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Diversity and paleoecology of Greek late Miocene mammalian faunas

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ABSTRACT

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The late Miocene of Macedonia has yielded several rich faunal assemblages, ranging from late Vallesian to late Turolian. They may be compared to the classical localities of Pikermi, Samos and Maragheh.

Taxonomic comparisons based upon updated faunal lists allowed us to compute faunal similarity indices, which were submitted to principal component and cluster analysis. On the graphs, "Ravin de la Pluie" is always remote from the other Macedonian fossil mammal localities: it can only be explained by its Vallesian age. The other Macedonian sites cluster next, demonstrating some provinciality of this area during the Turolian.

Comparisons of the frequencies of the various taxonomic groups support the installation of a more forested environment in the latest faunal set, Dytiko. The indices of diversity and the rank-abundance curves seem also to reflect a change of the ecological conditions during the Turolian: the fauna of "Ravin de la Pluie" and of the Vathylakkos-Prochoma-"Ravin des Zouaves" group is marked by the predominance of 1 or 2 species, while the species frequency of the Dytiko set is more balanced, suggesting warmer climate and less contrasted climatic conditions.

Another way of evaluating the ecological significance of the fossil assemblages is the analysis of the distribution of the body weight of each category of mammals in each fauna. When possible we used the cenogram method or a multivariate analysis of the number of species in each weight class (excluding small mammals, which are very rare in Macedonia); we have analysed in this way 25 fossil and 23 recent localities. We show that, although all the fossil localities are separated from the recent ones, it is possible to deduce an open environment in "Ravin de la Pluie" and a more forested one in Dytiko.

Introduction

Late Miocene fossil mammals localities are particularly common in insular and continental Greece. The oldest scientifically known is Pikermi in Attiki (Wagner, 1848; Gaudry, 1862–1867) dated as Turolian. The island of Samos has yielded several sites whose ages are certainly different; we decided to choose for our comparisons the richest locality, Quarry A, and the list of Solounias (1981), slightly revised. The locality of Halmyropotamos in the island of Euboa has been studied by Melentis

(1967). These last two localities are dated as Turolian. We have added two levels in the Maragheh area to extend our comparisons to Middle East localities (Mecquemen, 1924–1925; Bernor, 1978, 1986). We did not take into account the "lower Maragheh" level whose number of taxa is the poorest for this area. The sites of Northern Greece (Fig. 1) have been discovered in the first part of the twentieth century (Andrews, 1918; Arambourg and Piveteau, 1929) but several excavations have been conducted since the beginning of the seventies (Bonis et al., 1973; Bonis et al., 1988) and an

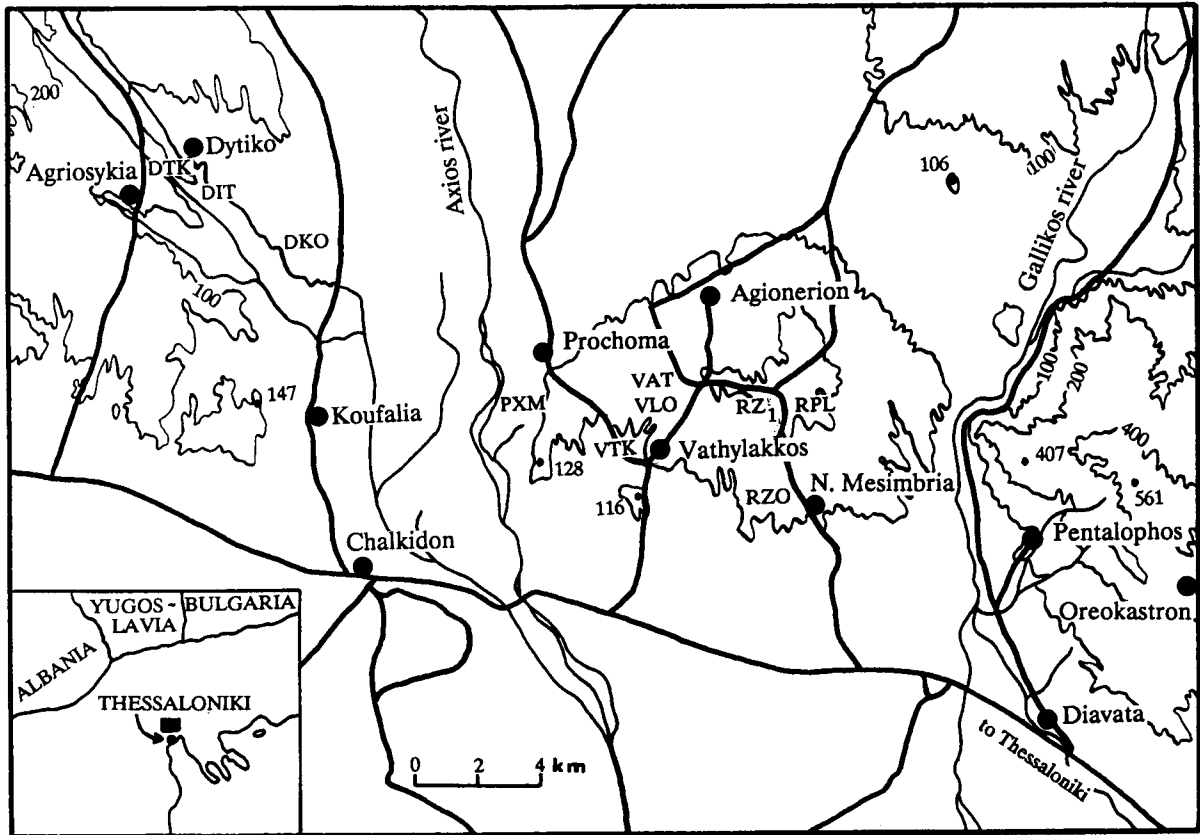


Fig. 1. Map of the fossil localities of Central Macedonia.

important new material has been unearthed. These sites can be arranged in three major sets, which can be dated by the stratigraphy and by the biochronology.

The stratigraphy can be briefly summarized as follows, mainly after Mercier (1973). From the bottom to the top there are:

—The Nea Messimbria Formation (Koufos, 1980), which consists of fluvial gravels and red clays, and which may reach 1000 m in thickness (Mercier, 1973). It contains the localities of “Ravin de la Pluie” (RPL) and “Ravin des Zouaves” n° 1 (RZ1);

—The Vathylakkos Formation (Koufos, 1980), which consists of fluvial white and grey sandy marls. This formation overlies unconformably the preceding one, as can be very clearly observed in the Vathylakkos ravine, about 2 km north of this village. It contains the localities of Vathylakkos 1 (VLO), 2 (VTK), 3 (VAT), Prochoma (PXM) and

“Ravin des Zouaves” n° 5 (RZO). A paleomagnetic study of the Prochoma area (Kondapoulou et al., in press) suggests that the fossil bearing beds belong to chron 8 and are equivalent to the early Turolian age of mammals.

—More to the NW, the Dytiko Formation (Koufos, 1980), consists mainly of fluvial gravel marls, grey or white sands and lacustrine limestones (Mercier, 1973). It contains the localities of Dytiko 1 (DTK), 2 (DIT) and 3 (DKO).

Bonis et al. (1988) have ascribed the faunas of the two later sets to the Turolian land mammal age (respectively early and late Turolian) and this has received general agreement. We (Bonis and Melentis, 1975) have also ascribed the fauna of the Nea Messimbria Fm to the Vallesian, but since this age has been questioned by other researchers (Bernor, 1985), it may be useful to reiterate some of our arguments, based upon the fauna from “Ravin de la Pluie”:

—The large giraffid called *Decennatherium pachecoi* by Geraads (1979) is primitive; it argues in favor of an early age. As Geraads (1979) has shown, the occurrence of this genus at Maragheh (Bosscha-Erdbrink, 1976) has not been firmly established;

—The murid *Progonomys cathalai* is a typically Vallesian species. The genus has been mentioned in the late Miocene locality of Sahabi (Münthe, 1987) but without adequate description or measurements and other identification (such as *Paraethomys*) are probably more likely;

—The two Hipparions, called *H. macedonicum* (a dwarf species) and *H. primigenium* by Koufos (1984, 1986) are similar to Vallesian species. The co-occurrence of two species cannot be used against a Vallesian age (Bernor, 1985) since there are two species in the Vallesian sites of Montredon (including a dwarf one: Eisenmann, 1988), Masia del Barbo (Sondaar, 1974) and possibly also Yassiören and Küçükçekmeçe (Eisenman, 1988). Of course, the first occurrence of a dwarf species at c. 8.5 m.y. in Maragheh (Bernor, 1986) does not preclude an earlier appearance at RPI. Also the similarities of the large species with the *H. primigenium* from the early Vallesian sites of Eppelsheim, Nombrevilla and Can Llobateres cannot be overlooked.

In sum, the relative stratigraphic position of the localities is not disputable, and we believe that the Vallesian age of RPI is firmly established even if still under debate (Bernor and Tobien, 1989).

The aim of this paper is:

(1) To test the faunistic similarities and differences to establish the likely paleogeographic relationships between these localities.

(2) To test several methods which could indicate the paleoecologic conditions by comparison with extant localities.

Some researches have been conducted on paleobiogeography and paleoecology of the late Miocene mammalian Greek faunas. Faunal comparisons between Greece and Iran have been made (Bernor, 1978) with zoogeographic analysis, clustering of different localities and conclusions on transgression of savanna communities into Western Europe and Indo-Pakistan. The problem of the ecology of the Greek late Miocene mammalian faunas has been taken up (Solounias and Dawson-

Saunders, 1988) from the study of the masticatory morphology of ruminants.

Conclusions drawn by Solounias and Dawson-Saunders (1988) would be that Samos and Pikermi ruminants were forest or woodland dwellers and that the extinct ruminant faunas are not similar to extant savanna adapted species. Some Greek sites are also included in a more general study (Nagatoshi, 1987) on habitats during the Miocene from literature analysis of sedimentology, floral or faunal evidences.

We take up the problem with faunal lists of the studied localities revised, when possible. Comparisons are made by faunal indices, pie diagrams, abundance curves or multivariate analysis of body weight.

Faunal lists

The revised faunal lists of the Macedonian sites are given below. The first two localities are of Vallesian age; Ravin des Zouaves n° 5, the three localities of Vathylakkos and Prochoma date from the early Turolian, while the localities of Dytko are late Turolian.

“Ravin de la Pluie” (RPL)

Tetralophodon sp., *Choerolophodon pentelicus*, Rhinocerotidae ind., *Hipparion primigenium*, *Hipparion macedonicum*, *Palaeotragus* cf. *coelophrys*, *Decennatherium* cf. *pachecoi*, *Bohlinia attica*, *Prostrepsiceros vallesiensis*, *Samotragus praecursor*, *Mesembriacerus melentisi*, Bovidae ind. (large size), *Protictitherium* cf. *gaillardi*, *Adcrocuta eximia leptoryncha*, *Progonomys cathalai*, Gliridae ind., Sciuridae ind., cf. *Palerinaceus* sp., *Ouranopithecus macedoniensis*, *Palaeonaja* sp., Boidae ind., *Testudo* sp.

“Ravin des Zouaves” n° 1 (RZ1)

Choerolophodon pentelicus, *Hipparion* cf. *macedonicum*, *Mesembriacerus melentisi*, *Samotragus praecursor*, *Ouzocerus gracilis*, *Ictitherium* cf. *hipparionum*, *Adcrocuta eximia*.

“Ravin des Zouaves” n° 5 (RZO)

Choerolophodon pentelicus, *Zygodolophodon tapiroides*, *Ceratotherium neumayri*, *Hipparion proboscideum*, *Hipparion dietrichi*, *Hipparion macedonicum*, *Microstonyx* sp., *Postpotamochoerus hyotherioides*, *Helladotherium duvernoyi*, *Palaeotragus* cf. *rouenii*, *Gazella* sp., *Prostrepsiceros rotundicornis*, *Prostrepsiceros zitteli*, *Nisidorcas planicornis*, *Palaeoreas zouavei*, *Tragoportax rugosifrons*, *Mesopithecus delsoni*, *Adcrocuta eximia*, *Ictitherium robustum*, *Chasmaporthetes* sp., *Machairodus* sp., ? *Valerymys* sp..

Vathylakkos 1 (VLO)

Hipparion dietrichi, *Palaeoreas lindermayeri*, *Nisidorcas planicornis*.

Vathylakkos 2 (VTK)

Choerolophodon pentelicus, Rhinocerotidae ind., *Hipparion dietrichi*, *Hipparion macedonicum*, *Microstonyx* sp., *Bohlinia attica*, *Gazella* sp., *Nisidorcas planicornis*, *Tragoportax rugosifrons*, *Mesopithecus* cf. *pentelicus*, *Ictitherium robustum*, *Ictitherium wongii*, *Plioviverrops orbignyi*, *Hystrix* sp.

Vathylakkos 3 (VAT)

Choerolophodon pentelicus, *Ceratotherium neumayri*, *Hipparion dietrichi*, *Hipparion macedonicum*, *Microstonyx* sp., *Dorcatherium* sp., *Samotherium boissieri*, *Bohlinia attica*, *Gazella* sp., *Nisidorcas planicornis*, *Prostrepsiceros zitteli*, *Palaeoreas lindermayeri*, *Tragoportax rugosifrons*, *Mesopithecus* cf. *pentelicus*, *Plesiogulo crassa*, *Ictitherium robustum*, *Ictitherium wongii*, *Plioviverrops orbignyi*, *Plioviverrops* cf. *guerini*, *Protictitherium intermedium*.

Prochoma (PXM)

Choerolophodon pentelicus, Chalicotheridae ind., *Hipparion dietrichi*, *Hipparion macedonicum*, *Helladotherium duvernoyi*, *Microstonyx* sp., *Gazella* sp., *Prostrepsiceros zitteli*, *Nisidorcas planicornis*,

Palaeoreas sp., *Tragoportax rugosifrons*, *Plioviverrops orbignyi*, *Ictitherium* sp., *Adcrocuta* sp.

Dytiko 1 (DTK)

Choerolophodon pentelicus, cf. *Ceratotherium neumayri*, *Hipparion mediterraneum*, *Hipparion matthewi*, *Hipparion periafricanum*, *Microstonyx* sp., Cervidae ind., *Bohlinia attica*, *Gazella* sp., *Palaeoreas lindermayeri*, *Protragelaphus theodori*, *Tragoportax gaudryi*, Ovibovinae ind., *Mesopithecus* cf. *pentelicus*, *Chasmaporthetes bonisi*, *Protictitherium crassum*, *Orycteropus* cf. *gaudryi*.

Dytiko 2 (DIT)

Choerolophodon pentelicus, *Hipparion matthewi*, *Dorcatherium* sp., *Bohlinia attica*, *Palaeotragus rouenii*, *Gazella* sp., *Palaeoreas lindermayeri*, *Tragoportax gaudryi*, Ovibovinae ind., *Mesopithecus* cf. *pentelicus*.

Dytiko 3 (DKO)

Chalicotherium sp., *Hipparion matthewi*, *Hipparion mediterraneum*, *Dorcatherium* sp., *Gazella* sp., *Hispanodorcus orientalis*, *Prostrepsiceros* n. sp., *Protragelaphus theodori*, *Tragoportax gaudryi*, *Mesopithecus* cf. *pentelicus*, *Hystrix* sp., *Protictitherium crassum*.

Indices of faunal similarity

We have tried to compare the Macedonian localities each other and to other upper Miocene sites from eastern Mediterranean. We have arranged together localities of the same age, to get longer and more significant faunal lists: RZ1 and RPI, both in the Nea Messimbria Formation, and topographically very close; VLO, VTK and VAT plus the “Vatilük” of Arambourg and Piveteau (1929); DTK, DIT and DKO. For Samos, since there is no evidence that all the quarries can be considered homogeneous neither chronologically nor ecologically, we have chosen the richest quarry, Quarry A, and used the faunal list provided by Solounias (1981), with a few taxonomic corrections. We have

slightly modified the published faunal lists of Pikermi (Gaudry, 1862–1867; Solounias, 1981) and Halmyropotamos (Melentis, 1967). We have also tentatively included under “Middle Maragheh” and “Upper Maragheh”, two sets of localities of this area (Bernor, 1986), because the faunal list of each single locality is very short, but we are well aware of the heterogeneity of these faunal lists.

We have not included the rodents because they are quite rare in all these localities, nor the Carnivores, because they have neither been fully studied yet in Macedonia, nor been revised recently in the other sites (Table 1).

Overall faunal similarity between two sites can be expressed by a number of indexes, of which we have selected Simpson's index of similarity and Pickford's index of distance. They are given by the formulae:

$$\text{Simpson's} = \frac{X \cap Y \text{ number of taxa common to the two sites}}{X \text{ or } Y \text{ number of taxa in the shorter list}} \times 100$$

$$\text{Pickford's} = \frac{(X - X \cap Y)(Y - X \cap Y) \text{ product of the number of taxa peculiar to each site}}{X \cdot Y \text{ product of the number of taxa in each site}} \times 100$$

They have the advantage over other indices (e.g. Dice's, Jaccard's or Otsuka's) of indicating maximum similarity (resp. 100 and 0) when all the taxa in one site are also present in the other, and maximum difference (resp. 0 and 100) when there is no taxon in common. Both indexes have been calculated at the generic and at the specific level. In this latter case, taxa not determined at the species level have been excluded when present in both considered sites (e.g. *Hipparion proboscideum* is excluded only when VAT is compared with RZO or SAM, but not in other comparisons). In Table 2, indexes at the specific level are to the left, at the generic level to the right.

The most obvious result is the remoteness of “Ravin de la Pluie”, which is very distant from all

other sites, but it is more difficult to picture the relationships of the other localities, merely by inspecting the tables. Therefore we have performed several multivariate analysis upon them: factor analysis, cluster analysis (Peters, 1971); of course, not all results are identical: they depend on the index used (Simpson or Pickford), the type of analysis (and sub-type, since there are, for instance, several clustering methods), and especially on the taxonomic level (specific or generic).

At the generic level, Ravin de la Pluie makes a cluster of its own, while all other sites are grouped together within one cluster, in a cluster analysis (Fig. 2). An other cluster groups together all the Greek localities except Samos; the Southern Greece sites, Pikermi and Halmyropotamos, are separated from the Northern ones. Samos is grouped with the two levels of Maragheh. In principal components analysis at the generic level performed either directly on the faunal lists, or on the matrices of faunal indexes (Fig. 3a), “Ravin de la Pluie” is widely separated from all other sites on the first component. The second axis of the analysis separates all Macedonian sites on the one side, all other sites on the other. The first clusters formed are also those aggregating the 4 Turolian Macedonian sites. It must be noted that, at this taxonomic level, VAT is more closely related to DIT than to RZO and PXM.

At the species level, the most noticeable difference is the position of Dytiko, which is very remote from the other Turolian Macedonian sites relatively to the first two axis (Fig. 3b), and which is never clustered with them before being clustered with other sites (which are, depending on the clustering method: RPI, all Turolian sites, all non-Macedonian Turolian sites, or Samos + Maragheh; of course, this variability arises from the weakness of these clusterings).

It seems, therefore, that the leading factor at the generic level, within the same broad time period, is geography, but it is more difficult to suggest an interpretation of the relationships at the specific level. Dytiko may be closer in age to Pikermi, Samos and Maragheh than to the other Macedonian sites, or it may simply postdate the establishment of closer geographic links between northern Greece, Asia Minor and Middle East. As

TABLE 1

Fossil mammalian faunal lists used for comparisons

	RZ1 RPL	RZ0	VTK VAT VLO	PXM	DKO DTK DIT	PIK	SAM	MMR	UMR	HAL
<i>Choerolophodon pentelicus</i>	+	+	+	+	+	+	+	+	+	
<i>Zygodolophodon tapiroides</i>		+				+				+
<i>Tetralophodon atticus</i>	-					+				
<i>Dinotherium giganteum</i>						+	+		+	+
<i>Chalicotherium goldfussi</i>			+	-	+					
<i>Ancylotherium pentelicum</i>				-		+	+		+	+
<i>Ceratotherium neumayri</i>		+	+		-	+	+	+		
<i>Dicerorhinus pikermiensis</i>						+	+			+
<i>Aceratherium</i> sp.			-			-	-			
<i>Chilotherium persiae</i>							+	+		
<i>Hipparion proboscideum</i>		+	-				+			
<i>Hipparion mediterraneum</i>					+	+				+
<i>Hipparion brachypus</i>						+				
<i>Hipparion primigenium</i>	+									
<i>Hipparion matthewi</i>					+		+	+	+	
<i>Hipparion periafricanum</i>					+					
<i>Hipparion prostylum</i>								-		
<i>Hipparion moldavicum</i>								-		
<i>Hipparion campbelli</i>									+	
<i>Hipparion koenigswaldi</i>										+
<i>Hipparion theniisi</i>										+
<i>Hipparion dietrichi</i>		+	+	+			+			
<i>Hipparion macedonicum</i>	+	+	+	+						
<i>Microstonyx</i> sp.		-	-	-	-	-	-	-	-	-
<i>Postpopamochoerus</i> sp.		-								
<i>Dorcatherium</i> sp.			-		-					
Cervid					-	-	-	-		-
<i>Helladotherium duvernoyi</i>		+		+		+	+	+		+
<i>Palaeotragus rouenii</i>		-			+	+	+			
<i>Palaeotragus coelophrys</i>	-						-	+	+	
<i>Samotherium boissieri</i>			+				+	+	+	
<i>Decennatherium</i> sp.	-									
<i>Bohlinia attica</i>	+		+		+	+				
<i>Gazella</i> sp.		-	-	-	-	-	-	-	-	-
<i>Prostrepsiceros rotundicornis</i>		+				+				+
<i>Prostrepsiceros zitteli</i>		+	+	+			+			
<i>Prostrepsiceros vallesiensis</i>	+									
<i>Prostrepsiceros houtumschindleri</i>								+		+
<i>Prostrepsiceros</i> n. sp.					+					
<i>Oioceros rothi</i>						+		+		
<i>Oioceros wegneri</i>							+			
<i>Oioceros atropatenes</i>								+	+	
<i>Nisidorcas planicornis</i>		+	+	+						
<i>Ouzocerus gracilis</i>	+									
<i>Hispanodorcas orientalis</i>					+					
<i>Samotragus praecursor</i>	+									
<i>Pachytragus laticeps</i>							+	+		
<i>Protoryx carolinae</i>						+				
<i>Protragelaphus skouzesi</i>						+	+	+		-
<i>Protragelaphus theodori</i>					+					
<i>Palaeoryx pallasii</i>						+	+			+
<i>Pseudotragus parvidens</i>						+	+			

TABLE 1 (continued)

	RZ1 RPL	RZ0	VTK VAT VLO	PXM	DKO DTK DIT	PIK	SAM	MMR	UMR	HAL
<i>Pseudotragus capricornis</i>							+			
<i>Tragoreas oryxoides</i>							+			
<i>Palaeoreas lindermayeri</i>			+	-	+	+				+
<i>Palaeoreas zouavei</i>		+		-						
<i>Criotherium argalioides</i>							+			
<i>Urmitherium polaki</i>									+	
<i>Mesembriacerus melentisi</i>	+									
<i>Tragoportax amalthea</i>						+				-
<i>Tragoportax rugosifrons</i>		+	+	+			+			
<i>Tragoportax gaudryi</i>					+	+		+	+	
<i>Hystrix</i> sp.			-		-	-				-
<i>Orycteropus gaudryi</i>					-		+			+
<i>Mesopithecus pentelicus</i>			-	-	-	+				
<i>Mesopithecus</i> n. sp.		+						-		
<i>Ouranopithecus macedoniensis</i>	+									
<i>Pliohyrax graecus</i>						+				+

TABLE 2

Indices of distance and similarity

Simpson Index																				
	RP1		RZ0		VAT		PXM		DIT		PIK		SAM		MMR		UMR		HAL	
RP1	100	100	017	036	023	036	018	030	017	045	018	050	009	036	008	036	008	027	000	018
RZ0			100	100	050	071	087	090	008	069	036	086	050	064	021	071	009	050	020	057
VAT					100	100	086	089	033	080	031	075	043	056	019	056	018	050	007	044
PXM							100	100	014	078	029	089	062	078	022	070	012	056	014	078
DIT									100	100	043	076	020	059	020	067	030	058	013	056
PIK											100	100	043	075	037	081	036	075	077	100
SAM													100	100	053	094	060	092	033	075
MMR															100	100	055	067	013	050
UMR																	100	100	018	050
HAL																			100	100
Pickford Index																				
	RP1		RZ0		VAT		PXM		DIT		PIK		SAM		MMR		UMR		HAL	
RP1	000	000	073	045	064	048	069	051	075	039	076	040	087	053	087	048	084	055	100	072
RZ0			000	000	027	011	006	004	087	014	051	013	036	022	064	011	085	029	066	021
VAT					000	000	008	005	048	006	057	013	043	027	067	019	072	030	087	032
PXM							000	000	008	013	065	008	030	015	069	017	079	024	080	012
DIT									000	000	042	011	070	023	065	013	058	025	076	022
PIK											000	000	034	008	047	009	054	016	018	000
SAM													000	000	031	002	030	005	053	012
MMR															000	000	029	017	075	025
UMR																	000	000	072	031
HAL																			000	000

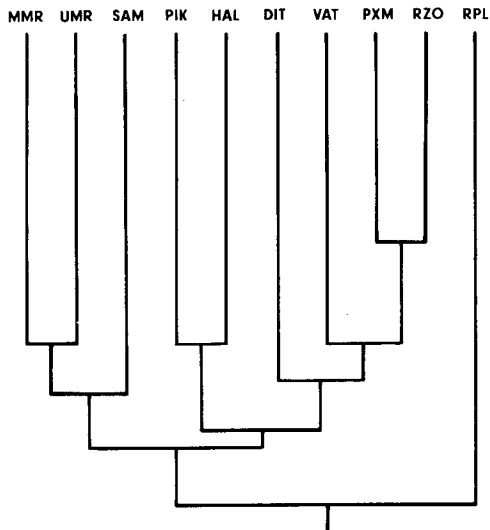


Fig. 2. Cluster analysis on taxonomy of some late Miocene fossil sites of Greece and Middle East at the generic level. *DIT*: Dytiko; *HAL*: Halmypotamos; *MMR*: Middle Maragheh; *PIK*: Pikermi; *PXM*: Prochoma; *RPL*: "Ravin de la Pluie"; *RZO*: "Ravin des Zouaves" n° 5; *SAM*: Samos; *UMR*: Upper Maragheh; *VAT*: Vathyakkos.

we shall see below, ecology is unlikely to be a major factor.

Anyhow, the best established result is the remoteness on the graphs of the locality "Ravin de la Pluie" and the Nea Messimbria Formation as a whole from the other late Miocene localities from Greece or Middle East, which can easily be explained by the earlier age, Vallesian, of the fossils (Bonis et al., 1975; Bonis et al., 1988).

Comparisons of the faunal assemblages

To compare the fossil assemblages of the different Macedonian sites, we have first to compute the number of individuals present in each site. For mammals, the minimum number of individuals (MNI) is often based upon dental remains (here: M/1). The micromammals being very few in these localities, the MNI is low. Nevertheless it is higher than 100 for "Ravin de la Pluie", "Ravin des Zouaves" and Dytiko. From the MNI of each site and the MNI of each species, it is easy to calculate the frequencies of each taxon and to construct pie-diagrams (Rose, 1981).

Frequencies of the various taxonomic groups

The faunal assemblage of the Nea Messimbria Formation (Fig. 4) is remarkable by its high percentage of artiodactyls (74,6%). Among them, bovids largely outnumber giraffids (70 vs 4.6%), although they are little diversified, since 4 species only are present, one of them being very rare. We may note the absence of suids, tragulids and cervids; these two latter families being usually forest dwellers, their absence might imply an open environment. Perissodactyls are uncommon (8.5%): there are few hipparions, chalicotheres are absent, and there is only a fragment of rhinoceros tooth. The percentage of carnivores is also very low (2.3%). On the contrary, primates are quite numerous (10%) but little diverse, since only 1 species is present.

The faunal assemblage of RZO (Fig. 5) has a high percentage of artiodactyls (65.6%) with 4.1% suids, 3.5% giraffids and 58% bovids. The last are rather diversified with 6 species. Tragulids and cervids are absent. Perissodactyls are much more numerous than in the Nea Messimbria formation (24.7%), especially *Hipparion*, but chalicotheres are still absent. Carnivores are slightly more numerous, but primates are few.

Prochoma (Fig. 6) is the only faunal assemblage where perissodactyls outnumber artiodactyls. They consist almost only of *Hipparion*, since there are no rhinoceros and only one tooth of a chalicotherid. Apart from this general picture, percentages must be considered with caution since all MNI are low.

In the Dytiko Formation (Fig. 7), artiodactyls are about as common as in most of the other localities (67%), but they are more diversified, since there are 55.8% bovids, 7.5% giraffids, 1.4% suids, 1.4% cervids and 1.4% tragulids. These two latter families, although rare, might suggest a more wooded environment. Among perissodactyls (25%), *Hipparion* largely predominate over a chalicotherid and a rhinoceros. Primates are uncommon (3%) and carnivores are rare (1.4%).

We have compared these percentages of the various groups of mammals in the Macedonian sites to those of Pikermi, estimated from the material collected by Gaudry and housed in the MNHN, Paris (Fig. 8). The data from Pikermi are

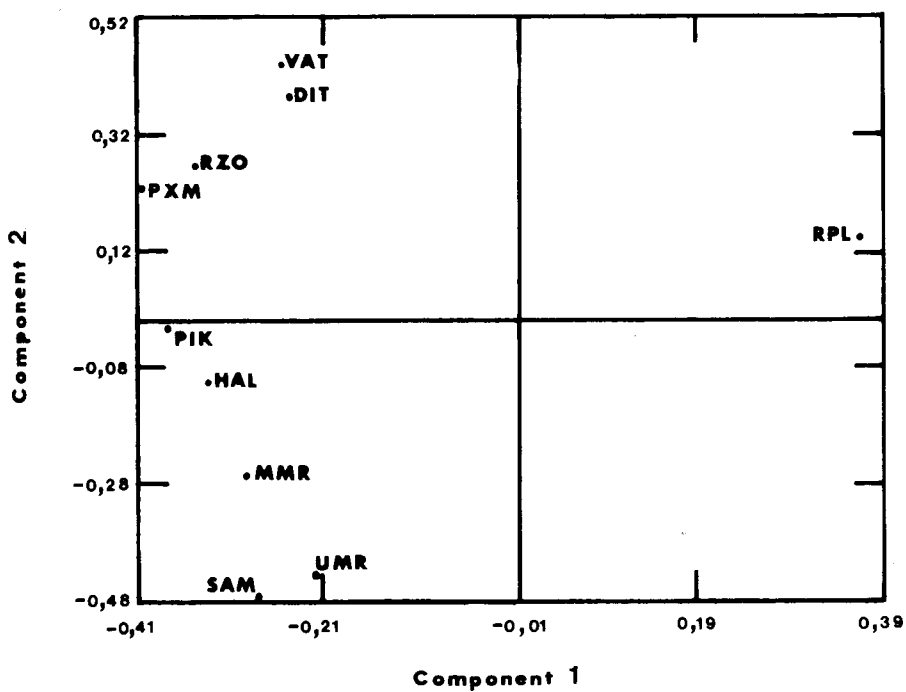
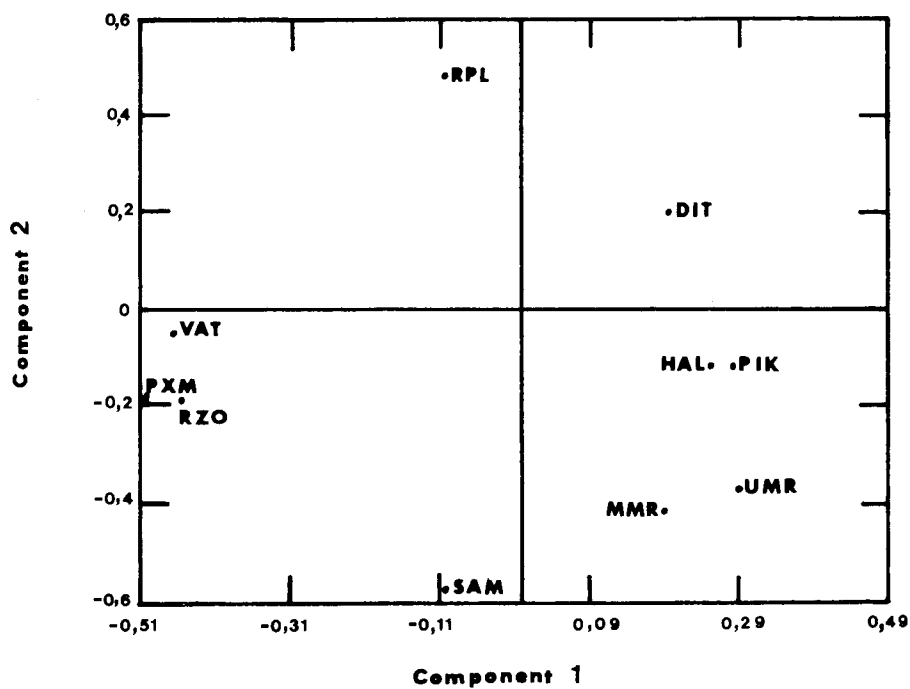


Fig. 3. Principal component analysis on the matrix of the faunal lists for some late Miocene sites of Greece and middle East. A. Generic level. B. Specific level. Legend as in Fig. 1.

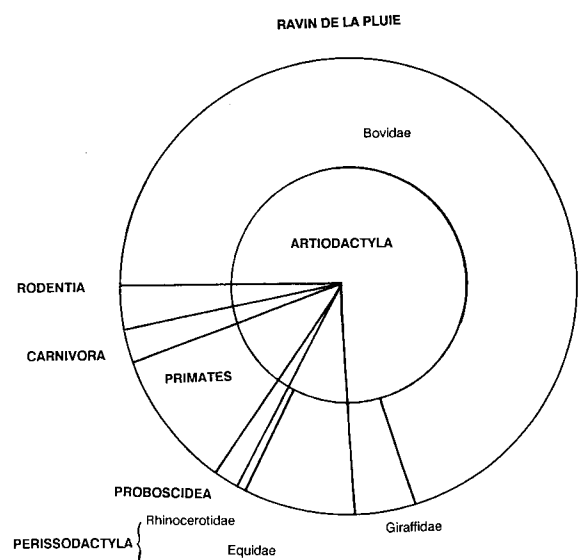


Fig. 4. Faunal composition of the mammal assemblage from "Ravin de la Pluie" (RPI). Minimum number of individuals (MNI): 130.

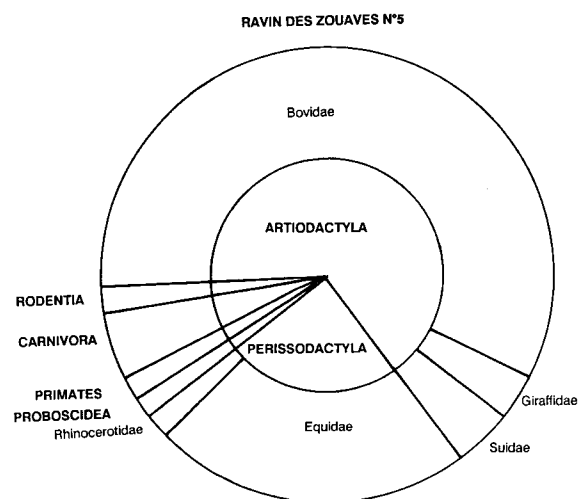


Fig. 5. Faunal composition of the mammal assemblage from "Ravin des Zouaves" n° 5 (RZO). Minimum number of individuals: 120.

less reliable, since a selection of the most supposedly interesting or spectacular specimens is likely to have occurred, either in the field or in the lab.. This would explain the large number of primates and carnivores, and of skulls compared to the number of mandibles.

Artiodactyls (41%) and perissodactyls (40%) are about equally numerous. Among the former,

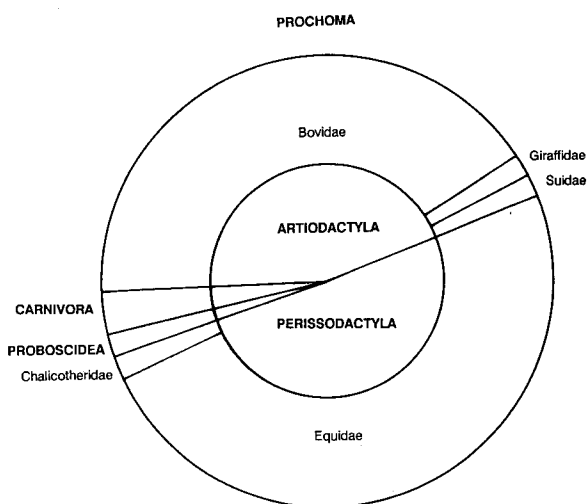


Fig. 6. Faunal composition of the mammal assemblage from Prochoma (PXM). Minimum number of individuals: 63.

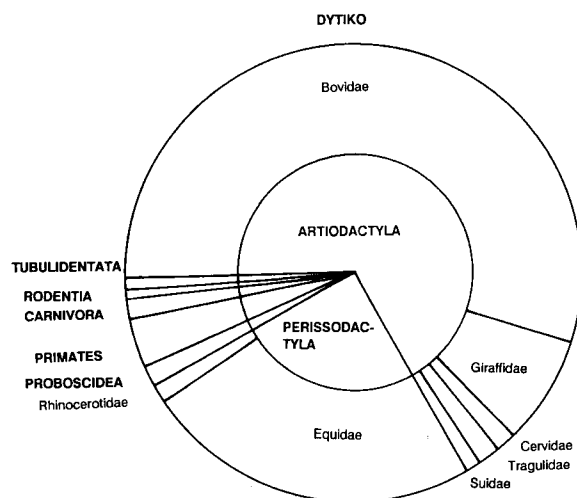


Fig. 7. Faunal composition of the mammal assemblage from the formation of Dytiko. Minimum number of individuals: 147.

bovids (30%) are less common than in Macedonia, but more diversified. Giraffids (4.6%) and suids (6%) are more common. There are some cervids, but no tragulids. Chalicotheres are present, and rhinoceros are not uncommon (5.5%). As we have mentioned above, carnivores (10%) and primates (6%) are relatively numerous.

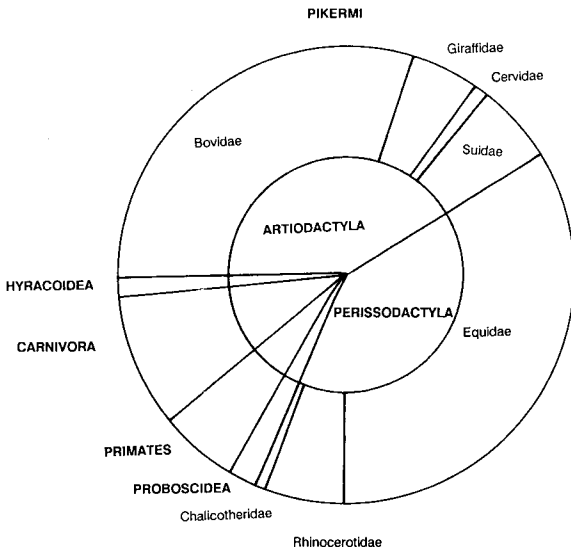


Fig. 8. Faunal composition of the mammal assemblage from Pikermi. Minimum number of individuals: 216.

Faunal diversity

The 3 most commonly used indices of faunal diversity are:

$L = \text{Simpson index}$

$$L = \sum_{i=1}^s \frac{n_i(n_i - 1)}{N(N - 1)}$$

where: n_i = MNI of the i^{th} species

N = total number of individuals, S = number of species.

This index is very sensitive to the frequency of the most common species. It increases with the predominance of one species, and is usually given in the shape $1 - L$: then, it is close to 1 when species abundances are equitable, as at Pikermi and Dytko, while the large number of *Samotragus* at RPI, and of *Hipparion* at PXM decrease the value of the corresponding indices.

$H' = \text{Shannon-Wiener index}$

$$H' = \sum_{i=1}^s \frac{n_i}{N} \ln \frac{n_i}{N}$$

This heterogeneity index is more sensitive to the frequency of rare species; it is greater when the various species are equally common;

$E = \text{Whittaker index}$

$$E = \frac{S \cdot n_{\max}}{\log N} - \log \frac{n_{\min}}{N}$$

where S is the number of species, increases with the evenness of the species frequencies (Table 3).

It is difficult to compare these indices calculated for the Macedonian with those obtained from the few other faunas where they have been calculated, because lack of micro-mammals strongly lessens the number of species and the total MNI. It would be meaningless to compare indices computed from micromammalian sites with those computed from the Macedonian ones. Therefore the indices are given here so that they can be compared with those of other large mammalian faunas in the future.

In Macedonia, we may note that the specific diversity increases during the Upper Miocene, from Ravin de la Pluie to Dytko.

Rank-abundance curves

An other means of depicting the relative frequencies of the various species in a site is to draw a rank abundance curve, where the frequencies of each species are plotted in decreasing order in ordinate versus their rank on a logarithmic abscissa. The resulting curve can be compared with the theoretical one corresponding to equitable frequencies (type 1 of Mac Arthur, 1957, 1960).

The curves for RPI and RZO (Fig. 9 and Fig. 10) diverge widely from the theoretical one, the 2 most common species being much more abundant. On the contrary the curves for Dytko and Pikermi (Figs. 11 and 12) follow more or less the theoretical curve, and have therefore more even frequencies without great predominance of 1 or 2 species; this could be explained by a more steady environment, warmer climate, or more diverse habitats, while the curves for RPI, and RZO might suggest more irregular ecological conditions (rainfalls, temperature...).

Conclusion on faunal assemblages

Comparison of the frequencies of the various families in the Macedonian sites show that while

TABLE 3

Indices of faunal diversity

	Total MNI	Number of species	Simpson index	Shannon-Weaver index	Whittaker index
Dytiko	147	23	0.912	2.60	15.7
PXM	60	13	0.810	1.93	9.7
RZO	120	22	0.854	2.40	13.6
RP1	130	19	0.808	2.42	11.7
Pikermi	216	32	0.920	2.93	20.2

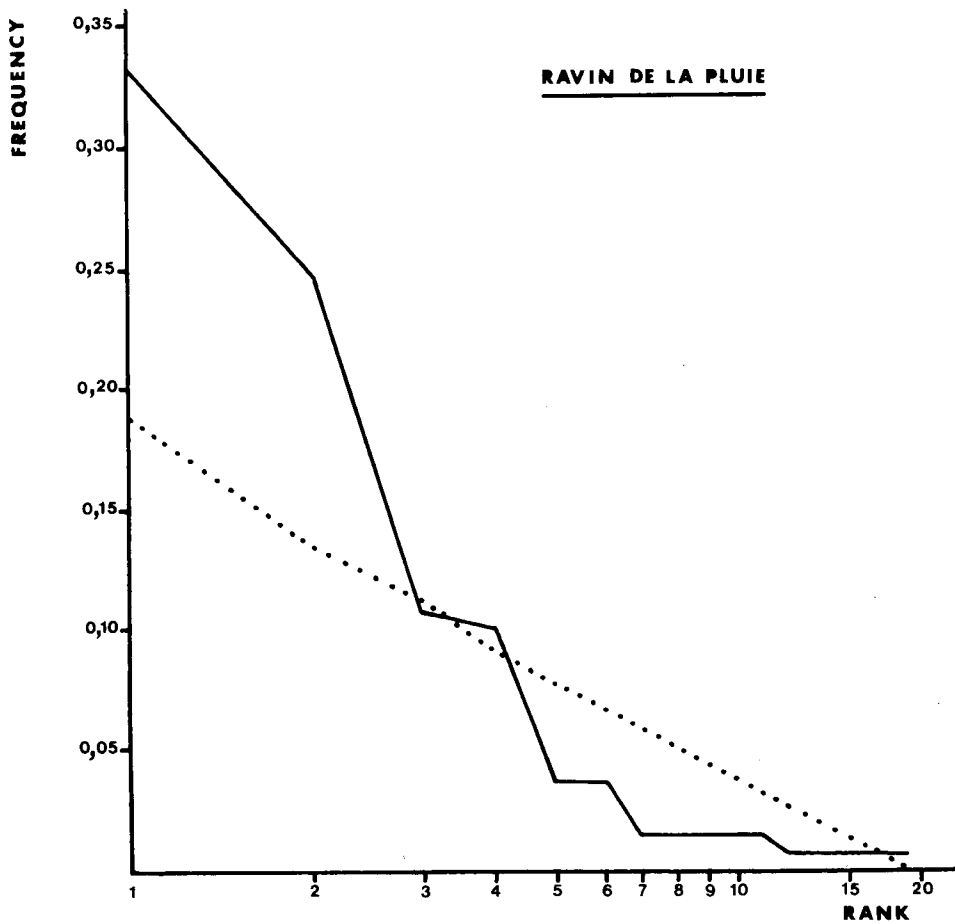


Fig. 9. Rank abundance curve for "Ravin de la Pluie". Dashed line is the expected curve according to Mac Arthur's type 1 model.

the frequency of some groups vary little (i.e. proboscideans, from 1.4 to 1.7%), others, like the carnivores or the primates, are more irregularly represented (from 1.4% at Dytiko, up to 5% at RZO for the carnivores and from 0 to 10% for the primates), but these differences in the fre-

quencies of the less common groups are likely to be taphonomically biased.

Except at PXM where the MNI is low, artiodactyls are predominant in the late Miocene of Macedonia. Among them, bovids are the most numerous, and their specific diversity increases

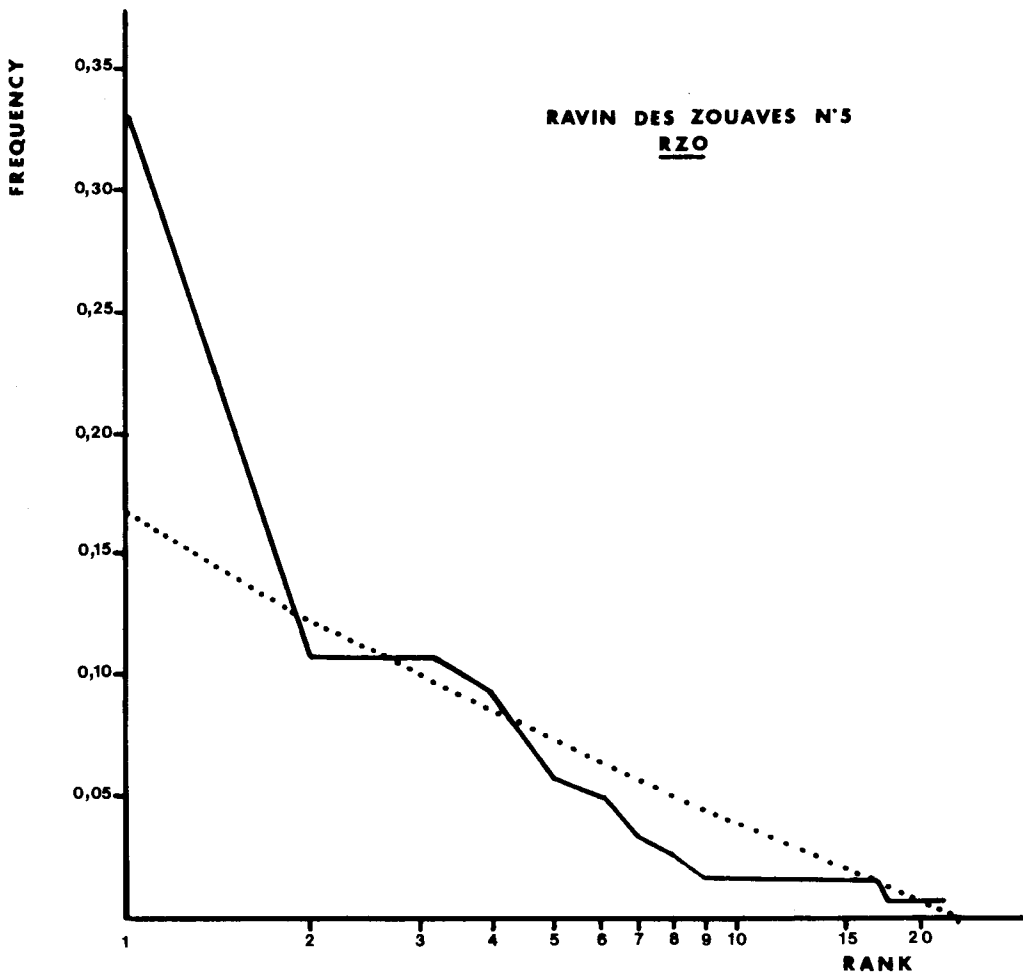


Fig. 10. Rank abundance curve for "Ravin des Zouaves" n° 5. Dashed line is the expected curve according to Mac Arthur's type 1 model.

from RPI to Dytiko. Giraffids are always present, but suids are either rare or absent. Cervids and tragulids are present at Dytiko only.

Among the perissodactyls, *Hipparion*'s species are always the most important group but one may notice they are uncommon at RPI.

Rarity or absence of micromammals in the Macedonian sites is certainly due to a taphonomic bias (e.g. depositional sorting), because screen-washing has been attempted at all sites.

Faunal diversity indices and curves show that Dytiko is the only assemblage with a well balanced fauna, i.e. a fauna in which there are no predominant species, whereas 1 or 2 species predominate in the other sites. According to Hutchinson (1961)

and Rose (1981), this might reflect more favourable ecological conditions at Dytiko (especially higher temperatures), while the other assemblages might have lived under stressed environments.

Analysis of the body weight repartition

Cenogram

The adaptations of a living mammal species are expressed in many ways. They are expressed by feeding habits, dentition, general morphology, morphology and proportions of the body and particularly of the limb bones, locomotor type or color of the hair and many other features. Body

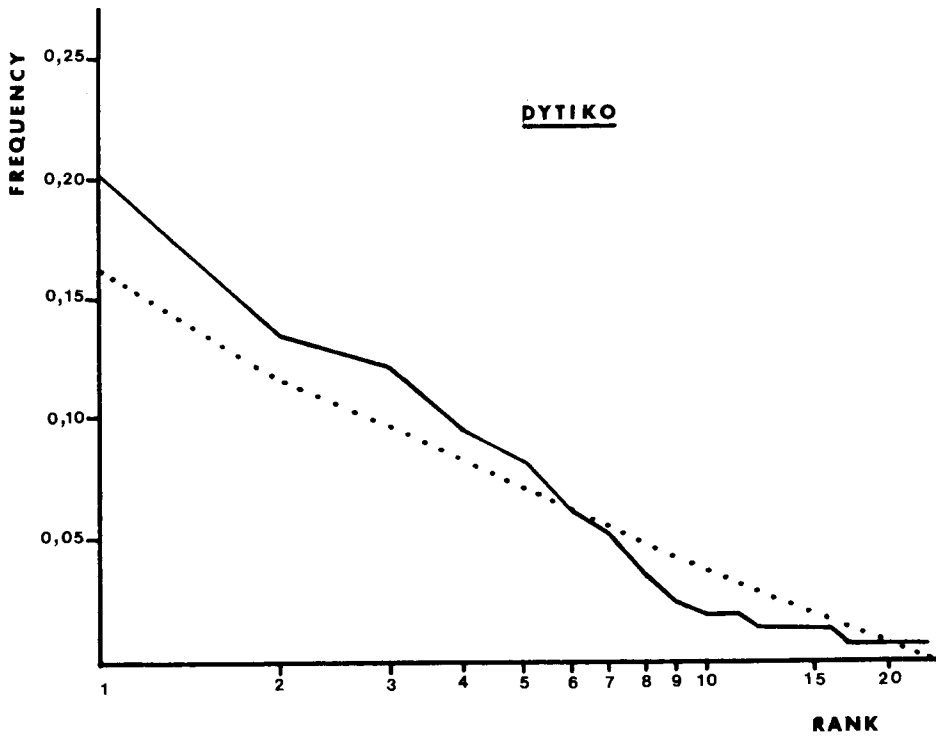


Fig. 11. Rank abundance curve for Dytiko formation. Dashed line is the expected curve according to Mac Arthur's type I model.

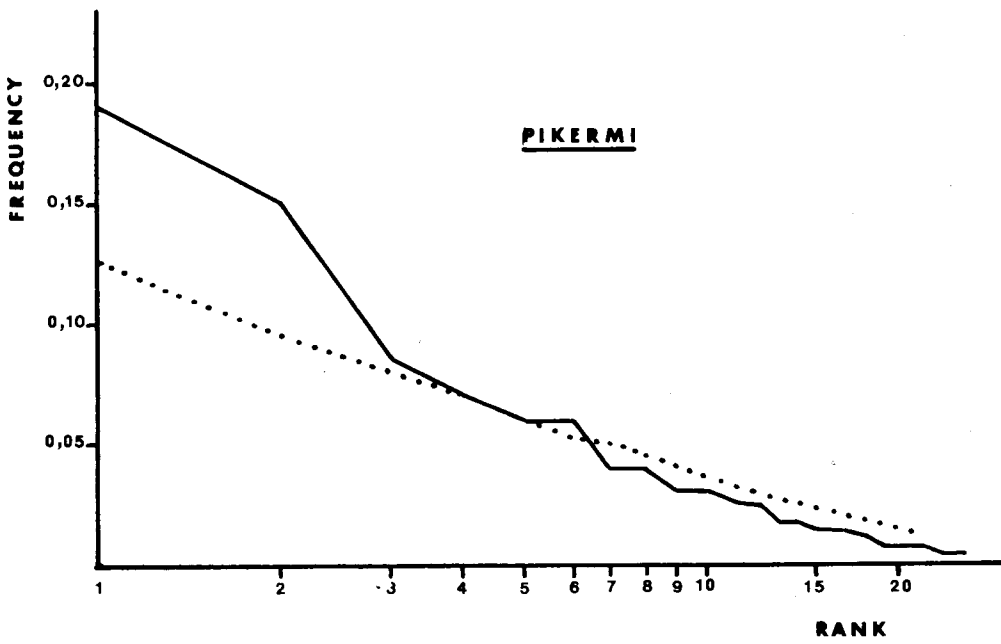


Fig. 12. Rank abundance curve for Pikermi. Dashed line is the expected curve according to Mac Arthur's type I model.

weight is also more or less linked with the ecological place of a species in a mammalian community and it is a part of the adaptation features which characterize this species. Importance of body size and body weight in mammalian communities has been stressed by several authors (Eisenberg, 1981; Peters, 1983). For Valverde (1964; 1967), each mammalian community can be generally considered as a self trophic chain more or less independent of the other vertebrate communities, amphibians, birds or reptiles. These communities (mammals, reptiles, birds or amphibians) are called microcommunities by Valverde (1964, 1967). Whatever the interactions between these microcommunities, each of them can be studied separately and compared to the other microcommunities of the same category in different areas. In this kind of microcommunities the body weight distribution is under control of both the environment and relationships between prey and predators. If the predators are generally median-sized with regard to the body size of the whole community, prey tend to be smaller or larger than the mean size of the predators. There is a general trend to increase or to decrease body size to escape predators. If the prey's weights are plotted on the Y axis and the species on the X axis in decreasing weight order, the graph which is obtained is called a cenogram. The shape of the graph depends on the predators' pressure and environment. In forest and closed environment there is a continuity in the curve, probably because the number of ecological niches is higher and there is a lowering of selective pressure level. In open environment there is a break in the curve generally for the medium sized prey, between 1 and 6 kg. The shape of the curve can also be different, the slope of the first part, larger weights, being steeply inclined for open environments probably because there are few species. The method has been applied to recent faunas (Valverde, *op. cit.*), to fossil Tertiary faunas (Legendre, 1986, 1988) and to Quaternary faunas (Cohen, 1988). For fossil animals the body weight is computed from the occlusal area of the lower M/1 (Gingerich, 1974; Gingerich and Ryan, 1979; Legendre, 1986; Gingerich and Smith, 1984; Gingerich and Rosenberg, 1982; Legendre and Roth,

1988). The localities of the late Miocene of Northern Greece are very poor in micro-mammals and in many cases it is impossible to know if there is a gap on the cenogram. One site, the "Ravin de la Pluie", has yielded some micro-mammals but not enough to have really a good idea on the shape of the inferior part of the curve (Fig. 13). The cenogram shows a steeply inclined slope in its first part and a break for the medium sized species, two conditions which would indicate an open environment. Looking at the graphs given by Legendre (1988) for recent communities of mammals, the "Ravin de la Pluie" cenogram fits very well with the curves established for the savanna faunas, as Rwindi-Rutschuru plain for instance (Legendre, 1988, Fig. 8). It is different from the curves established for recent forest faunas where the slopes of the curves remain similar for large and small mammals and the distribution of the species is continuous. It is also different from the recent desert environment faunas which have a curve with a very steeply inclined slope for large mammals and a very large gap between large and small mammals (Legendre, 1988, figs. 21, 24 et 25).

Multivariate analysis of the body weight repartition

Another way to analyse recent or fossil mammalian communities is to compare ecological diversity (Andrews et al., 1979). The mammals of the studied communities are divided in classes according to feeding habits, locomotor adaptation, taxonomy and body size or body weight. In Northern Greece localities, it is not possible to take into account feeding habits or locomotor adaptations because in faunas without micro-mammals there are very few categories in these classes. Moreover it is sometimes very hard to distinguish browsers from grazers in late Miocene faunas, particularly for giraffes and bovinds. Therefore, we used only body weights of herbivorous mammals, primary consumers at the beginning of mammalian trophic chains, whose weights are greater than 6 kg. Seven size categories have been chosen for recent or fossil faunas.

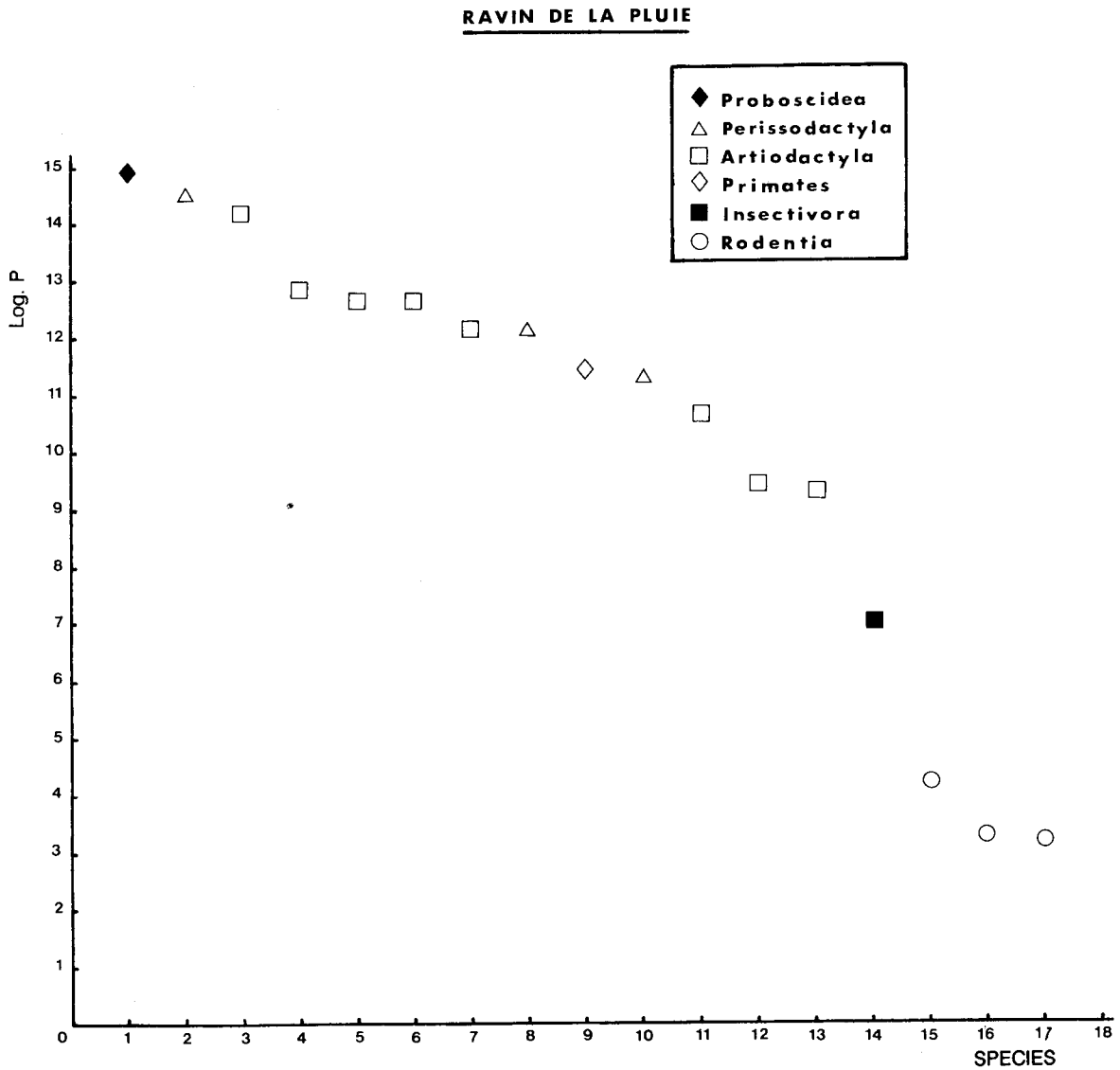


Fig. 13. Cenogram of fossil fauna from "Ravin de la Pluie".

06 kg < A < 14.9 kg
 15 kg < B < 39.9 kg
 40 kg < C < 109.0 kg
 110 kg < D < 269.0 kg
 270 kg < E < 539.0 kg
 540 kg < F < 1000.0 kg
 G > 1000.0 kg

Each fauna contains 10 species, or more, of mammals which correspond to the 7 size classes. We have chosen 23 recent faunas (Table 4) from tropical rain forest, open woodland, savanna or

flood plain and 26 fossil sites whose age range from middle Miocene to Pleistocene (Table 5). We did not find any temperate recent fauna in the Old World which could fulfil our definitions. The comparisons are made by multivariate analysis (correspondance analysis).

The data from recent and some fossil faunas were taken from several authors. The data from the Northern Greece sites and from the locality of Pikermi were taken from our own identifications. The results of the analysis (Fig. 14) show that 3

TABLE 4

Recent faunas used for the correspondance analysis

No.	Locality	Country	Ecology	Number of species	References
01	Transvaal	South Africa	Tropical forest	14	Rautenbach, 1978.
02	Mont Kivu	Zaire	Montane forest	16	Legendre, 1988.
03	Lamto	Ivory Coast	Tropical forest and savanna	26	Bourliere et al., 1974.
04	Makokou	Gabon	Tropical forest	23	Legendre, 1988.
05	La Maboké	Central Africa	Tropical forest	23	Legendre, 1988.
06	Tai	Ivory Coast	Tropical forest	21	Legendre, 1988.
07	Malaisie	Malaisia	Tropical forest	14	Legendre, 1988.
08	Transvaal 7	South Africa	Savanna woodland	14	Rautenbach, 1978.
09	Lokori	Kenya	Savanna woodland	13	Legendre, 1988.
10	Transvaal 2	South Africa	Montane grassland	17	Rautenbach, 1978.
11	Umfolozi	South Africa	Savanna woodland	21	Mentis, 1970.
12	Kafue	Zambia	Flood plain grassland	25	Sheppe and Osborne, 1971.
13	Birao	Central Africa	Flood plain grassland	19	Felix, 1953.
14	Rukwa valley	Tanzania	Flood plain grassland and woodland	31	Andrews et al., 1979.
15	Transvaal 5	South Africa	Arid bushland	32	Rautenbach, 1978.
16	Serengeti	Tazania	Savanna woodland	32	Legendre, 1988.
17	Transvaal 4	South Africa	Savanna woodland	17	Rautenbach, 1978.
18	Transvaal 9	South Africa	Savanna woodland	31	Rautenbach, 1978.
19	Zinave	Mozambica	Savanna woodland	26	Legendre, 1988.
20	Gabiro	Rwanda	Wooded grassland	20	Andrews et al., 1979.
21	Rwindi-Rutschuru	Rwanda	Arid bushland	10	Legendre, 1988.
22	Ihema	Rwanda	Arid bushland	15	Legendre, 1988.
23	Amboseli	Kenya	Arid bushland	23	Legendre, 1988.

variables are more important than the others ones: A, F and G.

A and E have respectively 29.8 and 36.1% of the total variance of the first axis. F has 71.9% of the variance of the second axis; it is followed by A with 11.7%. On the third axis, the more important variables are E, G and A. Plotting of the localities on the plan 1-2 (Fig. 14) shows that the recent tropical forest localities are grouped together with A; all are saturated for this variable which corresponds to the smallest body weights. A and these localities are on the opposite of E on the first axis and of F on the second one. The more open environment localities are more linked to F and little to E. Most of them are plotted on the graph along a line from A to F, from the open woodland near the tropical forest localities to the dry savannas, except two localities which are little apart. Mammals whose body weights are between 540 and 1000 kg are more numerous with regard to other mammals in open environments. On the other hand most of the fossil localities are plotted on the right part of

the first axis and out of the group of the recent ones. Two African fossil localities, Fort Ternan (middle Miocene) and Maboko (middle Miocene) plot among the recent faunas between tropical forest faunas and open environment fauna (FTE) or with savanna faunas (MBK). It is also the case of Pasalar and Yassiören, respectively dated from middle and late Miocene of Asia Minor. The site of Jebel Zelten (ZEL) plots very near the dry savanna faunas.

The late Miocene Greek localities are grouped together with more or less the same values on the second axis and not far from G variable. They are separated along the first axis, Dytiko being on the left part, closer to the forest and woodland localities than are the other ones. The Pleistocene sites are on the right part of the first axis, Voigstedt and Stranska-Skala are very far and very linked to the E variable and on the opposite of A. Ternifine, Oubeidyeh and Burgtonna opposite to A but on the dependance of both E and F. We may note the place of Zhou Kou Dian just with the bulk of late Miocene sites. The two levels of

TABLE 5

List of the fossil faunas used for the correspondence analysis

	Localities	Country	Number of species	Age	Bibliography
BUR	Burgtonna	Germany	14	Pleistocene	Hunermann, 1978; Kahlke, 1978a,b; Cohen, 1988.
CKT	Zhou Kou Dian loc.1	China	24	Pleistocene	Young, 1932.
OUB	Oubeidiyeh	Israël	19	Pleistocene	Tchernov and Guérin, 1985.
STR	Stranska Skala	Czechoslovakia	15	Pleistocene	Musil, 1972; Cohen, 1988.
TER	Terminfe	Algeria	20	Pleistocene	Geraads et al., 1986.
VOI	Voigstedt	Germany	16	Pleistocene	Wehrli, 1963; Cohen, 1988.
LGB	Langebaanweg PPM 3aN	South Africa	16	Pliocene	Hendey, 1981.
LGM	Langebaanweg QSM	South Africa	18	Pliocene	Hendey, 1981.
DJH	Jebel Hamrin	Iraq	13	Late Miocene	Thomas et al., 1980; Brunet and Heintz, 1983.
DIT	Dytiko	Greece	21	Late Miocene	our identification.
HAL	Halmypotamos	Greece	17	Late Miocene	Melentis, 1967.
LUK	Lukeino	Kenya	17	Late Miocene	Pickford 1978; Thomas, 1980.
MMR	Middle Maraghe	Iran	20	Late Miocene	Bernor 1978; Bernor, 1986.
RPI	Ravin de la Pluie	Greece	13	Late Miocene	our identification.
PMX	Prochoma	Greece	11	Late Miocene	our identification.
PIK	Pikermi	Greece	26	Late Miocene	Gaudry, 1862; Solounias, 1981.
RZO	Ravin des Zouaves no.5	Greece	17	Late Miocene	our identification.
SAM	Samos	Greece	28	Late Miocene	Solounias, 1981.
SAH	Sahabi	Libya	16	Late Miocene	Bernor and Pavlakis, 1987.
UMR	Upper Maraghe	Iran	15	Late Miocene	Bernor, 1978; Bernor, 1986.
VAT	Vathyiakkos	Greece	18	Late Miocene	our identification.
YAS	Yassioren	Turkey	15	Late Miocene	Ozansoy, 1957; Sickenberg, 1975.
FTE	Fort Ternan	Kenya	21	Middle Miocene	Shipman et al., 1981.
MBK	Maboko	Kenya	20	Middle Miocene	Andrews et al., 1981.
PAS	Pasalar	Turkey	15	Middle Miocene	Sickenberg, 1975; Köhler, 1987.
ZEL	Zelten	Libya	15	Middle Miocene	Hamilton, 1973; Savage and Hamilton, 1973.

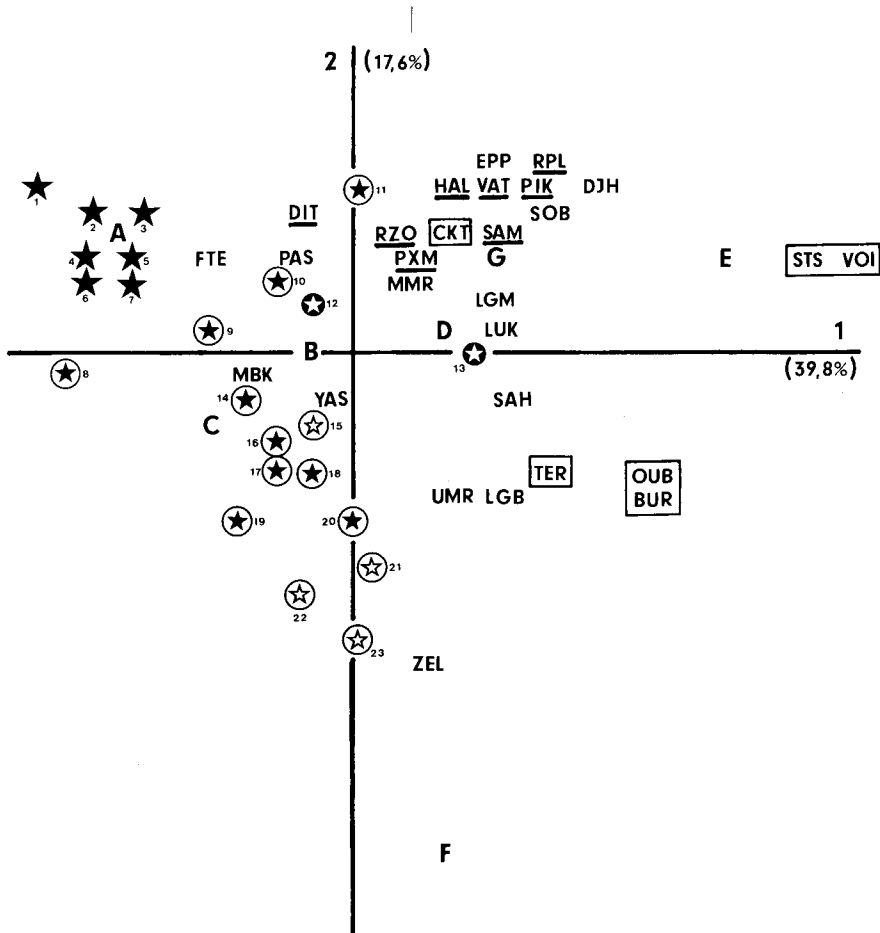


Fig. 14. Multivariate analysis (correspondance analysis) of recent and fossil faunas relative to the body weight of the large herbivorous mammals on the plan of the two first axis. Variables: A= 6–14.9 kg; B= 15–39.9 kg; C= 40–109 kg; D= 110–269 kg; E= 270–539 kg; F= 540–1000 kg; G= more than 1000 kg. Recent faunas: Black stars= forest; circled black stars= savanna woodland, montane and wooded grassland; circled white stars= arid bushland; white on black stars= flood plain grassland. For numbers see Table 4. Fossil faunas: For letters see Table 5. The Greek localities are underlined; the Pleistocene localities are framed.

Maragheh as well as the two levels of Langebaanweg are separated along the second axis.

On the plan 1–3 (Fig. 15), the recent faunas are less separated from the fossil ones but they plot nevertheless between A and G variables, smaller body size and larger body size. The tropical rain forest faunas stay near the A variable. The sites of Fort Ternan, Pasalar, Yassiören and Maboko are not far from each other and they are separated from the Greek localities which plot near G variable. In this plan, the two levels of Maragheh and the two levels of Langebaanweg are grouped respectively. Some Pleistocene localities plot very

far from the other sites; they are attracted by E variable and in opposition with G variable. This is the case of Voigstedt, Stranska Skala and, a little less, Oubeidyeh. The other Pleistocene localities plot not so far from G variable which represents the larger body weights. The late Miocene Greek localities plot also near the G variable except “Ravin de la Pluie” which is plotted with Sahabi and Maragheh.

In this multivariate analysis there is a striking difference between the bulk of the recent faunas and most of the fossil ones. The two sets plot separately, the latter being more or less linked with

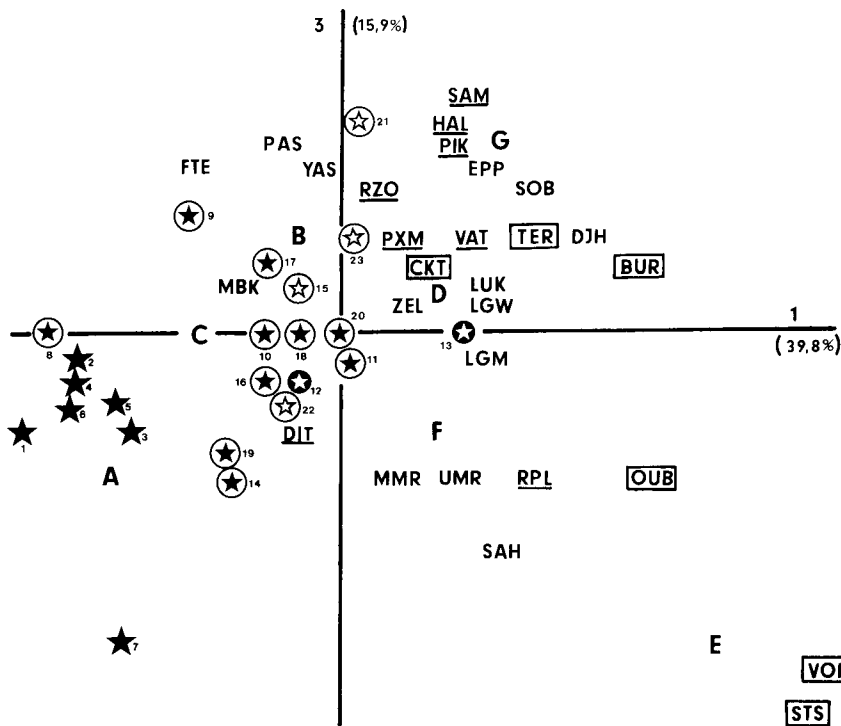


Fig. 15. Multivariate analysis (correspondance analysis) of recent and fossil faunas relative to the body weight of the large herbivorous mammals on the plan of the axis 1 and 3. For legend see Fig. 13.

E and G variables, two categories of large mammals. This is probably related to large extinction which occurred at the end of the Pleistocene, 9000 to 10,000 yr B.C. This large scale event has been noted in North and South America, in Europe and North Asia where 60% of the large herbivorous mammal genera disappeared, probably killed by skilled human hunters (Owen-Smith, 1989), whereas Africa and tropical Asia have suffered only minor extinction. Most of the Pleistocene genera do exist today in these areas. But recent works show that the reduction of very large herbivorous mammals can cause a large disturbance in ecosystems and it can be followed by extinctions of other large herbivorous mammals (Graham and Lundelius, 1984; Owen-Smith, 1989). Actually in most part of Africa this process has begun to act and, if there are nowadays 35 genera of large herbivorous mammals, no local fauna can reach such a number. There are more species in the heavy weight categories in the fossil localities. The richness in large herbivorous species of G and E

categories would be decreasing also in Africa even if, on the whole, the number of genera is not yet affected. In this point of view, it is interesting to see that the locality of Umfolozi plots with the fossil faunas; it is certainly because we have added to the list of the living species some species which are not present nowadays but which were present at the beginning of this century. Our study shows that the recent faunas cannot be used strictly as paleoecological models to reach conclusions for fossil faunas.

Conclusions

The comparison of the faunal indices of similarity as well as the principal component analysis and the cluster analysis at the generic level show a grouping between the Macedonian Turolian localities ("Ravin des Zouaves" n° 5, Vathyakkos, Prochoma and Dytiko) on one side and between two sets of sites, Pikermi and Halmyropotamos (Southern Greece) followed by Samos (Eastern

Greece) and Maragheh (Middle East) on the other. The locality of "Ravin de la Pluie" is isolated in the principal component analysis and separated from all the other localities at the first branching of the cluster analysis. At the species levels we obtain almost the same result but Dytiko is separated from the other Macedonian Turolian localities. Most of these results can be explained on biogeographical grounds: Northern Greece sites cluster together, they are linked with the southern Greece sites and, through Samos (Eastern Greece) and the Greco-Iranian faunal province (Bonis et al., 1979), to Maragheh (Middle East). The separation of "Ravin de la Pluie" from the other sites on the graph may be explained by a change in ecological conditions between Vallesian and Turolian, the geological level being more important for faunal similarities or differences than geographic localisation. The distinction of Dytiko in the specific multivariate analysis could be due to the slightly younger age of this locality versus the other Turolian sites of Greece (Bonis et al., 1988) or may be by the differences in general faunal composition without predominance of one or two species as in the other localities.

The analysis of the faunal assemblages of the late Miocene Macedonian mammalian sites shows that the frequency of some groups, the less common ones as Carnivora, can vary in large proportions probably for taphonomic bias reasons. Generally Artiodactyla are predominant, particularly the bovids except in Prochoma where the minimum number of individuals is the lower and *Hipparion* is dominant. But we must note the increase of bovids diversity from "Ravin de la Pluie" (Vallesian) to Dytiko (late Turolian). In fact the Dytiko fauna, more diversified, suggests more favorable ecological conditions, the same being indicated by the regular shape of the curve of faunal diversity. If the general landscape in Macedonia during the late Miocene times seems to have been an open one, with numerous giraffids or bovids and few suids, in Dytiko the environment was more forested with cervids and tragulids as components of the fauna.

The analysis of the body weight repartition can be made with two different methods. The ceno-

gram, curve of the repartition of the body size or body weight species after species, can be applied only to one locality, the "Ravin de la Pluie", which has yielded macro-mammals but also some micro-mammals. The curve has a steeply inclined first part and a break for the medium sized species which indicate an open environment. The multivariate analysis allow to separate very clearly the extant forest faunas from the open environment faunas, the proportions of large, medium or small sized species being very different. It is more difficult to analyse the fossil faunas. They are separated from the recent ones on the graph probably because nowadays there is a gap in the communities corresponding to large species, particularly the big game. Nevertheless we can note that, among the Macedonian mammalian fossil sites, the plotting of the locality of Dytiko on the graphs is the nearest of the recent forest dwelling faunas.

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