and complex structure. Moist forests are characterized by evergreen trees and epiphytes, while seasonally drier forests may be dominated by deciduous trees with few epiphytes (Lind and Morrison 1974). Moist evergreen forests in Africa receive as much as 2500 mm of rain per annum, with minor fluctuations in temperature and humidity throughout the year. Dry semideciduous forests receive from 1200 to 1600 mm of rain annually (White 1983). Woodlands are characterized by trees reaching up to 20 m in height with crowns forming a discontinuous canopy that covers at least 40% of the land surface; grasses dominate the woodland floor. In woodlands annual rainfall ranges from 500 to 1200 mm (Lind and Morrison 1974). Bushland is defined as a habitat in which bushes, multiple-stemmed plants intermediate between shrubs and trees, cover at least 40% of the land surface. Bushland typically occurs in areas where yearly precipitation ranges from 250 to 500 mm (White 1983). Wooded or bushed grasslands consist of areas where the tree or bush canopy covers from 10% to 40% of the land surface. Grasslands are dominated by grasses with scattered trees and shrubs covering up to 10% of the surface area. In East Africa, two distinct types of grasslands are recognized: derived and edaphic. Derived or secondary grasslands are maintained by regular burning or grazing and are characterized by very seasonal rainfall ranging from about 250 to 500 mm per year. Edaphic or primary grasslands occur in areas of waterlogged soils. In some permanent swamps the bulrush *Typha* may be dominant (White 1983). The term savanna is loosely defined to include areas where sec-

ondary grasslands are predominant. Deserts and semideserts occur in arid regions with sparse plant cover in which annual precipitation is usually less than 250 mm (White 1983).

The modern lower Omo Valley has a semiarid tropical climate. The vegetation is part of an *Acacia* savanna belt, but habitats range from closed forest communities sustained by the Omo River near its banks to seasonally dry grasslands in the plains away from the river (Carr 1976). Although past environments in the lower Omo Valley were probably quite different from modern ones (see below), it is likely that a mosaic of forests, woodlands, and grasslands in varying proportions characterized the region for much of the Plio-Pleistocene.

The paleobotanical record of the Shungura Formation is sparse and discontinuous but yields valuable data on the past vegetation of the lower Omo Valley (Fig. 3C). Fossil pollen provides information about both the taxonomic composition of past plant communities and the relative abundance of arboreal versus nonarboreal vegetation (Bonnefille 1994). High percentages of arboreal pollen indicate relatively closed woodlands or forests, while high percentages of grass pollen indicate more open environments. Some nonarboreal taxa such as *Typha* indicate wet environments, while taxa from the Chenopodiaceae and Amaranthaceae groups (abbreviated C/A) are indicative of arid conditions (Bonnefille 1995). The relative abundance of various pollen taxa in the sample is not, however, necessarily proportional to the representation of taxa in the original plant community. Pollen production, distribution, and depositional environments play a role in producing final pollen representation (Bonnefille 1995).

The earliest significant palynological sample from the Shungura Formation derives from Member B (Fig. 3C): a coprolite from Unit B-10 has 28% arboreal, 43% grass, 10% *Typha*, and 6% C/A pollen (Bonnefille and Dechamps 1983). A coprolite from Member C-7 shows a decrease in arboreal pollen to 21% and an increase in grass pollen to 47%, while *Typha* and C/A pollen percentages remain virtually unchanged. A sample from Unit C-9 shows a further decrease in arboreal pollen to 13%, and an increase in grass pollen to 60%, indicating a shift to more open conditions. Bonnefille and Dechamps (1983) view the pollen spectra from B-10 and C-7 as similar, but they note that the C-9 spectrum may reflect an incipient change in climatic conditions. A shift to more open and seasonally arid conditions is evident in a sample from E-4, which shows a decrease in arboreal taxa to 3% and an increase in grass pollen to 72%, a decrease in *Typha* to 1%, and an increase in C/A pollen to 16%. The last significant pollen sample comes from Tuff G, where arboreal pollen remains low, at 6%, but grass pollen decreases to 51%, *Typha* increases to 17%, and C/A pollen decreases to 3% (Bonnefille and Dechamps 1983). The Tuff G sample shows a prevalence of open habitats with marshy areas.

In addition to pollen, the Shungura sequence has yielded several samples of macrobotanical remains such as fruits and fossil wood (Fig. 3C). The earliest samples of macrobotanical remains in the Omo derive from Unit A-1, where the dominant species of fossil wood is *Garcinia huilensis.* This species is thought to indicate the prevalence of extensive gallery forests in the lower Omo Valley. Fossil fruit of *Antrocaryon* in Unit A-1 is indicative of humid tropical rain forests. *Antrocaryon* is a genus that today occurs primarily in dense and humid West and Central African forests (Bonnefille and Letouzey 1976). Thus, the sample from Unit A-1 indicates the presence of extensive riverine forests in the lower Omo Valley, with possible biogeographical connections to the West and Central African rain forests. Fossil fruit of *Antrocaryon* has also been found in Unit U-12 of the Usno Formation, correlative with Shungura Unit B-2, and the paleoenvironmental implications for U-12 are similar to those for Member A (Bonnefille and Letouzey 1976; Bonnefille and Dechamps 1983). Fossil wood samples from Members B, C, and D are rare, but Member D has wood of *Platysepalum chevalieri,* which is associated with closed riverine forests, and of *Psorospermum febrifugum,* associated with savanna. Member F fossil wood samples show a significant environmental changes in the lower Omo Valley: the dominant taxa are *Catophractes, Vitex, Ochna,* and *Rhus,* plant taxa associ-

ated with very dry savanna, but the persistence of gallery forests is indicated by samples of *Ficus* and *Garcinia.* Wood samples from G-2 to G-13 include *Rothmannia, Albizia, Bridelia, Celtis,* and *Ficus capensis,* which indicate humid and marshy gallery forests, while *Combretum, Kigelia,* and *Ozoroa* are indicative of more open savanna. Upper Member G, Unit G-29, has a large collection of fossil wood, with taxa that point to a rich and complex mosaic of habitats. Gallery forests persist in upper Member G, as attested by the presence of *Garcinia* and *Ficus,* but taxa such as *Acacia, Brachylaena,* and *Combretum,* which indicate dry savanna with scattered clumps of trees, are more abundant. Furthermore, a number of taxa, including *Zizyphus* and *Commiphora,* which occur in very dry habitats, make their first appearance in upper Member G (Bonnefille and Dechamps 1983). The fossil wood sample from Members J, K, and L is small, but there are specimens of *Steganotaenioxylon,* a taxon characteristic of arid habitats. This taxon indicates that the environments during the time of deposition of Members J to L were significantly more arid than in earlier times (Dechamps and Maes 1985). Thus, the paleobotanical record provides evidence that during most of the Plio-Pleistocene, the lower Omo Valley was characterized by a mosaic of habitats, including forests, woodlands, and grasslands, but that the proportions of the different habitats changed considerably through time.

Micromammals.—The Omo micromammals come mostly from excavated localities (Jaeger and Wesselman 1976; Wesselman 1984). The earliest significant assemblage of micromammals derives from B-10 (Fig. 3D). The assemblage includes murids, sciurids, shrews, bats, and galagos with strong affinities to species restricted to the closed forests of West and Central Africa. Some of these taxa indicate not only the presence of dense riverine forest along the Omo river but also a potential biogeographic connection between the Omo Valley and the equatorial forests of Central Africa (Wesselman 1984, 1995). Micromammals in Member C indicate major environmental changes in the Omo Valley. A micromammal assemblage from Unit C-8 has only one taxon considered to be primarily a forest form. There are a few species associated with savanna woodlands and wet savanna grasslands, while two species are indicative of dry savanna grassland (Wesselman 1984). Micromammal assemblages from Tuff F and Unit F-1 show a sharp increase in species indicative of xeric environments—dry savanna woodlands and grasslands (Fig. 3D). An assemblage from Unit G-3 has no species indicative of mesic or forested conditions (Wesselman 1984). Thus, the Omo micromammals point to mesic conditions during Member B times, with extensive forests dominating the landscape. The micromammals from Member C indicate drier, but still closed environments. The samples from Members F and G represent a shift to more arid and open savannas.

Remaining Problems.—The evidence from paleosols, paleobotanical remains, and micromammals provides a broad picture of environmental changes in the late Pliocene lower Omo Valley (Fig. 3). Although it is clear that a mosaic of forests, woodlands, and grasslands occurred in the lower Omo Valley throughout most of the Plio-Pleistocene, the importance of these different types of habitat changed considerably through time. The different lines of evidence reviewed thus far agree in their representation of paleoenvironments in Members A and B as heavily forested, with a prevalence of mesic conditions. Furthermore, the forests of Members A and B may have been extensive enough to maintain biogeographical connections with the humid forests of Central and West Africa. There is also agreement in the representation of environments in Members E and F as considerably drier and more open than those in Members A and B. However, the timing of this environmental shift to more-open habitats is not well resolved. Samples of paleosols, paleobotanical remains, and micromammals are sparse and discontinuous. Paleosols show a shift to more-arid conditions in Unit C-3, but this shift is not apparent in the palynological sample from Unit C-7. If an environmental shift occurred in lower Member C, as suggested by paleosols, there are no samples of fossil wood or micromammals in lower units of Member C to test this possibility. The nature of environments in lower Member G also remains problematic. The only pal-

ynological sample from Member G indicates an abundance of marshy habitats amidst grasslands, in agreement with the marshy-forest and open-savanna interpretation derived from fossil wood. Micromammals, however, indicate only dry and open savanna for lower Member G. Micromammal assemblages may represent highly localized conditions, while pollen samples are likely to be heavily biased toward wind-pollinated species and therefore are likely to represent taxa from a wide range of habitats (Bonnefille 1995). In fact, the Omo pollen spectra regularly contain montane forest taxa, whereas montane species are conspicuously absent from the Omo samples of fossil wood (Bonnefille and Dechamps 1983).

Thus, paleosols, paleobotanical remains, and micromammals show a broad shift toward more open and arid environmental conditions in the lower Omo Valley, a shift that is consistent with the evidence of oxygen isotopes from marine foraminifera. Nevertheless, the timing of this environmental shift in the Omo remains in doubt; the evidence of paleosols, paleobotanical remains, and micromammals is not continuous enough to elucidate the exact timing and rate of these changes. The Shungura Formation record of larger mammals, especially that of the Bovidae, is abundant and continuous, and thus presents us with a suitable database to study the nature and timing of environmental and faunal changes in the lower Omo Valley.

Materials and Methods

Collection Methods

The documentation of faunal change requires representative and comparable samples from the units of analysis. Recognizing this need, one of the authors (GGE) began a program of systematic collection of specimens from the American sector of the "type area" of the Shungura Formation (map Sectors 1 through 16 of de Heinzelin 1983) late in the 1968 field season. Eck and his survey crew followed this program throughout the 1969, 1970, 1971, and early part of the 1972 field seasons. During the daily search, Eck and his crew collected a restricted set of fossil specimens from those available on the surface. The set comprised all mammalian crania and mandibles or major fragments thereof, all mammalian jaw fragments and complete isolated teeth, all bovid horn cores or basal fragments, all mammalian astragali, and all ruminant metapodials or their distal ends. Because of special interests expressed by members of the expedition, all specimens of Primates and Carnivora were collected even if very fragmentary. Beginning in the south, in Sectors 15 and 16, and working northward, the survey crew searched small areas that were defined by easily recognized geographic features. They attempted to search the entire surface of an area with approximately equal intensity. As specimens were found, they were assigned to localities and the geographic positions of the localities were plotted on high-resolution aerial photographs (scale approximately 1:8000). At the end of each day, the area of search was also plotted on the aerial photographs and the next day's search was undertaken in a new area contiguous to those completed previously. In this manner, Eck and his crew searched essentially all of the well-exposed surfaces of Shungura Sectors 1 through 16.

Search discipline was relatively easy to maintain because the Shungura Formation is remarkably fossiliferous and thus search rewards were relatively constant. Interesting, important, and exciting specimens were discovered essentially every day. In addition, most sediment types, with the clear exception of the lacustrine sediments of middle Member G, produced fossils. Thus it was very difficult to predict where fossils might or might not be found and it usually "paid" to search everywhere with equal intensity. Stratigraphic bias in collection intensity was low because Eck and his crew usually worked in areas whose stratigraphic structure had not yet been determined. Geological crews led by Jean de Heinzelin and Paul Haesaerts determined the stratigraphic position of most of the localities a year or two after they were discovered, by using the positions of localities marked on the aerial photographs (see de Heinzelin 1983). The exceptions to these statements are the Basal Member and Members A and B, which have very limited exposures and thus were very in-

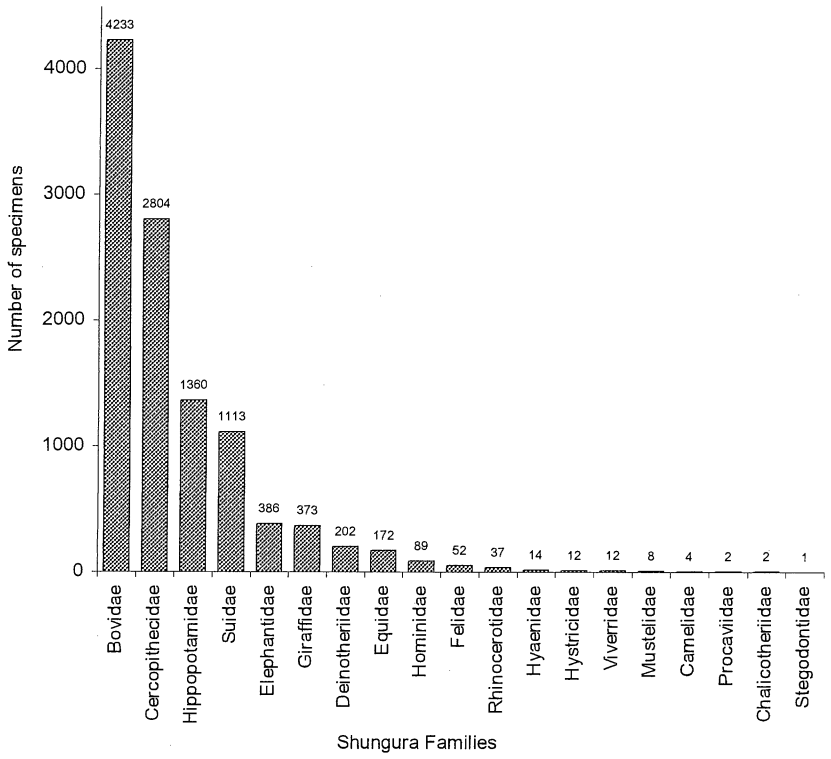

FIGURE 5. Abundance of Shungura Formation mammalian families based on the analytic database, which consists of 10,876 specimens in 19 families.

tensely searched in hopes of recovering the largest possible sample.

We thus feel that, given this collection routine, important stratigraphic or depositional collection biases were not introduced into the mammalian sample of the American contingent (with the exceptions noted above) and that the sample is reasonably representative of the fossils occurring on the surface in this area. It is interesting to note here that, near the end of his work establishing the stratigraphic position of the localities, Haesaerts (personal communication 1972) reported that his crews only rarely found specimens belonging to the search set described above, even though several members of his crew were assigned the task of looking for them. Haesaerts's observation suggests to us that Eck and his crew had already collected nearly all specimens belonging to the search set.

The Shungura Database

The paleontological record of the Shungura Formation compiled by the American contingent of the Omo Research Expedition is kept as a computerized database with 22,335 specimen records. A typical record includes the specimen number, skeletal element, taxon, locality number, sector, and stratigraphic level. Various sorting procedures then allowed us to develop an "analytic database" that includes only those types of specimens whose collection was consistent with the procedures detailed in the preceding section. Other collected specimens were eliminated from the analysis. The types of specimens eliminated from the analysis are described below:

1. Specimens from sectors other than 1 through 16 were not systematically collected and thus were removed from the analysis. Other specimens removed include those derived from unknown members or from localities that span multiple members.
2. Postcranial elements other than those collected systematically were removed from the analysis, as were all records of vertebrates other than mammals (crocodiles, turtles, fish, birds).

TABLE 2. Abundance of Shungura Formation families of mammals (number of specimens in analytic database).

	Member								
	B	C	D	E	F	G(L)	G(U)	H	Total
Bovidae	276	658	245	424	492	2099	34	5	4233
Cercopithecidae	237	1086	254	239	374	589	14	1	2804
Hippopotamidae	63	466	113	193	122	392	10	1	1360
Suidae	146	188	100	152	115	406	5	1	1113
Elephantidae	55	64	59	61	53	94			386
Giraffidae	34	110	33	48	29	119			373
Deinotheriidae	22	39	18	10	34	78	1		202
Equidae	24	30	11	14	26	65	2		172
Hominidae	5	22	16	11	17	17	1		89
Felidae	4	25	3	4	5	9	2		52
Rhinocerotidae	6	3	5	7	7	9			37
Hyaenidae		4	1	1		8			14
Hystricidae	2	2		3		5			12
Viverridae	3	5	2	1		1			12
Mustelidae	2	3			3				8
Camelidae	2				1	1			4
Procaviidae	1	1							2
Chalicotheriidae			1			1			2
Stegodontidae	1								1
Total	883	2706	861	1178	1278	3893	69	8	10876

3. Most of the Omo specimens were recovered from surface collections, but excavations were carried out in several localities. The purpose of excavation was the recovery of hominid remains rather than a representative sample of the member, and not all Shungura members were excavated. Therefore, samples found in excavations and those from surface collections are not comparable with respect to collection procedures, and members with excavated localities are not comparable to those without. Thus, all records from excavated localities were removed from the analysis.
4. Most Shungura specimens are isolated teeth, each probably representing a single individual animal. In some cases, however, specimens were found in a context that indicated that a single individual was represented by more than one specimen (the bones were in close proximity, and they had similar coloration and degree of wear). Multiple specimens likely to belong to a single individual were noted as such in the database. Only the most complete or diagnostic skeletal part from the various fossil fragments of a single individual was left in the analytic database to represent that individual.

This procedure results in the Shungura analytic database, in which each record is likely to represent one individual mammal collected from the surface in localities of known stratigraphic provenience. The analytic version of the Shungura faunal database has 10,876 specimens of mammals (Fig. 5) (see Bobe 1997), of which 4233 are bovids (Table 2). This study focuses on the most abundant of Shungura Formation families: the Bovidae, which constitutes almost 40% of the mammalian fauna. The 4233 specimens of bovids in the analytic database compose the basic data set used to generate the analyses, tables, and figures in this study. Table 3 and the Appendix provide a list and a frequency count of all bovids in the Shungura analytic database following the systematic framework of Gentry (1985), who described and identified the specimens. A few taxonomic modifications are based on the work of Harris (1991). Table 4 presents each taxon as a proportion of all bovids per member; this table then provides the relative abundance of bovid taxa across Shungura members.

Analytical Methods

The variables under study are displayed in a data matrix, such as Table 3, where columns

TABLE 3. Shungura bovid taxa across members (number of specimens in analytic database). Tribes in capital letters indicate the total number of specimens in that tribe.

	Member								
	B	C	D	E	F	G(L)	G(U)	H	Total
Tragelaphini sp.	5	11	1	2	3	9	0	0	31
Tragelaphus sp.	0	1	2	2	2	4	0	0	11
T. nakuae	22	163	62	106	38	214	0	0	605
cf. *T. gaudryi*	2	0	0	0	0	0	0	0	2
T. gaudryi	0	2	1	7	44	147	2	0	203
T. strepsiceros	0	0	0	0	0	1	0	0	1
T. pricei	0	1	0	0	0	0	0	0	1
TRAGELAPHINI	29	178	66	117	87	375	2	0	854
Bovini sp.	19	56	15	12	12	26	1	1	142
Syncerus sp.	3	9	0	1	0	5	1	0	19
S. acoelotus	1	4	0	0	0	1	0	0	6
Pelorovis sp.	1	4	0	0	3	6	0	0	14
BOVINI	24	73	15	13	15	38	2	1	181
Reduncini sp.	49	52	21	32	32	346	7	2	541
Redunca sp.	1	2	0	1	1	0	0	0	5
Kobus sp.	0	0	0	0	0	2	0	0	2
K. oricornus	8	0	0	0	0	0	0	0	8
K. ancystrocera	3	7	0	2	0	29	0	0	41
K. kob	2	1	1	0	0	1	0	0	5
K. sigmoidalis	0	0	7	19	16	204	1	0	247
K. ellipsiprymnus	0	0	0	0	0	1	0	0	1
Menelikia lyrocera	0	1	0	2	20	101	6	1	131
M. leakeyi	0	11	1	0	0	0	0	0	12
REDUNCINI	63	74	30	56	69	684	14	3	993
Hippotragini sp.	0	1	0	1	0	2	0	0	4
Hippotragus gigas	0	1	0	0	0	0	0	0	1
Oryx	0	1	0	0	0	0	0	0	1
HIPPOTRAGINI	0	3	0	1	0	2	0	0	6
Aepyceros shungurae	48	94	56	91	141	461	2	0	893
AEPYCEROTINI	48	94	56	91	141	461	2	0	893
Alcelaphini sp.	5	4	6	9	25	47	1	0	97
Damalops	1	0	0	0	0	0	0	0	1
Parmularius sp.	0	1	0	0	0	2	0	0	3
P. altidens	0	0	0	0	0	1	0	0	1
Megalotragus sp.	0	0	0	0	0	1	0	0	1
ALCELAPHINI	6	5	6	9	25	51	1	0	103
Antidorcas	0	1	0	0	1	1	0	0	3
A. recki	1	0	0	0	3	1	0	0	5
Gazella sp.	0	0	1	0	0	0	0	0	1
G. praethomsomi	0	0	0	0	1	2	0	0	3
Antilope subtorta	0	2	0	0	0	0	0	0	2
ANTILOPINI	1	3	1	0	5	4	0	0	14
Neotragini sp.	0	0	0	1	1	1	0	0	3
Raphicerus	0	0	0	1	0	1	0	0	2
NEOTRAGINI	0	0	0	2	1	2	0	0	5
OVIBOVINI	0	0	1	0	0	0	0	0	1
Bovidae sp.	105	228	70	135	149	482	13	1	1183
BOVIDAE (total)	276	658	245	424	492	2099	34	5	4233

represent geological strata (members) and rows represent different taxa (species, genera, and tribes). This data matrix can be studied across columns and across rows. The column categories are independent samples, but the row categories are considered to be dependent on one another, because the abundance, presence, or absence of any given taxon could theoretically influence similar parameters in other taxa (Ludwig and Reynolds 1988). In this study the emphasis is first on the characteristics of geological members (columns), and then on the taxa (rows). Subsequently, the approach is multidimensional: with the use of correspondence analysis columns and rows are considered simultaneously.

TABLE 4. Shungura bovid taxa as a proportion of the total number of bovids per member. Taxa with abundance <0.005 appear as 0.00.

	Member								
	B	C	D	E	F	G(L)	G(U)	H	Total
Tragelaphini sp.	0.02	0.02	0.00	0.00	0.01	0.00	0.00	0.00	0.01
Tragelaphus sp.	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00
T. nakuae	0.08	0.25	0.25	0.25	0.08	0.10	0.00	0.00	0.14
cf. *T. gaudryi*	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
T. gaudryi	0.00	0.00	0.00	0.02	0.09	0.07	0.06	0.00	0.05
T. strepsiceros	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
T. pricei	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
TRAGELAPHINI	0.11	0.27	0.27	0.28	0.18	0.18	0.06	0.00	0.20
Bovini sp.	0.07	0.09	0.06	0.03	0.02	0.01	0.03	0.20	0.03
Syncerus sp.	0.01	0.01	0.00	0.00	0.00	0.00	0.03	0.00	0.00
S. acoelotus	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Pelorovis sp.	0.00	0.01	0.00	0.00	0.01	0.00	0.00	0.00	0.00
BOVINI	0.09	0.11	0.06	0.03	0.03	0.02	0.06	0.20	0.04
Reduncini sp.	0.18	0.08	0.09	0.08	0.07	0.16	0.21	0.40	0.13
Redunca sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Kobus sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
K. oricornus	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
K. ancystrocera	0.01	0.01	0.00	0.00	0.00	0.01	0.00	0.00	0.01
K. kob	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
K. sigmoidalis	0.00	0.00	0.03	0.04	0.03	0.10	0.03	0.00	0.06
K. ellipsiprymnus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Menelikia lyrocera	0.00	0.00	0.00	0.00	0.04	0.05	0.18	0.20	0.03
M. leakeyi	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00
REDUNCINI	0.23	0.11	0.12	0.13	0.14	0.33	0.41	0.60	0.23
Hippotragini sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Hippotragus gigas	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Oryx	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
HIPPOTRAGINI	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Aepyceros shungurae	0.17	0.14	0.23	0.21	0.29	0.22	0.06	0.00	0.21
AEPYCEROTINI	0.17	0.14	0.23	0.21	0.29	0.22	0.06	0.00	0.21
Alcelaphini sp.	0.02	0.01	0.02	0.02	0.05	0.02	0.03	0.00	0.02
Damalops	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Parmularius sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
P. altidens	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Megalotragus sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ALCELAPHINI	0.02	0.01	0.02	0.02	0.05	0.02	0.03	0.00	0.02
Antidorcas	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A. recki	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00
Gazella sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
G. praethomsoni	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Antilope subtorta	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ANTILOPINI	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00
Neotragini sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Raphicerus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
NEOTRAGINI	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
OVIBOVINI	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Bovidae sp.	0.38	0.35	0.29	0.32	0.30	0.23	0.38	0.20	0.28
BOVIDAE (total)	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00

Geological members can be compared in terms of taphonomic factors, faunal composition, species richness, and diversity. For each member, we estimate a minimum number of species using the following criteria. Each taxon identified to the species level counts as one species. Taxa identified only to the genus level count as a species only if there are no specimens of the same genus identified to the species level. Taxa identified only to the tribe level count as a species only if there are no specimens of the same tribe identified to the genus or species level. In Table 3, for example, in the tribe Bovini of Member B, only *Syncerus acoelotus* is identified to the species level, so *S. acoelotus* counts as one species. Specimens identi-

fied only as *Syncerus* sp. or Bovini sp. do not necessarily contribute new species to the sample, so they are not counted as additional species. However, *Pelorovis* sp., although only identified to the genus level, contributes at least one species different from *S. acoelotus*, so *Pelorovis* sp. counts as one species. Thus, the minimum number of species of Bovini in Member B is two.

The minimum number of species in each member is used to calculate species richness and diversity. Species richness simply refers to the number of species in a community or assemblage, but the number of species depends on sample size. Species diversity takes into account not only the number of species but also the evenness of species abundance. A community with only one or two very abundant species and many rare ones has lower diversity than a community with many moderately abundant species. However, different combinations of richness and evenness can produce similar measurements of diversity. Although richness and diversity may be simple to compute, they are rarely easy to interpret. There are several indices of diversity in the published literature (e.g., May 1975; Grayson 1984; Ludwig and Reynolds 1988; Magurran 1988; Hayek and Buzas 1997). Some of these indices, however, require assumptions that the data do not meet. For example, the Shannon index assumes that all taxa in the group of interest are represented in the sample (Magurran 1988), an assumption that is unlikely to hold in most Shungura members. Other indices may correlate strongly with sample size, and thus be of little ecological value. In this study we use Fisher's alpha as the main diversity index for the study of species richness. Then we use the Berger-Parker and Simpson indices of diversity to focus on species dominance or evenness. The criteria and equations that apply to each of these measures of diversity are provided by Hayek and Buzas (1997), Magurran (1988), and Ludwig and Reynolds (1988).

Bovid diversity in each Shungura member is likely to be a function of ecological and taphonomic factors. In ecological terms, species diversity is known to vary with factors such as latitude, elevation, productivity, and environmental heterogeneity (Begon et al. 1990). In fossil assemblages, however, species diversity may also vary because of taphonomic factors such as time-averaging and differential preservation. These factors are assessed in considering the meaning of diversity measures in the Shungura assemblages.

To evaluate the environmental implications of the fauna in an assemblage, we need to infer the ecological characteristics of the species that compose the assemblage. The ecological characteristics of extinct species can be derived from various lines of evidence (Wing et al. 1992), an important one being functional anatomy. The principles of functional anatomy show a general correlation between form and function, and certain forms are adaptations to particular environments. For example, hypsodont dentition in living mammals is strongly associated with a diet based on grass, and grasses generally occur in open areas. Thus, fossil mammals with hypsodont teeth are inferred to be grazers and are characterized as inhabiting relatively open habitats. Some grazers, however, specialize on fresh grasses and thus tend to occupy marshy areas or wetlands. Another source of information comes from living relatives of extinct species. If a clade of living species typically occupies a particular habitat, e.g., open grasslands, we infer that an extinct close relative also occupied that habitat. This kind of taxonomic analogy has its limitations, because species may change their habitat preferences through time, or they may have enough behavioral flexibility to occupy different environments at different times. For Plio-Pleistocene Bovidae, however, taxonomic analogy seems to be fairly reliable (Vrba 1985b). Morphological and taxonomic data can be supplemented by stable carbon isotope analysis, which determines the relative amount of C_3 and C_4 plants consumed by an animal (Cerling and Harris 1999; Sponheimer et al. 1999). Another source of information comes from the depositional context itself. Analysis of sediments and soils provides information not only of depositional environments, e.g., floodplain deposits, but also of past temperatures and patterns of precipitation. In this study, we draw on a combination

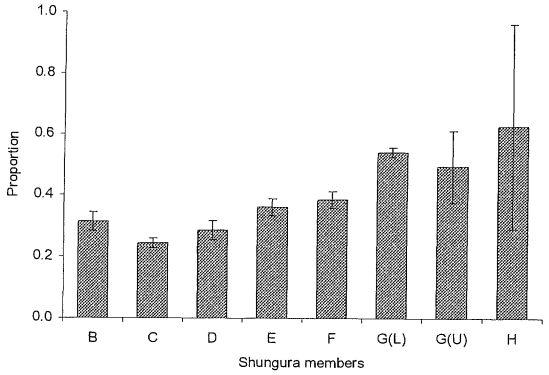

FIGURE 6. Bovid abundance as a proportion of all mammals per member of the Shungura Formation. Binomial error bars denote the 95% confidence interval.

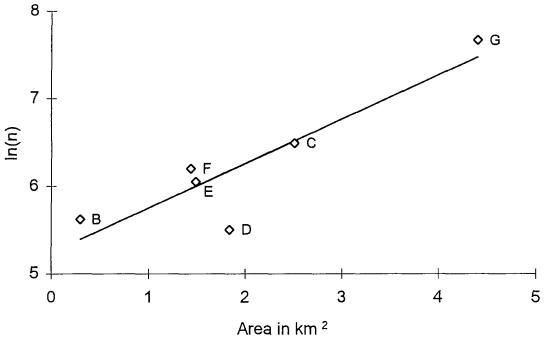

FIGURE 7. Log-log plot of bovid sample size (natural logarithm of the number of specimens) with area of exposure of Shungura members. Regression line with $r^2 = 0.805$, $p = 0.015$.

of these lines of evidence to infer the ecological preferences of bovid taxa.

The potential significance of differences in the abundance of bovid tribes across geological strata can be evaluated with a variety of statistical techniques. Here we use two different methods to evaluate each distribution. We apply the chi-square statistic to test the null hypothesis that taxonomic abundance has a uniform or homogeneous distribution across geological strata. Rejection of the null hypothesis indicates that a given taxon does not have an even distribution across strata. The chi-square statistic is applied only to absolute frequency data such as those in Table 3, from which we may then calculate relative abundances or proportions such as those in Table 4 and Figures 14–18 (Zar 1984; Fisher and van Belle 1993). Additionally, we use binomial 95% confidence limits to estimate the proportion or relative abundance of each bovid tribe in each Shungura member (equations in Buzas 1990).

In many faunal sequences, taxonomic relative abundances are greatly influenced by sample size: there is often a significant correlation between sample size and the relative abundances of a species (Grayson 1984). We use the nonparametric Spearman's rank-order correlation coefficient, r_s, to test the null hypothesis that there is no significant correlation between the relative abundance of bovid tribes and sample size across Shungura members (Zar 1984).

Relationships among various taxa, which include measurements of species association and covariation, can be studied with bivariate statistics. In modern communities, species associations are evaluated in terms of presence or absence. If two species usually occur together, they are highly associated, but positive covariation does not follow from association. Two species may usually co-occur, but high abundance of one may be accompanied by low abundance of the other. In this case, the two species have negative covariation, even if they are highly associated. Species that are highly correlated not only occur together but also show positive covariation. Here we analyze

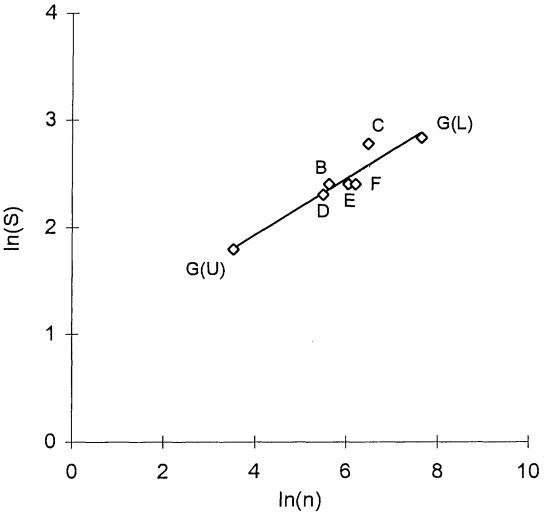

FIGURE 8. Log-log plot of the number of bovid species (natural logarithm) with bovid sample size (natural logarithm) per member. Regression line with $r^2 = 0.958$, $p = 0.001$.

covariation among bovid taxa with the nonparametric Spearman rank correlation coefficient. The null hypothesis is that the ranked abundances of bovid taxa across Shungura members are not correlated (Ludwig and Reynolds 1988).

Faunal assemblages can be compared and classified by means of various ordination techniques, such as principal component analysis or correspondence analysis. Ordination techniques display different communities along axes so that communities that resemble each other the most, on the basis of species composition, are grouped closer together. Among the commonly used ordination techniques, correspondence analysis is more robust than principal component analysis in dealing with nonlinear data (Ludwig and Reynolds 1988).

The correspondence analysis procedure analyzes contingency tables with cells containing frequency counts (e.g., Table 3). The procedure is particularly useful if the variables are nominal and contain many categories. Correspondence analysis displays graphically the relationship between two nominal variables. Categories that are similar to each other appear close together in the graphic display, and those that are different occur farther apart (Greenacre and Vrba 1984; Benzécri 1992; Greenacre 1993). In the correspondence analysis graphical output, each taxon is pulled to the geological member for which the taxon has a high profile, and each member is pulled to the taxon in which the member has a high profile. Thus we may obtain associations of taxa that have high profiles in a particular member, and of members that have high profiles for particular taxa. Interpretations of correspondence analysis graphs consist of examining the spread of taxa and sampling units across each axis in search of underlying ecological features that may explain the spread of points (Greenacre and Vrba 1984).

Results

Abundance and Diversity

Bovids are the most abundant family of mammals in the Shungura Formation (Fig. 5), but this abundance varies significantly across members (with Table 2 values, $\chi^2 = 416.7$; $p <$ 0.001). As shown in Figure 6, the relative abundance of bovids (as a proportion of all mammals) fluctuates between about 25% and 30% of all mammals in Members B, C, and D and increases thereafter to reach 54% in lower Member G. Sample size in Member H is too small to be of use in quantitative analyses of relative abundance, as reflected in the large confidence interval depicted in Figure 6, so this member is dropped from further analysis. The error bars in the relative abundance estimate of bovids in upper Member G are also rather large. Nevertheless, we retain upper Member G in the analysis, and consider with caution any interpretations derived from the faunal sample of this member.

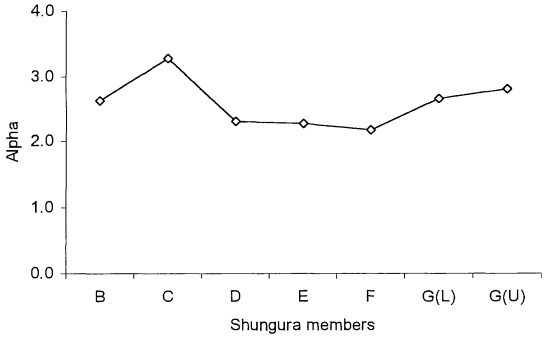

FIGURE 9. Bovid diversity measured by Fisher's alpha, which emphasizes species richness.

Sample size is known to be a confounding factor in studies of relative abundance and diversity (e.g., Grayson 1984; Magurran 1988; Hayek and Buzas 1997). In the Shungura Formation, bovid sample size varies considerably across members, as shown in Tables 3 and 5. This variation in sample size does not correlate significantly with the amount of time represented by each member ($r_s = 0.11$; $p > 0.5$). As shown in Figure 7, a good predictor of bovid sample size in the Shungura Formation is the area of exposure of each member ($r^2 = 0.81$; $p = 0.015$). The total number of bovid specimens per member, in turn, plays a critical role in determining the number of bovid species in each member. Figure 8 shows the relationship between bovid sample size and the number of species per member, with the data provided in Table 5. There is a clear increase in the number of bovid species with increase in sample size.

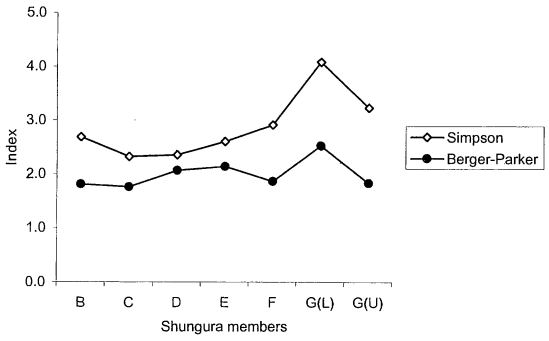

FIGURE 10. Berger-Parker and Simpson indices (inverse) measure species dominance, an aspect of diversity. A high index implies less dominance of the most abundant species, and thus greater diversity.

To compare species richness among members, we use Fisher's alpha (see Magurran 1988; Hayek and Buzas 1997). Figure 9 (also Table 5) shows a peak in species richness in Member C, followed by a decline in Members D to F, and an increase in Member G (upper and lower). There is no significant correlation between bovid sample size and species richness as measured by Fisher's index ($rs = 0.071$; $p > 0.5$).

Diversity is measured not only in terms of species richness but also in terms of the relative abundance or evenness of species distributions. In most members there are a few very abundant or dominant taxa and many less abundant ones. A simple index to measure species dominance is the Berger-Parker index (Table 5, Fig. 10). The Berger-Parker index, "one of the most satisfactory diversity measures available" (Magurran 1988: p. 41), expresses the relative dominance of the most abundant species in each sample. Table 5 and Figure 10 follow the convention of using the inverse value of the index, so that greater values imply less dominance and greater diversity (Magurran 1988). The Berger-Parker index shows a slight decline in species diversity, i.e., an increase in the dominance of the most abundant species, from Member B to Member C. Subsequently, there is an increase in diversity from Member C to Member E (the dominant species become less dominant) and then a peak in lower Member G. Among the many diversity measures that take into account the relative abundance of all taxa in the sample, the Simpson index is one of the most commonly used (Magurran 1988). In Table 5 we provide values of the Simpson index computed at the species level. Figure 10 shows that according to the Simpson index there is a decrease in bovid diversity (decrease in evenness) from Member B to Member C. Diversity increases after Member C and reaches a high peak in lower Member G. Thus, the Berger-Parker and Simpson indices provide a similar picture of changes in species diversity across members. Overall, bovid species are more evenly distributed in lower Member G than in other members (Fig. 10). With respect to richness, however, there is a peak in Member C, and high values in lower and upper Member G (Fig. 9).

Taphonomic Considerations

The quality of preservation of fossil specimens may have an effect on diversity esti-

TABLE 5. Characteristics of Shungura members: area of exposure, time span, bovid sample size, and biodiversity. n.d. = no data available; n.a. = not applicable.

	Member								
	B	C	D	E	F	G(L)	G(U)	H	Total
Bovid sample size	276	658	245	424	492	2099	34	5	4233
Area of exposure in square km	0.30	2.51	1.84	1.49	1.44	4.40	*	n.d.	12.0
Time span in Kyr	550	330	120	40	30	220	210	160	1660
Minimum number of species (S)	11	16	10	11	11	17	6	2	26
Fisher's alpha diversity	2.63	3.28	2.30	2.27	2.17	2.66	2.81	n.a.	3.7
Bovid sample size identified to tribe	171	430	175	289	343	1617	21	4	3050
Bovid sample size identified to genus	93	306	131	232	270	1186	12	1	2231
Bovide sample size identified to species	87	287	128	227	263	1164	11	1	2168
Abundance of most abundant species	48	163	62	106	141	461	6	n.a.	
Berger-Parker index (1/d)	1.81	1.76	2.06	2.14	1.87	2.52	1.83	n.a.	
Simpson's Diversity (1/D)	2.69	2.32	62.36	2.60	2.91	4.09	3.24	n.a.	

* Area of exposure under G(L) refers to all of Member G.

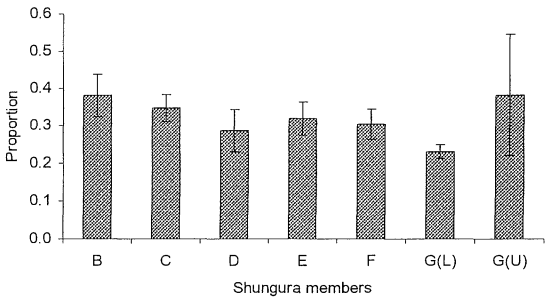

FIGURE 11. Abundance of bovid specimens identified to the family level only (Bovidae sp.) in Shungura Members B to G. Binomial error bars denote the 95% confidence interval.

mates. Localities or stratigraphic levels that yield well-preserved and easily identifiable specimens are likely to have more identified species than localities or stratigraphic levels with poor preservation, other factors being comparable. We can evaluate preservation and "identifiability" by the proportion of specimens identified only to the family level, i.e., identified to family as Bovidae sp. but not to a lower taxonomic level (tribe, genus, or species), from the total sample of bovids. The absolute and relative frequencies of specimens classified as Bovidae sp. are found in Tables 3 and 4. Figure 11 shows that the relative abundance of Bovidae sp. is comparable in Members B to F, but significantly lower in lower Member G. Thus, lower Member G has a higher relative abundance (Fig. 6) and better preservation (Fig. 11) of bovids than earlier members. Overall, as Figure 11 illustrates (see also Tables 4, 5), about 28% of bovid specimens in the Shungura analytic database are identified only as Bovidae sp., and 72% are identified to a tribe or lower taxonomic level.

This pattern of changing identifiability of bovid specimens may be due to differences in the abundance of various skeletal elements across the sequence. The percentage of bovid specimens identified below the family level varies with the skeletal element involved (see Table 6): 80% of isolated teeth, 85% of horn cores, 91% of cranial parts (other than horn cores), 88% of mandibles, and 3% of postcranial elements (metapodials and astragali) are identified to tribe, genus, or species. Thus, localities or stratigraphic levels with a high proportion of skull elements such as horn cores, mandibles, or maxillae are likely to have more recognized taxa than localities with a high proportion of isolated teeth or postcranial elements, all else being equal.

Table 7 provides the number and relative frequency of bovid specimens in each of several skeletal element categories. Figure 12 depicts the relative abundance of each body-part category as a proportion of all bovid speci-

TABLE 6. Percentage of skeletal elements identified to family only, and of those identified below the family level.

	No. of specimens	% per skeletal-element category
Isolated teeth identified to family only	365	19.8
Isolated teeth identified to tribe, genus, or species	1483	80.2
Isolated teeth (total)	1848	
Horn cores identified to family only	216	15.2
Horn cores identified to tribe, genus, or species	1204	84.8
Horn cores (total)	1420	
Crania identified to family only	9	8.8
Crania identified to tribe, genus, or species	93	91.2
Crania (total)	102	
Mandibles identified to family only	35	12.1
Mandibles identified to tribe, genus, or species	25	87.9
Mandibles (total)	290	
Metapodials identified to family only	251	94.4
Metapodials identified to tribe, genus, or species	15	5.6
Metapodials (total)	266	
Astragali identified to family only	307	100.0
Astragali identified to tribe, genus, or species	0	0.0
Astragali (total)	307	
Total number of bovids	4233	

TABLE 7. Bovid specimens according to skeletal-element representation.

	Member								
	B	C	D	E	F	G(L)	G(U)	H	Total
NUMBER OF SPECIMENS									
Isolated teeth	153	299	121	181	203	874	15	2	1848
Horn cores	52	145	64	124	169	859	6	1	1420
Crania and maxillae	10	22	3	15	19	31	1	1	102
Mandibles	16	65	19	37	20	129	3	1	290
Metapodials	22	61	12	35	34	94	8	0	266
Astragali	23	66	26	32	47	112	1	0	307
Total	276	658	245	424	492	2099	34	5	4233
RELATIVE ABUNDANCES									
Isolated teeth	0.55	0.45	0.49	0.43	0.41	0.42	0.44	0.40	0.44
Horn cores	0.19	0.22	0.26	0.29	0.34	0.41	0.18	0.20	0.34
Crania and maxillae	0.04	0.03	0.01	0.04	0.04	0.01	0.03	0.20	0.02
Mandibles	0.06	0.10	0.08	0.09	0.04	0.06	0.09	0.20	0.07
Metapodials	0.08	0.09	0.05	0.08	0.07	0.04	0.24	0.00	0.06
Astragali	0.08	0.10	0.11	0.08	0.10	0.05	0.03	0.00	0.07
Total	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00

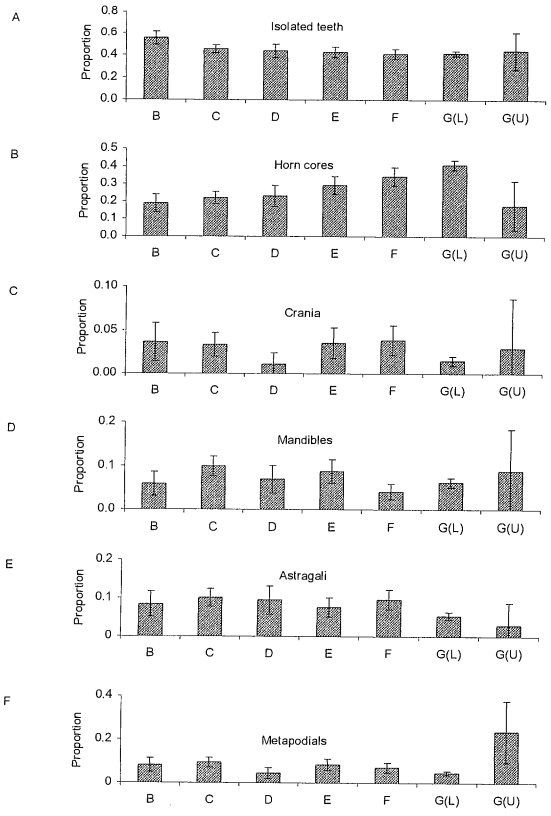

FIGURE 12. Relative abundance of bovid skeletal elements (i.e., proportion of all bovid specimens) in Shungura Members B to G. Binomial error bars denote the 95% confidence interval.

mens. It is noteworthy that the abundance of isolated teeth (Fig. 12A), the most common element in Members B to G, differs only marginally from an even distribution (chi-square test on Table 7 frequencies: $\chi^2 = 13.8$; with 6 df, $0.05 > p > 0.025$). The relatively homogeneously distributed abundance of isolated teeth indicates that isotaphonomic conditions prevailed in this part of the Shungura sequence. Other elements, however, show a more heterogeneous distribution. The relative abundance of horn cores, shown in Figure 12B, increases from Member B to lower Member G, and then declines in upper Member G ($\chi^2 = 86.8$; with 6 df, $p < 0.001$). The relative abundance of other cranial parts (crania, maxillae, and other cranial fragments) is depicted in Figure 12C, and shows no trend, although the distribution is not even ($\chi^2 = 19.7$; with 6 df, $p = 0.005$). The relative abundance of mandibles, shown in Figure 12D, is high in Members C and E, and low in Members B and F ($\chi^2 = 19.0$; with 6 df, $p < 0.005$). The relative abundance of postcrania is shown in Figures 12E and 12F. Astragali and metapodials combined are least abundant in lower Member G and most abundant in upper Member G. Astragali are most abundant in Members B, C, D, and F (Table 7, Fig. 12E). Two of these members, B and D, have units characterized by deep channeling. Metapodials are most abundant in upper Member G, characterized by la-

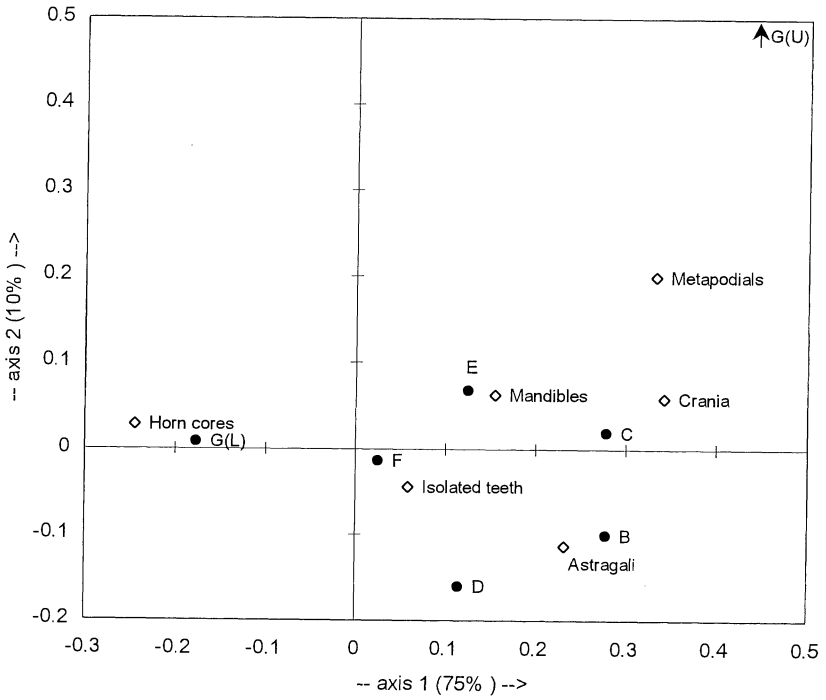

FIGURE 13. Correspondence analysis of bovid skeletal elements across Shungura members; $n = 4233$; axes 1 and 2 explain 85% of the variation.

custrine deposits. The distributions of astragali and metapodials taken separately differ significantly from an even distribution (for astragali, $\chi^2 = 26.4$; with 6 df, $p < 0.001$; for metapodials, $\chi^2 = 41.3$; with 6 df, $p < 0.001$).

A correspondence analysis of bovid skeletal element representation in Members B to upper G (with the frequencies in Table 7) is shown in Figure 13, which thus incorporates in a single multidimensional analysis the univariate patterns in Figure 12A–F. The category "isolated teeth" is positioned near the origin, which indicates that its distribution is relatively even across members. The first principal axis (horizontal) in Figure 13 shows a gradient of increasing representation of horn cores from Member B to lower Member G. Astragali are pulled most strongly in the directions of Members B and D, members characterized by deep channeling and high-energy depositional environments. Metapodials are pulled most strongly in the direction of upper Member G, characterized by low-energy depositional environments. There is a strong temporal trend in the position of Members B to lower G along the first axis, but this temporal trend breaks down with upper Member G. It would thus appear that the main shift in bovid skeletal element representation occurs between lower and upper Member G. In Figure 13, lower and upper Member G occur at opposite ends of the first principal axis, which otherwise follows a chronological sequence from Member B to lower Member G.

Taphonomic conditions as reflected in the representation of skeletal elements can be further analyzed by taking the position of each member along the first axis of Figure 13 and plotting this position along a stratigraphic axis, as shown in Figure 3E. With this method it becomes apparent that taphonomic conditions change only gradually from Member B to lower Member G, and abruptly from lower to upper Member G. The trend between Members B and lower G appears to be driven by the gradual increase in horn cores between these members (Fig. 12B). These results indicate that there are no major taphonomic shifts in the Shungura sequence in Members B to lower G. The shift in taphonomic conditions be-

tween lower and upper Member G is likely to be a direct consequence of the change in depositional environments, from fluvial conditions in lower Member G to lacustrine conditions in upper Member G.

With these taphonomic considerations in mind, we proceed to study the relative abundance of bovid tribes through the Shungura sequence. We begin with the most abundant tribe, the Reduncini, and continue with the other tribes in order of decreasing abundance.

Bovid Taxa

Reduncini.—The most abundant bovid tribe in the Shungura Formation is the Reduncini (Tables 3, 4). Modern Reduncini are medium-sized bovids with hypsodont teeth for grazing. Most species live near marshes or floodplains and always stay close to water. The horns, found only in males, are strongly ringed. There are two living genera of reduncines: the relatively large and gregarious *Kobus* and the smaller, less gregarious *Redunca.* Waterbuck, kob, puku, and lechwe, all species of the genus *Kobus*, typically live in woodland clearings, wetlands, and floodplains, where they are almost entirely grazers. The waterbuck, *Kobus ellipsiprymnus*, is one of the most water-dependent bovids, and its distribution is limited to areas with grass and some cover, always within a few kilometers of water. The kob, *Kobus kob*, typically occupies low-lying flats close to permanent water. Lechwes, *Kobus leche*, are one of the most aquatic antelopes, inhabiting flooded meadows bordering large rivers and lakes. The Nile lechwe, *Kobus megaceros*, inhabits the meadows of *Leersia* grass in southern Sudan. The various species of reedbuck, all genus *Redunca*, tend to live among tall grasses near water, although the mountain reedbuck, *Redunca fulvorufula*, prefers scrub-grass ecotones (Kingdon 1982, 1989; Spinage 1982; Estes 1991).

Most specimens of Reduncini from the Shungura Formation are the size of *Kobus*, but isolated teeth are not identified below the tribal level (Gentry 1985). The predominant species of *Kobus* in Member B is *K. oricornus*, but this species disappears from the subsequent Shungura record (Table 3). Specimens of *Kobus ancystrocera* are found in Members B, C, E, and lower G, but they only constitute about 1% of the bovid fauna. Harris (1991) suggests that the laterally diverging horn cores of *K. oricornus* and *K. ancystrocera* are an indication of adaptation to open marshy habitats, similar to those preferred by the modern lechwe. The most common reduncine, especially in Members D through lower G, is *K. sigmoidalis*, an extinct species that greatly resembles the modern waterbuck and is probably ancestral to it. Gentry (1985) documents a change in the morphology of *K. sigmoidalis* in Member G, a change that he identifies as the origin of the modern waterbuck, *K. ellipsiprymnus.* Like the waterbuck, *K. sigmoidalis* probably inhabited areas with grass and some cover, always close to water. Specimens of *K. sigmoidalis* constitute about 3% of all bovids in Member D but nearly 10% in lower Member G. Horn cores of *K. sigmoidalis* increase in size during this time (Gentry 1985). There are only five specimens of *Redunca* in the analytic database; these occur in Members B, C, E, and F. The reduncine *Menelikia lyrocera* is rare in lower members but reaches about 5% of the bovid fauna in Member F and lower Member G, and it is the most abundant bovid species in upper Member G. Gentry (1985) identified a new species of *Menelikia* in Members C and D. This species appears to be the same as *Menelikia leakeyi* described by Harris (1991) in the Koobi Fora Formation. Morphological analysis and comparisons with modern bovids show that *Menelikia* was a mixed feeder rather than a grazer, and that it fed on soft, tender vegetation (Spencer 1997). The vegetation preferred by *Menelikia* is thought to have been homogeneously distributed, in areas with little seasonal variation. These observations are particularly relevant in the interpretation of environments in upper Member G, where *Menelikia* is the dominant bovid.

The pattern of reduncine abundance across members is not homogeneous (chi-square test on Table 3 frequencies: $\chi^2 = 171.8$; with 6 df, $p < 0.001$). Overall, reduncines are very abundant in Member B, where they constitute almost 25% of the bovid fauna, as shown in Figure 14. But their abundance drops sharply to about 11% in Member C and remains low in Members D, E, and F. In lower Member G there is a sharp increase in reduncine abundance to over 30% of the bovid fauna. In upper Member G, reduncines are the dominant bovid, with *Menelikia lyr-*

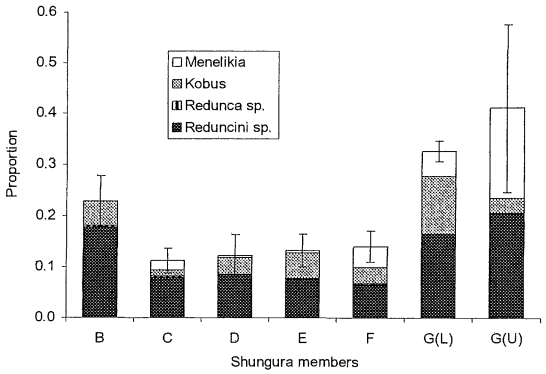

FIGURE 14. Reduncini as proportion of all bovids per member. Binomial 95% confidence intervals for the tribe as a whole.

ocera as the dominant species. The relative abundance of Reduncini is not significantly correlated with sample size ($r_s = -0.21$; $p > 0.5$).

Living species of the genus *Kobus* are strongly associated with edaphic grasslands and marshy habitats often close to woodlands and forests. Thus, the prevalence of reduncines in Member B, where almost all the specimens identified to genus belong to *Kobus* (Fig. 14), indicates that edaphic grasslands were an important component of the Omo habitats during deposition of this member. The drop in reduncine relative abundance in Members C through F indicates that edaphic grasslands, although present, had a diminished role in the mosaic of Omo habitats. *Menelikia's* appearance in Member C and its increases in abundance in Members F and G suggest that environmental conditions in Members C to G were different from those in Member B. The resurgence of Reduncini in lower Member G is made up largely of *Kobus sigmoidalis*, but *Menelikia lyrocera* is an important component. In pairwise comparisons of relative abundance among bovid species, *K. sigmoidalis* and *M. lyrocera* are significantly correlated ($r_s = 0.90$, $p < 0.05$), which suggests that competition between these two species was not a major factor in their abundance. *Menelikia's* presumed preference for habitats without good modern analogues (Spencer 1997), habitats different from those preferred by other reduncines, adds a measure of environmental heterogeneity to the mosaic of Member G (upper and lower) habitats.

The changes in the relative abundance of Reduncini in Members B and C occur in the absence of significant changes in taphonomic or depositional conditions (Figs. 3B, 4), whereas those changes in upper Member G, and to a lesser extent in lower Member G, are probably a consequence of the onset of deltaic and lacustrine environments (Fig. 3B). As discussed earlier, the onset of lacustrine environments in the basin resulted from tectonic, not climatic changes. In Members B and C, however, changes in the relative abundance of Reduncini may be driven by factors other than tectonics. The significant decrease in the abundance of Reduncini from Members B to Member C is consistent with the onset of drier climatic conditions reflected in paleosols (Fig. 3B). Thus, although Reduncini are most abundant in Members B and G, the high abundance has different environmental implications in each case.

Aepycerotini.—The tribe Aepycerotini is the second most abundant group of Shungura Bovidae (Tables 3 and 4). The modern impala, *Aepyceros melampus*, is a medium-sized, highly gregarious antelope, with hypsodont teeth and, in males, long, lyrate horns. Impalas are an ecotone or edge species that inhabits acacia savannas and light woodlands close to water. They have a diverse diet of leaves, short grasses, and occasional fruits, and they adapt to different habitats by grazing in some areas and browsing in others (Murray 1981; Kingdon 1982; Vrba 1984; Estes 1991). Plio-Pleistocene impala may have relied more heavily on browsing than the living species (Sponheimer et al. 1999).

The direct ancestor of the modern impala is *Aepyceros shungurae*, the most common species of bovid in the Shungura Formation. The extinct Shungura impala differs from the living form in its smaller size, longer premolar row, and shorter, thicker limb bones (Gentry 1985; Harris 1991). However, it is difficult to distinguish fossil *A. shungurae* from modern *A. melampus*, and Gentry (1985) rather arbitrarily assigns all *Aepyceros* specimens in Members A through G to *A. shungurae*.

Although the abundance of impalas across members is not evenly distributed ($\chi^2 = 34.5$; with 6 df, $p < 0.001$), *A. shungurae* is consistently the first or second most abundant species in each member. As shown in Figure 15, *Aepyceros* constitutes about 21% of the bovid fauna, and its relative abundance fluctuates around this mean,

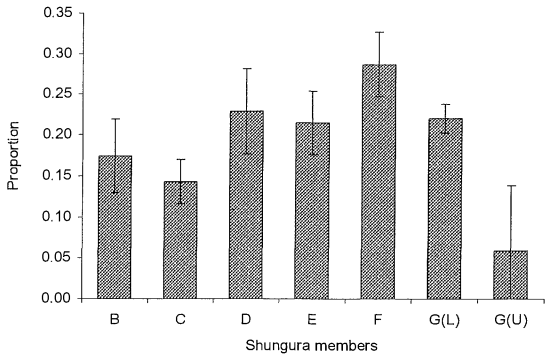

FIGURE 15. Aepycerotini as proportion of all bovids per member. Binomial 95% confidence intervals for the tribe as a whole.

with no significant correlation between relative abundance and sample size ($r_s = 0.29$; $p > 0.5$). The consistently high abundance of impala may be evidence of the adaptability of this species. Impala today remain one of the most successful African antelopes (Vrba 1984).

On morphological grounds (smaller horn cores, shorter legs, longer premolar row), it appears likely that *A. shungurae* inhabited more-closed woodlands than the living impala. These woodlands would have been a predominant element of the environment throughout the time of deposition of the Shungura sequence under consideration.

Tragelaphini.—Tragelaphini is the third most abundant tribe of Shungura bovids. Modern tragelaphines are medium-sized to large bovids found in much of Sub-Saharan Africa. Tragelaphines have deep bodies, long necks and legs, narrow heads with big ears, and horns that are keeled and spiraled. They are characterized by brachyodont teeth, an adaptation to a diet of leafy vegetation. They are selective browsers that typically live in woodlands. At one end of the tragelaphine-habitat spectrum is the bongo, *Boocercus euryceros,* which inhabits the thick lowland rain forests of West and Central Africa and montane forests in East Africa. The bongo browses on leaves and shoots of shrubs in forest openings, where new growth and leafy vegetation are found near ground level (Kingdon 1982; Hillman 1986). Bongo can be relatively gregarious, occasionally found in groups of up to 30 individuals, but group size varies seasonally and usually consists of just a few individuals (Estes 1991). At the other end of the tragelaphine ecological spectrum is the common eland, *Taurotragus oryx,* a gregarious species. The eland inhabits open plains and savannas, where it feeds on leaves and occasional fruits. In bongo and eland both sexes carry horns. All the other species of this tribe are in the genus *Tragelaphus,* in which only the males carry horns (Kingdon 1982; Estes 1991).

Most species of living *Tragelaphus* occupy relatively wooded or bushy habitats. The greater kudu, *Tragelaphus strepsiceros,* is a browser that lives in light forest or bushland. The lesser kudu, *T. imberbis,* is adapted to dry but closed thickets, where it feeds on the leaves of trees and shrubs. The bushbuck, *T. scriptus,* is a forest-edge species that inhabits thickets and dense bush, where it browses on leaves, digs for roots and tubers, and occasionally eats fruit. The sitatunga, *T. spekei,* and the nyala, *T. angasi,* are closely related species. The sitatunga is specialized to life in muddy swamps and marshes, where it browses on leaves and grazes on low-level vegetation, while the nyala is found in woodlands near water (Dorst and Dandelot 1969; Kingdon 1982; Estes 1991).

In the Shungura Formation analytic database, tragelaphines are represented by 854 specimens from at least four species (Table 3). The extinct species *Tragelaphus nakuae* is the most abundant tragelaphine in the sequence. Although in size, morphology, and orientation of the horn cores *T. nakuae* resembles the bongo, the habitat preferences of *T. nakuae* remain unclear. Gentry (1985) notes that *T. nakuae* undergoes notable changes in horn-core morphology between Member B and Member C, and further changes between Members F and G. The second most common Shungura tragelaphine is *T. gaudryi,* a species closely related to modern kudus. Other tragelaphines include specimens of *T. pricei,* a species probably close to the ancestry of the bushbuck, and *T. strepsiceros,* the greater kudu.

The abundance of Tragelaphini in the Shungura sequence is not homogeneous ($\chi^2 = 55.6$; with 6 df, $p < 0.001$). The relative abundance of Tragelaphini as a proportion of all bovids across Shungura members experiences two major changes, illustrated in Figure 16. There is a highly significant increase from about 10% in Member B to about 27% in Member C. This proportion is maintained in Members D and

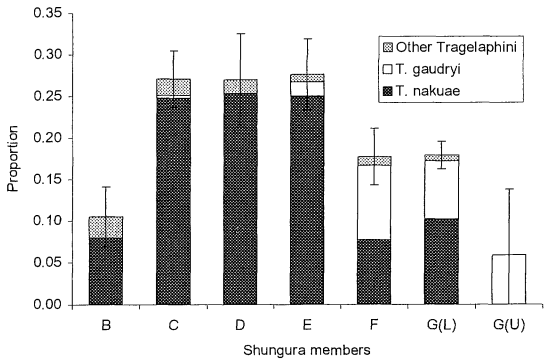

FIGURE 16. Tragelaphini as proportion of all bovids per member. Binomial 95% confidence intervals for the tribe as a whole.

E and decreases to under 20% in Member F and lower Member G. In upper Member G there are only two specimens of Tragelaphini, both belonging to *T. gaudryi*. The relative abundance of Tragelaphini does not correlate significantly with sample size ($r_s = 0.43$; $0.5 > p > 0.2$). In pairwise comparisons at the tribal level, there is only one significant correlation in the relative abundance of bovid tribes: a negative correlation exists between Tragelaphini and Reduncini ($r_s = -0.857$; $p = 0.05$). In correlations at the species level, however, *T. gaudryi* is positively correlated with both *Kobus sigmoidalis* ($r_s = 0.81$; $p < 0.05$) and *Menelikia lyrocera* ($r_s = 0.85$; $p < 0.05$), species that tend to be most abundant in Members F and G.

The changes in the relative abundance of Tragelaphini are mostly a reflection of the pattern of abundance seen in *T. nakuae* (Fig. 16). From a low proportion of the bovid fauna in Member B, *T. nakuae* increases its representation to constitute a quarter of all bovids in Members C, D, and E and then drops again in Member F and lower Member G. As *T. nakuae* drops in abundance in Members F and G, *T. gaudryi* increases. In Member F and upper Member G, *T. gaudryi* is more abundant than *T. nakuae* (Fig. 16).

The increase in tragelaphine abundance between Members B and C may reflect a shift in the environment of the lower Omo basin toward conditions favored by *T. nakuae*. If *T. nakuae* was like most species of living *Tragelaphus*, it probably avoided dense forests as well as open grasslands. Thus, the increase in tragelaphine abundance may signify a shift from dense forest to woodland or bushland conditions between Members B and C. The next major change occurs between Members E and F. Although tragelaphines as a whole, and *T. nakuae* in particular, decline at this time, *T. gaudryi* increases significantly. Gentry (1985) describes *T. gaudryi* as closely related to modern kudus. Like modern kudus, *T. gaudryi* was probably adapted to light forest and dry thickets, habitats that may have gained prevalence in Members F and G.

Bovini.—The tribe Bovini includes one of the most successful African large mammals, the African buffalo, *Syncerus caffer*, with populations that range from rain forests to savannas. Forest buffalo are smaller than their savanna counterparts, but the two forms interbreed wherever their ranges overlap. Bovines have large bodies, stout limbs, massive horns in both sexes, and a large and broad muzzle for grazing. They are always found close to thick cover and water, for they must drink daily. They are primarily grazers in dense riverine vegetation, although they also eat leaves in wooded habitats (Sinclair 1977; Kingdon 1982; Mloszewski 1983; Estes 1991).

Two genera of Bovini are recognized in the Shungura analytic database: *Syncerus* and *Pelorovis*. A third genus, *Simatherium*, has been reported from the French collection of the Shungura Formation (Geraads 1995). The specimens of *Syncerus* probably belong to a species closely related to the modern African buffalo (Gentry 1985) and may have had similar habitat preference. *Pelorovis* is an extinct large bovine with long, curved, and massive horn cores, suggesting it was probably adapted to more open conditions than *Syncerus*. Specimens of *Pelorovis* are present in Members B, C, F, and G, but in small numbers.

Figure 17 shows that Shungura Bovini are most abundant in Members B and C, and that their abundance decreases in Members D to lower G. A simple chi-square test for the distribution of Bovini across members shows that their abundance is significantly different from homogeneous ($\chi^2 = 119.2$; with 6 df, $p < 0.001$). The relative abundance of Bovini does not correlate significantly with sample size ($r_s = -0.32$; $p = 0.5$). The abundance of Bovini, and particularly of *Syncerus*, in Members B and C (Fig. 17) points to the presence of wet and closed habitats during deposition of these members.

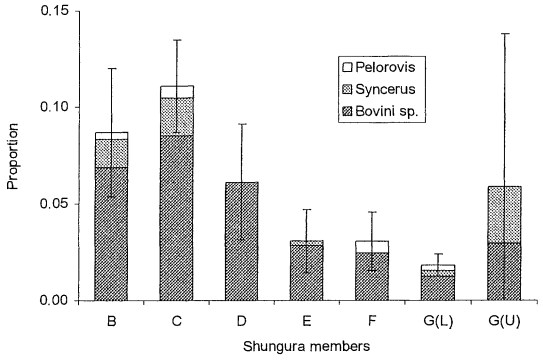

FIGURE 17. Bovini as proportion of all bovids per member. Binomial 95% confidence intervals for the tribe as a whole.

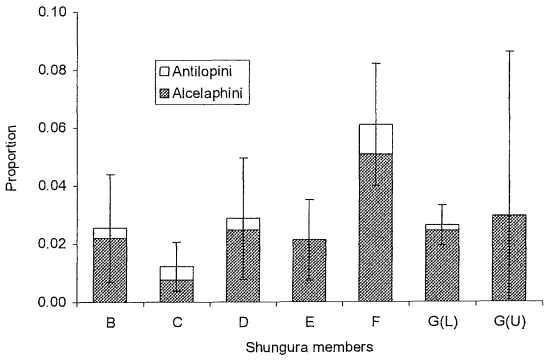

FIGURE 18. Alcelaphini and Antilopini as proportion of all bovids per member. Binomial 95% confidence intervals for both tribes combined.

Alcelaphini.—Alcelaphines are the most characteristic open-country dwellers of the African savannas. Alcelaphines are rather large, gregarious antelopes, with very hypsodont teeth for grazing and limbs with strong cursorial adaptations. Horns are present in both sexes. Modern alcelaphines include species of hartebeest in the genus *Alcelaphus*, topi and blesbok in the genus *Damaliscus*, and wildebeests in the genus *Connochaetes*. Although some hartebeests inhabit woodlands, nearly all alcelaphines prefer open savanna with short grasses (Vrba 1984; Estes 1991).

Alcelaphines are not common in the Shungura Formation, except perhaps in Member F (Tables 3, 4). Among alcelaphines, few specimens are identified below the tribal level, but *Damalops*, *Megalotragus*, and *Parmularius* occur in the sequence. The pattern of alcelaphine abundance is significantly different from an even distribution ($\chi^2 = 22.1$; with 6 df, $0.005 > p > 0.001$). The relative abundance of alcelaphines, shown in Figure 18, remains close to 2% in all members except for F, where there is a spike in the representation of this tribe. The relative abundance of Alcelaphini does not correlate significantly with sample size ($r_s = 0.35$; $0.5 p > 0.2$). Thus, although alcelaphines are rare in the Shungura Formation, their increase in abundance in Member F provides a strong indication that this member was deposited under seasonally drier and more open conditions than the other Shungura members under consideration.

Antilopini.—Antilopines are medium-sized antelopes with long and thin legs for very fast running. This group includes gazelles, gerenuk, and springbok, bovids that typically live in grasslands or bushland and can tolerate very dry conditions. Antilopines generally are selective feeders on foliage and herbage (Dorst and Dandelot 1969; Kingdon 1982; Estes 1991). For example, the springbok, *Antidorcas marsupialis*, can graze or browse, but the plants it eats typically occur in dry and open environments (Vrba 1987).

Antilopines are rare in the Shungura Formation, but at least three genera are represented: *Gazella*, *Antidorcas*, and *Antilope*. The sample size of Antilopini is too small for a chi-square evaluation, but the combined abundance of Antilopini and Alcelaphini, the two bovid tribes most closely associated with open habitats, is significantly different from a uniform distribution ($\chi^2 = 26.4$; with 6 df, $p < 0.001$). The relative abundance of Antilopini does not correlate significantly with sample size ($r_s = -0.18$; $p > 0.5$). Like the distribution of Alcelaphini, the relative abundance of Antilopini shows a spike in Member F (Fig. 18) and suggests the presence of open and seasonally dry conditions during deposition of Member F.

Hippotragini.—Modern hippotragines are medium-sized antelopes, mainly grazers, with hypsodont teeth. Species of *Hippotragus* typically inhabit bushland or light woodlands, while *Oryx* species range into very dry habitats (Vrba 1980a; Kingdon 1982; Estes 1991). Hippotragines are scarcely represented in the Shungura Formation. The Hippotragini sample in the analytic database consists of six specimens: one

horn core, one mandible fragment, and four isolated teeth. Hippotragini are completely absent from the record of the lower Omo Valley prior to Member C (including the French Shungura collection, Mursi and Usno Formations). Therefore, the appearance of *Hippotragus* and *Oryx* in Member C may indicate the spread of the dry woodlands, bushlands, and grasslands favored by these bovids.

Neotragini.—Modern neotragines form a very diverse group of small antelopes. Although there are two species of forest neotragines (*Neotragus pygmaeus* and *N. batesi*), most species of this tribe are adapted to relatively arid environments. Steenbok and grysbok, for instance, species of the genus *Raphicerus*, occur in bushland or light woodland. They browse on leaves and shoots of low shrubs and trees and sometimes graze on young grasses (Spinage 1986; Estes 1991).

Neotragines are poorly represented in the Shungura Formation. *Raphicerus* is represented by a horn core in Member E and a mandible fragment in G. Three other specimens, identified as Neotragini sp., occur in Members E, F, and G. Although the sample is minute, it is interesting to note that all five neotragine specimens occur in the later part of the Shungura sequence. The two specimens that are identified to the generic level correspond to arid-adapted neotragines.

Ovibovini.—There is only one specimen of Ovibovini in the Shungura Formation analytic database, in Member D. The specimen is a lower molar indistinguishable from those of the better-known South African Ovibovini, *Makapania broomi* (Gentry 1985). Isotopic and ecomorphological data indicate that *Makapania* was a mixed feeder with preference for grasses (Sponheimer et al. 1999). The Omo ovibovine may represent a brief incursion of this species into the Omo at a time when paleobotanical and micromammalian data suggest a relative opening of the environment.

In sum, bovid tribes show different patterns of abundance through the Omo sequence. Some significant changes in abundance appear to be a consequence of tectonic forces that brought about changes in depositional environments (e.g., the increased abundance of Reduncini in lower and upper Member G). Other changes occur in the absence of significant changes in depositional environments or taphonomic factors (e.g., those experienced by Reduncini and Tragelaphini between Members B and C). The overall patterns of abundance of bovid taxa are explored next, along with their paleoenvironmental implications.

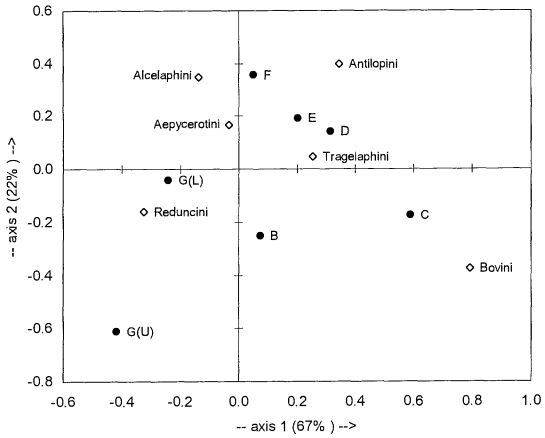

FIGURE 19. Correspondence analysis of bovid tribes in Shungura Member B to upper Member G. $n = 3034$; axes 1 and 2 explain 89% of the variation.

Patterns of Faunal Change

The univariate patterns of bovid abundance depicted so far are better understood when taken simultaneously in correspondence analyses. Rare taxa play only a minor role in the patterns generated by correspondence analysis. Thus, in the following analyses we exclude taxa with fewer specimens than there are members under consideration, i.e., with fewer than seven specimens. A correspondence analysis of bovid tribes across members is depicted in Figure 19. The positions of Members C to upper G along the first correspondence analysis axis follow a strictly chronological succession. At one end of the first axis there is Member C, with a high abundance of Bovini, while at the other end there is upper Member G, with a high abundance of Reduncini. Only Member B fails to line up in proper chronological order. Along the second axis, Members B to F form another chronological succession that approaches the pole dominated by Alcelaphini and Antilopini, the two bovid tribes most closely associated with dry and open habitats. Member B, being out of the chronological sequence along the first axis,

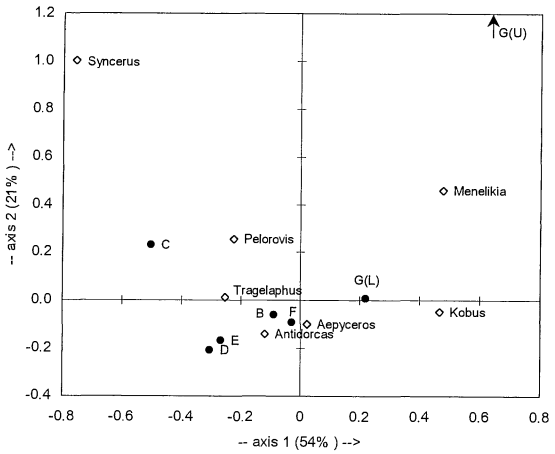

FIGURE 20. Correspondence analysis of bovid genera in Shungura Member B to upper Member G. $n = 2209$; axes 1 and 2 explain 76% of the variation.

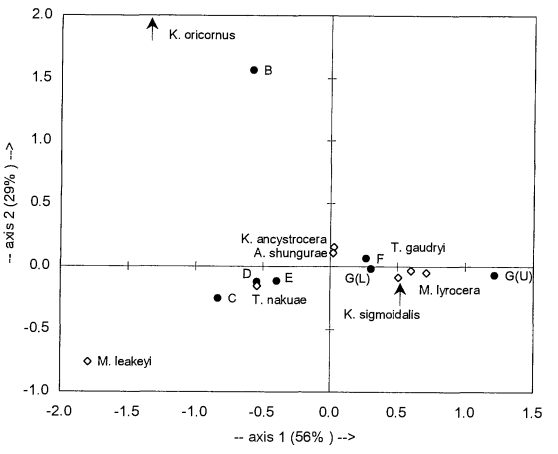

FIGURE 21. Correspondence analysis of bovid species in Shungura Member B to upper Member G. $n = 2138$; axes 1 and 2 explain 85% of the variation.

is pulled in the direction of both Bovini and Reduncini, the two bovid tribes most closely associated with wet and wooded habitats. The first dimension accounts for 67% of the variation and the second dimension accounts for 22%. Thus, nearly 90% of the variation in bovid tribal abundances across members is depicted in the two-dimensional representation of Figure 19.

A correspondence analysis of Shungura bovids at the genus level, with the data provided in Table 3, is depicted in Figure 20. As in Figure 19, Figure 20 shows a chronological placement of Shungura Members C to upper G along the first axis, with Member B placed out of sequence. In Figure 20, *Tragelaphus* occupies a similar position as Tragelaphini in Figure 19, a position in the direction of Members C, D, and E. *Aepyceros* occupies a similar position as Aepycerotini, a position in the direction of Members F and lower G. This is to be expected in tribes dominated by a single genus. The genera of Bovini *Syncerus* and *Pelorovis* occupy different positions in Figure 20, although both genera are pulled most strongly in the direction of Member C, where both have high relative abundances. The genera of Reduncini cluster relatively close together, although *Kobus* has a higher profile in lower Member G and *Menelikia* in upper Member G. The divergent position occupied by upper Member G is a consequence of the high relative abundance of *Menelikia* in that member.

A correspondence analysis of Shungura bovids at the species level is shown in Figure 21. This figure shows that congeneric species may have very different patterns of abundance. Thus, *Tragelaphus nakuae* is far apart from *T. gaudryi*; *Menelikia lyrocera* is far apart from *M. leakeyi*, and *Kobus oricornus* is far from *K. ancystrocera*, which is also far apart from *K. sigmoidalis*. In Figure 21 we find once again that the axis explaining most of the variation among members has a largely chronological component, but that Member B does not follow the pattern of the other members. In fact, the analysis in Figure 21 places Member B in opposition to all other members along the second axis. If instead of analyzing one axis at a time we look at the entire two-dimensional configuration, we see that there are three poles, composed of Members B, C, and upper G. The correspondence analysis figure suggests that there is a break between Members B and C, followed by gradual faunal transition between Members C and G.

Although there is variation in the correspondence analysis patterns from one taxonomic level to the next, there is a consistent theme running through Figures 19 to 21. The position of each member in these figures depends on the abundance of the different bovid taxa in that member. Overall, Shungura Members C to upper G show a pattern of changes in taxonomic abundance that correlates with time. At the tribal, generic, and species levels, Members C to upper G line up along the first axis in chronological order. The position of Member B is more

TABLE 8. Abundance of bovid taxa across 200-Kyr intervals (number of specimens in analytic database).

	Units						
	B2–B9 >3.0 Ma	B10–C3 3.0–2.8 Ma	C4–C8 2.8–2.6 Ma	C9–D5 2.6–2.4 Ma	E1–G8 2.4–2.2 Ma	G9–G27 2.2–2.0 Ma	Total
T. nakuae	2	24	131	90	276	81	604
T. gaudryi	0	0	0	3	161	40	204
Bovini	3	22	50	37	56	12	180
K. oricornus	1	7	0	0	0	0	8
K. ancystrocera	0	3	7	0	6	25	41
K. sigmoidalis	0	0	0	7	202	38	247
Menelikia	0	0	12	1	89	40	142
Hippotragini	0	0	2	1	3	0	6
Aepyceros	2	50	71	75	406	289	893
Alcelaphini	0	6	4	7	66	207	103
Antilopini	0	1	3	1	8	1	14
Total	8	113	280	222	1273	546	2442

variable, and Member B is the only member that does not fall along the chronological sequence. This pattern may be illustrated by plotting the position of members in the tribal analysis (Fig. 19) along a stratigraphic axis, as shown in Figure 3F. Figure 3F indicates that changes in bovid relative abundances between members C and upper G occurred gradually through time, but that changes in relative abundance between Members B and C were abrupt.

To further test the robustness of this pattern, instead of using the traditional subdivision into members we can subdivide the Shungura sequence into time intervals of 200,000 yr. The correspondence analyses carried out thus far are used to select taxonomic categories. Thus, among the Tragelaphini, for example, *Tragelaphus nakuae* and *Tragelaphus gaudryi* are used, since both species have a large sample size and cluster far apart from each other in the correspondence analysis figures. But tribes like Alcelaphini and Antilopini have small samples identified to genus or species, so in those cases we use tribes. The taxa and their abundance in this analysis of time intervals are shown in Table 8. A correspondence analysis of Table 8 is shown in Figure 22. The overall pattern between 3 and 2 Ma shows a shift in bovid relative abundances at 2.8 ± 0.1 Ma followed by another relatively significant change at 2.4 ± 0.1 Ma.

Thus, the overall patterns of changes in bovid abundances show a strong shift between Members B and C, or at about 2.8 Ma. As shown in Figures 3 and 4, this shift occurred in the absence of significant changes in depositional environments, taphonomic conditions, or rates of deposition. Further changes in bovid relative abundances continued to occur, albeit more gradually, between 2.8 and 2.0 Ma. A peak in the abundance of Alcelaphini and Antilopini at about 2.35 Ma may signify an expansion of habitats preferred by these bovids.

Paleoenvironmental Implications

To the extent that bovids serve as indicators of past environments, the changes in abundance presented in previous sections appear to reflect shifts in environmental conditions. Associations of modern bovid taxa with broad habitat categories have been demonstrated by Greenacre and Vrba (1984) and by Shipman and Harris (1988). Greenacre and Vrba's (1984) analysis of bovid tribes indicates that Alcelaphini and Antilopini are strongly associated with modern wildlife areas characterized by open and dry conditions. Shipman and Harris's (1988) analysis confirms the association of Alcelaphini and Antilopini with open and dry habitats and also demonstrates the association of Tragelaphini and Aepycerotini with closed and dry habitats, and of Reduncini and Bovini with closed and wet habitats. Although some of the associations of modern bovid tribes with particular kinds of habitats may be ancient (Vrba 1980b, 1985b; Greenacre and Vrba 1984), there may be some exceptions. In particular, as Spencer's (1997) analysis suggests, *Menelikia* was decidedly different in its feeding habits from all other Reduncini. The soft and tender, yet homogeneously distributed vegetation with little seasonal

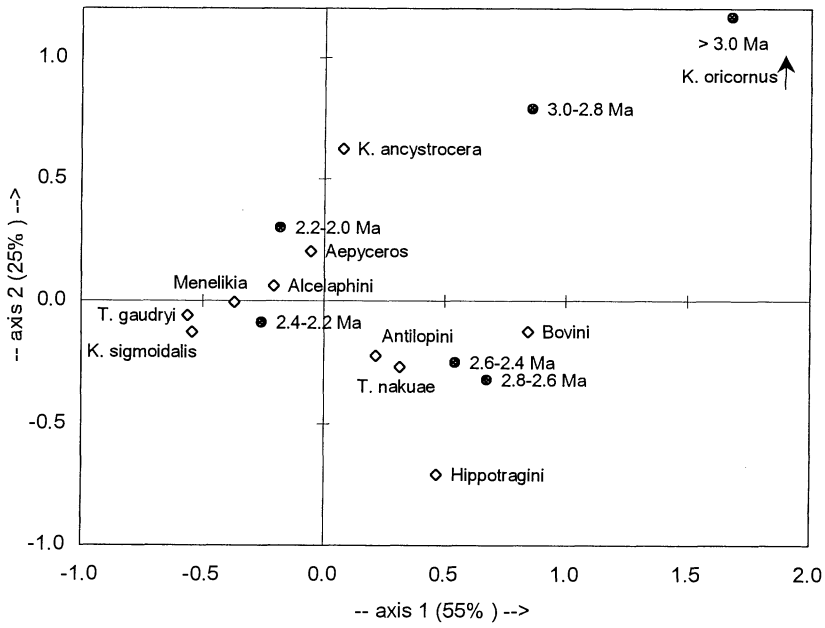

FIGURE 22. Correspondence analysis of bovid taxa across 200,000-yr intervals. $n = 2442$; axes 1 and 2 explain 81% of the variation.

variation that *Menelikia* would have fed upon may represent a habitat different from that preferred by other reduncines (Spencer 1997), a habitat that can be characterised as open and wet.

In Figure 3G, bovid abundances are used to indicate changes in the proportions of different types of environments in the Omo sequence from Member B to Member G. We distinguish the three types of environments defined by Shipman and Harris (1988) and add a fourth habitat in reference to *Menelikia*. Thus, the abundance of Bovini and Reduncini (without *Menelikia*) reflects the proportion of closed and wet environments, the abundance of Aepycerotini and Tragelaphini reflects closed and dry environments, and the abundance of Alcelaphini and Antilopini reflects open and dry environments. The abundance of *Menelikia* reflects open and wet environments. The fact that 51% of bovid specimens in Member B are indicative of closed and wet environments (Fig. 23) need not imply that closed and wet environments occupied 51% of the lower Omo Valley. Instead, it is the changes in this proportion through the sequence that are important. As Figure 23 indicates, bovids reflect a significant decrease in the proportion of closed and wet environments in the lower Omo Valley from Member B to Member C. This drop established a trend that continued in Members D, E, and F. These changes occurred in the absence of significant changes in depositional environments or taphonomic conditions. The proportion of closed and wet environments became more prevalent again in lower Member G but remained significantly less prevalent than in Member B (Fig. 23). The apparent resurgence of closed and wet environments in upper Member G must remain in doubt because its sample size is small (and the

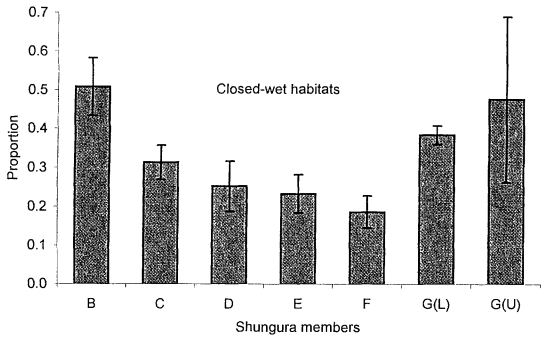

FIGURE 23. Abundance of bovids indicative of closed and wet habitats (Bovini and Reduncini without *Menelikia*) with 95% binomial confidence intervals.

confidence interval wide). However, as Figure 3G shows, environmental diversity and heterogeneity were greater in lower and upper Member G than in earlier times. Open and dry habitats seem to have played only a minor role in the Omo between 3 and 2 Ma, except perhaps at about 2.35 Ma (Figs. 3G, 18).

Discussion

The pattern of bovid taxonomic abundances in the lower Omo Valley shows a marked shift at about 2.8 Ma, between Shungura Members B and C (Figs. 3F, 19–22). This shift in abundances was followed by a prolonged and smooth faunal succession from Member C to upper Member G, or between about 2.8 and 2.0 Ma. In addition to the notable changes in relative abundances between Members B and C, the bovid fauna experienced an increase in species richness between these members (Fig. 9), accompanied by a slight decrease in species evenness (Fig. 10). The increase in richness in Member C was due to the first appearance in the basin of taxa such as *Tragelaphus gaudryi*, *Tragelaphus pricei*, *Menelikia leakeyi*, *Hippotragus gigas*, *Oryx*, and *Antilope subtorta*. These taxa were absent not only from the earlier members of the Shungura sequence (Members A and B of both the French and American collections), but also from the relatively large sample of the Usno Formation (n = 345 bovid specimens), which is correlative with lower Member B.

The analysis of bovid skeletal elements in the Shungura sequence indicates that only moderate changes in taphonomic conditions occurred between 3.0 and 2.1 Ma, i.e., between Member B and lower Member G, but significant changes occurred at about 2.1 Ma, between lower and upper Member G (Figs. 3E, 12, and 13). This pattern of taphonomic stability and change can be understood in relation to depositional environments in the lower Omo Valley. The large meandering river that dominated the basin in Members B through lower G brought a degree of stability to the mode of preservation of vertebrate remains. The onset of lacustrine depositional environments in upper Member G resulted from regional tectonic changes (de Heinzelin et al. 1976), not from changes in climate or precipitation, and produced a mode of preservation that differed from the preceding one. Although upper Member G samples are small, the lacustrine environment of upper Member G preserved significantly more metapodials and fewer horn cores than the fluvial environment of lower Member G (Figs. 12, 13).

Thus, the shift in taxonomic abundances between Members B and C occurred in the absence of a shift in taphonomic conditions, while the shift in taphonomic conditions between lower and upper Member G was not accompanied by a major shift in taxonomic abundances. The faunal shift between Members B and C is not related to changes in depositional environments, rates of deposition, sample size, or other taphonomic factors that affect preservation (Figs. 3, 4).

In the absence of evidence linking this shift in bovid abundance to local tectonic, depositional, or taphonomic factors, an explanation may be sought in the broader context of climate change in Africa. The timing of the major faunal changes in the Omo appears to coincide closely with changes in African climate recorded in terrigenous sediments off the coast of Africa at 2.8 Ma (deMenocal 1994; deMenocal and Bloemendal 1995). In addition to the coincidence in the timing of the pattern of faunal change, the environmental implications of the shift in bovid abundances are consistent with a transition from wet to dry habitats, albeit without a significant expansion of secondary grasslands (Figs. 3G, 23). As shown in Figure 23, the abundance of bovids associated with closed and wet habitats declined significantly between Members B and C, and continued to decline in Members D, E, and F. This decline was commensurate with an increase in bovids associated with closed but dry habitats. It is only in Member F, at about 2.35 Ma, that bovids associated with open and dry habitats showed a significant increase in abundance, even though they did not become a dominant component of the bovid fauna (Figs. 3G, 18). This peak at about 2.35 Ma occurred without significant changes in taphonomic conditions, although rates of deposition at this time reached their highest levels (Fig. 4). The bovid fauna of lower and upper Member G shows an increase in environmental heterogeneity at a time when depositional environments were shifting from fluvial to deltaic and then to lacustrine conditions (Fig. 3B,G).

This picture of environmental change (Fig. 3G) is also evident in the correspondence analysis graph of bovid tribes (Fig. 19). The idea that Member B had a higher proportion of closed and wet environments than later members follows from the suggestion that Bovini and Reduncini are the bovid tribes most closely associated with wet and wooded conditions (Greenacre and Vrba 1984; Shipman and Harris 1988). As shown in Figure 19, even though Member C has a high abundance of Bovini (Fig. 17), and Member G has a high abundance of Reduncini (Fig. 14), only Member B combines a high abundance of both tribes. Opposite from Member B along the second axis of Figure 19, Member F occurs in the direction of Alcelaphini and Antilopini, indicating that Member F represents the driest and most open paleoenvironments in the sequence. In an intermediate position we find Tragelaphini and Aepycerotini, associated with Members D and E.

The use of bovids as habitat indicators produces a rich and complex picture of environmental change in the lower Omo Valley, a picture that is consistent with several independent lines of evidence from both the Shungura Formation itself and from a broader context of climate in Africa. The evidence of micromammals and paleobotanical remains supports the interpretation derived from bovid abundances that Member B environments were closed and wet. As noted earlier, micromammals indicate the existence of biogeographical connections between the Turkana Basin and the humid forests of Central Africa during Member B times (Wesselman 1984, 1995). Fossil fruit of *Antrocaryon* in Member A and Usno U-12 (Bonnefille and Letouzey 1976) suggests that this biogeographical connection may have existed during much of Member A and Member B times, from about 3.6 to 2.85 Ma. The extension of this forested environment is highlighted by records of the rainforest gastropod *Potadoma* from Nachukui Formation sediments dating to about 3.4 Ma (Williamson 1985). Reed's (1997) analysis of ecological variables in Plio-Pleistocene African localities also supports this interpretation, in that Member B had a higher percentage of arboreal and frugivorous macromammal species than later Shungura members. However, the interpretation of closed or forested environments in Member B contradicts some of the conclusions of Boaz's (1977) study of Shungura mammals. Boaz found a more erratic pattern of faunal change in the Omo than suggested here. For example, he interpreted a peak of alcelaphines in Unit B-12 as indicative of a dry episode. However, the American Shungura analytic database has only 6 bovids from unit B-12 (Appendix), none of which belongs to Alcelaphini, although one specimen is *Aepyceros*. The French Shungura database has 57 bovids in Unit B-12, only one of which belongs to Alcelaphini, although 19 are *Aepyceros*. The peak of alcelaphines in Unit B-12 reported by Boaz (1977) apparently derives from lumping together as "alcelaphines" these 20 specimens in the French database. Although Alcelaphini sensu stricto and *Aepyceros* are closely related taxa (Gentry 1976, 1985; Vrba 1984), researchers (Vrba 1984, 1995; Shipman and Harris 1988; Harris 1991) agree that at least ecologically they are distinct and should be placed in different tribes. Thus, Boaz's interpretation of aridity in B-12 is an artifact of classification. Unit B-12, like most of Member B, was deposited under more mesic conditions than suggested by Boaz.

The environmental changes in Member C signaled by the bovid fauna coincide with a notable reduction in soil development and illuviation, and therefore in precipitation, beginning in unit C-3 (Fig. 3B). The reduction in soil development and illuviation between Members B and C occurred in the absence of significant changes in the rate of deposition between these members (Fig. 4). Also, palynological samples show a decrease in arboreal taxa in Member C compared with Member B, although this decrease is not as readily apparent in the sample from C-7 as it is in the sample from C-9 (Fig. 3C). Micromammals from C-8 compared with those from B-10 suggest a decline in forests with a continued presence of woodlands and thickets (Fig. 3D).

Bovids, together with independently derived lines of evidence, show that the drying trend established in Member C continued in Members D, E, and F (Figs. 3G, 23). Paleosols and fossil pollen in Member E suggest notably drier conditions than in earlier members: soils in Unit E-1 show little illuviation and consequently reflect low precipitation, while the pollen sample from E-4 shows the highest percentage of grass (72%)

and lowest percentage of arboreal vegetation (3%) in the sequence (Fig. 3). Micromammals from Member F indicate relatively dry and open conditions. The increased aridity suggested by bovids in Members D, E, and F coincides with regional (Bonnefille 1983) and high-latitude records of intensification of cooling and drying conditions between 2.5 and 2.3 Ma (e.g., Shackleton et al. 1984; Kukla 1987; Kennett 1995).

The environmental setting of lower Member G, beginning at about 2.3 Ma, was complex. Fossil pollen and wood indicate the presence of marshy forests alongside open and dry savanna (Bonnefille and Dechamps 1983). Among the bovids, reduncines again became very abundant, after their decline in Members C through F (Fig. 14), but unlike in Member B the reduncine fauna of lower Member G included a significant proportion of *Menelikia.* In lower Member G, bovids that are inferred to have occupied closed and wet habitats (e.g., *Kobus sigmoidalis, Kobus ancystrocera, Syncerus*) occurred alongside bovids that are inferred to have occupied drier, and perhaps more open, habitats (e.g., *Tragelaphus gaudryi* and Alcelaphini). Bovid abundance (Fig. 6), diversity (Figs. 9, 10), and preservation (Figs. 11–13) were exceptionally high. These parameters are commensurate with the heterogeneous nature of lower Member G environments (Fig. 3).

Upper Member G marks a major change in the depositional environments of the lower Omo Valley. The large, meandering river that characterized earlier times gave way to a major lake. Fossil wood shows that taxa indicative of very dry habitats made their first appearance in the basin at about 2 Ma (Bonnefille and Dechamps 1983). There is a further increase in the relative abundance of reduncines, but nearly all reduncines identified below the tribal level belong to *Menelikia.* If we follow Spencer's (1997) suggestion that *Menelikia* preferred habitats distinct from those of other reduncines, the high abundance of this genus adds an element of greater environmental heterogeneity.

The environmental reconstruction of Omo habitats in this study is in broad agreement with Alemseged's (1998) reconstruction based on the French collection of Shungura mammals. Alemseged, however, saw the most-significant faunal changes in the sequence occurring in Member G, which separates an "ancient" fauna in Members A to F from a more modern fauna in Members H to L. Although in this study we have not analyzed the fauna in Members H to L, preliminary analyses of the upper part of the Shungura sequence do indicate that significant faunal changes continued to occur in the basin after 2 Ma (Bobe and Behrensmeyer 1999). However, these changes still need to be assessed in terms of collection and taphonomic biases.

The overall pattern of late Pliocene faunal change detected in this study differs from the turnover pulse noted by Vrba (1985a, 1995) and from the prolonged shift noted by Behrensmeyer et al. (1997), although it contains elements of both. The Shungura bovids showed no major changes in abundances at 2.5 Ma, the timing of Vrba's original turnover pulse, but they showed marked changes at about 2.8 Ma, the older limit of Vrba's most recent assessment of the African record, which points to faunal turnover between 2.5 and 2.8 Ma. Behrensmeyer et al. (1997) noted a prolonged faunal shift in the late Pliocene record of the Turkana basin, between about 3.0 and 2.0 Ma, in agreement with the results presented here for the time interval between 2.8 and 2.0 Ma. It should be noted, however, that these studies have looked at different aspects of the fossil record: changes in relative faunal abundances (in this study) versus speciation and extinction events (Vrba 1995; Behrensmeyer et al. 1997).

It may be argued that changes in relative abundance are likely to be more sensitive to environmental and climatic signals than speciation and extinction events. Climatic change may affect the fauna in ways that do not necessarily lead to speciation or extinction. Thus, for example, as the preferred habitat of a species shrinks or expands, the abundance of the species may decrease or increase without resulting in extinction or speciation. These changes in abundance would not be noted in studies focusing on speciation and extinction only, except possibly through secondary effects on species presence or absence in small samples. Other types of faunal responses to climatic change, e.g., evolutionary responses by heterochrony (Vrba 1996), although important, are beyond the scope in this study.

Although the Omo bovids do appear to have

responded to broad environmental and climatic changes in Africa, the Omo bovid community had important attributes of long-term stability. Two species almost completely dominated the bovid fauna for at least one million years: *Aepyceros shungurae* and *Tragelaphus nakuae.* The most common species in Members B, F, and lower G is *A. shungurae.* The most common species in Members C, D, and E is *T. nakuae.* In those members in which *A. shungurae* is dominant, *T. nakuae* is the second or third most abundant species. In those members in which *T. nakuae* is dominant, *A. shungurae* is the second most abundant species. It was only at about 2.1 Ma, in upper Member G, after major depositional changes in the basin, that both of these species lost their dominance to *Menelikia lyrocera.*

Even the appearance of several new taxa in the basin, through speciation or migration, did not alter the dominance of *A. shungurae* and *T. nakuae.* Several species of bovids made their first continental-scale appearance in the fossil record in the Shungura Formation (see the Appendix for a distribution of Shungura Bovidae across submembers). The earliest record of *Tragelaphus gaudryi* is in Shungura Unit C-9. This species remained relatively rare for about 200 Kyr before it became an important element of the Omo bovid fauna. Similarly, *Kobus sigmoidalis* had its first appearance at about 2.6 Ma, in Unit C-6, after which it gradually increased in abundance to reach a peak in lower Member G. Other species of bovids appear to have come and gone with little effect on the rest of the bovid fauna. For example, *Tragelaphus pricei* made a brief appearance at 2.6 Ma, in Unit C-9; *Menelikia leakeyi* appeared in Unit C-5 only to disappear above Unit D-1, after about 200 Kyr; and *Antilope subtorta* made its only appearance in the Omo record in Unit C-5. Thus, the Omo bovid community had a certain degree of homeostasis and stability, in spite of the appearance and disappearance of some species, and the significant shifts in the proportions of different vegetational habitats.

The results obtained in this study can be compared with the records of other localities in the Turkana Basin and elsewhere in East Africa, but there are no other contemporaneous African localities that combine large samples with a relatively continuous record from 3 to 2 Ma. The Nachukui Formation has a long and relatively continuous sequence of deposits that overlap those of the Shungura Formation, but faunal samples from the Nachukui Formation are small. Harris and colleagues (1988) argue that the most significant faunal changes in the Nachukui sequence occurred at about 2 Ma, but they do not provide a quantitative analysis of the fauna, so this assertion is difficult to evaluate. Also, as already noted, a thorough quantitative analysis of the Shungura record younger than 2 Ma remains to be done. In spite of these limitations, the bovid samples of the Shungura and Nachukui Formations show some interesting differences. A comparison of tribal abundances at Shungura and Nachukui (with data published by Harris et al. [1988]) indicates that the proportion of Alcelaphini and Antilopini was consistently and significantly higher in the Nachukui area than in the Shungura area. In Members B to G, Alcelaphini and Antilopini combined make up 2.8% of the bovid fauna, while in correlative sediments of the Nachukui Formation (Lomekwi to Kalochoro Members) these tribes constitute 31.0% of the bovids (98 specimens in a sample of 316 bovids). The higher abundance of Alcelaphini and Antilopini in the Nachukui area is evidence of drier and more open habitats in that area. This difference between the two areas may be attributable to their position within the Plio-Pleistocene Turkana Basin. Sedimentological evidence indicates that the Shungura Formation was located along the axis of the Turkana Basin throughout the Plio-Pleistocene, whereas the Nachukui Formation occupied a marginal position in the basin (Feibel et al. 1991). The influence of the Plio-Pleistocene Omo river running along the axis of the basin would have resulted in consistently more forested, mesic, and stable habitats along the axis than at the margins of the basin. This argument may also explain differences in the bovid fauna between the Shungura and Usno areas: reduncines are the most abundant tribe of bovid in Shungura Member B, but they are virtually absent from correlative deposits of the Usno Formation (Appendix). Like the Nachukui Formation, the Usno Formation occupied a marginal position in the Turkana Basin (Feibel et al. 1991) and therefore sampled drier and more open habitats than the Shungura Formation.

The Koobi Fora Formation presumably sam-

pled both axial and marginal habitats (Feibel et al. 1991). Although Koobi Fora possesses faunal samples that are large enough for quantitative comparisons with the Shungura Formation, a 500-Kyr temporal hiatus at Koobi Fora, between 2.5 and 2.0 Ma, prevents direct comparison with Shungura Members D to lower G (Feibel et al. 1989). At those levels in which both formations posses comparable samples, there are some significant differences between the two areas (Koobi Fora data from Evolution of Terrestiral Ecosystems database [http://etedata.si.edu]). As at Nachukui, the relative abundance of Alcelaphini and Antilopini is consistently greater at Koobi Fora than in the Omo. For example, in the lower Tulu Bor Member at Koobi Fora Alcelaphini and Antilopini make up 11% of the bovid fauna (13 specimens in a sample of 114 bovid individuals), while in Shungura Member B these tribes make up 2.5% of the bovid fauna (see Table 3, Fig. 18), a significant difference in proportions at the 0.05 confidence level. In the upper Burgi Member at Koobi Fora, Alcelaphini and Antilopini make up 22.5% of the bovids (93 specimens in a sample of 413 bovid individuals), while these two tribes make up 3% of the bovid fauna in upper Member G (Table 3, Fig. 18), again a significant difference. Thus, the Koobi Fora Formation sampled marginal and axial habitats in the Turkana Basin (Feibel et al. 1991), and the abundance of Alcelaphini plus Antilopini at Koobi Fora is intermediate between that at Shungura and at Nachukui. Although Shungura, Usno, Nachukui, and Koobi Fora are broadly contemporaneous formations in the same sedimentary basin, taphonomic and sedimentary factors must be carefully analyzed before meaningful faunal comparisons can be carried out.

A comparison of the Shungura Formation with the Hadar Formation of northern Ethiopia reveals differences and similarities between two geographically distinct sedimentary basins. The majority of specimens from the Hadar Formation were recovered from sediments between the Sidi Hakoma Tuff (3.40 Ma) and the BKT-2 Tuff (2.92 Ma) (Gray 1980; Kimbel et al. 1996), thus spanning about 0.5 Myr. At Hadar, the most abundant bovid tribes are Reduncini (27% of all bovids), Aepycerotini (21%), Alcelaphini (16%), Tragelaphini (15%), and Bovini (12%). Although the rank order of the two most abundant tribes is the same in both formations, at Hadar the third rank is occupied by Alcelaphini rather than Tragelaphini (the third most abundant tribe in the Shungura Formation). The percentage contributions of the dominant bovid tribes and their rank order suggest that at both sites plant communities formed complex mosaics and that wet, edaphic grasslands were important constituents of the plant communities in both, as were drier woodlands. In addition, wetter woodlands and forests were important at Shungura, while, in contrast, open woodlands and grasslands were important at Hadar. Overall, then, the Hadar Formation may have had a somewhat drier, more open vegetational mosaic than did Shungura.

We have carried out preliminary correspondence analyses of the Hadar sample and have discovered some interesting differences between Hadar and Shungura. In the Shungura analyses (Figs. 3F, 19–21), there is clearly a strong temporal trend, with Members C through G occurring in their proper stratigraphic order as one proceeds along the first axis of the analysis. A similar analysis of the Hadar sample shows no similar temporal trend in the sampling units. Our results suggest that although plant communities appear to have become on average more open at both sites during the times under analysis, the pattern at Shungura resulted from a series of changes all leading in the same direction. In contrast, at Hadar the changes between sampling units were larger and often not in the same direction, so that only on average and over the whole time period do the plant communities become drier and more open. The changes seen at Hadar probably resulted principally from regional tectonic activity that caused major changes in local topography and hydrology (Yemane et al.1996). In contrast, the temporal trend in the Shungura Formation probably resulted from worldwide climatic changes, especially acute between about 2.8 and 2.3 Ma, that caused the initiation of glacial cycles in the north and drier climate in the tropics of Africa.

Much interest on the Omo fossil record has focused on its implications for human evolution (e.g., Howell 1968, 1978; Coppens 1994). Although the hominids per se are not the focus of

this study, early humans were an integral part of the Plio-Pleistocene Omo fauna, and, like the bovids, they may have responded to the climatic and environmental changes taking place around them (Bobe 1996, 1997). The same forces that led to the shift in bovid abundances in the Omo at 2.8 Ma may have resulted in the speciation event that gave rise to the *Paranthropus* clade, the earliest specimens of which occur in Shungura Unit C-5.

Although this study of Shungura bovids reveals some distinct patterns of faunal change, much work remains to be done to further our understanding of faunal evolution in the African Plio-Pleistocene. Ongoing work in the Turkana Basin promises to augment and refine the data available for comparisons between the Shungura, Nachukui, and Koobi Fora Formations, so that a more thorough integration of the data from these areas will become possible. Ongoing work in the Hadar region (Kimbel et al. 1996) may also expand the faunal sample between 3 and 2 Ma, so that comparisons between the Turkana and Hadar regions can be used to evaluate the effects of climate change in geographically distinct but contemporaneous sequences. To this end, it is critical that further sampling of the land mammal record be done in a carefully controlled and thorough manner, so we can discern the complex signals of taphonomic, environmental, and climatic forces.

Conclusions

The Omo Shungura vertebrate record represents one of the largest and most carefully controlled samples for deciphering the responses of land faunas to global-scale environmental change. This study demonstrates at least two different types of response for the family Bovidae to large-scale environmental change. First, the Omo bovids experienced an increase in richness and a rapid episode of change in taxonomic abundances at 2.8 ± 0.1 Ma (between Members B and C). Second, this episode was followed by a gradual and prolonged shift in abundances between 2.8 and 2.0 Ma (from Member C to upper Member G). This pattern of faunal change is apparent at different taxonomic levels and with differing temporal partitioning of the record. The analysis of bovid skeletal elements in the Shungura sequence indicates that only moderate changes in taphonomic conditions occurred between 3.0 and 2.1 Ma, but that significant changes in the mode of preservation accompanied the onset of lacustrine depositional environments at 2.1 Ma (between lower and upper Member G). A juxtaposition of taphonomic with taxonomic patterns shows that the shift in taxonomic abundances at about 2.8 Ma occurred in the absence of major changes in taphonomic conditions. The main changes in bovid relative abundances and diversity appear to have been driven by broad environmental and climatic changes in Africa. As environmental indicators, bovids show a transition in the Omo at about 2.8 Ma from closed and wet environments in Member B to closed but dry environments in Member C. This drying trend intensified in Members D, E, and F, between about 2.5 and 2.3 Ma. In lower Member G, between 2.3 and 2.1 Ma, there was an increase in bovid abundance and diversity, which may be a result of greater environmental heterogeneity. The pattern of environmental change depicted by the Shungura bovids is consistent with independently derived evidence of Omo paleoenvironments (from paleosols, paleoflora, and micromammals) and with regional and global evidence of climatic changes, especially acute between 2.8 and 2.3 Ma, that caused the initiation of glacial cycles in the north and drier climate in the tropics of Africa. Even though the Omo bovids showed distinct responses to large-scale climatic and environmental change, the Omo bovid community also had important attributes of long-term stability: two species, *Aepyceros shungurae* and *Tragelaphus nakuae*, dominated the community for nearly one million years. This analysis highlights the importance of carefully controlled collection procedures of fossil vertebrates and provides an important demonstration of the potential complexity in mode and rate of responses of land faunas to climatic change.

Acknowledgments

We are indebted to F. C. Howell, director of the American contingent of the Omo Research Expedition, for leading the multidisciplinary effort in the Omo that has made this kind of research possible. We also extend our appreciation to A. W. Gentry for his exemplary treatment of the Omo bovids. We thank the National Muse-

um of Ethiopia for access to the Shungura collections. We also thank N. Atkins, A. K. Behrensmeyer, J. Barry, K. Bobe, A. W. Gentry, F. C. Howell, E. S. Vrba, S. L. Wing, and an anonymous reviewer for providing comments and suggestions that have greatly improved the manuscript. Sincere thanks from R. B. to Tina, Alexa, Marisa, and René for so much encouragement and support. Funding for this research was provided by the Smithsonian's Scholarly Studies Program. This is publication 76 of the Evolution of Terrestrial Ecosystems Program.

Literature Cited

Alemseged, Z. 1998. L'Hominidé Omo-323: sa position phylétique et son environnement dans le cadre de l'évolution des communautés de mammifères du Plio-Pléistocène dans la basse vallée de l'Omo (Éthiopie). Ph.D. dissertation. Muséum national d'Histoire naturelle, Paris.

Arambourg, C. 1947. Contribution à l'étude géologique et paléontologique du Bassin du Lac Rodolphe et de la Basse Vallée de l'Omo, deuxième partie: Paléontologie. Mission Scientifique de l'Omo 1932–1933, 1(3). Paris.

Beden, M. 1976. Proboscideans from the Omo group formations. Pp. 193–208 *in* Coppens et al. 1976.

———. 1987. Les faunes Plio-Pléistocène de la basse vallée de l'Omo (Éthiopie), Tome 2. Les eléphantidés (Mammalia-Proboscidea). Editions du CNRS, Paris.

Begon, M., J. L. Harper, and C. R. Townsend. 1990. Ecology: individuals, populations, and communities. Blackwell Scientific, Boston.

Behrensmeyer, A. K. 1982. Time resolution in fluvial vertebrate assemblages. Paleobiology 8:211–227.

———. 1988. Vertebrate preservation in fluvial channels. Palaeogeography, Palaeoclimatology, Palaeoecology 63:183–199.

Behrensmeyer, A. K., N. E. Todd, R. Potts, and G. E. McBrinn. 1997. Late Pliocene faunal turnover in the Turkana Basin, Kenya. Science 278:1589–1594.

Benzécri, J. P. 1992. Correspondence analysis handbook. Dekker, New York.

Boaz, N. T. 1977. Paleoecology of Plio-Pleistocene Hominidae in the Lower Omo Basin, Ethiopia. Ph.D. dissertation. University of California, Berkeley.

Bobe, R. 1996. Pliocene environmental changes derived from faunal analysis of the Shungura Formation, Ethiopia. Journal of Vertebrate Paleontology 16(3):23A.

———. 1997. Hominid environments in the Pliocene: an analysis of fossil mammals from the lower Omo valley, Ethiopia. Ph.D. dissertation, University of Washington, Seattle.

Bobe, R., and A. K. Behrensmeyer. 1999. Environmental changes in early hominid evolution derived from analysis of fossil mammals from the lower Omo Valley, Ethiopia. Journal of Human Evolution 36(4):A3.

Bonnefille, R. 1983. Evidence for a cooler and drier climate in the Ethiopian uplands towards 2. 5 Myr ago. Nature 303:487–491.

———. 1994. Palynology and paleoenvironment of East African hominid sites. Pp. 415–427 *in* Corruccini and Ciochon 1994.

———. 1995. A reassessment of the Plio-Pleistocene pollen record of East Africa. Pp. 299–310 *in* Vrba et al. 1995.

Bonnefille, R., and R. Dechamps. 1983. Data on fossil flora. Pp. 191–207 *in* de Heinzelin 1983.

Bonnefille, R., and R. Letouzey. 1976. Fruits fossiles d'*Antrocaryon* dans la vallée de l'Omo (Ethiopie). Adansonia 16:65–82.

Brown, F. H. 1982. Tulu Bor Tuff at Koobi Fora correlated with the Sidi Hakoma Tuff at Hadar. Nature 300:631–633.

———. 1994. Development of Pliocene and Pleistocene chronology of the Turkana basin, East Africa, and its relation to other sites. Pp. 285–312 *in* Corruccini and Ciochon 1994.

———. 1995. The potential of the Turkana Basin for paleoclimatic reconstruction in East Africa. Pp. 319–330 *in* Vrba et al. 1995.

Brown, F. H., and C. S. Feibel. 1986. Revision of lithostratigraphic nomenclature in the Koobi Fora region, Kenya. Journal of the Geological Society, London 143:297–310.

Brown, F. H., and J. de Heinzelin. 1983. The lower Omo basin. Pp. 7–24 *in* de Heinzelin 1983.

Brown, F. H., I. McDougall, I. Davies, and R. Maier. 1985. An integrated Plio-Pleistocene chronology for the Turkana basin. Pp. 82–90 *in* E. Delson, ed. Ancestors: the hard evidence. Alan R. Liss, New York.

Burckle, L. H. 1995. Current issues in Pliocene paleoclimatology. Pp. 3–7 *in* Vrba et al. 1995.

Buzas, M. A. 1990. Another look at confidence limits for species proportions. Journal of Paleontology 64:842–843.

Carr, C. J. 1976. Plant ecological variation and pattern in the lower Omo basin. Pp. 432–467 *in* Coppens et al. 1976.

Cerling, T. E. 1992. Development of grasslands and savannas in East Africa during the Neogene. Palaeogeography, Palaeoclimatology, Palaeoecology 97:241–247.

Cerling, T. E., and J. M. Harris. 1999. Carbon isotope fractionation between diet and bioapatite in ungulate mammals and implications for ecological and paleoecological studies. Oecologia 120:347–363.

Cooke, H. B. S. 1976. Suidae from Plio-Pleistocene strata of the Rudolf basin. Pp. 251–263 *in* Coppens et al. 1976.

———. 1978. Faunal evidence for the biotic setting of early African hominids. Pp. 267–281 *in* C. J. Jolly, ed. Early hominids of Africa. Duckworth, London.

———. 1985. Pliocene-Pleistocene Suidae in relation to African hominid deposits. Pp. 101–115 *in* M. Beden et al., eds. L'environnement des hominidés au Plio-Pléistocène. Masson, Paris.

Coppens, Y. 1975. Evolution des hominidés et de leur environnements au cours du Plio-Pléistocène dans la basse vallée de l'Omo en Éthiopie. Comptes Rendus de l'Académie des Sciences D 281:1693–1696.

———. 1978. Evolution of the hominids and of their environment during the Plio-Pleistocene in the lower Omo valley, Ethiopia. Pp. 499–506 *in* W.W. Bishop, ed. Geological background to fossil man. Scottish Academic Press, Edinburgh.

———. 1994. East side story: the origin of humankind. Scientific American 270(5):88–95.

Coppens, Y., and F. C. Howell. 1976. Mammalian faunas of the Omo Group: Distributional and biostratigraphic aspects. Pp. 177–192 *in* Coppens et al. 1976.

———, eds. 1985. Les faunes Plio-Pléistocène de la basse vallée de l'Omo (Éthiopie), Tome 1. Périssodactyles-Artiodactyles (Bovidae). Editions du CNRS, Paris.

Coppens, Y., F. C. Howell, G. L. Isaac, and R. E. F. Leakey, eds. 1976. Earliest man and environments in the Lake Rudolf basin. University of Chicago Press, Chicago.

Corruccini, R. S., and R. L. Ciochon, eds. 1994. Integrative paths to the past: paleoanthropological advances in honor of F. Clark Howell. Prentice-Hall, Englewood Cliffs, N.J.

Coryndon, S. C. 1976. Fossil Hippopotamidae from Plio-Pleistocene successions of the Rudolf basin. Pp. 238–250 *in* Coppens et al. 1976.

Dechamps, R., and F. Maes. 1985. Essai de reconstitution des climats et des végétations de la basse vallée de l'Omo au Plio-

Pléistocène à l'aide de bois fossiles. Pp. 175–221 *in* M. Beden et al., eds. L'environnement des hominidés au Plio-Pléistocène. Masson, Paris.

Dechant Boaz, D. 1994. Taphonomy and the fluvial environment: examples from Pliocene deposits of the Shungura Formation, Omo Basin, Ethiopia. Pp. 377–414 *in* Corruccini and Ciochon 1994.

de Heinzelin, J., ed. 1983. The Omo group: archives of the International Omo Research Expedition. Musée Royale de l'Afrique Centrale Annale, série in 8°. Sciences Géologiques No. 85. Tervuren, Belgium.

de Heinzelin, J., and P. Haesaerts. 1983. The Shungura Formation. Pp. 25–127 *in* de Heinzelin 1983.

de Heinzelin, J., P. Haesaerts, and F. C. Howell. 1976. Plio-Pleistocene formations of the lower Omo basin, with particular reference to the Shungura Formation. Pp. 24–49 *in* Coppens et al. 1976.

deMenocal, P. B. 1995. Plio-Pleistocene African climate. Science 270:53–59.

deMenocal, P. B., and J. Bloemendal. 1995. Plio-Pleistocene climatic variability in subtropical Africa and the paleoenvironment of hominid evolution: a combined data-model approach. Pp. 262–288 *in* Vrba et al. 1995.

Dorst, J., and P. Dandelot. 1969. A field guide to the larger mammals of Africa. Houghton Mifflin, Boston.

Eck, G. G. 1976. Cercopithecoidea from the Omo Group deposits. Pp. 332–344 *in* Coppens et al. 1976.

Eck, G. G., N. G. Jablonski, and M. Leakey. 1987. Les faunes Plio-Pléistocène de la basse vallée de l'Omo (Éthiopie), Tome 3. Cercopithecidae de la formation de Shungura. Editions du CNRS, Paris.

Eisenmann, V. 1976. Equidae from the Shungura Formation. Pp. 225–233 *in* Coppens et al. 1976.

———. 1985. Les équidés des gisements de la vallée de l'Omo en Éthiopie. Pp. 13–65 *in* Coppens and Howell 1985.

Estes, R. D. 1991. The behavior guide to African mammals. University of California Press, Berkeley.

Feibel, C. S., F. H. Brown, and I. McDougall. 1989. Stratigraphic context of fossil hominids from the Omo Group deposits: northern Turkana basin, Kenya and Ethiopia. American Journal of Physical Anthropology 78:595–622.

Feibel, C. S., J. M. Harris, and F. H. Brown. 1991. Palaeoenvironmental context for the Late Neogene of the Turkana Basin. Pp. 321–346 *in* Harris 1991.

Fisher, L. D., and G. van Belle. 1993. Biostatistics: a methodology for the health sciences. Wiley, New York.

Gentry, A. W. 1976. Bovidae of the Omo Group deposits. Pp. 275–292 *in* Coppens et al. 1976.

———. 1985. The Bovidae of the Omo Group deposits, Ethiopia. Pp. 119–191 *in* Coppens and Howell 1985.

Geraads, D. 1995. *Simatherium shungurense* n. sp., un nouveau Bovini (Artiodactyla, Mammalia) du Pliocène terminal de l'Omo (Éthiopie). Annales de Paleontologie 81:87–96.

Grattard, J. L., F. C. Howell, and Y. Coppens. 1976. Remains of *Camelus* from the Shungura Formation, Ethiopia. Pp. 268–274 *in* Coppens et al. 1976.

Gray, B. T. 1980. Environmental reconstruction of the Hadar Formation (Hadar, Ethiopia). Ph.D. dissertation. Case Western Reserve University, Cleveland.

Grayson, D. K. 1984. Quantitative zooarchaeology. Academic Press, Orlando.

Greenacre, M. J. 1993. Correspondence analysis in practice. Academic Press, London.

Greenacre, M. J., and E. S. Vrba. 1984. Graphical display and interpretation of antelope census data in African wildlife areas, using correspondence analysis. Ecology 65:984–997.

Guérin, C. 1976. Rhinocerotidae and Chalicotheriidae (Mammalia, Perissodactyla) from the Shungura Formation, lower Omo Basin. Pp. 214–221 *in* Coppens et al. 1976.

———. 1985. Les rhinocéros et les chalicothères (Mammalia, Perissodactyla) des gisements de la vallée de l'Omo en Éthiopie. Pp. 67–89 *in* Coppens and Howell 1985.

Haesaerts, P., G. Stoops, and B. van Vliet-Lanoe. 1983. Data on sediments and fossil soils. Pp. 149–185 *in* de Heinzelin 1983.

Harris, J. M. 1991. Koobi Fora Research Project, Vol. 3. The fossil ungulates: geology, fossil artiodactyls, and palaeoenvironments. Clarendon, Oxford.

Harris, J. M., F. H. Brown, and M. G. Leakey. 1988. Stratigraphy and paleontology of Pliocene and Pleistocene localities west of Lake Turkana, Kenya. Contributions in Science (Los Angeles) No. 399.

Hayek, L. A., and M. A. Buzas. 1997. Surveying natural populations. Columbia University Press, New York.

Hillman, J. C. 1986. Aspects of the biology of the bongo antelope, *Tragelaphus euryceros* Ogilby 1837, in southwest Sudan. Biological Conservation 38:255–272.

Hooijer, D. A., and C. S. Churcher. 1985. Perissodactyla of the Omo Group deposits. Pp. 97–117 89 *in* Coppens and Howell 1985.

Howell, F. C. 1968. Omo research expedition. Nature 219:567–572.

———. 1978. Overview of the Pliocene and earlier Pleistocene of the lower Omo basin, southern Ethiopia. Pp. 85–130 *in* C. J. Jolly, ed. Early hominids of Africa. Duckworth, London.

Howell, F. C., and Y. Coppens. 1976. An overview of Hominidae from the Omo succession, Ethiopia. Pp. 522–532 *in* Coppens et al. 1976.

Howell, F. C., and G. Petter. 1976. Carnivora from Omo Group Formations, southern Ethiopia. Pp. 314–331 *in* Coppens et al. 1976.

Howell, F. C., P. Haesaerts, and J. de Heinzelin. 1987. Depositional environments, archeological occurrences and hominids from Members E and F of the Shungura Formation (Omo basin, Ethiopia). Journal of Human Evolution 16:665–700.

Jaeger, J. J., and H. B. Wesselman. 1976. Fossil remains of micromammals from the Omo Group deposits. Pp. 351–360 *in* Coppens et al. 1976.

Kennett, J. P. 1995. A review of polar climatic evolution during the Neogene, based on the marine sediment record. Pp. 49–64 *in* Vrba et al. 1995.

Kimbel, W. H., R. C. Walter, D. C. Johanson, K. E. Reed, J. L. Aronson, Z. Assefa, C. Marean, G. G. Eck, R. Bobe, E. Hovers, Y. Rak, C. Vondra, T. Yemane, D. York, Y. Chen, N. M. Evensen, and P. E. Smith. 1996. Late Pliocene Homo and Oldowan tools from the Hadar Formation (Kada Hadar Member), Ethiopia. Journal of Human Evolution 31:549–561.

Kingdon, J. 1982. East African mammals: an atlas of evolution in Africa, Vol. III. Parts C and D, Bovids. Academic Press, London.

———. 1989. Island Africa: the evolution of Africa's rare animals and plants. Princeton University Press, Princeton, N.J.

Kukla, G. 1987. Loess stratigraphy in central China. Quaternary Science Reviews 16:191–219.

Lind, E. M., and M. E. Morrison. 1974. East African vegetation. Longman, London.

Ludwig, A. J., and J. F. Reynolds. 1988. Statistical ecology: a primer on methods and computing. Wiley, New York.

Magurran, A. E. 1988. Ecological diversity and its measurement. Princeton University Press, Princeton, N.J.

May, R. M. 1975. Patterns of species abundance and diversity. Pp. 81–120 *in* M. L. Cody and J. M Diamond, eds. Ecology and evolution of communities. Belknap Press of Harvard University Press, Cambridge.

McDoughall, I. 1985. K-Ar and $^{40}Ar/^{39}Ar$ dating of the hominid-bearing Pliocene-Pleistocene sequence at Koobi Fora, Lake

Turkana, northern Kenya. Geological Society of America Bulletin 96:159–175.

McDougall, I., T. Davies, R. Maier, and R. Rudowski. 1985. Age of the Okote Tuff Complex at Koobi Fora, Kenya. Nature 316: 792–794.

McGougall, I., F. H. Brown, T. E. Cerling and J. W. Hillhouse. 1992. A reappraisal of the geomagnetic polarity time scale to 4 Ma using data from the Turkana Basin, East Africa. Geophysical Research Letters 19:2349–2352.

Mloszewski, M. J. 1983. The behavior and ecology of the African buffalo. Cambridge University Press, Cambridge.

Murray, M. G. 1981. Structure of association in impala, *Aepyceros melampus*. Behavioral Ecology and Sociobiology 9:23–33.

Reed, K. E. 1997. Early hominid evolution and ecological change through the African Plio-Pleistocene. Journal of Human Evolution 32:289–322.

Shackleton, N. J. 1995. New data on the evolution of Pliocene climatic variability. Pp. 243–248 *in* Vrba et al. 1995.

Shackleton, N. J., J. Backman, H. Zimmerman, D. V. Kent, M. A. Hall, D. J. Roberts, D. Schnitker, J. G. Baldauf, A. Desprairies, R. Homrighausen, P. Huddlestun, J. B. Keene, A. J. Kaltenback, K. A. Krumsiek, A. C. Morton, J. W. Murray, and J. Westberg-Smith. 1984. Oxygen isotope calibration of the onset of ice rafting and history of glaciation in the North Atlantic region. Nature 307:620–623.

Shipman, P., and J. Harris. 1988. Habitat preference and paleoecology of *Australopithecus boisei* in Eastern Africa. Pp. 343–381 *in* F. E. Grine, ed. Evolutionary history of the "robust" australopithecines. Aldine, New York.

Sinclair, A. R. E. 1977. The African buffalo. University of Chicago Press, Chicago.

Spencer, L. M. 1997. Dietary adaptations of Plio-Pleistocene Bovidae: implications for hominid habitat use. Journal of Human Evolution 32:201–228.

Spinage, C. A. 1982. A territorial antelope: the Uganda waterbuck. Academic Press, New York.

———. 1986. The natural history of antelopes. Facts on File, New York.

Sponheimer, M., K. E. Reed, and J. A. Lee-Thorp. 1999. Combining isotopic and ecomorphological data to refine bovid paleodietary reconstruction: a case study from the Makapansgat Limeworks hominid locality. Journal of Human Evolution 36: 705–718.

Suwa, G., T. D. White, and F. C. Howell. 1996. Mandibular postcanine dentition from the Shungura Formation, Ethiopia: crown morphology, taxonomic allocations, and Plio-Pleistocene hominid evolution. American Journal of Physical Anthropology 101:247–282.

Vrba, E. S. 1980a. The significance of bovid remains as indicators of environment and predation patterns. Pp. 247–271 *in* A. K. Behrensmeyer and A. P. Hill, eds. Fossils in the making. University of Chicago Press, Chicago.

———. 1980b. Evolution, species, and fossils: how does life evolve? South African Journal of Science, 76:61–84.

———. 1984. Evolutionary pattern and process in the sister-group Alcelaphini-Aepycerotini (Mammalia: Bovidae). Pp. 62–79 *in* N. Eldredge and S. M. Stanley, eds. Living fossils. Springer, New York.

———. 1985a. Ecological and adaptive changes associated with early hominid evolution. Pp. 63–71 *in* E. Delson. ed. Ancestors: the hard evidence. Liss, New York.

———. 1985b. Paleoecology of early Hominidae, with special reference to Sterkfontein, Swartkrans and Kromdraai. Pp. 345–369 *in* M. Beden et al., eds. L'environnement des hominidés au Plio-Pléistocène. Masson, Paris.

———. 1987. Ecology in relation to speciation rates: some case histories of Miocene-Recent mammals clades. Evolutionary Ecology 1:283–300.

———. 1988. Late Pliocene climatic events and hominid evolution. Pp. 405–426 *in* F. E. Grine, ed. Evolutionary history of the "robust" australopithecines. Aldine, New York.

———. 1995. The fossil record of African antelopes (Mammalia, Bovidae) in relation to human evolution and paleoclimate. Pp. 385–424 *in* Vrba et al. 1995.

———. 1996. Climate, heterochrony, and human evolution. Journal of Anthropological Research 52:1–28.

Vrba, E. S., G. H. Denton, T. C. Partridge, and L. H. Burckle, eds. 1995. Paleoclimate and evolution, with emphasis on human origins. Yale University Press, New Haven, Conn.

Walter, R. C., and J. L. Aronson. 1993. Age and source of the Sidi Hakoma Tuff, Hadar Formation, Ethiopia. Journal of Human Evolution 25:229–240.

Wesselman, H. B. 1984. The Omo micromammals: systematics and paleoecology of early man sites from Ethiopia. Contributions to Vertebrate Evolution 7:1–219.

———. 1995. Of mice and almost-men: regional paleoecology and human evolution in the Turkana basin. Pp. 356–368 *in* Vrba et al. 1995.

White, F. 1983. The vegetation of Africa: a descriptive memoir to accompany Unesco/AETFAT/UNSO vegetation map of Africa. Unesco, Paris.

Williamson, P. G. 1985. Evidence of an early Plio-Pleistocene rainforest expansion in East Africa. Nature 315:487–489.

Wing, S. L., H. D. Sues, R. Potts, W. A. DiMichele, and A. K. Behrensmeyer. 1992. Evolutionary paleoecology. Pp. 1–13 *in* A. K. Behrensmeyer, J. D. Damuth, W. A. DiMichele, R. Potts, H. D. Sues, and S. L. Wing, eds. Terrestrial ecosystems through time: evolutionary paleoecology of terrestrial plants and animals. University of Chicago Press, Chicago.

Yemane, T., C. F. Vondra, and J. Aronson. 1996. Provenance, tectonics, and climate change; Kada Hadar Member, Hadar Formation, Ethiopia. Geological Society of America Abstracts with Programs 28(6):72

Zar, J. H. 1984. Biostatistical analysis, 2d ed. Prentice-Hall, Englewood Cliffs, N.J.

Appendix

Omo bovid taxa of the Usno and Shungura Formations (number of specimens in the analytic database). Dx, Fx, G(L)x = submember provenance unknown. P = species present in Shungura Formation but not in analytic subset. Fr = species identified in the French Shungura collection only.

	USNO			Shungura Member B										
	U3/6	U12	U19	B2	B3	B6	B7	B7–10	B8	B9	B10	B11	B12	B(U)
Tragelaphini sp.	1	6	1			1					1	1		2
Tragelaphus sp.			2											
T. nakuae	1	43	1	1						1	7	2	1	10
cf. *T. gaudryi*									1		1			
T. gaudryi														
T. strepsiceros														
T. ?pricei														
Bovini sp.		27	1		1	1			1		10			6
Syncerus sp.													1	2
S. ?acoelotus											1			
Simatherium shungurense														
Pelorovis sp.													1	
Reduncini sp.		4									25	1		23
Redunca sp.											1			
Kobus sp.														
K. oricornus							1				4			3
K. ancystrocera														3
K. kob														2
K. sigmoidalis														
K. ellipsiprymnus														
Menelikia leakeyi														
M. lyrocera														
Hippotragini sp.														
Hippotragus gigas														
Oryx														
cf. *Aepyceros* sp. nov.														
Aepyceros shungurae		128	1				1	1			30	1	1	14
Alcelaphini sp.		4	1								1			4
?Damalops sp.														1
Pamularius sp.														
P. eppsi														
P. altidens														
Megalotragus sp.														
Antilopini sp.		3												
Antidorcas														
A. recki														1
Gazella														
G. praethomsoni														
Antilope aff. *subtorta*														
Neotragini sp.														
?Raphicerus														
Ovibovini														
Bovidae sp.	4	114	3	1			2	1	1	3	53	3	2	39
Total	6	329	10	2	1	2	4	2	3	4	134	8	6	110

Appendix. Extended.

Shungura Member C													
C0–2	C1	C2	C3	C4	C(M)	C4-7	C5-7	C5	C6	C7	C8	C9	C(U)
		1					4	4			1	1	
											1		
1		2	1	2	1	5	27	21	18	9	46	27	3
												2	
												1	
			1	2		6	7	4	3	4	17	12	
											1	8	
									1		1	2	
				1				1	2				
				3	1	4	10	6	9	2	11	3	3
							1	1					
							1		3		3		
								1					
									P				
							4	2	3	1	1		
							1						
									1				
											1		
												1	
		4		5	3	3	8	13	11	6	20	19	2
											3	1	
										1			
									1				
								2					
	1	1	1	9	1	12	25	20	31	10	59	53	5
1	1	8	3	22	6	30	88	75	83	33	165	130	13

Appendix. Continued.

	Shungura Member D								
	Dx	D1	D2	D1–3	D(M)	D3	D4	D(U)	D5
Tragelaphini sp.						1			
Tragelaphus sp.									2
T. nakuae	1	13		2		20	3	2	21
cf. *T. gaudryi*									
T. gaudryi							1		
T. strepsiceros									
T. ?pricei									
Bovini sp.		2				4	4	1	4
Syncerus sp.									
S. ?acoelotus									
Simatherium shungurense									
Pelorovis sp.									
Reduncini sp.	1	2				2	3	2	11
Redunca sp.									
Kobus sp.									
K. oricornus									
K. ancystrocera									
K. kob						1			
K. sigmoidalis		2	1			1			3
K. ellipsiprymnus									
Menelikia leakeyi		1							
M. lyrocera									
Hippotragini sp.									
Hippotragus gigas									
Oryx									
cf. *Aepyceros* sp. nov.									
Aepyceros shungurae		4	3	7		14	6	3	19
Alcelaphini sp.		2						2	2
?Damalops sp.									
Parmularius sp.									
P. eppsi									
P. altidens									
Megalotragus sp.									
Antilopini sp.									
Antidorcas									
A. recki									
Gazella		1							
G. praethomsoni									
Antilope aff. *subtorta*									
Neotragini sp.									
?Raphicerus									
Ovibovini									1
Bovidae sp.		13	1	10	1	9	11	3	22
Total	2	40	5	19	1	52	28	13	85

Appendix. Extended.

Shungura Member E										Shungura Member F							
E1	E2	E1–3	E3	E(M)	E3–4	E4	E(U)	E5	E5?	Fx	F0	F0–1	F1	F2	F3	F(U)	F5
			1		1								3				
2													2				
20	25	2	16		22	12	7	2		1		5	15	1	16		
1	1						3	2		3		2	24	1	14		
2	1		4		1	1	3				1		10			1	
						1											
										2					1		
5	4	1	10		2	5	3	2		2	4	4	11		10	1	
			1									1					
1							1										
3	8		2		1	2	3			1			6		9		
	2									4		1	11		4		
					1												
6	12		36	7	5	11	10	2	2	3	3	8	Fr 89	Fr 2	32	2	2
3			3			1			2	1	2	1	17		4		
													1				
													2		1		
																1	
			1											1			
			1														
29	23		41	4	11	9	12	5	1	5	7	14	72	4	45		2
72	76	3	116	11	44	42	42	13	5	22	17	36	263	9	136	5	4

Appendix. Continued.

	Shungura Member G(L)												
	G(L)x	G1	G2	G1–3	G3	G4	G3–5	G4–5	G5	G4–7	G7	G8	G7–9
Tragelaphini sp.		1			1	3			1		1		1
Tragelaphus sp.						1			2				
T. nakuae	3				8	27	5	1	45	4	11		22
cf. *T. gaudryi*													
T. gaudryi	1	5	4		2	26		2	49	3	7	5	5
T. strepsiceros													
T. ?pricei													
Bovini sp.		2			6	1	1		6		1		1
Syncerus sp.		1				2							
S. ?acoelotus									1				
Sim. shungurense		Fr											
Pelorovis sp.						6							
Reduncini sp.	4	1	1		6	25	1	2	92	7	21	10	21
Redunca sp.													
Kobus sp.									2				
K. oricornus													
K. ancystrocera		1				1			1				1
K. kob													
K. sigmoidalis	4	3	2		7	53	4		48	1	10		35
K. ellipsiprymnus		1											
Menelikia leakeyi													
M. lyrocera	1				5	8	1		19	1	16	2	14
Hippotragini sp.									2				
Hippotragus gigas													
Oryx													
cf. *Aepyceros* sp. nov.		Fr										Fr	
Aepyceros shungurae	4	6	2	1	29	42	1	3	34	14	3	7	21
Alcelaphini sp.	1	2	1		7	5	1		5	1	2	2	2
?Damalops sp.													
Parmularius sp.						1							
P. eppsi													
P. altidens											1		
Megalotragus sp.									1				
Antilopini sp.													
Antidorcas													
A. recki									1				
Gazella													
G. praethomsoni									1				1
Antilope aff. *subtorta*													
Neotragini sp.													
?Raphicerus						1							
Ovibovini													
Bovidae sp.	2	6	2	3	29	52	2	2	73	17	25	8	61
Total	20	29	12	4	100	254	16	10	383	48	98	34	185

Appendix. Extended.

Shungura Member G(L)								Shungura Member G(U)								Mb H		
G8–9	G9	G10	G11	G9–13	G12	G11–13	G13	G15	G16	G17	G18	G19	G23	G24	G27	H1	H4	Total
						1												39
						1												13
6	4	3	2	7	11	40	14											649
																		2
1	1			3	8	24	2					1			1			204
						1												1
																		1
	1		1			5	1		1							1		170
					1	1		1										19
																		6
																		Fr
																		14
2	11	6	5	10	10	84	27		5		1				1	1	1	545
																		5
																		2
																		8
			1	3	5	15	1											41
		1																5
	4	1	3		2	16	11		1									247
																		1
																		12
	5		1	6	1	16	5	3		1		1		1			1	131
																		4
																		1
																		1
																		Fr
7	11	8	8	15	14	172	59		1					1				1022
	4	2	1	3	1	3	4		1									102
																		1
		1																2
																		1
																		1
																		1
																		3
						1												3
																		5
																		1
																		3
																		2
							1											3
																		2
																		1
4	26	3	7	12	18	100	30		2	1	3	1	1	2	3	1		1304
20	67	25	29	59	71	480	155	4	11	2	4	3	1	4	5	3	2	4578