

The Late Miocene Mammal Faunas of the Mytilinii Basin, Samos Island, Greece: New Collection

17. Palaeoecology – Palaeobiogeography

by

George D. Koufos¹⁾, Dimitris S. Kostopoulos¹⁾ & Gildas Merceron²⁾

KOUFOS, G.D., KOSTOPOULOS, D.S. & MERCERON, G., 2009. The Late Miocene Mammal Faunas of the Mytilinii Basin, Samos Island, Greece: New Collection. 17. Palaeoecology – Palaeobiogeography. — Beitr. Paläont., 31:409–430, Wien.

Abstract

The palaeoecology of the Samos mammal faunas is studied using complementary methods. The analysis of the faunal diversity suggests that the Samos faunas are homogeneous, equilibrated and with normal taxonomic distribution. The faunal composition of the Samos faunas has been analyzed using the Minimum Number of Individuals (MNI), the taxonomy and the feeding preferences of the various groups of mammals. Dental meso- and micro-wear analysis indicates the dominance of intermediate feeders among the prevalent ungulates, i.e., the bovids, equids and giraffids, suggesting an open bushland with a thick grassy herbaceous layer landscape for the Turolian of Samos. The comparison of the Samos faunas with contemporaneous mammal assemblages from Continental Greece and Western Asia indicates the closer relation of the Samos faunas with the eastern ones.

Keywords: Late Miocene, Samos, Greece, Mammalia, Palaeoecology, Palaeobiogeography.

Zusammenfassung

Zur Studie der Paläoökologie der fossilen Säugetiere von Samos wurden unterschiedliche Methoden verwendet. Die Faunenzusammensetzung von Samos wurde mittels der

„kleinsten Anzahl an Individuen“ (Minimum Number of Individuals = MNI), der Taxonomie und der Nahrungspräferenzen der verschiedenen Säugergruppen analysiert. Die Analyse der Faunendiversität legt eine homogene und gleich alte Fauna mit einer normalen taxonomischen Verbreitung nahe. Meso- und micro-wear an Zähnen deuten eine Dominanz an Ungulaten an, die gemischte Nahrung bevorzugten. Dazu gehören Boviden, Equiden und Giraffiden, die für ein offenes Buschland mit dichtem Grasbewuchs im Turolium von Samos sprechen. Der Vergleich der Samos Faunen mit zeitgleichen Assoziationen vom kontinentalen Griechenland und aus Kleinasien deuten auf eine nähere Beziehung der Samos Faunen mit jenen aus dem Osten hin.

Schlüsselwörter: Obermiozän, Samos, Griechenland, Säugetiere, Paläoökologie, Paläobiogeographie.

1. Introduction

The palaeoecology of the Greek Neogene mammal faunas fascinated the palaeontologists from the early time of their discovery. In the main study of the Pikermi assemblage, GAUDRY (1862–67) already stressed out the relations of Pikermi fauna with the recent East African mammal communities. During the last 20 years, several studies have been carried out, providing new palaeoecological methods and important data on Eurasian Neogene environment. At the same time, a serious effort towards the study of the Neogene palaeoenvironmental conditions of Greece and the surrounding areas has been done (QUADE et al., 1994; SOLOUNIAS & DAWSON-SAUNDERS, 1988; BONIS et al., 1992, 1994, 1999; BONIS & KOUFOS, 1994; FORTELIUS et al., 1996; SOLOUNIAS et al., 1999; KOSTOPOULOS & KOUFOS, 2000; VALLI, 2005; MERCERON et al., 2005a, b, c, 2007a; SCOTT & MAGA, 2005; KOUFOS, 2006a; KOUFOS et al., 2006; STRÖMBERG et al., 2007). All the studies trying to determine the late Miocene palaeoenvironment of the Southeastern Mediterranean include the mammal

¹⁾ Prof. George D. KOUFOS & Dr. Dimitris S. KOSTOPOULOS, Aristotle University of Thessaloniki. Department of Geology. Laboratory of Geology and Palaeontology. GR-54124 Thessaloniki, Greece. e-mail: koufos@geo.auth.gr, dkostop@geo.auth.gr

²⁾ Dr. Gildas MERCERON, UMR CNRS5125-Paleoenvironment & Paleobiosphere, University Lyon 1-Campus la Doua. FR-69622 Villeurbanne cedex, France; e-mail: gildas.merceron@univ-lyon1.fr

faunas of Samos in their data, because they are very rich and have been known for many years. Thus, there are several articles referring to the palaeoenvironmental conditions of Samos.

The palynological analysis of the lower horizons (Mavratzei Fm. according to KOSTOPOULOS et al., this volume) of the Miocene deposits of the Mytilinii Basin, Samos, tries to give some information about the palaeoenvironmental conditions (IOAKIM & SOLOUNIAS, 1985). The Mavratzei Fm is considered to be of middle Miocene - earliest Vallesian age (KOSTOPOULOS et al., this volume). The pollen samples were taken from the lignitic clays that are placed below a basalt flow dated to $11.2 \pm 0.7 - 10.88 \pm 0.4$ Ma (WEIDMANN et al., 1984). According to the recent subdivision of the Neogene, a latest middle Miocene age is quite possible for the pollen. The flora suggests a mixture of dense closed woodland with swampy areas and more open woodland with a dense ground cover of grasses (IOAKIM & SOLOUNIAS, 1985). Although the Mytilinii Fm., including the mammalian faunas, is quite younger (<8.0 Ma, see KOUFOS et al., this volume), the same authors tried to expand their results to them as well as to the Greek and Turkish late Miocene faunas, assuming warm temperate communities, more resembling the European Oligocene laurophyllous woodlands. This is, however, in contrast to later studies, suggesting that during the Astaracian/Vallesian boundary, the Southeastern Mediterranean conditions changed to being drier and more open, and gradually extended to the west, allowing the Vallesian Faunal Change with a remarkable renewal in the mammal communities (AGUSTÍ et al., 1999; AGUSTÍ & ANTÓN, 2002; AGUSTÍ et al., 2003; BONIS et al., 1992, 1999; KOUFOS, 2006a). Some years later, SOLOUNIAS & DAWSON-SAUNDERS (1988) suggested a forest-woodland environment, based on the masticatory morphology of the Samos and Pikermi late Miocene ruminants. But the stable isotopic analysis of the late Miocene Mytilinii Fm. indicates woodlands or forests for Samos (QUADE et al., 1994). SOLOUNIAS et al. (1999), using stable isotopes, palaeobotanical data, masticatory patterns and dental microwear also suggested a sclerophyllous woodland or forest for the "Pikermian Biome", established during late Miocene in Eastern Mediterranean and Samos. Recently STRÖMBERG et al. (2007) studied the evolution of Eastern Mediterranean ecosystems, using the phytolith assemblages preserved in direct association with faunas, and they arrived at the conclusion that the Miocene assemblages are dominated by pooid open-habitat grasses, while forest indicator phytoliths are rare in the late Miocene (9.0-7.0 Ma). Their analysis rejects the above mentioned opinion of SOLOUNIAS et al. (1999) for a sclerophyllous woodland or forest with rare grasses environment during Turolian. In the present article we shall try to give some more information about the palaeoenvironment of the late Miocene of Samos, using the data from the study of the newly collected mammal assemblages from the fossiliferous sites of Mytilinii Fm.

2. Material

The reconstruction of the palaeoenvironment from the fossil faunas strongly depends upon the taphonomy and the field-work procedures. The newly collected material from Samos comes from various single lenses formed by fluvial-fluviolacustrine action. The material from Adrianos ravine (MTL fauna) exceeds 1000 identified specimens from three well-defined fossil lenses. In Potamies ravine the MLN (~90 specimens) and MYT (~130 specimens) faunas are relatively poor, but they come from single fluvial lenses. The stratigraphic position, the fauna and the age of the three faunal assemblages from Samos, discussed in previous chapters of this volume (KOSTOPOULOS et al., this volume; KOUFOS et al., this volume), are as following:

MLN: early Turolian, ~7.5 Ma: *Hyaenictitherium* cf. *wongii*, *Protictitherium crassum*, *Hipparion* aff. *proboscideum*, *Hipparion* aff. *prostylum*, "*Diceros*" *neumayri*, *Palaeotragus rouenii*, *Palaeotragus* sp., *Samotherium boissieri*, *Gazella pilgrimi*, *Tragoptax* sp., *Miotragocerus* sp., ?*Palaeoryx* sp. (KOUFOS, this volume-a; VLACHOU & KOUFOS, this volume; KOSTOPOULOS, this volume-a, b)

MYT: early middle Turolian, ~7.3 Ma: "*Diceros*" *neumayri*, *Diboplos pikermiensis*, *Ancylotherium pentelicum*, *Hipparion* cf. *proboscideum*, *Hipparion* cf. *forstenae*, *Hipparion prostylum*, *Hipparion* cf. *matthewi*, *Samotherium major*, *Sporadotragus parvidens*, *Gazella pilgrimi*, *Pachytragus zermalisi* n. sp., *Palaeoryx* sp., ?*Majoreas* sp. (GIAOURTSAKIS, this volume; GIAOURTSAKIS & KOUFOS, this volume; KOSTOPOULOS, this volume-a, b; VLACHOU & KOUFOS, this volume).

MTL A/B/C: late middle Turolian, ~7.1 Ma: *Pseudomerionis pythagorasi*, '*Karminata*' *provocator*, *Spermophilinus* cf. *bredai*, *Pliospalax* cf. *sotirisi*, *Adrocota eximia*, *Hyaenictitherium wongii*, *Plioviverrups orbignyi*, *Machairodus giganteus*, *Metailurus parvulus*, *Parataxidea maraghana*, *Choerolophodon pentelici*, *Zygolophodon turicensis*, *Orycteropus gaudryi*, *Pliohyrax graecus*, "*Diceros*" *neumayri*, *Diboplos pikermiensis*, *Ancylotherium pentelicum*, *Hipparion brachypus*, *Hipparion dietrichi*, *Hipparion proboscideum*, *Hipparion* cf. *matthewi*, *Hipparion* cf. *forstenae*, *Microstonyx major*, *Palaeotragus rouenii*, *Palaeotragus* sp., *Samotherium major*, *Helladotherium duvernoyi*, *Gazella pilgrimi*, *Gazella* cf. *capricornis*, *Gazella mytilinii*, *Miotragocerus valenciennesi*, *Tragoptax rugosifrons*, *Sporadotragus parvidens*, *Skoufotragus laticeps*, *Palaeoryx pallasi*, *Palaeoryx majori*, *Urmiatherium rugosifrons* (GIAOURTSAKIS, this volume-a; GIAOURTSAKIS & KOUFOS, this volume; KONIDARIS & KOUFOS, this volume; KOSTOPOULOS, this volume-a, b; KOUFOS, this volume-a, b, c; SYLVESTROU & KOSTOPOULOS, this volume; VASILEIADOU & SYLVESTROU, this volume; VLACHOU & KOUFOS, this volume).

The Samos faunal assemblages have been compared with a series of well-dated faunas from Continental Greece and Turkey. Some more significant mammal assemblages, such

Localities	MLN	MYT	MTL	PXM	RZO	PIK	DYTI	PER	AKK	KTD	KTA/B
Taxa S	12	13	33	14	25	30	23	26	28	14	23
MNI	19	27	167	64	121	204	146	134	195	52	54
Simpson 1-L	0.898	0.892	0.940	0.802	0,850	0,907	0,896	0,906	0,909	0,918	0,931
Shannon H'	2.379	2.375	3.087	1.985	2.473	2.792	2.584	2.695	2.728	2.440	2.960
Equitability E	0.957	0.926	0.883	0.752	0.768	0.821	0.824	0.827	0.819	0.925	0.944

Table 1: Species diversity indices for the Samos and some Greek and Turkish Turolian localities.

as the old Samos ones, the Pikermi and the Maragheh faunas are also included.

- Ravin des Zouaves-5 (RZO), Axios valley, MN 11, ~8.2 Ma
- Prochoma-1 (PXM), Axios valley, MN 11/12, ~7.5 Ma
- Vathylakkos (VATH), Axios valley, MN 11/12, ~7.5 Ma
- Dytiko (DYTI), Axios valley, MN 13
- Perivolaki (PER), Thessaly, MN 12, 7.3-7.1 Ma
- Pikermi (PIK), Attica, MN 12, ~7.0 Ma; the faunal list is based on Gaudry's collection at the Muséum National d'Histoire Naturelle de Paris which eventually comes from one site and could be considered homogeneous.
- Kerassia (KER), Evia Island, MN 11-12
- Samos Q5, MN 13, 6.9-6.7 Ma
- Kemiklitepe D (KTD), MN 11, ~7.7 Ma
- Kemiklitepe A-B (KTA-B), MN 12, ~7.2 Ma
- Akkaşdağı (AKK), MN 12, ~7.1 Ma
- Lower Maragheh, (LMRG), 9.0-8.2 Ma
- Middle Maragheh (MMRG), 8.2-8.0 Ma
- Upper Maragheh (UMRG), 8.0-7.6 Ma

Faunal lists were taken from KOUFOS (2006c, with minor corrections and included bibliography), KOUFOS et al. (2006), SEN (1994, 2005), BERNOR et al. (1996), SOLOUNIAS (1981).

3. Species Diversity

Species diversity is used to express the homogeneity, equilibrium and normality of a faunal assemblage and depends on both the species richness and the evenness with which individuals are distributed among species (SOKAL & ROHLF, 1998). Among several diversity indices based on Minimum Number of Individuals, we performed the Simpson dominance Index (1-L), which weighs towards the abundance of the most common taxon, the Shannon-Wiener Index (H'), depending on the frequency of the taxa and Equitability (E), which compares actual diversity to the maximum possible one. The Minimum Number of Individuals (MNI) for the Greek assemblages is given in Appendix 1.

Simpson's Index (1-L) is given by the formula:

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

n_i = MNI of the i^{th} species, N = total number of individuals and S = number of species.

Shannon-Wiener Index (H') is given by the formula:

$$1-L = 1 - \sum_{i=1}^s \frac{n_i}{N} \times \ln \frac{n_i}{N}$$

n_i = MNI of the i^{th} species, N = total number of individuals, S = number of species

Equitability (E) is given by the formula:

$$E = H' / \ln S$$

S = total number of species.

Although the low number of individuals and species of most assemblages under comparison (Tab. 1) severely affect the Simpson index, most sites indicate relatively equilibrated faunas, making due allowance. The even wealthier, the RZO and PXM faunal assemblages appear less equilibrated than MLN and MYT, whereas the MTL fauna stands out as the most diversified and equilibrated (Tab. 1). As one would expect, evenness looks greater in poorer faunal association as a result of sampling bias (Tab. 1); PXM and RZO are exceptions again, suggesting a low diversity that is certainly influenced by the high frequency of particular taxa (*Tragoportax rugosifrons* represent 30.3% of RZO MNI and "*Hipparion dietrichi*" 34% of PXM MNI). The equitability of the MTL assemblage perfectly matches the values obtained for the most well-sampled Turolian faunas, such as PIK, PER, AKK and DYTI (Tab. 1).

4. Dental Mesowear and Microwear

The available material from the localities MYT and MLN is scarce and cannot allow definitive judgments on the dietary habits for most of the included taxa, and subsequently on the environmental trends. The fossil material from the contemporaneous MTL localities (MTLA, MTLB, and MTLC) on Samos Island is abundant enough to investigate feeding preferences of both bovids and equids through

Extinct Species	N	LS	LR	LB	HS	HR	HB
Fossil from MYT localities							
<i>Skoufotragus zemalisorum</i>	3	0	0	0	33.3	66.7	0
<i>Hipparion</i> cf. <i>prostylum</i>	4	0	50.0	50.0	0	0	0
Fossil from MTL localities							
<i>Gazella</i> cf. <i>capricornis</i>	8	0	12.5	0	12.5	75.0	0
<i>Miotragocerus valenciennesi</i>	4	0	0	0	0	100	0
<i>Skoufotragus laticeps</i>	32	0	3.1	6.3	6.3	84.4	0
<i>Palaeoryx</i> ssp.	6	0	33.3	0	16.7	50.0	0
<i>Sporadotragus parvidens</i>	6	0	0	16.7	0	83.3	0
<i>Hipparion</i> cf. <i>forstena</i>	5	0	40.0	40.0	0	20.0	0
<i>Hipparion</i> cf. <i>matthewi</i>	3	0	66.7	33.3	0	0	0
<i>Hipparion proboscideum</i>	6	0	33.3	50.0	0	16.7	0
<i>Hipparion dietrichi</i>	4	0	25.0	50.0	0	25.0	0
Extant Species							
All Browsers	81	0.0	0.0	0.0	76.5	23.5	0.0
<i>Alces alces</i> (aa)	30	0	0	0	100	0	0
<i>Odocoileus hemonius</i> (oh)	33	0	0	0	48.5	51.5	0
<i>Odocoileus virginianus</i> (ov)	18	0	0	0	88.9	11.1	0
All Grazers	469	13.0	17.3	19.8	4.7	43.7	1.5
<i>Alcelaphus buselaphus</i> (AB)	76	5.3	15.8	22.4	11.8	42.1	2.6
<i>Bison bison</i> (BB)	15	0	26.7	73.3	0	0	0
<i>Connochaetes taurinus</i> (CT)	52	5.8	13.5	23.1	15.4	36.5	5.8
<i>Equus burchelli</i> (EB)	121	33.9	32.2	33.9	0	0	0
<i>Equus grevyi</i> (EG)	29	41.4	34.5	24.1	0	0	0
<i>Hippotragus equinus</i> (HE)	26	0	15.4	0	3.8	80.8	0
<i>Hippotragus niger</i> (HN)	20	0	0	15	0	85.0	0
<i>Kobus ellipsyrhinus</i> (KE)	22	0	4.5	0	0	95.5	0
<i>Redunca redunca</i> (RR)	77	1.3	5.2	2.6	5.2	85.7	0
<i>Syncerus caffer</i> (SC)	31	0	0	0	0	93.5	6.5
All Intermediate feeders	337	5.0	4.2	0.9	46.6	43.0	0.3
<i>Aepyceros melampus</i> (Me)	17	0	0	0	35.3	64.7	0
<i>Capricornis sumatrensis</i> (Ca)	22	0	0	0	31.8	63.6	4.5
<i>Cervus canadensis</i> (Cc)	19	0	0	0	47.4	52.6	0
<i>Equus asinus</i> (Ea)	17	11.8	11.8	5.9	23.5	47.1	0
<i>Gazella granti</i> (Gg)	17	11.8	0	0	47.1	41.2	0
<i>Gazella thomsoni</i> (Gt)	146	5.5	4.8	1.4	52.7	35.6	0
<i>Ovibos moschatus</i> (Om)	52	9.6	9.6	0	44.2	36.5	0
<i>Tragelaphus scriptus</i> (Ts)	47	0	0	0	48.9	51.1	0

Table 2: Meso-wear variables distribution (percentages) on second upper molars for extant taxa and on M1, M2 or M3 for extinct species. N = number of specimens; L = low relief; H = high relief; S = sharp cusp; R = round cusp; B = blunt cusp.

dental wear analyses. These dietary reconstructions will be helpful to understand the niche partitioning among these meso-herbivorous species, and to characterize the past environments of Samos during Middle Turolian, MN 12 (KOSTOPOULOS et al., 2003; KOUFOS et al., this volume). Because they are abundant and diverse, the guild of these mammals gives information on past ecosystems and environments (e.g. PLUMMER & BISHOP, 1994). Here we combine two taxon-free approaches, dental mesowear and microwear analyses, to reconstruct the feeding-styles of these extinct meso-herbivorous mammals. While dental mesowear pattern provides a long-term dietary

signal, the dental microwear signature gives information about the food items consumed for the last few days or weeks (FORTELIUS & SOLOUNIAS, 2000; TEAFORD & OYEN, 1989).

4.1. Material and Methods

Tabs. 2, 3 list the fossil species investigated in the present dental meso- and micro-wear analyses, respectively. Several modern species with known dietary differences were also examined as a baseline series for comparison with the fossil

Localities	Species	N	Ns		Ls		Np		Tot		Pp	
			m	sem	m	sem	m	sem	m	sem	m	sem
MLN	<i>Hipparion</i> aff. <i>proboscideum</i>	1	32.0		154.1		40.0		72.0		55.6	
	<i>Hipparion</i> aff. <i>prostylum</i>	1	27.0		195.0		46.0		73.0		63.0	
	<i>Gazella pilgrimi</i>	2	22.5	12.5	136.2	9.9	68.5	7.5	91.0	5.0	76.0	12.4
	<i>Miotragocerus</i> sp.	2	26.0	1.0	151.7	2.4	32.0	9.0	58.0	10.0	54.1	6.2
	<i>Tragoptax</i> sp.	1	25.0		116.6		49.0		74.0		66.2	
MYT	<i>Hipparion</i> cf. <i>prostylum</i>	7	41.0	1.6	167.5	10.1	31.7	4.3	72.7	5.1	42.8	2.5
	<i>Hipparion</i> cf. <i>proboscideum</i>	1	41.0		147.3		24.0		65.0		36.9	
	<i>Skoufotragus zemalisorum</i>	4	17.0	2.9	120.8	8.1	53.5	5.5	70.5	5.5	75.7	3.6
	<i>Sporadotragus parvidens</i>	2	32.0	8.0	138.5	8.5	42.5	22.5	74.5	14.5	53.2	19.9
MTL	<i>Hipparion</i> cf. <i>forstenae</i>	6	32.8	2.4	149.3	9.5	38.2	12.1	71.0	10.4	47.0	9.2
	<i>Hipparion</i> cf. <i>matthewi</i>	3	35.7	2.2	134.8	9.5	36.7	15.5	72.3	14.7	46.4	10.6
	<i>Hipparion proboscideum</i>	6	37.2	2.0	193.5	14.6	20.0	6.9	57.2	6.9	31.6	7.0
	<i>Hipparion dietrichi</i>	4	32.8	4.6	158.6	22.3	36.0	14.3	68.8	13.8	46.3	13.5
	<i>Hipparion brachypus</i>	1	37.0		163.1		13.0		50.0		26.0	
	<i>Gazella</i> cf. <i>capricornis</i>	8	33.1	2.5	136.3	9.4	30.0	4.8	63.1	3.6	45.7	6.1
	<i>Gazella mytilinii</i>	1	16.0		68.3		49.0		65.0		75.4	
	<i>Gazella pilgrimi</i>	3	33.7	2.4	130.5	5.1	32.3	7.4	66.0	8.5	48.0	4.8
	<i>Miotragocerus valenciennesi</i>	7	27.6	2.4	166.6	13.5	43.6	9.7	71.1	8.6	56.7	7.7
	<i>Skoufotragus laticeps</i>	32	32.1	1.5	142.0	6.4	40.0	4.2	72.1	3.8	51.7	3.1
	<i>Palaeoryx</i> ssp.	5	35.9	1.9	149.9	14.6	33.1	9.7	69.0	8.3	44.0	8.9
<i>Urmatherium rugosifrons</i>	2	34.5	8.5	175.7	32.1	37.0	21.0	71.5	12.5	48.1	21.0	
<i>Sporadotragus parvidens</i>	5	27.4	5.5	141.6	13.2	43.2	12.5	70.6	8.3	57.1	11.5	
Extant	Intermediate feeders	156	25.5	0.7	151.9	3.3	37.0	1.6	62.5	1.6	56.3	1.3
	Grazers	171	25.4	0.4	172.0	3.1	15.4	0.7	40.8	0.9	35.7	0.9
	Browsers	214	21.2	0.5	134.5	2.5	34.6	1.0	55.8	1.1	60.6	0.8

Table 3: Summary statistics (mean [m] and standard deviation of the mean [s.e.m.]) of dental micro-wear variables on extinct taxa from the MTL localities of Samos and extant species in the respective diet category.

data. These extant taxa were chosen for their range of diets and habitat preferences. Tabs. 2, 3 lists these modern species that compose the meso- and micro-wear comparative databases (FORTELIUS & SOLOUNIAS, 2000; MERCERON et al., 2007b). Most of the MTL species are included in the mesowear analysis, whereas only two species from MYT, *Hipparion* cf. *prostylum* and *Skoufotragus zemalisorum*, are included. Eventually, no species from MLN was included because of the sample size limitations.

Mesowear analysis. Dental mesowear reflects the degree of attritive and abrasive wear on the occlusal molar surface. The former is due to the tooth/tooth contact and results in high crown relief and sharp cusp apices. Abrasive wear is due to the alteration of enamel tissues by food during mastication. In contrast to attritive wear, abrasion obliterates dental facets, resulting in lower crown relief and more round apices. Occlusal relief is classified as high (H) or low (L), and cusp shape is classified as sharp (S), round (R) or blunt (B) (FORTELIUS & SOLOUNIAS, 2000; KAISER & FORTELIUS, 2003; MERCERON et al., 2007b). For consistency of the data, the datasets of fossil and living species here are composed of specimens for whom both variables

were scored. Then, six conditions were identified: low relief with sharp [LS], round [LR] or blunt [LB] cusp(id)s and high relief with sharp [HS], round [HR] or blunt [HB] cusp(id)s (Tab. 2). This latter category is uncommon. FORTELIUS & SOLOUNIAS (2000) scored such conditions for few individuals amongst grazing ungulates. No fossil specimen investigated here displays such dental mesowear patterns. Hierarchical cluster analysis with single linkage (nearest neighbors) is applied following the standard hierarchical amalgamation method.

Microwear analysis. Dental microwear patterns give information on the physical properties of the last food items consumed by an individual (TEAFORD & OYEN, 1989). Depending on both measurements and densities of microwear scars, three main feeding styles defined from ecological data may be recognized: grazers, browsers and intermediate feeders. Due to the abrasiveness of monocotyledons (CARNELLI et al., 2001; KAUFMAN et al., 1985; MACNAUGHTON et al., 1985), grazers have higher densities of scratches and lower ones of pits than browsers. The intermediate feeders have a value that overlaps the range of both grazers and browsers (MERCERON et al., 2007b;

Parameter		df	SS	MS	F	p
Log Ns	Factor	14	15.42	1.10	10.84	0.000
	Error	616	62.27	0.10		
Log Ls	Factor	14	7.33	0.52	7.70	0.000
	Error	616	41.68	0.06		
Log Np	Factor	14	99.89	7.13	23.89	0.000
	Error	616	183.06	0.29		
Log Pp	Factor	14	22.42	1.60	17.54	0.000
	Error	616	55.98	0.09		
Log Tot	Factor	14	37.09	2.65	25.41	0.000
	Error	616	63.93	0.10		

Extinct species	Localities	Extant species		
		Intermediate feeders	Grazers	Browsers
<i>Hipparion cf. forstenae</i>	MTL		Np Tot	Ns
<i>H. cf. matthewi</i>	MTL			
<i>H. proboscideum</i>	MTL	Np Pp		Ns Ls Np Pp
<i>Gazella cf. capricornis</i>	MTL		Tot	Ns
<i>G. pilgrimi</i>	MTL			
<i>H. dietrichi</i>	MTL		Tot	
<i>H. cf. prostylum</i>	MYT	Ns	Ns Np Tot	Ns Pp
<i>Miotragocerus vallengiensesi</i>	MTL		Np Tot Pp	
<i>Skoufotragus laticeps</i>	MTL	Ns	Ns Ls Np Tot Pp	Ns Tot
<i>Sk. zemalisorum</i>	MYT		Np Tot Pp	
<i>Palaeoryx ssp.</i>	MTL		Tot	
<i>Sporadotragus parvidens</i>	MTL		Np Tot	

Table 4: ANOVAs and multi-comparisons HSD tests (extinct species versus extant taxa through diet categories).

SOLOUNIAS & SEMPREBON, 2002). Number of scratches (Ns), length of scratches (Ls), number of pits (Np), percentage of pits (%-p) and total number of microwear scars (Tot) are computed following the protocol shown in MERCERON et al. (2004, 2005a). All variables are log-transformed to ensure normality and homoscedasticity. Then, univariate analyses of variance (ANOVAs hereafter) and the Tukey's Honestly Significant Difference (HSD hereafter) multiple comparisons tests are applied to determine the sources of significant variation between extinct and extant species (Tabs 3, 4), (SOKAL & ROHLF, 1998).

4.2. Results and Discussion

Based on the dental mesowear analysis, the six fossil antelopes from the MTL localities plot with extant grazers (Tab. 2; Fig. 1). However, they all differ from extant grazers, except *G. pilgrimi*, in having more microwear scars on their shearing molar facets, and especially pits (Tabs 3, 4; Fig. 2). *Palaeoryx ssp.* (including both *Palaeoryx pallasi* and *Palaeoryx majori* samples), *Gazella cf. capricornis*, and *Skoufotragus laticeps*, also differ from browsers especially in having more scratches (Tabs 3, 4; Fig. 2). The combination of mesowear and microwear analyses clearly support

that these antelopes were intermediate feeders, highly involved in grazing. Based on the microwear pattern, *G. pilgrimi* does not show any significant differences to any of the extant species in their diet categories. Through the mesowear pattern, *G. pilgrimi* is clustered with grazing species. In spite of the low sample size, the high scratch density probably excludes browsing habits. The results on all of these species are quite consistent with those from previous studies based on microwear analysis or on ecomorphology (SOLOUNIAS & DAWSON-SAUNDERS, 1988; SOLOUNIAS & MOELLEKEN, 1999). Based on both morphology and microwear pattern *Skoufotragus laticeps* (= *Pachytragus laticeps*) is depicted as an intermediate feeder (SOLOUNIAS & DAWSON-SAUNDERS, 1988; SOLOUNIAS et al., 1995), although previous microwear analysis categorize this antelope as highly engaged in grazing (KOUFOS et al., 2006; SOLOUNIAS & MOELLEKEN, 1992). MERCERON et al. (2007a) also depict the closely associated *Protoryx* sp. from the late Vallesian of Northern Greece as an intermediate feeder. Based on ecomorphology, SOLOUNIAS & DAWSON-SAUNDERS (1988) also describe *Palaeoryx* sp. as an intermediate feeder.

The other two bovids, *Sporadotragus parvidens* and *Miotragocerus valenciennesi*, do not significantly differ from browsing and intermediate feeders, but they do differ

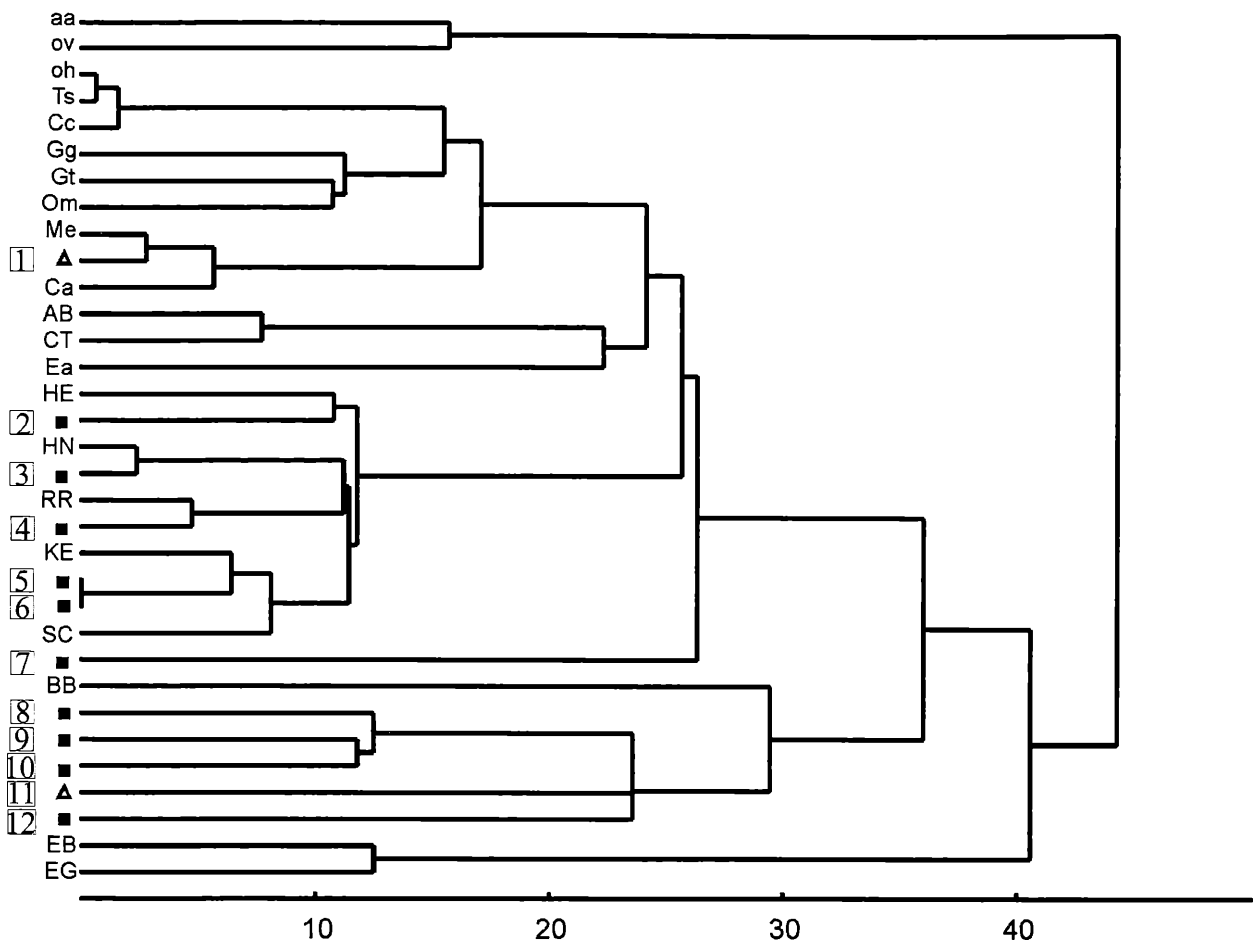


Figure 1: Hierarchical cluster diagram plotting meso-wear datasets of extinct bovids and equids from the MTL localities (MTLA, B, C) and 21 recent taxa after FORTELIUS & SOLOUNIAS (2000) and MERCERON et al. (2007).

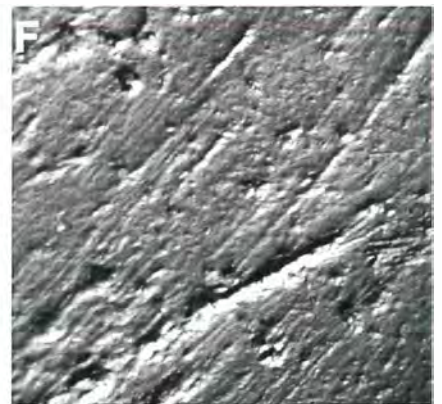
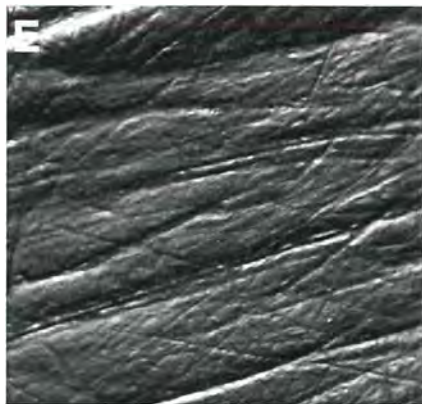
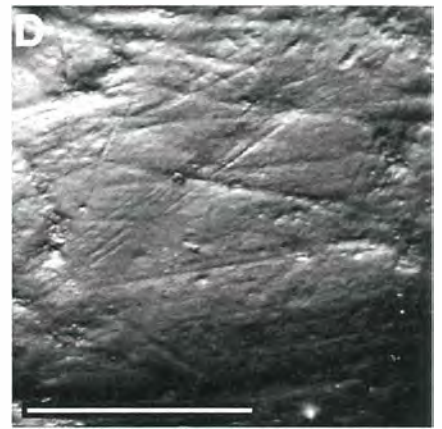
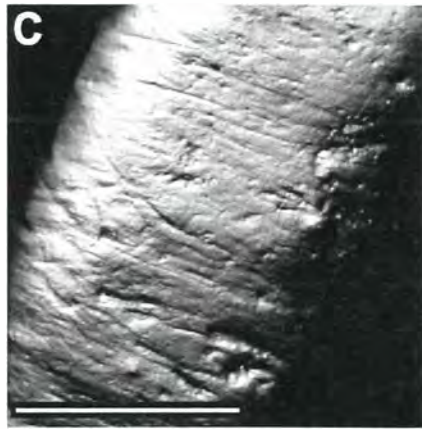
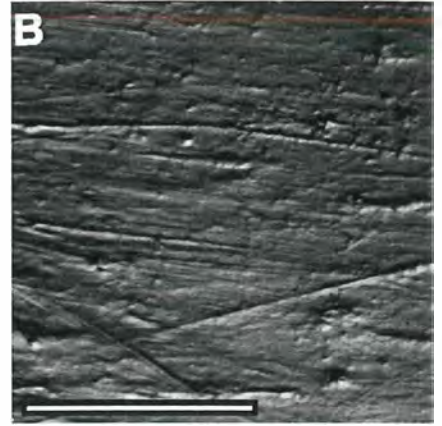
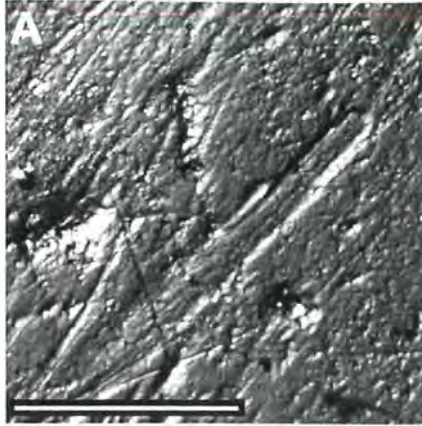
The present-day species are clustered in diet categories and symbolized as follows: Upper case letters for grazers, lower case letters for browsers and a combination of upper- and lower case letters for intermediate feeders (see abbreviations in Tab. 2). Open triangles are for MYT taxa and closed squares for MTL taxa. 1: *Skoufotragus zemalisorum*, MYT; 2: *Gazella cf. capricornis*, MTL; 3: *Sporadotragus parvidens*, MTL; 4: *Skoufotragus laticeps*, MTL; 5: *Gazella pilgrimi*, MTL; 6: *Miotragoceros valenciennesi*, MTL; 7: *Palaeoryx* ssp., MTL; 8: *Hipparion cf. forstenae*, MTL; 9: *Hipparion cf. proboscideum*, MTL; 10: *Hipparion dietrichi*, MTL; 11: *Hipparion cf. prostylum*, MYT; 12: *Hipparion cf. matthewi*, MTL.

from mere grazers (Tabs 3, 4; Fig. 2). However, the higher values of scratches, plus the dental mesowear data, allow us to propose an intermediate feeding style more engaged in browsing than the former antelopes. This is quite consistent with previous ecomorphological and microwear studies that describe the *Miotragoceros*-relative species as either browsers or intermediate feeders (MERCERON et al., 2005b, c; 2006; SOLOUNIAS & DAWSON-SAUNDERS, 1988) and *Sporadotragus parvidens* as an intermediate feeder (SOLOUNIAS & DAWSON-SAUNDERS, 1988). The last two species from MTL, *Gazella mytilinii* and *Urmiatherium rugosifrons*, are very poorly represented and were subsequently excluded from the mesowear analysis. The dental microwear pattern of *G. mytilinii* (1 individual) indicates that its last meals were based on dicotyledoneous plants rather than on grasses. Two individuals represent *U. rugosifrons*. In contrast to *G. pilgrimi*, the higher scratch density over pits indicates grazing habits. However, no

conclusions can be proposed for these two species because of the small sample size. In the same way, *Hipparion cf. forstenae*, *H. cf. matthewi*, *H. cf. proboscideum* and *Hipparion dietrichi* from the MTL localities at Samos, plot with *Bison bison* (BB), an extant grazer (Tab. 2; Fig. 1). A fifth species, *Hipparion brachypus*, is not included in the analysis since it is represented by a single individual only. Its dental microwear pattern is rich in scratches and poor in pits, indicating the possible consumption of graminoids. Based on the dental microwear analysis, *H. cf. proboscideum* significantly differs from both browsers and intermediate feeders in having a lower incidence of pitting. This equid also differs from browsers in having longer and a greater number of scratches (Tabs 3, 4; Fig. 2). The combination of both microwear and mesowear signatures clearly supports grazing habits for *H. cf. proboscideum*. In contrast, *H. cf. forstenae* differs from extant grazers in having more microwear features and especially more pits, and from

Figure 2: Light micrographs showing the dental micro-wear pattern on the molar shearing facets of *Skoufotragus laticeps* (A, MTLA 148), *Sporadotragus parvidens* (B, MTLA 434), *Gazella cf. capricornis* (C, MTLA 493), *Miotragocerus aff. valenciennesi* (D, MTLA 190), *Hipparion cf. proboscideum* (E, MTLA 288), and *Hipparion cf. forstenae* (F, MTLA 338).

Scale bar = 300 μ m.



browsers in having a greater number of scratches (Tabs. 3, 4; Fig. 2). Together, the mesowear and microwear pattern indicate an intermediate feeding style for this population of *H. cf. forstenae*. *H. cf. mattherwi* plots with the extant grazing *Bison* in the mesowear analysis. No significant differences in dental microwear pattern are detected between *H. cf. mattherwi* and extant species. The high scratch number would exclude pure browsing habits. However, the small sample size strongly limits interpretations on feeding habits for this species. *Hipparion dietrichi* from the MTL localities does not differ from extant species, but from grazers, in having more microwear scars (Tot). The high number of scratches indicates more affinities with intermediate feeders than with browsers (Tabs 3, 4). Previous studies (HAYEK et al., 1992; KOUFOS et al., 2006)

describe *H. dietrichi* as more engaged in grazing than *H. proboscideum*, which is quite contrary to the present results from the fossil assemblages from MTL. The microwear signal depicted for *H. cf. prostylum* from MYT differs from extant species in having more scratches, and especially from grazers in having more pits. The low sample size for these two populations of *H. prostylum* forbids us to make definitive judgments about its feeding habits.

The other equid from MYT, *H. cf. proboscideum*, is represented by one individual, the dental microwear pattern of which indicates that its last meal was not composed of soft foliages (Tab. 3). *Sporadotragus parvidens* from MYT (2 individuals) has higher values of pits and scratches, indicating probable mixed feeding habits (Tab. 3). As said above, no further interpretation can be proposed here for

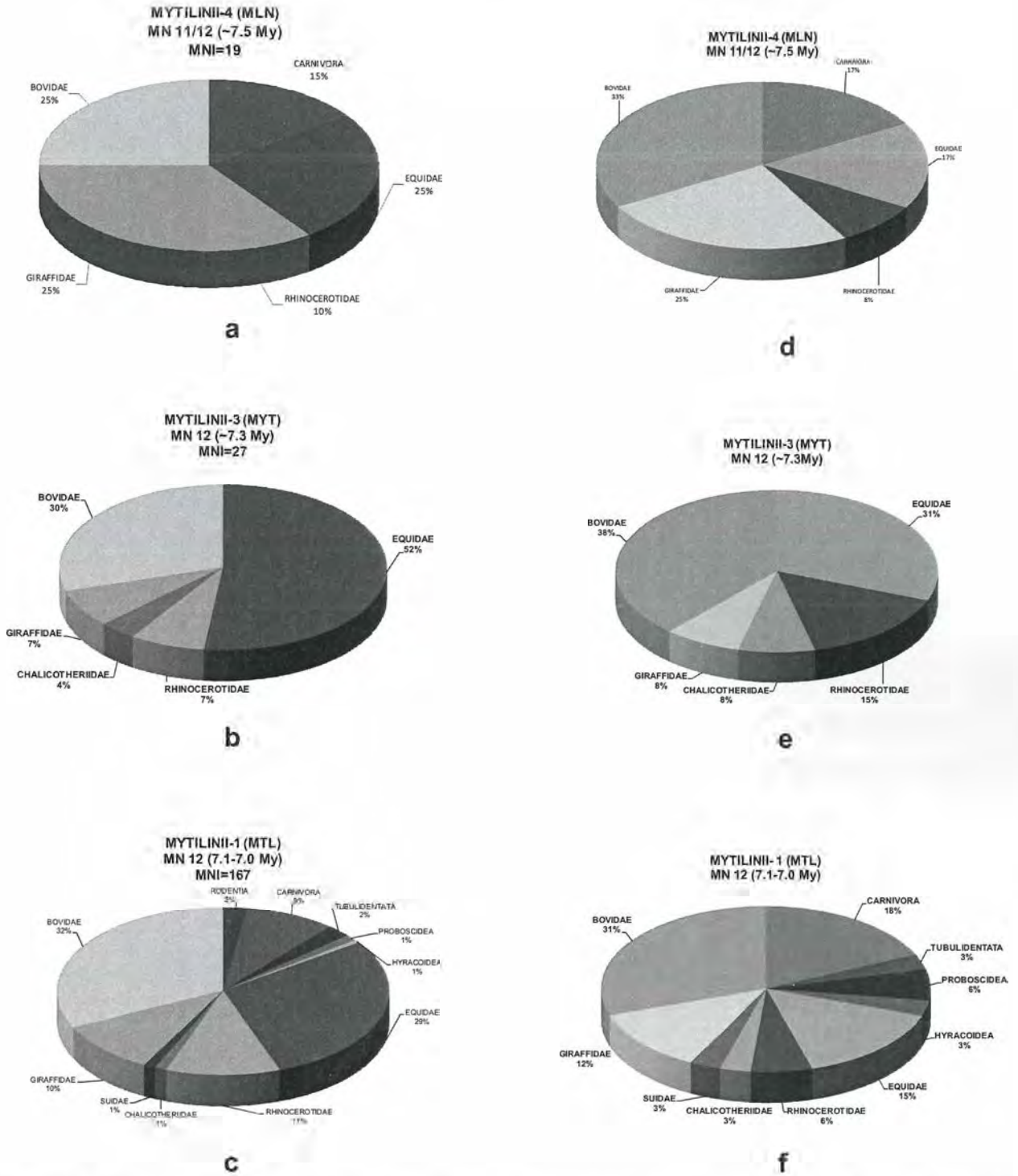
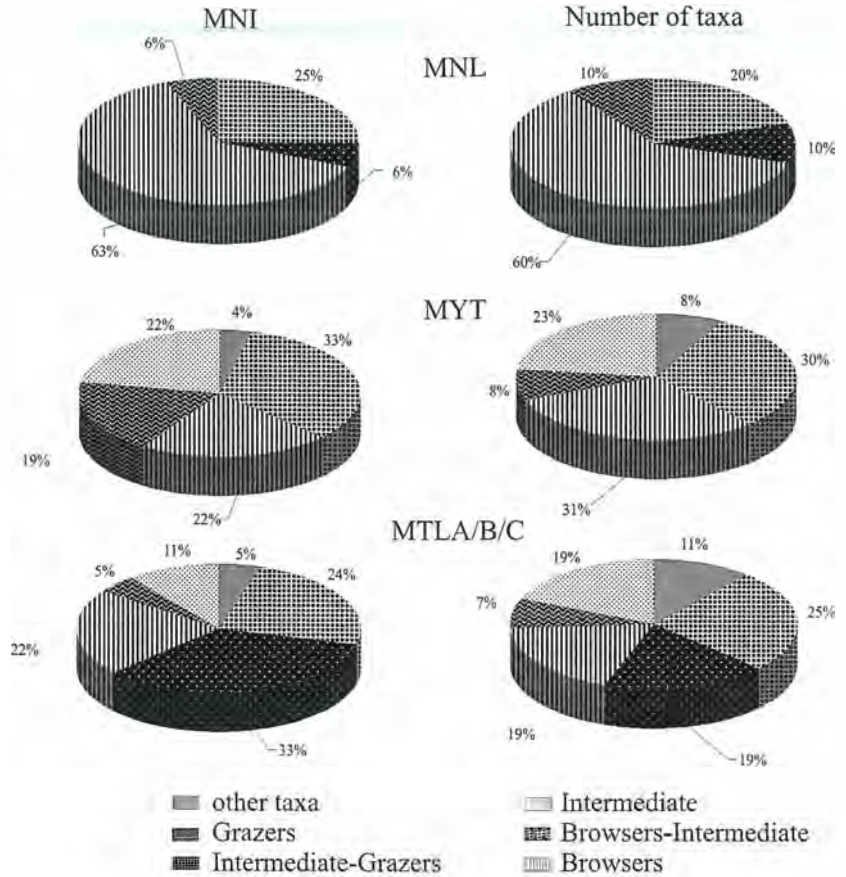


Figure 3: Pie-diagrams giving the faunal composition of the three Samos mammal assemblages on the basis of MNI per family (a, b, c) and species number per family (d, e, f).

these species in the MYT vicinity. *Skoufotragus zemalisorum*, represented by four individuals, displays a mesowear pattern similar to *Aepyceros melampus*, an intermediate feeder (Fig. 1). Its dental microwear pattern indicates browsing habits because it combines low scratch density and high pitting. Together with the mesowear signal, the approach depicts *Sk. zemalisorum* as a probable browser. This is quite in contrast to what has been found for *Sk. laticeps* from MTL (Tabs 3, 4). This may suggest an increase of

graminoids in the diet of early caprine-like species during the Middle Turolian. Unfortunately, the small sample size of *Skoufotragus zemalisorum* does not allow us more interpretations in terms of dietary adaptations or environmental dynamics. The species from the oldest investigated fossil site (MLN) are poorly represented. The dental microwear pattern of the three bovids and the two equids might indicate feeding habits more engaged in browsing than the species from the MTL localities (Tab. 3).

Figure 4: Pie-diagrams comparing the three faunal assemblages of Samos according to the feeding preferences of herbivore mammals, based on the MNIs and on the number of species per dietary group.



5. Faunal Composition

As palaeoecological interpretations based strictly on taxonomy might be influenced by the frequency of rare and/or endemic taxa, we performed a faunal composition analysis of the Samos assemblages, based on both taxonomy (= number of determined species per family or group category) and MNI (= Minimum Number of Individuals per family or group category). The profiles of the Samos mammal faunas, MLN, MYT and MTL are compared with each other, as well as with some Greek and Asian Turolian faunas.

The faunal composition of the three Samos assemblages is given in Fig. 3. It is worth mentioning here that the interpretations of the MLN and MYT faunas are with some reservation, because of their poorness (19 and 27 individuals, respectively). The MTL fauna is, however, quite rich (167 individuals/33 species), allowing safer conclusions. In both the strict taxonomic and the MNI-taxonomic analysis the dominance of bovids, giraffids and equids is clear in all Samos assemblages (Fig. 3). These three families represent more than 50%, by means of number of identified species (Figs. 3d-f) or 75% (of 19 individuals), 89% (of 27 individuals) and 71% (of 167 individuals) of the total number of individuals in the MLN, MYT and MTL faunas respectively. In spite of their low number of species, rhinos and chalicotheres participate in all Samos assemblages with relatively high percentages (>10%). Biased by the sample size, carnivores appear artificially exaggerated in MLN and underestimated in MYT; they

appear quite diversified in MTL, representing 18% of the taxa, but with a relatively low number of individuals (9% of the MNI; Fig. 3c). The MTL fauna also contains a few proboscideans, hyracoids, tubulidentates and suids (Figs. 3c, f). The absence of most of these groups from MLN and MYT faunas is probably artificial, as the old collections from corresponding localities let one assume. However, the primates, tragulids and tapirids are absent in all Samos faunas, even in the old collections. Even though cervids are not detected in the new collection, the family is weakly represented in old samples from Q5 and Q6 (SOLOUNIAS, 1981; KOSTOPOULOS, 2006). In spite of the limited data from MLN and MYT, the three Samos faunas show a similar taxonomic composition with a possible increase of bovids, equids and rhinocerotids from late early (MLN) to late middle (MTL) Turolian (Fig. 3).

Combining information on the feeding preferences of the Samos herbivore species, provided by the micro- and mesowear analyses, as well as by bibliographic data (SOLOUNIAS et al., 1999, 2000; NOW, 2007), the dietary spectra of the three Samos assemblages based either on MNI's or on the number of taxa are given in Fig. 4. Five feeding categories have been distinguished: pure grazers, intermediate feeders with an intense grazing signal, generalized intermediate feeders, intermediate feeders with a clear browsing signal, and pure browsers. Pure grazers slightly increase from the late early Turolian MLN faunal assemblage to the middle Turolian ones (MYT, MTL), where they represent about a fourth of the fauna. Strict browsers look more unstable; they show an important increase at the beginning of

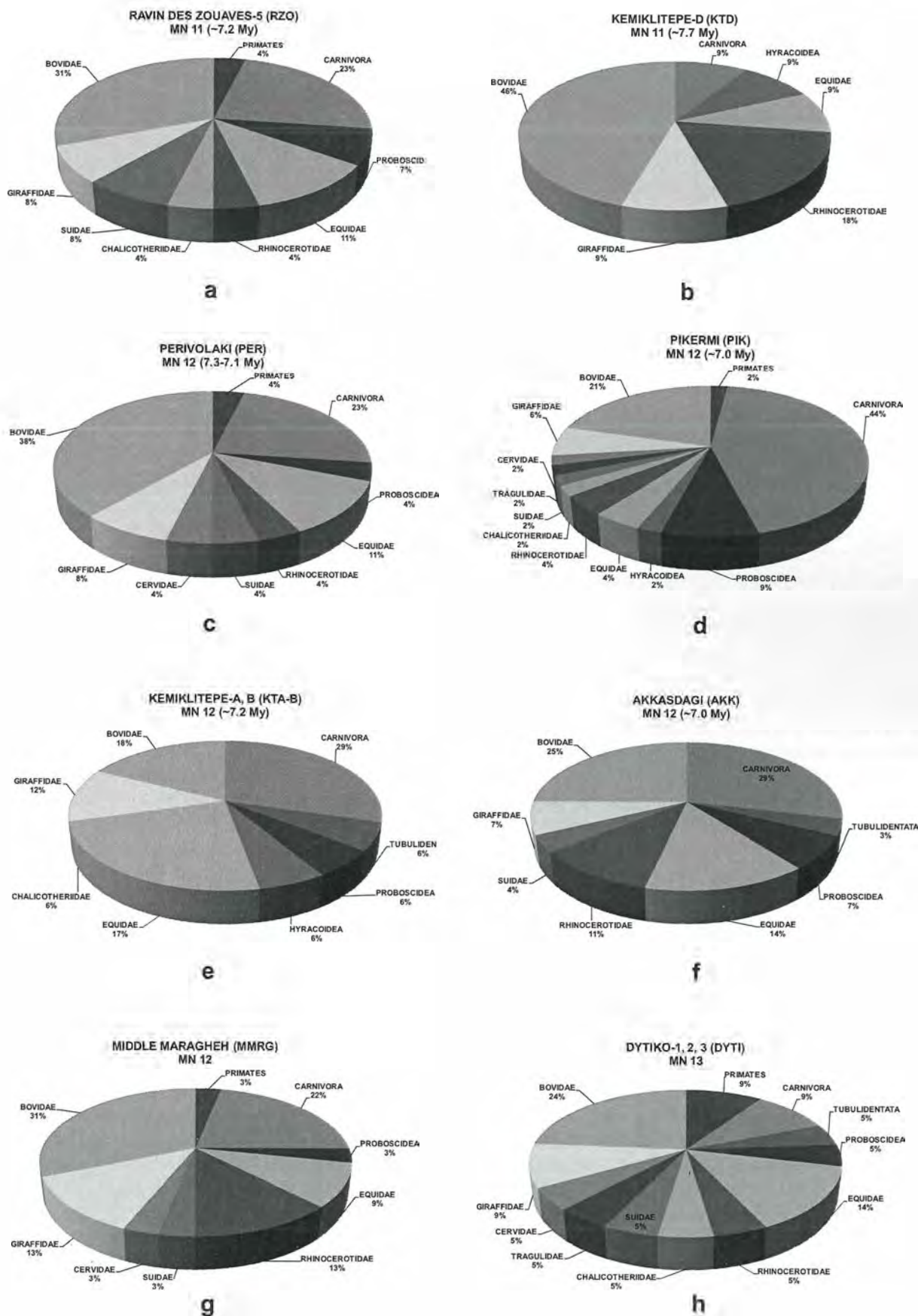
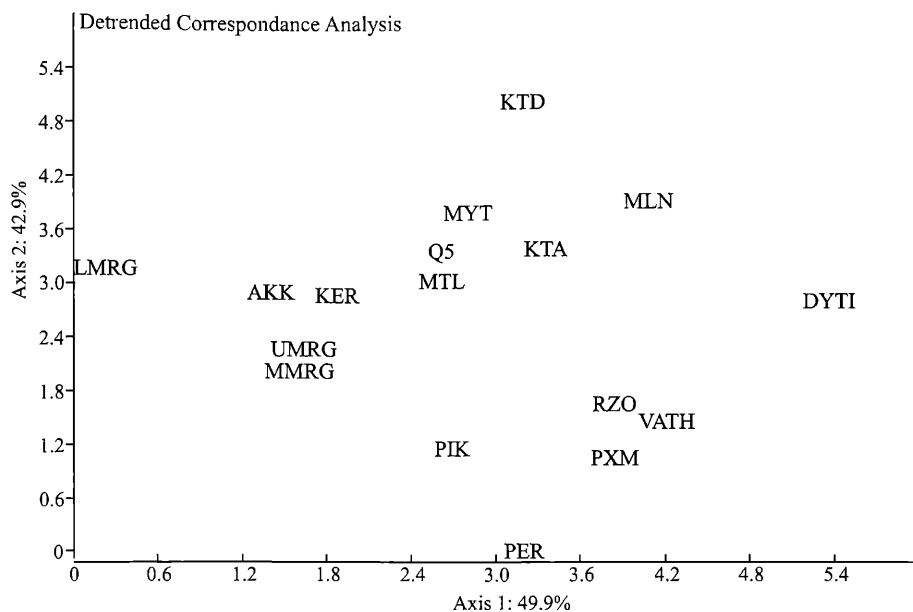


Figure 5: Pie-diagrams indicating the faunal composition of several Turolian mammal assemblages from Greece, Turkey and Iran on the basis of number of species per family.

Figure 6: Detrended Correspondence Analysis comparing the Turolian mammal assemblages of Southeastern Europe and Western Asia based on the presence/absence of 110 species.

AKK = Akkaşdağı, Turkey; DYTI = Dytiko-1, 2, 3, Greece; KER = Kerassia, Greece; KTA-B = Kemiklitepe-A, B, Turkey; KTD = Kemiklitepe-D, Turkey; LMRG = Lower Maragheh, Iran; MLN = Mytilinii-4, Greece; MMRG = Middle Maragheh, Iran; MTL = Mytilinii-1, Greece; MYT = Mytilinii-3, Greece; PER = Perivolaki, Greece; PIK = Piker-mi, Greece; PXM = Prochoma-1, Greece; Q5 = Samos Quarry-5, Greece; RZO = Ravin des Zouaves-5, Greece; VATH = Vathylakkos-1, 2, 3; UMRG = Upper Maragheh, Iran. Data for the Greek faunas was taken from KOUFOS (2006c, with modifications), for Turkish ones from SEN (1994, 2005) and for Iranian ones from BERNOR et al. (1996).



AKK = Akkaşdağı, Turkey; DYTI = Dytiko-1, 2, 3, Greece; KER = Kerassia, Greece; KTA-B = Kemiklitepe-A, B, Turkey; KTD = Kemiklitepe-D, Turkey; LMRG = Lower Maragheh, Iran; MLN = Mytilinii-4, Greece; MMRG = Middle Maragheh, Iran; MTL = Mytilinii-1, Greece; MYT = Mytilinii-3, Greece; PER = Perivolaki, Greece; PIK = Piker-mi, Greece; PXM = Prochoma-1, Greece; Q5 = Samos Quarry-5, Greece; RZO = Ravin des Zouaves-5, Greece; VATH = Vathylakkos-1, 2, 3; UMRG = Upper Maragheh, Iran. Data for the Greek faunas was taken from KOUFOS (2006c, with modifications), for Turkish ones from SEN (1994, 2005) and for Iranian ones from BERNOR et al. (1996).

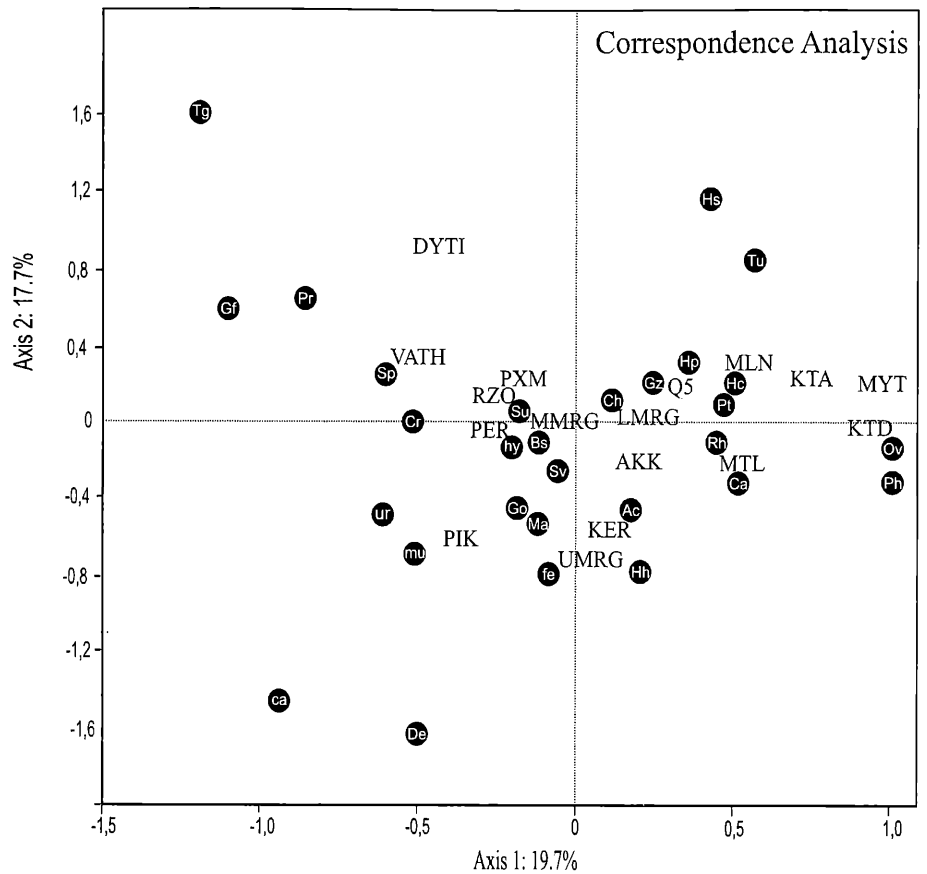
middle Turolian (MYT) reaching a relative balance with grazers, but they slightly decrease again towards the late middle Turolian (MTL). Intermediate feeders are certainly the predominant dietary category in Samos assemblages, representing 72% of the MLN assemblage (73% in number of taxa), 41% of MYT (42% in number of taxa) and 60% of MTL (45% in number of taxa). Its prevalence among other categories is obviously indicative of the general environmental pattern, ruling out open grasslands and closed forests. Nevertheless, during late middle Turolian (MTL), there is a clear shift among intermediate feeders to more grazing-dependent species, probably suggesting an environmental trend to more open/dry conditions. The increased presence of "*Diceros*" *neumayri* in MTL in comparison to its balanced occurrence with *Diboplos pikermiensis* in the lower fossil horizons of Samos (GI-AOURTSAKIS, this volume) as well as the replacement of the intermediate feeder *Skoufotragus zemalisorum* by the grazer *Skoufotragus laticeps* in MTL (KOSTOPOULOS, this volume-b) are also in favor of the expansion of more open and dry habitats towards late middle Turolian.

Comparison of the taxonomic composition of the Samos assemblages with a set of faunas from Continental Greece, Turkey and Iran covering the whole Turolian (Fig. 5), indicates great similarity. As on Samos, all assemblages are characterized by the dominance of bovids, giraffids and equids, and by the weak presence of other groups such as cervids, tragulids and tapirids. The greatest number of bovids occurs in MTL, Ravin des Zouaves 5, Perivolaki and Middle Maragheh faunas, with ten taxa and more than 30% of the identified species (Figs. 3f, 5a, c, g) while their exaggerated presence in Kemiklitepe D (Fig. 5b) is probably due to the limited sample size. In the modern open African faunas the number of bovid taxa varies from 8-20 (LEGENDRE, 1989, appendix). The greatest number

of giraffids is 4, which is observed in Middle Maragheh (13%; Fig. 5g) and MTL (12%; Fig. 3f), while it varies from 1-3 in the rest of the faunas (Fig. 5). The equids are usually represented by 2-5 species, representing 10-15% of the fauna. As was already mentioned by earlier authors (SONDAAR, 1971; FORSTÉN, 1968), the greatest number of equid taxa (5 species, 15%; Fig. 3f) is observed in the Samos fauna (MTL) and Akkaşdağı (4 taxa, 14%; Fig. 5f), and although Middle Maragheh shows a similar equid diversity, the family is represented there by a significantly smaller percentage of the total population (9%). Taking into account both the number of species and their proportion in the taxonomic composition, it seems that the eastern Turolian faunas were richer in *Hipparion* species. The hyracoids are always rare, and apart from Samos, they are recorded in Pikermi and Kemiklitepe (Figs. 5b, d, e). The primates in the Turolian faunas of Southeastern Europe are represented by the cercopithecoid *Mesopithecus*, which is repeatedly present in the faunas of Continental Greece, as well as in middle Maragheh (2-4%; Figs. 5a, c, d, g). On the contrary, primates are absent in the new and old Samos collections, as well as in the Turkish ones (Figs. 3, 5b, e, f). The hypothesis that this is due to limited or poor collections cannot be valid as there is a great number of Turolian fossils from both sides of the Aegean Sea, and if the species was present, it should be found. Its absence could be related to different palaeoecological conditions. The tubulidentates are represented by a single species, *Orycteropus gaudryi*, which is more common and abundant in the more eastern Turolian faunas; in Continental Greece, the species is recorded in the Vallesian of Axios Valley (BONIS et al., 1994), as well as in the late Turolian Dytiko assemblage (Fig. 5h) documented by a single mandibular fragment, and in the late Miocene locality Drazi of Evia Island represented by a partial skull (KOUFOS, this

Figure 7: Correspondence Analysis comparing the taxonomic composition of the Turolian mammal assemblages of South-Eastern Europe and Western Asia based on five carnivoran and 24 herbivore/omnivore categories (Appendix 2).

ca: canids; fe: felids; hy: hyaenids; mu: mustelids; ur: ursids; Pr: primates; De: deinotheriids; Go: gomphotheriids; Ma: mammutids; Ch: chalicotheriids; Ac: aceratheriids; Rh: rhinocerotins; Ph: pliohyracids; Hh: *Hipparion* of *H. brachypus* lineage; Hc: *Hipparion* of *H. mediterraneum* lineage; Hp: *Hipparion* of *H. dietrichi* lineage; Hs: hystricids; Tu: tubulidentates; Su: suids; Tg: tragulids; Cr: cervids; Gf: giraffins; Pt: palaeotragins; Sv: sivatheriins; Gz: gazellins; Sp: spiral-horned antelopins; Ca: caprine-like bovids; Ov: ovibovine-like bovids; Bs: boselaphins. Assemblage abbreviations as in Fig. 6.



volume). On Samos, *Orycteropus* is very common in the new MTL fauna (3% of taxa; Fig. 3f) but it is also very common in the old samples from Q1, Q4 and Q5 (SONDAAR, 1971). The genus is also frequent in the Turkish faunas of Kemiklitepe A-B and Akkaşdağı (Figs. 5e, f). The strong signal of *Orycteropus* could imply dry conditions.

The carnivores are represented by a relatively high number of taxa, especially in some faunas, such as that of Pikermi, with 21 species (44% of the taxa). In the other faunas, the number of carnivoran species usually varies from 1-8 or between 18%-29%; the greatest number is observed in Akkaşdağı (8 taxa, 29%) and Perivolaki (7 taxa, 23%) (Figs. 5c, f). The dominance of the hyaenids in all Turolian faunas is characteristic with *Adcrocuta eximia* and *Hyaenictitherium wongii* playing the main role. The obviously extreme range in the number of carnivores is difficult to explain, but it might be related to the environmental spectrum. NAGEL & KOUFOS (this volume) suggest that the Samos carnivore guild does neither fit heavily wooded, nor typical savannah environments.

A significant change in the taxonomic composition is observed in the Dytiko fauna (Fig. 5h), which is characterized by an increased signal of cervids (5%) and tragulids (5%) (BOUVRAIN & BONIS, 2007) parallel to a reduction of bovid taxa (24%). Although cervids occasionally appear on Samos and in Turkey, they seem to be more frequent in Continental Greece, documented in Perivolaki, Pikermi, Dytiko and the latest Turolian Greek fauna of Maramena, in which they are represented by a single taxon, but with a plethora of specimens (AZANZA, 1995). Tragulids are always rare

and apart from Dytiko, they were also traced in the Vathy-lakkos fauna, dated to MN 12, ~7.5 Ma (ARAMBOURG & PIVETEAU, 1929). The taxonomic composition (presence/absence matrix for 110 species) of a set of 17 Turolian mammal assemblages from Greece, Turkey and Iran has been analyzed using Detrended Correspondence Analysis (Past software®, HAMMER & HARPER, 2007), in order to spread out points at the left edge of the plot, provided by the simple correspondence analysis (Fig. 6; original matrix available on request). The Turolian faunal assemblages are divided into two geographically controlled groups along the first ordination axis, which explains about 50% of total variation; the right group includes Greek faunal assemblages, while the left includes Turkish and Iranian ones, plus the Samos assemblages. Kerassia (KER) is evidently out of order, because of the limited number of identified taxa at species level. The interpretation of the second axis (~43%) is not as obvious as the first one, but it could be considered as showing two opposite environmental gradients. The first one concerns the “eastern faunas”, with Kemiklitepe D and MLN to the one extreme, and Akkaşdağı (plus Middle and Upper Maragheh; MMRG, UMRG) to the other; it looks linear and certainly time-controlled, since assemblages are arranged in chronological order from early to late Turolian (MN 11 to MN 13). The other gradient refers to the “western faunas”, with Dytiko to the one extreme and Pikermi and Perivolaki to the other, and it looks independent of time, or non-linear, if time has been taken into account. It is quite possible that in both cases, the distribution of faunal assemblages indicates an increase of their

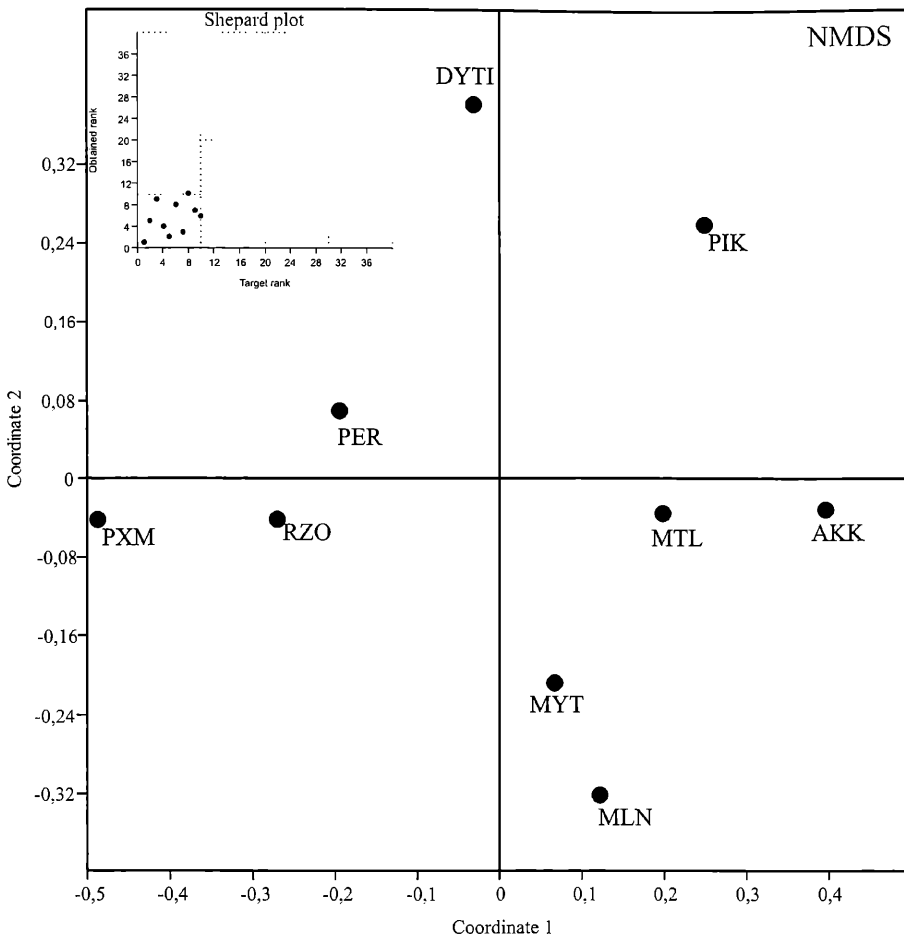


Figure 8: Non-Metric Multi-Dimensional Scaling Analysis based on MNI taxonomic composition, comparing a set of Turolian Greek and Turkish mammal assemblages (abbreviations as in Fig. 6).

Data in Appendix 1; the MNI for the AKK fauna was taken from VALLI (2005).

open/arid characteristic towards the bottom of the plot. In order to explain more radically the ecological account of association of different groups of Turolian mammals we performed a Correspondence Analysis (Past software®, 2007) on a subset of the original matrix (Appendix 2; Fig. 7). In this analysis, the species are grouped in distinct taxonomical categories that might correspond to a different ecological profile. The carnivores are clustered in five groups (canids, felids, hyaenids, mustelids and ursids). The herbivores are grouped in 24 categories, most of them reflecting subfamily or tribal level, or sharing morphotype. Although the first and second ordination axes explain only 19.7% and 17.7% of the data-spreading respectively, the analysis provides interesting information. The mammal assemblages are well-split into two groups along the first axis, with those of Samos and Turkey in the right part of the plot, and those of Continental Greece in the left one (Fig. 7). The Maragheh successive faunas are shared between these two groups. The “eastern faunas” are characterized by the strong signal of all kinds of hipparionine horses, pliohyraxes, ovibovine-like and caprine-like bovids, tubulidentates and hystrioids, most of them associated with intermediate to open environments (Fig. 7). On the other side of the plot, the “western faunas” are split into two parts (Fig. 7). The upper one includes only Dytiko, and it is characterized by the strong signal of tragulids, primates, and giraffines, all related to woodland environments. The lower group shows an arrangement of the assemblages along the second axis,

from Vathylakkos, Prochoma and Ravin des Zouaves 5 at the top to Pikermi and Kerassia at the bottom, due to the increasing impact of all kinds of proboscideans, ursids, felids, and mustelids. The analysis implies a clear environmental gradient across the Eastern Mediterranean during Turolian, with more open and arid conditions to the east in accordance with other studies (STRÖMBERG et al., 2007; KOSTOPOULOS, 2009 and listed literature). A Non-Metric Multi-dimensional Scaling (Past software®, 2007) with Morisita index on a MNI abundance data-matrix for a subset of the previous assemblages was also performed (Fig. 8). The obtained Shepard stress value of 0.19 is relatively high, indicating that a considerable amount of information has been lost during the reduction of dimensionality (HAMMER & HARPER, 2006). Even so, the distribution of the involved mammal assemblages does not significantly differ from those of previous analyses, showing the opposite ecological profile of Turolian “western” and “eastern” faunas (KOSTOPOULOS, 2009). Bearing in mind that the open and rather arid assemblage of Akkaşdağı (SCOTT & MAGA, 2005) and the relatively closed and humid Dytiko (BONIS et al., 1992; KOUFOS, 2006b) are placed on the opposite extremes of the plot, an open/arid (down/right) to closed/humid (up/left) environmental gradient could be assumed. Hence, in both geographical regions, there is a tendency to increase the open character from late MN 11/early MN 12 to late MN 12; in the west, this trend seems to be reversed towards MN 13, increasing the humidity and tree density.

6. Conclusions

The faunal composition of the Samos assemblages is dominated by bovids, giraffids and equids (mainly running horses), while the cervids, tragulids, and tapirids are weak to absent. This faunal composition is very close to the general pattern observed in the Turolian faunas of the Eastern Mediterranean. The study of the dental meso- and micro-wear of the MTL herbivores indicates that the dominance of the intermediate feeders over grazers and browsers clearly excludes the dominance of open grasslands and dense forests, as well as supporting the existence of grass/bushy vegetation on Samos during Middle Turolian. Such an interpretation was also proposed in other peri-Mediterranean localities from the Balkan-Turkish area (KOUFOS et al., 2006; MERCERON et al., 2005b, c, 2006). The phytolith assemblages clearly indicate the existence of wide tracks with a wealthy herbaceous vegetal layer including C3 graminoids (STRÖMBERG et al., 2007). The multivariate analysis of the feeding preferences of the Samos herbivores suggests open bushlands and a clear trend to more open/dry conditions from late early Turolian onwards.

The Turolian faunas of Continental Greece (RZO, VATH, PXM, PER, PIK, KER, DYTI) and the West-Asian ones (KTD, KTA-B, AKK, LMRG, MMRG, UMRG) are well-correlated with the modern relatively open environments (open woodlands, open bushlands, open grasslands) (BONIS et al., 1992, 1994, 1999; KOUFOS, 2006c; KOUFOS et al., 2006). The strong similarity of the faunal composition of the Samos faunas to these Turolian assemblages indicates a similar palaeoenvironment. However, there are differences between the faunal assemblages of Continental Greece and those from Samos and Turkey that need further investigation (KOSTOPOULOS, 2009). Taking into account all the above mentioned results of the various analyses and methods, it was possible to determine the palaeoenvironment of Samos. During latest Astaracian and Vallesian the extended lacustrine deposits as well as the pollen found in Mavratzei Fm (IOAKIM & SOLOUNIAS, 1985; IOAKIM & KOUFOS, this volume) indicate relatively closed/humid conditions with swamps and marshes.

The beginning of Turolian is marked by a dry phase which started earlier (Astaracian/Vallesian boundary), gradually extending to the west and affecting Western Europe during middle Vallesian. In the Eastern Mediterranean, the mammal signal indicates relatively open and dry conditions (AGUSTÍ et al., 1999; AGUSTÍ & ANTÓN, 2002; AGUSTÍ et al., 2003; BONIS et al., 1992, 1994, 1999; KOUFOS, 2006a); the landscape became more open with bushes, shrubs and a thick grass layer, including C3-graminoids as is shown by the dental wear (see above) and the phytolith assemblages (STRÖMBERG et al., 2007).

The dental wear of the Samos assemblages indicates the dominance of the intermediate feeders, suggesting bushy/grassy vegetation and thus a relatively open bushland with a well-developed grassy floor. These conditions seem to become exaggerated towards late middle Turolian.

7. Acknowledgements

The excavations on Samos have been supported by the Prefecture of Samos and the “Konstantinos and Maria Zimalis” Foundation. The Municipality of Mytilinii provided generous help, too. The Natural History Museum of the Aegean offered us the premises for the preparation and storage of the fossils. G.M. is grateful to Th. Kaiser and E. Schulz for discussions. G.M. was financially supported by the Humboldt Foundation (Germany) and the Singer-Polignac Foundation (France). Thanks are also due to Dr. D. Geraads for reviewing the original manuscript and making useful comments and suggestions.

8. References

- AGUSTÍ, J. & ANTÓN, M., 2002. Mammoths, Sabertooths, and Hominids. — 1:1–314, New York (Columbia University Press).
- AGUSTÍ, J., SANZ DE SIRIA, A. & GARCÉS, M., 2003. Explaining the end of the hominoid experiment in Europe. — *Journal of Human Evolution*, 45:145–153, New York.
- AGUSTÍ, J., CABRERA, L., GARCÉS, M., LLENAS, M., 1999. Mammal turnover and global climate change in the late Miocene terrestrial record of the Valles-Penedes basin (NE Spain). — [in:] AGUSTÍ, L., ROOK, L. & ANDREWS, P. (eds). *Hominoid Evolution and climatic change in Europe, The evolution of the Neogene terrestrial ecosystems in Europe*, 1:397–412, London (Cambridge Univ. Press).
- ARAMBOURG, C. & PIVETEAU, J., 1929. Les Vertébrés du Pontien de Salonique. — *Annales de Paléontologie*, 18:59–138, Paris.
- AZANZA, B., 1995. The Vertebrate locality of Maramena (Macedonia, Greece) and the Turolian-Ruscinian boundary (Neogene). 14. Cervidae (Artiodactyla, Mammalia). — *Münchener Geowissenschaftliche Abhandlungen*, 28:157–166, München.
- BERNOR, R.L., SOLOUNIAS, N., SWISHER III, C.C., VAN COUVERING, J.A., 1996. The correlation of three classical “Pikermian” mammal faunas – Maragheh, Samos, Pikermi – with the European MN Unit System. — [in:] BERNOR, R.L., FAHLBUSCH, V., MITTMAN, H.-W. (eds). *The evolution of Western Eurasian Neogene Mammal Faunas*. – 137–154, New York (Columbia University Press).
- BONIS, L. de & KOUFOS, G.D., 1994. Our ancestors’ ancestor: *Ouranopithecus* is a Greek link in human ancestry. — *Evolutionary Anthropology*, 4(3):75–83, New York.
- BONIS, L. de, BOUVRAIN, G. & KOUFOS, G.D., 1999. Palaeoenvironments of the hominoid primate *Ouranopithecus* in the late Miocene deposits of Macedonia, Greece. — [in:] AGUSTÍ, L., ROOK, L. & ANDREWS, P. (eds). *Hominoid Evolution and climatic change in Europe, The evolution of the Neogene terrestrial ecosystems in Europe*. – 1:205–237, London (Cam-

- bridge Univ. Press).
- BONIS, L. de, BOUVRAIN, G., GERAADS, D. & KOUFOS, G.D., 1992. Diversity and palaeoecology of Greek late Miocene mammalian faunas. — *Palaeogeography, Palaeoclimatology, Palaeoecology*, 91:99–121, Amsterdam.
- BONIS, L. de, BOUVRAIN, G., GERAADS, D., KOUFOS, G.D., SEN, S. & TASSY, P., 1994. Les gisements de mammifères du Miocène supérieur de Kemiklitepe (Turquie). 11. Biochronologie, paléoécologie et relations paléobiogéographiques. — *Bulletin Muséum National d'Histoire Naturelle, Paris, 4^{ème} sér., sect. C*, 16:225–240, Paris.
- BOUVRAIN, G. & BONIS, L. de, 2007. Ruminants (Mammalia, Artiodactyla: Tragulidae, Cervidae, Bovidae) des gisements du Miocène supérieur (Turolien) de Dytiko (Grèce). — *Annales de Paléontologie*, 93(2): 121–147, Paris.
- CARNELLI, A.L., MADELLA, M. & THEURILLAT, J.-P., 2001. Biogenic silica production in selected alpine plant species and plant communities. — *Annals of Botany*, 87:425–434.
- FORSTÉN, A.-M., 1968. Revision of the palaeartic *Hipparion*. — *Acta Zoologica Fennica*, 119:1–134, Helsinki.
- FORTELIUS, M. & SOLOUNIAS, N., 2000. Functional characterization of ungulate molars using the abrasion–attrition wear gradient: a new method for reconstructing paleodiets. — *American Museum Novitates*, 3301:1–36, New York.
- FORTELIUS, M., WERDELIN, L., ANDREWS, P., BERNOR, R.-L., GENTRY, A., HUMPHREY, L., MITTMANN, H.-W. & VIRATANA, S., 1996. Provinciality, Diversity, Turnover, and Palaeoecology in Land Mammal Faunas of the Later Miocene of Western Eurasia. — [in:] BERNOR, R.L., FAHLBUSCH, V., MITTMANN, H.-W. (eds). *The evolution of Western Eurasian Neogene Mammal Faunas*. — 137–154, New York (Columbia University Press).
- GIAOURTSAKIS, I.X., this volume. The Late Miocene Mammal Faunas of the Mytilinii Basin, Samos Island, Greece: New Collection. 9. Rhinocerotidae. — *Beiträge zur Paläontologie*, 31:157–187, Wien.
- GIAOURTSAKIS, I.X. & KOUFOS, G.D., this volume. The Late Miocene Mammal Faunas of the Mytilinii Basin, Samos Island, Greece: New Collection. 10. Chalicotheriidae. — *Beiträge zur Paläontologie*, 31:189–205, Wien.
- IOAKIM, C. & SOLOUNIAS, N., 1985. A radiometrically dated pollen flora from the upper Miocene of Samos Island, Greece. — *Revue de Micropaléontologie*, 28(3):197–204, Paris.
- IOAKIM, C. & KOUFOS, G.D., this volume. The Late Miocene Mammal Faunas of the Mytilinii Basin, Samos Island, Greece: New Collection. 3. Palynology. — *Beiträge zur Paläontologie*, 31:27–35, Wien.
- HAMMER, O. & HARPER, D., 2006. Paleontological data analysis. — 1–351, New York (Blackwell Publ.).
- HAYEK, C.L.-A., BERNOR, R.L., SOLOUNIAS, N. & STEIGERWALD, P., 1992. Preliminary studies of Hipparionine horse diet as measured by tooth microwear. — *Annales Zoologici Fennici*, 28:187–200, Helsinki.
- KAISER, T., & FORTELIUS, M., 2003. Differential mesowear in occluding upper and lower molars: opening mesowear analysis for lower molars and premolars in hypsodont horses. — *Journal of Morphology*, 258: 67–83.
- KAUFMAN, P.B., DAYANANDAN, P. & FRANKLIN, C.I., 1985. Structure and function of silica bodies in the epidermal system of grass bodies. — *Annals of Botany*, 55:487–507.
- KONIDARIS, G. & KOUFOS, G.D., this volume. The Late Miocene Mammal Faunas of the Mytilinii Basin, Samos Island, Greece: New Collection. 8. Proboscidea. — *Beiträge zur Paläontologie*, 31:139–155, Wien.
- KOSTOPOULOS, D.S., 2006. The late Miocene vertebrate locality of Perivolaki, Thessaly, Greece. 9. Cervidae and Bovidae. — *Palaeontographica, Abt. A*, 276(1-6):151–183, Stuttgart.
- KOSTOPOULOS, D.S., 2009. The Pikermian Event: temporal and spatial resolution of the Turolian large mammal fauna in SE Europe. — *Palaeogeography, Palaeoclimatology, Palaeoecology*, 274:82–95, Amsterdam.
- KOSTOPOULOS, D.S., this volume – a. The Late Miocene Mammal Faunas of the Mytilinii Basin, Samos Island, Greece: New Collection. 13. Giraffidae. — *Beiträge zur Paläontologie*, 31:299–343, Wien.
- KOSTOPOULOS, D.S., this volume – b. The Late Miocene Mammal Faunas of the Mytilinii Basin, Samos Island, Greece: New Collection. 14. Bovidae. — *Beiträge zur Paläontologie*, 31:345–389, Wien.
- KOSTOPOULOS, D.S. & KOUFOS, G.D., 2000. Palaeoecological remarks on Plio-Pleistocene mammalian faunas. Comparative analysis of several Greek and European assemblages. — [in:] KOUFOS, G. & IOAKIM, C. (eds). *Mediterranean Neogene cyclostratigraphy in marine-continental deposits*. — *Bulletin of the Geological Society of Greece, special publ.*, 9:139–150, Athens.
- KOSTOPOULOS, D.S., SEN, S. & KOUFOS, G.D., 2003. Magnetostratigraphy and revised chronology of the late Miocene mammal localities of Samos, Greece. — *International Journal of Earth Sciences*, 92:779–794, Berlin.
- KOSTOPOULOS, D.S., KOUFOS, G.D., SYLVESTROU, I.A., SYRIDES, G.E. & TSOMPACHIDOU, E., this volume. The Late Miocene Mammal Faunas of the Mytilinii Basin, Samos Island, Greece: New Collection. 2. Lithostratigraphy and Fossiliferous Sites. — *Beiträge zur Paläontologie*, 31:13–26, Wien.
- KOUFOS, G.D., 2006a. Palaeoecology and chronology of the Vallesian (late Miocene) in the Eastern Mediterranean region. — *Palaeogeography, Palaeoclimatology, Palaeoecology*, 234:127–145, Amsterdam.
- KOUFOS, G.D., 2006b. The large mammals from the Miocene/Pliocene locality of Silata, Macedonia, Greece with implications about the Latest Miocene palae-

- oecology. — *Beiträge zur Paläontologie*, 30:293–313, Wien.
- KOUFOS, G.D., 2006c. The Neogene mammal localities of Greece: faunas, chronology and biostratigraphy. — *Hellenic Journal of Geosciences*, 41(1):183–214, Athens.
- KOUFOS, G.D., this volume - a. The Late Miocene Mammal Faunas of the Mytilinii Basin, Samos Island, Greece: New Collection. 5. Carnivora. — *Beiträge zur Paläontologie*, 31:57–105, Wien.
- KOUFOS, G.D., this volume - b. The Late Miocene Mammal Faunas of the Mytilinii Basin, Samos Island, Greece: New Collection. 6. Tubulidentata. — *Beiträge zur Paläontologie*, 31:107–125, Wien.
- KOUFOS, G.D., this volume - c. The Late Miocene Mammal Faunas of the Mytilinii Basin, Samos Island, Greece: New Collection. 7. Hyracoidea. — *Beiträge zur Paläontologie*, 31:127–137, Wien.
- KOUFOS, G.D., MERCERON, G., KOSTOPOULOS, D.S., VLACHOU, T.D. & SYLVESTROU, I., 2006. The late Miocene Vertebrate locality of Perivolaki, Thessaly, Greece. 11. Palaeoecology and Palaeobiogeography. — *Palaeontographica*, Abt. A, 276:201–221, Stuttgart.
- KOUFOS, G.D., KOSTOPOULOS, D.S. & VLACHOU, T.D., this volume. The Late Miocene Mammal Faunas of the Mytilinii Basin, Samos Island, Greece: New Collection. 16. Chronology. — *Beiträge zur Paläontologie*, 31:397–408, Wien.
- LEGENDRE, S., 1989. Les communautés de mammifères du Paléogène (Eocène supérieur et Oligocène) d'Europe occidentale: structures, milieux et évolution. — *Münchner Geowissenschaftliche Abhandlungen*, 16:1–110, München.
- MACNAUGHTON, S.J., TARRANTS, J.L., MACNAUGHTON, M.M. & DAVIS, R.H., 1985. Silica as a defense against herbivory and a growth promotor in African grasses. — *Ecology*, 66:528–535.
- MERCERON, G., VIRIOT, L. & BLONDEL, C., 2004. Tooth microwear pattern in roe deer (*Capreolus capreolus*, L.) from Chizé (Western France) and relation to food composition. — *Small Ruminant Research*, 53:125–138.
- MERCERON, G., BLONDEL, C., BONIS, L. de, KOUFOS, G.D. & VIRIOT, L., 2005a. A new dental microwear analysis: application to extant Primates and *Ouranopithecus macedoniensis* (Late Miocene of Greece). — *Palaios*, 20:551–561.
- MERCERON, G., BONIS, L. de, VIRIOT, L. & BLONDEL, C., 2005b. Dental microwear of fossil bovids from Northern Greece: paleoenvironmental conditions in the Eastern Mediterranean during the Messinian. — *Palaeogeography, Palaeoclimatology, Palaeoecology*, 217:173–185, Amsterdam.
- MERCERON, G., BONIS, L. de, VIRIOT, L. & BLONDEL, C., 2005c. Dental microwear of the Late Miocene bovids of Northern Greece: the Vallesian/Turolian environmental changes as explanation of the disappearance of *Ouranopithecus macedoniensis*? — *Bulletin de la Société Géologique de France*, 176:475–484, Paris.
- MERCERON, G., BLONDEL, C., VIRIOT, L., KOUFOS, G.D., & BONIS, L. de, 2007a. Dental microwear analysis on bovids from the Vallesian (Late Miocene) of the Axios Valley in Greece: reconstruction of the habitat of *Ouranopithecus macedoniensis* (Primates, Hominoidea). — *Geodiversitas*, 29:421–433, Paris.
- MERCERON, G., SCHULTZ, E., KORDOS, L. & KAISER, T.M., 2007b. Paleoenvironment of *Dryopithecus* branchoi at Rudabánya, Hungary: evidence from dental meso- and micro-wear analyses of large vegetarian mammals. — *Journal of Human Evolution*, 53:331–349, New York.
- MERCERON, G., ZAZZO, A., SPASSOV, N., GERAADS, D. & KOVACHEV, D., 2006. Bovid paleoecology and paleoenvironments from the late Miocene of Bulgaria: evidence from dental microwear and stable isotopes. — *Palaeogeography, Palaeoclimatology, Palaeoecology*, 241:637–654, Amsterdam.
- NOW, 2007. Neogene Old World (database with the Neogene localities and their faunal lists). — www.helsinki.fi/science/now/database.htm.
- HAMMER, O. & HARPER, D., 2007. Paleontological Statistics, Past software. — <http://folk.uio.no/ohammer/past/>
- PLUMMER, T.W. & BISHOP, L.C., 1994. Hominid paleoecology at Olduvai Gorge, Tanzania as indicated by antelope remains. — *Journal of Human Evolution*, 27:47–75, New York.
- QUADE, J., SOLOUNIAS, N. & CERLING, T.E., 1994. Stable isotopic evidence from paleosol carbonates and fossil teeth in Greece for forest or woodlands over the past 11 Ma. — *Palaeogeography, Palaeoclimatology, Palaeoecology*, 108:41–53, Amsterdam.
- SCOTT, R.S. & MAGA, M., 2005. Paleoecology of the Akkaşdağı hipparions (Mammalia, Equidae), late Miocene of Turkey. — *Geodiversitas*, 27(47):809–830, Paris.
- SEN, S. (ed.), 1994. Les gisements de mammifères du Miocène supérieur de Kemiklitepe, Turquie. — *Bulletin du Muséum National d'Histoire Naturelle*, Paris, 4^{ème} sér., 16:1–240, Paris.
- SEN, S. (ed.), 2005. Geology, mammals and environments at Akkaşdağı, late Miocene of Central Anatolia. — *Geodiversitas*, 27(4):509–830, Paris.
- SOKAL, R.R. & ROHLF, J.F., 1998. Biometry: The principles and practice of statistics in biological research. — 1–887, New York (Freeman & Co).
- SOLOUNIAS, N., 1981. The Turolian fauna from the island of Samos, Greece. — *Contributions Vertebrate Evolution*, 6:1–232, Basel.
- SOLOUNIAS, N. & DAWSON-SAUNDERS, B., 1988. Dietary adaptations and paleoecology of the late Miocene ruminants from Pikerimi and Samos in Greece. — *Palaeogeography, Palaeoclimatology, Palaeoecology*, 65:149–172, Amsterdam.
- SOLOUNIAS, N. & MOELLEKEN, S.M.C., 1992. Dietary adaptation of two goat ancestors and evolutionary considerations. — *Geobios*, 25:797–809, Lyon.
- SOLOUNIAS, N. & MOELLEKEN, S.M.C., 1999. The Mi-

- ocene gazelle from Greece as a model for detecting Darwinian evolutionary change. — *Annales Musei Goulandris*, 10:291–308, Athens.
- SOLOUNIAS, N. & SEMPREBON, G., 2002. Advances in the reconstruction of ungulate ecomorphology with application to early fossil equids. — *American Museum Novitates*, 3366:1–49, New York.
- SOLOUNIAS, N. & MOELLEKEN, S.M.C. & PLAVCAN, J.M., 1995. Predicting the diet of extinct bovids using masseteric morphology. — *Journal of Vertebrate Paleontology*, 15:795–805.
- SOLOUNIAS, N., PLAVCAN, J.M., QUADE, J. & WITMER, V., 1999. The paleoecology of the Pikermian biome and the savanna myth. — [in:] AGUSTÍ, L., ROOK, L. & ANDREWS, P. (eds). *Hominoid Evolution and climatic change in Europe, The evolution of the Neogene terrestrial ecosystems in Europe*. — 1:427–444, London (Cambridge Univ. Press).
- SOLOUNIAS, N., SCOTT MCGRAW, W., HAYEK, L.-A., WERDELIN, L., 2000. The paleodiet of the Giraffidae. — [in:] VRBA, E. & SCHALLER, G. (eds). *Antelopes, Deer and Relatives – 84–95*, New Haven (Yale University Press)
- SONDAAR, P.Y., 1971. The Samos Hipparion. — *Proceedings of the Koninklijke Nederlandse Akademie van het Wetenschappen, B*, 74:417–441, Amsterdam.
- STRÖMBERG, C.A.E., WERDELIN, L., FRIIS, E.M. & SARAÇ, G., 2007. The spread of grass-dominated habitats in Turkey and surrounding areas during the Cenozoic: phytolith evidence. — *Palaeogeography, Palaeoclimatology, Palaeoecology*, 250:18–49, Amsterdam.
- SYLVESTROU, I.A. & KOSTOPOULOS, D.S., this volume. The Late Miocene Mammal Faunas of the Mytilinii Basin, Samos Island, Greece: New Collection. 12. Suidae. — *Beiträge zur Paläontologie*, 31:283–297, Wien.
- TEAFORD, M.F. & OYEN, O.J., 1989. In vivo and in vitro turnover in dental microwear. — *American Journal of Physical Anthropology*, 80:447–460.
- VALLI, A., 2005. Taphonomy of the late Miocene of Akkaşdağı, Turkey. — *Geodiversitas*, 27(47):793–808, Paris.
- VASSILEIADOU, K. & SYLVESTROU, I.A., this volume. The Late Miocene Mammal Faunas of the Mytilinii Basin, Samos Island, Greece: New Collection. 4. Micromammals. — *Beiträge zur Paläontologie*, 31:37–55, Wien.
- VLACHOU, T.D. & KOUFOS, G.D., this volume. The Late Miocene Mammal Faunas of the Mytilinii Basin, Samos Island, Greece: New Collection. 11. Equidae. — *Beiträge zur Paläontologie*, 31:207–281, Wien.
- WEIDMANN, M., SOLOUNIAS, N., DRAKE R.E. & CURTIS J., 1984. Neogene stratigraphy of the Mytilini Basin, Samos Island, Greece. — *Geobios*, 17(4):477–490.

Appendix

MNI	MLN	MYT	MTL	PXM	RZO	PIK	DYTI	PER
<i>Mesopithecus pentelicus</i>	0	0	0	0	0	12	5	0
<i>Mesopithecus delsoni</i>	0	0	0	0	2	0	0	4
<i>Ursavus depereti</i>	0	0	0	0	0	0	0	1
<i>Hyaenictitherium wongii</i>	1	0	6	0	2	0	0	0
<i>Machairodus giganteus</i>	0	0	1	0	1	0	0	0
<i>Metailurus parvulus</i>	0	0	1	0	0	0	0	0
<i>Parataxidea maraghana</i>	0	0	2	0	0	0	0	0
<i>Plioviverrups orbignyi</i>	0	0	1	1	1	3	0	2
<i>Protictitherium crassum</i>	2	0	0	0	0	0	1	0
<i>Chasmaporthetes bonisi</i>	0	0	0	0	1	0	1	0
<i>Ictitherium viverrinum</i>	0	0	0	1	1	0	0	0
<i>Adcrocuta eximia</i>	0	0	4	1	2	6	0	2
<i>Promephitis larteti</i>	0	0	0	0	0	0	0	1
<i>Promeles palaeoattica</i>	0	0	0	0	0	0	0	1
<i>Plesiogulo crassa</i>	0	0	0	0	0	0	0	1
<i>Choerolophodon pentelici</i>	0	0	1	1	1	2	1	0
<i>Zygalophodon turicensis</i>	0	0	1	0	1	1	0	0
<i>Tetralophodon atticus</i>	0	0	0	0	0	1	0	0
<i>Deinotherium giganteum</i>	0	0	0	0	0	1	0	0
<i>Deinotherium sp.</i>	0	0	0	0	0	0	0	1
<i>Pliohyrax graecus</i>	0	0	1	0	0	2	0	0
<i>Orycteropus gaudryi</i>	0	0	4	0	0	0	1	0
<i>Ancylotherium pentelicum</i>	0	1	2	0	0	2	0	0
<i>Macrotherium macedonicum</i>	0	0	0	0	0	0	1	0
<i>Chalicotherium goldfussi</i>	0	0	0	9	1	0	0	0
<i>Diceros neumayri</i>	1	1	17	0	2	7	1	1
<i>Diboplus pikermiensis</i>	0	1	2	0	0	4	0	0
<i>Hipparion "dietrichi"</i>	0	0	0	22	11	0	0	14
<i>Hipparion dietrichi</i>	0	0	18	0	0	0	0	0
<i>Hipparion forstenae</i>	0	3	11	0	0	0	0	0
<i>Hipparion proboscideum</i>	2	3	11	0	4	0	0	0
<i>Hipparion brachypus</i>	0	0	6	0	0	32	0	0
<i>Hipparion matthewi</i>	0	3	4	1	13	0	12	20
<i>Hipparion mediterraneum</i>	0	0	0	0	0	41	20	5
<i>Hipparion periafricanum</i>	0	0	0	0	0	0	3	0
<i>Hipparion prostylum</i>	3	5	0	0	0	0	0	0
<i>Microstonyx major</i>	0	0	2	1	3	12	2	2
<i>Propotamochoerus hysudricus</i>	0	0	0	0	1	0	0	0
<i>Palaeotragus rouenii</i>	1	0	3	0	2	3	2	2
<i>Palaeotragus sp.</i>	1	0	1	0	0	0	0	0

MNI	MLN	MYT	MTL	PXM	RZO	PIK	DYTI	PER
<i>Helladotherium duvernoyi</i>	0	0	2	1	2	4	0	7
<i>Samotherium boissieri</i>	3	0	0	0	0	0	0	0
<i>Samotherium major</i>	0	2	11	0	0	0	0	0
<i>Boblinia attica</i>	0	0	0	0	0	3	9	0
<i>Dremotherium pentelici</i>	0	0	0	0	0	1	0	0
<i>Pliocervus graecus</i>	0	0	0	0	0	1	2	0
<i>Lucentia sp.</i>	0	0	0	0	0	1	0	2
<i>Gazella capricornis</i>	0	0	10	0	0	15	0	0
<i>Gazella cf. sclosseri</i>	0	0	0	0	0	0	2	0
<i>Gazella deperdita</i>	0	0	0	0	0	0	14	0
<i>Gazella mytilinii</i>	0	0	9	0	0	0	0	0
<i>Gazella pilgrimi</i>	1	1	2	3	4	0	0	5
<i>Gazella sp.</i>	0	0	0	0	2	0	0	1
<i>Miotragocerus valenciennesi</i>	1	0	3	0	0	7	0	2
<i>Tragoportax rugosifrons</i>	0	0	1	14	40	0	0	23
<i>Miotragocerus macedoniensis</i>	0	0	0	0	0	0	30	0
<i>Tragoportax amalthaea</i>	0	0	0	0	0	8	0	0
<i>Tragoportax sp.</i>	2	0	0	0	0	0	2	0
<i>Nisidorcas planicornis</i>	0	0	0	4	7	0	0	12
<i>Dytikodorcas longicornis</i>	0	0	0	0	0	0	5	0
<i>Hispanodorcas orientalis</i>	0	0	0	0	0	0	4	0
? <i>Majoreas sp.</i>	0	1	0	0	0	0	0	0
<i>Oioceros rothi</i>	0	0	0	0	0	6	0	0
<i>Palaeoreas lindermayeri</i>	0	0	0	0	0	18	8	0
<i>Palaeoreas/Helladorcas sp.</i>	0	0	0	1	0	0	0	2
<i>Palaeoreas zouavei</i>	0	0	0	0	2	0	0	0
<i>Protragelaphus skouzesi</i>	0	0	0	0	0	3	0	0
<i>Protragelaphus theodori</i>	0	0	0	0	0	0	18	0
<i>Sporadotragus parvidens</i>	0	1	4	0	0	3	0	0
<i>Protoryx carolinae</i>	0	0	0	0	0	1	0	0
<i>Skoufotragus laticeps</i>	0	0	17	0	0	0	0	6
<i>Skoufotragus zemalisorum</i>	0	4	0	0	0	0	0	0
<i>Palaeoryx majori</i>	0	0	4	0	0	0	0	0
<i>Palaeoryx pallasii</i>	0	0	3	0	0	2	0	1
<i>Palaeoryx sp.</i>	1	1	0	0	0	0	2	0
<i>Urmiatherium rugosifrons</i>	0	0	2	0	0	0	0	0
<i>Prostrepsiceros rotundicornis</i>	0	0	0	0	2	2	0	0
<i>Prostrepsiceros axiosi</i>	0	0	0	4	13	0	0	0
<i>Prostrepsiceros fraasi</i>	0	0	0	0	0	0	0	15
<i>Pheraios chryssomallos</i>	0	0	0	0	0	0	0	1

Appendix 1: Minimum Number of Individuals (MNI) per species for the Samos and other Greek Turolian assemblages. Assemblage abbreviations as in Fig. 6.

	MLN	MYT	MTL	Q5	RZO	KER	PER	VATH	PXM	PIK	DYTI	KTD	AKK	KTA	LMRG	MMRG	UMRG
Primates	0	0	0	0	1	0	1	1	0	1	2	0	0	0	0	1	0
Hyaenidae	2	0	3	2	5	1	2	4	3	7	2	0	4	2	0	2	3
Mustelidae	0	0	1	0	0	0	3	1	0	5	0	0	1	0	0	1	1
Felidae	0	0	2	1	1	2	0	1	0	6	0	1	0	1	0	2	3
Ursidae	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0
?Canidae	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Deinotheriidae	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Gombotheriidae	0	0	1	0	1	1	0	1	1	2	0	0	2	0	1	1	1
Mammutidae	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0
Chalicotheriidae	0	1	1	0	0	0	0	1	1	1	1	0	1	1	0	1	1
Aceratheriinae	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	1	1
Rhinocerotinae	0	2	2	2	1	2	1	1	0	2	1	2	1	1	0	1	1
Pliohyracidae	0	0	1	0	0	0	0	0	0	1	0	1	0	1	0	0	0
<i>H. brachypus</i> lineage	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0
<i>H. dietrichi</i> lineage	1	1	1	1	1	0	1	1	1	0	1	1	1	1	1	1	1
<i>H. mediterraneum</i> lineage	1	3	3	2	2	0	2	1	1	1	1	1	2	2	0	2	0
Hystriidae	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0
Tubulidentata	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0
Suidae	0	0	1	1	2	1	1	1	1	1	1	0	1	0	1	1	1
Cervidae	0	0	0	1	0	0	1	0	0	2	1	0	0	0	0	1	0
Tragulidae	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0
Giraffinae	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0
Sivatheriinae	0	0	1	1	1	1	1	0	1	1	0	0	1	0	0	1	0
Palaeotraginae	2	1	2	2	1	1	1	1	0	1	1	2	1	1	1	2	1
gazelles	1	1	3	3	2	0	2	1	1	1	2	1	2	1	2	2	1
spiral-horned bovids	0	0	0	1	4	0	3	3	2	4	4	1	0	0	1	5	0
capra-like bovids	0	2	4	2	0	0	2	0	0	3	0	1	2	1	1	2	1
ovibovine-like bovids	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0
Boselaphini	0	0	2	2	1	1	2	1	1	2	1	0	2	0	1	2	0

Appendix 2: Number of species per taxonomical categories, reflecting subfamily or tribal level or sharing morphotype for 17 Turolian assemblages from Greece, Turkey and Iran. Data from KOUFOS (2006c), KOUFOS et al. (2006), SEN (1994, 2005), BERNOR et al. (1996), SOLOUNIAS (1981). Assemblage abbreviations as in Fig. 6.