7. Comparability of fossil data and its significance for the interpretation of hominin environments

A case study in the lower Omo Valley, Ethiopia

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Abstract

Unraveling the context in which the evolution and diversification of early hominins occurred has become one of the core and highly debated subjects in paleoanthropology. Over the past three decades substantial progress has been made due to the proliferation of fieldwork and a consequently expanding fossil record, and development of new methods of analysis. The present study uses data of fossil mammals from the Shungura Formation of Ethiopia, with specimens collected semi-independently by French and American research teams who worked in the southern and northern parts of the Shungura area respectively. We compare these two samples in terms of collection methods, taxonomy, taphonomy, and local environmental differences. The following results were obtained: (1) No major taphonomic differences were observed between the two collections. The effect of a major taphonomic shift that occurred in the middle of Member G (G-13) is observed in both samples and is caused by the important change in the depositional environment from fluvial to lacustrine conditions. (2) The French team collected more specimens than the American team, in part because it had a larger area of exposures, and it spent two extra seasons in the field. Additionally, the French team collected more large-sized taxa including their postcranial elements, while the American team recovered a restricted set of postcranial bones. In contrast, the American team collected more primates and carnivores than the French team. (3) Despite these differences, comparable taxonomic composition and number of species are observed in both collections. (4) A study of changes in relative abundance in bovid tribes indicates that similar patterns of variation through time are observed in both samples. This is considered to be evidence for the prevalence of generally similar habitats (and habitat change through time) in the north and

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south of the Shungura area. (5) However, habitat differences may have occurred locally, as inferred by differences in taxonomic abundances at the species level. For example, the bovid *Menelikia lyrocera* was more common in the southern parts of the Shungura exposures, while *Kobus sigmoidalis* was more common in the north. (6) Finally, the present study underscores the importance of the quality of data in unraveling past environments and patterns of faunal changes through time. Well-controlled and standardized collecting methods and systematic documentation procedures are critical for future fieldwork activities. This will improve the quality of our data, facilitate comparisons across regions, and lead to more robust hypotheses.

Introduction

Our understanding of the origin, diversification, and evolution of early hominins is tightly linked to our knowledge of the paleoenvironments in which these processes took place. Over the last few decades, increasing attention has been paid to the environmental context of human evolution. New hypotheses have been proposed, and novel approaches developed for paleoenvironmental research. Some of these approaches rely on the hominin fossils themselves. The functional anatomy of postcranial elements may be used to provide information about locomotion and therefore about substrate (Senut, 1980; Senut and Tardieu, 1985; Susman and Stern, 1991; Stern, 2000; Ward, 2002). However, our understanding of the adaptive significance of anatomical characters is limited. The hominin fossil record has also been used to elucidate evolutionary patterns and possible links to climatic and environmental change (e.g., Vrba, 1988), but the rarity and discontinuity of this record make potential links between evolutionary patterns and broader climatic factors highly problematic (e.g., White, 1995; Behrensmeyer et al., 1997). Other approaches used to investigate the paleoenvironments and paleoecology of Plio-Pleistocene hominins in Africa include the analysis of fossil pollen, the study of paleosols and their isotopic composition, and the analysis of vertebrate remains that are commonly encountered in the fossil record. In the study of fossil vertebrates, the most common methods rely on faunal composition and taxonomic abundance data to derive paleoenvironmental information from hominin localities (e.g., Coppens, 1975; Geraads and Coppens, 1995; Bobe and Eck, 2001; Bobe et al., 2002; Alemseged, 2003; Suwa et al., 2003). Other approaches rely on ecomorphology or on the analysis of ecological community structure. Ecomorphology deals with interpreting fossil remains in terms of functional anatomy and its relationship to environmental conditions (e.g., Kappelman, 1988; Spencer, 1997; Bishop, 1999). These approaches have strengths and weaknesses, and whenever possible they should be combined and cross-checked to evaluate the consistency of their respective signals.

One of the better known attempts to tie human evolution to environmental and climatic changes is the “turnover pulse hypothesis” (Vrba, 1988, 1992, 1995, 1999). This idea posits that most if not all speciation and extinction is due to climatic change: the majority of evolution occurs fairly rapidly and is concentrated during periods of dramatic climatic change causing significant pulses of speciation and/or extinction over time. Turnover pulses are concentrations of first and last appearance data (FADs and LADs) of species’ temporal ranges, as shown for bovids (Vrba, 1995), and more recently for cercopithecids (Frost, 2002, 2007) and carnivores (Lewis and Werdelin, 2007). However, calculating the number of FADs and LADs is not as clear-cut as it might appear (e.g., Hill, 1987; White, 1995). In particular, detecting the timing of major biotic changes and potential links to climatic signals derived from other sources, such as marine sediments and stable isotopes (deMenocal, 1995; deMenocal and Bloemendal, 1995; Kennett, 1995; Shackleton, 1995; Denton, 1999), has 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; Alemseged, 2003). For Vrba (1988, 1995, 2000), the major turnover pulse among bovids occurred 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) analyzed various mammalian taxa to suggest that the most important episode of faunal change occurred at around 1.8 Ma. Based on their study on the Shungura fauna, Bobe and Eck (2001) and Bobe et al. (2002) indicate that an episode of significant faunal change occurred at about 2.8 Ma and was followed by an interval of stability from 2.7 to 2.5 Ma. Geraads and Coppens (1995) and Alemseged (2003) on the other hand detected major faunal change at around 2.3 Ma in the Shungura sequence. Finally Frost (2002, 2007) showed that major turnover in monkeys happened at around 3.4 and 2.0 Ma, in broad agreement with the results of Lewis and Werdelin (2006) in their analysis African carnivores.

All studies discussed above have contributed considerably to our understanding of the relationships between mammalian evolution and climate change, and to different aspects of paleoenvironment and paleoecology in the Plio-Pleistocene of Africa. Particularly, the results of these studies have shed light on the role played by environment and climate in shaping the evolution of our own family since ca. 6 Ma. Nonetheless, discrepancies among these studies clearly demonstrate the complexity of the issues. One important aspect of these approaches is that they are all susceptible to the quality and comparability of the data, which depends in turn on how well we control biases introduced by taphonomy, collection strategies, and stratigraphic and provenance uncertainties.

In this study we address the issue of data comparability using information from the well-known Shungura Formation in the southwest of Ethiopia. Our main goal is to explore the differences and similarities of two fossil samples that were collected from comparable sedimentary contexts, time interval, and geographic areas, but by two independent paleontological teams. The large data set from the Shungura Formation, where American and French research teams conducted fieldwork during the 1960s and 1970s, is used for the comparative study. Given that both collections come from the same stratigraphic context and sedimentary basin we expect the two research teams to document similar taphonomic, paleoenvironmental, and paleoecological information.

The Shungura sequence is unrivalled by any hominin bearing Plio-Pleistocene site for its continuity, abundance of fossils, and quality of dating methods used. All these added together make this sequence the best candidate to undertake comparisons in terms of taxonomic abundance, species richness, taphonomic and collecting biases. The fact that there are two independent samples of fossil fauna provides an opportunity to evaluate equivalent fossil assemblages of the same geological age and region.

The Shungura Formation: Background

The Shungura Formation is located in the lower Omo Valley of southwestern Ethiopia, west of the Omo River and north of Lake Turkana (Brown and Heinzelin, 1983) (Figure 1). The composite stratigraphic section of the formation measures nearly 800 m and radiometric ages indicate that it covers the time span from at least 3.6 Ma to about 1 Ma (Feibel et al., 1989) (Figure 2). The sedimentary cycles of the formation are grouped into 12 members (Basal, A, B, C, D, E, F, G, H, J, K, and L), each (except the Basal Member) commencing with a volcanic tuff designated by the same letter. The sequence is typically composed of fluvial sediments, but episodes of lacustrine deposition also occurred, particularly in the Basal Member, upper Member G, and upper Member L (de Heinzelin and Haesaerts, 1983).

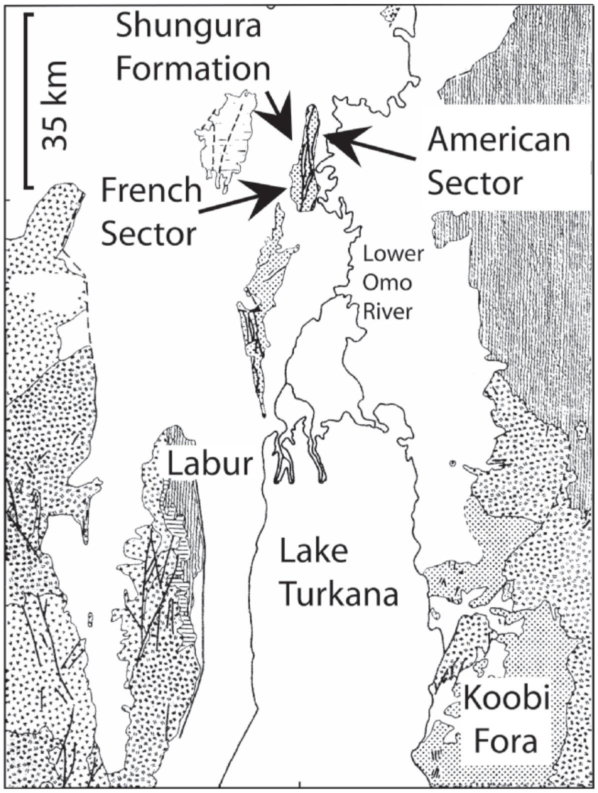

Figure 1. Geographic position and distribution of major rock types in the lower Omo valley and Turkana. (Adapted from de Heinzelin, 1983).

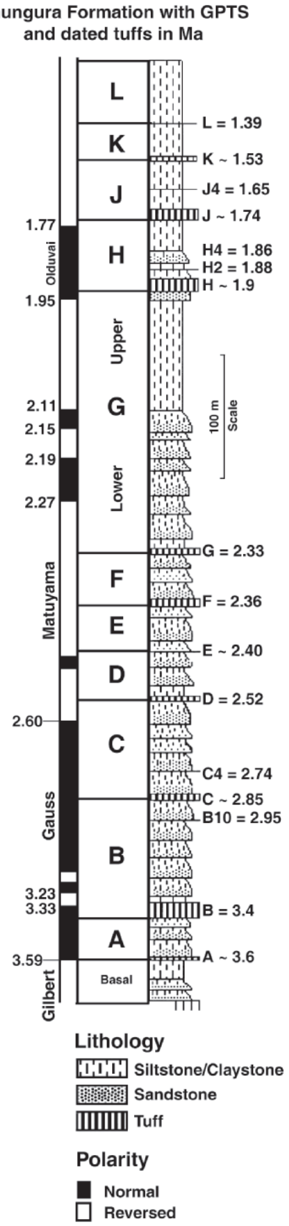

Figure 2. Stratigraphic column of the Shungura Formation (after de Heinzelin, 1983).

The Mission Scientifique de l'Omo, led by C. Arambourg in 1932 and 1933, was the first expedition to conduct systematic paleontological work in the lower Omo Valley (Arambourg and Coppens, 1967; Coppens, 1976). In 1966, the International Omo Research Expedition (IORE) was created under the direction of L.S.B. Leakey, C. Arambourg, and F.C. Howell (Coppens et al., 1976). In 1967, three contingents of the IORE independently explored the sedimentary exposures of the Omo region. The French one, under the direction of C. Arambourg and Y. Coppens, worked principally in the "type area" of the Shungura Formation. The Kenyan contingent, under the direction of R.E.F. Leakey, and the American contingent, under the direction of F.C. Howell, worked farther to the north, the Kenyans in the Kibish and Mursi Formations, and the Americans in the Usno Formation. In 1968, quitting his research in the Mursi and Kibish Formations, Leakey moved to the Koobi Fora area of northern Kenya. Howell on the other hand arranged with Arambourg to move south and jointly explored the type area of the Shungura Formation. The American contingent ceased work in the lower Omo Valley at the end of the 1974 field season, and the French expedition continued until 1976.

In the nine years of fieldwork between 1967 and 1976 (no fieldwork was conducted by either team in 1975), nearly 50,000 paleontological specimens were collected, 21,858 by the Americans and 27,409 by the French. Most of these were recovered during surface survey, but large paleontological excavations were also carried out, producing 6,692 American and 3,417 French specimens (see Johanson et al., 1976).

About 220 hominin specimens were recovered by the two research teams. The oldest hominin remains were recovered from Member B and the Usno Formation. Most specimens are teeth and span the interval from 3.3 to ca.1.0 Ma. There are 21 hominin specimens between 3.3 and 3.0 Ma, 45 between 3.0 and 2.5 Ma, 145 between 2.5 and 2.0 Ma, 3 between 2.0 and 1.5 Ma, and 3 between 1.5 and 1.0 Ma (Suwa, 1990). Among these specimens a "gracile australopithecine" is recognized in Member B of the Shungura Formation and Usno (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). *Australopithecus 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 and Coppens, 1974; Howell et al., 1987; Suwa et al., 1996).

Comparative Studies

DEPOSITIONAL ENVIRONMENTS AND TAPHONOMY

As noted above, nearly all of the richly fossiliferous deposits of the Shungura Formation consist of fluvial sediments laid down by a major river similar in size to the modern Omo River. These sediments consist of sands deposited in the river channel, silts deposited on the banks of the river near the channel, and, silty clays deposited during periods of high water more distal to the channel. The fossil specimens were dominated by elements resistant to damage: jaw fragments and teeth, dense postcranial elements, and bovid horn cores. This is evidence for hydraulic sorting, which is not a surprise in a depositional context characterized by a major river system (Alemseged et al., 1996; Bobe and Eck, 2001; Alemseged, 2003). While it is hard to determine to what extent this differential representation of diverse skeletal elements affects the resulting fossil taxonomic composition in the Shungura Formation, it is possible to use differences in relative abundance of skeletal elements between the two collections to evaluate some taphonomic aspects of the two samples. This is done by comparing the relative change of the number of skeletal elements through time in both collections, which allows the assessment of taphonomic conditions in relation to depositional environments. The results show that patterns of variation through time of the number of isolated teeth collected by both teams are very similar (Table 1, Figure 3). It is true that in almost all members the French team collected more teeth, particularly in lower Member G, which reflects the greater total number of specimens collected by this team. However, as one moves from one member to the next, the number of teeth collected fluctuates in the same manner in both samples. A similar pattern is observed when postcranial elements are considered (Table 1, Figure 4). These two observations are probably indicative of similar changes in both areas with respect to taphonomic context. The differences observed, particularly in lower Member G where the French sample is much larger, can be attributed mainly to differences in the number of specimens (NISP) between the two collections.

To make each sample comparable to one another we used ratios of the number of teeth or postcranial elements to the total number of specimens (Table 1, Figures 5 and 6). Isolated teeth constitute a high proportion of specimens

Table 1. Number of specimens for various skeletal elements (top) and ratios of the numbers of teeth and postcrania vs. the total of skeletal elements (bottom) in the American and French collections

American collection	**A**	**B**	**C**	**D**	**E**	**F**	**G(L)**	**G(U)**	**H**	**J**	**K**	**L**	**Total**
Isolated teeth	29	576	1607	556	661	725	2190	113	236	103	159	128	7,083
Mandibles	1	56	220	74	108	67	301	26	37	16	8	20	934
Crania	3	87	273	87	178	217	1002	41	44	21	29	37	2,019
Postcrania	6	168	858	136	310	283	706	254	144	70	62	90	3,087
Total	39	887	2958	853	1257	1292	4199	434	461	210	258	275	13,123
French collection													
Isolated teeth	233	1008	1744	233	1000	659	5555	495	309	48	118	342	11,744
Mandibles	11	68	169	30	125	66	903	68	30	5	19	16	1,510
Crania	6	73	136	42	102	64	1172	85	32	8	45	17	1,782
Postcrania	84	281	1034	186	544	253	2908	772	288	84	229	97	6,760
Total	334	1430	3083	491	1771	1042	10538	1420	659	145	411	472	21,796
Ratios													
American collection	**A**	**B**	**C**	**D**	**E**	**F**	**G(L)**	**G(U)**	**H**	**J**	**K**	**L**	**Total**
Isolated teeth	0.744	0.649	0.543	0.652	0.526	0.561	0.522	0.26	0.512	0.49	0.616	0.465	0.54
Mandibles	0.026	0.063	0.074	0.087	0.086	0.052	0.072	0.06	0.08	0.076	0.031	0.073	0.071
Crania-maxillae	0.077	0.098	0.092	0.102	0.142	0.168	0.239	0.094	0.095	0.1	0.112	0.135	0.154
Postcrania	0.154	0.189	0.29	0.159	0.247	0.219	0.168	0.585	0.312	0.333	0.24	0.327	0.235
French collection													
Isolated teeth	0.698	0.705	0.566	0.475	0.565	0.632	0.527	0.349	0.469	0.331	0.287	0.725	0.539
Mandibles	0.033	0.048	0.055	0.061	0.071	0.063	0.086	0.048	0.046	0.034	0.046	0.034	0.069
Crania-maxillae	0.018	0.051	0.044	0.086	0.058	0.061	0.111	0.06	0.049	0.055	0.109	0.036	0.082
Postcrania	0.251	0.197	0.335	0.379	0.307	0.243	0.276	0.544	0.437	0.579	0.557	0.206	0.31

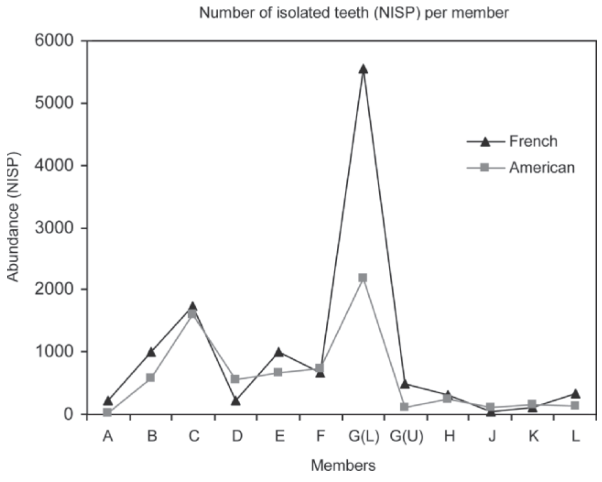

Figure 3. Number of isolated teeth (NISP) per member for American and French localities showing similar variation patterns through time: r = 0.9, α = 0.05.

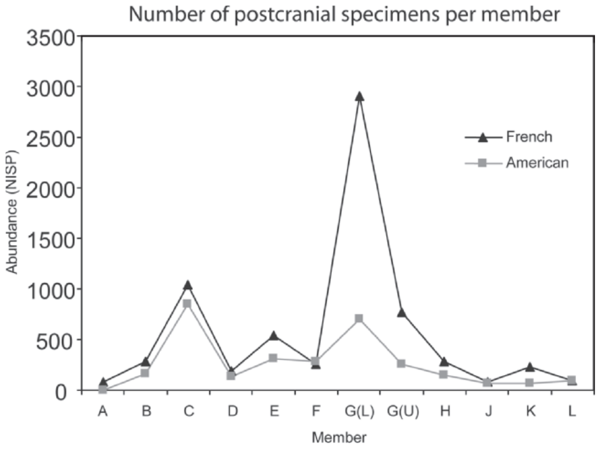

Figure 4. Number of postcranial specimens (NISP) per member for American and French localities showing similar variation patterns through time: r = 0.77, α = 0.05.

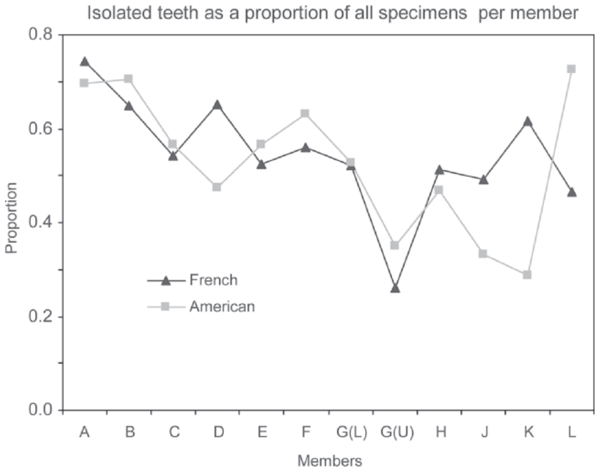

Figure 5. Variation through time of isolated teeth as a proportion of all specimens per member for the American and French collections: r = 0.74, α = 0.05.

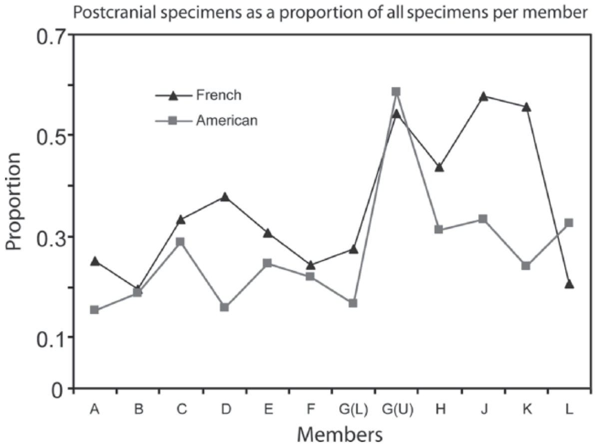

Figure 6. Variation through time of postcranial elements as a proportion of all specimens per member for the American and French collections: r = 0.75, α = 0.05.

in both collections, and show similar patterns of change through time, except for Member D and the younger levels of the sequence (Figure 5). Ratios of both teeth and postcranial elements to the total are significantly correlated when Members J and K are not included. The most striking observation is the drop in the proportion of isolated teeth in the transition from lower Member G to upper Member G observable in both collections. Likewise, the proportion of postcrania shows similar patterns of fluctuation and there is a clear increase of this proportion in the transition from lower G to upper G (Figure 6). Again, we interpret these observations to indicate similarities of taphonomic conditions, at least those related to depositional environments, in both the American and French samples. The relative decrease in teeth and increase in postcrania in the transition from lower to upper Member G is evidence for a transition from a high-energy river system to a low-energy lacustrine system. In other words, teeth, which are more resistant to damage than postcrania, are well represented in both fluvial and lacustrine systems. However, postcranial elements are relatively more common in the lacustrine (lower energy) than in the riverine (higher energy) setting. These results corroborate conclusions drawn previously from geological data and other sources (Brown and Heinzelin, 1983; Haesaerts et al., 1983).

ABUNDANCES AT HIGHER TAXONOMIC CATEGORIES

Among the 42,481 specimens that can be identified at the ordinal level, 11 orders of mammals are represented, with artiodactyls clearly predominating, primates having high abundance, and carnivores being uncommon among the mammals of medium to very large body size (Table 2, Figure 7). Out of this total 25,764 and 16,718 come from the French and American localities, respectively. The remaining specimens are identifiable either as Mammalia indet. or belong to nonmammalian taxa, which are not considered in this study. In the combined sample 74% of the total is composed of artiodactyls. However, when this percentage is calculated for the two samples separately, artiodactyls account for 81% of mammals in the French database and only 67% in the American. This shows that there is a relative bias against artiodactyls in the American sample. However, frequency distributions using the Kolmogorov–Smirnov test both at

Table 2. Numbers of specimens identified at the ordinal level. Kolmogorov–Smirnov's D value of 0.333, for α = 0.05

	American	French	Total
Artiodactyla	11,053	20,731	31,784
Primates	3,632	3,052	6,684
Proboscidea	743	1,259	2,002
Perissodactyla	390	510	900
Rodentia	724	96	820
Carnivora	149	113	262
Chiroptera	10	0	10
Insectivora	10	0	10
Lagomorpha	3	3	6
Hyracoidea	3	0	3
Tubulidentata	1	0	1
Total	16,718	25,764	42,481

Table 3. Number of specimens identified at the family level. Kolmogorov–Smirnov's D value of 0.143, for α = 0.05

Macromammals	American	French	Total
Bovidae	6,295	11,007	17,302
Hippopotamidae	2,448	5,472	7,920
Cercopithecidae	3,482	2,917	6,399
Suidae	1,770	3,087	4,857
Elephantidae	517	1,062	1,579
Giraffidae	535	1,007	1,542
Equidae	332	397	729
Deinotheriidae	225	196	421
Hominidae	147	135	282
Rhinocerotidae	55	109	164
Felidae	85	42	127
Hyaenidae	16	22	38
Hystricidae	15	10	25
Camelidae	5	16	21
Mustelidae	12	3	15
Chalicotheriidae	3	4	7
Procaviidae	3	0	3
Orycteropodidae	1	0	1
Total	15,946	25,486	41,432

ordinal and familial level show that the two samples do not differ significantly (Tables 2 and 3), but abundance comparisons made between the two samples at different taxonomic levels reveal some interesting differences. Comparing numbers of specimens of the first five most common orders (Artiodactyla, Primates, Proboscidea, Perissodactyla, and Carnivora) collected by the two teams shows that the French collected more of every group with the exception of primates and carnivores (Table 2, Figure 7). In other words, in both collections artiodactyls are the most common and carnivores the least, but more primates and carnivores were collected by the American than the French team. This is also reflected when abundance comparison is made at family level. For the first ten most common families (Bovidae, Hippopotamidae, Suidae, Cercopithecidae, Elephantidae, Giraffidae, Equidae, Deinotheriidae, Hominidae, and Rhinocerotidae), there are more specimens in the French collection than there are in the American (Table 3, Figure 8). One major exception is the Cercopithecidae, of which the American team collected more specimens.

It is clear that the intrinsic nature of sediments, where some are more fossiliferous than others, and the size of areas explored by the different teams, have affected the overall difference in the number of specimens collected. However, other factors may explain some of the differences observed above. Among these, differences in collection protocols between the two teams have played a role. The higher number of total mammalian specimens collected by the French can be explained in part by the fact that they included postcranial elements of all taxa, even those of very large mammals such as hippopotamids. Consequently, while most mammalian families constitute comparable percentages in both the French and the American collections, hippopotamids comprise 21% of the French but only 16% of the American collections (Figures 9 and 10). This illustrates that the American team was biased against large mammals, particularly their postcrania (see Eck, 2007). In comparison, cercopithecids differ clearly in their relative abundance in the two collections, constituting 22% in the American but only 12% in the French collection (Figures 9 and 10). The higher number of cercopithecids amassed by the American

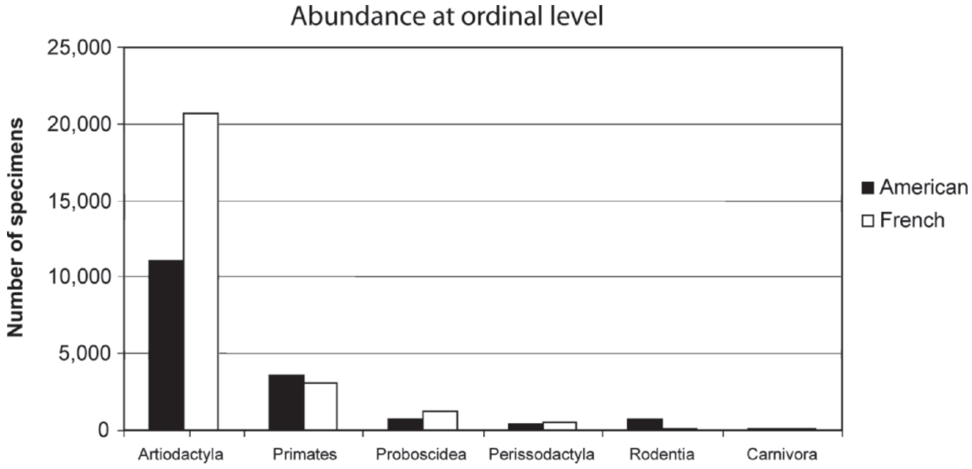

Figure 7. Comparative abundance of the first six most common mammalian orders in the French and American samples.

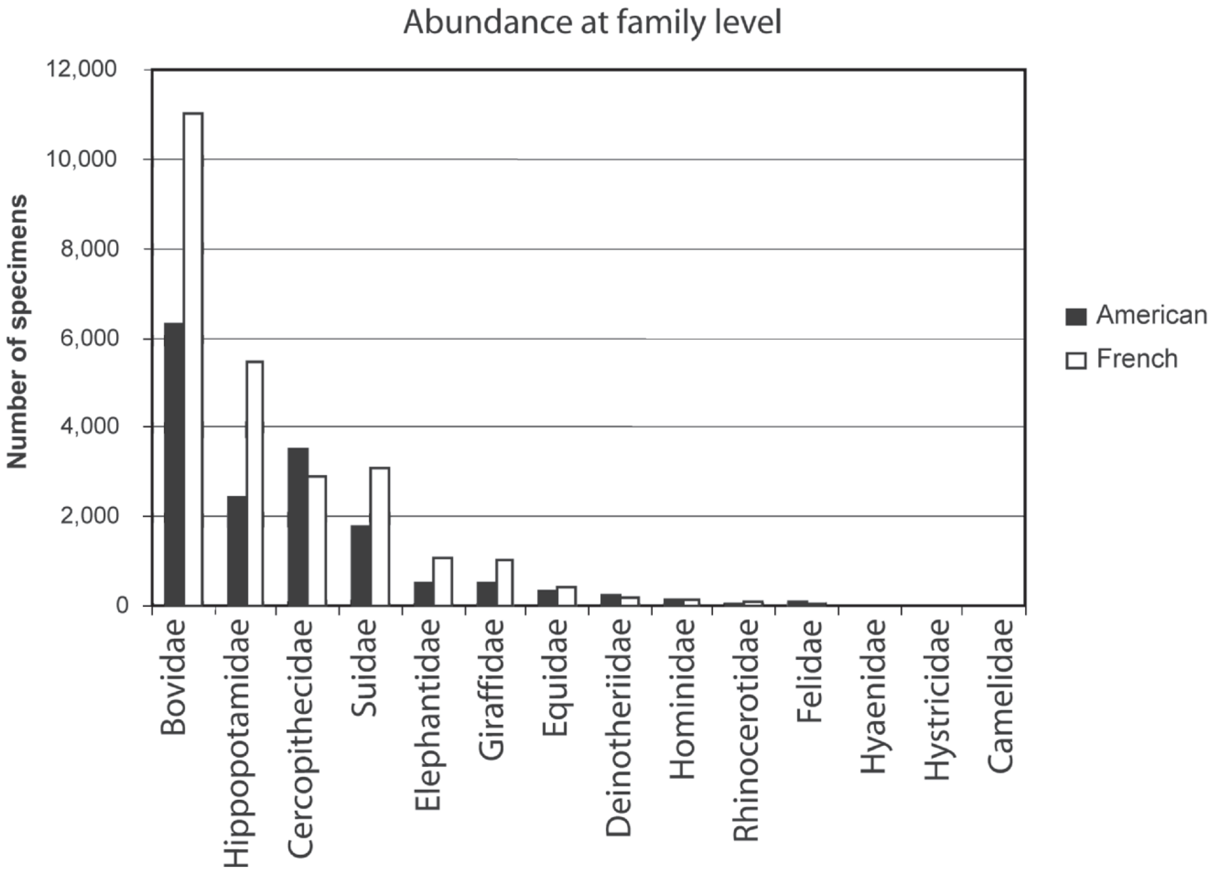

Figure 8. Comparative abundance of the first 14 most common mammalian families in the French and American samples.

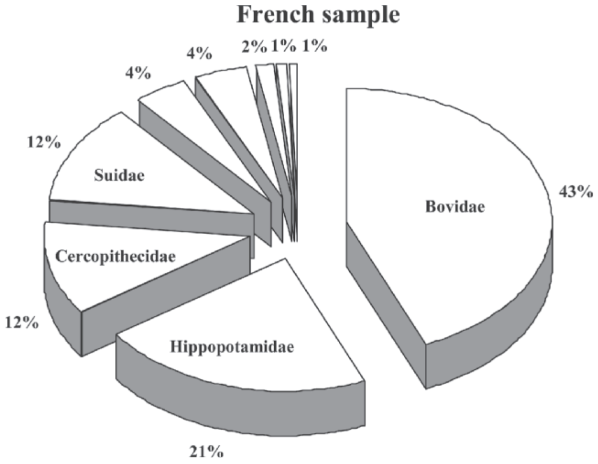

Figure 9. Percentages of the most common mammalian families within the French collection.

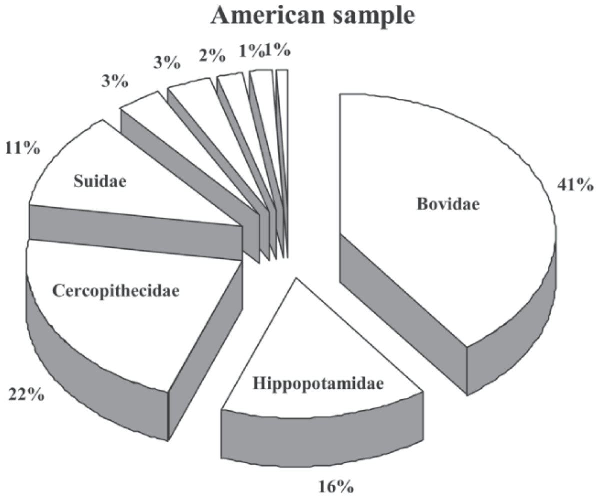

Figure 10. Percentages of the most common mammalian families within the American collection.

contingent is noteworthy considering that the overall French sample exceeds the American sample by almost 10,000 specimens. It is clear that the American team was collecting monkeys with higher intensity than other major taxa, which accounts for the differences observed (see Eck, 2007). Thus, paleoenvironmental interpretations based on abundance of monkeys relative to other major taxa should be considered with caution.

TAXONOMIC ABUNDANCE: VARIATION THROUGH TIME

Given that similar taphonomic history can be assumed in the Shungura sequence for both collections, taxonomic abundance variation through the sequence could be evaluated using some taxa. Bovid tribes are used for this purpose for the widely accepted reason that they are very common and habitat specific. Four tribes – Reduncini, Alcelaphini, Aepycerotini, and Tragelaphini are considered. We used these four tribes and looked at how their relative abundances vary through the Shungura sequence in the American and French samples.

Results of comparisons between the two collections do not show major differences in relative abundance variation through time from Members B to upper G among the taxa under consideration (Table 4, Figures 11–14). Patterns of variation are almost identical for Reduncini, Tragelaphini, and Alcelaphini and similar fluctuation patterns are observed in both collections for Aepycerotini, even though after Member E American proportions are higher for the latter. These observations indicate that overall, despite the considerable differences in the number of specimens collected by the two research teams, relative abundance variation patterns of major bovid groups are similar in both samples. We conclude therefore that in general the Shungura area was characterized by similar type of habitats both in northern and southern parts. In other words, the two research teams sampled areas that overall were characterized by comparable depositional and paleoenvironmental conditions. As a result both samples document similar patterns of changes through time in terms of taphonomy and taxonomic abundance.

Table 4. Number of specimens of bovid tribes across the members of the Shungura Formation in the American and French collections

French	**B**	**C**	**D**	**E**	**F**	**G(L)**	**G(U)**
Tragelaphini	41	110	21	69	74	731	66
Bovini	37	50	5	12	20	53	5
Reduncini	110	76	15	30	68	1645	198
Hippotragini	0	0	0	0	1	6	1
Aepycerotini	69	92	30	29	68	545	124
Alcelaphini	6	11	4	3	26	68	33
Antilopini	2	0	1	0	0	8	5
American	**B**	**C**	**D**	**E**	**F**	**G(L)**	**G(U)**
Tragelaphini	29	178	66	117	87	375	2
Bovini	24	73	15	13	15	38	2
Reduncini	63	74	30	56	69	684	14
Hippotragini	0	3	0	1	0	2	0
Aepycerotini	48	94	56	91	141	461	2
Alcelaphini	6	5	6	9	25	51	1
Antilopini	1	3	1	0	5	4	0

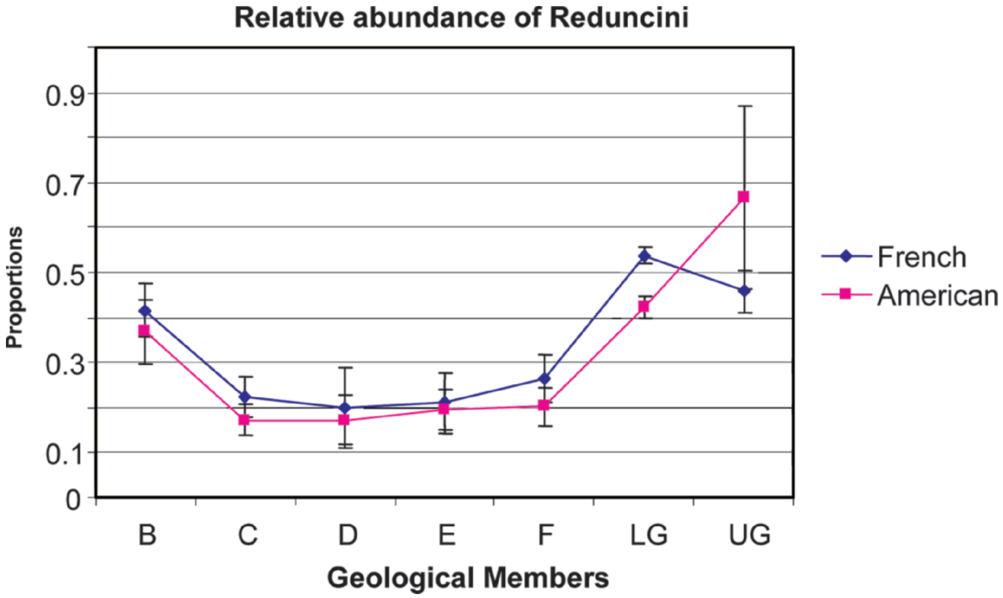

Figure 11. Abundance variation through time of Reduncini in the American and French collections. (95% CI calculations based on Buzas, 1990).

ARE THERE LOCAL HABITAT DIFFERENCES?

As mentioned above, although the French sample is larger than the American one, both collections are characterized by similar species richness. Excluding micromammals, there are 55 species of mammals in the French collection and 60 species in the American one. This shows that the higher number of specimens in the French collection is caused in part by the inclusion of more postcranial elements rather than sampling more paleohabitats. Likewise, abundances of major bovid tribes are similar in both collections and

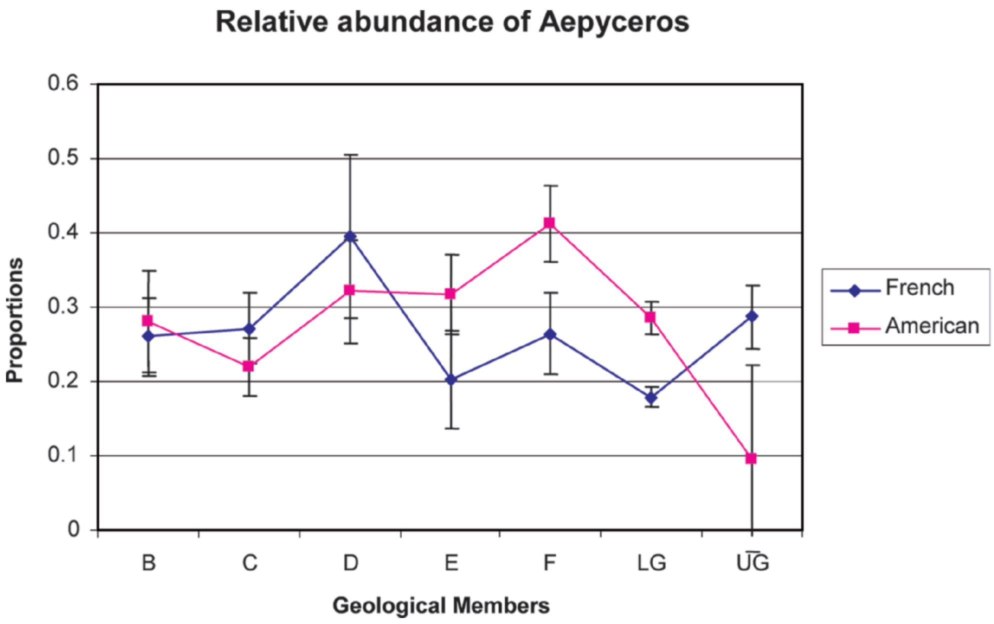

Figure 12. Abundance variation through time of Aepycerotini in the American and French collections (95% CI calculations based on Buzas, 1990).

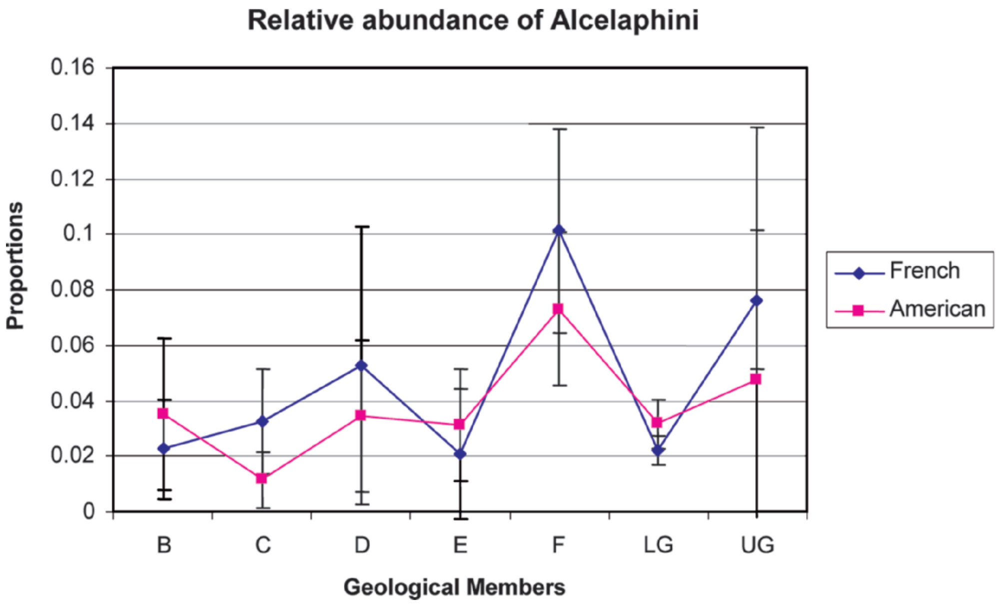

Figure 13. Abundance variation through time of Alcelaphini in the American and French collections (95% CI calculations based on Buzas, 1990).

show a high degree of comparability in terms of taxonomic diversity both in time and space. These observations lead to us to conclude that the overall underlying paleoenvironmental and paleoecological conditions both in the southern and northern parts of Shungura were similar. However, it is possible that there were local habitat differences characterized by higher or lower proportions of various species. A correspondence analysis (CA) was

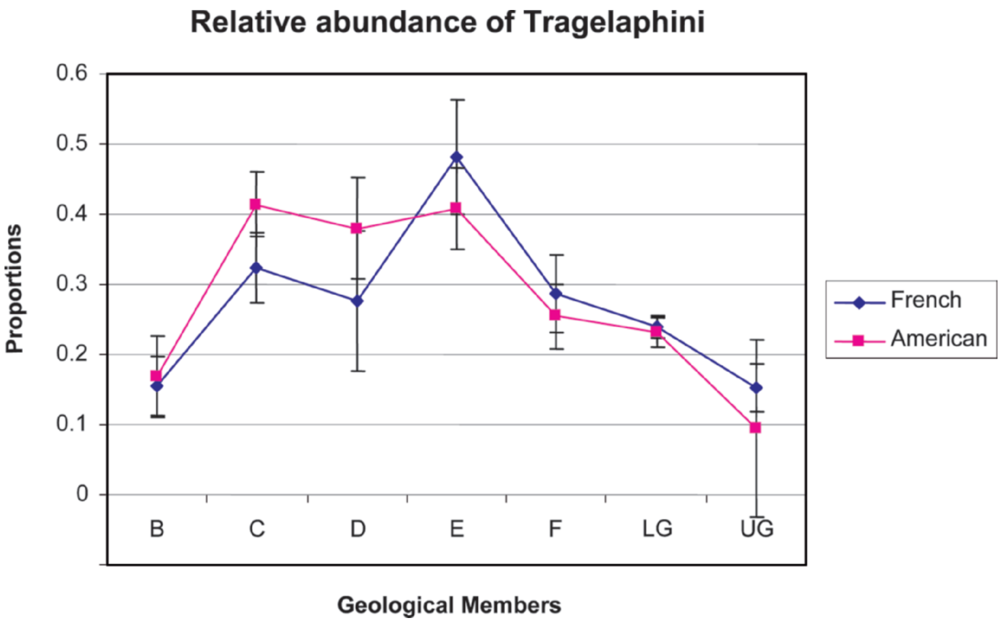

Figure 14. Abundance variation through time of Tragelaphini in the American and French collections (95% CI calculations based on Buzas, 1990).

chosen to look into this question. CA allows projecting rows and columns simultaneously onto a two- or three-dimensional graph, thus allowing us to see which taxa have higher or lower proportions in which localities. CA is a statistical visualization method for picturing the associations between the levels of a two-way contingency table. It is a geometric technique for displaying the rows and columns as points in a low-dimensional space, such that the positions of the row and column points are consistent with their associations in the table. In our case the objective is to explore if localities are particularly characterized by a given taxon or group of taxa. The expectation is that there should not be significant differences among localities of the two teams in terms of species proportions. Based on these assumptions we conducted an analysis at lower taxonomic levels (genera and species) in a restricted time interval, lower Member G (dating from ~2.3 to 2.1 Ma) (see Table 5). This interval was chosen because of the high abundance of fossils from a relatively restricted time period. Some localities that are within this interval did not yield large enough numbers of fossil and were excluded from the analysis. We also excluded upper Member G because it differs from lower Member G in depositional environments, taphonomic conditions, and abundance of fossils. As stated above, the transition from lower G to upper G is characterized by a shift from fluvial to lacustrine conditions, with a lake expanding to the north from the center of the Turkana Basin. The geographic distribution of the localities considered is presented in Figure 15.

A correspondence analysis on localities from lower Member G using genera and species as variables shows that there is some differentiation between the French and the American localities, implying that there may be local faunal (and perhaps habitat) differences (Figure 16). A similar analysis using only bovid species shows a stronger differentiation between French and American localities, with a higher proportion of *Menelikia lyrocera* in French localities and *Kobus sigmoidalis* in

Table 5. Abundance of selected mammalian species and genera in lower Member G localities

Locality	Stratigraphic level	*T. nakuae*	*T. gaudryi*	*M. lyrocera*	*K. sig moidalis*	*K. ancystrocera*	*A. shungurae*	*Kolpochoerus*	*Notochoerus*	*Metridiochoerus*
Omo29	G(L)	62	38	8	6	2	117	22	36	14
Omo47	G8	103	25	39	0	7	42	104	24	25
Omo48	G12	15	1	1	0	4	10	4	1	0
Omo75	G(L)	130	57	50	27	16	171	105	64	40
Omo113	G10–11	2	0	17	0	11	0	0	0	0
Omo210	G3	7	1	4	5	0	5	0	3	0
Omo309	G6	0	0	1	7	0	5	0	0	0
Omo308	G4	1	2	2	5	0	0	1	0	0
Omo310	G8	1	0	66	0	1	0	3	0	1
Omo323	G8	28	2	81	0	5	3	31	4	5
SH 1	G8–9	12	27	6	2	3	22	13	15	0
Omo50	G(L)	16	3	9	0	4	16	10	9	4
Omo311	G8	0	0	13	0	0	2	4	0	0
L7	~G5	22	38	14	37	0	18	16	12	12
L16	G4	11	7	5	32	1	20	6	2	1
L25	G13	7	0	5	11	0	40	10	5	0
L35	G5	8	5	2	4	1	10	3	1	1
L43	G12	2	0	2	5	0	1	0	0	2
L67	~G8	19	3	8	36	0	5	0	4	0
L73	G12	6	1	2	3	0	15	2	1	2
L74	G4	5	0	1	4	0	1	2	4	0
L80	G4	5	12	1	10	0	0	5	0	0
L112	G7	2	0	5	3	0	0	3	0	0
L627	G12	21	21	4	4	6	109	27	6	6

American localities (Figure 17). These two species of Reduncini might have preferred only part of the Shungura paleolandscape, suggesting possible local habitat differences between the two areas.

Can this pattern be extrapolated over the whole range of the Shungura area? And, is there any consistent differentiation in the distribution of these taxa in the north and south? To answer these questions we considered only the tribe Reduncini (and its species), and examined their distribution in the whole geographic range covered by the two research teams. The goal was to see if there were relative abundance differences among closely related species of this tribe (in this case *Menelikia lyrocera*, *Kobus sigmoidalis*, and *Kobus ancystrocera*) in the southern and northern parts of the Shungura area. If these differences exist, this would indicate possible local differences in habitat, which the various species of Reduncini would occupy, even though they shared general adaptations to waterlogged environments characteristic of the tribe as a whole.

For this purpose, abundances in each locality were plotted on the maps redrawn from those published at a scale of 1:10,000 by de Heinzelin (1983). For localities to be comparable we used ratios of taxonomic abundances that are represented by different sizes and colors of circles as illustrated in Figure 18. This was done because the term “locality” covers a wide range of collecting units, from a single spot where only one

Figure 15. Geographical distribution of American (top) and French (bottom) localities from lower Member G of the Shungura Formation.

fossil specimen was collected (common in the American collection), to huge areas where thousands of fossils were amassed (such as the French Locality Omo-75). For every taxon (species, tribe) and anatomical element (horn cores, teeth, postcrania), we calculated its relative abundance as the ratio of its total number (numerator) to the number of the same element in the immediately higher taxonomic category (denominator). For instance, abundance of Tragelaphini teeth at locality Omo-323 is the ratio (N = Tragelaphini teeth from locality Omo-323)/(N = Bovid teeth from Omo-323), but abundance of *Tragelaphus nakuae* horn cores in the same locality is the ratio (N = *T. nakuae* horn cores from Omo-323)/(N = *Tragelaphus* horn cores from Omo-323). Thus, the size of the circles is proportional to the denominator and its color (lighter or deeper) reflects the abundance of the numerator. In Figure 18 for example *Menelikia* horn cores are compared to the number of Reduncini horn cores. A deeper color means that the *proportion* of *Menelikia* is greater, while the size of the circle, which is proportional to the number of Reduncini horn cores, reflects the *significance* of this proportion at this particular locality. Since for many localities the number of collected specimens is low, the computed ratios are not always significant. For instance, if only one reduncin horn core is found in a locality, the relative abundance of the occurring species will be one, but the small size of the resulting circle will reflect the insignificance of that particular locality. It is important to note that this method allows us to control taphonomic or collecting bias, because the results are not altered by differential preservation of teeth vs. long bone or selective collecting of horn cores vs. teeth.

Obviously, color depth cannot have the same meaning for all taxa, as there are rare and common ones. To estimate the "rarity" or "commonness" of taxa, we could have calculated the average proportion in the whole collection, but this would have given too much weight to the rich

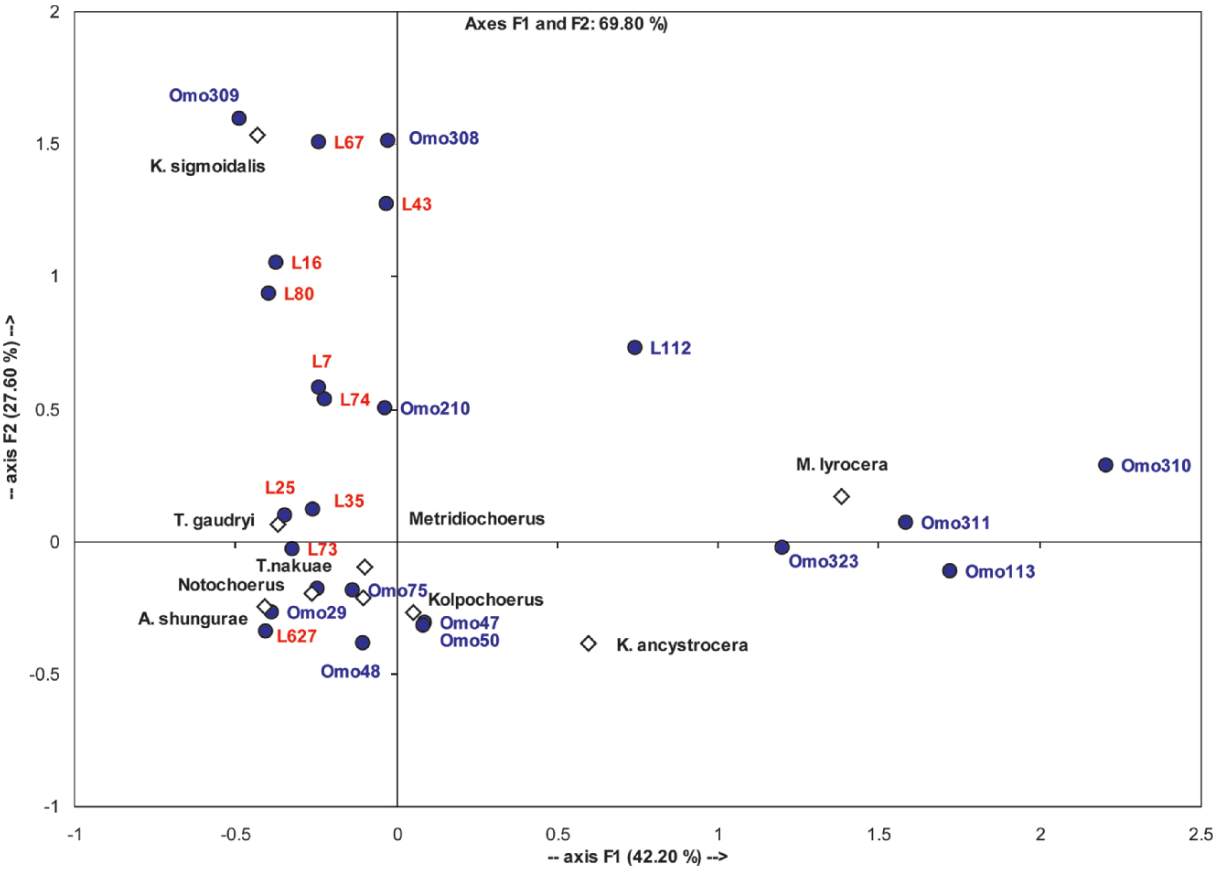

Figure 16. Correspondence analysis showing locality distributions on axes 1 and 2. Each point represents a locality. The American and French localities tend to separate. In this analysis columns represent mammalian taxa and rows represent localities. Omo = French localities, L = American localities.

localities. Alternatively, calculating the mean of ratios (sum of the ratios in each locality, divided by the number of localities) would have given too much weight to less fossiliferous localities. Thus, we compared these ratios to the average ratios in the 71 localities that yielded more than 100 specimens. Circle color reflects this ratio (the higher the proportion, the deeper the color), as follows:

very rare (very light color): less than half the average proportion;
rare (light color): between half and the average proportion;
common (deep color): between the average and twice the average;
very common (very deep color): more than twice the average.

For Reduncini horn cores, these ratios are: Reduncini/Bovidae=0.28; *Menelikia*/Reduncini = 0.24; *Kobus ancystrocera*/Reduncini = 0.07; *Kobus sigmoidalis*/Reduncini = 0.28. However, before analyzing differences at the species level within the Reduncini, we calculated the relative abundance of the tribe itself compared to the total number of bovids in different localities using the same approach. This was done by dividing the number of Reduncini horn cores in every locality considered by the total number of bovid horn cores in that same locality. The ratio indicates that the relative distribution of the tribe Reduncini in the north and south was not even. Figure 19 (column A) shows that we have comparable number of bovids in the north and south as is illustrated by the comparability of the size of the circles, but we have more

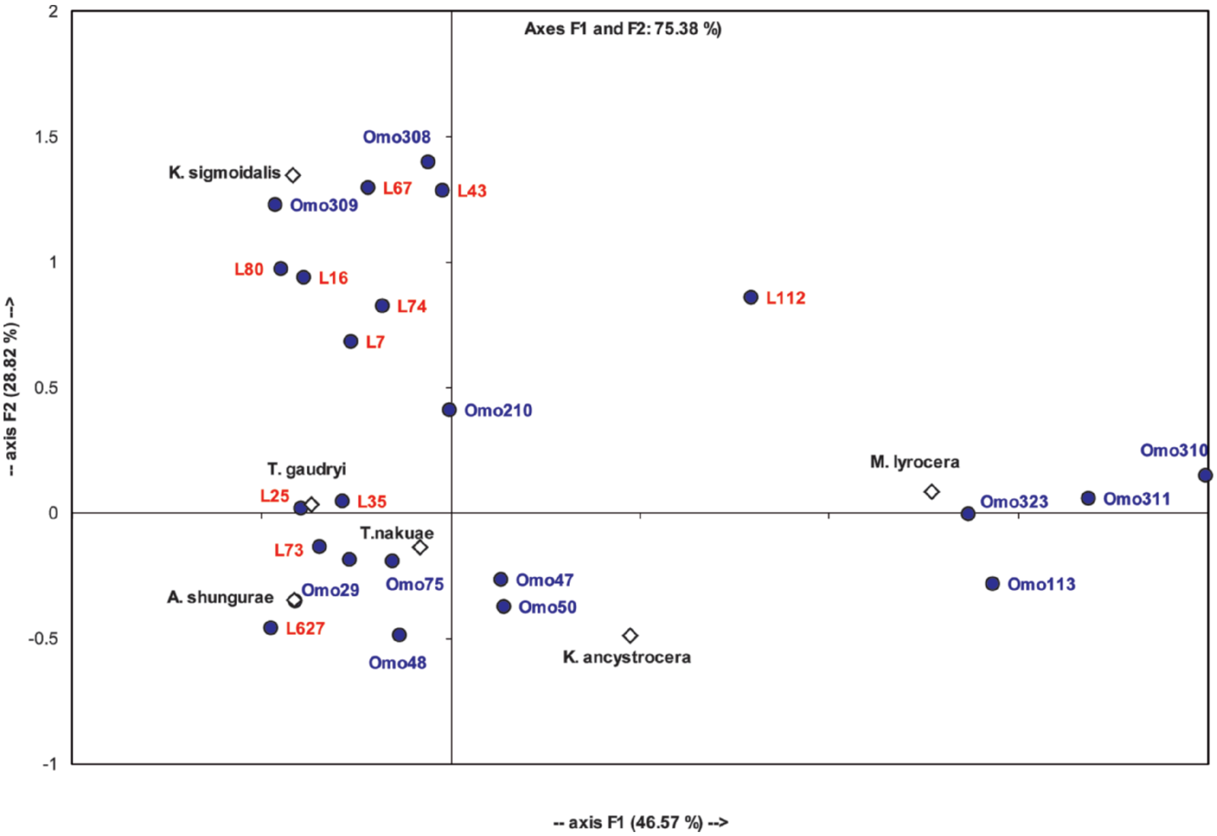

Figure 17. Correspondence analysis showing locality and taxa profiles on axes 1 and 2. Note the separation along the first axis of *Menelikia lyrocera* and *Kobus sigmoidalis*, two species of the tribe Reduncini.

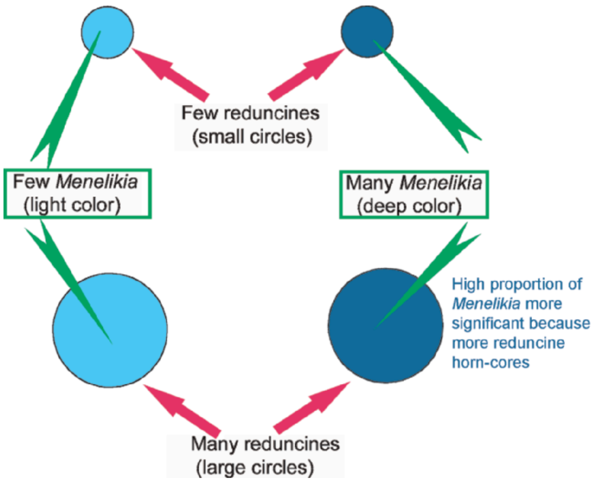

Figure 18. Schematic representation of the relative proportion of a taxon in a locality. The size of the circles is proportional to the denominator and its color (lighter or deeper) reflects the abundance of the numerator. In this example *Menelikia* horn cores are compared to the number of Reduncini horn cores. A deeper color means that the proportion of *Menelikia* is greater, while the size of the circle, which is proportional to the number of Reduncini horn cores, reflects the significance of this proportion at this particular locality.

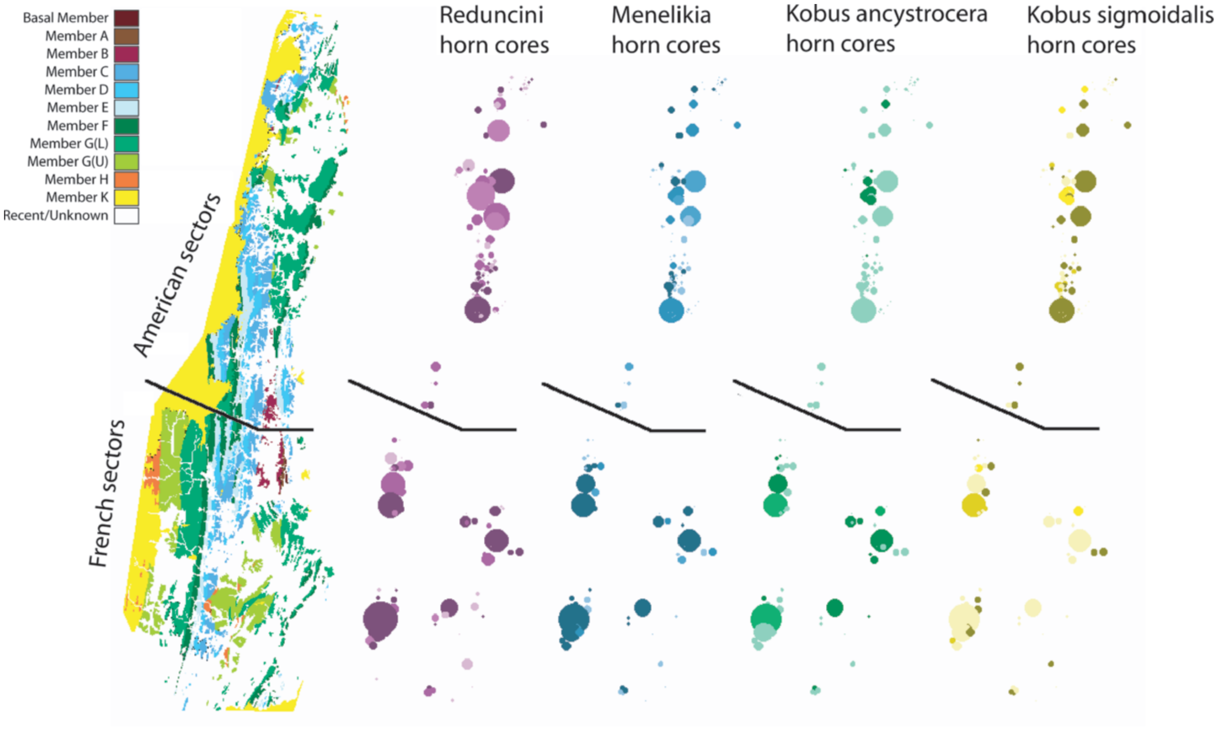

Figure 19. Distribution of Reduncini and its species over the whole range of the Shungura area for the French and American localities in the north and south. Every circle represents a locality. The depth of the color indicates the proportion of the taxa in a particular locality. Note that Reduncini are more common in the south than in the north in general. However, specimens of *Menelikia lyrocera* and *Kobus ancystrocera* are more common in the south, while those of *Kobus sigmoidalis* are more common in the north. These differences are statistically significant, $X^2 = 153$, $P < 0.001$.

deep-color circles in the south pointing to a relatively higher number of Reduncini in the area, as shown also by the table below (322 horn cores on the American collection from units G3–G13, 432 in the French one).

	American collection	French collection
Kobus ancystrocera	28	61
Kobus sigmoidalis	193	82
Menelikia lyrocera	101	289

Given the differences in the relative abundance of Reduncini in the north and south, we undertook the same calculation for the different species within this tribe to see if they also show differences in their relative abundance in different geographic secotrs. Horn cores of *Menelikia lyrocera*, *Kobus ancystrocera*, and *Kobus sigmoidalis* are used for this purpose. The result shows that there are more large-size circles in the south than in the north confirming the relative higher abundance of the tribe Reduncini in the south. However, looking at the depth of colors of circles reveals that there are more deep colored circles in the south for *M. lyrocera* and *K. ancestrocera* showing the higher relative abundance of these tow species in the south, i.e. in the French localities. In contrast for *K. sigmoidalis*, there are more deep colored circles in the north. This indicates that specimens of *Menelikia* and

Kobus ancystrocera are more common in the south (French localities), while those of *K. sigmoidalis* are more common in the north (American Localities) (Figure 19 column B, C, D) and this difference is significant (X2 = 153, $p<0.001$). This may provide evidence for local ecological differences within the lower Omo basin during lower Member G times.

The inverse abundance of the two most common reduncine species (*M. lyrocera* and *K. sigmoidalis*) had already been noticed by Gentry (1985) who linked his observation to ecological differences, since he assumed that *Menelikia* was an open-country form. Alemseged (1998) further substantiated this ecological separation, but following Spencer (1997) he assumed that *Menelikia* was adapted to more wooded environments. The preferred kind of habitat of these two extinct species remains to be determined by further ecomorphological studies, but our results provide some evidence that these species may have lived in different habitats, or may have excluded each other. Their abundances were negatively correlated among Shungura localities, and overall *K. sigmoidalis* was more common in the north whereas *M. lyrocera* was so in the south. Further studies should test the possibility of local habitat differences in the lower Omo Basin. Results of such studies could shed light on issues pertaining to habitat preferences of hominin species.

Geraads and Coppens (1995) found that in Member G the American team collected more bovid horn cores relative to teeth than the French team, while the French collected proportionately more teeth. Eck (2007) found the same results and suspects that these differences were introduced because the French team less consistently collected horn cores. However, the same pattern may be produced by the French collecting a greater proportion of teeth, especially fragmentary ones. Even though the American team collected more horn cores than the French team, there is no reason to believe that either team was particularly biased for or against horn cores of any particular taxon. Therefore, it is likely that the differences in taxonomic abundances based on horn cores within each collection reflect the reality on the ground. In this contribution we have shown that both collections are generally comparable in taxonomic composition and patterns of relative abundance, but at finer levels of resolution there are some intriguing differences. Eck's (2007) suspicion that differences in skeletal element abundances between the two teams introduced taxonomic biases within the collections does not distinguish taphonomic from taxonomic biases. We suggest that some of these differences may have environmental causes, but further work in the Shungura Formation would be required to settle the issue of environmental vs. collection factors.

Summary

The present study addressed issues that relate to data comparability and standardization based on fossil collections from the well-dated Shungura Formation in southwestern Ethiopia. Large numbers of specimens (ca. 50, 000) were collected by French and American research teams working semi-independently in the same stratigraphic sequence and adjacent areas. Here we compared various aspects of the two collections and found important similarities and differences. Taphonomic analyses pertaining to depositional environments show that there are no major differences between the two samples. A major taphonomic shift in the middle of Member G (between units G-13 and G-14) is observed in both samples and is caused by a major change in depositional environments, from fluvial to lacustrine conditions. Effects of this taphonomic shift are expressed in a higher proportion of postcranial elements relative to isolated teeth as depositional environments became more lacustrine. The question of collection bias was addressed by comparing abundances (NISP) of different taxa among the two collections. In this regard, in general the French team collected more specimens than the American team; however, the American team collected more primates and carnivores. In contrast, the French in general recovered more remains of large-sized mammals as well as more postcranial elements of macromammals (other than primates) than the Americans.

Despite these differences, similar taxonomic composition and species richness is documented in both samples. In other words, the types of animals that roamed the paleo-Omo landscape at a given time were found in both areas, in the north and south. In addition a comparative approach that used abundance variation of bovid tribes through time indicated that similar patterns of variation are observed in both samples. This is considered to be additional evidence for the prevalence of generally similar habitats in the northern and southern parts of the Shungura area.

While this is generally true, habitat differences may have occurred locally. Using species of the tribe Reduncini, we were able to demonstrate that some species were more frequent in the southern localities (French) and others in the northern localities (American). In particular, we have shown that *Menelikia lyrocera* was more common in the south while *Kobus sigmoidalis* was so in the north. This means that even if the Shungura area was characterized by generally similar type of habitat in the south and north at any given time, there may have been local ecological differences, indicated by inferred differences in the habitat preference of these species.

Conclusion

The late Cenozoic fossil record of Africa is growing fast as a result of the proliferation of fieldwork activities in different parts of the continent over the past decades. Major projects are being conducted in Chad, Ethiopia, Kenya, Tanzania, Malawi, South Africa, and Morocco, to mention some. Several international multidisciplinary research groups undertaking fieldwork in these countries have amassed large numbers of faunal remains including hominins. The faunal collections are useful to understand the paleobiodiversity of a given area and time period. In addition they are one of the best sources of information in exploring the paleoenvironments and paleoecology of our ancestors. Moreover, studies that are carried out to understand the effects of regional and global climatic changes on faunal and hominin evolution require data that are extracted from these collections. In short, data that are recovered in the field remain our primary sources of information in the study of biological, environmental, and ecological evolution of hominins and associated fauna in the Miocene, Pliocene, and Pleistocene. However, research groups tend to work independently following their team-defined approaches, as illustrated by the present study, and there is little or no standardization in the documentation of these fossil collections.

Even though different projects undertake their field activities separately, their research goals are often very similar and the questions they address are strongly linked to each other. While they are explored by separate projects, many paleontological sites are located in the same temporal range and geographical areas; and even sometimes belong to the same sedimentary basin. It is therefore imperative that the various projects coordinate their efforts to maximize the amount of data and information that can be extracted from these irreplaceable resources. For several scientific and nonscientific reasons, it is usually not possible to coordinate different field projects to work together. Yet it is critical that we reach some minimum agreement on how fossil data should be collected in a standardized fashion, so as to establish comparable databases that can subsequently be used for regional and even global understanding of patterns of human evolution.

The present study on comparability of data underscores the importance of the quality of data in unraveling past environments and patterns of change through time. Well-controlled collecting methods and systematic documentation procedures are necessary for the data to be used for these purposes. One way of doing this is to encourage information exchange among different research groups conducting fieldwork in geographically and temporally comparable sites. This can be accomplished in many different ways ranging from informal discussions about current research on specific sites to organized symposia and workshops in which standards and methodologies can be discussed in a comparative fashion. There have been some initiatives over the last few years in this regard that need to be encouraged and expanded. More importantly, a mechanism of data exchange needs to be established among researchers. This will facilitate not only our endeavor towards improving the quality and soundness of databases but also will make our interpretations and hypotheses easier to test and evaluate.

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