

Multivariate study of late Cenozoic mammalian faunal compositions and paleoecology

L. de BONIS¹, G. BOUVRAIN², D. GERAADS³ and G. KOUFOS⁴

SUMMARY

In order to get some informations on paleoenvironment of some fossils sites we compared these sites with recent localities with respect to the taxonomic categories and the body weights of the different species. We used the number of species taxonomic categories and the repartition of body weights in some recent or fossil localities for a multivariate study. The striking parallelism between recent forest and savanna faunas plotting and the fossil localities allows to get some important evidences on the paleoenvironment.

The composition of a mammalian fauna is determined by several factors such as evolution, geography or environment. Therefore, by comparison with recent faunas, it would be possible to get some indications or evidences on the paleoecology of fossil localities by inferring from that which exists in recent communities. But, when comparing recent and fossil faunas, there is a major bias caused by the presence of man and its drastic consequence on animal wild life. African mammals seem less concerned than others by recent extinctions and would constitute the best model although several large mammals have disappeared during the last two centuries. Nevertheless, in order to use only African fau-

nas we have taken for our comparisons some Plio-Pleistocene faunas from Europe and Asia.

Some authors have used several variables to look for a link between faunal composition and paleoecology such as locomotion, feeding habits, taxonomy (ordinal level) and body size or body weight (Andrews et al., 1979 ; Valverde 1964, 1967 ; Legende, 1988). The initial aim of this work being to study late Miocene mammalian communities from Greece, we used only the latter two which can be applied to all our fossil sites. We did not take into account the micro-mammals whose presence or absence is highly dependant on the type of deposits and hydraulic sorting.

TAXONOMY

We decided to choose different taxonomic categories of different levels. For instance we conserved one category for Carnivora or for Proboscidea but several categories for Artiodactyla (Giraffidae, Hip-

1. Lab. Paléontologie Vertébrés et Paléontologie humaine, Université de Poitiers, U.A CNRS 720, 86022 Poitiers — France
2. Lab. Paléontologie Vertébrés et Paléontologie humaine, Université Paris VI, U.A. CNRS 720, 75230 Paris Cedex — France
3. Lab. Paléontologie Vertébrés et Paléontologie humaine, Université Paris VI, U.A. CNRS 49, 75230 Paris Cedex — France
4. Department of Geology, Aristotelou University, 540 06 Thessaloniki — Greece.

TABLE 1a. Recent localities.

N°	Locality	Country	Ecology	Number of species	References
01	Transvaal 10	South Africa	Tropical forest	39	Rautenbach, 1978.
02	Mont Kivu	Za're	Montane forest	40	Legendre, 1988.
03	Lamto	Ivory Coast	Tropical forest and savanna	51	Bourliere et al., 1974.
04	Makokou	Gabon	Tropical forest	45	Legendre, 1988.
05	La Maboké	Central Africa	Tropical forest	42	Legendre, 1988.
06	Ta'	Ivory Coast	Tropical forest	45	Legendre, 1988.
07	Malaisie	Malaisia	Tropical forest	35	Legendre, 1988.
08	Transvaal 7	South Africa	Savanna woodland	31	Rautenbach, 1978.
09	Lokori	Kenya	Savanna woodland	23	Legendre, 1988.
10	Transvaal 2	South Africa	Montane grassland	36	Rautenbach, 1978.
11	Kafue	Zambia	Flood plain grassland	53	Sheppe and Osborne, 1971.
12	Rukwa valley	Tanzania	Flood plain grassland and woodland	52	Andrews et al., 1979.
13	Transvaal 5	South Africa	Arid bushland	55	Rautenbach, 1978.
14	Serengeti	Tanzania	Savanna woodland	65	Legendre, 1988.
15	Transvaal 4	South Africa	Savanna woodland	33	Rautenbach, 1978.
16	Transvaal 9	South Africa	Savanna woodland	62	Rautenbach, 1978.
17	Zinave	Mozambique	Savanna woodland	41	Legendre, 1988.
18	Gabiro	Rwanda	Wooded grassland	25	Andrews et al., 1979.
19	Rwindi-Rutschuru	Rwanda	Arid bushland	27	Legendre, 1988.
20	Amboseli	Kenya	Arid bushland	42	Legendre, 1988.

TABLE 1b. Fossil localities.

Localities	Country	Number of species	Age	Bibliography
AFY Afyon (Gülyazi)	Turkey	19	Pleistocene	Becker-Platen et al., 1975
BUR Burgtonna	Germany	17	Pleistocene	Hunermann, 1978 ; Kahlke, 1978a, b ; Cohen, 1988.
CKT Zhou Kou Dian loc.1	China	52	Pleistocene	Young, 1932
ETO Etouaires	France	28	Pleistocene	Heintz et al., 1974
MAL Malusteni	Roumania	20	Pleistocene	Simionescu, 1930
OUN Oubeidiyah	Israël	32	Pleistocene	Tchernov and Guérin, 1985.
SEN Sénèze	France	27	Pleistocene	Heintz et al., 1974
STS Stranska Skala	Czechoslovakia	30	Pleistocene	Musil, 1972 ; Cohen, 1988.
SVA Saint Vallier	France	27	Pleistocene	Mein, 1990
TER Ternifine	Algeria	26	Pleistocene	Geraads et al., 1986.
VIA Viallette	France	16	Pleistocene	Heintz et al., 1974
VGS Voigstedi	Germany	25	Pleistocene	Wehrli, 1963 ; Cohen 1988.
VMI Venta Micena	Spain	24	Pleistocene	Agusti, 1987
LGM Langebaanweg QSM	South Africa	37	Pliocene	Hendey, 1981.
LGS Langebaanweg PPM 3aN	South Africa	33	Pliocene	Hendey, 1981.
ARO Arquillo	Spain	20	Late Miocene	Golpe, 1974.
AZA Azambujeira	Portugal	14	Late Miocene	Antunes, Ginsburg and Mein, 1983.
CLL Can Llobateres	Spain	41	Late Miocene	Mein, 1990.
CPO Can Ponsic	Spain	27	Late Miocene	Golpe, 1974.
DHA Jebel Hamrin	Iraq	17	Late Miocene	Thomas et al., 1980 ; Brunet and Heintz, 1983.
DIT Dytiko	Greece	22	Late Miocene	Bonis et al., 1988 ; Bonis et al. 1991.
EPP Eppelsheim	Germany	26	Late Miocene	Thenius, 1959.
HAL Halmyropotamos	Greece	21	Late Miocene	Melentis, 1967.
LUK Lukeino	Kenya	18	Late Miocene	Pickford 1978 ; Thomas, 1980.
LVF Los Valles de Fuentidueña	Spain	28	Late Miocene	Alberdi et al., 1981.
MRM Middle Maraghe	Iran	25	Late Miocene	Bernor, 1986.
MRS Upper Maraghe	Iran	17	Late Miocene	Bernor, 1986.
PIK Pikermi	Greece	48	Late Miocene	Gaudry, 1862 ; Solounias, 1981.
PMX Prochorma	Greece	13	Late Miocene	Bonis et al., 1988 ; Bonis et al., 1990.
RPI Ravin de la Pluie	Greece	15	Late Miocene	Bonis et al., 1988 ; Bonis et al., 1990.
RZO Ravin des Zouaves n°5	Greece	21	Late Miocene	Bonis et al., 1988 ; Bonis et al., 1990.
SAM Samos	Greece	47	Late Miocene	Solounias, 1981.
SHB Sahabi	Libya	29	Late Miocene	Bernor and Pavlakis, 1987.
SOB Soblay	France	19	Late Miocene	Guérin and Mein, 1971.
VAT Vathylakkos	Greece	23	Late Miocene	Bonis et al., 1988 ; Bonis et al., 1990.
VDM Venta del Moro	Spain	23	Late Miocene	Aguirre and Robbles, 1973.
YAS Yassiören	Turkey	23	Late Miocene	Ozan soy, 1957 ; Sickenberg, 1975.
BUK Bukwa	Kenya	13	Middle Miocene	Pickford, 1981.
CMA Can Mata	Spain	18	Middle Miocene	Agusti et al., 1985.

Localities	Country	Number of species	Age	Bibliography
DZE Jebel-Zelten	Libya	22	Middle Miocene	Hamilton, 1973 ; Savage and Hamilton, 1973.
FTN Fort Ternan	Kenya	26	Middle Miocene	Shipman et al., 1981.
GUM Gumba	Kenya	23	Middle Miocene	Pickford, 1981.
KAR Karungu	Kenya	23	Middle Miocene	Pickford, 1981.
LGR La Grive	France	63	Middle Miocene	Guérin, Mein, 1971.
MAB Maboko	Kenya	23	Middle Miocene	Andrews et al., 1981.
MOR Mormorot	Kenya	18	Middle Miocene	Pickford, 1981.
NAP Napak	Ouganda	27	Middle Miocene	Pickford, 1986.
PAS Pasalar	Turkey	30	Middle Miocene	Sickenberg, 1975 ; Köhler, 1987.
SAM Sant Mamet	Spain	14	Middle Miocene	Agusti et al., 1985.
SAS Sansan	France	36	Middle Miocene	Mein, 1990.

popotamidae, Bovidae...) insofar as we think they indicate important ecological differences. We took 20 taxonomic categories (tabl. 1) which were applied to 72 recent, Plio-Pleistocene or Miocene localities (tabl. 2). We numbered the species corresponding to our categories and compared all the localities to each other by mean of multivariate correspondance factor analysis (Benzecri, 1976).

a — Comparison of the recent faunas

We compared first the recent forest or more open environment African faunas (fig. 1). The first factor has clearly an ecological meaning. It separates the forest localities which cluster together from the other ones. The variables which have the most important contribution on this factor are Primates (63 %), La-

gormorphia (7,8 %) and Pholidota (7,7 %). The second factors shows the differences between three Transvaal faunas with several Lagomorpha contribution (56 %) and the other open countries faunas without, or with few rabbits but with Rhinocerotidae (20 %) and Giraffidae (6,8 %). The allotment of the other variables is more or less similar in all the localities and they are less important in this analysis.

If we add in the analysis a locality of Malaysia (fig. 2), the results are similar but a little less clear.

TABLE 2. Taxonomic categories used in the different analysis

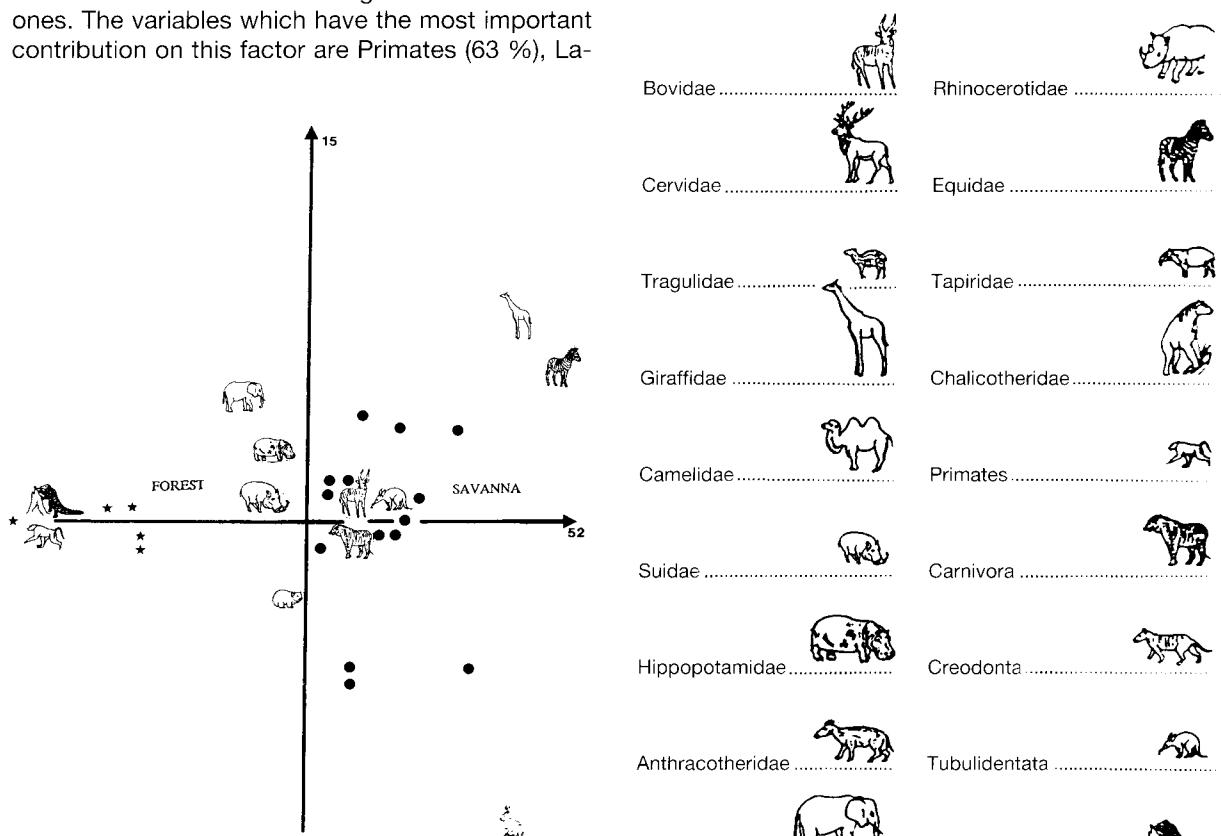


FIGURE 1. Multivariate study (Correspondance Factor Analysis) of the taxonomic compositions of recent African mammalian faunas. Plotting of the localities and variables on the plan of the first and the second factors. Stars : forest faunas, black circles : open environment faunas. For the taxonomic groups see table 2.

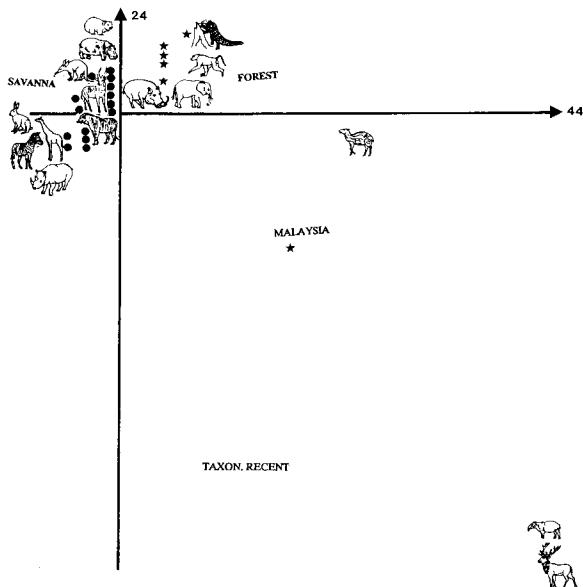


FIGURE 2. Multivariate study (C.F.A.) of the taxonomic compositions of recent mammalian African and Malaysian faunas. Legend : see fig. 1.

The originality of the Malaysian fauna gives a great importance to some variables (Tapiridae and Cervidae); it is near the African forest faunas on the first factor but it is well separated by the second one. On the other hand, while most of the total variance is expressed by the Malaysian fauna, the two groups of African sites, forest and more open environments, are less separated each other.

b — Comparison of the recent and late Miocene localities (fig. 3).

The two sets, recent and fossil, are separated by the first factor. There is a good parallelism on the second factor which separates, between the recent faunas, the open environment ones in the upper part and the forest ones in the lower part of the graph. We may note the peculiar position of the Malaysian forest fauna which is a little isolated from the African ones. It means that the ecological differences can be as important as the geographic's. In the right half of the graph, the fossil faunas are separated into two groups and we can say that it is on the same basis as for the recent sites. Forest faunas are in the lower part (Spain, France or Germany) and the open environment faunas are in the upper part (Greece, Turkey, Iran, Irak or Africa).

We can note that the Spanish localities of Arquillo and Venta del Moro plot very near the open environment localities of Greece.

The most important variables on the first factor are Primates (26,6 %) in the left side of the graph and Equidae (13,6 %), Rhinocerotidae (12,2 %) and Giraffidae (10,3 %) in the right side. The second factor can be considered as expressing ecological differences and the most important contributions are Bo-

vidae (19,2 %) for the open environment faunas versus Cervidae (18 %), Primates (16 %) and Tapiridae (13,6 %) for the more forested areas.

c — Comparison of all the recent and fossil faunas (fig. 4).

The first factor allows to distinguish the middle Miocene African faunas from all the other ones. Very important are some variables like Creodonta, Ant-hracotheriidae, Hyracoids or Tragulids. Some of these taxa are became extinct by the Middle Miocene in Eurasia and the distance is amplified by their presence. The second factor separates the other fossil faunas and the recent ones, the later's being divided in open environment and forested localities but we cannot see any clear cut division into the former's.

d — Comparison of all the fossil faunas (fig. 5).

The results are not very different from those of the latter analysis for the first factor but the second factor separates more open environment from more forested fossil localities. In the first category there are all the Greek late Miocene localities, Yassiören in Turkey, the two levels of Maraghe in Iran, Jebel Hamrin in Irak, Sahabi and Langebaanweg in Africa or the Pleistocene Turkish site of Afyon. In the second set we find the European middle Miocene sites, the western European Vallesian sites and most of the Pleis-

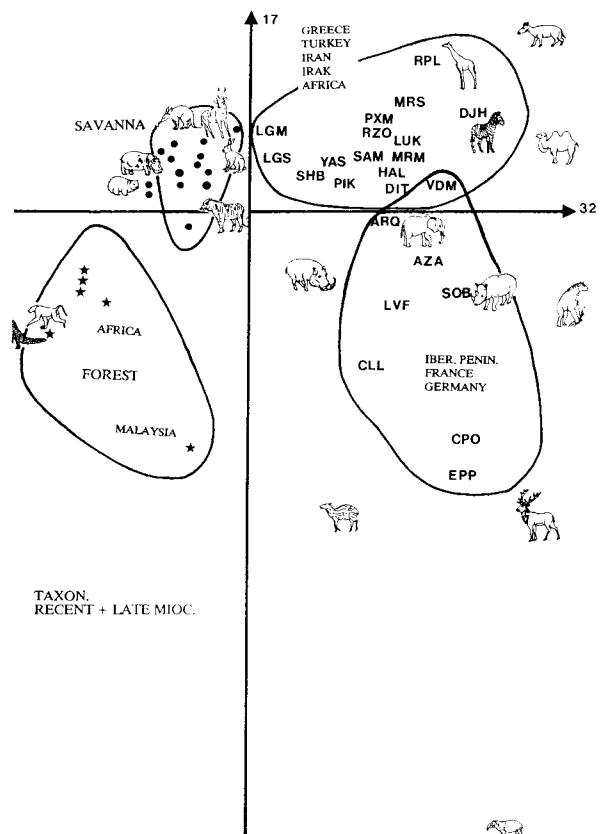


FIGURE 3. Multivariate study (C.F.A.) of the taxonomic compositions of recent, late Miocene and Pliocene mammalian faunas. Legend : see fig. 1 and tab. 1 and 2.

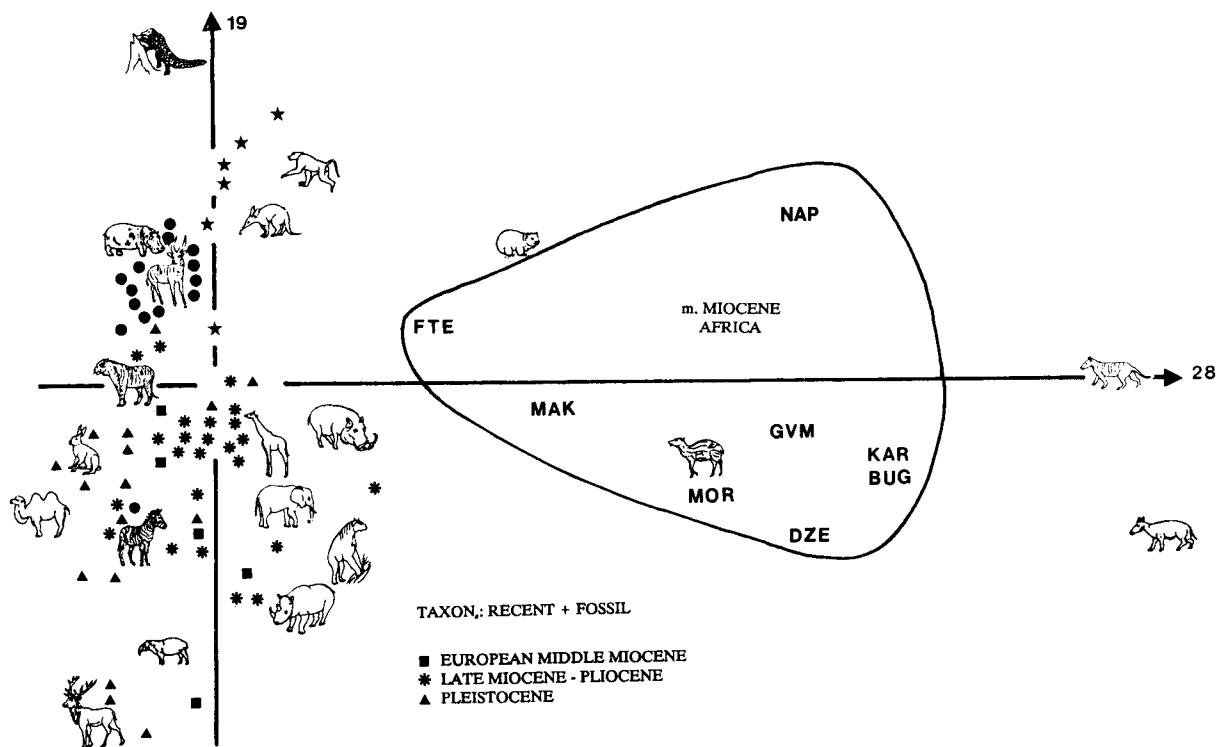


FIGURE 4. Multivariate study (C.F.A.) of the taxonomic compositions of recent, Miocene and Plio-Pleistocene mammalian faunas. Legend : see fig. 1 and tab. 1 and 2.

tocene ones. The late Miocene localities of Venta del Moro and Arquillo in Spain and the Israelian Pleistocene site of Oubeidiyeh are more or less intermediate between the two groups.

The most important contributions for this factor are Cervidae (25,3 %) for one part and Bovidae (25,3 %), Giraffidae (21,2 %) and, far behind, Equidae (7 %) for the other part.

e — Comparison of the fossil localities except those of the African middle Miocene (Fig. 6)

The first factor separates the localities of the late Miocene of Greece, Turkey, Iran, Irak and African

with some Pleistocene sites of the same area (Afyon and Ternifine) from the other ones from the middle or late Miocene and Plio-Pleistocene. The localities of Oubedyieh, Venta del Moro, Arquillo and Soblay are more or less intermediate between the two sets. Here again, Cervidae (24,3 %), Bovidae (21 %) and Giraffidae (21,3 %) are the most important variables.

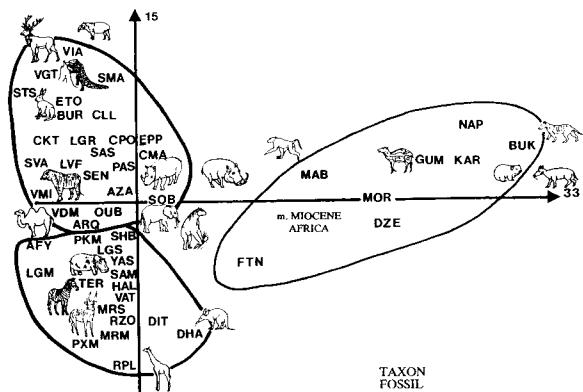


FIGURE 5. Multivariate study (C.F.A.) of the taxonomic compositions of Miocene and Plio-Pleistocene mammalian faunas. Legend: see tab. 1 and 2.

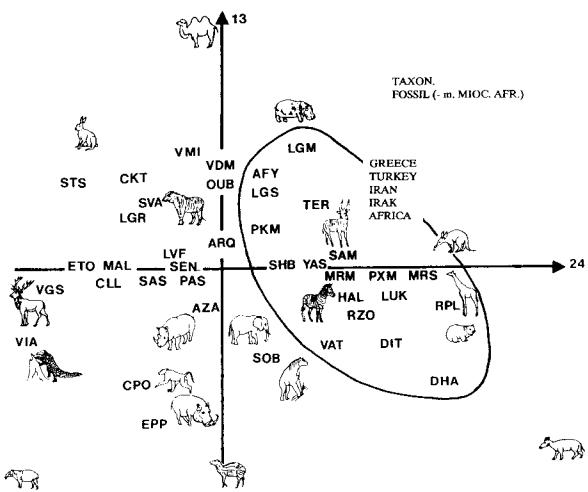


FIGURE 6. Multivariate study (C.F.A.) of the taxonomic compositions of European Middle Miocene, late Miocene and Plio-Pleistocene mammalian faunas. Legend : see tab. 1 and 2.

f — Comparison of the late Miocene localities (fig. 7).

They are very well separated in two sets by the first factor (degree of wood cover), Spain, France and Germany on one side, and Africa, Turkey, Iran and Greece on the other side. Iran and Greece, except Pikermi, are separated from Africa and Turkey by the second factor.

BODY SIZE AND TAXONOMY

Body size or body weight variations among the faunas give for recent mammalian localities more or less the same results as the taxonomic analysis. The different species of the studied faunas are put into seven categories of body weight (A to G) from 6 to more than 1,000 kg (tab. 3). The numbers of species in each category for every fauna constitute the seven variables acting in the analysis. These results are less clear with the fossil faunas and it seems that the distribution of the body size has largely been modified during the Holocene. If we use both taxonomy and body size as variables, we obtain good result in separating recent and fossil faunas as well as the dif-

ferent ecological types. We do not present the analysis with the African middle Miocene sites which retain the most important part of the total variance.

a — Body weights of recent faunas (fig. 8)

Body weights allow to separate, in the recent communities, the forest faunas from the other ones. The most important difference is the presence of relatively many small mammals in closed environment. The most important contributions of the variables are A, i.e. 6 to 14,9 kg, (46,2 %) on ne part, D, i.e. 110 to 269 kg, (24,2 %) and F, i.e. 540 to 1,000 kg (24,2 %) in the other part. In this way we may observe the location of a Transvaal locality (Tr. 10) which clusters near the forest localities. In fact Transvaal 10 is a more or less deforested area, an open country with relictual forests and with relatively few large mammals because human predation. The categories D and F, which are very poor for this localities, are big games, therefore they have been more or less destroyed by hunting.

TABLE 3. *Body weights categories.*

06 kg	< A < 14,9 kg	110 kg	< D < 269,0 kg
15 kg	< B < 39,9 kg	270 kg	< E < 539,0 kg
40 kg	< C < 109,0 kg	540 kg	< F < 1 000,0 kg

G > 1 000,0 kg

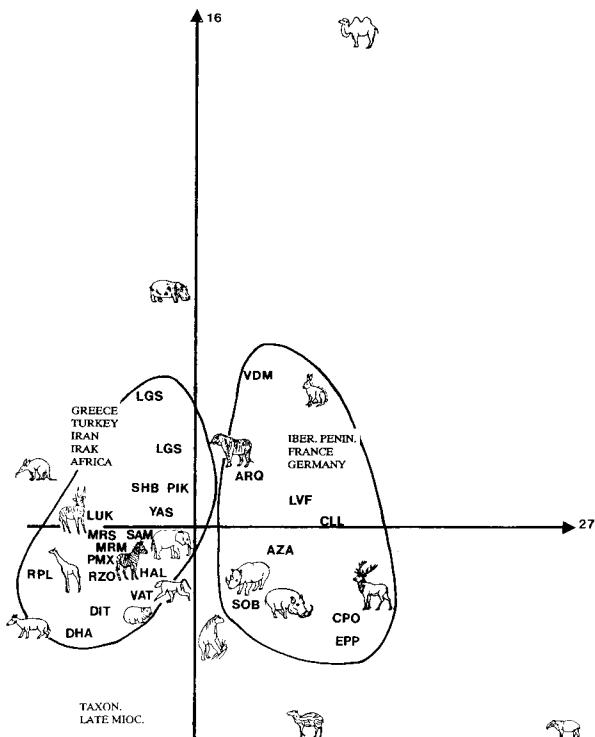


FIGURE 7. Multivariate study (C.F.A.) of the taxonomic compositions of late Miocene mammalian faunas. Legend : see tab. 1 and 2.

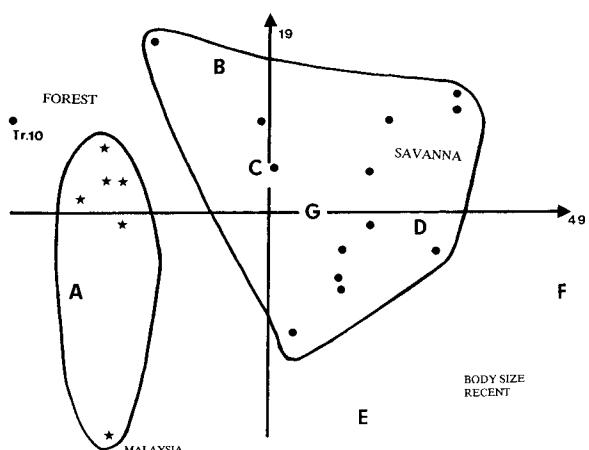


FIGURE 8. Multivariate study (C.F.A.) of recent mammalian faunas with respect to the body weights of the species. Legend : see fig. 1 and tab. 3.

b — Body weights and taxonomy for recent Miocene and Plio-Pleistocene localities (fig. 9)

The first factor separates principally the recent from the fossil faunas. On the second axis we can see on the left side the differences between the forest faunas and the savannah faunas and on the right side an homologous difference between the late Miocene and Pleistocene localities of Eastern Europe, middle East and Africa and Pleistocene localities of Western Europe. Some fossil sites like Arquillo, Azambujeira, Venta del Moro and Soblay cluster near the south-eastern Europe ones. We can remark also the place of most of the Pleistocene European sites which cluster at the extreme right and indicate probably an environment relatively forested.

In this analysis, the first factor corresponds to the contributions of Primates (24,6 %) in the left part and

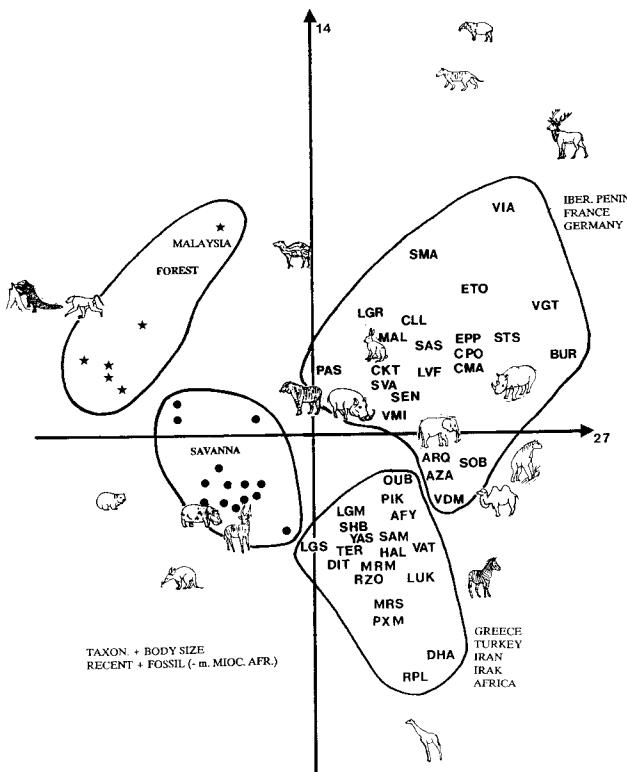


FIGURE 9. Multivariate study (C.F.A.) of recent, Miocene (without the middle Miocene of Africa) and Plio-Pleistocene mammalian faunas with respect to body weights of the species and the taxonomic categories. Legend : see fig. 1 and tab. 1, 2, 3.

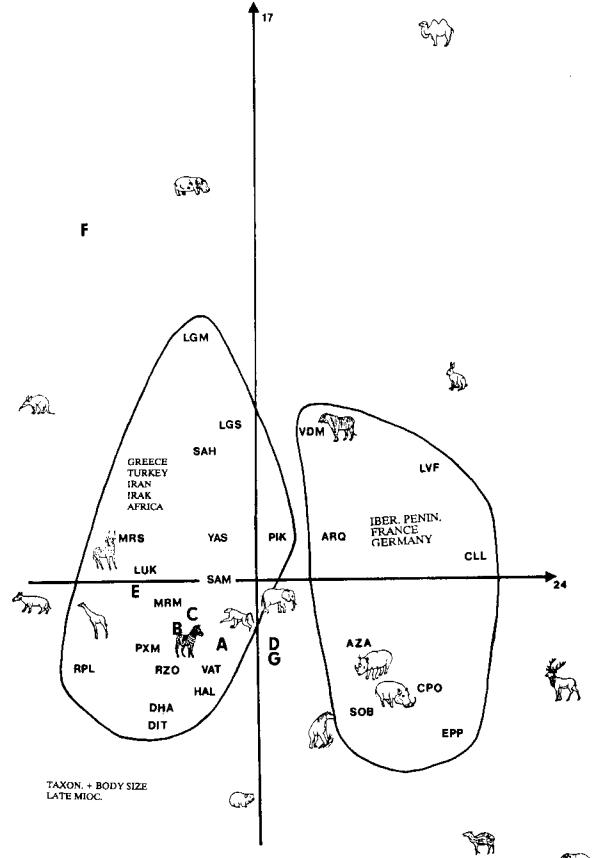


FIGURE 10. Multivariate study (C.F.A.) of late Miocene and Pliocene mammalian faunas with respect to body weights of the species and the taxonomic categories. Legend : see tab. 1, 2, 3.

Cervidae (15,4) in the right part of the graph, in other words probably an opposition between African faunas and European Pleistocene faunas. The ecological characteristics appear on the second factor with Cervidae (25,9 %) and Primates (10,6 %) in one side and Giraffidae (17,3 %) and Bovidae (13,8 %) in the other side.

c — Body weights and taxonomy for late Miocene localities (fig. 10)

The first factor separates the Vallesian or Turolian localities of Greece, Turkey, Iran, Irak or Africa from the Vallesian or Turolian localities of western Europe. In fact it separates the more open environment sites from the other ones. Some localities from western Europe are not so far from the other set, but they do not cluster with any one. The meaning of the differences along the second axis remains unclear except that it separates some localities with numerous relatively large mammals (F variable) and carnivores from other ones in which these categories are less abundant.

CONCLUSION

Generally, a few percent of the whole variance is expressed by the first and the second factors. The percent is very lesser for the other factors. It means that there are not a great difference between the number of species for each category in the different localities. But this difference allows nevertheless to separate clearly the types of environment. The most important difference is between the middle Miocene African faunas and the other ones. In fact, the presence in Africa at that time of several archaic taxa hides the other differences and the corresponding factor is a biogeographic one. The second is between the recent and other fossil localities. The third, which is the most interesting for us, is between open and more forested environment. When the Plio-Pleistocene of Europe are acting in the analysis, they cluster with the forested localities of the European Vallesian sites. It does not mean of course that the climate was the same but it means rather than the country was more forested and housed more browser animals than grazer's. The taxonomic analysis seems to be a good tool to deal with paleoecology but in the future it would be better to use only faunas

coming from almost the same geological level. The results are not very different if we add the body size or body weight as other variables. If, within the recent communities, the body weight variation between the different species allows to recognize forest

faunas from savanna faunas, it is more difficult to do the same with the fossil communities. We can remark that when taxonomy and body size are used together, the body variables are less important than the taxonomic ones.

BIBLIOGRAPHY

- AGUIRRE E., ROBLES F., THALER L., LOPEZ N., ALBERDI M.T. and FUENTES C. (1973): Venta del Moro, nueva fauna finimiocenica de Moluscos y vertebrados. *Est. Geol.*, 29 : 569-578, Madrid.
- AGUSTÍ I. (1987): Introducció : Història del Jaciment de Venta Micena. *Paleont. Evol. Mem. Esp.* 1 : 3-9, Sabadell.
- AGUSTÍ I., CABRERA L. and MOYA SOLA S. (1985): Síntesis estratigráfica del Neogeno de la fosa del Valles Penedès. *Paleont. Evol.*, XVIII : 57-81, Sabadell.
- ALBERDI M. T., LOPEZ N., MORALES J., SESE C. and SORIA D. (1981): Bioestratigrafía y biogeografía de la fauna de Mamíferos de los valles de Fuentidueña. *Est. Geol.*, 37 : 503-511, Madrid.
- ANDREWS P., LORD J. M. and NESBIT EVANS E. M. (1979): Patterns of ecological diversity in fossil and modern mammalian faunas. *Biol. J. Linn. Soc.*, 11 : 177-205, London.
- ANDREWS P., MEYER G. E., PILBEAM D. R., VAN COUVERING J. A. and VAN COUVERING J. A. H. (1981): The Miocene fossil beds of Maboko Island, Kenya : Geology, Age, Taphonomy and Palaeontology. *J. Hum. Evol.*, 10 (1) : 35-48, London.
- BECKER-PLATEN J. D., SICKENBERG O. and TOBIEN H. (1975): Die Gliederung der känozoischen sediments der Türkei nach Vertebraten. Faunengruppen. *Geol. Jahrb.*, B, 15 : 19-45, Hannover.
- BENZECRI J. P. (1976): L'analyse des données, Dunod, t. 1, 631 p., t. 2, 616 p, Paris.
- BERNOR R. L. (1978): The mammalian systematics, biostratigraphy and biochronology of Maragheh and its importance for understanding late Miocene Hominoid zoogeography and evolution. Ph. D. Dissertation, University of California, 314 p, Los Angeles.
- BERNOR R. L. (1986): Mammalian biostratigraphy, Geochronology and Zoogeographic relationships of the Late Miocene Maragheh Fauna, Iran. *J. Vert. Pal.*, 6 (1) : 76-95, Washington.
- BERNOR R. L. and PAVLAKIS P. P. (1987): Zoogeographic Relationships of the Sahabi large mammal fauna (Early Pliocene, Libya). in : Neogene Paleontology and Geology of Sahabi, Alan R. Liss, 349-383, New York.
- BONIS L. de, BOUVRAIN G. and KOUFOS G. (1988): Late Miocene localities of the lower Axios Valley (Macedonia, Greece) and their stratigraphic significance. *Modern Geology*, 13 : 141-147, London.
- BONIS L. de, BOUVRAIN G., GERAADS D. and KOUFOS G. (1990): Composition and species diversity in late Miocene faunal assemblages of Northern Greece. *Bull. Soc. Geol. Grèce.*, 25(2), 395-404.
- BOURLIERE F., MINNER E. and VUATTOUX R. (1974): Les grands mammifères de Lamto, Côte d'Ivoire. *Mammalia*, 38 : 433-447, Paris.
- BRUNET M. and HEINTZ E. (1983): Interprétation paléoécologique et relations biogéographiques de la faune de Vertébrés du Miocène supérieur d'Injana, Irak. *Pal. Pal. Pal.*, 44 : 283-293, Amsterdam.
- COHEN F. (1988): Etude de quatre faunes du Pléistocène d'Europe selon deux méthodes paléoécologiques : les cénogrammes et les spectres fauniques. *Mém. DEA* Paris VI : 1-76, Paris.
- GAUDRY A. (1862-1867): Animaux fossiles et Géologie de l'Attique. F. Savy ed. : 1-472, Paris.
- GERAADS D., HUBLIN J. J., JAEGER J. J., TONG H., SEN S. and TOUBEAU P., 1986: The pleistocene Hominid site of Ternifine, Algeria : new results on the environment age and human industries. *Quaternary Research*, 25 : 380-386, London.
- GUERIN C. and MEIN P. (1971): Les principaux gisements de Mammifères miocènes et pléistocènes du domaine rhodanien. *Doc. Lab. Geol. Univ. Lyon.* h.s. : 131-170, Lyon.
- GOLPE J. (1974): Faunas de Yacimientos con Suiformes en el Terciario español. *Paleont. Evol.*, VIII : 1-87, Sabadell.
- HAMILTON W. R. (1973): The lower miocene ruminants of Gebel Zelten, Libya. *Bull. Brit. Mus. (Nat. Hist.)*, Geol., 21 (3) : 73-150, London.
- HEINTZ E., GUERIN C., MARTIN R. and PRAT F. (1974): Principaux gisements villafranchiens de France : listes fauniques et biostratigraphie. Ve congrès du Néogène méditerranéen. *Mém. BRGM* n° 78, 1 : 169-182, Orléans.
- HENDEY Q. B. (1981): Palaeoecology of the late tertiary fossil occurrences in "E" Quarry, Langebaanweg, South Africa, and a reinterpretation of their geological context. *Ann. S. Afr. Mus.*, 84 (1) : 1-104, Cape town.
- HUNERMANN K. A. (1978): Das wildschwein (*Sus scrofa* L.) aus dem Jungpleistozän von Burgtonna in Thüringen. *Quartärpal.*, Akad. Verlag., 3 : 123-127, Berlin.
- KAHLKE H. D. (1978a): Die Cerviden Reste aus den Travertinen von Burgtonna in Thüringen. *Quartärpal.*, Akad. Verlag., 3 : 113-122, Berlin.
- KAHLKE H. D. (1978b): Die Rhinocerotidenreste aus den Travertinen von Burgtonna in Thüringen. *Quartärpal.*, Akad. Verlag., 3 : 129-135, Berlin.
- KOHLER M. (1987): Boviden des turkischen Miozäns (Känozoikum und Braunkohlen der Türkei). *Pal. I. Evol.*, 21 : 133-246, Sabadell.
- LEGENDRE S. (1988): Les communautés de mammifères du Paléogène (Éocène supérieur et Oligocène) d'Europe occidentale : structures, milieux et évolution. Thèse d'Etat, Université Montpellier : 1-118, Montpellier.
- MEIN P. (1990): Updating of MN Zones. In : "European Neogene Mammal chronology". Edit. E.H. Lindsay et al., Plenum Press : 73-90, New York.
- MELENTIS J. (1967): Studien über Fossile Vertebraten Griechenlands. 19. Die Pikermifauna von Halmyropota-

- mos (Euböa, Griechenland). *Ann. Geol. Pays Hell.*, 19 : 283-411, Athens.
- MUSIL R. (1972): Stranska Skala I 1910-1945. *Anthropos* C 20, n.s., 12 : 1-204, Brno.
- OZANSOY F. (1957): Faunes de Mammifères du Tertiaire de Turquie et leurs révisions stratigraphiques. *Bull. Min. Res. Expl. Inst. Turkey*, 49 : 29-48, Ankara.
- PICKFORD M. (1978): Stratigraphy and mammalian paleontology of the late Miocene Lukeino Formation. In: *Geological Background to Fossil Man*, W.W. Bishop edit. : 238-262, London.
- PICKFORD M. (1981): Preliminary Miocene Mammalian biostratigraphy for Western Kenya. *J. Hum. Evol.*, 10 : 73-97, London.
- PICKFORD M., SENUT B., HADOTO D., MUSISI J. and KARIINA C. (1986): Nouvelles découvertes dans le Miocène inférieur du Napak, Ouganda oriental. *C.R. Acad. Sc. Paris*, ser. II, 302 (1) : 47-52, Paris.
- RAUTENBACH I. L. (1978): Ecological distribution of the mammals of the Transvaal (Vertebrata : Mammalia). *Ann. Transv. Mus.*, 31 : 131-156, Johannesburg.
- SAVAGE R. J. G. and HAMILTON W. R. (1973): Introduction to the Miocene Mammal faunas of Gebel Zelten, Libya. *Bull. Brit. Mus (Nat. Hist.) Geol.*, 22 (8) : 513-527, London.
- SHEPPE W. and OSBORNE T. (1971): Patterns of use of a flood plain by Zambian mammals. *Ecological Monographs*, 41 : 179-205, London.
- SICKENBERG O. (1975): Die Gliederung des höheren Jungtertiärs und Altquartärs in der Türkei nach Vertebraten und ihre Bedeutung für die internationale Neogen-Stratigraphie. *Geol. Jahrb.*, 15, B : 1-167, Hannover.
- SIMIONESCU I. (1930): Vertebratele plicocene dela Malusteni (Covurlui). *Acad. Rom. Publ. Adam.*, IX, 49 : 1-69, Bucarest.
- SOLOUNIAS N. (1981): The Turolian Fauna from the island of Samos, Greece. *Cont. Vert. Evol.*, 6 : 1-232, New York.
- TCHERNOV E. (1985): Conclusion sur la faune du gisement pléistocène ancien d'Oubeidiyeh (Israël) : implications paléoécologiques, biogéographiques et stratigraphiques. *Mém. Trav. Centre Rech. Français de Jérusalem*, 5 : 351-398, Paris.
- THENIUS E. (1959): Tertiär — 2e partie — In : "Handbuch der Stratigraphischen Geologie". Edit. F. Lotze : 1-308, Stuttgart.
- THOMAS H., SEN S. and LIGABUE G. (1980): La faune miocène de la formation Agha Jari du Jebel Hamrin (Irak). *Proc. Koninkl. Nederl. Akad.*, ser. B, 83 (3) : 269-287, Amsterdam.
- THOMAS H. (1980): Les bovidés du Miocène supérieur des couches de Mpesida et de la formation de Lukeino (district de Baringo, Kenya). Actes 8e Congrès Panafricain Prehistoire et Etudes quaternaires. Nairobi 1977. Eds : R. Leakey and B. Agot : 82-91, Nairobi.
- VALVERDE J. A. (1964): Remarques sur la structure et l'évolution des communautés de vertébrés terrestres. *Terre et Vie*, 111 : 121-154, Paris.
- VALVERDE J. A. (1967): Estructura de una comunidad de vertebrados terrestres. *Monogr. Est. biol. Donana*, 1 : 1-129, Madrid.
- WAGNER A. (1848): Urweltliche Säugetier-ueberreste aus Griechenland. *Abh. bayer. Akad. Wiss.*, 5 : 333-378, München.
- WEHRLI H. (1963): Das Pleistozän von Voigtstedt. *Pal. Abh. Abt. 4, Paläozoo.*, 2 (2/3) : 221-292, Berlin.
- YOUNG C. C. (1932): On the Artiodactyla from the Sinanthropus site at Choukoutien. *Pal. Sin.*, 8 (2) : 1-100, Beijing.