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TAPHONOMICAL AND PALEOENVIRONMENTAL STUDY OF OMO-33, A LATE PLIOCENE HOMINID LOCALITY OF THE LOWER OMO BASIN, ETHIOPIA

Zeresenay ALEMSEGHED¹, Denis GERAADS², Yves COPPENS³ & Claude GUILLEMOT⁴

KEY WORDS

Paleoenvironment, Taphonomy, Late Pliocene, Shungura, Omo, Ethiopia.

MOTS CLES

Paléoenvironnement, Taphonomie, Pliocène Supérieur, Shungura, Omo, Ethiopie.

ABSTRACT

Multivariate analyses are carried out in order to understand the taphonomy and paleoenvironment of Omo-33, an upper Pliocene Hominid locality of the Shungura formation, in the Omo Basin of south western Ethiopia. Teeth and post cranial parts are not evenly distributed within the excavated zone indicating differential deposition of various skeletal elements, at different points of the river, by the effect of hydraulic sorting. Besides, comparisons of this locality with others of similar age show the existence of preferential association between taxa, and specially of Hominids with those of open and dry environment.

RESUME

Etude taphonomique et paléoenvironnementale d'Omo-33, une localité à Hominidés du Pliocène supérieur de la Basse Vallée de l'Omo, Ethiopie.- Des analyses multivariées ont été effectuées afin de comprendre la taphonomie et le paléoenvironnement d'Omo-33, localité à Hominidés du Pliocène supérieur de la Formation de Shungura, du bassin de l'Omo, dans le sud-ouest éthiopien. Les dents et les os post crâniens ne sont pas répartis uniformément à l'intérieur de la zone fouillée, suggérant un dépôt différentiel des divers éléments anatomiques. Par ailleurs la comparaison de cette localité avec d'autres d'âges voisins démontre l'existence d'associations préférentielles de taxons, spécialement des Hominidés avec ceux de milieux ouverts et secs.

1 *Université Pierre et Marie Curie, Laboratoire de Paléontologie des Vertébrés, Case 106, 4 Place Jussieu, 75252 Paris Cedex 05, France*

2 *UMR 152, Musée de l'Homme, Place du Trocadéro, 75116 Paris et Université Pierre et Marie Curie, Laboratoire de Paléontologie des Vertébrés, Case 106, 4 Place Jussieu, 75252 Paris Cedex 05, France*

3 *Collège de France, 11 Place Marcelin-Berthelot, 75005 Paris, France*

4 *Maison des Etudes Ethiopiennes, P.O. Box - 5554, Addis Ababa, Ethiopia*

INTRODUCTION

Numerous researchers have worked in the lower Omo basin for different purposes. Thanks to them the geology and the palaeontology of this region are fairly well known, and its importance for the study of our ancestors and their environment is widely acknowledged (ARAMBOURG, 1947; COPPENS & HOWELL, 1976; HOWELL & COPPENS, 1983). The "Mission Scientifique de l'Omo" was the first important research team to carry out substantial geological works in this region (HOWELL & COPPENS, 1983).

In the sedimentary basin, the Mursi formation being the oldest, the Shungura formation is the most important for its thickness, fossil content and continuity (HEINZELIN & HAESAERTS, 1983). These authors have indicated that its total thickness is about 776 m, with an age ranging from 3.6 to 1.16 Myrs (FEIBEL *et al.*, 1989). The sediments of this formation are characterised by different depositional environments: fluvial, deltaic, and lacustrine, the first being the most important (HEINZELIN & HAESAERTS, 1983: fig. 72). In the Shungura Formation, the existence of considerable faunal evolution and climatic changes with time have already been globally suggested by different authors (COPPENS, 1975 a & b; GENTRY, 1985; BEDEN, 1987). This was supported later by palynological studies (BONNEFILLE, 1976; BONNEFILLE & VINCENS, 1985) and by general ecological considerations (BOAZ, 1985). Furthermore GERAADS & COPPENS (1995) have tested these global changes with a multidimensional study in which they pointed out that these changes were neither regular nor continuous.

Nevertheless, and despite all these efforts, detailed studies of localities, which would allow us to reconstruct the paleoenvironment of different localities for limited time and space, have never been carried out. The aim of this work is therefore, to consider the Hominid locality Omo-33, dated as 2.36 Ma, from the paleoenvironmental point of view. The advantage of this approach is that it minimises the time and space factors, thus avoiding mixing assemblages from different areas and/or time periods.

The use of mammalian faunas as indicators of paleoenvironment and paleoecology is one of the commonest methods used in the Plio-Pleistocene of Africa (ARAMBOURG, 1947; COPPENS, 1975 a & b; GENTRY, 1985; GERAADS & COPPENS, 1995; VRBA 1979, 1980). It is true that this method is usually limited by the lack of abundant data, we believe however that the formation in question provides us with the necessary information.

MATERIAL AND METHOD

Omo-33, like L398 (a locality of the same formation excavated by an American research team), is situated at the base of the member F (HEINZELIN & HAESAERTS, 1983: fig. 35). It is characterised by fluvial sediments. This locality (Omo-33) was excavated in the years 1973-1974 by a French research team (HOWELL & COPPENS, 1976). It has yielded a rich mammalian fauna including remains of *Australopithecus* and *Homo*. Part of the fauna was studied by one of us (ALEMSEGHED, 1994) in an unpublished "mémoire de DEA". The data used in the present paper come from the French catalogue which has recently been updated by C. GUILLEMOT in Addis Ababa. All information concerning each specimen are provided in this catalogue.

A multidimensional graphical technique called correspondence analysis has been employed for this study. This was conducted with the help of the software SPAD.N (Système Portable pour l'Analyse des Données). A similar method has been used and explained by GREENACRE *et al.* (GREENACRE & VRBA, 1984).

This study has two parts: first we will consider the locality in question in detail; secondly all localities from Members E and F will be taken into account.

1. Detailed Consideration of the Locality Omo-33

The importance of the consideration of detailed studies of localities before dealing with any paleoenvironmental and paleoecological reconstruction has been underlined by many authors (BEHRENSMEYER, 1978; BEHRENSMEYER & DECHANT-BOAZ, 1980; KLEIN & CRUZ-URIBE, 1984; MCGEE & MARTIN, 1995). Systematically excavated under the direction of two of us (GUILLEMOT & COPPENS), this locality has been divided into 104 squares, each square representing an area of 50 X 50 cm. All specimens are registered by square. Since the number of specimens in each square is very limited we regrouped the adjacent squares to come out with eight larger sectors (Fig. 1). These eight sectors do not include peripheral specimens which were not encompassed in either of the squares. Due to this fact, the total number of specimens collected therefrom is less than that which was collected from the whole locality.

Data : For each sector we counted the different skeletal parts belonging to different taxa. The cranial parts and horn cores are too small in number to be included in the study. For this reason we considered the teeth and the post crania only. It is also important to note that, in the

Fig. 1 : A sketch tentatively showing the different squares, sectors as well as the course of the river based on the orientation of long bones for the excavated part of the locality. Big and small arrows indicate differences in the speed of the river.

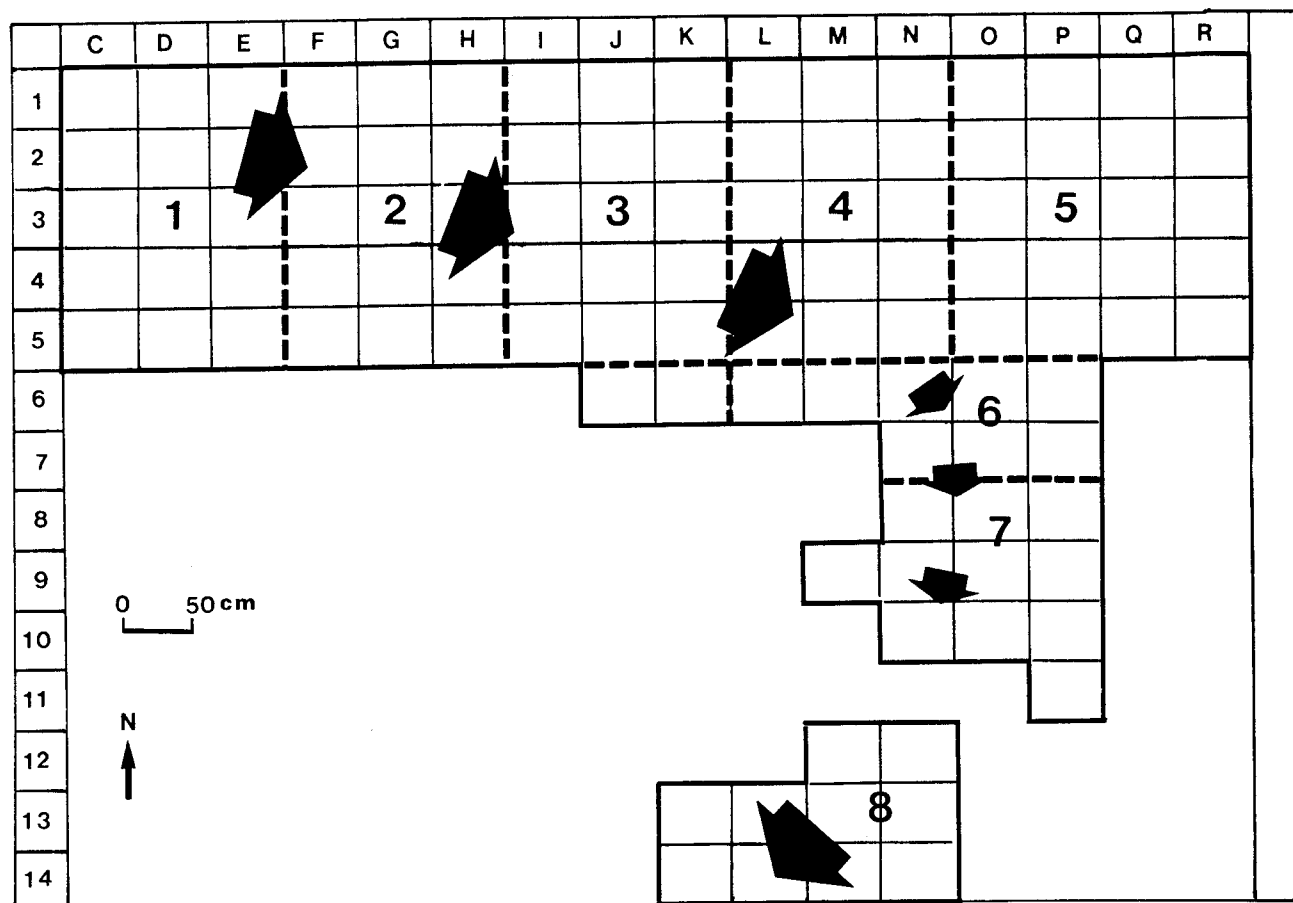


Table 1 : Number of teeth or post cranial elements belonging to each taxon **strictly** included in each sector.

	GIRAFT	SUIDT	HIPPOP	HIPPOT	CERCOT	BOVIDP	BOVIDT
SECTOR1	2	12	1	24	12	6	36
SECTOR2	6	14	4	33	10	8	42
SECTOR3	10	20	5	57	16	10	80
SECTOR4	6	11	2	40	25	6	47
SECTOR5	13	22	7	64	35	11	88
SECTOR6	1	3	2	8	4	4	14
SECTOR7	0	2	2	7	2	3	9
SECTOR8	2	3	0	4	2	1	10

detailed study of the locality, taxa are considered at family level, since determinations are not complete for lower taxonomical category, specially for the post crania.

Variables : The seven variables, columns of the contingency table, (Tabl. 1) are : Giraffid teeth, Suid teeth, Hippopotamid post crania, Hippopotamid teeth,

Cercopithecid teeth, Bovid post crania, Bovid teeth.

Sample units: These are the eight sectors and they represent the rows of the contingency table (Tabl. 1).

Results : The first axis of this analysis clearly reflects taphonomic factor. For the taxa considered, it separates the teeth on the right and the post crania on the left (Fig.

2). When we project the sectors onto the cloud of skeletal parts we note that 6 and 7 are on the left whereas 1-5 and 8 are on the right. This means that, post cranial elements are relatively better represented in 6 and 7 than in others.

As has been pointed out by some authors (HANSON, 1980; LYMAN, 1994, p. 404-416) in fluvial deposits the linear density of a given skeletal part is inversely proportional to its mean transport velocity, but directly proportional to its burial rate, i.e. the number of skeletal elements deposited per given period of time in the flowing river. Besides it can easily be conceived that the force of the river and its velocity change with differences in the topography of the bed. This phenomenon may happen abruptly and within short distances, where we have for example, widening of river mouth, increasing of bed depth, change in direction (as in meandering rivers), change in inclination or some possible combinations.

Therefore in general, in a fast flowing river, skeletal parts with higher density, teeth in our case, will have higher probability of burial and will be better represented, as in sectors 1-5 and 8. However in either of the cases listed above, where the river would lose its force all skeletal elements would have a temporary but similar probability of burial as in sectors 6 and 7. This explains the relative better representation of post cranial parts in 6 and 7. Sector 8 can be considered to

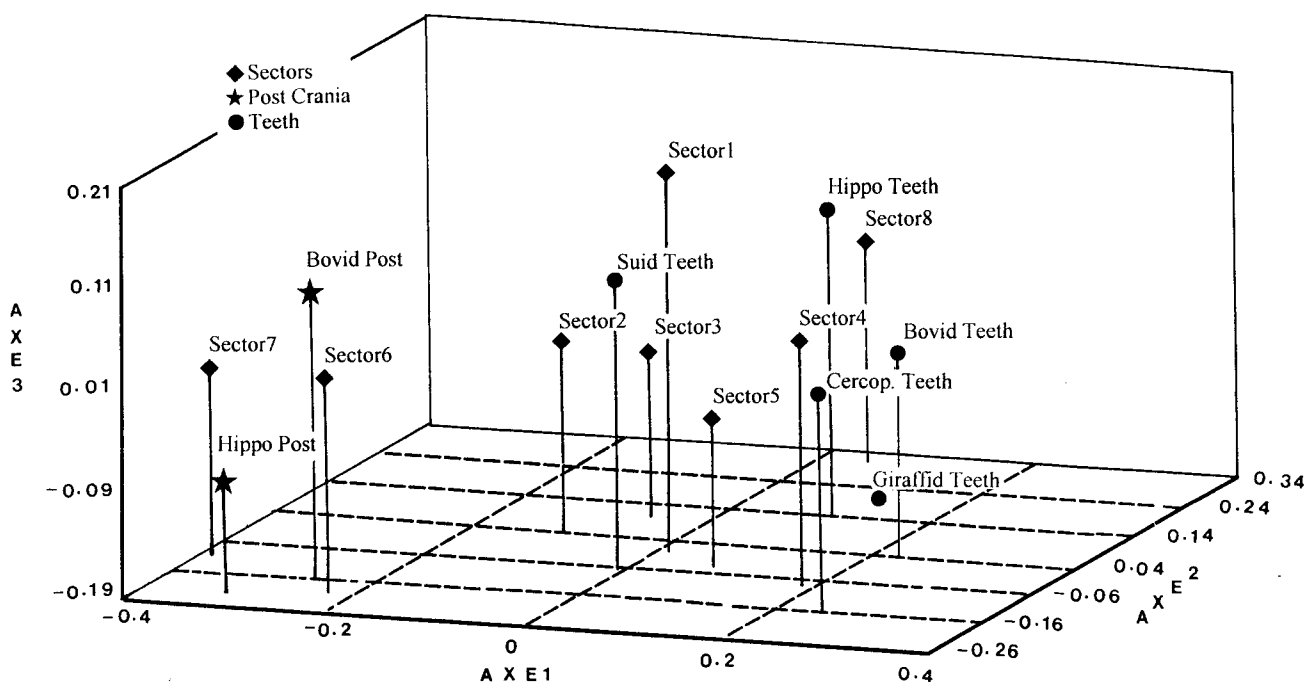
be the starting point for the river to regain its force. Fig. 1 tentatively shows the course of the river based upon the orientation of long bones for the excavated part of the locality. However, as stated above this is one of the possibilities but likely, we believe, so that this phenomenon would occur.

2. Environmental study of the locality

Besides the micro mammals, the mammalian taxa encountered in this locality are the following : *Dinotherium bozasi*, *Elephas recki* cf. *shungurensis*, *Ceratherium simum*, *Diceros bicornis*, *Hipparion* sp., *Kolpochoerus limnetes*, *Notochoerus scotti*, *Notochoerus euilus*, *Metridiochoerus jacksoni*, *Hexaprotodon protamphibius*, *Hippopotamus aethiopicus?*, *Sivatherium maurusium*, *Giraffa jumae*, *Giraffa gracilis*, *Giraffa pygmaeus*, Bovini indet., *Tragelaphus nakuae*, *Tragelaphus gaudryi*, *Kobus* sp., *Menelikia lyrocera*, *Connochaetes* sp., *Damaliscus* sp., *Aepyceros shunguruae*, *Pseudocivetta ingens*, *Papio* sp., *Rhinocolobus turkanaensis*, *Theropithecus brumpti*, *Theropithecus oswaldi*, *Australopithecus boisei?*, and *Homo habilis?*. Nonetheless, the paleoenvironmental studies will be considered only in the light of the taxa which are relatively abundant in the localities belonging to the Members E & F.

To begin with, we present the factors that could bias our

Fig. 2 : Position of sectors and the two skeletal elements of the different taxa in the space 1-3 (Contribution of the first three axes, to the total inertia : 35.39%, 28.16%, 18.13%)



interpretations and the ways by which we tried to overcome (minimise) this problem.

1. Time sampled : In such type of studies the time sampled has to be a compromise between two facts (VRBA, 1980). Firstly it should be long enough to reduce to insignificance the effects of possible catastrophes or seasonal patterns in the final sample. It must not however be too long to lead to include mixed environmental information. For the taxa considered, the time limit taken into account, which is about 0.07 my (Members E & F), seems to us compatible with these facts.

2. Area sampled : When we take samples (localities in our case) we should warrant that the area sampled is not too big to include different climate or habitat zones. The localities that we consider are small enough to avoid mixing up of different zones.

3. The influence of depositional environments on the different skeletal parts is evident. This has been shown in the first part of this paper. Differences exist even within fluvial deposits. Bearing this in mind, for all paleoenvironmental studies, we considered not only those localities which belong to the same depositional conditions but also we take in to account the same anatomical elements separately.

Finally we employed a multidimensional method. In essence this provides us with graphics which are the results of the total consideration of all factors independently of the absolute abundance of each taxon in each locality.

Data : In the first place we counted the total number of each anatomical element (ex. tooth, horn) belonging to each taxon in each locality. We then prepared a contingency table in which the lines and columns represent the localities (sample units) and the taxa (variables) respectively (Tabl. 2).

Variables : The taxa which represent the variables (columns) are : *Aepyceros*, *Alcelaphini*, *Reduncini*, *Tragelaphini*, *Bovini*, *Theropithecus*, *Hexaprotodon*, *Kolopochoerus*, *Notochoerus*, *Metridiochoerus*, *Giraffa*, *Hippopotamus*, *Elephas*, *Hominidae*.

Sample units : These are all the localities which belong to the Members E and F.

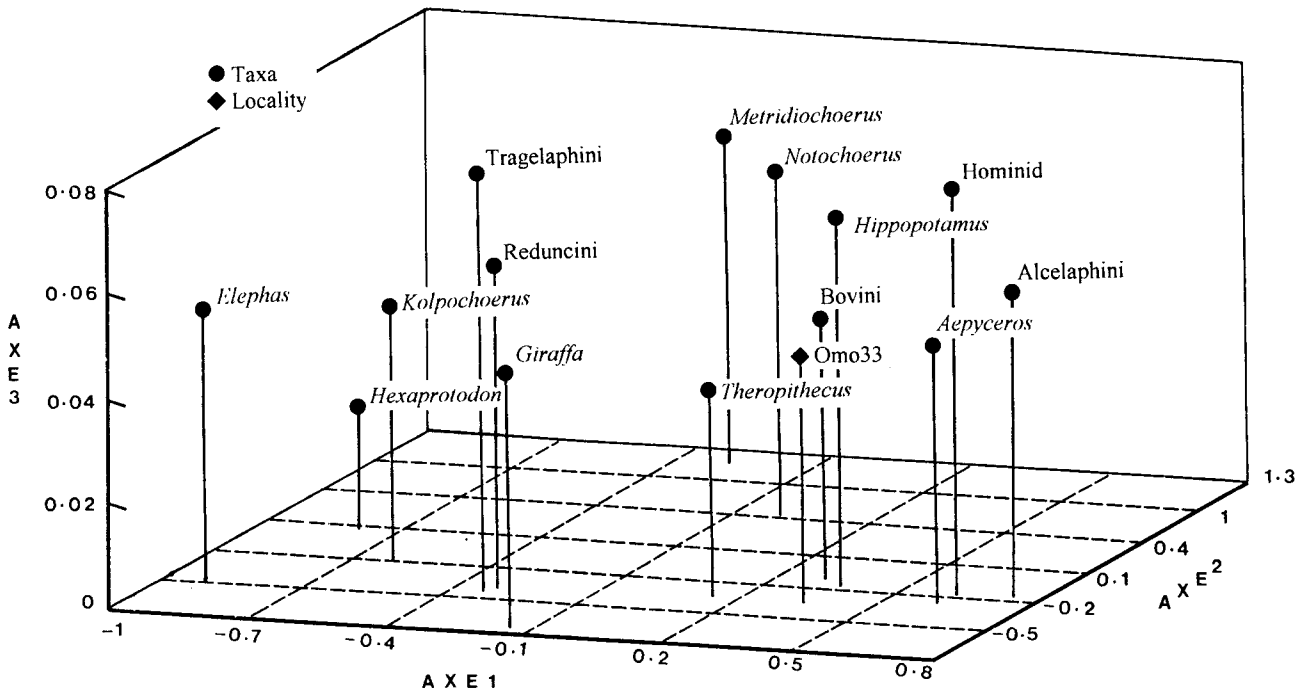
Results : The result of the analysis which was performed on the 15 localities and 14 variables (total of each taxon) is satisfactory since the first two principal axes account for 75.60 % of the total inertia. In fact, the associations that we see in Fig. 3. correspond to parallel fluctuations of the abundance of the taxa which are on the same side of the graphic, in the whole faunal composition, for the time limit and the localities considered. We believe therefore that these associations can be interpreted in terms of paleoenvironmental preferences.

We observe an association of *Alcelaphini*, *Aepyceros*, *Hominidae*, *Theropithecus*, *Bovini*, *Notochoerus*, *Metridiochoerus* and *Hippopotamus* on the one hand and *Reduncini*, *Tragelaphini*, *Kolpochoerus*, *Elephas*, *Hexaprotodon* and *Giraffa* on the other hand. In the first group there exist taxa like *Bovini* and *Aepyceros* which are rather generalist (mixed feeders), it is

Table 2 : Number of specimens belonging to each taxon in each locality.

	<i>Aepyceros</i>	<i>Alcelaphini</i>	<i>Reduncini</i>	<i>Tragelaphini</i>	<i>Bovini</i>	<i>Theropithecus</i>	<i>Hexaprotodon</i>	<i>Kolpocho.</i>	<i>Notocho.</i>	<i>Metridiocho.</i>	<i>Giraffa</i>	<i>Hippopot.</i>	<i>Elephas</i>	<i>Hominid</i>
OM01C	0	1	5	3	0	2	0	0	0	0	5	0	0	0
OM042	3	1	2	12	1	9	25	1	9	0	2	0	1	2
OM01E	0	0	1	2	0	1	1	0	0	0	1	0	1	0
OM076	14	13	22	20	12	18	52	21	31	13	5	3	2	5
OM0199	1	0	4	1	1	5	7	1	2	0	0	0	0	0
OM0167	2	0	0	1	0	3	0	0	0	0	0	0	0	0
OM0129	4	0	2	2	1	1	11	1	2	2	1	0	2	0
OM033	149	203	43	62	59	154	270	90	22	9	63	14	3	21
OM058	6	2	8	7	3	8	11	6	4	0	16	0	2	0
OM057	10	2	22	26	6	16	97	10	5	0	17	3	3	9
OM04	3	0	2	2	1	4	12	4	4	0	2	0	1	1
OM0151	1	0	4	4	0	14	19	2	4	0	3	0	3	0
OM0207	0	0	3	4	0	2	24	2	0	0	6	0	0	3
OM071	9	0	8	12	2	8	34	42	5	0	8	0	5	0
OM044	1	0	0	8	1	11	15	15	4	2	6	0	1	2

Fig. 3 : Position of different taxa and the locality Omo-33 in the space 1-3 (Contribution of the first three axes, to the total inertia : 36.6%, 22.6%, 16.4%).



however well known that species of Alcelaphini are adapted to more vegetationally open habitats (DORST & DANDELLOT, 1976; VRBA, 1980). On the contrary, in the second group, species of Reduncini are mostly wet grass grazers in swamps and grass lands but are associated with larger areas containing high proportion of wood cover. As to species of Tragelaphini they live in forests or woodlands. Moreover, morphological and metric characters, in particular the crown height of suids reveal that *Kolpochoerus* and *Metridiochoerus-Notochoerus* might have lived respectively in covered and open environments for this time limit (COOKE, 1976; HARRIS, 1983). Therefore these two groups (left and right) should globally represent a distinction between open/dry and humid/woodland environments.

GERAADS & COPPENS (1995) have shown the existence of a fluctuating equilibria between at least two types of environments for the stratigraphic limit they considered. This has been noted in the present paper, for the time limit taken into account, by the existence of two groups of taxa with different adaptations. However these authors pointed out an association of all suids indicating similar ecological adaptation but opposition between Reduncini and Tragelaphini. The present work indicates that *Kolpochoerus* opposes *Notochoerus-Metridiochoerus*. But Reduncini and Tragelaphini remain together, a phenomenon which has not been noted by GERAADS & COPPENS (1995) for another stratigraphic limit.

These two observations do not contradict, but it simply means that the equilibria followed a rather complex fluctuation pattern between more than two types of environments.

As has been shown in the first part there exist a clear difference between the various skeletal parts as far as their deposition is concerned. For this reason we performed a second analysis for the same localities and the same taxa but exclusively represented by teeth (Tabl. 3). In Fig. 4 we observe that there is no much difference as to the taxonomic association.

Finally, considering in general that paleontological localities and their fossil assemblages represent a given living paleocommunity, we projected the localities (sample units) onto the cloud of points of taxa in order to see the position of Omo-33 (Fig. 3 and Fig. 4). It is situated in the middle of the taxa which frequent open and/or dry environment which indirectly explains the paleoenvironment of this locality.

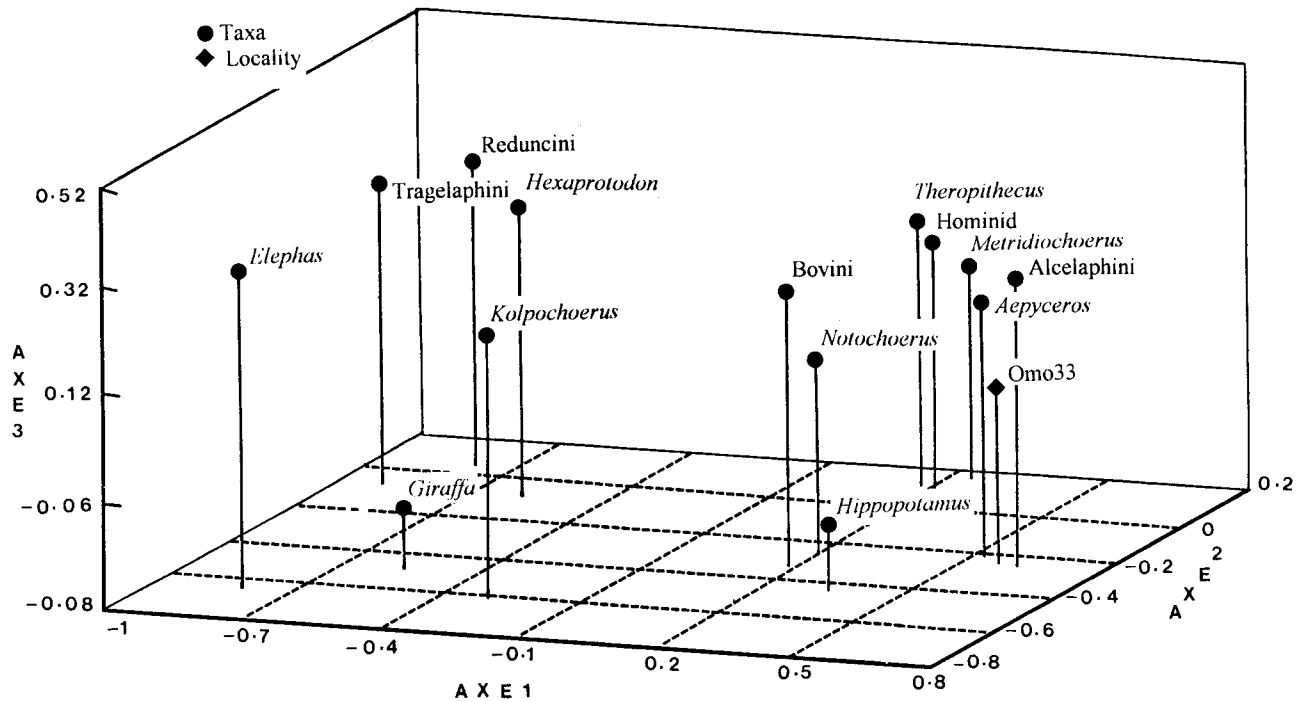
CONCLUSION

For formations where localities yield large number of specimens the use of multivariate analyses, the results of which are independent of absolute values (abundance), seems to us a good method for paleoenvironmental studies. Nevertheless these should be always preceded by detailed taphonomic studies. In the present paper we have attempted to place the

Table 3 : Number of teeth belonging to each taxon in each locality.

	Aepyceros	Alcelaphini	Reduncini	Tragelaphini	Bovini	Theropithecus	Hexaprotodon	Kolpocho.	Notocho.	Metridiocho.	Giraffa	Hippopot.	Elephas	Hominid
OMO1C	0	1	5	3	0	0	0	0	0	0	3	0	0	0
OMO42	3	1	2	12	1	8	15	1	9	0	2	0	1	1
OMO1E	0	0	1	2	0	0	0	0	0	0	0	0	1	0
OMO76	12	11	21	17	12	14	33	20	31	8	3	2	2	4
OMO199	0	0	4	0	1	3	4	1	2	0	0	0	0	0
OMO167	2	0	0	1	0	2	0	0	0	0	0	0	0	0
OMO129	4	0	2	1	1	1	5	1	2	0	1	0	2	0
OMO33	142	197	43	58	55	139	254	85	22	6	60	13	3	19
OMO58	6	2	5	4	2	7	6	5	3	0	5	0	2	0
OMO57	9	2	18	20	4	11	42	8	4	0	6	2	3	9
OMO4	3	0	2	2	1	2	8	3	4	0	0	0	1	1
OMO151	1	0	4	4	0	12	16	2	4	0	3	0	3	0
OMO207	9	0	3	3	0	0	8	2	0	0	6	0	0	2
OMO71	1	0	8	12	2	8	21	40	5	0	8	0	4	0
OMO44	2	0	0	8	1	10	2	15	4	1	5	0	1	2

Fig. 4 : Position of different taxa represented exclusively by teeth and the locality Omo-33 in the space 1-3 (Contribution of the first three axes, to the total inertia : 37.27%, 19.23%, 16.32%).



Hominid locality Omo-33 in the taphonomic and paleoenvironmental context. The latter was done mainly based on the bovids of which we know more or less the environment. More over we have noted some associations of non-bovid taxa with either of the bovid group. Of interest here are the Suidae. For the time limit

considered, *Kolpochoerus* seems to be associated with bovids of bushes or woodlands where as *Metridiochoerus* and *Notochoerus* seem to prefer open environments. These observations are coherent with what has been proposed by COOKE based on morphological characters. Besides, we are aware that

different genera and species of the Hominid family have been reported to have occupied different niches. We underline that, consideration of Hominids in family level and Suids in genus level can only permit us to understand their environment very globally. Therefore, further studies of other localities of this formation for different Members and lower taxonomical categories are to be carried out.

REFERENCES

- ALEMSEGHED, Z. (1994) - Etude Faunique et Paléocologique d'Omo-33, Un Site à Hominidés du Pliocène Supérieur d'Ethiopie. Mémoire de DEA de l'Université de Montpellier II et de Paris VI. (unpublished, deposited at the library of the "Laboratoire de paléontologie de Paris").
- ARAMBOURG, C. (1947) - Mission scientifique de l'Omo (1932-1933). Contribution à l'étude géologique et paléontologique du bassin du lac Rodolphe et de la basse vallée de l'Omo. Ed. Muséum, Paris, 1: 231-559.
- BEDEN, M. (1987) - Données préliminaires à l'étude des Elephantidés de l'Omo. In: "Les faunes Plio-Pléistocènes de la basse vallée de l'Omo (Ethiopie)", COPPENS, Y. & F.C. HOWELL (Eds.), *Cahiers de paléontologie*, travaux de paléontologie est-africaine, Ed. CNRS, Paris, 2: 1-159.
- BEHRENSMEYER, A.K. (1978) - The habitat of Plio-Pleistocene hominids in East Africa: Taphonomic and microstratigraphic evidence. In: "Early hominids of Africa", JOLLY, C. (Ed.). Ed. Duck worth, London: 166-189.
- BEHRENSMEYER, A.K. & D.E. DECHANT-BOAZ (1980) - The Recent Bones of Amboseli National Park, Kenya, in Relation to East African Paleocology. In: "Fossils in the Making, Vertebrate Taphonomy and Paleocology", BEHRENSMEYER, A.K. & A.P. HILL (Eds.) *Prehistoric Archaeology and Ecology series*: 72-93.
- BOAZ, N.T. (1985) - Early paleoecology in the Omo basin, Ethiopia. In: "L'environnement des Hominidés au Plio-Pléistocène". Fondation Singer-Polignac & Ed. Masson, Paris: 279-308.
- BONNEFILLE, R. (1976) - Palynological evidence for an important change in the vegetation of the Omo Basin between 2.5 and 2 Million years. In: "Earliest Man and environments in the Lake Rudolf Basin", COPPENS, Y., F.C. HOWELL, G.LI. ISAAC & R.F.E. LEAKEY (Eds.). University of Chicago Press, Chicago: 421-431.
- BONNEFILLE, R. & A. VINCENS (1985) - Apport de la palynologie à l'environnement des Hominidés d'Afrique orientale. In: "L'environnement des Hominidés au Plio-Pléistocène". Fondation Singer-Polignac & Ed. Masson, Paris: 237-278.
- COOKE, H.B.S. (1976) - Suidae from Plio-Pleistocene strata of the Rudolf basin. In: "Earliest Man and environments in the Lake Rudolf Basin", COPPENS, Y., F.C. HOWELL, G.LI. ISAAC & R.F.E. LEAKEY (Eds.). University of Chicago Press, Chicago: 251-263.
- COPPENS, Y. (1975a) - Evolution des Mammifères, de leurs fréquence et de leurs associations, au cours du Plio-Pléistocène dans la basse vallée de l'Omo en Ethiopie. *C.R. Acad. Sc. Paris*, 281: 1571-1574.
- COPPENS, Y. (1975b) - Evolution des Hominidés et de leur environnement au cours du Plio-Pléistocène dans la basse vallée de l'Omo en Ethiopie, *C.R. Acad. Sc. Paris*, 281: 1693-1696.
- COPPENS, Y. & F.C. HOWELL (1976) - Mammalian Faunas of the Omo Group: Distributional and Biostratigraphical Aspects. In: "Earliest Man and environments in the Lake Rudolf Basin", COPPENS, Y., F.C. HOWELL, G.LI. ISAAC & R.F.E. LEAKEY (Eds.), University of Chicago Press, Chicago: 177-192.
- DORST, J. & P. DANDELLOT (1976) - Guide des grands mammifères d'Afrique. Ed. Delachaux & Niestle, Paris: 187-279.
- FEIBEL, C.S., F.H. BROWN & I. McDUGALL (1989) - Stratigraphical Context of Fossil Hominids From the Omo Group Deposits: Northern Turkana Basin, Kenya and Ethiopia. *Am. J. Phys. Anthropol.*, 78 (4) : 595-622.
- GENTRY, A.W. (1985) - The bovidae of the Omo Group Deposits, Ethiopia. In: "Les faunes Plio-Pléistocènes de la basse vallée de l'Omo (Ethiopie)", COPPENS, Y. & HOWELL F.C. (Eds.), *Cahiers de paléontologie*, travaux de paléontologie est-africaine. Ed. CNRS, Paris, 1: 119-191.
- GERAADS, D. & Y. COPPENS (1995) - Evolution des faunes de Mammifères dans le Plio-Pléistocène de la basse vallée de l'Omo (Ethiopie) : Apport de l'analyse factorielle. *C.R. Acad. Sci. Paris*, 320: 625-637.
- GREENACRE, M.J. & E.S. VRBA (1984) - Graphical display and interpretation of antelope census data in African wild life areas, using correspondence analysis. *Ecology*, 65 (3) : 984-997.
- HANSON, C.B. (1980) - Fluvial Taphonomic Processes: Models and Experiments. In: "Fossils in the Making, Vertebrate Taphonomy and Paleocology", BEHRENSMEYER, A.K. & A.P. HILL (Eds.), *Prehistoric Archaeology and Ecology series*: 156-181.
- HARRIS, J.M. (1983) - Family Suidae. In: "Koobi Fora Research Project. The fossil ungulates: Proboscidea, Perissodactyla, and Suidae", HARRIS, J.M. (Ed.). Clarendon Press, Oxford. 2: 215-302.
- HEINZELIN, J. de & P. HAESAERTS (1983) - The Shungura Formation In: "Archives of the International

- Omo Research Expedition”, HEINZELIN, J. de (Ed.), *Annales du Musée Royal de l’Afrique Centrale*, Série 8, Sciences Géologiques, Tervuren. 85: 25-185.
- HOWELL, F.C. & Y. COPPENS (1976) - An overview of hominidae from the Omo succession, Ethiopia. *In*: “Earliest Man and environments in the Lake Rudolf Basin”, COPPENS, Y., F.C. HOWELL, G.LI. ISAAC & R.F.E. LEAKEY (Eds.). University of Chicago Press, Chicago. 522-532.
- HOWELL, F.C. & Y. COPPENS (1983) - The Omo Group. *In*: Archives of the International Omo Research Expedition, HEINZELIN, J. de (Ed.), *Annales du Musée Royal de l’Afrique Centrale*, Série 8, Sciences Géologiques, Tervuren. 85: 1-5.
- KLEIN, R.G. & K. CRUZ-URIBE (1984) - The Analysis of Animal Bones From Archaeological Sites. *Prehistoric Archaeology and Ecology Series*. The University of Chicago Press, Chicago: 63-98.
- LYMAN, R.L. (1994) - Vertebrate Taphonomy. Cambridge Manuals in Archaeology. Cambridge University Press, Cambridge: 524 p.
- McGEE, E. & L. MARTIN (1995) - Chance and the taphonomy of the hominoid assemblage from the middle Miocene site at Palsalar, Turkey. *J. Hum. Evol.*, 28: 325-341.
- VRBA, E.S. (1979) - Phylogenetic analysis and classification of fossil and recent Alcelaphini (Family Bovidae, Mammalia). *J. Linn. Soc. (Zoology)*, 11 (3): 207-228.
- VRBA, E.S. (1980) - The significance of bovid remains as indicators of environment and predation pattern. *In*: “Fossils in the Making, Vertebrate Taphonomy and Paleoecology”, BEHRENSMEYER, A.K. & A.P. HILL (Eds.), *Prehistoric Archaeology and Ecology series*. The University of Chicago Press, Chicago: 247-271.

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