

Available online at www.sciencedirect.com

SCIENCE @ DIRECT®



Journal of Human Evolution 44 (2003) 1–28

An integrated approach to taphonomy and faunal change in the Shungura Formation (Ethiopia) and its implication for hominid evolution

Zeresenay Alemseged*

Institute of Human Origins, Arizona State University, P.O. Box 874101, Tempe, AZ 85287-4101, USA

Received 8 May 2002; accepted 10 January 2003

Abstract

Environmental and faunal changes through time have been recorded for many African Plio-Pleistocene sites. Fossil evidence suggests that there is a continuous, if not uniform, transformation of the fauna and flora from the Pliocene through the end of Pleistocene. However, discerning major biotic turnovers and linking them to global and regional climatic changes have been complicated by many factors, notably taphonomy and discontinuity of the fossil evidence, notwithstanding the considerable work of some researchers (e.g., Vrba, E.S., 1988. Late Pliocene climatic events and hominid evolution, in: Grine, F. (Ed.), *Evolutionary History of the “Robust” Australopithecines*. De Gruyter, New York, pp. 405–426, Vrba, E.S., 1995. The fossil record of African (Mammalia, Bovidae) in relation to human evolution and paleoclimate, in: Vrba, E.S., Denton, G.H., Partridge, T.C., Burkle, L.H. (Eds.), *Paleoclimate and Evolution, with Emphasis on Human Origins*. Yale University Press, New Haven, pp. 385–424). A sample of over 22,000 fossils collected by the French Omo Expedition, from the Shungura Formation of Ethiopia, was analyzed using an integrated approach to investigate taphonomic and faunal change patterns. The following results are obtained: (1) Univariate and multivariate studies support continuous faunal change from Member A through Member G of the Shungura sequence; (2) Correspondence analysis (CA) on extant bovids in African game parks shows that bovid tribes and genera are generally characterized by habitat specificity; (3) Taphonomic studies demonstrate that the relative abundance of different skeletal elements varies according to depositional environment; (4) CA on 73 localities of the Shungura Formation and 19 mammalian taxa points to a major faunal change around the base of Member G dated to ca. 2.3 Ma. This transformation is characterized by a change to open and edaphic grassland as a dominant type of environment; (5) This major faunal change correlates in time with the appearance of *A. boisei*. It is tentatively suggested that this major biome change is associated with an anagenetic speciation from *A. aethiopicus* to *A. boisei*.

© 2003 Elsevier Science Ltd. All rights reserved.

Keywords: faunal change; taphonomy; pliocene; hominid evolution; Shungura Formation, Ethiopia

* Corresponding author. Tel.: +1-480-727-6580; fax: +1-480-727-6570
E-mail address: zeray@asu.edu (Z. Alemseged).

1. Introduction

Most researchers agree that the origin, diversification and extinction of Plio-Pleistocene African faunas, including hominids, resulted from environmental changes, which in turn are caused by climatic changes (e.g., Coppens, 1975a,b; Vrba, 1988, 1995, 2000; Behrensmeyer et al., 1997; Bobe and Eck, 2001). Studies on bovids from South and East African sites suggest, in particular, that hominid evolution and diversification are triggered and accelerated by environmental changes that caused major biotic turnover due to global climatic changes (Vrba, 1988, 1995, 2000). However, determining the number of First Appearance Datum (FAD) and Last Appearance Datum (LAD), which are the basis for drawing conclusions on the relationship between faunal evolution and regional and global climatic changes, is not as straightforward as it might appear (e.g., Hill, 1987; White, 1995). In particular, detecting the timing of major biotic changes and linking them to the relatively well-documented and continuous climatic signals derived from other sources, such as marine sediments and stable isotopes (deMenocal, 1995; deMenocal and Bloemendal, 1995; Shackleton, 1995; Kennett, 1995; Denton, 1999), have resulted in discrepancies between different approaches (Vrba, 1988, 1995, 2000; Feibel et al., 1991; Behrensmeyer et al., 1997; Bobe and Eck, 2001; Bobe et al., 2002). For Vrba (1988, 1995, 2000), the major faunal turnover is situated in the interval 2.8–2.5 Ma. Other researchers indicate that major faunal changes in East Africa occurred at around 2 Ma (Harris et al., 1988; Feibel et al., 1991). Behrensmeyer et al. (1997) suggested that the most important faunal change occurred at around 1.8 Ma. Bobe and Eck (2001) and Bobe et al. (2002) indicate, based on their study on the lower Omo Basin fauna, that the interval 2.7–2.5 Ma was a period of stability and an episode of rapid faunal change occurred between 2.9–2.7 Ma.

Some of the potential sources of these discrepancies are: (1) the discontinuous nature of sedimentary sequences; (2) the difficulty to distinguish biological signals from taphonomic signals within each site; (3) the use of different taxonomic groups which might result in different signals; and (4)

problems related to comparing sites of different taphonomic histories. One way of addressing these problems, which is one of the goals of this paper, is to comprehend patterns of environmental and faunal changes of sites separately before drawing regional and/or global conclusions. Similar studies have been carried out for some African Plio-Pleistocene sites using different approaches (e.g., Shipman and Harris, 1988; Feibel et al., 1991; Reed, 1997; Bobe and Eck, 2001). Some of these studies, if not all, have attempted to tie observed biotic changes with physical causes, such as regional and global climatic changes. However, the discontinuous nature of the fossil record did not, in some cases, allow researchers to make comparison between different stratigraphic levels.

The abundance of fossils, the large number of localities, and the continuity of the sequence in the Shungura Formation give good opportunity to document faunal changes through time. In the present paper both univariate and multivariate studies are used to study environmental and faunal changes in the Shungura Formation. French and American expeditions undertook separate but equivalent collections from the northern and southern portions of the exposures. This is interesting as it allows comparison of datasets collected by two different teams from the same basin and time interval. Other researchers have analyzed fossils collected by the American contingent (Bobe and Eck, 2001; Bobe et al., 2002). This paper provides an analysis based primarily on an independent dataset—the French collection.

2. The Shungura Formation: background

Even though the first fossils were recovered from the Lower Omo Valley by du Bourq de Bozas (du Bourq de Bozas, 1903, 1906), the mission led by Arambourg, Mission Scientifique de l'Omo, was the first to conduct systematic paleontological work in the region (Coppens, 1976). In 1966 the International Omo Research Expedition was created under the direction of Howell, Arambourg (replaced by Coppens in 1968) and Leakey

(Coppens, 1976), and recovered thousands of vertebrate fossils, including hominids (Howell and Coppens, 1974, 1976; Coppens, 1975; Leakey, 1976; Boaz, 1977; Leakey and Leakey, 1978). The Shungura Formation, which is the subject of this study, is located in the Lower Omo Basin, which is the northerly continuation of the Turkana basin into Ethiopia (Brown and de Heinzelin, 1983). Radiometric ages indicate that the Formation covers a time span from 3.6 to 1.16 Ma (Feibel et al., 1989). Different sedimentary cycles of the Formation are grouped into 12 members (Basal, A, B, C, D, E, F, G, H, J, K and L), each commencing by a volcanic tuff designated by the same letter (Fig. 1a). The three main depositional conditions of this formation are: fluvial, deltaic and lacustrine, the first being the most common. As a result, the Omo fauna remains are in general fragmentary and represented mainly by isolated teeth and other resistant skeletal elements, such as mandibles.

Faunal changes from the bottom to the top of the Shungura Formation have been documented for different taxonomic groups (Coppens, 1975a,b; Cooke, 1976; Eck, 1976; Wesselman, 1984; Gentry, 1985a,b; Beden, 1985, 1987; Eisenmann, 1985; Guérin, 1985; Bobe and Eck, 2001). Specialists of each group have recognized changes throughout the sequence in morphology and/or relative abundance of species, genera or tribes within the respective taxa they studied. For example, elephants show rapid increase in the number of plates, hypsodonty, and plates become more folded (Beden, 1985). Suids have smaller premolars, but longer and more hypsodont molars through time (Cooke, 1976). On the other hand, micromammals show considerable change in their relative abundance, (Wesselman, 1984) (Fig. 1d). In addition, evidence that comes from palynology (Fig. 1c; Bonnefille and Dechamps, 1983), paleosols and depositional environments (Fig. 1b; Heesaerts et al., 1983) point to changes in environmental conditions from the base to the top of the Shungura Formation.

The two international research teams (French and American) collected about 220 hominid specimens. The oldest specimens were recovered from Member B and the Usno Formation. Most

specimens are teeth and come from the interval 3.3 Ma to 1.0 Ma. Thus, there are 21 specimens between 3.3 and 3.0 Ma, 45 between 3.0 and 2.5, 145 between 2.5 and 2.0, 3 between 2.0 and 1.5 and 3 between 1.5 and 1.0 (Suwa, 1990). Among these specimens, a gracile australopithecine is recognized in Member B of the Shungura Formation and Usno (e.g. Howell and Coppens, 1973; Suwa, 1988). In member C, *Australopithecus aethiopicus* is identified (Arambourg and Coppens, 1967, 1968; Coppens, 1976; Suwa, 1988, 1990; Suwa et al., 1996). This species is believed to have existed up to Lower Member G (Suwa et al., 1996). *A. boisei* and *Homo* sp. are recognized at the base of Member G; however, the genus *Homo* could have existed during the times of Member E (Howell et al., 1987; Suwa et al., 1996).

3. Environmental and faunal change studies

3.1. Materials and methods

Over 50,000 fossil specimens were collected from the Shungura and adjacent Formations by both American and French research teams. In this study I use a subset of the French Omo material collected with a high degree of stratigraphic control (Guillemot, pers. comm.). The collecting team recovered all mammalian crania and mandibles, all mammalian jaw fragments and complete isolated teeth, as well as all bovid horn cores. All primate and carnivore specimens were also collected. Post-cranial elements of bovids and other small to medium-sized mammals were collected, but that of large mammals, such as elephants, hippos and rhinos, were not recovered at the same rate. Counts of specimens were conducted on a pre-existing computerized database that has recently been updated by Claude Guillemot. Primary taxonomic identifications were undertaken by specialists of each group. Denis Geraads and I contributed to the re-identification of some bovid material collected during the last field season in 1976. The number of specimens varies considerably from one Member to the other: only six specimens were recovered from the Basal Member, whereas 11,990 were amassed from Member G.

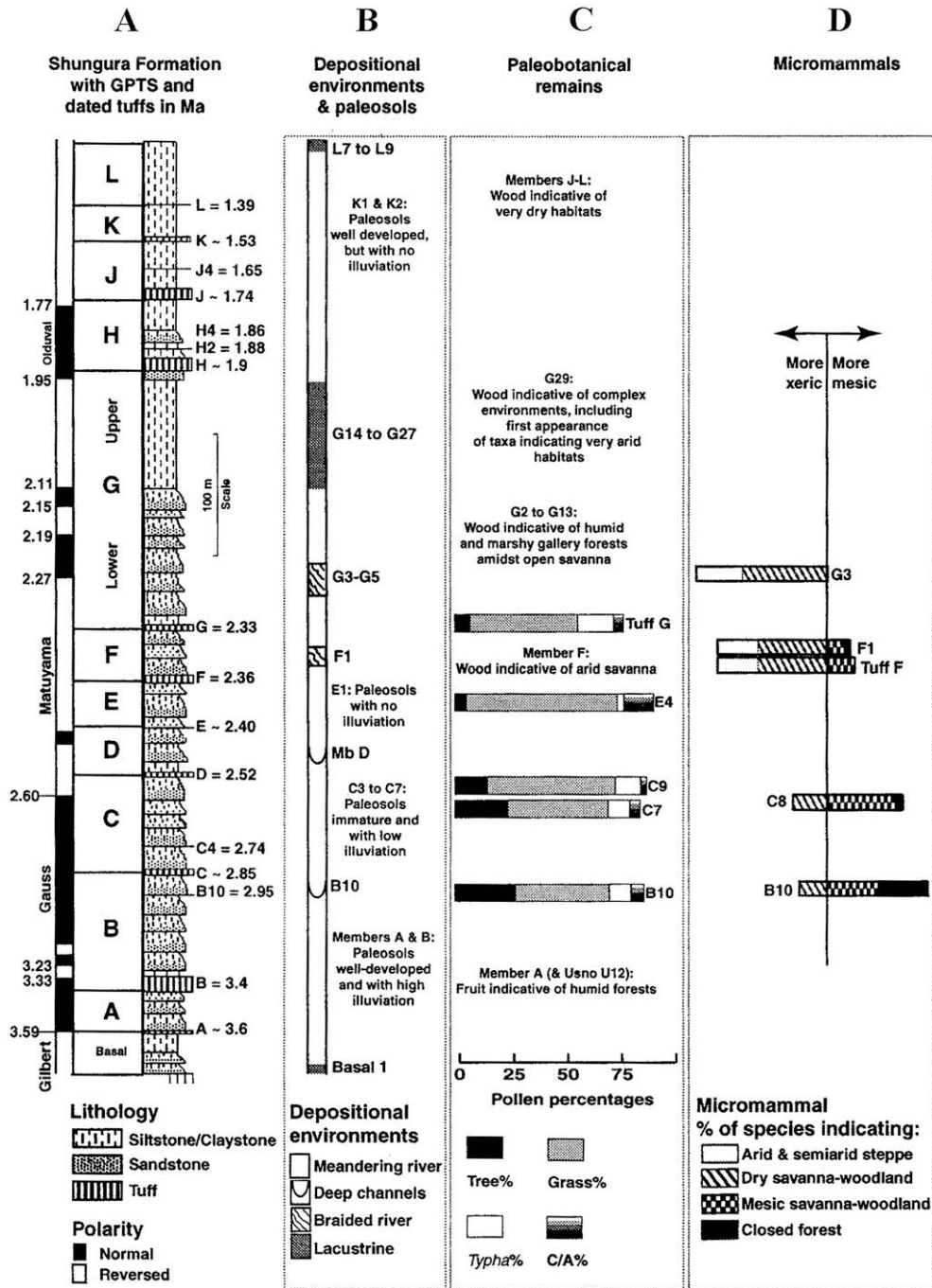


Fig. 1. Juxtaposition of stratigraphy and different sources of evidence for environmental changes through time in the Shungura Formation. Adapted from Bobe & Eck (2001). Original data on paleosols (B), paleobotanical remains (C) and micromammals (D) come, respectively, from Heesaerts et al. (1983), Bonnefille & Dechamps (1983) and Wesselman (1984). C/A%= Chenopodiaceae/Amaranthaceae.

Table 1

Abundance (number of specimens) of the thirteen most common mammalian families across Members of the Shungura Formation

	Basal	A	B	C	D	E	F	G	H	J	K	L	Total
Bovids	3	20	383	559	134	285	356	5451	349	99	68	137	7844
Hippopotamids	3	86	164	751	85	366	222	2183	217	19	96	149	4341
Suids	0	125	160	193	30	224	154	1121	98	10	14	68	2197
Cercopithecids	0	15	224	545	57	146	103	544	3	0	1	6	1644
Giraffids	0	5	61	113	14	68	54	315	7	1	3	8	649
Elephantids	0	2	60	61	26	44	18	178	7	1	8	8	413
Equids	0	7	24	39	7	13	48	166	14	5	0	28	351
Deinotheriids	0	2	18	14	0	12	7	39	5	0	0	0	97
Hominids	0	0	6	15	1	13	13	31	0	0	0	0	79
Rhinocerotids	0	2	10	2	3	7	9	29	0	1	0	3	66
Felids	0	0	0	0	0	2	0	31	1	0	0	0	34
Hyaenids	0	0	2	2	0	2	2	7	0	0	0	0	15
Camelids	0	0	7	0	1	0	2	4	0	0	0	0	14
Total	6	264	1119	2294	358	1182	988	10099	701	136	190	407	17744

Among the 22,022 vertebrate specimens identifiable to skeletal element, 17,744 belong to the 13 most abundant families (Table 1). The remaining specimens either belong to rare taxa, including non-mammals, or are not attributed to any family due to their fragmentary nature.

In this study, both univariate and multivariate approaches are employed. The first is used to compare different levels of the Shungura Formation in terms of faunal composition of taxa that are common in the sequence and are believed to be environmentally informative. These include bovids, suids and cercopithecids. Some common groups, such as equids, are not included in this analysis because paleoenvironmental conclusions that can be drawn from them are not as well established as in the groups considered here. In the second place, data from the Shungura Formation are analyzed using multivariate analysis of datasets arrayed in different contingency tables (Tables 5–8). Correspondence analysis is chosen for its relative robusticity in dealing with nonlinear data (Ludwig and Reynolds, 1988). When this method is applied to a contingency table with cells containing frequency counts (e.g., Tables 3, 5 and 7), the resulting graphs depict clusters of points in which closely related variables are grouped together. Thus, if localities of a given faunal assemblage and taxa from these localities are the two

variables used as rows and columns, then in the resulting graph, taxa with similar habitat preference would be close to each other as would be localities of similar taxonomic composition (Greenacre and Vrba, 1984; Benzecri, 1992). Each correspondence analysis is preceded by a chi-square test for a null hypothesis of independence of rows and columns. Since correspondence analysis is used to address different problems, definitions of variables will differ and will be explained for every analysis.

3.2. Faunal change in Shungura—Univariate approach

Percentages of tribes and/or genera of the three most common and most environmentally informative taxa (i.e., bovids, suids and cercopithecids) are used to look into environmental changes from one stratigraphic level to the other (Table 2). Among these tribes and genera only those encountered throughout the sequence are considered. In Members A and B bovids account for 29% of specimens assigned to large mammals. Among the different tribes, alcelaphines constitute only 2%, whereas reduncines account for 48% (Table 2). In Members C and D, alcelaphines, bovines and *Aepyceros* have the same percentage as the preceding members (Table 2). The percentage of reduncines is

Table 2
Abundance of tribes and genera of the three environmentally informative taxa in pairs of members and Member G

	<i>Aepyceros</i>	<i>Alcelaphini</i>	<i>Reduncini</i>	<i>Tragelaphini</i>	<i>Bovini</i>	<i>Theropithecus</i>	<i>Papio</i>	<i>Colobus</i>	<i>Kolpochoerus</i>	<i>Notochoerus</i>	<i>Metridiochoerus</i>
Lower G	454	52	1580	592	57	336	22	24	338	176	108
EF	54	19	93	104	28	102	27	8	105	70	17
CD	61	5	60	50	27	345	4	20	66	30	4
AB	44	4	1 03	28	37	169	16	24	28	204	8

marked by a considerable decrease relative to AB, whereas tragelaphines show a relative increase. In members E and F the percentage of alcelaphines increases. *Aepyceros* and bovines show a decrease in the transition from members CD to EF (Table 2). In lower G the percentage of reduncines increases compared to other bovid tribes. The decrease in the percentage of tragelaphines is significant and alcelaphines show a decrease as well. The overall increase in alcelaphines through time probably indicates relative increase in grasslands. In Member G reduncines account for about 57% of the bovines, indicating that the type of habitat they live in was the most common in these levels.

Among suids, *Notochoerus* shows a considerable decrease and *Kolpochoerus* is the dominant suid in members C and D. In the transition from Members CD to EF *Metridiochoerus* shows a relative increase, whereas *Notochoerus* continues to decrease (Table 2). Similar trends continue in Member G with a considerable increase of *Metridiochoerus*. The continuous increase in *Metridiochoerus* percentage through time indicates that grasslands were becoming more common.

Within cercopithecids, *Theropithecus* is dominant and colobines account for 11% in Members AB (Table 2). In the transition from AB to CD colobines show a decrease, while little change is recorded for *Theropithecus*. In EF there is an increase in *Papio*, but *Theropithecus* remains the most abundant. The transition to G is mainly characterized by similar trends, but there is a slight increase in colobines.

Overall, as inferred from the taxa considered here, the transition from AB to CD levels is characterized by a decrease in precipitation, but with no evidence of considerable decrease in forest habitat. During this transition, humid habitats where reduncines lived are the most affected. Grasslands are probably becoming part of the main paleolandscape in Shungura for the first time in Members E and F. From the high percentage of reduncines it can be inferred that wet substrate habitats (e.g., edaphic grasslands) increased considerably in the transition from EF to G. These conclusions concern only the Shungura Formation, but are in general agreement with results

obtained by other researcher in which a continuous trend towards a more open environment has been suggested (e.g., Bonnefille and Vincens, 1985; Bobe et al., 2002). However, this study shows that in Member G, though environments become more open, there are also evidences of increase in precipitation.

3.3. Environmental and taphonomic studies—multivariate approach

The objective of the following study is to assess taphonomic and environmental aspects of the Shungura Formation using a correspondence analysis method. This is conducted using XL-Stat software on datasets arrayed in different contingency tables as rows and columns. After a test of independence of active rows and active columns in the contingency table for a given degree of freedom and probability P , a decision is made on the significance of the dependence between the rows and the columns. The results are then depicted as clusters of points on two-dimensional graphs with the first two axes that contribute to most of the variation.

First taphonomic questions will be addressed by using differential representations of skeletal elements in different depositional conditions. Second, environmental problems will be tackled by comparing relative abundance of different taxa in localities that are distributed in the Shungura sequence. This approach differs from the one used above, in which pairs of members were compared in terms of their taxonomic composition, for two reasons. Primarily, comparisons of faunal abundance are not made among members, but localities. This allows sampling of a given environment, and does not lump different environments that co-occurred at the same time. Secondly, localities of all Members are considered simultaneously in order to detect faunal breaks (if any) in the Shungura sequence. Before applying the method to Plio-Pleistocene fossils and localities, however, the same method will be used to analyse modern bovid taxa from African game parks. This will be followed by taphonomic studies and finally correspondence method will be applied to the Shungura fauna.

3.4. Correspondence analysis on modern parks and bovids

Bovoid tribes and genera from 29 African game parks are used (Table 3). Data are derived from various publications, notably Vrba (1980), Greenacre and Vrba (1984), Shipman and Harris (1988), and more information can be obtained from Alemseged (1998a). The data are presented in a contingency table where variable 1 and variable 2 are represented by game parks and taxa (tribes and genera) respectively (Table 3).

The result of the correspondence analysis conducted on all parks and bovid taxa considered at tribal level shows three clusters (Fig. 2). The first cluster (open–dry) consists of Alcelaphini and Antilopini associated with the generally open and dry parks of Etosha, Kalahari, Omo, Nairobi, Serengeti and Ngorongoro. A second group of taxa (woodland), Tragelaphini–Bovini–Aepycerotini is associated with Timbavati, Hluhluwe, Mkuzi, Kruger, Manyara and Kwange. A third cluster of Reduncini–Hippotragini–Cephalophini (wet) is associated with Arli, Mupa, Luando, Comoe, Deux Bale, W, Penjari, Quicama, Kafue, Boubu Ndjida, Bicuara, Po, Saint-Floris, Kaninji, Fina, Yankari and Turkana. The correspondence analysis thus distinguishes three main habitat types: open dry (group I), wet (edaphic grassland) (group II) and woodland (group III). Overall the associations between bovid tribes and game parks are in agreement with what is traditionally accepted (e.g., Greenacre and Vrba, 1984). Comparable results were obtained by Shipman and Harris (1988), with some exceptions.

A second correspondence analysis on the same game parks, with taxa considered at the generic level, shows comparable clusters of game parks and taxa (Fig. 3). However, even though the overall tendencies of associations are comparable, this analysis reveals the environmental specificity of certain genera within the generally accepted environment for their tribe. For example, *Antidorcas* and *Oryx* are closely associated, whereas *Taurotragus* is isolated. *Gazella* is closer to *Damaliscus* than it is to *Antidorcas*, probably indicating similar environmental preferences, even though they belong to different tribes. This

cautions against oversimplification in attributing different species and genera to the same habitat as the general environmental preference of their tribe. Finally, the two correspondence analyses above indicate that this approach can be used to study the relationship between relative abundances of taxa and their habitat preferences. Nonetheless, its application to fossil fauna is complicated by the biased representation of taxonomic abundances in any fossil assemblage.

3.5. Taphonomic considerations

A series of factors intervene during the transition from biocoenose to taphocenose (e.g., Behrensmeyer, 1975). Taphonomic considerations are thus essential as they provide information on how to address problems pertaining to paleo-environmental reconstruction and ecological studies (Behrensmeyer, 1975, 1982, 1988). In addition, actualistic studies show that biases related to body weight, habitat differences, and predators modify relative abundances of taxa in fossil assemblages (Behrensmeyer, 1975, 1993; Behrensmeyer and Dechant Boaz, 1980). Increasing sample sizes of contemporaneous paleofauna could provide information on the original proportion between taxa when the same taxa are encountered in many localities. One way to do this is to compare fossil assemblages from a large number of localities in a given stratigraphic sequence. Fossil assemblages from the Shungura Formation allow us to do this comparison.

Another major taphonomic problem is the role of the depositional environment and its influence on the ratio between different taxa and skeletal elements. Vertebrate bones differ considerably in size, density, weight and shape. As a result they are affected differently by various transporting agents. In fluvial environments small and light elements, such as ribs, are transported faster than cranial parts, mandibles and teeth (Voorhies, 1969; Behrensmeyer, 1975). As a consequence, there is a biased representation of different skeletal elements in fossil assemblages. The fact that there is a large number of localities, and that detailed sedimentological and stratigraphic studies have been conducted in the Shungura Formation, allows one

Table 3
Abundance of bovid tribes and genera in 29 African Game Parks

	Alcela.	Antilop.	Aepycer.	Trage.	Redun.	Bovini	Hippotra.	Cephalo.	Alcelap.	Connoch.	Damalis.	Antidor.	Gazella	Aepyceros	Taurotra.	Tragela.	Kobus	Redunca	Syncerus	Hippotragus	Oryx	Ourebia	Raphicerus	Cephalo.	Sylvicap.
Kruger	10000	0	153000	11124	4730	24200	1400	1300	0	9360	640	0	0	153000	424	10700	3220	1510	24200	1400	0	100	5000	300	1000
Manyara	0	0	700	25	55	1500	0	0	0	0	0	0	0	700	0	25	15	40	1500	0	0	0	0	0	0
Quiçama	0	0	0	5500	1500	8000	1500	3500	0	0	0	0	0	0	2500	3000	0	1500	8000	1500	0	0	0	2500	1000
Bicuara	500	0	150	450	150	100	500	500	0	500	0	0	0	150	250	200	100	50	100	500	0	50	100	0	500
Luando	0	0	0	900	2250	150	3000	1100	0	0	0	0	0	0	200	700	1750	500	150	3000	0	250	0	100	1000
Mupa	250	0	0	750	1600	0	200	500	0	250	0	0	0	0	200	550	600	1000	0	200	0	500	500	0	500
Mkuzi	1397	0	9394	533	69	0	0	4	0	1397	0	0	0	9394	0	533	0	69	0	0	0	0	6	1	3
Hluhluwe	3509	0	4894	3202	1009	2195	0	15	0	3509	0	0	0	4894	0	3202	820	189	2195	0	0	0	0	0	15
Kafue	119	0	2	42	198	85	31	70	19	100	0	0	0	2	2	40	78	120	85	31	0	50	40	30	40
Kwange	2630	0	8000	5450	1250	13000	2620	2000	0	2500	130	0	0	8000	1800	3650	1000	250	13000	2500	120	0	3000	0	2000
Kalahari	20558	24040	0	6569	0	0	16070	710	14180	6378	0	24040	0	0	6569	0	0	0	0	0	16070	0	1645	0	710
Nairobi	1348	845	633	78	105	0	0	2	1095	253	0	0	845	633	58	20	90	15	0	0	0	0	2	0	2
Turkana	2023	1059	0	0	0	0	4500	0	0	0	2023	0	1059	0	0	0	0	0	0	0	4500	0	0	0	0
Serengeti	455000	190000	65000	9500	5500	50000	2500	0	18000	410000	27000	0	190000	65000	7000	2500	3000	2500	50000	2500	0	1000	0	0	0
Ngorongoro	13630	5000	0	400	120	60	0	0	100	13530	0	0	5000	0	400	0	60	60	60	0	0	650	0	0	0
Etosha	4600	12000	0	2500	0	0	296	250	600	4000	0	12000	0	0	500	2000	0	0	0	296	0	505	500	0	250
Arli	190	0	0	80	1240	65	1900	2150	100	0	90	0	0	0	0	80	1185	55	65	1900	0	0	0	0	2150
Deux Bale	453	0	0	198	227	40	1200	651	453	0	0	0	0	0	0	198	176	51	40	1200	0	11736	0	153	498
Po	543	0	0	108	287	248	777	482	543	0	0	0	0	0	0	108	99	188	248	777	0	0	0	0	482
Saint-Floris	3022	0	0	0	3224	1813	504	0	907	0	2115	0	0	0	0	0	3224	0	1813	504	0	4613	0	0	0
Bouba Ndji.	7128	0	0	1800	7056	1746	4356	5451	6984	0	144	0	0	0	954	846	1386	5670	1746	4356	0	7864	0	51	5400
Yankari	675	0	0	0	653	675	360	0	675	0	0	0	0	0	0	0	653	0	675	360	0	17000	0	0	0
Fina	2975	0	0	0	1283	0	3938	0	2975	0	0	0	0	0	0	0	1283	0	0	3938	0	2775	0	0	0
Penjari	9367	0	0	0	19737	3480	5014	2466	8768	0	599	0	0	0	0	0	18915	822	3480	5014	0	2100	0	0	2466
Comoé	8000	0	0	1000	7500	500	100	13000	8000	0	0	0	0	0	0	1000	7500	0	500	100	0	0	0	6500	6500
Kainji	6436	0	0	550	4827	118	5886	1413	6436	0	0	0	0	0	0	550	4827	0	118	5886	0	0	0	157	1256
W	1440	0	0	240	6120	4140	2850	0	1020	0	420	0	0	0	0	240	6120	0	4140	2850	0	0	0	0	0
Omo	2090	646	0	947	0	350	0	0	0	0	2090	0	646	0	944	3	0	0	350	0	0	0	0	0	0
Timbavati	1247	0	4659	78	33	0	0	0	0	1247	0	0	0	4659	0	78	0	33	0	0	0	0	0	0	0

Alcela. (*Alcelaphini*), Antilop. (*Antilopini*), Aepycer. (*Aepycerotini*), Trage. (*Tragelaphini*), Redun. (*Reduncini*), Hippotra. (*Hippotragini*), Cephalo. (*Cephalophini*), Alcelap. (*Alcelaphus*), Connoch. (*Connochaetes*), Damalis. (*Damaliscus*), Antidor. (*Antidorcas*), Taurotra. (*Taurotragus*), Tragela. (*Tragelaphus*), Cephalo. (*Cephalophus*), Sylvicap. (*Sylvicapra*)

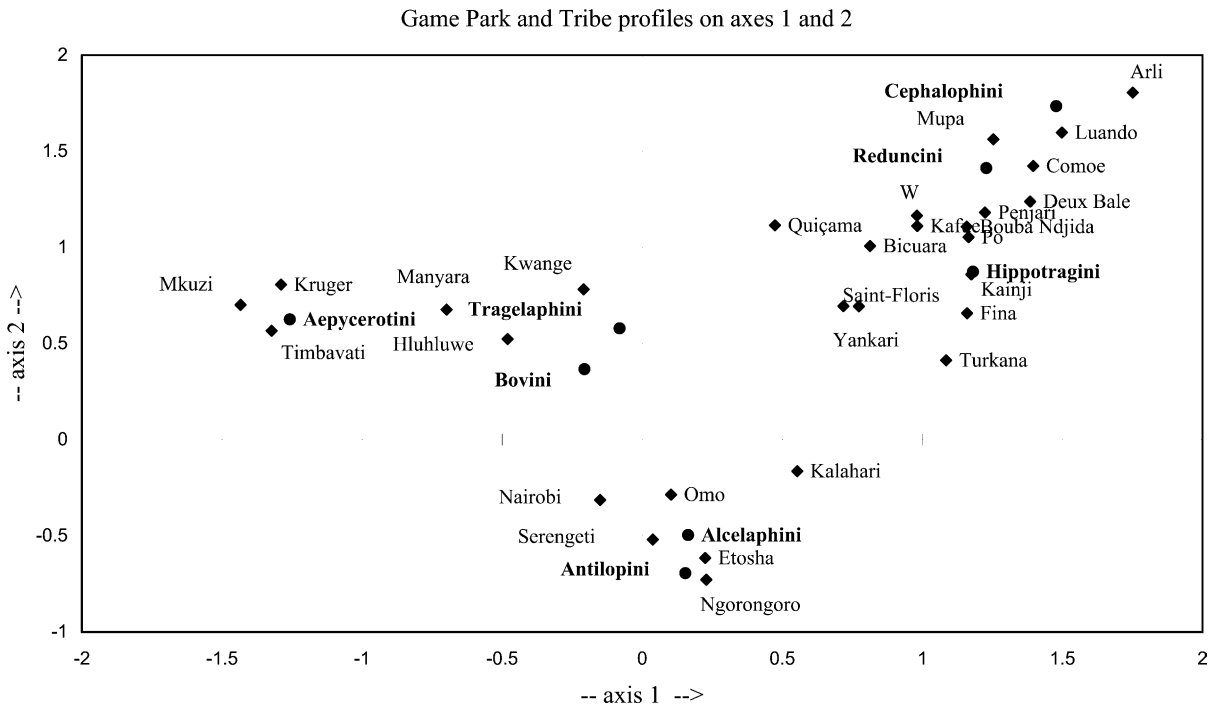


Fig. 2. Correspondence analysis showing game park and bovid tribe profiles on axes 1 and 2. Chi-square distance on data=3586196.9026 ~ degrees of freedom=392, Corresponding probability: 0.0001, Limit Chi2 for the chosen confidence range=439.1645. Using this test one should reject the hypothesis of independence. Variable1: representing the rows, variable1 is constituted by 29 African game parks (Table 3). Variable2: this represent the columns and is constituted by tribes and genera of bovinds encountered in the parks (Table 3).

to pose questions pertaining to the relationship between fossil assemblages and depositional environments.

3.5.1. Correspondence analysis on depositional environment and skeletal elements

For this study I counted the total number of skeletal elements of all taxa in all localities that are characterized by the same depositional condition. Thus, in the contingency table (Table 4) Variable1 (rows) represents various types of depositional environments and Variable2 (columns) is represented by skeletal elements.

The results of the correspondence analysis show that there are four groups of skeletal elements (Fig. 4): teeth, mandibles–maxillae, crania–horn cores, and postcrania. By superimposing the row profiles (depositional environments) on the column profiles (skeletal elements) (Fig. 4), one

can see that postcranial elements are closely associated with low energy depositional environments such as lacustrine, deltaic, mud flat and ephemeral streams, whereas the rest of the skeletal elements are grouped mainly with relatively high energy fluvial conditions: channel, levee and flood plain. This observation could be explained by the fact that skeletal elements that survive to become fossils in fluvial conditions are relatively more dense and resistant, as a result they have higher probability of being buried in high-energy depositional environments. In contrast, the relatively high percentage of postcranial elements in depositional environments of less energy, such as lacustrine, deltaic etc., support the interpretation that they are less preservable in fluvial conditions.

While dentognathic elements generally are more abundant in fluvial conditions than postcranial

Game Park and Genus profiles on axes 1 and 2

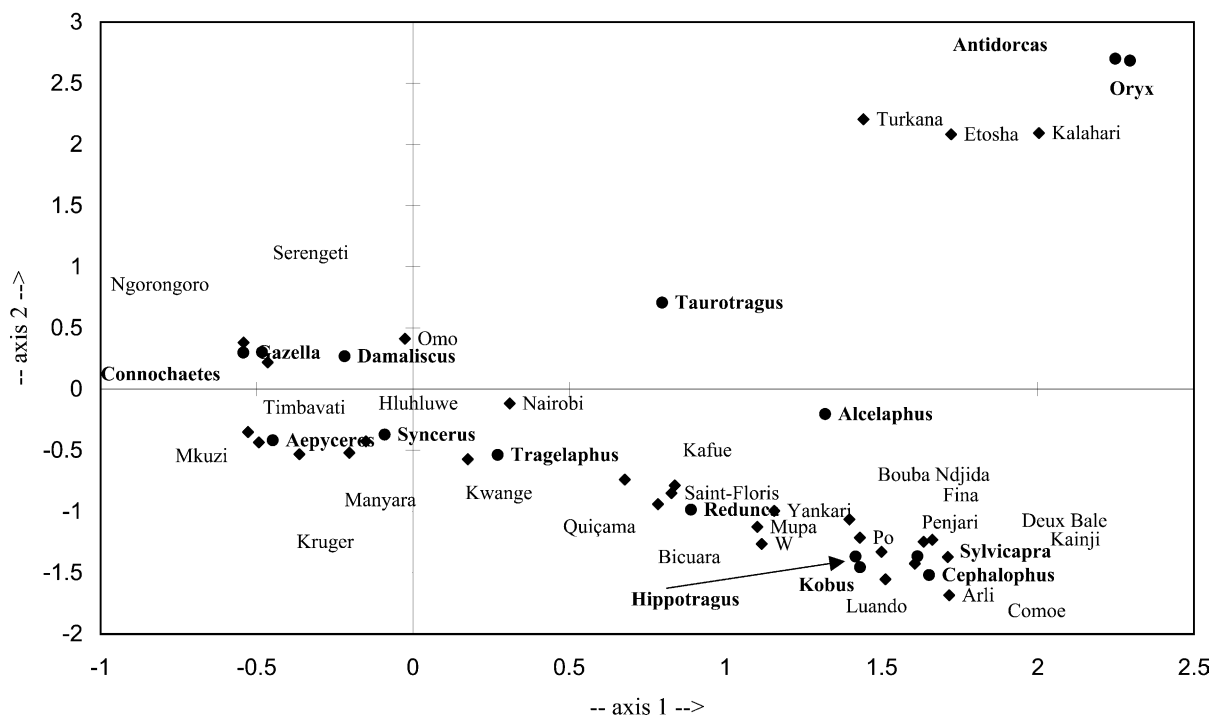


Fig. 3. Correspondence analysis showing game park and bovid genera profiles on axes 1 and 2.

elements, indicating similar pre- and post-burial reactions of these elements to transport and other agents, one can see in Fig. 4 that maxillae and mandibles are close to each other, as are crania and horn cores, with teeth occupying a distinct position. Based on this analysis there are four groupings characterized by skeletal element abundance in different depositional environments. The above observation indicates that the relative abundance of skeletal elements (proportions) is not random in different depositional environments. Based on experimental evidence using modern skeletons (mainly from ungulates), Voorhies (1969) and Behrensmeyer (1975) classified different skeletal elements according to their degree of susceptibility to transport. This corresponds to the transportability of a given element in a fluvial context. They concluded that five groups could be established, with a sixth non-tested group (group NT).

Group I—Ribs, vertebrae, sacra, sterna, sesamoids, patellae

Group I/II—Scapulae, ulnae, phalanges, astragali, calcanei, carpals and other tarsals.

Group II—Femora, tibiae, humeri, radii, metapodials, pelvis

Group II/III—Hemi-mandibles

Group III—Crania, horn cores, mandibles, teeth

Group NT—Epiphyses, fibulae, maxillae and diaphyses

It is interesting to note that results obtained here are in general agreement with the classification proposed by Voorhies (1969) and Behrensmeyer (1975). However, Voorhies and Behrensmeyer did not test maxillae. Based on the correspondence analysis, I suggest further subdivision of Group III into three sub-divisions namely teeth, crania+horn cores, and mandible+

Table 4

Abundance of skeletal elements in localities of the Shungura Formation that are characterized by similar depositional environments

	Teeth	Crania	Maxillae	Mandibles	Horn Cores	Postcrania	Total
Deltaic	386	20	12	50	72	552	1092
Ephemeral streams	63	6	6	10	18	179	282
Flood plain	313	14	10	37	30	165	569
Lacustrine	328	5	5	12	17	407	774
ChaLeve	107	4	1	5	5	47	169
ChaLevFP	8563	156	184	760	601	3178	13442
ChaLevFPDel	13	1	2	3	0	10	29
ChaLevFPLac	10	1	1	0	4	27	43
ChaLevFPMF	1441	20	37	116	34	834	2482
ChaLevMFDel	960	27	56	221	68	254	1586
MFDel	540	31	15	68	107	586	1347
Total	12724	285	329	1282	956	6239	21815

Variable1: representing the rows, variable 1 corresponds to various depositional environments. The Shungura Formation is mainly characterized by fluvial, deltaic and lacustrine conditions (de Heinzelin 1983). The first is the most common. In this study environments are further subdivided into channel (**Cha**), levee (**Lev**), flood plain (**FP**) and swamp. Nevertheless, as localities are not necessarily characterized by only one of these, some were grouped. In addition, some localities are characterized by deltaic (**Del**), mudflat (**MF**), Lacustrine (**Lac**) and ephemeral conditions. Variable2 represents the columns and is constituted by skeletal elements (teeth, crania, mandibles or cranial fragments, horn cores and post crania) belonging to all mammalian taxa. Therefore, in the contingency table (Table 5), the box $K(i, j)$ represents the total number of skeletal elements j collected from localities characterized by depositional environment i .

maxillae. However it should be underscored that more experiments in modern systems are needed to confirm this proposed subdivision of skeletal elements.

3.5.2. Taphonomic patterns in Shungura

The skeletal element distributions obtained above can be used to evaluate taphonomic aspects of members of the Shungura Formation through time. For this purpose, correspondence analysis is applied to different skeletal elements and Members A to G of the Shungura Formation (Table 5). The result (Fig. 5) shows that Upper G is most distinct in terms of the skeletal element proportion. This can be explained by the fact that there is a major change in depositional environment at the base of Upper G where depositional conditions change from fluvial to lacustrine, becoming more favorable for the preservation of postcrania. Members A through Lower G are grouped showing that taphonomic conditions were relatively stable throughout the sequence. One exception is Member D, which occupies an intermediate position between Upper Member G and the others.

Depositional environment and the other factors listed above are not the only source of bias. The original proportions (ratio of abundance) between taxa and skeletal elements could be modified by other factors, particularly carnivores. The degree to which the latter affects the faunal and skeletal composition is difficult to determine. Nonetheless, we know that teeth, mandibles, maxillae and horn cores are probably less affected by carnivores due to their low nutritional value (Hill, 1978, 1980). It has also been shown above and elsewhere that these elements react in general in the same way to transporting agents. This implies they are vulnerable to similar taphonomic agents and processes before, during and after transport. On the other hand, as shown above, using modern bovids and African game parks that multivariate analysis can be used for environmental studies (Figs. 2 and 3). However, as demonstrated in the preceding section, skeletal elements are not uniformly distributed in different localities (Fig. 4). It is difficult to determine to which degree this differential representation affects taxonomic composition.

Depositional environment and skeletal element profiles on axes 1 and 2

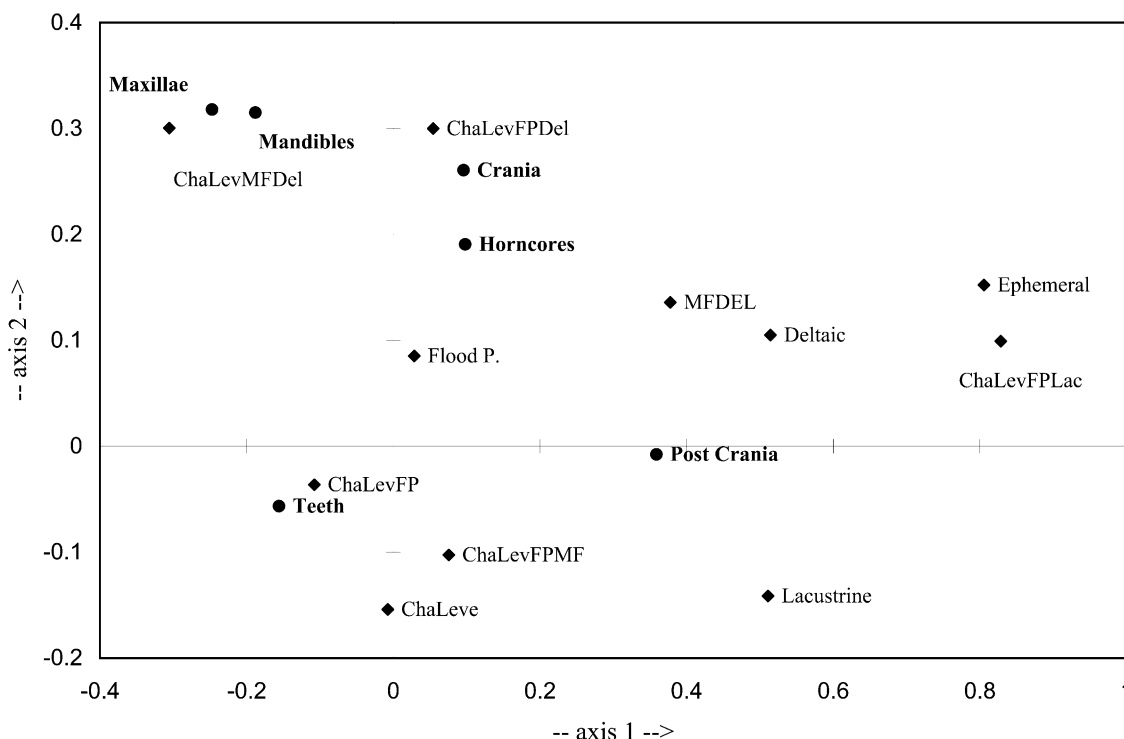


Fig. 4. Correspondence analysis showing depositional environment and skeletal element profiles on axes 1 and 2. Chi-square distance on data=1731.5539 ~ degrees of freedom=50; Corresponding probability: 0.0001; Limit Chi2 for the chosen confidence range=67.5048; ChaLevMFDel=Channel+Levee+Mud Flat+Deltaic, ChaLevFP=Channel+Levee+Flood Plain, ChaLevFPDel=Channel+Levee+Flood Plain+Deltaic, ChaLevFPMF=Channel+Levee+Flood Plain+Mud Flat, ChaLeve=Channel+Levee and ChaLevFPLac=Channel+Levee+Flood Plain+Lacustrine.

Table 5
Abundance of skeletal elements in Members A through Upper G of the Shungura Formation

	Teeth	Crania	Maxillae	Mandibles	Horn cores	Postcrania	Total
A	188	1	3	8	5	74	279
B	955	12	15	78	37	272	1369
C	1592	53	23	144	64	273	2149
D	194	12	9	23	18	192	448
E	928	29	27	97	45	462	1588
F	2926	43	25	133	65	673	3865
G (Lower)	4766	129	183	682	699	2682	9141
G (Upper)	436	15	10	55	53	726	1295
Total	11985	294	295	1220	986	5354	20134

Moreover, as shown above and demonstrated elsewhere, postcranial elements are affected more than cranial elements under fluvial conditions. So,

in order to avoid the effects of these variables in the faunal studies, I will consider only teeth, mandibles, cranial parts and horn cores that, to

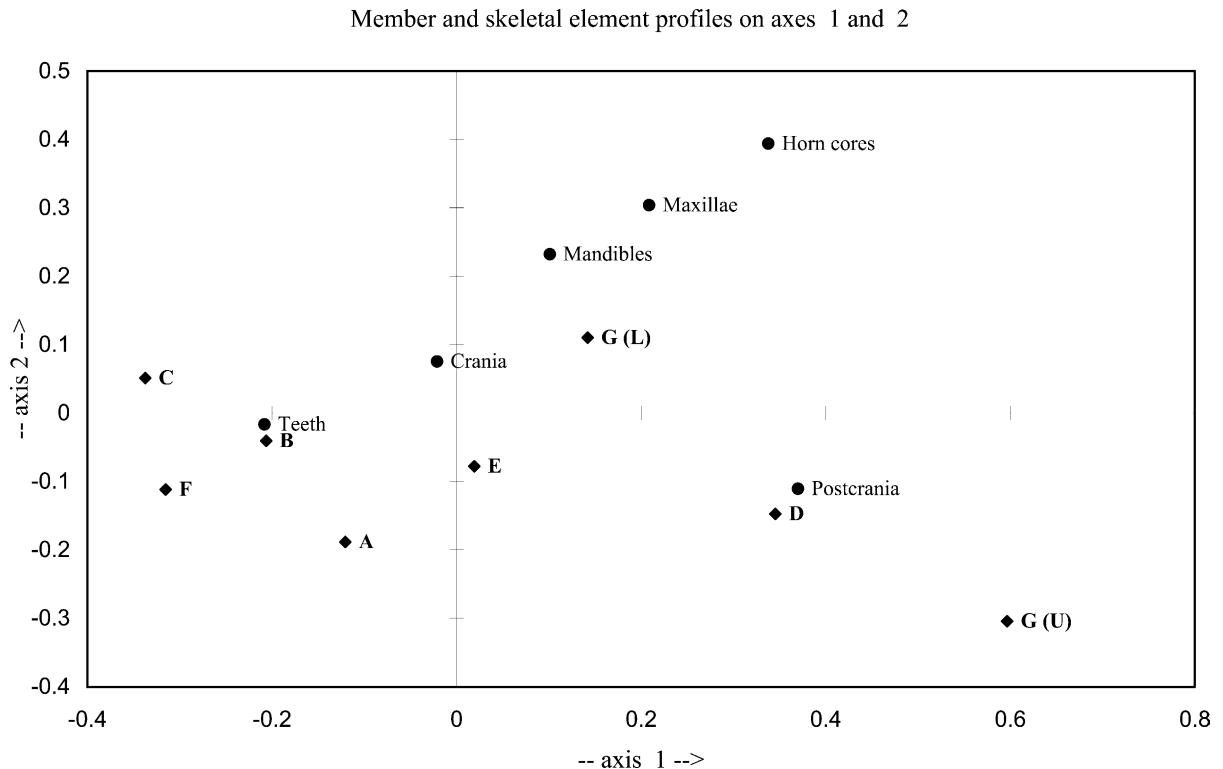


Fig. 5. Correspondence analysis showing geological Members and skeletal element profiles on axes 1 and 2. Note that Upper G, at bottom right, is well separated from others showing its unique taphonomic nature. Others are grouped showing that isotaphonomy can be justified for Members A through Lower G.

some degree, behave similarly. Also, postcranial elements were not collected in the same intensity as cranial parts for various reasons, and are subject to unknown sampling biases. Another reason to avoid postcranial elements in this study is that they are rarely attributed to lower taxonomic categories (tribes, genera and species).

3.6. Correspondence analysis on Shungura fauna

3.6.1. Correspondence analysis 1 (Shungura Members vs. Mammalian families)

The first correspondence analysis was conducted on all members of the Shungura Formation and taxa considered at the family level (Table 6). In this table, abundance of taxa has been summed up to the respective family. The abundance of every family in each member has been added, such that in Table 7 the cell $K(i, j)$ represents the total number of specimens belonging to the family j

encountered in Member i . The result of the correspondence analysis shows (Fig. 6) that cercopithecids are relatively more abundant in Member C than in other Members. Giraffids, deinotheriids and suids are clustered with the oldest levels A, B and D. Hippopotamids, elephantids and hominids are associated with Members E and F. The position of Member F, which is close to the origin, might suggest that this Member is not especially dominated by any taxa at the family level. Bovids are closely associated with lower Member G and equids with upper Member G. Considering only the three most abundant and environmentally informative families (i.e., bovids, suids and cercopithecids), plus hominids, the plot shows (Fig. 7) similar patterns in which suids associate with Members A, B, D, and E, cercopithecids “attract” Member C, and bovids are strongly associated with lower Member G.

Table 6
Abundance (number of specimens) of mammalian families in Members of the Shungura Formation

	Bovidae	Cercopithecidae	Suidae	Equidae	Deinotheriidae	Giraffidae	Elephantidae	Hippopotamidae	Hominidae	Total
Upper G	411	12	132	56	2	10	12	311	2	948
Lower G	2735	382	622	78	36	223	88	1186	22	5372
Member F	167	69	60	23	5	30	8	107	3	472
Member E	131	68	99	7	6	42	13	204	8	578
Member D	8	6	9	2	0	6	2	4	0	37
Member C	195	363	93	26	12	55	24	309	10	1087
Member B	200	200	115	13	16	46	16	103	3	712
Member A	15	9	93	4	1	2	0	63	0	187
Total	3862	1109	1223	209	78	414	163	2287	48	9393

Table 7
Abundance (number of specimens) of mammalian tribes and genera in Members of the Shungura Formation

	<i>Aepyceros</i>	Alceaphini	Reduncini	Tragelaphini	Bovini	<i>Theropithecus</i>	<i>Papio</i>	<i>Colobus</i>	<i>Hexaprotodon</i>	<i>Kolpochoerus</i>	<i>Notoch.</i>	<i>Metridioch.</i>	<i>Hipparion</i>	<i>Equus</i>	<i>Deinoth.</i>	<i>Giraffa</i>	<i>Elephas</i>	<i>Hippopot.</i>	<i>Australopith.</i>	<i>Homo</i>	Total
Upper G	88	60	235	24	4	5	4	3	127	97	24	11	11	45	2	10	12	184	1	1	948
Lower G	454	52	1580	592	57	336	22	24	1160	338	176	108	35	43	36	223	88	26	14	20	5384
Member F	30	17	54	48	18	47	21	1	107	30	48	15	23	0	5	30	8	10	6	0	518
Member E	24	2	39	56	10	55	6	7	201	75	22	2	7	0	6	42	13	3	5	3	578
Member D	2	0	4	2	0	4	2	0	4	2	7	0	2	0	0	6	2	0	0	0	37
Member C	59	5	56	48	27	341	2	20	306	64	23	4	26	0	12	55	24	3	10	0	1085
Member B	40	4	97	26	33	162	16	22	103	18	121	8	13	0	16	46	16	0	6	0	747
Member A	4	0	6	2	4	7	0	2	60	10	83	0	4	0	1	2	0	3	0	0	188
Total	701	140	2071	798	153	957	73	79	2068	634	504	148	121	88	78	414	163	229	42	24	9485

Notoch. (*Notochoerus*), Metridioch. (*Metridiochoerus*), Deinoth. (*Deinotherium*), Hippopot. (*Hippopotamus*), Australopith. (*Australopithecus*).

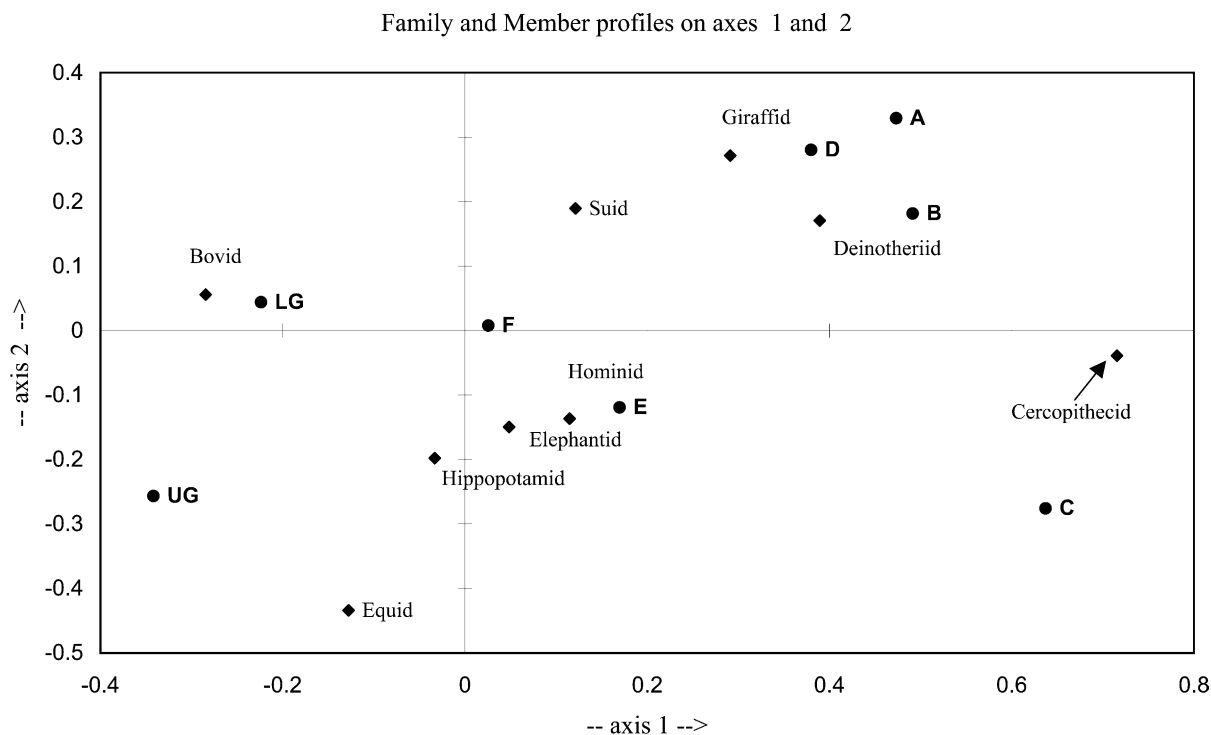


Fig. 6. Correspondence analysis showing Member and mammalian family profiles on axes 1 and 2. Taxa are considered at family level and taxonomic abundance for every Member is sums of number of specimens encountered in localities from the respective Member.

3.6.2. Correspondence analysis 2 (*Shungura Members vs. genera and tribes*)

A second correspondence analysis conducted on the same Members, but taxa are considered at lower taxonomic levels (Table 7), tribes and genera, reveals chronology as an important discriminating factor (Fig. 8). The first axis separates members according to their stratigraphic level, indicating that there was a continuous change of the faunal composition in the Shungura Formation through time. I have shown above that isotaphonomy could be warranted for Members A through Lower G (Fig. 5), thus alignment of different members is probably best interpreted as a taxonomic (environmental) signal. This result underscores the generally acknowledged fact that there is environmental and taxonomic change throughout the Shungura sequence (Coppens 1975a,b; Cooke, 1976; Eck, 1976; Wesselman, 1984; Gentry, 1985a,b; Beden, 1985, 1987;

Eisenmann, 1985; Guérin, 1985). However, Upper G is situated further right probably showing juxtaposition of taxonomic and taphonomic factors that make this submember distinct from others (Fig. 8). Among the first group of localities (A through Lower G), Member F does not follow the same pattern as the others for the second axis (Fig. 8). The reason for this is that Member F is dominated by alcelaphines, which are rare in other members.

It is tempting to interpret distances between members on the first principal axis of Fig. 8 in terms of major and minor environmental changes. For example, changes from C to D would be relatively minor whereas D to E, and F to G would be relatively major (Fig. 8). However, Members (A, B, C etc.) include lumped localities from the same period of time that sample different types of environments. A more environmentally sensitive approach would, therefore, be to consider localities separately, regardless of their stratigraphic position.

Family and Member profiles on axes 1 and 2

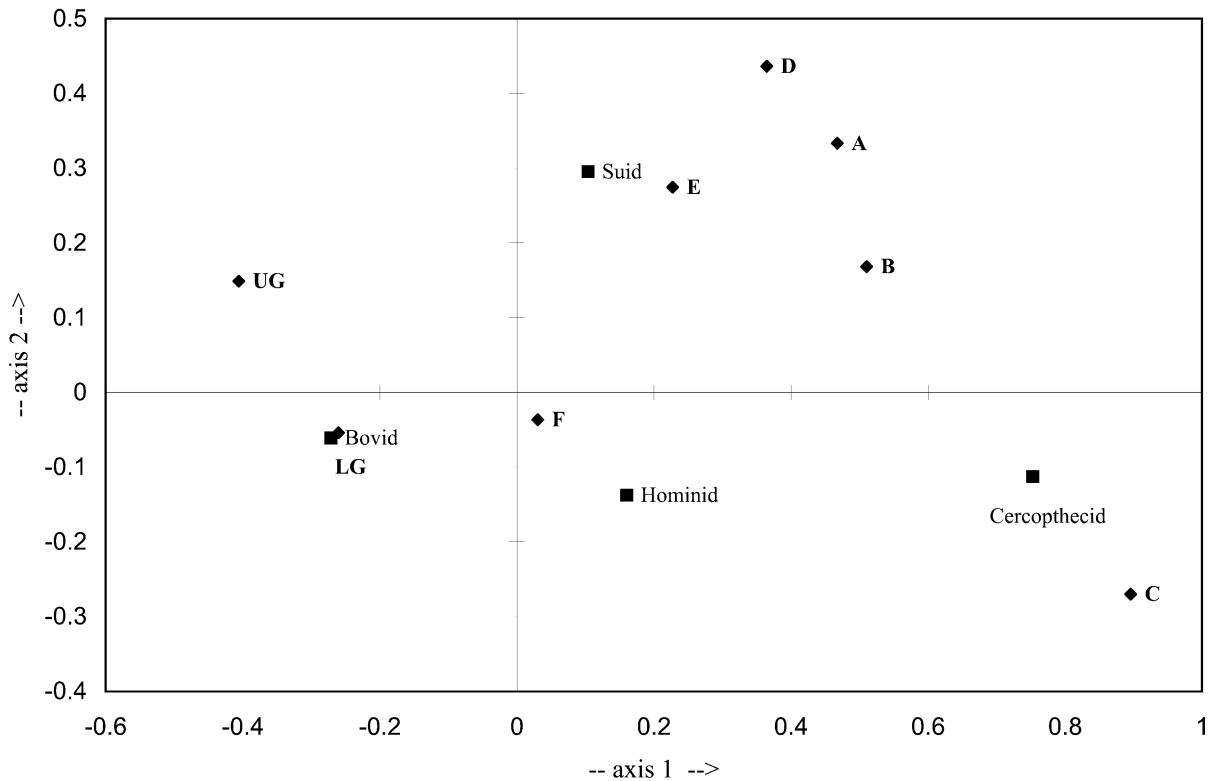


Fig. 7. Correspondence analysis showing Member and mammalian family profiles on axes 1 and 2. Here only the three environmentally informative taxa (bovids, suids and cercopithecids) and hominids are depicted. Note that suids are abundant in most of the lower stratigraphic levels as cercopithecids are in Member C. Bovids are very closely associated with Member G, particularly lower Member G.

3.6.3. Correspondence analysis 3 (*Localities vs. Genera and Tribe*)

In this analysis localities are considered separately and are assumed to sample a given environment or environmental complex. Abundance of taxa in localities from the same member are not summed up as in preceding analysis. Note that even though row profiles in the graphs show Members (A, B, C, etc.) to facilitate interpretation of results, every point represents a locality. The data are presented in a contingency table (Table 8) in which localities and fossil taxa represent rows and columns respectively.

Correspondence analysis conducted on all localities (variable1) and 19 taxa (variable2) shows,

on axis 1 (Fig. 9), similar patterns to that observed above when localities were combined according to their stratigraphic levels (Fig. 8). While localities from Members A–F are separated from those of Members G and above, they are not separated among themselves according to their stratigraphic levels (Fig. 9). This shows that there are environmental changes through time in the Shungura Formation (as inferred from the changes in faunal composition), but they are not as significant as those in lower Member G. In other words, the fact that localities of Members A–F are not discriminated in this analysis shows that changes were not abrupt enough from one level to the other to alter the faunal composition as much as in lower

Member profiles on axes 1 and 2

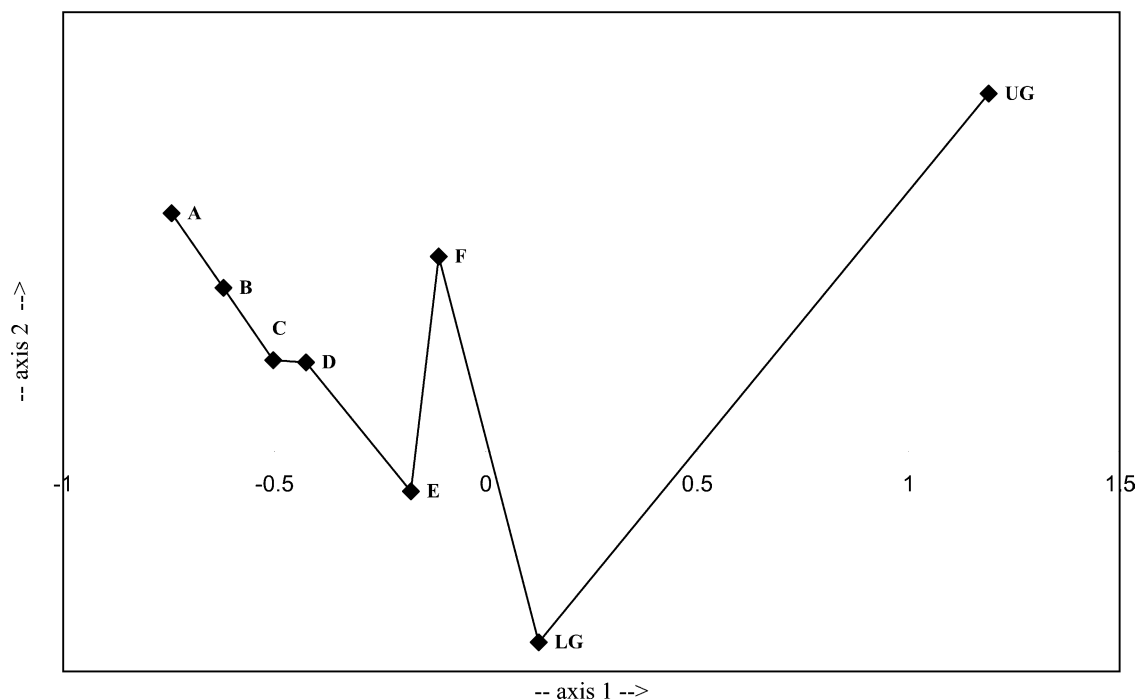


Fig. 8. Correspondence analysis showing Member profiles axes 1 and 2. In this analysis columns are constituted by lower taxonomic categories (tribes and genera). Note that on axis 1 Members are aligned according to their stratigraphic level and that Upper G (UG) is the most distinct. See text for explanation.

Member G. While there are a few exceptions showing the presence of the type of habitat that generally characterized Lower G in Members A–F, this result shows that the faunal composition of localities from the two stratigraphic levels differ considerably. Thus, it appears that the most important faunal transformation in the Shungura sequence occurred at the base of Member G at around 2.3 Ma.

One way to interpret the results obtained above is to look at the distribution of taxa used in the analysis. Fig. 10 shows the column profiles (taxa) used for this same analysis. The taxa on the right side are more open environment dwellers compared to the ones on the left. Comparing pairs of related taxa further supports this interpretation. *Deinotherium* vs. *Elephas*, *Notochoerus* vs. *Metridiochoerus* and *Kolpochoerus*, *Hipparion* vs. *Equus* and *Australopithecus* vs. *Homo*, represent, in gen-

eral, wooded habitat and grassland dwelling taxa respectively (Coppens, 1975a,b; Cooke, 1976; Eck, 1976; Wesselman, 1984; Gentry, 1985a,b; Beden, 1985, 1987; Eisenmann, 1985; Guérin, 1985; Bobe and Eck, 2001). Interpreting bovid tribes in this analysis is more complicated than for other groups. In the univariate studies above, the abundance of most bovid tribes increases in Member G. In other words, lower Member G is dominated by bovinds and other grassland dwelling taxa. Among bovinds, reduncines account for 59% followed by tragelaphines (21%) and *Aepyceros* (16%). The prevalence of reduncines points to the dominance of edaphic grassland. The relative abundance of grassland dwelling, non-bovid taxa as compared to their more wooded environment relatives (i.e., *Deinotherium* vs. *Elephas*, *Notochoerus* vs. *Metridiochoerus* and *Kolpochoerus*, *Hipparion* vs. *Equus* and *Australopithecus* vs. *Homo*) shows that

Table 8

Abundance (number of specimens) of taxa in localities of the Shungura Formation.

Unit	Locality	<i>Aepyceros</i>	<i>Alcelaphini</i>	<i>Reduncini</i>	<i>Tragelaphini</i>	<i>Bovini</i>	<i>Theropithecus</i>	<i>Papio</i>	<i>Hippartion</i>	<i>Equus</i>	<i>Deinotherium</i>	<i>Giraffa</i>	<i>Elephas</i>	<i>Australopithecus</i>	<i>Homo</i>	<i>Colobus</i>	<i>Hexaprotodon</i>	<i>Kolpochoerus</i>	<i>Notochoerus</i>	<i>Metridiochoerus</i>
KAL(-L9)	K7	28	31	20	1	0	2	2	4	21	0	5	6	0	1	0	0	34	0	4
KAL(L)	K6	1	1	0	0	0	0	0	14	8	3	1	0	0	0	0	0	6	1	0
KAL(K or L)	K10	0	0	0	3	1	0	0	1	0	19	1	2	0	0	0	74	6	2	0
KAL(G-H)	K5	0	0	1	0	0	0	0	0	0	0	0	2	0	0	0	0	5	0	0
H4-H7	OMO74	4	1	105	1	0	1	0	0	2	2	0	1	1	0	0	8	27	3	0
G28&29	OMO100	27	4	31	11	1	2	1	0	0	0	1	1	0	0	2	24	3	6	6
G28&29	OMO2	0	5	1	0	0	0	0	0	2	0	0	1	0	0	0	2	0	0	0
G27&28	OMO78	9	5	37	7	1	0	0	1	5	0	1	0	0	0	1	11	16	12	0
G27&G28	OYE.0	2	6	7	0	0	0	0	2	6	0	0	0	0	0	0	1	0	0	0
G27&G24	OMO214	3	0	11	2	0	0	1	3	8	0	0	0	0	0	0	7	0	0	1
G12-G13	OMO55	27	1	41	26	1	5	3	0	0	1	10	0	0	0	1	32	6	3	7
G12&G13	OMO280	5	0	22	1	9	3	0	0	0	2	13	7	0	0	0	11	0	3	0
G3-G13	OMO50	14	0	58	16	1	12	1	2	4	5	5	1	0	0	0	47	12	9	4
G8,G9&G12	OMO184	16	0	23	22	1	8	0	1	0	0	2	0	0	0	2	7	18	1	3
G3-G13	OMOSH1	19	0	65	39	4	18	1	0	0	0	30	0	0	1	0	38	16	25	0
G1-G13	OMO93	9	0	31	7	0	12	0	0	0	1	2	0	0	0	0	20	7	1	0
G12	OMO48	23	1	49	29	0	16	1	0	0	0	5	1	0	0	1	27	19	1	2
G11	OMO113	0	0	18	0	0	1	0	0	2	0	0	0	0	0	0	0	0	0	0
G8	OMO47	29	5	330	115	10	41	5	4	2	1	53	1	2	2	5	267	96	17	26
G8	OMO323	3	0	67	2	2	0	0	0	0	0	2	0	2	2	0	0	0	0	0
G7 or G8	OMO195	3	1	21	5	0	1	0	0	2	1	4	0	1	0	4	23	10	4	2
G7	OMO222	3	0	13	6	1	1	0	0	0	0	7	1	0	2	0	11	1	2	1
G7-G8	OMO290	4	0	10	0	0	0	0	0	0	0	2	0	0	0	0	3	3	4	1
G6 & G8	OMO244	20	1	5	4	1	3	0	0	0	0	1	0	0	0	0	4	6	1	4
G6&G8	OMO309	3	0	39	0	0	1	0	0	0	0	0	0	0	0	0	0	3	0	1
G5-G8	OMOSH2	3	1	15	9	1	1	0	0	0	0	5	3	0	0	0	0	0	0	0
G4 or G5	OMO1B	5	0	10	15	3	1	0	0	1	7	1	4	0	0	0	31	15	4	6
G4	OMO203	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	5	0	1	0
G4	OMO25	2	1	7	4	1	1	0	0	1	0	1	3	0	0	0	4	3	0	0
G3	OMO210	2	7	3	2	2	2	1	0	0	0	1	0	0	0	0	5	0	2	0
G1-G13	OMO75	49	7	241	89	10	66	0	9	22	11	30	25	0	10	3	251	45	38	19
G3-G8	OMO75I	6	1	28	5	0	11	1	1	1	0	4	3	0	1	0	22	1	3	3
G12 & G13	OMO75N	40	0	75	28	1	30	1	0	0	0	18	0	0	1	80	16	10	6	
G1-G13	OMO75S	35	2	184	48	2	27	5	1	3	0	10	23	1	1	1	87	34	18	11
G1-G5	OMO29	113	18	205	97	2	33	3	5	2	7	15	10	0	1	3	156	20	22	12
G3 & G6	OMO230	3	0	4	5	0	1	0	0	0	0	0	0	0	0	0	6	1	1	0
G3	OMO141	1	2	5	2	0	12	0	0	0	0	0	0	2	0	3	7	3	5	0
G1	OMO35	15	3	7	13	4	26	0	12	3	0	2	3	6	0	0	13	3	1	0
G(BASE)	OMO6	1	1	3	3	1	2	0	0	0	0	0	3	0	0	0	3	0	0	0

Table 8 (continued)

Unit	Locality	<i>Aepyceros</i>	<i>Alcelaphini</i>	<i>Reduncini</i>	<i>Tragelaphini</i>	<i>Bovini</i>	<i>Theropithecus</i>	<i>Papio</i>	<i>Hipparion</i>	<i>Equus</i>	<i>Deinotherium</i>	<i>Giraffa</i>	<i>Elephas</i>	<i>Australopithecus</i>	<i>Homo</i>	<i>Colobus</i>	<i>Hexaprotodon</i>	<i>Kolpochoerus</i>	<i>Notochoerus</i>	<i>Metrictchoerus</i>
F	OMO1C	0	1	5	3	0	2	0	0	0	4	5	0	0	0	0	0	0	0	0
F	OMO42,	3	1	2	12	1	9	2	1	0	0	2	1	0	0	1	25	1	9	0
F2-F3	OMO1E	0	0	1	2	0	1	5	1	0	0	1	1	0	0	0	1	0	0	0
F1-F3	OMO76	14	13	22	20	12	18	5	20	0	0	5	2	3	0	0	52	21	31	13
F1-F3	OMO199	1	0	4	1	1	5	6	0	0	0	0	0	0	0	0	7	1	2	0
F1	OMO167	2	0	0	1	0	3	1	0	0	0	0	0	0	0	0	0	0	0	0
F(BASE)	OMO129	4	0	12	2	1	1	0	1	0	0	1	2	0	0	0	11	1	2	2
E5-F1	OMO58	6	2	8	7	3	8	2	0	0	1	16	2	0	0	0	11	6	4	0
E3-F1	OMO57	10	2	22	26	6	16	5	1	0	2	17	3	4	1	5	97	10	5	0
E	OMO4	3	0	2	2	1	4	0	0	0	0	2	1	0	1	0	12	4	4	0
E3	OMO151	1	0	4	4	0	14	0	0	0	0	3	3	0	0	0	19	2	4	0
E3	OMO207	0	0	3	4	0	2	1	0	0	0	6	0	0	0	0	24	2	0	0
E1	OMO71	9	0	8	12	2	8	0	5	0	4	8	5	0	0	2	34	42	5	0
E1	OMO44	1	0	0	8	1	11	0	1	0	0	6	1	1	1	0	15	15	4	2
D5	OMO9	2	0	3	0	0	1	1	2	0	0	4	0	0	0	0	0	0	7	0
D3	OMO175	0	0	1	2	0	3	1	0	0	0	2	2	0	0	0	4	2	0	0
C or E	OMO84	7	2	5	4	3	14	1	2	0	2	1	1	1	0	1	15	4	2	2
C8	OMO18	31	1	36	29	14	211	0	18	0	6	30	9	9	0	8	89	30	7	0
C8	OMO239	0	1	4	2	0	6	0	0	0	0	1	0	0	0	0	11	2	0	0
C5-C9	OMO52	0	0	0	0	0	6	0	0	0	0	1	3	0	0	0	1	0	0	0
C4-C8	OMO154	10	0	4	4	2	33	0	1	0	3	7	0	0	0	0	71	8	1	0
C4-C9	OMO40	1	0	0	6	1	28	0	4	0	1	10	9	0	0	7	83	11	5	1
C6	OMO132	3	0	1	0	5	28	0	0	0	0	2	0	0	0	1	7	1	4	0
C9&C5	OMO53	7	1	6	3	2	15	1	1	0	0	3	2	0	0	3	29	8	4	1
B12	OMO3-0	12	1	3	4	2	14	5	1	0	0	2	3	0	0	1	15	1	7	0
B-10	OMO212	0	0	0	2	0	6	4	0	0	4	2	0	2	0	0	8	1	9	2
B10	OMO41	3	0	5	4	3	14	4	6	0	1	5	1	0	0	0	24	6	21	3
B-10	OMO28	24	3	89	9	26	118	3	4	0	7	34	12	2	0	15	29	6	42	1
A-B	OMO20-1	0	0	0	2	0	6	0	0	0	4	2	0	2	0	0	8	1	9	2
B-10	OMO112	1	0	0	5	2	4	0	2	0	0	1	0	0	0	6	19	3	33	0
A3-A4	OMO81	2	0	0	6	3	3	0	3	0	0	2	0	0	0	6	22	4	47	0
A-1	OMO127	0	0	0	0	0	0	0	1	0	2	0	0	0	0	0	43	3	5	0
B-2	OMO229	20	0	56	7	19	59	1	0	0	5	25	0	0	0	13	20	5	32	0
A-3	OMO128								0	0	0	49	0	0	0	11	17	2	28	0

Columns and rows are mammalian taxa and localities (or group of localities) respectively. The number of rows is low compared to the 600 localities established by the French contingent. The difference is due to, first many localities have yielded only few specimens and thus could not be considered for these types of studies. Secondly, some localities that yielded small numbers of fossils but fit into the same stratigraphic level and geographic location were grouped. Chi-square distance on data=8092.9901 ~df=1008, Corresponding probability: 0.0001, Limit Chi2 for the chosen confidence range=1082.9731. Hypothesis of independence rejected based on this test.

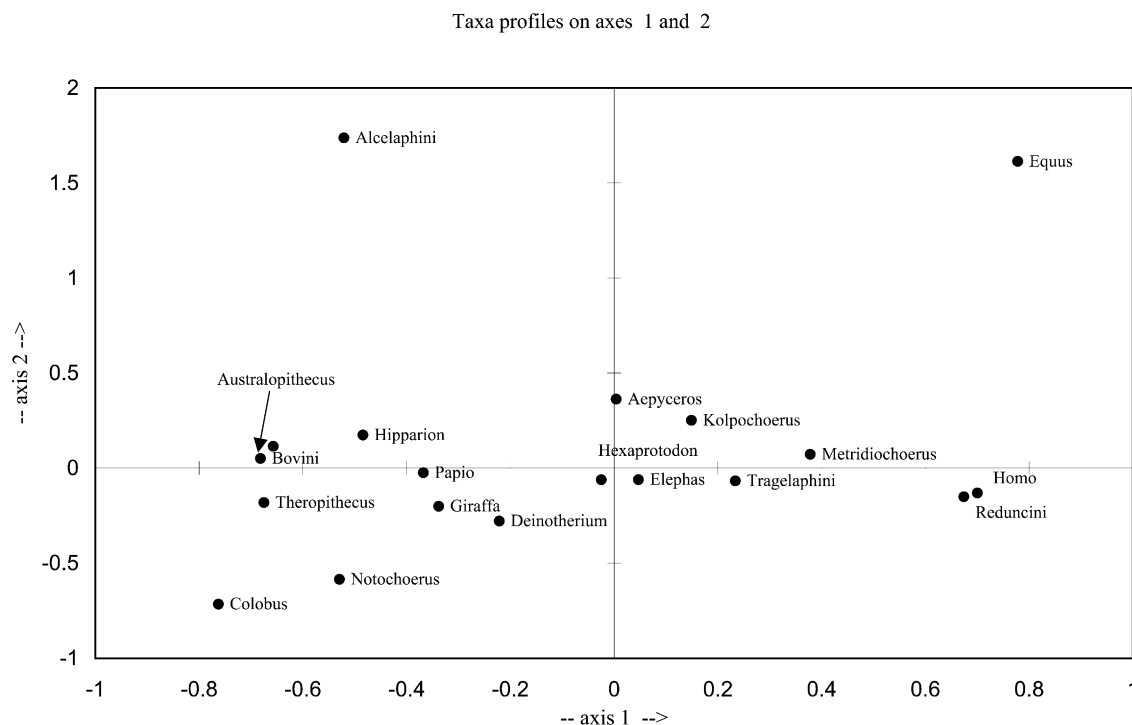


Fig. 10. Correspondence analysis showing taxa profiles on axes 1 and 2. This is the same analysis as in Fig. 9, but depicts the column profiles. See text for explanation.

19 mammalian taxa points to a major biotic change in the region corresponding with the base of Member G, dated to ca. 2.3 Ma. This transformation is characterized by a change to open and edaphic grassland as the dominant type of environment. This change, however, is to be considered in terms of relative abundance between taxa, and not necessarily in terms of evolutionary changes (speciation and extinction) and migration, though these factors, no doubt, contributed to it. In other words, the Shungura fauna which was characterized by “earlier taxa” before 2.3 Ma was *dominated* but not replaced by the “latter ones” (Figs. 9 and 10). This major regional faunal change correlates in time with the appearance of *Australopithecus boisei*. It is tentatively suggested that this major biome change is associated with the anagenetic speciation in the *A. aethiopicus*–*A. boisei* lineage. But as the present study deals only with the Shungura Formation, this remains to be supported by data from other

sites of similar age where the two taxa are encountered.

Several researchers have indicated the presence of a well-developed forest and humid and warm climate in East Africa during the Miocene (Yemane et al., 1985; Burckle, 1995). In contrast, the Pleistocene is characterized by open and dry savanna with marked seasonality, at least in East Africa (Cooke, 1978, 1985; Feibel et al., 1991; Cerling, 1992; Bonnefille, 1995; Potts, 1998). The Pliocene is regarded as a transitional period in which contrasting climatic oscillations are inferred (Burckle, 1995; deMenocal, 1995; deMenocal and Bloemendal, 1995). Furthermore, Shackelton et al. (1984) showed that early Pliocene was hot; the temperature then decreased considerably and attained its minimum around 2.5 Ma. deMenocal and Bloemendal (1995) also showed, based on marine sediments, that the climate during the Plio-Pleistocene oscillated between humid and dry conditions.

Various studies on the Shungura sequence indicate the presence of forest, gallery forest, montane forest, woodland, scrub (thickets), wooded grassland or open grassland at one time or the other. Data used in the present study also indicate the existence of at least two of the above cited environments at any given time, between 3.6 and 1.16 Ma, in Shungura. These conclusions are in agreement with data obtained by Jaeger and Wesselman (1976), Wesselman (1984, 1995) and Boaz, (1977). In addition, palynological data from older Members of the Shungura Formation support this conclusion in general (see Fig. 1c).

Both univariate and multivariate approaches in the present study point to changes in faunal composition between 3 and 2 Ma in the Shungura Formation. Even if this has been suggested previously, modalities and interpretations of these changes differ. These differences do not relate only to the Shungura Formation, but also to other East African Plio-Pleistocene sites (Vrba, 1988, 1995; Behrensmeyer et al., 1997; Feibel et al., 1991; Bobe and Eck, 2001). Results of the present study are in agreement with those obtained by Behrensmeyer et al. (1997) in that there is a continuous environmental and faunal change between 3.0 and 1.8 Ma. Moreover, the proposed gradual faunal change between 3 and 2 Ma put forward by Bobe and Eck (2001) is supported by this work, but no rapid change is observed between 2.9–2.7 Ma. Changes are also observed in the present study around this time period. That is, in the transition from stratigraphic levels AB to CD there is a decrease in precipitation (Table 2) as inferred from the univariate studies conducted above. However, based on results of the correspondence analysis, where isotaphonomy can be justified (Fig. 9), this does not represent the most important change in the sequence. Bobe and Eck (2001) used similar data, from the same Formation, based on collections made by the American contingent. In their studies, patterns of faunal change were analyzed by considering localities of the same geologic member as a variable. Instead, in the present study, each locality is assumed to sample a given type of habitat, and is considered as a unit. That allows one to see clusters of localities grouped as a

function of their taxonomic composition. Another source of differences could be that in the present study bovids, suids and cercopithecids were used and that postcranial elements were not included in the multivariate analysis for taphonomic reasons. A future joint project will compare the French and American data sets to examine any differences introduced by collecting biases.

Results of the present study can be used to examine some aspects of Vrba's turnover pulse hypothesis (Vrba, 1988, 1995), which hypothesizes that the 2.7 to 2.5 Ma interval was characterized by rapid faunal change. According to the univariate analyses of the present study (Table 2), the Shungura fauna documents important environmental changes towards more dry and relatively less wooded habitats around Member C. This does not, however, represent the most important change in the Shungura sequence, which occurs after 2.5 Ma based on the results of the correspondence analysis described in this study. It is worth noting that White (1995), Kimbel (1995) and Frost (2002), who used suids, hominids and cercopithecids respectively to study FADs and LADs, did not find any unique increase in FADs and LADs at around 2.5 Ma. Behrensmeyer et al. (1997) indicated that, although their data show significant species turnover occurred during the 3.0–1.8 Ma interval, there is no marked pulse affecting different groups between 2.8 and 2.5 Ma. These authors added that the biggest turnover was found at around 1.8 Ma. It should be noted, however, as pointed out by Bobe and Eck (2001), Vrba (1988, 1995) and Behrensmeyer et al. (1997) focus on evolutionary changes that include speciation, extinction and migration (Vrba, 1995), i.e., FADs and LADs (turnover), which provides a different level of analysis of faunal change compared with the abundance data used in the present study. I concur with Bobe and Eck (2001) in that "changes in relative abundance are likely to be more sensitive to environmental and climatic signals than speciation and extinction events. Climatic changes may affect the fauna in ways that do not necessarily lead to speciation and extinction". A change in the preferred habitat of a given species may change its relative abundance, but not necessarily lead to its extinction.

The above discussion shows that there is no consensus on the date of the major faunal turnover. This may be due to our inability to distinguish biological signals from taphonomic ones, or it could be attributable to other problems with the data. It is well known that taphonomic biases affect paleontological data in general and FADs and LADs in particular (e.g., Behrensmeyer, 1975; Hill, 1987; Kimbel, 1995; White, 1995; Behrensmeyer et al., 2000). Variable treatments of different taxonomic groups could also result in different signals (Hill, 1987, Vrba, 1988, 1995; Kimbel, 1995; Vrba, 1995; White, 1995; Behrensmeyer et al., 1997). In addition, data that come from different sites could result in different faunal change patterns owing to their unique taphonomic history and probable differences in local paleoenvironment. Nonetheless, as is the case in the present study, several researchers have shown that major faunal changes postdate 2.5 Ma (e.g., Kimbel, 1995; Geraads and Coppens, 1995; Behrensmeyer et al., 1997).

4.1. Habitat preferences of Shungura hominids

Four hominid species have been identified in the Shungura Formation: *Australopithecus* sp., *Australopithecus aethiopicus*, *Australopithecus boisei* and *Homo* sp. The first is encountered mainly in Member B. This part of the sequence is dominated by wet and relatively closed habitats and open habitats are rare. Remains of *A. aethiopicus* were collected from Members C through G (Suwa et al., 1996). The associated fauna indicates that it lived in similar habitat as *Theropithecus brumpti*, which is considered a gallery forest species (e.g., Leakey 1993). The habitat preference of *A. boisei* in Shungura was reconstructed by Alemseged (1998b) based on the fossil assemblage from locality Omo-323 of unit G-8 Shungura Formation from which a fragmentary cranium of *A. boisei* (Omo-323-1976-896) was recovered (Alemseged et al., 2002). In these levels, *A. boisei* was associated with taxa that lived in edaphic grassland, particularly the reduncine *Menelikia lyrocera*. This is in agreement with Reed's habitat reconstruction of this species (Reed, 1997). Suwa (1988), Suwa et al. (1996), Wood et al. (1994) showed the presence of important morphological changes within the East

African robust australopithecine lineage around 2.3 Ma. This coincides in time and space with the major environmental transformation that took place in the Shungura sequence, as documented in the present study. It has also been shown that *A. aethiopicus* lived in habitats that are more forested than that of *A. boisei*, probably gallery forests, at least, in East Africa (see above). It is suggested here, therefore, that environmental change discerned in the present study is associated with the appearance of *A. boisei*. As edaphic grasslands became more prevalent in the lower Member G, *A. boisei* seems (or at least correlates in time) to be the result of an adaptation to the new environmental context. However, this hypothesis needs to be examined in light of data that are derived from other sites of comparable age, before a regional conclusion can be reached.

Acknowledgements

I would like to thank Denis Geraads, Rene Bobe, Kaye Behrensmeyer and Kaye Reed for comments on an earlier version of this paper. I also thank Terry Harrison and two anonymous reviewers for their comments and suggestions.

References

- Alemseged, Z., 1998a. L'Hominidé Omo-323: sa position phylétique et son environnement dans le cadre de l'évolution des communautés de mammifères du Plio-Pleistocène dans la basse vallée de l'Omo (Ethiopie). Ph.D. dissertation, Museum National d'Histoire Naturelle, Paris.
- Alemseged, Z., 1998b. On the habitat preference of *Australopithecus boisei*. Dual Congress, Johannesburg, South Africa.
- Alemseged, Z., Coppens, Y., Geraads, D., 2002. A hominid cranium from Omo description and taxonomy of Omo-323-1976-896. *Am. J. Phys. Anthropol.* 117, 103–112.
- Arambourg, C., Coppens, Y., 1967. Sur la découverte dans le Pléistocène inférieur de la vallée de l'Omo (Ethiopie) d'une mandibule d'australopithecien. *C. R. Acad. Sci., Paris* 265, 589–590.
- Arambourg, C., Coppens, Y., 1968. Découverte d'un australopithecien nouveau dans les gisements de l'Omo (Ethiopie). *S. Afr. J. Sci.* 64, 58–59.
- Beden, M., 1985. Les Proboscidiens des grands gisements à Hominidés Plio-Pleistocène d'Afrique orientale. Fondation Singer-Polignac, Paris, pp. 21–44.

- Beden, M., 1987. Données préliminaires à l'étude des Elephantidés de l'Omo, in: Coppens, Y., Howell, F.C. (Eds.), *Les faunes Plio-Pléistocènes de la basse vallée de l'Omo (Ethiopie)*. 2. CNRS, Paris.
- Behrensmeyer, A.K., 1975. The taphonomy and paleoecology of Plio-Pleistocene vertebrate assemblages east of the Lake Rudolf, Kenya. *Bull. Mus. Comp. Zool. Harvard* 146, 473–578.
- Behrensmeyer, A.K., 1993. The bones of Amboseli: The taphonomic record of ecological change in Amboseli Park, Kenya. *Nat. Geogr. Res. Expl.* 9, 402–421.
- Behrensmeyer, A.K., Kidwell, S.M., Gastaldo, R.A., 2000. Taphonomy and paleobiology. *Paleobiology* 26(Supplement), 103–144.
- Behrensmeyer, A.K., 1982. Time resolution in fluvial vertebrate assemblages. *Paleobiology* 8, 211–227.
- Behrensmeyer, A.K., 1988. Vertebrate preservation in fluvial channels. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 63, 183–199.
- Behrensmeyer, A.K., Dechant-Boaz, D., 1980. The recent bones of Amboseli National Park, Kenya, in relation to East African paleoecology, in: Behrensmeyer, A.K., Hill, A.P. (Eds.), *Fossils in the Making: Vertebrate Taphonomy and Paleoecology*. University of Chicago Press, Chicago, pp. 72–92.
- Behrensmeyer, A.K., Todd, N.E., Potts, R., McBrinn, G.E., 1997. Late Pliocene faunal turnover in the Turkana Basin, Kenya. *Science* 278, 1589–1594.
- Benzecri, 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.
- Bobé, R., Eck, G.G., 2001. Response of African bovids to Pliocene climatic change. *Paleobiology* 27(Supplement to No. 2, *Paleobiology Memoirs* 2), 1–47.
- Bobé, R., Behrensmeyer, A.K., Chapman, R.E., 2002. Faunal change, environmental variability and Late Pliocene hominin evolution. *J. Hum. Evol.* 42, 475–497.
- Bonnefille, R., Dechamps, R., 1983. Data on fossil flora, in: de Heinzelin (Ed.), *The Omo Group. Archives of the International Omo Research Expedition*. 85. *Ann. Sci. Géol. Musée Royal de l'Afrique Centrale Tervuren, Tervuren*, pp. 191–207.
- Bonnefille, R., Vincens, A., 1985. Apport de la palynologie à l'environnement des Hominidés d'Afrique orientale. L'environnement des hominidés au Plio-Pléistocène. *Fondation Singer-Polignac, Paris*, pp. 237–278.
- Bonnefille, R., 1995. A reassessment of the Plio-Pleistocene pollen record of East Africa, in: Vrba, E.S., Denton, G.H., Partridge, T.C., Burkle, L.H. (Eds.), *Paleoclimate and Evolution*. Yale University Press, New Haven, pp. 299–310.
- Brown, F.H., de Heinzelin, J., 1983. The Lower Omo Basin. *Archives of the International Omo Research Expedition*, in: de Heinzelin, J. (Ed.), *The Omo Group. Ann. Sci. Géol. Musée Royal de l'Afrique Centrale, Tervuren*, pp. 7–24.
- Burkle, L.H., 1995. Current issues in Pliocene paleoclimatology, in: Vrba, E.S., Denton, G.H., Partridge, T.C., Burkle, L.H. (Eds.), *Paleoclimate and Evolution, with Emphasis on Human Origins*. Yale University Press, New Haven, pp. 3–7.
- de Bourg de Bozas, 1903. D'Addis Ababa au Nil par le lac Rodolphe. *La géographie*, 91–112.
- Cerling, T.E., 1992. Development of grasslands and savannas in East Africa during the Neogene. *Paleogeogr. Paleoclimatol. Paleoecon.* 97, 241–247.
- Cooke, H.B.S., 1976. Suidae from Plio-Pleistocene strata of the Rudolf Basin, in: Coppens, Y., Howell, F.C., Isaac, G.L., Leakey, R.E. (Eds.), *Earliest Man and Environments in the Lake Rudolf Basin*. University of Chicago Press, Chicago, pp. 251–263.
- Cooke, H.B.S., 1978. Plio-Pleistocene Suidae from Hadar, Ethiopia. *Kirtlandia* 29, 1–63.
- Cooke, H.B.S., 1985. Plio-Pleistocene Suidae in relation to African hominid deposits. L'environnement des hominidés au Plio-Pléistocène. *Fondation Singer-Polignac, Paris*, pp. 101–117.
- Coppens, Y., 1975a. Evolution des Mammifères, de leurs fréquence et de leurs associations, au cours du Plio-Pléistocène dans la basse vallée de l'Omo en Ethiopie. *C.R. Acad. Sci., Paris D* 281, 1571–1574.
- Coppens, Y., 1975b. Evolution des Hominidés et de leurs environnements au cours du Plio-Pléistocène dans la basse vallée de l'Omo en Ethiopie. *C.R. Acad. Sci., Paris D* 281, 1693–1696.
- Coppens, Y., 1976. Introduction, in: Coppens, Y., Howell, F.C., Isaac, G.L., Leakey, R.E. (Eds.), *Earliest Man and Environments in the Lake Rudolf Basin*. University of Chicago Press, Chicago, pp. 173–176.
- de Heinzelin, J., 1983. The Omo group: Archives of the International Omo Research Expedition, in: de Heinzelin, J. (Ed.), *The Omo Group. Ann. Sci. Géol. Musée Royal de l'Afrique Centrale, Tervuren*.
- deMenocal, P.B., 1995. Plio-Pleistocene African climate. *Science* 270, 53–59.
- deMenocal, P.B., Bloemendal, J., 1995. Plio-Pleistocene climatic variability in subtropical Africa and the paleoenvironment of hominid evolution: A combined data model approach, in: Vrba, E.S., Denton, G.H., Partridge, T.C., Burkle, L.H. (Eds.), *Paleoclimate and Evolution with Emphasis on Human Evolution*. Yale University Press, New Haven, pp. 262–288.
- Denton, G.H., 1999. Cenozoic climate change, in: Bromage, T.G., Schrenk, F. (Eds.), *African Biogeography, Climate Change, & Human Evolution*. Oxford University Press, Oxford, pp. 94–114.
- Eck, G.G., 1976. Cercopithecoidae from Omo Group deposits, in: Coppens, Y., Howell, F.C., Isaac, G.L., Leakey, R.E. (Eds.), *Earliest Man and Environments in the Lake Rudolf Basin*. University of Chicago Press, Chicago, pp. 332–344.
- Eisenmann, V., 1985. Les Equidés des gisements de la vallée de l'Omo en Ethiopie, in: Coppens, Y., Howell, F.C. (Eds.), *Les faunes Plio-Pléistocènes de la basse vallée de l'Omo*

- (Ethiopie). Cahiers de Paléontologie, travaux de paléontologie est-africaine. CNRS, Paris, pp. 17–55.
- Feibel, C.S., Brown, F., McDougall, I., 1989. Stratigraphical context of fossil hominids from the Omo Group Deposits: Northern Turkana Basin, Kenya and Ethiopia. *Am. J. Phys. Anthropol.* 78, 623–632.
- Feibel, C.S., Harris, J.M., Brown, F.H., 1991. Paleoenvironmental context for the Late Neogene of the Turkana Basin, in: Harris, J.M. (Ed.), Koobi Fora Research Project, Volume 3. The Fossil Ungulates: Geology, Fossil Artiodactyls, and Paleoenvironments. Clarendon, Oxford, pp. 321–346.
- Frost, S., 2002. East African cercopithecoid fossil record and its relationship to global climatic changes. *Am. J. Phys. Anthropol.* 32(Supplement), 72–73.
- Gentry, A.W., 1985a. The Bovidae of the Omo Group Deposits, Ethiopia, in: Coppens, Y., Howell, F.C. (Eds.), Les faunes Plio-Pléistocènes de la basse vallée de l’Omo (Ethiopie). Cahiers de Paléontologie, travaux de paléontologie est-africaine. CNRS, Paris, pp. 121–191.
- Gentry, A.W., 1985b. Pliocene and Pleistocene Bovidae in Africa. L’environnement des hominidés au Plio-Pleistocène. Fondation Singer-Polignac, Paris, pp. 119–132.
- Geraads, D., Coppens, Y., 1995. Evolution des faunes des mammifères dans le Plio-Pléistocène de la basse vallée de l’Omo (Ethiopie): Apport de l’analyse factorielle. *C.R. Acad. Sci., Paris* 320, 625–637.
- Guérin, C., 1985. Signification paléoécologique des Rhinocerotidae et Chalicotheriidae (Mammalia, Perissodactyla) des gisements à Hominidés du Plio-Pléistocène d’Afrique. L’environnement des hominidés au Plio-Pleistocène. Fondation Singer-Polignac, Paris, pp. 45.
- Greenacre, M.J., Vrba, E.S., 1984. A correspondence analysis of biological census data. *Ecology* 65, 984–997.
- Harris, J.M., Brown, F.H., Leakey, M.G., 1988. Stratigraphy and paleontology of Pliocene and Pleistocene localities west of Lake Turkana, Kenya. *Contributions in Science* 399, 1–128.
- Heesaerts, P., Stoops, G., Van Vliet-Lanoe, B., 1983. Data on sediments and fossil soils, in: de Heinzelin, J. (Ed.), The Omo Group. 85. *Ann. Sci. Géol. Musée Royal de l’Afrique Centrale, Tervuren*, pp. 149–186.
- Hill, A., 1987. Causes of perceived faunal change in the later Neogene of East Africa. *J. Hum. Evol.* 16, 583–596.
- Hill, A.P., 1980. Early postmortem damage to the remains of some contemporary East African mammals, in: Behrensmeyer, A.K., Hill, A.P. (Eds.), Fossils in the Making: Vertebrate Taphonomy and Paleoecology. University of Chicago Press, Chicago, pp. 131–155.
- Howell, F.C., Coppens, Y., 1973. Deciduous teeth of Homiidae from the Plio-Pleistocene of the lower Omo Basin, Ethiopia. *J. Hum. Evol.* 2, 461–472.
- Howell, F.C., Coppens, Y., 1974. Inventory of remains of Homiidae from Plio-Pleistocene formations of the lower Omo Basin, Ethiopia, (1967–1972). *Am. J. Phys. Anthropol.* 40, 1–16.
- Howell, F.C., Coppens, Y., 1976. An overview of Homiidae from the Omo succession, Ethiopia, in: Coppens, Y., Howell, F.C., Isaac, G.L., Leakey, R.E. (Eds.), Earliest Man and Environments in the Lake Rudolf Basin. University of Chicago Press, Chicago, pp. 522–532.
- Howell, F.C., Haesaerts, P., de Heinzelin, J., 1987. Depositional environments, archaeological occurrences and hominids from Member E and F of the Shungura Formation (Omo Basin, Ethiopia). *J. Hum. Evol.* 16, 665–700.
- Jaeger, J.-J., Wesselman, H.B., 1976. Fossil remains of micro-mammals from the Omo Group Deposits, in: Coppens, Y., Howell, F.C., Isaac, G.L., Leakey, R.E. (Eds.), Earliest Man and Environments in the Lake Rudolf Basin. University of Chicago Press, Chicago, pp. 351–360.
- Kennett, J.P., 1995. A review of polar climatic evolution during the Neogene, based on the marine sediment record, in: Vrba, E.S., Denton, G.H., Partridge, T.C., Burkle, L.H. (Eds.), Paleoclimate and Evolution, with Emphasis on Human Origins. Yale University Press, New Haven, pp. 49–64.
- Kimbel, W.H., 1995. Hominid speciation and Pliocene climatic change, in: Vrba, E.S., Denton, G.H., Partridge, T.C., Burkle, L.H. (Eds.), Paleoclimate and Evolution, with Emphasis on Human Origins. Yale University Press, New Haven, pp. 425–437.
- Leakey, M.G., Leakey, R.E., 1978. The fossil hominids and an introduction to their context, 1968–1974. Koobi Fora Research Project. Clarendon Press, Oxford.
- Leakey, R.E., 1976. New Hominid fossils from the Koobi Fora Formation in northern Kenya. *Nature* 261, 574–576.
- Ludwig, A.J., Reynolds, J.F., 1988. *Statistical Ecology: A Premier on Methods and Computing*. Wiley, New York.
- Potts, R., 1998. Environmental hypotheses of human evolution. *Yrbk. Phys. Anthropol.* 41, 93–136.
- Reed, K.E., 1997. Early hominid evolution and ecological change through the African Plio-Pleistocene. *J. Hum. Evol.* 32, 289–322.
- Shackleton, N.J., Backman, J., Zimmerman, H., Kent, D.V., Hall, M.A., Roberts, D.C., Schnitker, D., Baldauf, J.G., Keltenback, A.J., Krumsiek, K.A., Morton, A.C., Murry, J.W., Westberg-Smith, J., 1984. Oxygen isotope calibration of the onset of ice rafting and history of glaciation in the North Atlantic region. *Nature* 307, 620–623.
- Shackleton, N.J., 1995. New data on the evolution of Pliocene climatic variability, in: Vrba, E.S., Denton, G.H., Partridge, T.C., Burkle, L.H. (Eds.), Paleoclimate and Evolution, with Emphasis on Human Origins. Yale University Press, New Haven, pp. 242–248.
- Shipman, P., Harris, J., 1988. Habitat preference and paleoecology of *Australopithecus boisei* in Eastern Africa, in: Grine, F. (Ed.), Evolutionary History of the “Robust” Australopithecines. De Gruyter, New York, pp. 343–381.
- Suwa, G., 1988. Evolution of the “Robust” australopithecine in the Omo succession: evidence from mandibular premolar morphology, in: Grine, F. (Ed.), Evolutionary History of the “Robust” Australopithecines. De Gruyter, New York, pp. 199–222.
- Suwa, G., 1990. A comparative analysis of hominid dental remains from the Shungura and Usno Formations,

- Omo Valley, Ethiopia. Ph.D. Dissertation, University of California, Berkeley.
- Suwa, G., White, T.D., Howell, F.C., 1996. Mandibular post-canine dentition from the Shungura Formation, Ethiopia: crown morphology, taxonomic allocation, and Plio-Pleistocene hominid evolution. *Am. J. Phys. Anthropol.* 101, 247–282.
- Voorhies, M.R., 1969. Taphonomy and population dynamics of an early Pliocene vertebrate fauna, Knox County, Nebraska. *Contrib. Geol., Univ. Wyoming Spec. Pap.* 1, 1–69.
- Vrba, E.S., 1980. The significance of bovid remains as indicators of environment and predation patterns, in: Behrensmeyer, A.K., Hill, A.P. (Eds.), *Fossils in the Making: Vertebrate Taphonomy and Paleoecology*. University of Chicago Press, Chicago.
- Vrba, E.S., 1988. Late Pliocene climatic events and hominid evolution, in: Grine, F. (Ed.), *Evolutionary History of the “Robust” Australopithecines*. De Gruyter, New York, pp. 405–426.
- Vrba, E.S., 1995. The fossil record of African Antelopes (Mammalia, Bovidae) in relation to human evolution and paleoclimate, in: Vrba, E.S., Denton, G.H., Partridge, T.C., Burkle, L.H. (Eds.), *Paleoclimate and Evolution, with Emphasis on Human Origins*. Yale University Press, New Haven, pp. 385–424.
- Vrba, E.S., 2000. Major features of Neogene mammalian evolution in Africa, in: Partridge, T.C., Maud, R.R. (Eds.), *The Cenozoic of Southern Africa*. Oxford University Press, Oxford, pp. 277–304.
- Wesselman, H.B., 1984. The Omo micromammals: systematics and paleology of early man sites from Ethiopia. *Contrib. Vert. Evol.* 7, 1–219.
- Wesselman, H.B., 1995. Of Mice and Almost-Men: Regional Paleoecology and Human Evolution in the Turkan Basin, in: Vrba, E.S., Denton, G.H., Partridge, T.C., Burkle, L.H. (Eds.), *Paleoclimate and Evolution, with Emphasis on Human Origins*. Yale University Press, New Haven, pp. 356–368.
- White, T.D., 1995. African Omnivores: Global climatic change and Plio-Pleistocene hominids and suids, in: Vrba, E.S., Denton, G.H., Partridge, T.C., Burkle, L.H. (Eds.), *Paleoclimate and Evolution, with Emphasis on Human Origins*. Yale University Press, New Haven, pp. 369–384.
- Wood, B.A., Wood, C., Konigsberg, L., 1994. *Paranthropus boisei*: an example of evolutionary stasis? *Am. J. Phys. Anthropol.* 95, 117–136.
- Yemane, K., Bonnefille, R., Faure, H., 1985. Paleoclimatic and tectonic implications of Neogene microflora from the north-western Ethiopian Highlands. *Nature* 318, 653–656.