

EVOLUTION OF BOVID DIVERSITY IN THE PLIO-PLEISTOCENE OF AFRICA

DENIS GERAADS

*URA 49 du CNRS, Musée de l'Homme, place du Trocadéro,
F-75116 PARIS and Laboratoire de Paléontologie des Vertébrés, Université Paris VI,
4 place Jussieu, F-75252 PARIS Cedex 05.*

(Received October 10, 1992; in final form July 1, 1993)

The diversity of the family Bovidae (Mammalia) in the Plio-Pleistocene of Africa is estimated by several indices and rank-abundance curves. The broad observed pattern in East and South-Africa is an increase in diversity during the second part of the Pliocene, followed by a decrease in the latest Pliocene or earliest Pleistocene. These changes are diachronic in the various areas, as are other faunal changes (in successive order, in Lake Turkana basin: West Turkana, Omo, Koobi Fora). High diversity is associated with a higher number of abundant species, whereas the subsequent, less diverse, assemblages have only 1 or 2 very abundant species. The decrease in diversity might be a consequence of the latest Pliocene global cooling, resulting in a decrease in primary productivity and other related parameters. There is, however, some evidence that more favourable conditions were restored afterwards.

KEYWORDS: Bovidae, diversity, Pliocene, Pleistocene, Africa.

INTRODUCTION

Faunal changes in the Plio-Pleistocene of Africa deserve investigation because of their probable correlation with human evolutionary events (Vrba, 1989). These changes are likely to be sensitive to a wide range of external factors (including predator/prey relationships, human impact, interspecific competition...) even though, usually, they have been interpreted in terms of climatic evolution.

In the late Cenozoic, ruminants are perhaps the mammals most commonly studied to this end, often by reference to their modern counterparts. Vrba (1980, 1984, 1985a, 1985b) has studied the changes in the percentages of Alcelaphines + Antilopines, bovids of open dry habitat in the modern world, among all bovids. Multivariate studies (Greenacre & Vrba, 1984; Denys, 1990), by incorporation of data from many sites and taxa allow sorting and grouping of faunas, but the underlying factors can only be revealed by comparison with modern faunas, a method which should be used cautiously (de Bonis et al., 1992).

One might expect that anatomical adaptations should help reconstructing the environment (e.g. Solounias and Dawson-Saunders, 1988), but the sharp limitation of data available for fossils leaves room for very rough ecological classifications only: e.g.,

Correspondence to: Dr Denis Geraads, Lab. Paléontologie Vertébrés, Case 106, 4 Place Jussieu, 75252 Paris Cedex 05, France

Andrews et al., (1979) classify all mammals into 6 feeding types only, 6 locomotory types... These classifications may contribute to demonstrate environmental changes over large time-periods, but are unlikely to be able to distinguish between closely similar assemblages (e.g. 2 successive levels of a Pleistocene site), where environments vary little.

MATERIAL AND METHODS

Of course, many of the ecological descriptors designed for recent assemblages are not applicable to fossils. However, one of the descriptive approaches most commonly used in recent communities, the study of species-abundance relations, together with the numerous measurements of richness, diversity, and evenness, can be applied, although they have seldom been used in mammalian palaeontology (Rose, 1981; Cruz-Uribe, 1988; Sese, 1991; de Bonis et al., 1992).

These analyses are all based upon the computation of the number of species (S) and, usually, the number of individuals in each species (N_i). Another estimate of species abundance, relative biomass ($N_i \times$ individual weight), which emphasizes unevenness (Pagel et al., 1991) can be used in modern communities, but its application to fossil faunas is difficult.

However, there are some limitations to the application of these analyses to fossil assemblages (see e.g. Behrensmeyer, 1991).

First, in mammalian palaeontology, we have no access to the number of individuals, but only to the number of specimens, bones, teeth, and fragments. Ideally, a Minimum Number of Individuals (MNI) can be computed from this (Cruz-Uribe, 1988; Cruz-Uribe and Klein, 1988), but this is often not so straightforward, since in many cases of the Plio-Pleistocene of Africa there are several clusters of closely related species (e.g. gazelles, or members of the genus *Equus*,...) where fragmentary specimens are not identifiable to species. It is also clear that collecting bias have altered the relative proportions of some groups; e.g., primates and carnivores are much more systematically collected than hippos or elephants.

Another bias arises from the differences in death rates, leading to an over-representation in the thanatocoenoses of species with short life-spans (Western, 1980). This is partly compensated by the greater durability of larger bones (larger size being highly correlated with longer life-span) but one can easily guess that correction of these factors, although feasible, would be largely speculative, and too much dependent upon the type of sedimentary facies.

For all these reasons, I believe that it would be meaningless to compare whole mammalian assemblages from all over Africa during several million years. I have therefore restricted my analysis to a single family, Bovidae, which I have chosen for the following reasons:

- they are always present and always the most numerous and diverse (in number of species) of large mammals;
- their life-spans (10 to 20 years for most of them) are not greatly unequal, even for very different sizes, and one may reasonably assume that the differential preservation of their remains roughly compensates these differences;
- they are likely to be sensitive to a number of external factors which may also influence hominid evolution, such as climate, predation patterns or competition with non-bovid herbivores.
- there is at least one frequently preserved part, horn-core (and skull), which is always identifiable to species-level, or at least, which can be distinguished from other species in the same site.

I have therefore used the number of bovid horn-cores and skulls, which is probably a good estimate of the number of individuals. I have computed them for most of the important African Plio Pleistocene mammal localities (see appendix). A drawback is the absence of horns in the female of many species, but there is no way to cope with this problem, since this sexual dimorphism may be present or absent in closely related species. When they are all identified to species (but this is seldom the case), I have also added jaws and teeth (sometimes only last lower molar): this has the advantage of increasing the sample; I have checked for Elandsfontein (data from Cruz-Uribe and Klein, 1991) that indices based upon the number of horn-cores only, or the number of horn-cores + teeth, or the NI calculated from the horn-cores, are not significantly different (Table 1). In the South-African cave sites, however, cranial remains are very few, and I have used dentitions instead.

Table 1 Comparison of some diversity and evenness indices computed from frontlets + horn-cores or frontlets + horn-cores + dentitions at Elandsfontein, using data from Klein and Cruz-Uribe, 1991, table 3 and figure 5.

	<i>S</i>	<i>N</i>	<i>H'</i>	<i>HB</i>	<i>H''</i>	<i>1/BP</i>
frontlets + horn-cores	18	556	2.43	2.36	2.40	6.46
frontlets + horn-cores + dentitions	18	1918	2.52	2.50	2.51	5.96
MNI from horn-cores	18	349	2.50	2.39	2.45	6.58

To avoid mixing of different assemblages, I have always tried to use the finest possible stratigraphic levels. However, this degree of resolution varies with the sites: a single layer at Olduvai certainly represents a much shorter time-period than a Koobi Fora member; even if the latter are probably too short to document significant changes in the ecological balance, it is probably more fruitful to compare sites in the same area. There are two more reasons for doing so. First, the overall similarity in environmental conditions at any one place eliminates one possible source of difference. Secondly, some sites are more subject to "Hominid-bias" (selection of some species by hunting or scavenging) than others, which are virtually unaffected and more natural. It is certainly closer to the truth to assume that the Hominid-bias is roughly the same for all Olduvai levels than to compare them directly to any other contemporaneous East-African localities.

Although I do not claim to have overcome all taphonomic biases, I believe that it is therefore possible to get a good approximation of the original assemblages through:

- choice of a limited, rather homogeneous taxonomic group;
- choice of easily determinable anatomical parts (horn-cores, skulls and teeth when there is no ambiguity), whose relative abundances cannot be much different from those of the individuals themselves;
- comparisons of successive assemblages within limited areas.

Anyhow, the observed changes in the values of indices through time are greater than those which might result from taphonomic differences. As table 2 shows, even significant differences in number of species or relative abundances do not greatly modify the indices, which are therefore rather "robust".

Table 2 Simulation of the variations of the relative abundances of 8, 10 or 12 species represented by 200 cranial specimens. Even with relatively large fluctuations (e.g., the most common species is twice as common as the second one, or both are equally common), indices vary little.

	<i>S</i>	<i>N</i>	<i>H'</i>	<i>HB</i>	<i>H''</i>	<i>I/BP</i>
1:	10	200	1.47	1.39	1.42	2
2:	8	200	1.48	1.42	1.44	2.86
3:	12	200	1.56	1.47	1.50	2.5
Ni(1): 100, 50, 20, 10, 5, 5, 5, 2, 2, 1.						
Ni(2): 70, 70, 30, 15, 10, 2, 2, 1.						
Ni(3): 80, 60, 30, 10, 10, 2, 2, 2, 1, 1, 1.						

DIVERSITY INDICES

The number of species, *S*, is often used since it can be obtained from a mere faunal list. However, it has the great inconvenience of being strongly dependent on sample size, *N*. It can, therefore, be used only when the latter is very large, what can best be achieved by mixing a number of sites over broad time periods: general patterns emerge for the whole Tertiary, for instance (Langer, 1987; Janis, 1989), but for limited samples, estimating "diversity" by the number of species can be greatly misleading.

Richness indices taking sample size into account, such as Margalef's ($(S-1)/\ln N$) or Menhinick's (S/\sqrt{N}) can be compared only after assumption of a fixed relation between *S* and *N*, especially if sample sizes vary greatly, as here, but nothing supports this assumption. The same is true of the diversity parameter of the logseries distribution, α (defined by $S = \alpha \log_e [1 + N/\alpha]$; Williams, 1964). The same problem, again, arises with the method called rarefaction, allowing to compute (Ludwig & Reynolds, 1988) the expected number of species for a sample whose size (*N*) is smaller than that of the reference sample. If the distribution in both samples is different, a number of species lower than expected, for instance, may result from lower richness OR from lower evenness (or both), and the results are, therefore, difficult to interpret.

Other indices do not depend only on *S* and *N*; since they are influenced by the distribution of *N* across *S*, they also describe the structure of the taxonomic community.

The frequently used Shannon's diversity index, $H' = -\sum [N_i/N * \log_x N_i/N]$ assumes that all species have been sampled, which is seldom, if ever, the case in palaeontology. However, this index has the practical (but not theoretical) advantage that, even with very different sample sizes, it does not vary with *N*, provided that the proportions N_i/N remain constant. Indeed, Cruz-Urbe (1988) has shown empirically that H' and Margalef's richness index are much less dependent on sample size (provided that it is > 25) than is the number of species, *S*.

The last two diversity indexes are strongly correlated. They have the advantage of being applicable to finite samples, and their use has often been recommended (Pielou, 1975; Alatalo, 1981):

- Shannon's index applied to finite samples becomes $H'' = H' - (S-1)/N$;
- Brillouin's index involves the computation of factorials: $HB = [1/\ln(N!) - \sum 1/N(N_i!)]/N$

Evenness or dominance may also be estimated by a large number of indices (Magurran, 1988). Again, a strong limitation arises from the very different sample sizes, and from the fact that, in most cases, not all species have been sampled. Among the convenient indices, the reciprocal of Berger-Parker index = $1/BP = N/N_{imax}$, where N_{imax} is the number of specimens in the most abundant species, measures the dominance of the most common species. However, it varies erratically when samples are small, so that only comprehensive samples (e.g. whole Omo members) can be compared.

RESULTS (Fig. 1-4)

I have computed these indexes for all areas, and plotted them against ages for East African sites (Omo, West Turkana, Koobi Fora, Olduvai) in Fig. 1-4. The general patterns are:

1) Omo

There is a slight decrease in diversity from member B to member D, followed by a sharp increase until lower member G, and then a decrease to later members, but J-K-L have low numbers of specimens. However, evenness is greater in the upper part of the Shungura Formation than in G. I have also computed H" and HB for 31 sets of localities of homogeneous size ($35 < N < 65$ for most sets) in the Shungura Formation, thus of similar taphonomic context. The climax of diversity at 2.2 m.y. is clearly displayed, irrespective of S (Fig. 4).

2) West Turkana

There is a steady increase of the values of indexes from the base to the top of the Lomekwi Formation (from ≈ 3.2 to 2.5 m.y.), with a decrease at KLI, 1 m.y. later. The Pliocene increase parallels the one seen at Omo, but seems to be earlier here. It must be noted, however, that samples sizes are here very small.

3) Koobi Fora

Again, sample sizes are small here, and this probably accounts for the wide range of values at each time-period. On the average, however, the same pattern emerges: increase in diversity from the Upper Burgi Formation to the KBS member, followed by a decrease in the Okote member. The curves for evenness indices are similar. Localities in the Karari Ridge (areas 105, 129, 130, 131) have lower values than others in the upper Burgi Formation; this might be due either to their slightly more recent ages (Brown and Feibel, 1991), or to a different environment. Although all localities are not precisely dated, changes here occur slightly later than at Omo.

4) Olduvai

The earliest localities of lower bed I, DK I, FLK I and level 6 of FLKN I, plus BK II in lower bed II, have the highest diversity values. All other localities in bed I, lower and middle bed II have lower indices.

5) South-Africa

All these have values consistently higher than their East African contemporaries, perhaps because of partial mixing of faunas (Partridge et al., 1991). All indices decrease from Sterkfontein member 4 to Kromdraai, but increase later to Swartkrans member 2 and Elandsfontein.

6) North-Africa

Plio-Pleistocene sites there are still poorly known, and are difficult to compare since they derive from very different areas and depositional environments, but most values are similar to East African equivalents.

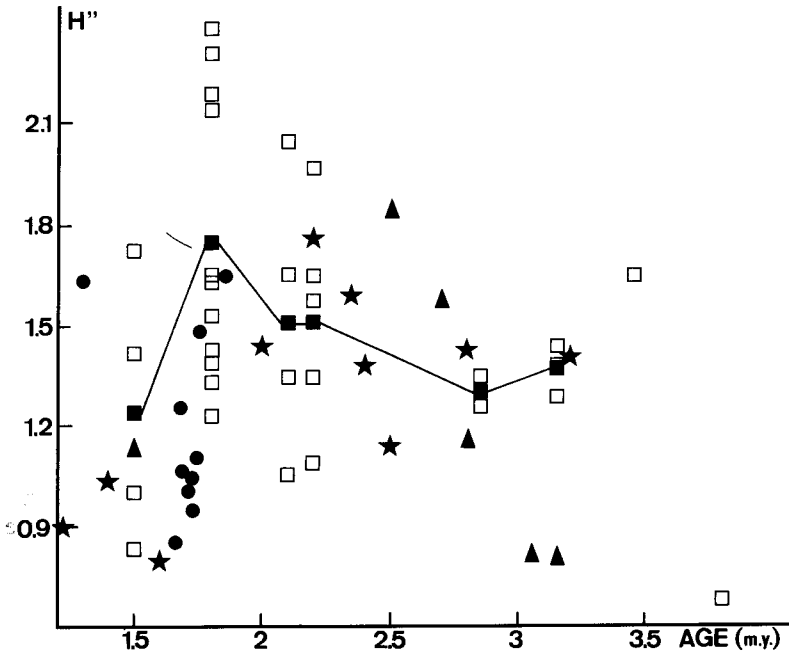


Figure 1 Plot of modified Shannon's index, H'' , versus age in million years, for Bovid East African assemblages. Open squares: individual values for Koobi Fora (member/area); the line joins the averages for each level (solid squares). Stars: Omo Shungura. Triangles: West Turkana. Circles: Olduvai.

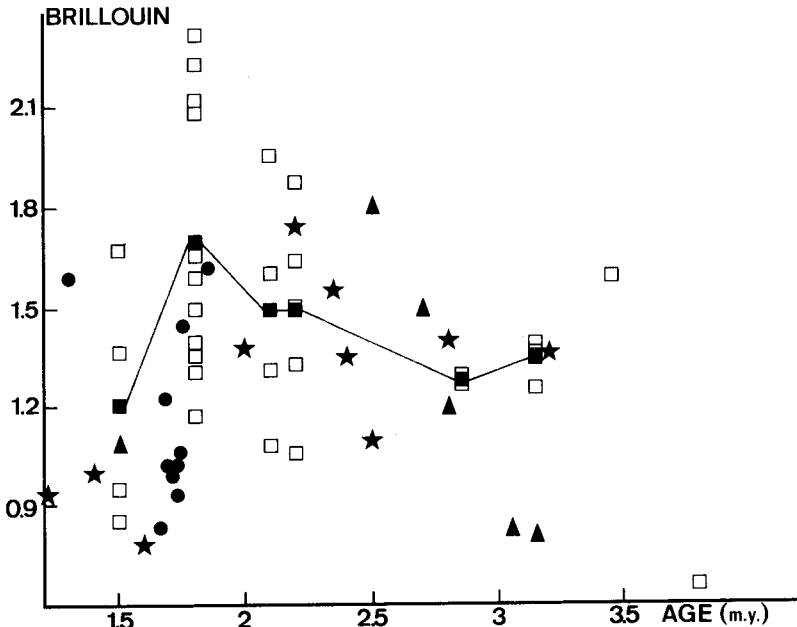


Figure 2 As for Fig. 1, but Brillouin's index (HB) in ordinate.

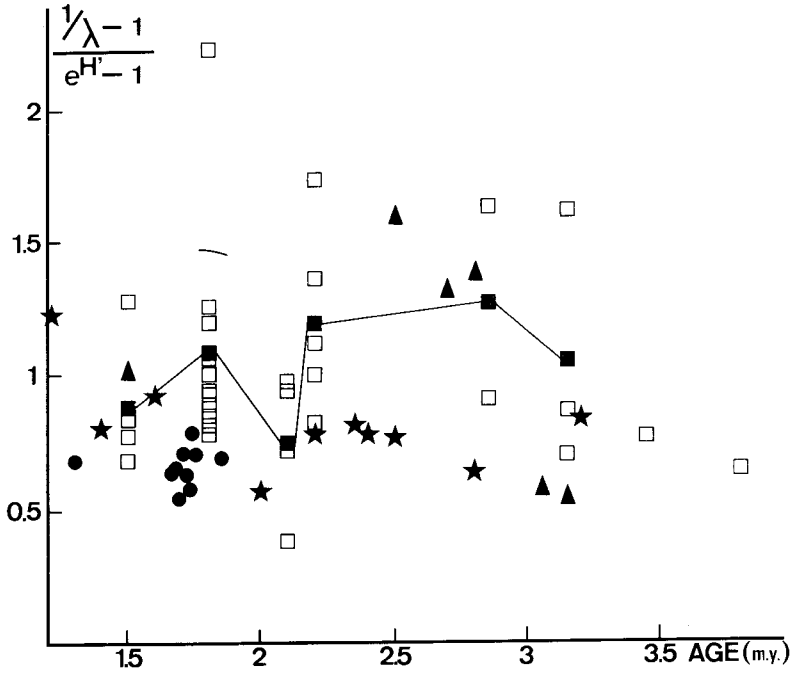


Figure 3 As for Fig. 1-3, but inverse Berger-Parker index in ordinate.

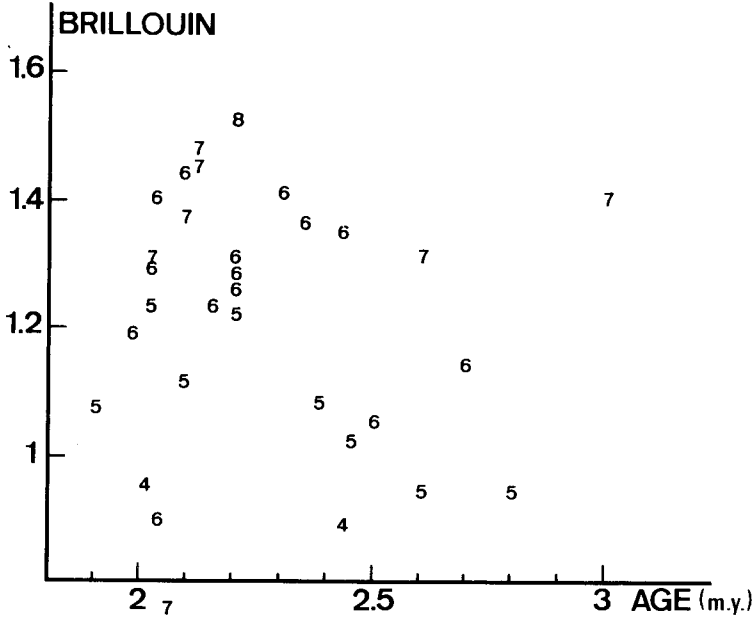


Figure 4 Plot of HB versus age for 31 sets of localities of the Omo Shungura Formation (data from the unpublished computer printout). The code for each set is the number of species, S.

In short, the three main areas in the Turkana Basin display similar patterns of evolution of species diversity around the Plio-Pleistocene: there is first an increase during the late or latest Pliocene, immediately followed by a decrease. Plio-Pleistocene South-African localities, and the earlier part of the Olduvai sequence (which covers a much shorter time-span), might be interpreted as documenting only the descending part of the curve.

The climax of diversity is reached at slightly different periods: about 2.5 m.y. ago at West Turkana, 2.2 at Omo, around 2 at Koobi Fora and perhaps Olduvai.

RANK-ABUNDANCE CURVES

The usual way of studying the distribution of N individuals across S species is to distribute the number of individuals in each species (N_i) among classes, called octaves, whose upper boundary is n times greater than the preceding one, the number of species in each class being plotted in ordinate. Any logarithmic base can be used, but I have chosen $n=2$, since S is very small. The shape of the curve can be compared, then, with theoretical models, the most common ones being the lognormal and the logseries; the distribution fitting can be estimated by χ^2 or Kolmogorov-Smirnov tests.

In the small data sets analysed here, χ^2 is not applicable, and K-S is almost always non significant. Furthermore, as Taylor (1977) pointed out, most of the lognormal distribution is "veiled" when S and N are small, and the remaining part of the curve is only slightly different from the logseries curve. Therefore, I have chosen to compare visually the curves for fossil bovid faunas to each other rather than to theoretical models (fig. 5-7).

I have used only sites where $S = 8$ and $N = 50$. Each class includes its upper boundary (i.e. class 1 includes species with 1 individual, class 2 with 2, class 3 with 3 or 4, class 4 with 5 to 8, class 5 with 9 to 16, class 6 with 17 to 32, etc.).

RESULTS

Most of the Pliocene East-African sites do not follow closely the logseries model, especially because of an excess in abundant species. A very consistent pattern emerges from localities dated between 3 and 2 m.y. This is especially true of Ndolanya, Omo E, Omo F, and Omo lower G, but not of Omo C. The modal class of the logseries curve is under-represented, but the common and abundant species are over-represented. The resulting cumulative curve (fig. 5) displays a plateau at intermediate octaves, and a steep second half. Omo upper G-H is very different, and follows more closely the logseries model, although there is an excess of species in the modal octave. There is no clear distinction between an intermediate flat level and a steep second part: all this second half of the curve is gently ascending.

A similar pattern can be recognized at Olduvai. At DK I and FLK I in lower bed I, there are several abundant species. At FLKN I, at the top of bed I, and also at HWK East II, in lower bed II, there are only 1 or 2 abundant, or very abundant, species, but fewer common species (1 or 2 octaves above modal octave) than expected, and more rare species. The resulting curves for these localities (fig. 6) reach more quickly high levels (at octave 5, for instance, all of them are above the curves for DK I and FLK I) but their second parts are less steep.

At West Turkana and Koobi Fora, there are few "localities" (stratigraphic member in one geographic area) with $N = 50$, but most of them have very high S/N ratios and

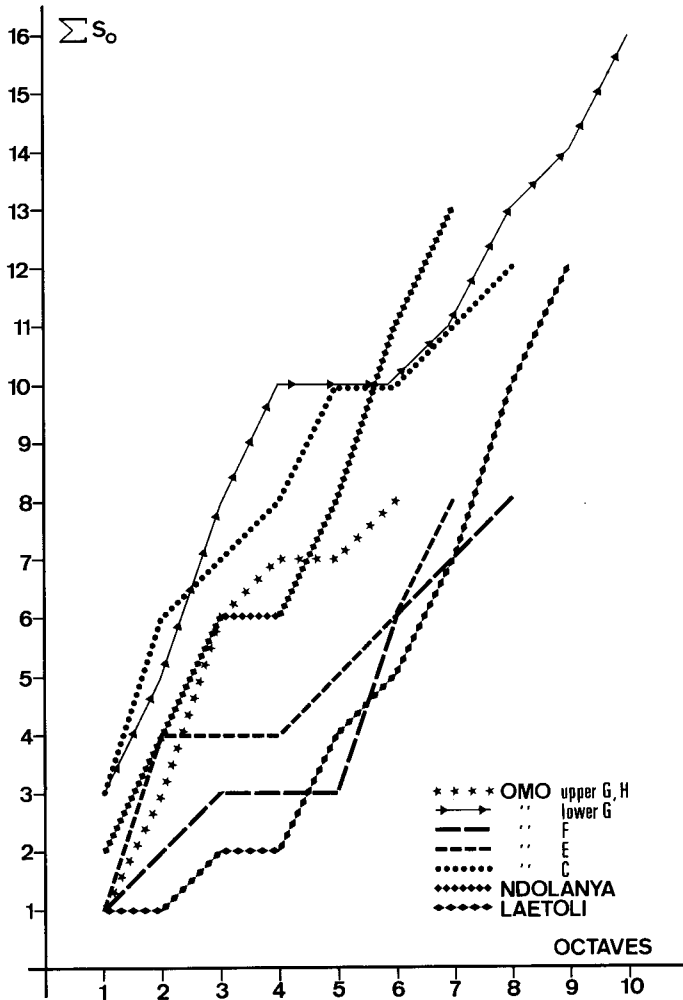


Figure 5 Rank-abundance curves of Bovid species for Laetoli and Omo Shungura. Cumulative number of species (S_0) in ordinate, octaves of species-abundance in abscissa (1: 1 specimen; 2: 2 specimens; 3: 3-4 specimens; 4: 5-8 specimens; 5: 9-16 specimens...)

consequently very high numbers of rare species. The distributions are usually in good agreement with the logseries model, but this may simply stem from the low number of specimens. The earlier locality where $N > 50$ is the upper Burgi Formation in area 130, in the Karari Ridge, which has 14 rare species and 1 (*Kobus sigmoidalis*) very common one; this must be strongly biased taphonomically. Other suitable localities all belong to the KBS member, and all have very similar, regular steep shape, similar to Olduvai DK I-FLK I and Omo lower G (but without the intermediate flat level). The Bovid assemblage of the KBS member in area 103 follows even rather closely the broken-stick model, the most equitable state of species-abundance relations.

All curves for South-African localities are steep and regular, except the curve for Swartkrans member 1, which is flat for the octaves of common species, and has only 2 very abundant species.

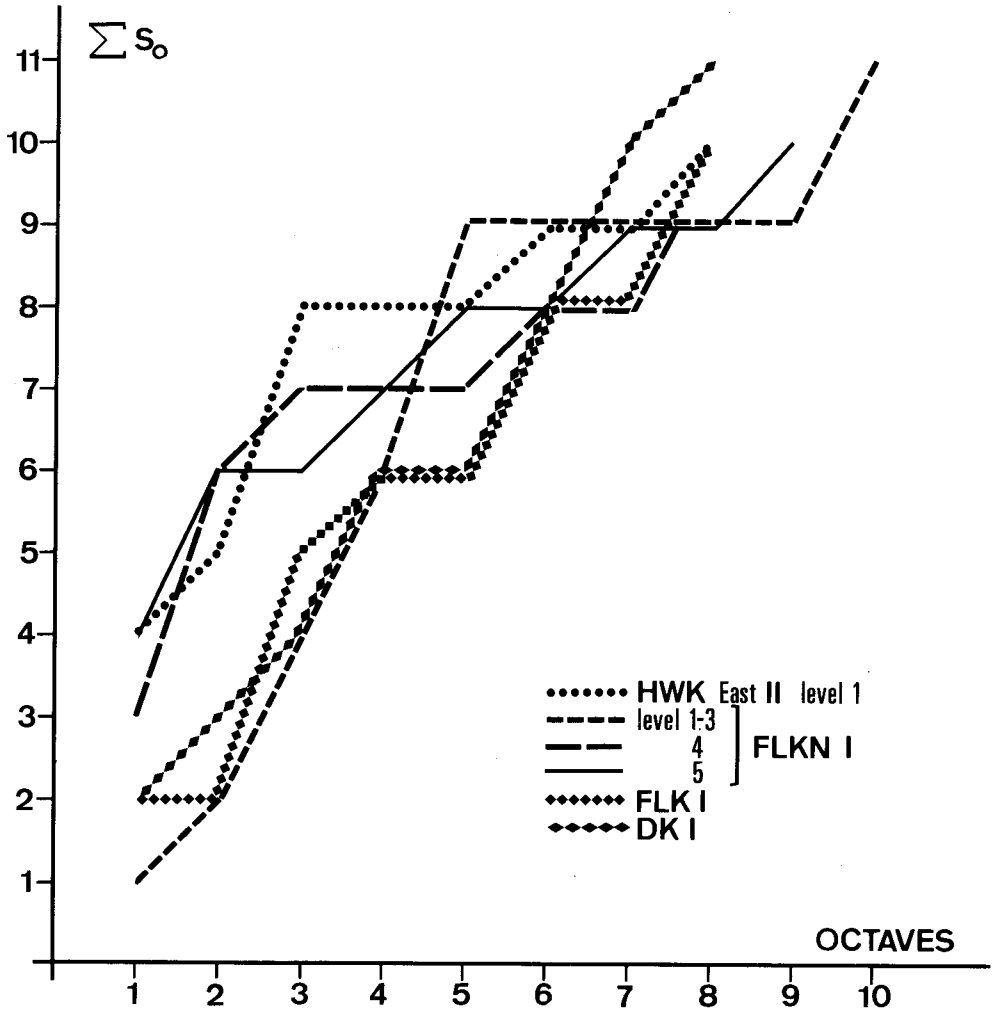


Figure 6 As for Fig.5, for Olduvai.

Of the 2 relevant sites in North-Africa, Ahl al Oughlam and Ain Boucherit, the former, and earlier, has more species of intermediate abundance. As far as the two sites can be compared (one is a fissure-filling on the Atlantic coast, the other an open-air site in Eastern Algeria), they do not document the same evolution as in the rest of Africa.

INTERPRETATION

Although species-diversity is a widely used concept, it is far from being fully understood (Brown, 1988). Apart from some very general and obvious rules (e.g. diversity is greater in the tropics than in the Arctic, in forests than in deserts...), it cannot be explained in a simple way. Currie (1991) has shown that the best correlate of species diversity in the 4

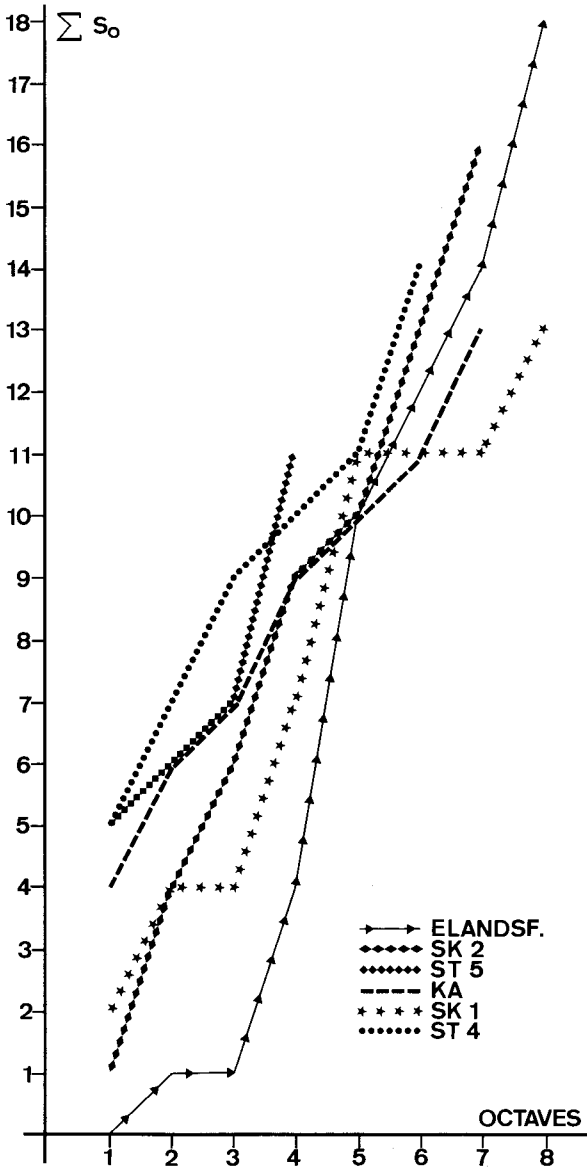


Figure 7 As for Fig. 5-6, for South-African localities.

classes of terrestrial vertebrates in North-America is potential evapotranspiration, a measure of available energy, of which temperature or solar radiation are approximations. Often, and especially at the family level, the diversity/productivity curve has a humped shape, with a peak of diversity at intermediate level of productivity, in accordance with Tilman's model (1982), observed by Abramsky and Rosenzweig (1984) for some rodents. This may not be valid at higher taxonomic levels, however, since the peaks are

reached at different levels of productivity in each family or order, as Owen (1990) has shown. There is no doubt that the scales (spatial and taxonomic) influence the observed pattern.

It has also been suggested (Owen, 1990) that species richness might be dependent upon environmental disturbance (such as erratic variations in temperature or rainfall). Moderate disturbance would allow a greater number of species to co-exist, while species-diversity would be lower in either more stable, or excessively stressed environments.

Examination of the species-abundance curves at sites where S and N are large enough, especially Omo Shungura members E-G, Olduvai lower bed I and most South-African sites, show that high diversity is associated with several common and abundant species, suggesting favourable conditions.

The succeeding decrease in diversity and increase in the number of uncommon and rare species, with only one or two very abundant species, could be interpreted as the effect, down the slope of the hump, of an increase (right slope) or decrease (left slope) of disturbance and/or productivity. Choice between these hypotheses should involve examination of correlated climatic events.

Indeed, we may notice, first, the apparent synchronism between the dates of changes in faunal diversity and the periods of known faunal and climatic changes. Gradual cooling at the end of the Pliocene (Zinderen-Bakker and Mercer, 1986) resulted in the expansion of savannas, increase in proportion of grazing antelopes and perhaps emergence of *Homo*. At West Turkana, major changes took place in the upper Lomekwi Formation (Harris et al., 1988); at Omo during member G of the Shungura Formation (Coppens, 1975; Bonnefille, 1976; Gentry, 1985; Bonnefille and Vincens, 1985); at Koobi Fora, the expansion of grassland, as well as disappearance of some antelopes (*Kobus oricornis*, *Tragelaphus nakuae*) post-date same changes at Omo (Bonnefille, 1984; Bonnefille and Vincens, 1985; Vincens, 1987; Feibel and Harris, 1991). In South-Africa, Vrba (1985b) has noted a sharp increase in Alcelaphines + Antilopines between Sterkfontein member 4 and Swartkrans member 1; two species only form the bulk of the bovid fauna in this latter site.

In each case, therefore, changes in diversity are associated with ecological or taxonomic changes, with the same diachronism: West Turkana pre-dates Omo, which pre-dates Koobi Fora.

Correlation with global climatic fluctuations (Zinderen-Bakker and Mercer, 1986) is not straightforward. Major cooling started at ± 2.5 m.y.; it resulted in opening of environments, and probably decrease of available energy and productivity, of plant diversity and habitat heterogeneity, and perhaps in more marked climatic irregularity. This might explain decrease of diversity at West Turkana, while only further cooling (around 2 m.y.) affected other areas of the Turkana basin, and Olduvai.

Some later localities (Omo J-K-L, Kromdraai, Elandsfontein, Ternifine) have more even assemblages, as shown by higher evenness indices and/or steeper curves. This suggests that a new equilibrium was reached by middle and late lower Pleistocene times.

CONCLUSION

The analysis of mammalian diversity and species-abundance relations is probably an efficient way of studying late Cenozoic ecological changes. Some of the biases mentioned above could probably be reduced, but the small sample size for large mammals remains the chief limitation, especially in North-Africa. Only rodents would overcome this problem, while retaining some of the advantages of bovids, but their

ecological links with hominids are certainly weaker. Cruz-Uribe (1988) has even noticed that sometimes they give opposite results. Recovery of large, homogeneous, samples of large mammals remains of prime importance for the understanding of environmental changes.

Acknowledgements

I thank E. Vrba and F. Surlyk for comments on an earlier version of this paper, and Y. Coppens, College de France, for constant support.

References

- Abramsky, Z., and Rosenzweig, M.L., 1984. Tilman's predicted productivity-diversity relationship shown by desert rodents. *Nature*, **309**: 150-151.
- Alatalo, R.V., 1981. Problems in the measurement of evenness in ecology. *Oikos*, **37**: 199-204.
- Amani, F., 1991. La faune du gisement à Hominidés du Jebel Irhoud. Contribution à l'étude de la chronologie et de l'environnement du Quaternaire marocain. *Unpubl. thesis univ. Rabat*.
- Andrews, P., Lord, J.M. and Nesbit-Evans, E.M., 1979. Patterns of ecological diversity in fossil and modern mammalian faunas. *Biological Journal of the Linnean Society*, **11**: 177-205.
- Arambourg, C., 1979. *Vertébrés villafranchiens de l'Afrique du Nord (artiodactyles, carnivores, primates, reptiles, oiseaux)*. Singer-Polignac, Paris.
- Behrensmeyer, A.K., 1991. Terrestrial Vertebrate accumulations. Chap. 6: 291-335, in: P.A. Allison and D.E.G. Briggs, *Taphonomy: releasing the data locked in the fossil record*. Plenum Press, New York.
- Bonis, L.de, Bouvrain, G., Geraads, D. and Koufos, G. 1992. Diversity and paleoecology of Greek late Miocene mammalian faunas. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **91**: 99-121.
- Bonnefille, R., 1976. Palynological evidence for an important change in the vegetation of the Omo basin between 2.5 and 2 million year. In: Y. Coppens, F.C. Howell, G.L.I. Isaac and R.E.F. Leakey (Eds), *Earliest Man and environments in the Lake Rudolph basin*. Univ. Chicago Press, p.421-432.
- Bonnefille, R., 1984. Cenozoic vegetation and environments of early Hominids in East Africa. In: *The evolution of the East Asian environment*, vol. 2: 579-612, Centre of Asian Studies, Hong Kong.
- Bonnefille, R. and Vincens, A. 1985. Apport de la palynologie à l'environnement des Hominidés d'Afrique Orientale. In: *L'environnement des Hominidés au Plio-Pléistocène*. Fondation Singer-Polignac. Masson, Paris, p.237-278.
- Brown, F.H. and Feibel, C.S., 1991. Stratigraphy, depositional environments and palaeogeography of the Koobi Fora Formation. In: J.M. Harris (Editor): *Koobi Fora Research Project*, Vol. 3, The fossil Ungulates: geology, fossil Artiodactyls and palaeoenvironments, Clarendon Press, Oxford, p.1-30.
- Brown, J.H. 1988. Species diversity. In: A.A. Myers and P.S. Giller (Eds), *Analytical Biogeography*. Chapman & Hall, London, p.57-89.
- Coppens, Y. 1975. Evolution des Hominidés et de leur environnement au cours du Plio-Pléistocène dans la basse vallée de l'Omo en Ethiopie. *Comptes Rendus de l'Académie des Sciences*, Paris, D, 281: 1693-1696.
- Cruz-Uribe, K. 1988. The use and meaning of species diversity and richness in archaeological faunas. *Journal of Archaeological Science*, **15**(2): 179-196.
- Cruz-Uribe, K. and Klein, R.G. 1986. Pascal Programs for computing taxonomic abundances in samples of fossil Mammals. *Journal of Archaeological Science*, **13**: 171-187.
- Currie, D.J. 1991. Energy and large-scale patterns of animal- and plant-species richness. *American Naturalist*, **137**(1): 27-49.

- Denys, C. 1990. Implications paléoécologiques et paléobiogéographiques de l'étude de rongeurs plio-pléistocènes d'Afrique Orientale et Australe. *Mémoires des Sciences de la terre, Université P. et M. Curie*, **428** p.
- Feibel, C.S., Harris, J.M. and Brown, F.H. 1991. Palaeoenvironmental context for the late Neogene of the Turkana basin. In: J.M. Harris (Editor): *Koobi Fora Research Project* Vol. 3, The fossil Ungulates: geology, fossil Artiodactyls and palaeoenvironments, Clarendon Press, Oxford, p. 321-370.
- Gentry, A.W. 1985. The Bovidae of the Omo group deposits, Ethiopia. In: Y. Coppens and F.C. Howell (Editors), *Les faunes plio-pléistocènes de la basse vallée de l'Omo (Ethiopie)*, vol. 1. p. 119-191.
- Gentry, A.W. 1987. Fossil Bovidae from Laetoli. In: M.D. Leakey and J.M. Harris (Editors), *Laetoli: a Pliocene site in Northern Tanzania*, Clarendon Press, Oxford, p. 378-408.
- Gentry, A.W. and Gentry, A., 1978. Fossil Bovidae (Mammalia) of Olduvai Gorge, Tanzania, Part II. *Bulletin of the British Museum Natural History Geology*, **30**(1): 1-83.
- Geraads, D., 1981. Bovidae et Giraffidae (Artiodactyla, Mammalia) du Pléistocène de Ternifine (Algerie). *Bulletin du Muséum national d'Histoire Naturelle*, ser. 4, C, **3**(1): 47-86.
- Greenacre, M.J. and Vrba, E.S., 1984. Graphical display and interpretation of antelope census data in African wildlife areas, using correspondence analysis. *Ecology*, **65**(3): 984-997.
- Harris, J.M. 1991. Family Bovidae. In: J.M. Harris (Editor): *Koobi Fora Research Project*, Vol. 3, The fossil Ungulates: geology, fossil Artiodactyls and palaeo-environments, Clarendon Press, Oxford, p. 139-320.
- Harris, J.M., Brown, F.H. and Leakey, M.G. 1988. Stratigraphy and palaeontology of Pliocene and Pleistocene localities west of Lake Turkana, Kenya. *Natural History Museum of the Los Angeles County, Contributions Science*, **399**: 1-128.
- Janis, C.M., 1989. A climatic explanation for patterns of evolutionary diversity in Ungulate Mammals. *Palaeontology*, **32**(3): 463-481.
- Klein, R.G. and Cruz-Uribe. 1991. The bovids from Elandsfontein, South Africa, and their implications for the age, palaeoenvironment, and origins of the site. *African Archaeological Review*, **9**: 21-79.
- Langer, V.P., 1987. Evolutionary patterns of Perissodactyla and Artiodactyla with different types of digestion. *Zeitschrift für zoologische Systematik und Evolutionsforschung*, **25**: 212-236.
- Ludwig J.A. and Reynolds, J.F., 1988. *Statistical ecology: a primer on methods and computing* J. Wiley, New York.
- Magurran, A.E., 1988. *Ecological diversity and its measurement*. Croom Helm, London.
- Owen, J.G., 1990. Patterns of mammalian species richness in relation to temperature, productivity, and variance in elevation. *Journal of Mammalogy*, **71**(1): 1-13.
- Pagel, M.D., Harvey, P.H. and Godfrey, H.C.J. 1991. Species-abundance, biomass, and resource use distributions. *American Naturalist*, **138**(4): 836-850.
- Partridge, T.C., Tobias, P.V. and Hughes, A.R. 1991. Paléoécologie et affinités entre les Australopithécins d'Afrique du Sud. Nouvelles données de Sterkfontein et de Taung. *L'Anthropologie*, **95**: 363-378.
- Pielou, E.C. 1975. *Ecological diversity*. Wiley, New York.
- Raynal, J.-P., Geraads, D., Texier, J.-P. and Sbihi-Alaoui F.Z. 1990. Un nouveau gisement paléontologique du Plio-Pléistocène du Maroc: Ahl al Oughlam (ancienne carrière Deprez). *Comptes Rendus de l'Académie des Sciences*, Paris, Sér. II, **310**: 315-320.
- Rose, K.D. 1981. Composition and species diversity in Paleocene and Eocene mammal assemblages: an empirical study. *Journal of Vertebrate Palaeontology*, **1**(3-4): 367-388.
- Sesé, C., 1991. Interpretación paleoclimática de las faunas de micromamíferos de Mioceno, Plioceno y Pleistoceno de la cuenca de Guadix-Baza (Granada, España). *Estudios geológicos*, **47**: 73-83.
- Solounias, N. and Dawson-Saunders, B. 1988. Dietary adaptations and paleoecology of the late Miocene Ruminants from Pikermi and Samos in Greece. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **65**: 149-172.
- Tilman, D. 1982. *Resource competition and community structure*. Princeton Univ. Press.

- Vincens, A., 1987. Environnements botanique et climatique des Hominides de l'Est Turkana, Kenya, entre 2,0 et 1,4 millions d'années: apport de la palynologie. In: J.A. Coetzee (Editor), *Palaeoecology of Africa*, Balkema, Rotterdam, 18: 257-269
- Vrba, E. S. 1976. The fossil Bovidae of Sterkfontein, Swartkrans and Kromdraai. *Transvaal Museum Memoirs*, 27:1-166.
- Vrba, E.S. 1980. The significance of bovid remains as indicators of environment and predation patterns. In: A.K. Behrensmeyer et A.P. Hill, *Fossils in the making*, p.247-271, Univ. Chicago Press.
- Vrba, E. S. 1984. Patterns in the fossil record and evolutionary processes. In: M.W. Ho and P.S. Saunders (Editors), *Beyond Neo-Darwinism*, p.115-142, Academic Press, London.
- Vrba, E.S. 1985a. Ecological and adaptative changes associated with early Hominid evolution. In: E.Delson (Editor), *Ancestors: the hard evidence.*, p. 63-71, Alan Liss, New York.
- Vrba, E.S. 1985b. Palaeoecology of early Hominidae, with special reference to Sterkfontein, Swartkrans and Kromdraai. In: *L'environnement des Hominidés au Plio-Pleistocene*. Fondation Singer-Polignac. Masson, Paris, p. 345-369
- Vrba, E.S. 1989 The environmental context of the evolution of early Hominids and their culture. In: R. Bonnichsen and M.H. Sorg (Eds), *Bone modification*. Center for the Study of the first Americans, Orono, Maine. p. 27-42.
- Walter, R.C., Manega, P.C., Hay, R.L., Drake, R.E. and Curtis, G.H. 1991. Laser-fusion $^{40}\text{Ar}/^{39}\text{Ar}$ dating of Bed I, Olduvai Gorge, Tanzania. *Nature*, 354: 145-149.
- Western, D., 1980. Linking the ecology of past and present mammals communities. In: A.K.Behrensmeyer et A.P. Hill, *Fossils in the making*, p.41-54, Univ. Chicago Press.
- Williams, C.B., 1964. *Patterns in the balance of nature and related problems in quantitative ecology*. Academic Press, London.
- Zinderen Bakker, E.M.van, and Mercer, J.H., 1986. Major late Cainozoic events and palaeo-environmental changes in Africa in a worldwide context. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 56: 217-235.

APPENDIX

List of the localities, with source of data, approximative age (A), number of species (S), number of specimens (N) and number of specimens in each species (N_i).

	A	S	N	N_i
North-Africa				
Ahl al Oughlam (Raynal <i>et al.</i> , 1990, and unpubl.)	2.5	7	84	40, 15, 12, 6, 6, 4, 1.
Aïn Boucherit (Arambourg, 1979, and unpubl.)	2	7	110	48, 39, 16, 3, 2, 1, 1.
Ternifine (Geraads, 1981, and unpubl.)	0.7	11	224	82, 55, 54, 16, 7, 4, 2, 1, 1, 1, 1.
J. Irhoud (Amani, 1991)	0.1	12	58	21, 9, 8, 5, 4, 3, 3, 1, 1, 1, 1, 1.
East-Africa				
Laetoli (Gentry, 1987)	3.5	12	775	175, 136, 117, 97, 85, 55, 54, 28, 15, 9, 3, 1.

	A	S	N	N _i
Ndolanya beds (Gentry, 1987)	2.7	13	167	36, 36, 23, 22, 20, 9, 9, 3, 3, 2, 2, 1, 1.
Omo Shungura (Gentry, 1985)				
Member B	3.2	7	60	23, 15, 14, 3, 2, 2, 1.
" C	2.8	12	192	92, 55, 16, 10, 7, 3, 2, 2, 2, 1, 1, 1.
" D	2.5	7	65	31, 23, 7, 1, 1, 1, 1.
" E	2.45	8	143	56, 49, 20, 11, 2, 2, 2, 1.
" F	2.35	8	201	79, 39, 31, 26, 19, 4, 2, 1.
" lower G	2.2	16	1075	337, 260, 205, 104, 91, 47, 7, 6, 4, 4, 3, 2, 2, 1, 1, 1.
" upper G, H	2	9	53	29, 6, 4, 3, 3, 3, 2, 2, 1.
" J	1.6	4	10	6, 2, 1, 1.
" K	1.4	5	16	9, 2, 2, 2, 1.
" L	1.2	5	8	4, 1, 1, 1, 1.
Olduvai (Gentry & Gentry, 1978)				
DKI	1.85	11	277	120, 44, 39, 29, 26, 7, 5, 3, 2, 1, 1.
FLK I	1.75	10	206	79, 73, 18, 17, 7, 4, 3, 3, 1, 1.
FLKN I level 6	1.74	6	54	23, 23, 4, 2, 1, 1.
" " 5	1.73	10	250	170, 56, 9, 7, 2, 2, 1, 1, 1, 1.
" " 4	1.72	9	108	65, 31, 3, 2, 2, 2, 1, 1, 1.
" " 1-3	1.71	11	760	414, 293, 11, 9, 9, 8, 6, 4, 3, 2, 1.
HWK E II level 1	1.69	10	122	80, 26, 4, 3, 3, 2, 1, 1, 1, 1.
" " 2	1.68	9	94	50, 23, 11, 4, 2, 1, 1, 1, 1.
" " 3-5	1.67	6	72	49, 17, 2, 2, 1, 1.
BK II	1.3	12	80	28, 26, 7, 5, 3, 3, 2, 2, 1, 1, 1, 1.
West Turkana (Harris <i>et al.</i> , 1988)				
Lomekwi 4	3.15	6	21	15, 2, 1, 1, 1, 1.
Lomekwi 5	3.05	6	16	11, 1, 1, 1, 1, 1.
Lomekwi 9	2.8	7	10	4, 1, 1, 1, 1, 1, 1.
Lomekwi 1	2.7	7	21	5, 4, 3, 3, 3, 2, 1.
Kangatukuseo 2	2.5	12	21	4, 3, 2, 2, 2, 2, 1, 1, 1, 1, 1.
Kalochoro 1	1.5	5	15	7, 3, 2, 2, 1.
Koobi Fora (Harris, 1991)				
Member/area				
Moiti/250	3.8	4	19	14, 3, 1, 1.
Lokochot/117	3.45	11	41	13, 12, 5, 2, 2, 2, 1, 1, 1, 1, 1.
Low. Tulu Bor/117	3.15	8	29	11, 6, 6, 2, 1, 1, 1, 1.
Lower T.B./202	3.15	6	12	3, 3, 2, 2, 1, 1.
Lower T.B./204	3.15	10	24	11, 5, 1, 1, 1, 1, 1, 1, 1, 1.
Upper T.B./202	2.85	7	11	3, 3, 1, 1, 1, 1, 1.
Upper T.B./203	2.85	7	22	9, 5, 3, 2, 1, 1, 1.
Upper Burgi/14	2.2	9	30	12, 4, 4, 3, 2, 2, 1, 1, 1.
Upper Burgi/100	2.2	11	43	10, 7, 6, 5, 3, 3, 2, 2, 2, 2, 1.

	A	S	N	N _i
Upper Burgi/102	2.2	11	20	6, 3, 2, 2, 1, 1, 1, 1, 1, 1.
Upper Burgi/104	2.2	5	9	3, 2, 2, 1, 1.
Upper Burgi/115	2.2	7	14	4, 3, 3, 1, 1, 1, 1.
Upper Burgi/105	2.1	13	48	10, 9, 5, 5, 4, 4, 3, 2, 2, 1, 1, 1, 1.
Upper Burgi/129	2.1	6	12	6, 2, 1, 1, 1, 1.
Upper Burgi/130	2.1	15	57	36, 4, 2, 2, 2, 2, 1, 1, 1, 1, 1, 1, 1, 1.
Upper Burgi/131	2.1	12	40	13, 12, 3, 2, 2, 2, 1, 1, 1, 1, 1, 1.
KBS/6	1.8	7	15	5, 3, 3, 1, 1, 1, 1.
KBS/8B	1.8	6	17	7, 4, 3, 1, 1, 1.
KBS/12	1.8	8	17	7, 2, 2, 2, 1, 1, 1, 1.
KBS/15	1.8	10	21	7, 5, 2, 1, 1, 1, 1, 1, 1, 1.
KBS/101	1.8	11	15	3, 2, 2, 1, 1, 1, 1, 1, 1, 1.
KBS/102	1.8	17	74	17, 16, 7, 5, 5, 5, 4, 3, 3, 2, 1, 1, 1, 1, 1, 1, 1.
KBS/103	1.8	19	130	23, 17, 16, 14, 13, 10, 8, 6, 4, 3, 3, 3, 2, 2, 2, 1, 1, 1, 1.
KBS/104	1.8	17	89	15, 14, 12, 9, 7, 6, 5, 5, 4, 2, 2, 2, 2, 1, 1, 1, 1.
KBS/105	1.8	8	19	6, 4, 4, 1, 1, 1, 1, 1.
KBS/119	1.8	9	21	5, 4, 3, 3, 2, 1, 1, 1, 1.
KBS/123	1.8	18	77	15, 14, 11, 9, 6, 4, 4, 2, 2, 2, 1, 1, 1, 1, 1, 1, 1, 1.
Okote/1	1.5	5	23	13, 6, 2, 1, 1.
Okote/1A	1.5	9	31	15, 5, 3, 2, 2, 1, 1, 1, 1.
Okote/3	1.5	5	10	6, 1, 1, 1, 1.
Okote/103	1.5	10	22	5, 4, 3, 2, 2, 2, 1, 1, 1, 1.
South-Africa				
Cave sites:				
(Vrba, 1976)				
Sterkfontein 4	2.6	14	108	28, 24, 22, 13, 5, 4, 3, 2, 2, 1, 1, 1, 1, 1.
Swartkrans 1	1.7	13	241	95, 70, 13, 12, 11, 10, 8, 8, 8, 2, 2, 1, 1.
Kromdraai	1.5	14	301	169, 41, 35, 17, 12, 8, 7, 4, 2, 2, 1, 1, 1, 1.
Sterkfontein 5	1.5?	11	34	7, 7, 5, 5, 372, 1, 1, 1, 1, 1.
Swartkrans 2	1.3?	16	251	55, 46, 33, 29, 25, 21, 11, 8, 5, 5, 3, 3, 2, 2, 2, 1.
Elandsfontein	0.7	18	556	86, 86, 83, 70, 61, 36, 27, 25, 13, 12, 11, 10, 10, 9, 5, 5, 2.
(Klein and Cruz-Uribe, 1991)				