

Feeding habits of the first European colobine, *Mesopithecus* (Mammalia, Primates): evidence from a comparative dental microwear analysis with modern cercopithecids

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ABSTRACT

This study aims to characterize the feeding habits of the first European colobines, *Mesopithecus* (late Miocene), through the analysis of its molar microwear pattern. Fifty-seven adult individuals of *Mesopithecus* (from Greece and Bulgaria) are compared to 162 wild-shot specimens representing nine modern species of African and Asian cercopithecids. Through the combination of a principal component analysis and analyses of variances, *Mesopithecus* displays significant differences with its extant colobine relatives. Actually, there is no significant difference between the *Mesopithecus* samples and *Chlorocebus aethiops* and *Papio hamadryas*. An intra-specific test dedicated to *Mesopithecus pentelicus* reveals no difference between the Bulgarian and the Greek samples. To sum up, the species of *Mesopithecus* were not leaf eaters like their present-day colobine relatives. Considering its wide paleogeographic range, its post-cranial anatomy, the paleoenvironmental data, and the present dietary reconstruction as a whole, the species of *Mesopithecus* can be depicted as semi-terrestrial monkeys opportunists in term of feeding preferences.

KEY WORDS

Mammalia,
Primates,
Cercopithecoids,
Neogene,
Europe,
diet,
ecology.

RÉSUMÉ

Habitudes alimentaires du premier colobiné européen, Mesopithecus : apports de l'analyse comparative des micro-usures dentaires avec des cercopithécidés actuels.

Cette étude vise à déterminer les habitudes alimentaires des premiers colobinés européens, du genre *Mesopithecus* (Miocène supérieur) par l'analyse du type de micro-usure dentaire sur les molaires. Cinquante-sept spécimens attribués à *Mesopithecus* sont comparés à 162 individus sauvages représentant neuf espèces actuelles de cercopithécidés africains et asiatiques. À travers une analyse en composante principale couplée à des analyses de variances, *Mesopithecus* apparaît significativement différent des colobinés actuels. Aucune différence significative n'est détectée entre les *Mesopithecus* et *Chlorocebus aethiops* et *Papio hamadryas*. Une analyse interspécifique dédiée à *Mesopithecus pentelicus* ne révèle aucune différence entre les échantillons bulgares grecs. En résumé, les espèces de *Mesopithecus* se distinguent des colobinés actuels, principalement folivores. En prenant en compte les données paléoenvironnementales, leur distribution paléogéographique, leur anatomie postcrânienne, et leurs habitudes alimentaires ici reconstituées, les *Mesopithecus* peuvent être dépeints comme des singes semi-terrestres et généralistes vis-à-vis de leur bol alimentaire.

MOTS CLÉS

Mammalia,
Primates,
Cercopithécoïdes,
Néogène,
Europe,
alimentation,
écologie.

INTRODUCTION

From the late Miocene to Pleistocene, cercopithecids have known a high specific diversity in Western Eurasia. Four genera are known: *Macaca* Lacépède, 1799, *Paradolichopithecus* Necrasov, Samson & Rădulescu, 1961, *Dolichopithecus* Depéret, 1889, and *Mesopithecus* Wagner, 1839. *Mesopithecus* from the late Miocene is the first representative of the family in Europe. The first occurrence of the genus was traced at Wissberg (Germany) dated to early Vallesian (MN 9). However, as Andrews *et al.* (1996) claim, the sole known teeth of Wissberg may come from different *Dinotherium-Sands* horizons with different ages. Actually, *Mesopithecus* is known from Turolian deposits. The genus is recognized at Grossulovo (Ukraine), an early Turolian locality (Semenov 2001) for which no independent age calibration has been performed. *Mesopithecus* from the locality "Ravin des Zouaves 5", RZO of Axios Valley (Macedonia, Greece) is therefore the first reliable occurrence of the genus in Europe (Bonis *et al.* 1990). The faunal assemblage from this locality is dated to the lower part of the early Turolian (late Miocene, 8.7-7.5 Ma); the magnetostratigraphy sug-

gests a correlation to Chron C4r.1r (8.23-8.07 Ma) indicating an age of ~8.2 Ma (Koufos 2006a). The genus *Mesopithecus* was also recognized in the locality Nikiti 2 (Koufos 2009, this volume). The locality is dated to the lowermost early Turolian, MN 11 (Koufos 2006a) confirming the certain early Turolian appearance of *Mesopithecus* in Eurasia. *Mesopithecus* is recognized as an early colobine; *Microcolobus tugenensis* Benefit & Pickford, 1986 from 11 Ma deposits of Kenya is probably the first representative of the subfamily (Benefit & Pickford 1986). The cranial and dental features root *Mesopithecus* at the knot splitting colobine and presbytini tribes (Szalay & Delson 1979; Strasser & Delson 1987; Bonis *et al.* 1990). Whereas the 10 modern genera of colobines are only distributed in Asia and Africa (Rowe 1996), *Mesopithecus* was widespread from France to Pakistan (with the exception of Anatolia) during the Turolian (Heintz *et al.* 1981; Andrews *et al.* 1996; Harrison & Delson 2007).

The paleobiology of *Mesopithecus* is particularly interesting because its occurrence in Eurasia is more or less synchronous to the extinction of the Miocene hominoids (Andrews *et al.* 1996). Two main hypotheses can explain this synchronism: changes in

climate and vegetation at the end of the Vallesian (Bonis *et al.* 1999; Agustí *et al.* 2003; Nelson 2003; Merceron *et al.* 2005a; Koufos 2006c) and/or direct ecological competition between the hominoids and cercopithecoids. The lack of co-occurrence of both hominoids and cercopithecoids rather supports the first hypothesis. Recently an isolated hominoid tooth assigned to cf. *Ouranopithecus* Bonis & Melentis, 1977 was discovered in the Bulgarian locality of Azmaca dated to Turolian ages (Spasov & Geraads 2008). *Mesopithecus* is hitherto absent in this locality but bearing in mind that this monkey is quite well known in the Turolian of Bulgaria (Koufos *et al.* 2003), it would support a co-existence of cercopithecoids and hominoids in Eastern Europe at least.

Contrary to the cercopithecines, the modern colobines are more involved in folivory (Rowe 1996 and citations therein). Besides, they display peculiar anatomical features of their gastrointestinal tracts. They have a forestomach which is divided into a proximal *presaccus* and a *saccus* (for complete review of gastrointestinal tract, see Chivers 1994; Kay & Davies 1994; Lambert 1998). A low acidity rate in these two former chambers is required to maintain fermentation in optimal conditions. During fermentation, carbohydrates, and especially polysaccharides (e.g., cellulose from the plant cell-walls) are reduced into disaccharide sugars, which are easily hydrolyzed during the transit through the small intestine before absorption. Chivers (1994) and Kay & Davies (1994) suspect that the folivory amongst colobines may have arisen from diets rich in seeds. This hypothesis is based on two facts. First, the two oldest cercopithecoids, *Prohylobates* Fourtau, 1918 and *Victoriapithecus* von Koenigswald, 1969, were not highly involved in folivory since they have cercopithecine-like molars (Benefit 2000). Second, fruits do not usually have complex molecules difficult to digest whereas seeds have many carbohydrates as complex as those found in foliage. This means that seeds might have been a link between frugivory and folivory (Chivers 1994).

Thus the question is, was *Mesopithecus* a leaf eater like its modern relatives or a fruit/seed eater as the extant cercopithecines? The present article is an effort to answer to this question trying to estimate the dietary habits and therefore its palaeobiology,

using dental microwear. Dental microwear, the study of scars on enamel facets resulting from abrasion with food items gives direct information of what an individual ate over a period of time in the past (Walker *et al.* 1978; Teaford & Oyen 1989).

ABBREVIATIONS USED IN TEXT

PCA	Principal Component Analysis;
LSD test	Fischer's Least Significant Differences test;
HSD test	Tukey's Honest Significant Differences test;
Nfs, Nws	Number of fine and wide scratches, respectively;
Nlp, Nsp	Number of large and small pits respectively;
Np, Pp	Number and percentage of pits, respectively;
Ns, Ls	Number and length of scratches respectively.

Localities

HD	Hadjidimovo-1 locality;
K	Kalimantsi locality;
PER	Perivolaki locality;
PIK	Pikermi locality;
RZO	Ravin des Zouaves-5 locality;
VTK	Vathylakkos-2 locality.

Institutions

AMPG	Athens Museum of Palaeontology and Geology;
MNHN	Muséum nationale d'Histoire naturelle, Paris;
MNHN-CG	Specimens from the "Catalogue général" housed in MNHN;
NHMW	Naturhistorisches Museum, Wien;
RMCA	Royal Museum of Central Africa, Tervuren;
ZSM	Zoologische Staatssammlung of Munich;
SNG	Naturmuseum Senckenberg, Frankfurt.

MATERIAL

A total number of 57 adult individuals of *Mesopithecus* (Appendix 1) are studied in this article. They belong to various Greek and Bulgarian Turolian localities. This fossil material is housed in the following European museum or institutions: the Assenovgrad Museum, a paleontological division of the National Museum of Natural History of Sofia (Bulgaria), the Muséum national d'Histoire naturelle, Paris (France), the Naturhistorisches Museum in Wien (Austria), the University of Vienna (Austria), the Athens Mu-

TABLE 1. — Dietary composition of extant cercopithecids.

Name	Diet	Publications
<i>Chlorocebus aethiops</i>	Fruits, seeds, leaves, animal prey	Struhsaker 1967; Rowe 1996; Nakawaga 2003; Lambert 2005
<i>Colobus polykomos</i>	Leaves, seeds	Mac Key 1978; Rose 1978; Baranga 1983; Dasilva 1994; Rowe 1996; Daegling & McGraw 2001
<i>Lophocebus albigena</i>	Fruits (59%), seeds, leaves (5%), flowers (3%), animal prey including reptiles and insects	Chalmers 1968; Rowe 1996; Lambert 2005
<i>Macaca fascicularis</i>	Fruits (64%), seeds, buds, leaves, animal prey	Richard <i>et al.</i> 1989; Rowe 1996
<i>Nasalis larvatus</i>	Leaves (44%), seeds (20%), fruits (17%), flowers (3%), animal prey	Yeager & Kool 1994; Rowe 1996
<i>Papio anubis</i>	Fruits, seeds, tubers, roots, leaves, flowers, animal prey	Nagel 1973; Rowe 1996
<i>Papio cynocephalus</i>	Fruits, seeds, leaves, flowers, tubers, roots, animal prey	Hausfater & Maccuskey 1980; Rhine <i>et al.</i> 1986, Norton <i>et al.</i> 1987; Rowe 1996
<i>Papio hamadryas</i>	Grass seeds, roots, tubers, leaves, animal prey	Nagel 1973; Rowe 1996
<i>Theropithecus gelada</i>	Grasses (90%), seeds, leaves, animal prey	Kawai 1979; Iwamoto 1993; Rowe 1996

seum of Palaeontology and Geology (Greece), and the University of Thessaloniki (Greece). The richest sample comes from Pikermi (Appendix 1) including the typical *Mesopithecus pentelicus* Wagner, 1839 and dated to the uppermost middle Turolian, MN 12 at ~7.0 Ma (Koufos 2006a and reference therein). The RZO sample includes *M. delsoni* Bonis, Bouvrain, Geraads & Koufos, 1990 and it is dated to early Turolian at ~8.2 Ma (Bonis *et al.* 1990; Koufos 2006a). Two other middle Turolian Greek localities VTK and PER include *Mesopithecus*. This form has intermediate characters and dimensions between *M. delsoni* and *M. pentelicus* and it is referred to as *M. delsoni/pentelicus* (Bonis *et al.* 1997; Koufos 2006b). The locality VTK is dated to the lowermost middle Turolian, MN 12 at ~7.5 Ma, while the locality PER to middle Turolian from 7.3–7.1 Ma (Koufos 2006a, Koufos *et al.* 2006b). The Bulgarian material of *Mesopithecus* comes from the locality of Hadjidi-movo-1 dated to the middle Turolian MN 12; it is determined to *M. delsoni/pentelicus* (Koufos *et al.* 2003; Koufos 2009, this volume). The Kalimantsi sample includes several specimens which belong to *M. pentelicus*; the material comes from the upper levels of Kalimantsi dated to the middle Turolian MN 12 (Koufos *et al.* 2003).

A set of 162 wild-shot adult specimens representing nine present-day species of cercopithecoid (including cercopithecine and colobine) with known differences in diet is here used for comparisons (Table 1; Appendix 2). These extant species were selected because they cover a large spectrum of dietary habits, from leaf-eaters like *Nasalis larvatus* (Wurmb, 1787) to fruit/seed eaters like *Lophocebus albigena* (Gray, 1850), to grass-eater *Theropithecus gelada* (Rüppell, 1835). Table 1 summarizes feeding habits for these extant species.

METHODS

High-resolution epoxy resin replicas of the upper and lower second molars for extant species were made following traditional methods (Ungar 1996). Because fossil material is scarce, the fossil samples are enlarged in including the first and third with second molars. Such samples including all molars should be then considered with caution. Also, no accurate intra-population (sexual differences) studies can be conducted. Regarding dental microwear analyses, many protocols from casting steps to quantification were employed (for a review, see

TABLE 2. — Descriptive statistics on extant cercopithecids and populations of *Mesopithecus* Wagner 1839. Abbreviations: **Ls**, length of scratch (μm); **m**, mean; **N**, number of individuals; **Nws**, number of wide scratches; **Nlp**, number of large pits; **Nfs**, number of fine scratches; **Nsp**, number of small pits; **Pp**, percentage of pits; **sem**, standard error of the mean.

	N	Ls (μm)		Nws		Nlp		Nfs		Nsp		Pp (%)	
		m	sem	m	sem	m	sem	m	sem	m	sem	m	sem
<i>Chlorocebus aethiops</i>	16	95.9	3.7	1.8	0.4	4.9	0.7	31.8	2.4	41.2	3.7	56.8	2.9
<i>Colobus polykomos</i>	21	131.7	5.9	1.7	0.3	4.5	0.5	20.0	1.6	35.5	3.0	63.3	2.9
<i>Lophocebus albigena</i>	25	99.0	3.4	1.8	0.4	9.1	0.7	32.2	1.7	47.6	3.2	61.7	2.1
<i>Macaca fascicularis</i>	20	88.4	2.4	0.9	0.2	6.5	0.7	37.6	2.6	50.6	2.7	59.8	1.9
<i>Nasalis larvatus</i>	15	141.2	8.8	0.4	0.2	3.8	1.0	21.7	2.2	25.9	3.1	57.0	3.0
<i>Papio anubis</i>	27	102.6	3.9	1.7	0.3	11.2	1.0	24.7	1.7	41.5	4.0	65.0	1.9
<i>P. cynocephalus</i>	20	111.0	7.0	1.6	0.3	7.3	0.8	25.5	1.4	40.8	3.8	62.1	2.5
<i>P. hamadryas</i>	9	102.5	9.7	1.6	0.6	7.8	1.5	28.0	2.1	43.3	7.2	61.4	2.5
<i>Theropithecus gelada</i>	9	123.2	13.1	1.2	0.4	4.0	1.0	21.6	2.4	8.7	1.8	33.6	3.4
<i>Mesopithecus delsoni</i>	3	83.0	7.0	0.7	0.3	8.7	2.2	26.7	3.2	43.0	7.5	64.4	7.2
RZO	3	83.0	7.0	0.7	0.3	8.7	2.2	26.7	3.2	43.0	7.5	64.4	7.2
<i>M. delsoni/pentelicus</i>	13	98.9	3.4	1.2	0.3	6.5	0.8	31.8	2.6	40.5	4.6	57.8	3.6
HD	6	105.6	4.9	1.5	0.5	6.8	1.3	29.2	4.3	40.2	7.1	59.4	6.0
PER	4	91.4	3.9	0.8	0.5	6.5	1.9	36.8	4.8	42.5	11.8	54.7	8.3
VTK	3	95.5	7.8	1.2	0.4	5.7	0.7	30.3	4.1	38.7	2.4	58.8	3.6
<i>M. pentelicus</i>	41	110.3	4.1	1.4	0.2	5.4	0.4	28.3	1.4	40.4	2.4	59.7	1.8
PIK	30	113.8	5.0	1.5	0.2	5.3	0.5	27.5	1.6	39.7	2.9	59.5	2.2
K	11	100.8	6.2	1.1	0.4	5.8	0.9	30.6	3.0	42.4	4.1	60.1	3.0

Ungar *et al.* 2008). The protocol of Merceron *et al.* (2005b) is here considered (see also Merceron *et al.* 2004, 2007). Data were collected on the dental facet 9, located on the lingual protocone facet for upper molars and on the buccal hypoconid facet for the lower molars (Kay & Hiiemae 1974; Maier 1977). All microwear scars crossing a 0.09 mm^2 ($300 \times 300 \mu\text{m}$) area using Optimas v. 6.2 image analysis software (Media Cybernetics) are quantified. The pits are clearly distinguishable from scratches; however, the distinction between elongated pits and short wide scratches may be unreliable. Microwear scars are then defined as pits or scratches as follows: pits have a width to length ratio greater than $\frac{1}{4}$, and scratches have a lower ratio (Grine 1986). Using Optimas v. 6.2, the pits are marked with a dot and the scratches with a line which is automatically measured as the “length of scratch” (Ls). After counting the number of pits (Np) and

the number of scratches (Ns), the microwear scars are assigned to a category depending on their size (length of major axis for pits and width for scratches). Subsequently, the numbers of wide scratches (Nws; width $> 15 \mu\text{m}$), fine scratches (Nfs; width $< 15 \mu\text{m}$), large pits (Nlp; major axis $> 15 \mu\text{m}$), and small pits (Nsp; major axis $< 15 \mu\text{m}$) are determined. The percentage of pits ($\text{Pp} = 100 \cdot \text{Np} / [\text{Np} + \text{Ns}]$) is then computed (Table 2).

The data is here investigated through the combination of a Principal Component Analysis (PCA hereafter) and analyses of variance. The PCA framework is built with extant specimens and raw data. Then, fossil specimens are inserted as supplementary data and therefore do not interfere with the model. The PCA generates six independent new variables based on the six initial variables of microwear pattern: Nfs, Nsp, Nlp, Nws, Ls and Pp (Tables 3; 4). In order to support interpretations, the inter- and intra-specific

TABLE 3. — Results of principal component analysis of dental micro-wear pattern of nine extant species of cercopithecid. Eigenvalue and percentage of the total variance for each component.

Component	Eigenvalues	% Total variance
1	2.31	38.53
2	1.37	22.77
3	1.02	17.01
4	0.72	12.01
5	0.51	8.51
6	0.07	1.18

differences in distribution along the new computed variables (components) are tested through analyses of variance (Tables 5; 6). The sources of variation are then determined by the combination of a Tukey's Honest Significant Differences test with a Fischer's Least Significant Differences test; the latter being less conservative than the former (Table 7). A rank transformation is conducted before each set of analyses to avoid violations of parametric test assumptions (Conover & Iman 1980; Sokal & Rohlf 1998).

RESULTS

The graphic distribution of the extant and extinct cercopithecids through PCA is given in Figure 1. Along the first component (38.53 % of the total variance), the distribution of the specimens is mainly controlled by the positive weight of the variable Ls (length of scratch) and the negative ones of Nsp, Nlp, and Pp (number of small pits, number of large pits, percentage of pits, respectively, Fig. 1; Tables 3; 4). The variable Nfs (number of fine scratches, and the couple Pp (percentage of pits) and Ls (length of scratch) in a lesser extent, contribute to the spread of the extant specimens along the second component (22.77 % of the total variance; Fig. 1; Tables 3; 4). The spread of specimens along the third component (17.01 % of the total variance) is controlled by the variable Nws (number of wide scratches, Tables 3; 4). According to the Kaiser' criterion, the drop in percentage of the total variance expressed from the third to the next eigenvalues allow us to disregard coordinates from the fourth component (Tables 3; 4) (Kaiser 1960).

EXTANT SPECIES

Along the first component, there is a trend from *Theropithecus gelada*, a grass-eater, to extant colobines (*Nasalis larvatus* and *Colobus polykomos* (Zimmermann, 1780)) highly involved in folivory, up to a cluster of cercopithecids with low coordinates (Fig. 1). The latter taxa display various feeding habits including leaves, fruits, seeds, and even underground vegetal parts. These differences in the distribution of the specimens are significantly supported (Tables 5-7) and are due to the variation of the variables Nsp, Nlp, Pp, and Ls (Tables 2; 7; Fig. 2). Along the second component there is a trend from the two colobines (*N. larvatus* and *C. polykomos*) to *Macaca fascicularis* (Raffles, 1821); the former ones have fewer fine scratches than the cercopithecid (Tables 2; 7; Fig. 2A-D). This differential spread between extant species along the second axis is significantly supported (Tables 5-7; Fig. 1). As mentioned above, the spread along the third component is mainly controlled by the variable Nws. This variable displays high variability for most of the species (Table 2), resulting in very few significant differences between species. In fact, *N. larvatus* is the only taxon which significantly differs from others.

MESOPITHECUS VERSUS EXTANT SPECIES

The three *Mesopithecus* samples (*M. delsoni*, *M. delsoni/pentelicus*, and *M. pentelicus*) plot far from *T. gelada* and their two extant relatives, *N. larvatus* and *C. polykomos* (Tables 2; 7; Fig. 1). Such distribution is due to a heavy pitting (Table 2; Fig. 2). Indeed, the distribution of the *Mesopithecus* samples through the PCA supports affinities with cercopithecids involved in frugivory, in seed predation or in a generalist diet. It should also be noted here that no significant difference is detected between the *Mesopithecus* samples on one hand and *Chlorocebus aethiops* (Linnaeus, 1758) and *Papio hamadryas* (Linnaeus, 1758) on the other hand. *Chlorocebus aethiops* is a semi-terrestrial cercopithecine foraging on fruits, leaves, seeds and animal prey (Nakawaga 2003; Rowe 1996 and citations therein). The second is a terrestrial monkey consuming various items from the ground such as grass and tubers.

TABLE 4. — Results of principal components analysis of dental microwear pattern of nine extant species of cercopithecoid. Communities r and square communities r^2 between variables and axis. Abbreviations: see text.

Component Variables	1		2		3		4		5		6	
	r	r^2										
Ls	0.676	0.458	0.443	0.196	-0.120	0.014	0.119	0.014	-0.564	0.318	0.013	0.000
Nws	0.085	0.007	-0.091	0.008	-0.973	0.947	0.150	0.022	0.123	0.015	0.012	0.000
Nlp	-0.644	0.415	0.105	0.011	-0.242	0.059	-0.682	0.465	-0.222	0.049	-0.030	0.001
Pp	-0.804	0.647	0.531	0.282	0.007	0.000	0.197	0.039	0.003	0.000	0.180	0.033
Nfs	-0.175	0.031	-0.931	0.867	0.016	0.000	0.057	0.003	-0.294	0.086	0.112	0.013
Nsp	-0.869	0.755	-0.045	0.002	-0.018	0.000	0.420	0.176	-0.205	0.042	-0.156	0.024

TABLE 5. — Results of inter-specific (including extant and extinct cercopithecoids) analyses of variance. Coordinates were rank-transformed before running analysis.

	df	Component 1				Component 2				Component 3			
		SS	MS	F	p	SS	MS	F	p	SS	MS	F	p
Effect	11	237 698	21609	7.0158	< 0.001	212 867	19352	6.0473	< 0.001	88 941	8086	2.1285	0.019
Error	207	637 572	3080			662 403	3200			786 329	3799		
Total	218	875 270				875 270				875 270			

TABLE 6. — Results of intra-specific analyses of variance. Intra-specific differences are investigated for *M. pentelicus* between the populations from Pikermi and Kalimantsi. Coordinates were rank-transformed before running analysis.

df	Component 1				Component 2				Component 3				
	SS	MS	F	p	SS	MS	F	p	SS	MS	F	p	
Effect	1	161.02	161.02	1.1256	0.295	127.22	127.22	0.8840	0.353	127.22	127.22	0.8840	0.353
Error	39	5578.98	143.05			5612.78	143.92			5612.78	143.92		
Total	40	5740.00				5740.00				5740.00			

MESOPITHECUS VERSUS MESOPITHECUS

There is no significant difference between the distributions of the three *Mesopithecus* samples. This likely supports similar feeding habits between these three forms (Tables 2; 5-7; Fig. 2). The intra-specific analysis does not detect any significant difference between the two samples of *M. pentelicus* (Bulgaria versus Pikermi; Tables 2; 5; 6).

DISCUSSION

The paleobiology of *Mesopithecus* is still under debate. As mentioned above, the colobines are highly involved in folivory. Even in the case of *Semnopithecus*, a terrestrial colobine, leaves con-

tribute more than 70 % to its diet (Dela 2007; Sayers & Norconk 2008). So, with the exception of the latter species, most of the modern colobines are arboreal forest dwellers (Rowe 1996). *Mesopithecus* postcrania do not support an arboreal mode of locomotion. In fact, the calcaneal morphology of *Mesopithecus* would indicate a semi-terrestrial mode of locomotion (Youlatos 2003). However, the distal part of the hindlimb does not seem to be so discriminating since a recent thorough analysis concludes that depending on statistical protocols, the metric data of the calcaneum may depict *Mesopithecus* as an arboreal monkey as well (Escarguel 2005). Anyway, the postcranial morphology and proportions in comparison to the extant cercopithecids indicate at least a semi-terrestrial mode of

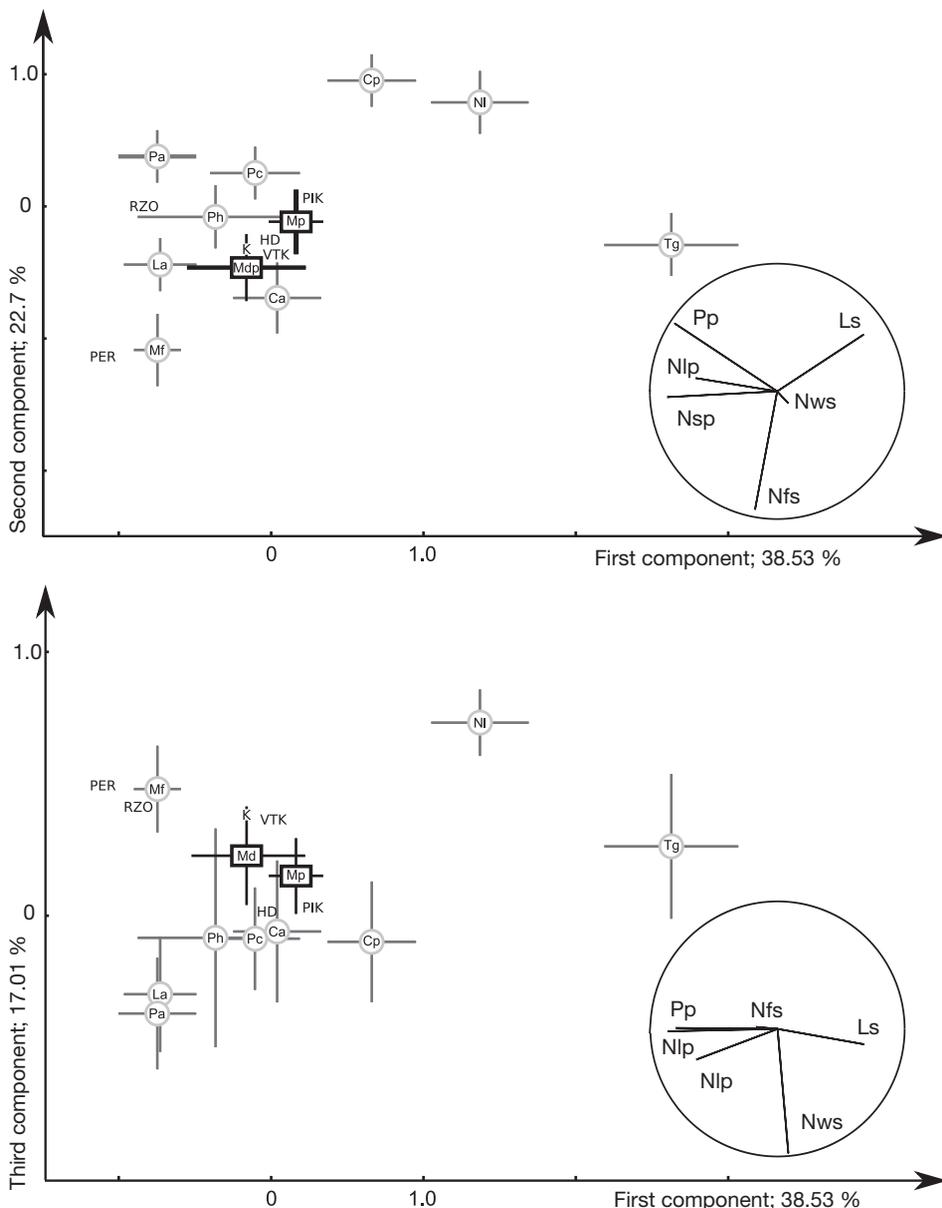


FIG.1. — Distribution (mean and standard error of the mean) of extant and extinct cercopithecids along the first and second components of the Principal Component Analysis. The specimens of *Mesopithecus* Wagner, 1839 are included as supplementary data. Extant species: **Ca**, *Chlorocebus aethiops* (Linnaeus, 1758); **Cp**, *Colobus polykomos* (Zimmermann, 1780); **La**, *Lophocebus albigena* (Gray, 1850); **Mf**, *Macaca fascicularis* (Raffles, 1821); **NI**, *Nasalis larvatus* (Wurmb, 1787); **Pa**, *Papio anubis* (Lesson, 1827); **Pc**, *Papio cynocephalus* (Linnaeus, 1766); **Ph**, *Papio hamadryas* (Linnaeus, 1758); **Tg**, *Theropithecus gelada* (Rüppell, 1835). Fossil specimens are plotted according to where they were unearthed: **HD**, Hadjidimovo 1 (Bulgaria); **K**, Kalimantsi (Bulgaria); **PER**, Perivolaki (Greece); **PIK**, Pikermi (Greece); **RZO**, Ravin des Zouaves 5 (Greece); **VTK**, Vathylakkos 2 (Greece). Also, all specimens belonging to *M. delsoni/pentelicus* or to *M. pentelicus* Wagner, 1839 symbolized as **Mdp** and **Mp**, respectively.

TABLE 7. — Results on pairwise comparisons. Significance at $\alpha < 0.05$ is indicated in normal font for the Fisher's Least Significant Difference test and in bold font for both Tukey's Honest Significant Difference and Fisher's Least Significant Difference tests. Abbreviations along the first line refer to the initials of the genera and species mentioned on the first row.

	M. d	M. dp	M. p	Ch. a	C. p	L. a	M. f	N. l	P. a	P. c	P. h	T. g
<i>M. delsoni</i>												
<i>M. delsoni/pentelicus</i>												
<i>M. pentelicus</i>												
<i>C. aethiops</i>												
<i>C. polykomos</i>	C1	C2	C2	C2								
<i>L. albigena</i>		C1	C1	C1	C1, C2							
<i>M. fascicularis</i>		C1	C1, C2	C1	C1, C2	C3						
<i>N. larvatus</i>	C1	C1, C2	C1, C2, C3	C1, C2 , C3	C3	C1, C2 , C3	C1, C2					
<i>P. hanubis</i>		C2	C1	C1, C2	C1	C2	C2, C3	C1, C3				
<i>P. cynocephalus</i>		C2		C2	C2	C2	C2, C3	C1, C3				
<i>P. hamadryas</i>					C2		C2	C1, C2, C3				
<i>T. gelada</i>	C1	C1	C1	C1	C1, C2	C1	C1	C2	C1, C2	C1	C1	

locomotion (Gabis 1961; Szalay & Delson 1979; Zapfe 1991; Delson 1994; Koufos *et al.* 2003). *Mesopithecus* had therefore the opportunity to forage on trees and ground.

The presence of semi-terrestrial monkeys in Eastern Europe during Turolian agrees with the paleoenvironmental data. The carbon isotope signature in tooth enamel of herbivorous mammals excludes the presence of C4 grasslands in the Eastern Mediterranean (Bocherens *et al.* 1994; Quade *et al.* 1994, 1995; Zazzo *et al.* 2002; Merceron *et al.* 2006) whereas faunal analyses undoubtedly exclude closed-forested ecosystems (Bonis *et al.* 1992, 1999; Fortelius & Solounias 2000; Eronen & Rook 2004; Koufos 2006a, 2009, this volume; Koufos *et al.* 2006a, 2008; Spassov *et al.* 2006). The microwear analyses on the ungulates from several investigated localities of the Eastern Mediterranean point out a large spectrum of dietary habits from browse to graze amongst ruminants and equids. These studies suggest the existence of open areas displaying a rich herbaceous vegetal layer including graminoids and patches of trees and/or bushes (Solounias *et al.* 1999; Merceron *et al.* 2005a, 2006; Koufos *et al.*

2006a, 2008). Based on phytolith assemblages, the presence of C3 graminoids is attested in the region (Strömberg *et al.* 2007) thus restraining interpretations from isotope analyses (Bocherens *et al.* 1994; Quade *et al.* 1994) which linked the lack of C4 plants to the dominance of forested habitats. Although the different environmental indicators are in accordance with the locomotion mode of *Mesopithecus*, they cannot conclude on its feeding preferences since fruit-dominated and leaf-dominated primates may share the same environment exploiting different ecological niches (Rowe 1996).

As Benefit (2000) reports, the bilophodonty of the earliest cercopithecoids was initially wrongly interpreted as an adaptation to a leaf-dominated diet. Since then, bilophodonty has been interpreted as a response to the need for a more efficient grinding mechanism to chew fruits (Lambert *et al.* 2004). Benefit (2000) also supports the last hypothesis since the shearing molar crests of *Mesopithecus* are lower than in the extant colobines suggesting a diet rich in fruits. Based on the present results, the feeding habits of the "three" *Mesopithecus* are alike. They cannot be depicted as leaf-eaters. Seeds,

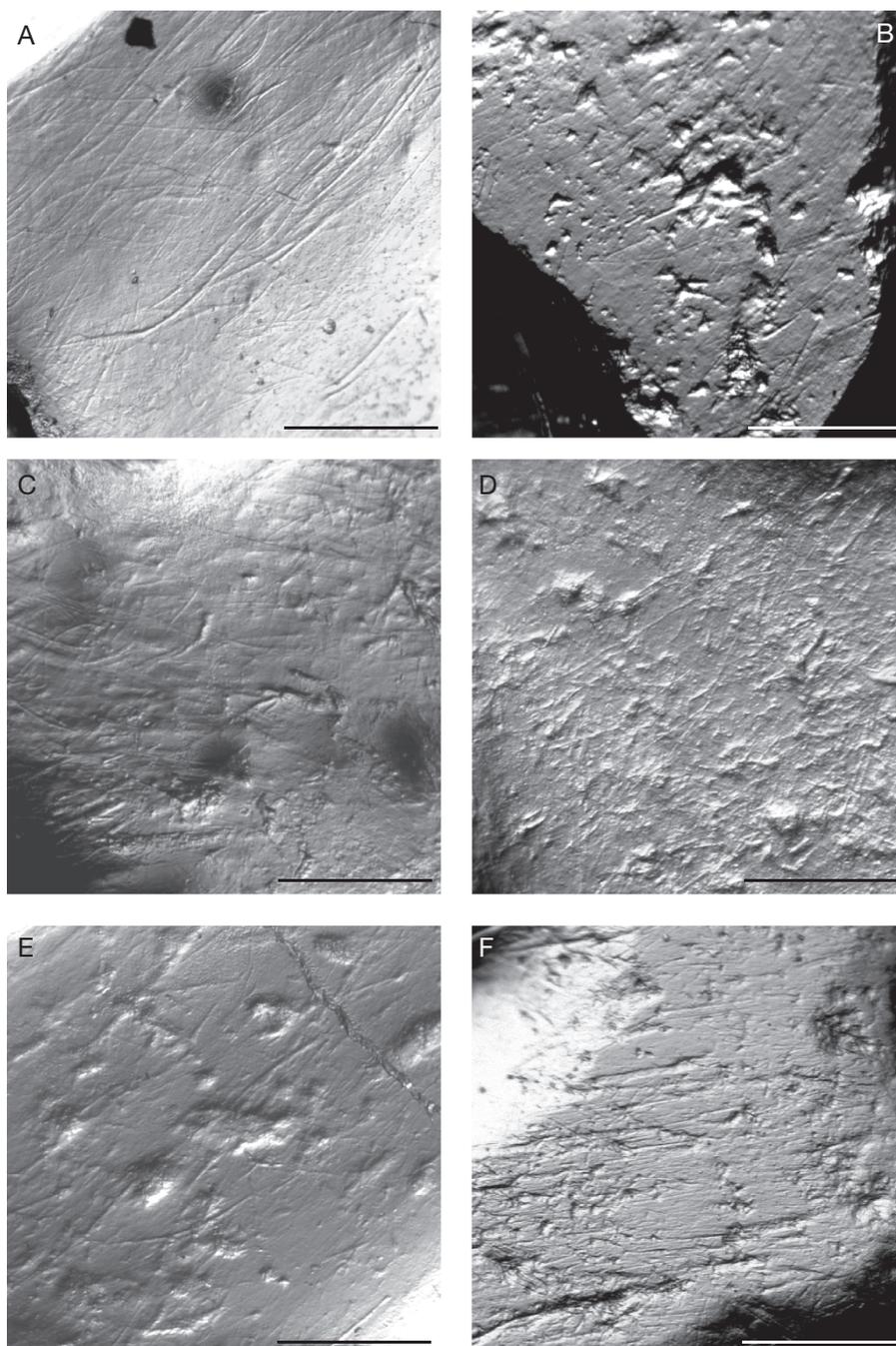


FIG. 2. — Dental facets nine of second molars for extant and extinct cercopithecid displaying dental microwear scars: **A**, *Nasalis larvatus* (Wurmb, 1787) (ZSM-1907-4023); **B**, *Lophocebus albigena* (Gray, 1850) (RMCA-83-006-0276); **C**, *Chlorocebus aethiops* (Linnaeus, 1758) (MNHN-CG-1972-309); **D**, *Papio hamadryas hamadryas* Linnaeus, 1758 (SNG-15831); **E**, *Mesopithecus delsoni/pentelicus* (HD-340); **F**, *M. pentelicus* (NHMW-1998z77-14). Scale bars: 300 μ m.

fruits or even underground vegetal parts were some of the main components in their diet. However, the ingestion of such hard/brittle or tough items does not exclude soft fruits and foliage in their diet since the cercopithecoid-like molars display two functionalities: high crests acting as blades for shearing and lophs as wedges to break hard items (Lucas & Teaford 1994).

Both mode of locomotion and feeding habits of *Mesopithecus* are in agreement with its wide dispersion in Western Eurasia (with the exception of Anatolia and Iberic peninsula) suggesting opportunistic feeding habits. Most of the extant colobine taxa are restricted to forested habitats and to folivory whereas *Mesopithecus* was widely dispersed in different provinces with various environmental and climatic conditions. As mentioned above, *Mesopithecus* (*M. delsoni*, *M. delsoni/pentelicus*, and *M. pentelicus*) probably had feeding preferences similar to *C. aethiops* and *P. hamadryas*. Actually, considering the post-cranial anatomy and the mode of locomotion, the similarities are greater with *C. aethiops*. Another similarity between this modern monkey and *Mesopithecus* is their wide range of geographic distribution. In fact, the vervet monkey occupies a large spectrum of habitats (swamps, riverine forests, savanna woodlands or even scrublands merging the dry Sahel) from Senegal to South Africa and feeds on fruits, seeds, and leaves (Rowe 1996).

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