

N. Jb. Geol. Paläont. Mh.	1997, H. 5	255-265	Stuttgart, Mai 1997
---------------------------	------------	---------	---------------------

New material of *Mesopithecus* (Mammalia,  
Cercopithecidae) from the late Miocene of  
Macedonia, Greece

By Louis de Bonis, Poitiers, Genevieve Bouvrain, Paris,  
Denis Geraads, Paris, and George D. Koufos, Thessaloniki

With 3 figures and 1 table in the text

DE BONIS, L.; BOUVRAIN, G.; GERAADS, D. & KOUFOS, G. D. (1997): New material of *Mesopithecus* (Mammalia, Cercopithecidae) from the late Miocene of Macedonia, Greece. - N. Jb. Geol. Paläont. Mh., 1997 (5): 255-265; Stuttgart.

**Abstract:** New material of *Mesopithecus*, including two cranial parts, is described from the late Miocene (early Turolian) locality of "Vathylakkos 2" (VTK) of the lower Axios valley, Macedonia, Greece. Its morphological characters are similar to those of the type material of *Mesopithecus pentelicus* from Pikermi. However the size of the lower and upper molars either reaches the maximal values of *M. pentelicus* or exceeds them indicating similarities with *M. delsoni*. Thus the VTK material of *Mesopithecus* is referred to *M. cf. pentelicus*. The biostratigraphical significance of the genus, as well as its palaeoecology are discussed.

**Zusammenfassung:** Neue *Mesopithecus*-Reste aus dem Obermiozän von "Vathylakkos-2" stimmen in ihren Merkmalen mit denen von *Mesopithecus pentelicus* aus Pikermi überein. Jedoch sind die oberen Molaren größer und erinnern in ihren Dimensionen an *M. delsoni*. Da nicht alle Merkmale erkennbar sind, wird das neue Material als *M. cf. pentelicus* bezeichnet. Die Gattung wird auf ihre biostratigraphische und paläo-ökologische Bedeutung hin betrachtet.

### Introduction

Several primate remains, hominoids or cercopithecoids, have been recovered from the late Miocene localities of the lower Axios valley (Macedonia, Greece) but until now, they never occur together at the same level. The late Miocene deposits of Axios valley have been divided in three formations:

- a) Nea Messimvria Formation (late Vallesian),
- b) Vathylakkos Formation (early Turolian), and
- c) Dytiko Formation (late Turolian), (BONIS et al. 1988).

0028-3630/97/1997-0255 \$ 2.75

© 1997 E. Schweizerbart'sche Verlagsbuchhandlung, D-70176 Stuttgart

The hominoid *Ouranopithecus macedoniensis* has been found only in Nea Messimvria Formation. Until now cercopithecoid remains are known from the lower level of the Vathylakkos Formation with *Mesopithecus delsoni* and from the Dytiko Formation with *Mesopithecus* cf. *pentelicus*, *Mesopithecus* aff. *pentelicus* and *Mesopithecus* cf. *monspessulanus* (BONIS et al. 1990). Some mandibular remains identified as *Mesopithecus pentelicus* are also referred from the localities "Ravin de Vatilük" and "Ravin X" (ARAMBOURG & PIVETEAU 1929), but unfortunately we could not find them in the Muséum National d'Histoire Naturelle of Paris (MNHN). In the wider area of Macedonia (Greece) *M. pentelicus* was found in the locality of Maramena, Strymon basin (KULLMER & DOUKAS 1995). In addition the cercopithecoid *Dolichopithecus rusciniensis* was recognized in the Ruscinian locality of "Megalo Emvolon", near Thessaloniki (KOUFOS et al. 1991). Some remains of *Mesopithecus* and *Dolichopithecus* are referred from the Ruscinian locality of Dorkovo, Bulgaria (THOMAS et al. 1986).

New material of cercopithecoids has recently been unearthed at the locality "Vathylakkos 2" (VTK) situated in the core of the Vathylakkos Formation. So this material can fill the gap in the cercopithecoid succession of the Axios valley. The material belongs to the collection of the Laboratory of Geology and Palaeontology, University of Thessaloniki (LGPUT) and of the MNHN of Paris (Brailon collection). The Brailon collection was offered to MNHN of Paris by BRAILLON, a medical doctor, who collected fossils from various countries, and nobody knows when he collected the fossils in Greece.

#### Systematic Palaeontology

Order: Primates LINNEAUS, 1758

Suborder: Anthroipoidea MIVART, 1864

Infraorder: Catarrhini GEOFFROY, 1812

Superfamily: Cercopithecoidea GRAY, 1821

Family: Cercopithecidae GRAY, 1821

Subfamily: Colobinae JERDON, 1867

Genus: *Mesopithecus* WAGNER, 1839

*Mesopithecus* cf. *M. pentelicus* WAGNER, 1839

Locality: "Vathylakkos-2", VTK, lower Axios valley, Macedonia, Greece.

Age: Early Turolian, MN 11 (late Miocene).

Material: Skull, VTK-56 (LGPUT collection); posterior part of the skull, unnumb. (MNHN); right maxilla with M<sup>1</sup>-M<sup>3</sup>, unnumb. (MNHN); right upper canine, unnumb. (MNHN); right I<sub>2</sub>, unnumb.

(MNHN); left lower canine, unnumb. (MNHN); right lower canine, unnumb. (MNHN); left P<sub>4</sub>, unnumb. (MNHN); right M<sub>1</sub>, unnumb. (MNHN); left M<sub>1</sub>, unnumb. (MNHN); left M<sub>2</sub>, unnumb. (MNHN); right M<sub>2</sub>, unnumb. (MNHN).

**Description:** The skull VTK-56 (Fig. 1) is crushed and the facial region is strongly damaged; the cranial roof and the maxilla with both P<sup>3</sup>-M<sup>3</sup> rows are well preserved. The orbits are partially preserved. The supraorbital torus is small and it is divided into two parts by a depression in the middle. There is a slight depression behind the supraorbital torus but

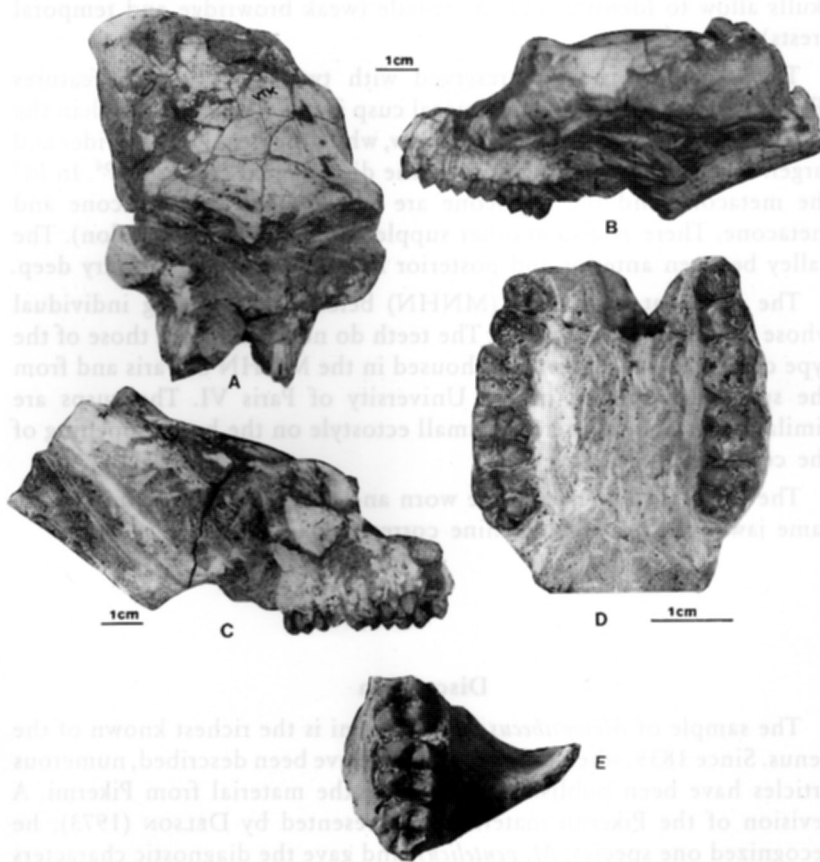


Fig. 1. *Mesopithecus* cf. *M. pentelicus*, "Vathylakkos 2" (VTK), late Miocene (early Turolian), Macedonia, Greece.

A-D: Skull, VTK-56 (Collection of the University of Thessaloniki). A: dorsal view; B: left lateral view; C: right lateral view; D: occlusal view of the maxilla;

E: Maxilla with M<sup>1</sup>-M<sup>3</sup>, MNHN unnumb. (BRAILLON collection).

this may be due to the deformation of the skull. The orbits are compressed dorsoventrally and their dimensions cannot be given. The interorbital distance can be estimated as being between 10–12 mm. The zygomatic arches are strong and they begin above the first lobe of  $M^2$ . The temporal crests are weakly developed. The palate is parabolic, wide and deep. The anterior border of the choanae are situated at the level of the mesial border of  $M^3$ .

The fragment of skull of the MNHN lacks the face as well as the basal portion. The supra-orbital torus is weak. The interorbital distance is relatively short. The temporal crests are weak. The characters of these two skulls allow to identify them as female (weak browridge and temporal crests).

The dentition is well preserved with typically colobine features (Fig. 1). On the premolars, the buccal cusp is remarkably higher than the lingual one. The mesial fovea is narrow, while the distal one is wider and larger. There is a small cingulum in the distolingual corner of  $P^4$ . In  $M^3$  the metacone and the hypocone are smaller than the paracone and metacone. There is also another supplementary fifth cusp (talon). The valley between anterior and posterior lobe of the molars is very deep.

The fragment of maxilla (MNHN) belongs to a young individual whose  $M^3$  is not fully erupted. The teeth do not differ from those of the type collection of *M. pentelicus* housed in the MNHN of Paris and from the specimens housed in the University of Paris VI. The cusps are similarly crested and there is a small ectostyle on the buccal opening of the central valley.

The available lower teeth are worn and they probably belong to the same jaw. The size of the canine corresponds to a male.

### Discussion

The sample of *Mesopithecus* from Pikermi is the richest known of the genus. Since 1839, when the first remains have been described, numerous articles have been published, describing the material from Pikermi. A revision of the Pikermi material was presented by DELSON (1973); he recognized one species, *M. pentelicus*, and gave the diagnostic characters of the genus and species. In the description of the *Mesopithecus* material from the lower Axios valley (Macedonia, Greece) a generic and specific diagnosis is given (BONIS et al. 1990). In the same year HOHENNEGER & ZAPFE (1990) published a biometric study of *Mesopithecus*. More recently ZAPFE (1991) revised all the material of *Mesopithecus* from Pikermi and

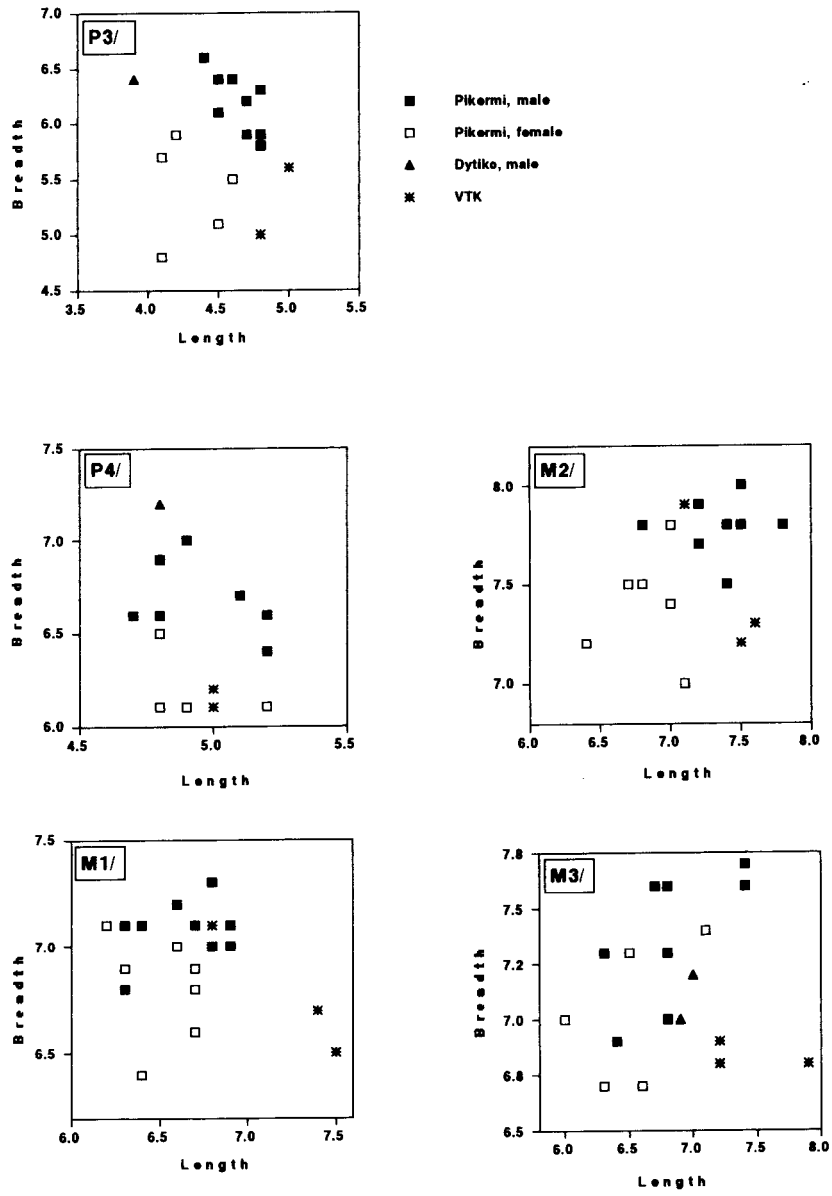


Fig. 2. *Mesopithecus*. Bivariate plot of the upper cheek teeth dimensions.

from the new locality of Chomateres, found near the old site. He determined two subspecies *M. p. pentelicus* and *M. p. microdon*, giving also diagnoses for the genus, species and subspecies.

The new cranial material from VTK is quite similar to the Pikermi one identified as *M. p. pentelicus* ZAPFE 1991. The frontal part in all these skulls is similar. The depression behind the supraorbital torus and the glabella seems to be slightly deeper than those of the Pikermi skulls. However the deformation of the cranial roof possibly accounts for these differences. The dental morphology is also quite similar to that of the Pikermi material. However the metrical comparison of the teeth leads to ambiguous conclusions. The premolars do not exceed the size of the larger specimens of Pikermi material (Fig. 2) while the molars can reach the size of the larger specimens of Pikermi or can be even larger (Fig. 2). For the lower molars  $M_1$  does not differ from the mean of the Pikermi sample and  $M_2$  fits better with the larger specimens of Pikermi, situated closer to *M. delsoni* (Fig. 3).

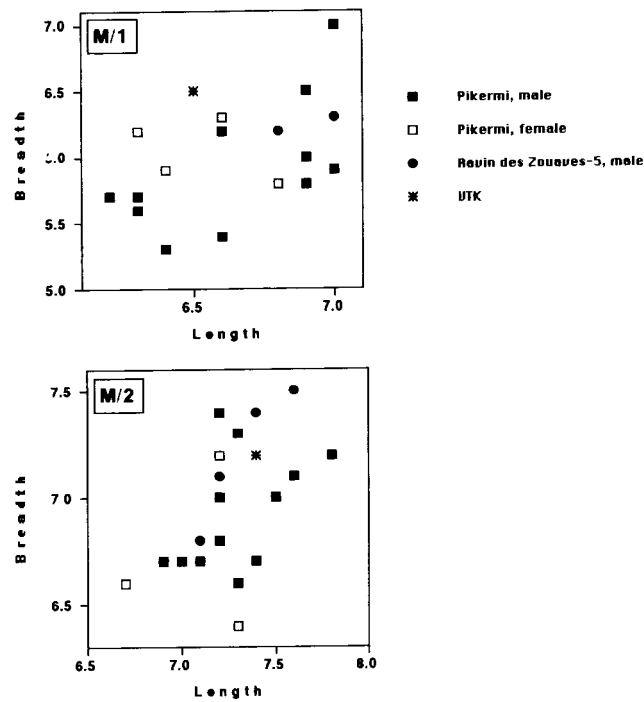


Fig. 3. *Mesopithecus*. Bivariate plot of  $M_1$  and  $M_2$  dimensions.

Another subspecies, *M. p. microdon*, has also been described by ZAPPE (1991) for one mandible coming from the site of Chomateres near Pikermi. This subspecies is smaller than the nominal one and so it differs clearly from our material.

Two male skulls of *Mesopithecus* have been described from the Dytiko localities of Axios valley as *M. aff. pentelicus* (BONIS et al. 1990). One of them (DKO-38) is well preserved and can be compared with the studied one. The supraorbital torus is thicker and more pronounced than that of our material. The depression behind the supraorbital torus is also deeper, while the temporal crests are thicker than those of the studied skull. These differences could be due to sexual dimorphism. The interorbital distance seems to be similar in these skulls, while the molar row is slightly longer in the Vathylakkos material than in DKO-38 (22 mm versus 18.6 mm respectively).

A new species, *M. delsoni*, was described for some mandibular remains found in the locality "Ravin des Zouaves-5" (RZO) of the Axios valley. The species differs from *M. pentelicus* by its larger size, deeper mandibular corpus, thicker inferior transverse torus, less inclined alveolar planum, flattened anterior face of the symphysis, large honing facet of P<sub>3</sub>, weaker and rounded metalophid of P<sub>3</sub> and well developed hypoconulid of M<sub>3</sub> (BONIS et al. 1990). A comparison with the studied material is difficult because there is no mandibular corpus in the VTK material. Nevertheless,

Table 1. *Mesopithecus* cf. *M. pentelicus*, "Vathylakkos 2" (VTK); late Miocene (early Turolian), Macedonia, Greece. Measurements of the upper and lower cheek teeth. Abbreviations: L = Length, b<sub>1</sub> = anterior breadth, b<sub>2</sub> = posterior breadth, l = left, r = right.

			p <sup>3</sup>	p <sup>4</sup>	M <sup>1</sup>	M <sup>2</sup>	M <sup>3</sup>	p <sup>3</sup> , p <sup>4</sup>	M <sup>1</sup> , M <sup>3</sup>	p <sup>3</sup> , M <sup>3</sup>
LGPUT VTK-56	l	L	5.0	5.0	7.4	7.6	7.2	10.0	22.0	31.7
		b <sub>1</sub>	5.6	5.2	6.7	7.3	6.9			
		b <sub>2</sub>			6.5	7.0	5.8			
	r	L	4.8	5.0	7.5	7.5	7.2	9.9	22.2	31.5
		b <sub>1</sub>	5.7	6.1	6.5	7.2	6.9			
		b <sub>2</sub>			6.0	6.8	5.7			
MNHN unumb.	r	L			[6.8]	7.1	7.9		[22.0]	
		b <sub>1</sub>				7.3	[6.4]			
		b <sub>2</sub>			7.1	7.9	[6.8]			
			P <sub>3</sub>	P <sub>4</sub>	M <sub>1</sub>	M <sub>2</sub>	M <sub>3</sub>			
MNHN unumb.	l	L			6.5					
		b <sub>1</sub>			[5.6]					
		b <sub>2</sub>			6.5					
MNHN unumb.	r	L				7.4				
		b <sub>1</sub>				6.7				
		b <sub>2</sub>				7.2				

the large size of most of the teeth, especially  $M^2$  and  $M^3$  (Fig. 2D, E) could be convenient for *M. delsoni*. Concerning this latter species ZAPFE (1991) refers that the possibility for the holotype to be a male specimen of *M. pentelicus* cannot be excluded. But, in fact, we have, in the type locality "Ravin des Zouaves-5" (RZO), three mandibles (2 males and 1 female) which show the same characteristics. Any important deformation must be excluded and the shape of the anterior part of the mandibles, as well as of the symphysis are clearly different from those of *M. pentelicus*. In addition, the index height of the mandibular corpus/length of the tooth row, following ZAPFE (1991), is 48.3 to 62.3 for *M. pentelicus pentelicus* of Pikermi and 64.4 for *M. p. microdon*. The same index reaches 66 for *M. delsoni* despite the larger size of the teeth.

Another species is *M. monspessulanus*, distinguished from *M. pentelicus* by its smaller size and the slightly narrower lower molars. The known material of *M. monspessulanus* consists mainly of mandibular remains and isolated teeth; only five badly preserved upper teeth are known (DELSON 1973). Thus a comparison with the studied skull is quite difficult. But the small size of this species does not fit at all the worn isolated lower teeth of "Vathylakkos-2".

The material from Vathylakkos is quite incomplete and, from the above comparisons, it could be referred to *M. pentelicus*, as well as to *M. delsoni*. Thus at the moment it is better to refer it to *Mesopithecus* cf. *M. pentelicus*. Since the excavations in Axios valley are continuing this identification can be changed if new material will allow better comparisons and determinations.

### Conclusion

The late Miocene deposits of the lower Axios valley have been dated in former articles. The faunal data of the Vathylakkos Fm, included the locality "Vathylakkos 2" (VTK), suggest an early Turolian age, MN 11 (BONIS et al. 1988, KOUFOS 1990). Moreover magnetostratigraphic data from the locality of "Prochoma 1" (PXM), also included in the Vathylakkos Fm, suggest an age between 9.2–9.6 Ma, corresponding to the early Turolian (KONDOPOULOU et al. 1992). According to these datings the studied skull belongs to the early Turolian forms of *Mesopithecus*.

Finally the localities of Macedonia, Greece, including *Mesopithecus*, are the following:

a) "Ravin des Zouaves-5" (RZO). The large-sized species *M. delsoni* has been found in this locality. The locality is dated as latest Vallesian – early Turolian and it is considered as older than Pikermi (BONIS et al. 1986, Koufos 1990).



- b) "Vathylakkos 2" (VTK). A medium-sized *M. cf. pentelicus* is described from this locality; the same species is also described from the localities "Ravin de Vatilük" and "Ravin X" (ARAMBOURG & PIVETEAU 1929). All these localities were dated to the early Turolian (MN 11) and they are considered older than Pikermi and slightly younger than RZO (BONIS et al. 1988, KOUFOS 1990).
- c) "Dytiko" localities. A medium-sized form similar to *M. pentelicus* has been recognized in the localities of Dytiko. Another small-sized form similar to *M. monspessulanus* is also referred from these localities (BONIS et al. 1990). The localities of Dytiko have been dated to late Turolian (MN 13) and they are considered younger than Pikermi (BONIS et al. 1988, KOUFOS 1990).
- d) "Maramena" (MA). Recently the presence of *M. pentelicus* is recorded in the locality of Maramena (Serres basin) dated to Turolian/Ruscinian or MN 13/MN 14 (KULLMER & DOUKAS 1995). Only milk teeth are described in this article and thus a comparison with the Axios valley material is impossible.

The genus *Mesopithecus* is represented by different species through the late Miocene (Turolian) of Macedonia (Greece) in different chronological levels (KOUFOS 1993). In the future better material will allow a clear identification of these species and the genus *Mesopithecus* will offer more in the biochronology of the Turolian of Greece.

The postcranial skeleton of *Mesopithecus* is characterized by mixed features. Some morphological characters (robustness of the long bones, joint morphology of the elbow, straight ulnar shaft, more posteromedially reflected medial epicondyle of humerus, and stout phalanges) are indicative for a terrestrial adaptation. On the other hand, characters such as the deep supraradial fossa on the distal humerus, the shallow radial notch on the ulna, the short tarsus and the moderately long posterior phalanges suggest an arboreal environment (SZALAY & DELSON 1979). Therefore, a semiterrestrial lifestyle has been proposed for *Mesopithecus* (DELSON 1973, 1975; SZALAY & DELSON 1979). In all localities *Mesopithecus* is always associated with an open (savanna) fauna, a fact that agrees with the semiterrestrial lifestyle of *Mesopithecus*.

The palaeoecological study of the lower Axios faunas has provided some more data, confirming the lifestyle of *Mesopithecus*. As it was referred above, *Mesopithecus* was found in the localities RZO, VTK (early Turolian) and in Dytiko localities (late Turolian). The factor analysis of the late Miocene faunas of Macedonia gave interesting results about the palaeoenvironment and the palaeoclimatic conditions in the area. The

Turolian faunas suggest an "open" savanna-like environment with some trees and shrubs; however along the river or near water points trees were also developed. The late Turolian faunas of Dytiko are always separated from the others in the factor analysis and suggest a more humid/forested character (presence of cervids and tragulids), while in RZO and Vathy-lakkos localities there are no cervids (BONIS et al. 1992).

In the Dytiko fauna a small-sized form similar to *M. monspessulanus* is present. SZALAY & DELSON (1979) have noted that the younger species of *Mesopithecus* at the end of Miocene beginning of the Pliocene (*M. monspessulanus*) are probably adapted to a more arboreal dwelling. This seems to fit well the palaeoecological conditions of the Axios valley.

### Acknowledgements

The excavations in Macedonia, Greece have been supported by L. S.B. Leakey Foundation, French CNRS and Collège de France. Many thanks to Prof. L. GINSBURG, Dr. S. SEN and Dr. D. GOUJET (Muséum National d'Histoire Naturelle, Paris) for access to collections, as well as for their help to find the old specimens.

### References

- ARAMBOURG, C. & PIVETEAU, J. J. (1929): Les Vertébrés du Pontien de Salonique. – Ann. Paléont., **18**: 59–138; Paris.
- BONIS, L. DE; BOUVRAIN, G. & KOUFOS, G. D. (1988): Late Miocene mammal localities of the lower Axios valley (Macedonia, Greece) and their stratigraphical significance. – Modern Geol., **13**: 141–147; London.
- BONIS, L. DE; BOUVRAIN, G.; GERAADS, D. & KOUFOS, G. D. (1990): New remains of *Mesopithecus* (Primates, Cercopithecidae) from the late Miocene of Macedonia with the description of a new species. – J. Vert. Paleont., **10**: 473–483; New York.
- (1992): Diversity and palaeoecology of Greek late Miocene mammalian faunas. – Pal., Pal., Pal., **91**: 99–121; Amsterdam.
- DELSON, E. (1973): Fossil colobine monkeys of the circum Mediterranean region and the evolutionary history of the Cercopithecidae (Primates, Mammalia). – Ph. D. dissertation, Columbia University, New York, 856 pp.
- (1975): Evolutionary history of the Cercopithecidae. [In:] SZALAY, F. (ed.): Approaches to Primate Palaeobiology. – Contrib. Primatol., **5**: 167–217; Basel.
- HOHENNEGER, J. & ZAPFE, H. (1990): Craniometric investigations on *Mesopithecus* in comparison with two recent colobines. – Beitr. Paläont. Österr., **16**: 111–143; Wien.

- KONDOPOULOU, D.; SEN, S.; KOUFOS, G. D. & BONIS, L. DE (1990): Magneto- and bio-stratigraphy of the late Miocene mammalian locality of Prochoma (Macedonia, Greece). – *Paleont. i Evolucio*, **24–25**: 135-139.
- KOUFOS, G. D. (1990): The hipparions of the lower Axios valley (Macedonia, Greece). Implications for the Neogene stratigraphy and the evolution of hipparions. [In:] LINDSAY, E., FAHLBUSCH, V. & MEIN, P. (eds.): *European Neogene Mammal Chronology*: 321–338; Plenum Press, New York.
- (1993): Review of the Neogene primates of Macedonia (Greece) and their biostratigraphic significance. [In:] Honorary volume for Prof. A. PANAGOS: 527–539; Athens.
- KOUFOS, G. D.; SYRIDES, G. E. & KOLIADIMOU, K. K. (1991): A Pliocene primate from Macedonia (Greece). – *Hum. Evol.*, **21**: 283–294; New York.
- KULLMER, O. & DOUKAS, K. (1995): The vertebrate locality Maramena (Macedonia, Greece) at the Turolian-Ruscinian boundary (Neogene). 6. The deciduous dentition of *Mesopithecus pentelicus* WAGNER (Primates, Mammalia). – *Münchner Geowiss. Abh.*, **28**: 65–74; München.
- SZALAY, F. & DELSON, E. (1979): *Evolutionary history of the Primates*. Academic Press, New York, 580 pp.
- THOMAS, H.; SPASSOV, N.; KOJUMGIEVA, E.; POIDEVIN, J.-L.; POPOV, V.; SEN, S.; TASSY, P. & VISSET, D. (1986): Résultats préliminaires de la première mission paléontologique franco-bulgare à Dorkovo (arrondissement de Pazardjik, Bulgarie). – *C. R. Acad. Sci. Paris*, **302**: 1037–1042; Paris.
- ZAPFE, H. (1991): *Mesopithecus pentelicus* WAGNER aus dem Turolien von Pikermi bei Athen, Odontologie und Osteologie. – *Neue Denkschr. Naturhist. Mus.*, **5**: 1–203; Wien.

Bei der Tübinger Schriftleitung eingegangen am 1. Juli 1996.  
Zum Druck angenommen am 19. Juli 1996.

Anschrift der Verfasser:

Prof. Dr. L. DE BONIS, Université de Poitiers, Laboratoire de Geobiologie, Biochronologie et Paléontologie Humaine, 40 av. du Recteur Pineau, F-86022 Poitiers;  
Drs. G. BOUVRAIN and D. GERAADS, Université Paris VI, Laboratoire de Paléontologie des Vertébrés et Paléontologie Humaine, 4 pl. Jussieu, F-75005 Paris; Prof. Dr. G. D. KOUFOS, Aristotle University of Thessaloniki, Laboratory of Geology and Palaeontology, GR-54006 Thessaloniki.