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COMPOSITION AND SPECIES DIVERSITY IN LATE MIOCENE FAUNAL ASSEMBLAGES OF NORTHERN GREECE

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A B S T R A C T

The faunal assemblages of the late Miocene of Macedonia are compared each other, and with those of the classic localities of Samos and Pikermi. Revised faunal lists allowed us to compute similarity indices, which demonstrate the remoteness of Ravin de la Pluie, a Vallesian site, and the clustering of the lower Turolian localities of PXM and VAT. Comparisons of the frequencies of the various taxonomic groups show a sharp increase in the number of Hipparions in sites later than RPl and a general increase of the faunal diversity during the Turolian.

Σ Υ Ν Ο Ψ Η

Στην εργασία αυτή γίνεται μια σύγκριση των πανίδων θηλαστικών του Ανωτέρου Μειοκαίνου της Μακεδονίας, τόσο μεταξύ τους, όσο και μ' εκείνες των κλασσικών θέσεων του Πικερμίου και της Σάμου. Δίνονται νέοι πιο πλήρεις κατάλογοι πανίδων, που επέτρεψαν τον υπολογισμό διαφόρων "δεικτών ομοιότητας". Με βάση αυτούς τους δείκτες βρέθηκε, ότι η θέση Ravin de la Pluie (RPl) του Βαλλέζιου είναι απομακρυσμένη απ' όλες τις άλλες, και ότι οι θέσεις Prochoma 1, Ravin des Zouaves 5 και Vathylakkos 3 του Κατώτερου Τουρόλιου αποτελούν μια συγκέντρωση. Από συγκρίσεις της συχνότητας εμφάνισης των διαφόρων ταξονομικών ομάδων αποδεικνύεται μια αξιοσημείωτη αύξηση του αριθμού των ιππαρίων στις νεότερες από την RPl θέσεις και μια γενική αύξηση της πανιδικής ποικιλλίας κατά το Τουρόλιο.

INTRODUCTION

Fossil vertebrates localities in Macedonia (Northern Greece) were found in the beginning of the twentieth century (Andrews, 1918; Arambourg and Piveteau,

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1929), In the recent years several new localities have been excavated which have yielded many fossil vertebrates ranging in age from late Vallesian to late Turolian (Bonis et al., 1988), in other words from 9-10 myr to 6 myr. These localities can be assembled into three different sets. The oldest quarries, Ravin de la Pluie (RP1) and Ravin des Zouaves n° 1 (RZ1) are into the Nea Messimbria Formation (NMF). The fauna indicates clearly a Vallesian age (*contra* Bernor, 1985). The second set with the Ravin des Zouaves n° 5 quarry (RZO), the Vathylakkos group and the locality of Prochoma, dates from early Turolian, older than the well known locality of Pikermi. The last one is composed of the three sites of Dytiko whose age is late Turolian. The purpose of this paper is to compare the faunal composition and species diversity of the different late Miocene localities of Macedonia. When it is possible we have added in the comparisons two localities of the same geographical area, Pikermi in southern continental Greece and Samos quarry A in the island of Samos in the Aegean sea.

The faunal composition is given by similarity or distance indices, the species diversity is expressed by pie-diagrams and faunal diversity indices. The results in some cases allow to hypothesize on the type of mammal community and to look for chronological, geographical or ecological differences between communities.

SYSTEMATIC COMPARISONS

The Table 1 gives the faunal list of large mammals for the Macedonian sites, plus Pikermi and Samos Quarry A. Faunal lists for the Macedonian sites and Pikermi are mainly taken from our own studies (Bonis et al., 1988; Koufos, 1987; Geraads, 1988, and unpublished; see also Marinos & Symeonidis, 1972; Symeonidis, 1973, 1978; Melentis, 1967). 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 united the three close localities of Vathylakkos: VAT, VTK and VLO, plus the "Vatilük" of Arambourg; we did the same with the three localities of Ditiko: DTK, DKO and DIT, and with the two Vallesian localities of RZ1 and RP1.

	RZ1		VAT		DTK		
			VTK		DIT		
	RP1	RZO	VLO	PXM	DKO	PIK	SAM
Choerolophodon pentelicus	+	+	+	+	+	+	+
Zygolophodon tapiroides		+				+	
Tetralophodon atticus	sp					+	
Dinotherium giganteum						+	+

	RZ1		VAT		DTK		
			VTK		DIT		
	RP1	RZO	VLO	PXM	DKO	PIK	SAM
Chalicotherium goldfussi			+	?	+		
Ancylotherium pentelicum				?		+	+
Ceratotherium neumayri		+	+		cf	+	+
Dicerorhinus pikermiensis						+	+
Aceratherium sp.			+			+	+
Hipparion proboscideum		+	cf				+
Hipparion mediterraneum					+	+	
Hipparion brachypus						+	
Hipparion primigenium	+						
Hipparion matthewi					+		+
Hipparion periafricanum					+		
Hipparion dietrichi		+	+	+			+
Hipparion macedonicum	+	+	+	?			
Microstonyx sp.		+	+	+	+	+	+
Postpotamochoerus sp.		+					
Dorcatherium sp.			+		+		
Cervid					+	+	+
Helladotherium duvernoyi		+		+		+	+
Palaeotragus rouenii	cf	cf			+	+	+
Palaeotragus coelophrys	cf						cf
Samotherium boissieri			+				+
Decennatherium cf. *pachecoi*	+						
Bohlinia attica	+		+		+	+	
Gazella sp.		+	+	+	+	+	+
Prostrepsiceros rotundicornis		+				+	+
Prostrepsiceros zitteli		+	+	+			+
Prostrepsiceros vallesiensis	+						
Prostrepsiceros n.sp.					+		
Oioceros rothi						+	
Oioceros wegneri							+
Nisidorcas planicornis		+	+	+			
Ouzocerus gracilis	+						
Hispanodorcas orientalis					+		
Samotragus praecursor	+						
Pachytragus laticeps							+
Protoryx carolinae						+	
Protragelaphus skouzesi						+	+

			VAT		DTK		
	RZ1		VTK		DIT		
	RP1	RZO	VLO	PXM	DKO	PIK	SAM
Protragelaphus theodori					+		
Palaeoryx pallasi						+	+
Pseudotragus parvidens						+	+
Pseudotragus capricornis							+
Tragoreas oryxoides							+
Palaeoreas lindermayeri			+		+	+	
Palaeoreas zouavei		+		sp			
Criotherium argalioides							+
Mesembriacerus melentisi	+						
Tragoportax amaltheus						+	
Tragoportax rugosifrons		+	+	+			+
Tragoportax gaudryi					+	+	
Hystrix sp.			+		+	+	
Orycteropus gaudryi					cf		+
Mesopithecus pentelicus			cf		cf	+	
Mesopithecus n.sp.		+					
Ouranopithecus macedoniensis	+						
Pliohyrax graecus						+	
Plioviverrops orbignyi			+			+	+
Plioviverrops guerini			cf				
Protictitherium gaillardi	cf						
Protictitherium intermedium			+				
Protictitherium crassum					+		
Adcrocuta eximia	+	+	+	+		+	+
Ictitherium hipparionum			+			+	+
Ictitherium robustum		+	+			+	+
Plesiogulo crassa			+			sp	
Chasmaporthetes bonisi		+			+		
Machairodus sp.		+	+			+	+
N =	15	21	26	12	22	33	33

Table-1. Faunistic list of the Axios Valley localities, Pikermi and Samos.

Some groups have not yet been studied in detail, and, therefore, *Gazella*, Cervids, *Microstonyx*, *Hystrix*, *Orycteropus* and *Machairodus* have been excluded from the comparisons at the species level. We have also excluded at this level *Palaeotragus coelophrys*, whose specific identity at Samos and Ravin de la Pluie is uncertain, and *Aceratherium*, poorly represented in the continental sites

mentionned here (*Chilotherium* is not listed at Samos A, because we believe that *A.samium* does not belong to this genus *contra* Solounias, 1981).

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

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

$$\text{Pickford index: } = \frac{(X-X\cap Y)(Y-X\cap Y)}{X.Y} \quad \frac{\text{product of the number of taxa peculiar to each site}}{\text{product of the number of taxa in each site}} \times 100$$

We have not used other indices (e.g. Dice's, Jaccard's, or Otsuka's), which take into account both the number of taxa in common and the number of taxa in the richest site: we believe that they are misleading, since they do not indicate maximum similarity even if all the species of one site are also present in the other. Both indices were calculated at the generic and at the specific levels. The results are given in Tab. 2, 3. Indices at the generic level are to the left, at the specific level to the right.

	RZO		VATHYL		PXM		DYTIKO		PIK		SAM	
RP1	44	76	39	62	44	60	38	77	35	69	50	79
RZO			15	25	4	11	17	78	8	41	18	25
VATHYL					5	9	18	53	16	39	17	31
PXM							16	83	13	56	19	27
DYTIKO									16	49	27	73
PIK											5	20

Table-2. Pickford's distances for the studied localities.

	RZO		VATHYL		PXM		DYTIKO		PIK		SAM	
RP1	38	21	46	27	36	25	38	14	54	23	38	15
RZO			67	56	91	80	61	11	83	11	67	61
VATHYL					91	87	60	29	68	43	64	29
PXM							73	12	82	37	73	67
DYTIKO									70	37	55	18
PIK											81	55

Table-3. Simpson's index of similarity for the studied localities.

Not surprisingly, Ravin de la Pluie is the most excentric of all sites. Well established is the closeness, on both indices and on both levels, between Prochoma, Ravin des Zouaves N^{O} 5 and Vathylakkos, and there can be no doubt that

all these sites belong to a single faunal unit, with only minor ecological and/or chronological differences between them.

Also closely clustered are Samos and Pikermi. The similarity of these sites has already been emphasized by Solounias (1981). Compared, by both indices, with the Vathylakkos-RZO-PXM group, Pikermi is very consistently closer at the generic level, while Samos is closer at the specific level. We find the same kind of difference for the Ditiko sites: they are rather central at the generic level but still more remote than RPl at the specific level. On the whole, at the generic level, R.Pl. is very remote, while at the specific level, Ditiko and R.Pl. are the most remote.

Leaded by the results previously published (Bonis et al., 1988) concerning the relative chronology of the sites, we can propose an explanation, or at least a working hypothesis, for the discrepancies between the results at the specific and generic levels: the generic distance might be more an expression of the geographic or ecological similarity, the specific distance an expression of the chronological one, although these factors cannot be treated separately. For instance, the great distance between RPl + RZl and the other sites at the generic level is certainly also partly due to their earlier age. Similarly, we do not know what are the relative bearing of ecology and geography on the closeness of Samos and Pikermi, as compared to the Turolian Macedonian sites.

COMPARISONS OF THE FAUNAL ASSEMBLAGES

The fossil assemblage collected in any paleontological site is, of course, an image of the fauna which lived in that particular area and time-period. From this taphocoenosis, an imperfect sample of the biocoenosis, paleontologists have long been trying to draw conclusions about climate, vegetation and paleoecology. For relatively late (Pleistocene) faunas, one may compare the sites by infering the paleoecology of the fossil species from those of their living close relatives, but this would be risky for late Miocene faunas. One can use instead various indices and graphic methods to depict the specific diversity and the relative frequencies of the various species (or other taxonomic categories) in each site. Of course, the samples of the fossil faunas must be large enough to be representative of the thanatocoenosis. In every case, one has to compute the number of individuals present in the site. For Mammals, the Minimum Number of Individuals (MNI) is usually based upon dental remains; here we have used the lower left molars. In case there are very few micromammals, as in Macedonia, the MNI is usually not very high. Nevertheless, it is higher than 100 for Ravin de la Pluie, Ravin des Zouaves and Dytiko. It is lower than 100 at Prochoma and the indices for this site are thus less reliable.

FREQUENCY DIAGRAMS

From the MNI of each site and the MNI of each species, it is easy to calculate the frequencies of each taxon, which can be used to construct pie-diagrams. In the macedonian sites other than PXM, the Artiodactyls are by far the largest group, making up from 65 to 75% of the fauna. Within the Artiodactyls, Cervids and Tragulids are rare or absent, Bovids being the most common group. Perissodactyls are uncommon at Ravin de la Pluie, where they consist only of *Hipparion*, but increase in the other sites and even outnumber the Artiodactyls at Prochoma. Primates may be numerous; at Ravin de la Pluie they are indeed the second most common group, after Bovids.

It would be interesting to compare these frequencies with those from other upper Miocene sites, but this is presently impossible because we do not know their MNIs, which are not published. Moreover, the fossils should come from a single stratigraphic layer, which is not the case at Samos and Maragheh. For Pikermi, although it has been recently surmised that two levels had been confused under this name, we have tried to compute the frequencies from the fossils housed in the Muséum National d'Histoire Naturelle, Paris. The result (fig. 1) is only approximative, since there are many possible errors. Artiodactyls and Perissodactyls are about equally numerous. Among the Artiodactyls, Bovids, although the most common group, are less abundant relatively to the Suids and Giraffids.

INDICES OF FAUNAL DIVERSITY

In each site, the faunal diversity can be figured by several indices, whose relative significance have been often discussed (Rose, 1981a and b; Gheerbrant, 1989). We will use here the 3 indices most frequently used:

Simpson's index:

$$L = \sum \frac{n_i(n_i-1)}{N(N-1)}$$

where n_i is the MNI of species i (every species), N is the total number of individuals (= d MNI) in the site. The larger L, the lower the specific diversity. This index is often used as 1 - L; it is then close to 1 when the fauna is well-balanced. Thus at Ravin de la Pluie (Table) a bovid (*Samotragus*) is predominant, and the index is low; the reverse is true at Ditiko.

SHANNON-WIENN 'S INDEX

$$H' = \sum \frac{n_i}{N} \times \ln \frac{n_i}{N}$$

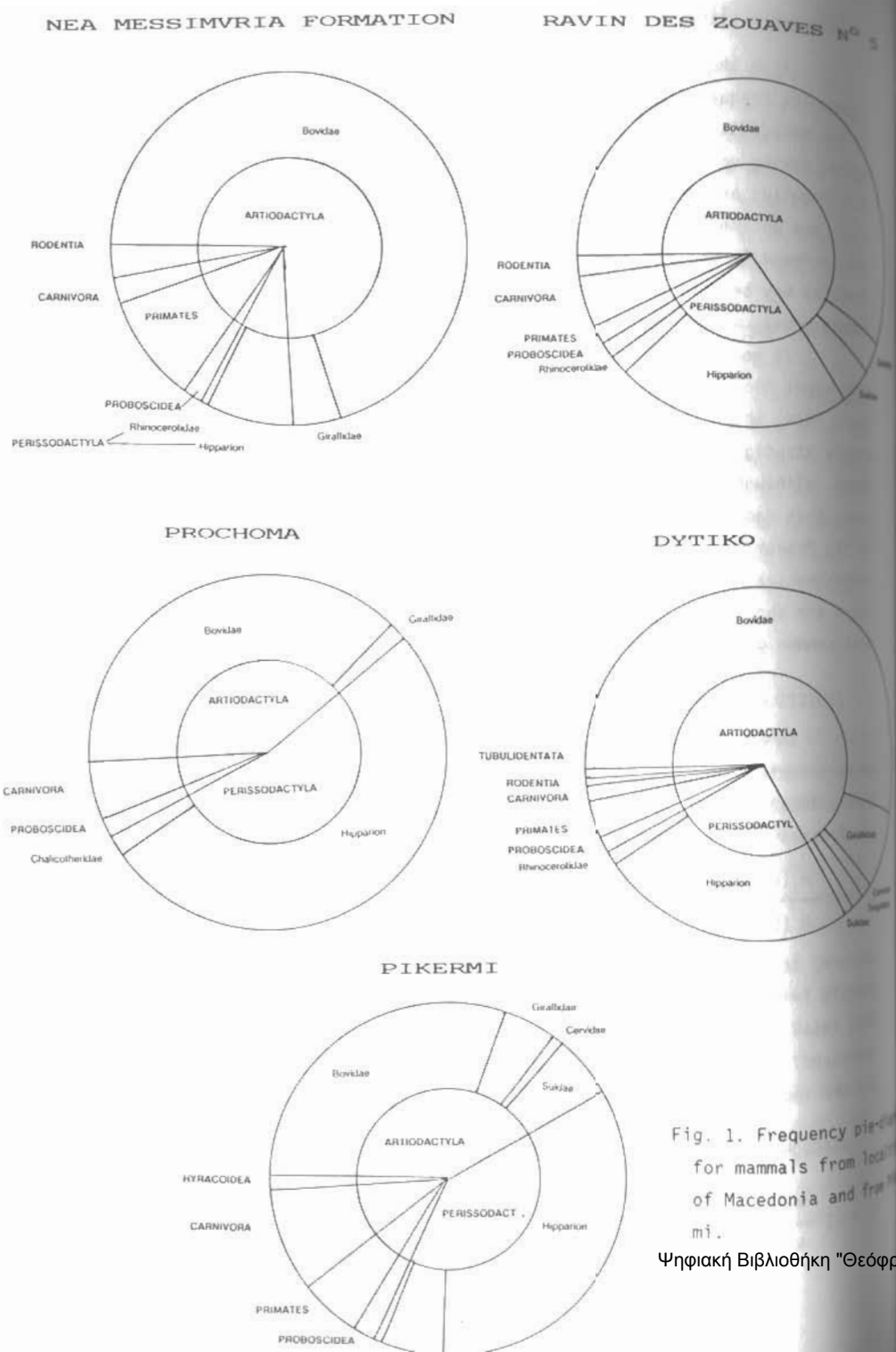

Fig. 1. Frequency pie-
for mammals from loca
of Macedonia and fro
mi.

This index is a figure of the specific diversity and faunal balance (Rose, 1981; Gheerbrant, 1989).

WHITTAKER'S INDEX:

$$E = \frac{S}{\log(n_{max}/N) - \log(n_{min}/N)}$$

where S is the total number of species n_{max}/N the frequency of the most common species, n_{min}/N the frequency of the least common species. This index increases when the fauna is well-balanced. It is very sensitive to the number of species.

	N	S	1-L	H'	E
Ditiko	147	23	0.912	2.60	15.7
PXM	60	12	0.810	1.96	9.0
RZO	120	22	0.854	2.40	13.6
RP1	130	19	0.808	2.42	11.7

Table-4. Indices of faunal diversity for the studied localities.

CONCLUSIONS

The most striking feature in the faunal assemblages of the Macedonian late Miocene localities seems to be the almost complete lack of micromammals, except some teeth of rodents or insectivores in RP1 or RZO. There is certainly a bias in the fossil record. We can invoque an hydraulic sorting during the fluvial transport of large versus micro-mammals but it exists in all the localities and we did not find any locality of low energy. For faunal comparisons with other localities we must take in account only the similarly-sized mammals. In the frequency diagrams, the Macedonian localities are more or less homogeneous except Prochoma (PXM) whose number of *Hipparion* specimens is higher. There is possibly a collecting bias, because the locality has been discovered on a railway excavation and the first fossils which have been collected had been unearthed by scrapers; in this case the *Hipparion* remains, more robust, would be more numerous. Another bias for this locality could be indicated by the low number of specimens and species and the low indices of diversity. At Pikermi, where Perissodactyls and Artiodactyls are equally numerous, the smaller quantity of Bovids versus Suids, could indicate a slightly different climate, probably more humid.

Other studies will continue to give more precisions in a next article.

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