

NEW REMAINS OF *MESOPITHECUS* (PRIMATES, CERCOPITHECOIDEA) FROM THE LATE MIOCENE OF MACEDONIA (GREECE), WITH THE DESCRIPTION OF A NEW SPECIES

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ABSTRACT—Numerous remains of *Mesopithecus* have recently been recovered from the late Miocene mammalian localities of Macedonia, northern Greece. Three mandibles from the early Turolian are identified as *M. delsoni*, sp. nov., probably ancestral to *M. pentelicus* of Pikermi. Others, dated to the latest Turolian, differ from *M. pentelicus*, but most of the teeth are so worn that they must be identified as *Mesopithecus*, aff. *M. pentelicus*. A last set, coming also from the latest Turolian, could possibly be attributed to *Mesopithecus*, cf. *M. monspessulanus*. The evolution of the genus *Mesopithecus* can be used as a biostratigraphic tool in late Miocene continental deposits.

INTRODUCTION

The late Miocene continental deposits of the lower Axios valley (Macedonia, Greece) contain several fossiliferous localities which have yielded a rich vertebrate fauna (Bonis et al., 1986, 1987). A hominoid primate, *Ouranopithecus macedoniensis*, has been found in a Vallesian locality (Ravin de la Pluie), but some cercopithecoid remains (skulls, jaws, and limb bones) have also been unearthed from other sites: Ravin des Zouaves 5 (RZO), Dytiko 1 (DTK), Dytiko 2 (DIT), and Dytiko 3 (DKO). These sites date from the early Turolian (RZO) and from the late Turolian (DTK, DIT, and DKO). We identify these cercopithecoid remains as belonging to *Mesopithecus* Wagner, 1839 (see Appendix). Arambourg and Piveteau (1929) have reported the discovery of some *Mesopithecus* remains in the late Miocene of Macedonia from the localities of Vathylakkos and Ravin X, but we were unable to find these fossils in the collections of the Muséum National d'Histoire Naturelle, Paris; however, E. Delson was kind enough to send us measurements and photographs of the specimens.

SYSTEMATIC PALEONTOLOGY

Order PRIMATES Linnaeus, 1758
Suborder ANTHROPOIDEA Mivart, 1864
Infraorder CATARRHINI Geoffroy, 1812
Superfamily CERCOPITHECOIDEA Gray, 1821
Family CERCOPITHECIDAE Gray, 1821

Subfamily COLOBINAE Jerdon, 1867
MESOPITHECUS Wagner, 1839

The genus *Mesopithecus* has been erected for the species *pentelicus* by Wagner (1839), with a fragmentary skull from Pikermi (Attiki, Greece) as the type (housed in the Bayerische Staatssammlung für Paläontologie und Historische Geologie, München, n° AS II 11). Many specimens from the same locality have been described (Gaudry, 1862–1867) and numerous remains are now housed in several museums. *M. pentelicus* has also been reported from other localities of about the same age, but no one has documented any differences from the type specimens except for the mandible from Maraghe, Iran (Delson, 1973). In fact, this homogeneity results principally from the similarities of the teeth, which are often not characteristic for an identification at the species level. For example “in size the known teeth of *Libypithecus markgrafi* are nearly indistinguishable from those of the roughly contemporaneous *Mesopithecus* species, except that M_3 is larger in the Egyptian fossil and its P_3 protocone is reduced” (Szalay and Delson, 1979). Still, the skulls of these two genera are clearly very different. We believe that, with good samples of well-preserved material from well-defined localities, it is possible to show an evolutionary trend within the genus *Mesopithecus* during the late Miocene. *Mesopithecus* bears the typical characters of the cercopithecids. It has been included in the subfamily Colobinae because of several shared derived characters (see Strasser and Delson, 1987):

TABLE 1. *Mesopithecus*. Measurements of lower cheek teeth and mandibles. Abbreviations: **b1**, breadth of the trigonid; **b2**, breadth of the talonid; **F**, female; **I**, left; **L**, length; **L. symph.**, length of symphysis; **MD**, depth of the mandible below P_4 and M_2 ; **M**, male; **r**, right; **DIT**, Dytiko 2; **DKO**, Dytiko 3; **DTK**, Dytiko 1; **MPL**, Montpellier (Muséum National d'Histoire Naturelle, Paris); **MRG**, Maragha (Muséum National d'Histoire Naturelle, Paris); **PIK**, Pikermi (Muséum National d'Histoire Naturelle, Paris); **PVH**, Pikermi (Laboratoire de Paléontologie des Vertébrés et Paléontologie Humaine, University of Paris 6); **RZO**, Ravin des Zouaves 5 (Laboratory of Geology and Paleontology, Thessaloniki).

												MD		L.
												bel. M ₂	bel. P ₄	symp.
			P ₃	P ₄	M ₁	M ₂	M ₃	P ₃₋₄	M ₁₋₃	P ₃ -M ₃	Sex			
DIT 22	l	L	5.5	4.8	6.5	6.7	8.3	11.3	22.0	33.7	M	18.3	20.5	
		b1	4.7	4.2		5.9	6.0							
		b2			5.6	5.6	5.4							
DKO 38	r							12.2	23.6		M	19.3	19.5	
DTK 235	l	L	6.4	5.2			9.1	11.1	24.0	36.0	M?			
		b1	4.4	5.3			6.3							
		b2					5.7							
DTK 240	l								22.3		F			
MPL uncat.	l	L	4.8	4.3	5.8	6.2	8.2	9.5	20.7	30.8				
		b1	4.1	4.1	4.7	5.3	5.7							
		b2			4.7	5.4	5.2							
MRG 1905-10	r	L	7.3	5.5	7.1	7.4	9.6	13.0	24.7	38.0	M	19.5	19.8	
		b1	4.5	5.0	6.3	7.0	6.8							
		b2			6.1	6.8	6.1							
MRG 1905-10	l	L	7.3	5.2	7.2	7.7	9.3	13.0	24.4	37.7	M			
		b1	4.5	5.2	6.2	7.4	7.1							
		b2			6.2	7.3	6.3							
PIK 01	l	L	5.2	5.1	6.6	7.2	8.6	10.7	23.0	34.3	F	16.0	16.5	21.3
		b1	4.2	4.9	5.8	6.8	6.9							
		b2			6.3	7.2	6.6							
PIK 02	l	L	4.9	5.2	6.4	7.3	8.7	10.0	23.7	34.0	F	17.5	18.0	
		b1	4.4	4.9	5.7	6.6	6.6							
		b2			5.9	6.4	5.8							
PIK 03	r	L	5.3	4.7	6.0	6.7	9.1	10.5	22.5	33.5	F	15.5	17.0	20.0
		b1	4.0	4.8	5.6	6.6	6.5							
		b2			6.0	6.5	6.4							
PIK 04	l	L			6.6	7.5	8.8		23.8		M	18.5	19.7	22.1
		b1			5.7	6.6	6.9							
		b2			6.2	7.0	6.7							
PIK 05	r	L	6.0	5.4	7.0	7.2		11.4			M	19.3	22.2	24.8
		b1	4.0	4.5	7.0	7.0								
		b2			6.5	6.9								
PIK 06	l	L	5.9	4.9	6.3	7.0	9.0	11.4	23.0	35.3	M	22.9	22.7	
		b1	4.1	4.3	5.4	6.3	6.4							
		b2			5.7	6.7	6.2							
PIK 07	r	L	6.0	5.2	7.0	7.6	9.0	11.5	23.4	35.3	M	18.5	19.9	
		b1	4.0	4.8	5.9	6.9	6.7							
		b2			5.8	7.1	6.5							
PIK 08	l	L		5.2	6.9	7.8	9.0		24.1		M	20.3	21.4	27.8
		b1		4.8	5.9	6.9	6.6							
		b2			6.5	7.2	6.5							
PIK 09	r	L	6.0	5.5	6.2	6.9	8.8	12.0	22.8	34.7	M	19.1	19.7	25.0
		b1	4.2	4.7	5.5	6.4	6.5							
		b2			5.7	6.7	6.6							
PIK 21	l	L	6.0	5.4	6.0	7.2	8.8	11.1	22.6	34.5	M			
		b1	4.0	4.8		6.9	6.5							
		b2				7.4	6.1							
PIK 34	r	L	5.5	5.5	6.9	7.3	8.8	10.7	23.2	34.6	M	20.2	21.2	24.5
		b1	4.3	5.0	6.0	6.8	6.5							
		b2				7.2	6.6							
PVH 2	r	L	6.2	5.5	6.4	7.3	8.9	11.4	23.3	34.5	M	16.8	17.7	24.5
		b1	6.3	4.5	5.3	6.3	6.2							
		b2			5.3	6.6	5.6							
PVH 2	l	L	6.1	5.4	6.3	7.4	8.9	11.9	23.0	35.3	M			
		b1	5.0	4.5	5.3	6.3	6.5							
		b2			5.6	6.7	6.1							

TABLE 1. (Continued)

												MD		L.
												bel. M ₂	bel. P ₄	symph.
			P ₃	P ₄	M ₁	M ₂	M ₃	P ₃₋₄	M ₁₋₃	P _{3-M₃}	Sex			
PVH 3	r	L					9.3	10.5	22.6	33.7	F			
		b1					6.3							
PVH 4	r	L	5.8	5.5	6.9	7.2	9.3	12.0	23.9	36.1	M	21.3	21.4	26.0
		b1	4.8	4.5	5.3	6.5	6.5							
		b2			5.8	6.8	6.5							
PVH 4	l	L	5.6	5.2	6.6	7.1	9.2	10.7	24.1	34.5	M			
		b1	5.5	4.6	5.4	6.3	6.3							
		b2			5.4	6.7	6.4							
PVH 12	r	L	5.3	4.9	6.8	7.3	8.3	10.6	22.5	33.4	F	17.3	17.9	20.1
		b1	4.7	4.2	5.6	6.4	6.2							
		b2			5.8	6.2	5.7							
PVH 12	l	L	5.2	5.0	6.3	7.2	7.5	10.7	21.0	32.8	F			
		b1	3.9	4.7	5.7	6.8	6.7							
		b2			6.2	6.4	5.9							
RZO 159	r	L	5.8	5.4	6.8	7.1	11.1	11.9	25.0	38.2	M	25.2	24.1	29.4
		b1	4.2	4.8	5.7	6.8	7.1							
		b2			6.2	7.0	6.6							
RZO 159	l	L	6.8	5.1	7.0	7.2	10.3	12.2	24.5	37.0				
		b1	4.3	5.2	6.5	7.0	7.3							
		b2			7.0	7.1	7.0							
RZO 160	r	L	6.4	7.7	7.0	7.6	10.5	12.5	25.5	39	M		22.4	27.8
		b1	5.2	4.8	6.0	7.2	7.1							
		b2			6.3	7.5	6.9							
RZO 160	l	L	6.7	5.1	6.9	7.4	10.5	12.2	25.3	38.4				
		b1	5.1	5.1	6.0	7.0	7.1							
		b2			6.5	7.4	7.0							
RZO 161	r	L				7.4	9.2				F	20.6		
		b1					7.0							
		b2					6.5							

- high dental cusps;
- reduced thumb;
- reduced proximal articular facet between ecto-cuneiform and cuboid.

Several features demonstrate that *Mesopithecus* belongs to the stem group of the subfamily, before the split between Colobini and Presbytini: the molar flare is still present, the thumb is reduced but not missing, and the medial groove for the flexor tibialis on the astragalus is shallow. Thus, it can be considered as Colobinae, incertae sedis (Szalay and Delson, 1979).

Following in part Szalay and Delson (1979) and Strasser and Delson (1987) we can give the following diagnosis for *Mesopithecus* Wagner, 1839:

Medium-sized colobine with: corpus depth more or less constant between P₃ and M₃, neither increasing forward as in the baboons nor backward as in the Colobini and most Presbytini; molar flare greater than in recent colobines but less than in Cercopithecinae; and male P₃ with a relatively low anterior edge and honing facet.

Mesopithecus can be compared with other more or less contemporaneous circum-Mediterranean genera of colobine monkeys. *Libypithecus* from the early Pliocene of Wadi Natrun in Egypt is chiefly known by a cranium. It differs from *Mesopithecus* by a narrower

interorbital septum, a longer snout, a stronger and longer sagittal crest, and a larger M³. *Dolichopithecus* from the Pliocene of Europe is larger, and it differs from *Mesopithecus* by a longer snout, a larger P₃, and the narrower M₁ and M₂. The Algerian locality of Menacer (Marceau; see Arambourg, 1959) has yielded a colobine-like monkey larger than *Mesopithecus* and a cercopithecine with macaque-like teeth (Delson, 1973, 1975; Thomas and Petter, 1986). Finally, a small colobine is known from the late Miocene of the Siwalik hills (? *Presbytis* in Szalay and Delson, 1979), but according to these authors the only known teeth would not differ from *Mesopithecus* and "could almost as easily be included in *Mesopithecus*, but this would imply a zoogeographical relationship which is completely unfounded on present evidence" (Barry et al., 1985).

We propose for the type species of the genus, *Mesopithecus pentelicus* Wagner, 1839, the following revised diagnosis:

Medium-sized *Mesopithecus*; relatively long face for a colobine, upper margin of the nasal opening just above the lower margin of the orbit, low orbits, torus orbitalis weak or moderate, males with a weak and always very short sagittal crest; rounded gonial area, shallow mandibular ramus, steeply inclined planum alveolare, weak inferior transverse torus; P₃ with a well-marked and short metalophid; well-marked fovea

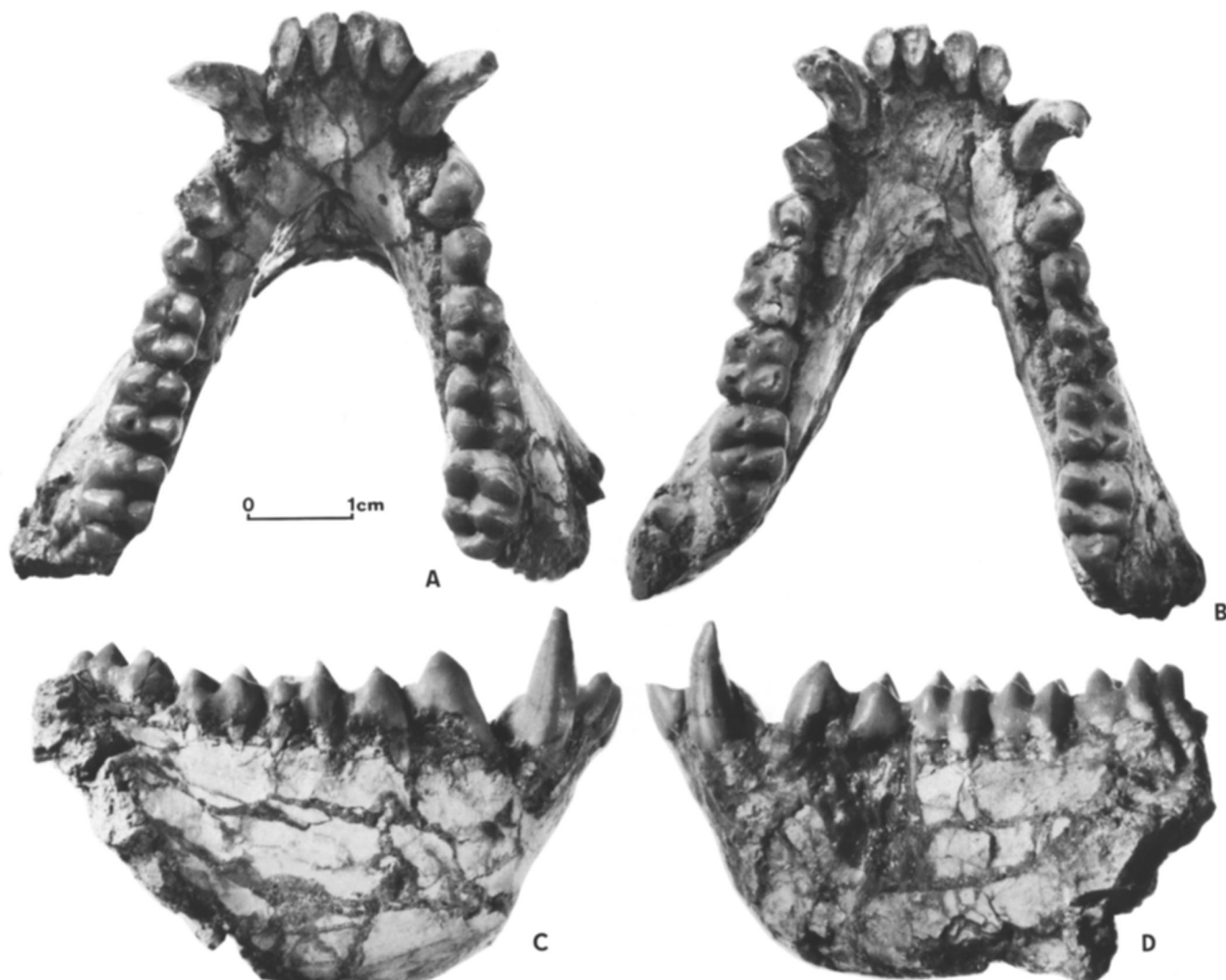


FIGURE 1. *Mesopithecus delsoni*, sp. nov., mandible, RZO 159, holotype. A, Occlusal view; C, right lateral view; D, left lateral view. B, Mandible, RZO 160, occlusal view. Ravin des Zouaves 5, late Miocene (early Turolian), Macedonia, Greece. Collection of the University of Thessaloniki.

on the premolars; M_3 hypoconulid of variable size but usually small. Forelimb clearly shorter than the hind limb; humeral medial epicondyle more backwardly directed than in recent colobines.

The other species of the genus, *Mesopithecus monspessulanus*, differs from *M. pentelicus* by its smaller size, narrower M_{1-2} , more reduced molar flare, more mesiodistally compressed cusps on the lower molars, and less retroflected medial epicondyle.

MESOPITHECUS DELSONI, sp. nov.

Holotype—RZO 159, nearly complete adult male mandible, housed in the Laboratory of Geology and Paleontology, University of Thessaloniki, Greece.

Referred Specimens—RZO 160 (nearly complete old male mandible) and RZO 161 (fragmentary right dentary with worn teeth).

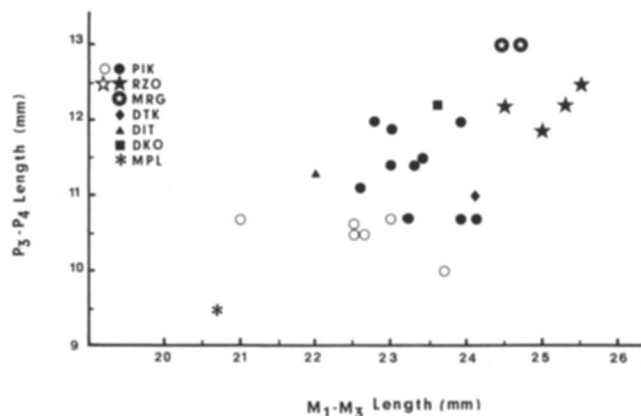


FIGURE 2. *Mesopithecus*. Bivariate plot of lower cheek teeth lengths. Open shapes indicate female, black = male. PIK: Pikermi; RZO: Ravin de Zouaves 5; MRG: Maraghe; DTK: Dytiko 1; DIT: Dytiko 2; DKO: Dytiko 3; MPL: sables de Montpellier.

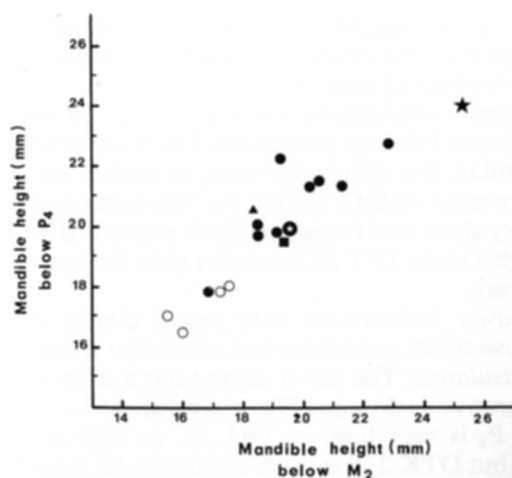


FIGURE 3. *Mesopithecus*. Bivariate plot of mandibular height. Symbols as in Figure 2.

Type Locality—Ravin des Zouaves 5 (RZO), Macedonia, Greece.

Age—Early Turolian (late Miocene).

Etymology—In honor of Eric Delson, for his numerous works on cercopithecoids.

Diagnosis—*Mesopithecus* of large size, deep corpus mandibularis; flattened anterior face of the symphysis, planum alveolare little inclined, thick inferior transverse torus. P_3 with a large honing facet, weak and rounded metalophid, and shallow foveae; well-developed M_3 hypoconulid.

Description—The mandibles differ from those of *M. pentelicus* by the very deep corpus (Table 1, Figs. 1, 3). The anterior face of the symphysis is less convex, the planum alveolare is less inclined, the fossa genio-glossa is deeper, and the inferior transverse torus is larger and more prominent. The incisors are similar to those of Pikermi specimens, and they also have an enamelled lingual face in contrast with the condition found in cercopithecines. The canines, although worn or eroded, are probably narrower than those of *M. pentelicus* relative to the cheek teeth, and they look slightly twisted in anterior view; the mesial groove is shallower. The premolars are slightly larger, but the molars are definitely larger than those of *M. pentelicus*, thus the proportions are different (Fig. 2). P_3 has a different shape: the honing facet is higher and more important; there is no epiconid (=metaconid), which is sometimes present in *M. pentelicus*; the metalophid is weak and blunt, separating the two shallow foveae. On P_4 , as on most P_4 from Pikermi, the metaconid is higher than the protoconid. Trigonid and talonid are separated by a lateral groove on one P_4 . The molars



FIGURE 4. *Mesopithecus delsoni* sp. nov., holotype (RZO 159), right side of mandible in occlusal view. Collection of the University of Thessaloniki, Ravin des Zouaves 5, late Miocene (early Turolian), Macedonia, Greece.

are larger than those of Pikermi, but their morphology is similar except M_3 , which is relatively larger and whose hypoconulid is larger and divided into two cusps (Figs. 4, 5).

The mandibles and dentitions of recent cercopithecids are relatively homogeneous; this is often true also of fossil species. The differences that we have noted between *M. pentelicus* and the mandibles from RZO are much more important than those we find within a recent species (Fig. 5). We think that these mandibles belong to a new species. The statistical differences from *M. pentelicus* from Pikermi are highly significant for several measurements, according to *t*-tests, as shown below:

OTHER SPECIES OF *MESOPITHECUS* FROM MACEDONIA

Description

Two crania of aged males (with heavily worn dentition) are known from the late Turolian. They are

measurements	N	Pikermi				RZO			
		\bar{x}	S^2	N		\bar{x}	S^2	<i>t</i>	
Length M_3	17	8.82	0.179	5		10.32	0.482	6.01	highly significant
Breadth M_3	17	6.52	0.043	5		7.12	0.012	6.19	highly significant
LP_3-P_4	15	11.05	0.384	4		12.20	0.060	3.58	highly significant
LM_1-M_3	17	23.09	0.586	4		25.07	0.189	4.94	highly significant

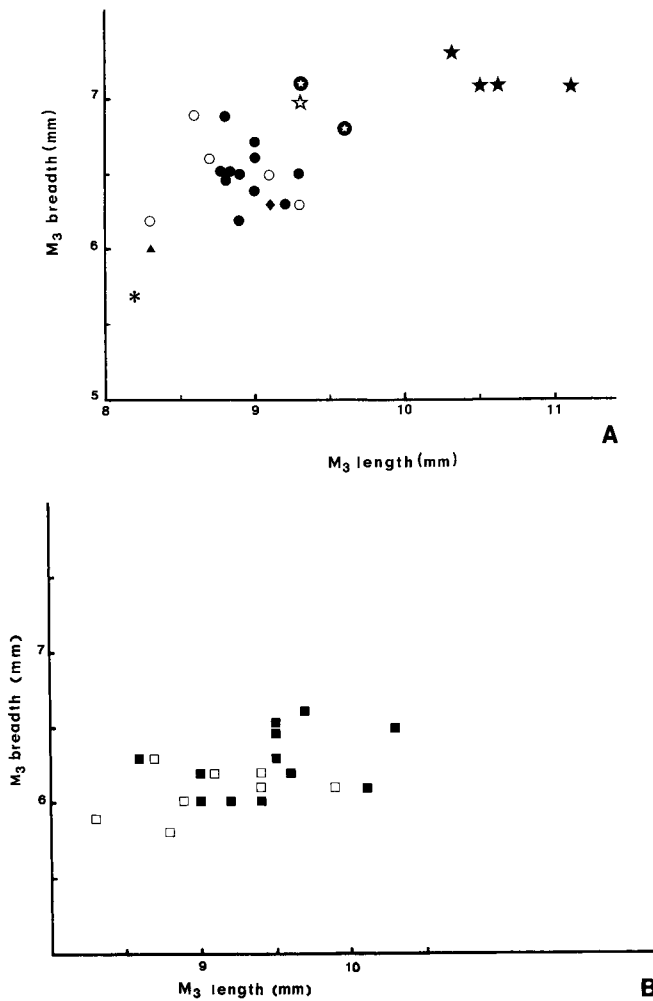


FIGURE 5. Bivariate plot of M_3 length and trigonid breadth. **A**, *Mesopithecus*. Symbols as in Figure 2. **B**, *Colobus guereza occidentalis*, West Africa. Open squares = female; black squares = male.

similar in size to skulls of *Mesopithecus pentelicus* but while DIT 21 (Dytiko 2) is completely crushed, DKO 38 (Dytiko 3; Fig. 6) differs in some characters: the orbits are smaller and not so low, being slightly higher than wide; the supraorbital torus is thicker; the jugal bone is higher under the orbit and looks more like that of *Semnopithecus* than *Colobus*; the suborbital fossa looks a little deeper; the temporal lines, well marked, meet abruptly 4 cm behind the torus just on the frontoparietal suture; the parietal region is badly preserved but it seems that a sagittal crest was present ending at the nuchal crest (Fig. 6). The skulls of the Pikermi males have only a very short sagittal crest or no crest at all. The external auditory duct is short. As on the Pikermi skulls, there is a clear sulcus supramastoideus, which is very weak or absent on most recent colobine skulls.

All the upper teeth are heavily worn, so it is im-

possible to distinguish any morphologic detail. Their size, when measurements are possible, is similar to that of *M. pentelicus* (Table 2).

The corpus mandibularis is shallow but no more so than on some Pikermi mandibles. The fossa genioglossa is similar, the transverse torus is thicker on DTK 235 but weaker on DIT 22 (Fig. 7). This latter mandible has a very short and steeply inclined planum alveolare. Although a male, DIT 22 is smaller than the mandibles of Pikermi.

The lower incisors are very small, clearly smaller than those of *M. pentelicus* and more like those of *M. monspessulanus*. The lower canine has a deep medio-lingual groove as do some Pikermi canines. The honing facet of P_3 is very high on DIT 22, as high as in *M. delsoni*; but DTK 235 is more similar to *M. pentelicus*, with a shallower mesial edge and honing facet, blunt metalophid, and shallow foveae. The molars of DTK 235 are similar to those of *M. pentelicus*, but those of DIT 22 are slightly smaller, fitting better with *M. monspessulanus*.

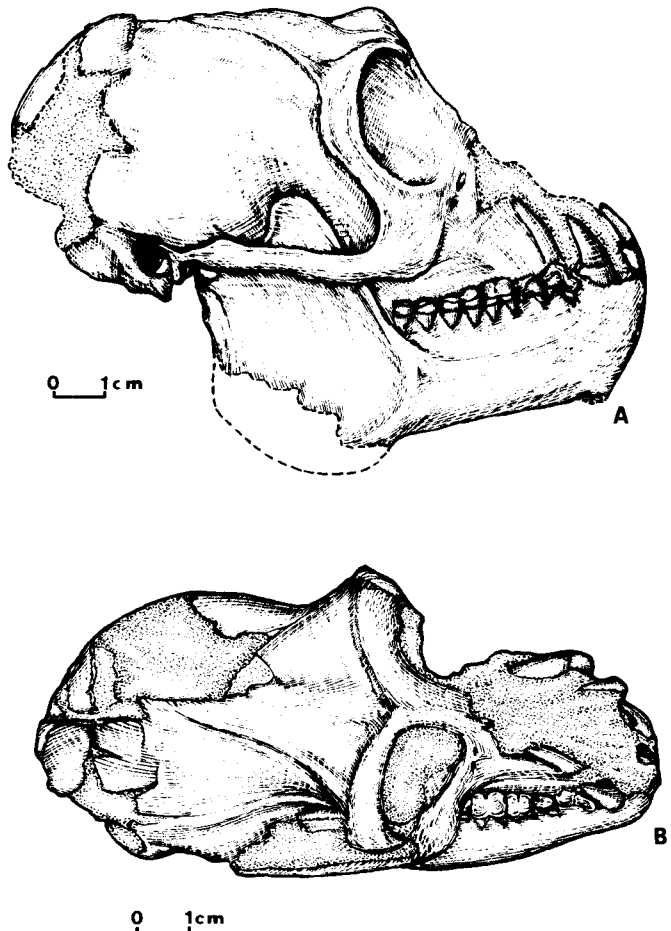


FIGURE 6. *Mesopithecus*, aff. *M. pentelicus*. Skull and mandible, DKO 38. Right lateral view; **B**, dorsal view. Dytiko 3, late Miocene (Turolian), Macedonia Greece. Collection of the University of Thessaloniki.

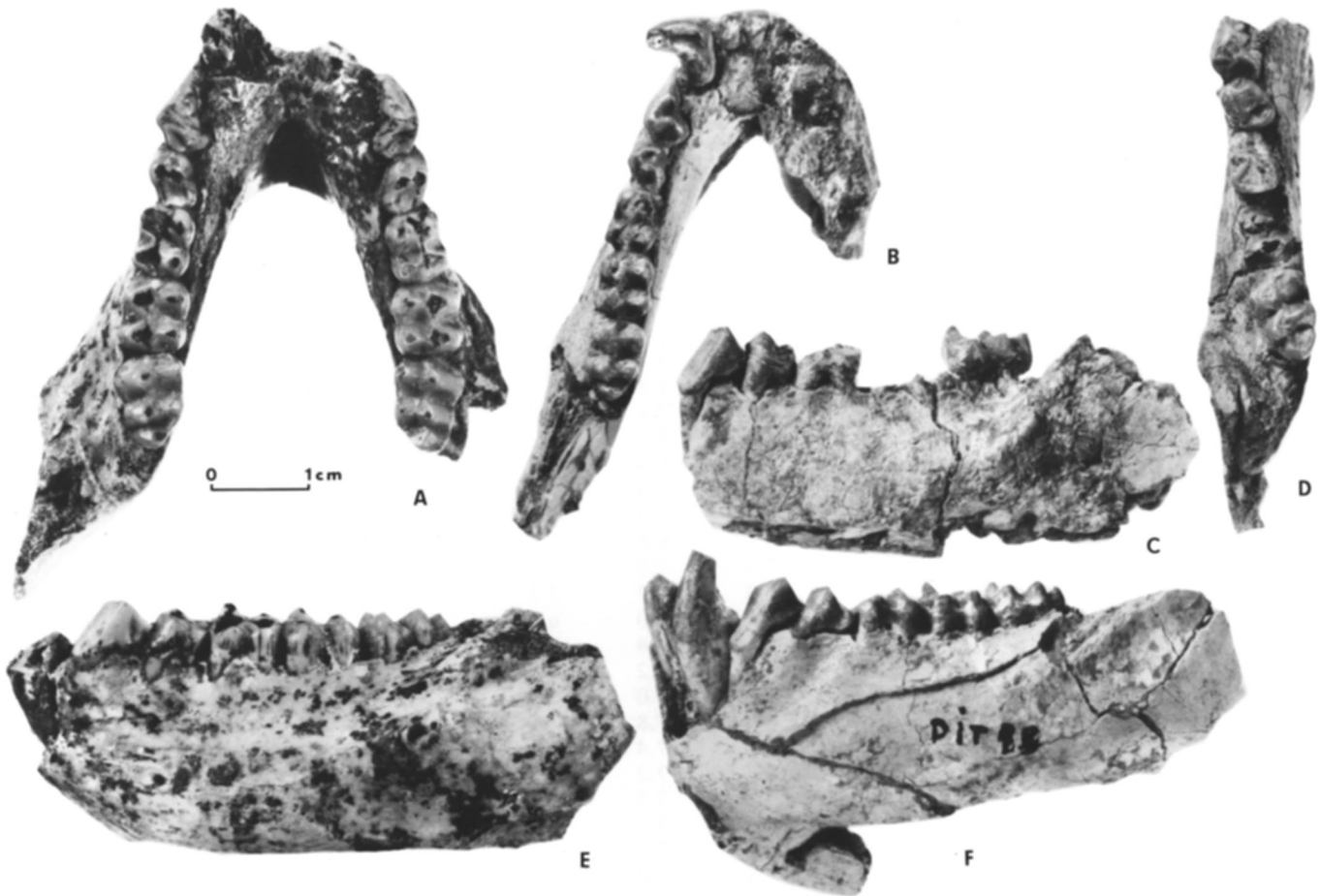


FIGURE 7. A, E, *Mesopithecus*, cf. *M. delsoni*, mandible (MRG 1905-10). Maragha, late Miocene, Iran. Collection of the Muséum National d'Histoire Naturelle, Paris. A, Occlusal view; E, left lateral view. B, F, *Mesopithecus*, cf. *M. monspessulanus*, mandible (DIT 22). Dytiko 2, late Miocene (Turolian), Macedonia, Greece. Collection of the University of Thessaloniki. B, Occlusal view; F, left lateral view. C, D, *Mesopithecus*, cf. *M. pentelicus*, mandible (DTK 235). Dytiko 1, late Miocene (Turolian), Macedonia, Greece. Collection of the University of Thessaloniki. C, Left lateral view; D, occlusal view.

The size of the two distal humeri is similar to that of the Pikermi males or slightly larger (DIT 23). The epicondylus medialis of DKO 39 is less backwardly directed, as in *M. monspessulanus* (Faculté des Sciences de Lyon n° FSL 320 002) from Montpellier. Radius and ulna (DKO 40) have a length similar to that of *M. pentelicus* but the radius has a more oval cross section; the ulna is slightly more slender and the proximal articular facet for the radius is smaller (Fig. 8).

The bones of the hind limb are more numerous and can be divided into two size groups (Figs. 8, 9). Most are as large as those from Pikermi. As noted by Strasser and Delson (1987) the proximal articular facet between the cuboid and ectocuneiform is lacking (DTK 236 and DTK 237). The bones of DIT 24 are smaller, similar in size to the Pikermi female bones. The most parsimonious explanation would thus be to consider DIT 24 as a female, but this limb differs from the others by some peculiar characters that cannot be explained by sexual dimorphism: the tibial malleolus is longer;

the external beak of the astragalus is more protruding; the astragalus neck is longer and correlatively, the articular part of the calcaneus is also longer; on the fifth metatarsal, the articular facet for the cuboid is almost perpendicular to the shaft and to the facet for the fourth metatarsal. On the other fifth metatarsals from Dytiko and Pikermi this facet is oblique to the long axis of the bone. At Pikermi, the female bones do not differ morphologically from those of the males (but we have seen no female astragalus), except for a calcaneus which does not look much different from that of DIT 24.

Taxonomic Status of the Dytiko Remains

All the specimens from Dytiko 3 (DKO) are roughly of the same size and there is no reason to distinguish two different species. The remains differ from *Mesopithecus pentelicus* by the smaller orbits, the stronger supra-orbital torus, the longer sagittal crest, the smaller lower incisors, the less backwardly reflected epicon-

TABLE 2. *Mesopithecus*. Measurements of upper cheek teeth. Abbreviations: **b1**, breadth of first lobe; **b**, length of the second lobe; others as in Table 1.

			P ³	P ⁴	M ¹	M ²	M ³	P ³⁻⁴	M ¹⁻³	P ³ -M ³	Sex
DIT 025		L	3.9	4.8			7.0	9.2			M
		b1	6.4	7.2			7.2				
		b2					6.4				
DIT 80							6.9			30.5	M
							7.0				
DKO 038	r								18.6		M
DTK 240	l								19.0		
PIK 010	l	L	4.7	4.8	6.8	7.2	7.4	10.0	21.2	31.1	M?
		b1	6.2	6.9	7.3	7.9	7.6				
		b2			7.3	7.7	7.0				
PIK 12	r	L	4.8	5.2	6.9	7.8	6.8	10.2	21.7	32.7	M
		b1	6.3	6.6	7.1	7.8	7.6				
		b2			6.9	7.1	7.3				
PIK 13	l	L	4.6	5.1	6.9	7.4	6.8	9.7	21.4	31.0	M
		b1	6.4	6.7	7.0	7.5	7.0				
		b2			6.7	7.2	6.4				
PIK 16	r	L	4.6	5.2	6.6	6.8	6.6	10.4	20.4	30.3	F
		b1	5.5	6.1	7.0	7.5	6.7				
		b2			6.3	6.7	5.3				
PIK 17	l	L	4.1	4.8	6.7	7.0	6.3	9.5	21.0	29.7	F
		b1	5.7	6.5	6.6	7.4	6.7				
		b2			6.8	7.2	5.9				
PIK 20	l	L	4.1		6.3	7.0	6.0		19.5	28.3	F?
		b1	4.8		6.9	7.8	7.0				
		b2			6.3	7.4	6.1				
PIK 21A	r	L	4.5	4.8	6.7	7.2	6.4	9.8	20.6	30.2	M
		b1	6.1	6.6	7.1	7.7	6.9				
		b2			6.7	7.2	5.8				
PIK 35	l	L	4.4	4.9	6.4	7.5	6.7	10.0	21.5	32.0	M
		b1	6.6	7.0	7.1	8.0	7.6				
		b2			6.9	7.5	6.3				
PIK 253	l	L	4.5	4.8	6.6			9.5			M
		b1	6.4	6.6	6.9						
		b2			7.2						
PIK 303A	r	L	4.5	4.9	6.7	6.4	9.0	20.0	29.6		F
		b1	5.1	6.1	6.6	7.2	6.7				
		b2			6.6	6.9	5.9				
PVH 05	r	L	4.2	4.2	6.2	6.7	6.5	9.2	20.1	29.2	F
		b1	5.9	6.6	7.1	7.5	7.3				
		b2			6.9	7.3	6.3				
PVH 06	r	L		4.9	6.7	7.4	7.1		22.0		F
		b1		7.0	6.9	7.8	7.4				
		b2			6.7	7.5	6.5				
PVH 07	r	L	4.8	5.2	6.8	7.4	7.4	9.5	21.3	31.0	M
		b1	5.9	6.4	7.0	7.8	7.7				
		b2			6.1	7.1	7.6				
PVH 08	r	L	4.8	4.8	6.3	6.8	6.3	9.8	20.0	30.0	M
		b1	5.8	6.6	6.8	7.8	7.3				
		b2			6.7	7.3	6.2				
PVH 09	r	L	4.7	4.7	6.3	7.5	6.8	9.5	21.0	30.4	M
		b1	5.9	6.6	7.1	7.8	7.3				
		b2			6.8	7.3	6.2				
PVH 11	r	L	4.5	4.8	6.4	7.1		9.7			F
		b1	6.1	6.1	6.4	7.0					
		b2			6.2	6.7					

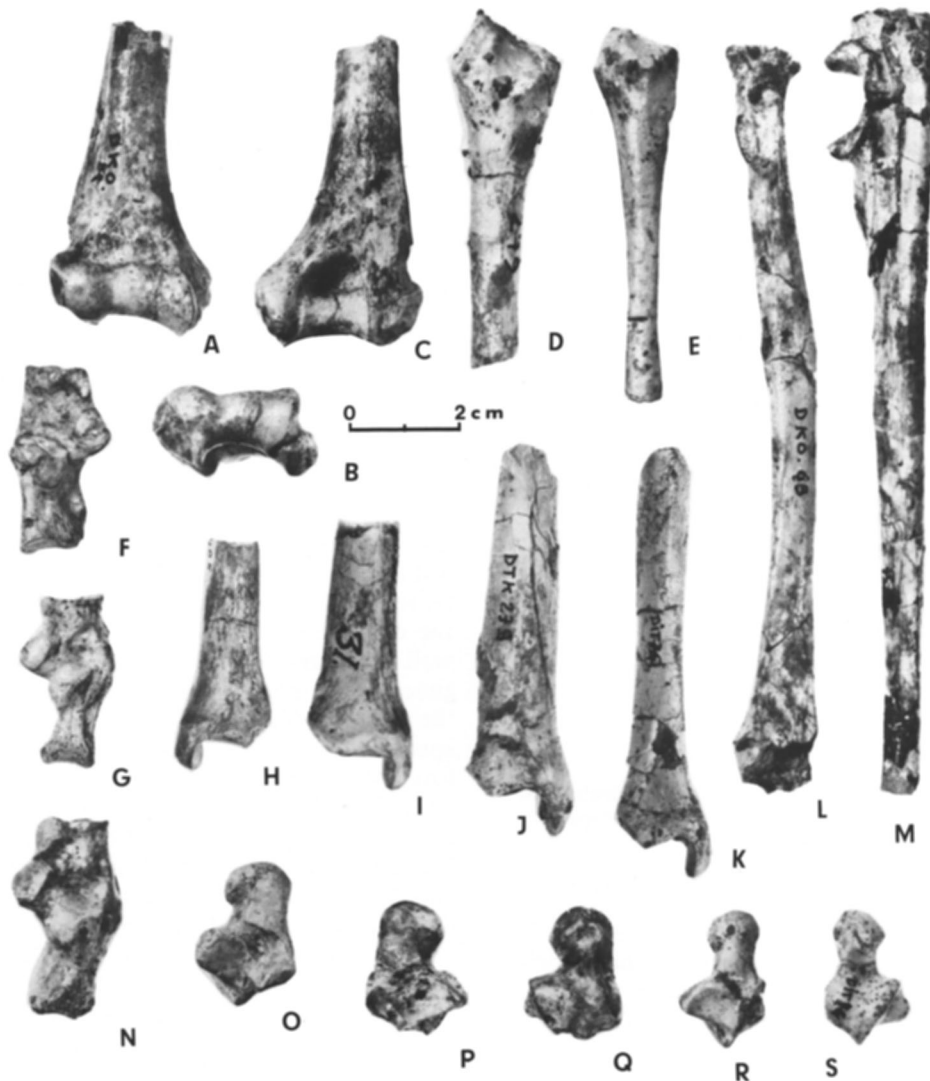


FIGURE 8. *Mesopithecus* spp., limb bones. A, B, C, F, L, M, P, Q, *Mesopithecus*, aff. *M. pentelicus*. Dytiko 3, Collection of the University of Thessaloniki. A–C, Right distal humerus DKO 39, in anterior (A), dorsal (B), and distal (C) views; F, left calcaneus, DKO 44, dorsal view; L, left radius, DKO 40, anterior view; M, left ulna, DKO 40; P, Q, left astragalus, DKO 44, plantar view (P), dorsal view (Q). D, J, N, O, *Mesopithecus*, cf. *M. pentelicus*. Dytiko 1, Collection of the University of Thessaloniki. D, Right fifth metatarsal, DTK 239, dorsal view; J, right tibia, DTK 239, anterior view; N, right calcaneus, DTK 236, dorsal view; O, right astragalus, DTK 236, plantar view. E, G, K, R, S, *Mesopithecus*, cf. *M. monspessulanus*. Dytiko 2, Collection of the University of Thessaloniki. E, Right fifth metatarsal, DIT 24, dorsal view; G, right calcaneus, DIT 24, dorsal view; K, right tibia, DIT 24, anterior view; R, right astragalus, DIT 24, plantar view; S, right astragalus, DIT 24, dorsal view. H, I, *Mesopithecus pentelicus*, Pikermi, Collection of the Muséum National d'Histoire Naturelle, Paris. H, Left female tibia PIK 028, anterior view; I, right male tibia PIK 405, anterior view. Scale for A–C, F–S = 2 cm, for D, E = 4 cm.

dylus medialis of the humerus, the oval section of the radial shaft, and the small radial facet of the ulna. Unfortunately the teeth are all worn and no interesting feature is visible. Their size is that of *M. pentelicus* and these fossils are thus identified as *M.*, aff. *M. pentelicus* since the shape of the skull could indicate a different taxon.

Some specimens are known from Dytiko 1 (DTK). They differ significantly neither from the DKO nor

from the Pikermi material and they are identified as *M.*, cf. *M. pentelicus*.

At Dytiko 2 (DIT), the crushed skull and some teeth and bones are similar to the material from DKO, and they are identified as *M.*, aff. *M. pentelicus*. But the hind limb DIT 24 and the mandible DIT 22 (which may belong to the same species) are of smaller size; they are similar to *Mesopithecus monspessulanus* and might belong to that species. Some features of the hind

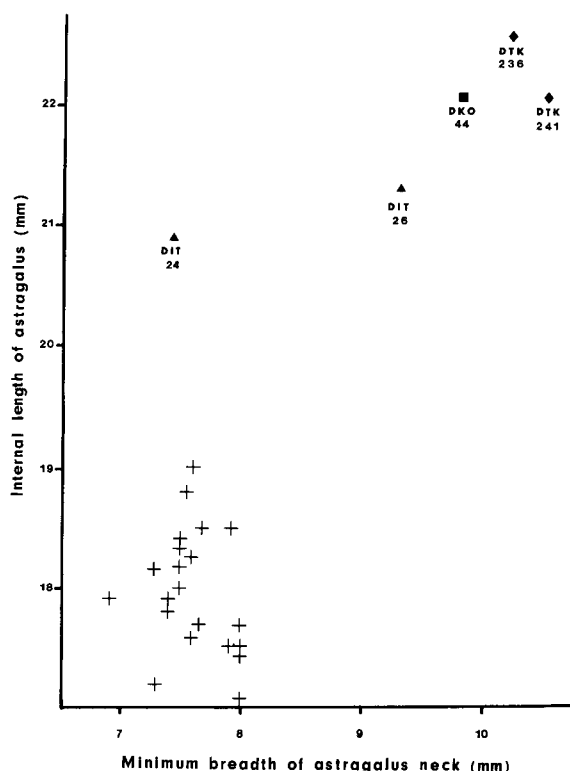


FIGURE 9. Bivariate plot of astragalus measurements. Symbols in Figure 2; crosses = male and female *Pygathrix* (*Rhinopithecus*) *roxellanae*, China.

limb (long tibial malleolus, long astragalar neck, orientation of the proximal articular facet of the fifth metatarsal) are reminiscent of Cercopithecinae rather than of Colobinae.

As mentioned above, we have not seen the material from Vathylakos (=Vatilük in Arambourg and Piveteau, 1929) found by Arambourg, but the measurements kindly provided by E. Delson (pers. comm.) of the lower M_3 n° Slq 942 housed in the Muséum National d'Histoire Naturelle, Paris (length = 10.0 mm, breadth = 7.0 mm) show that this material is intermediate in size between the Ravin des Zouaves and the Pikermi specimens.

CONCLUSION

The Greek localities with *Mesopithecus* have been dated from different levels of the Turolian (later late Miocene). RZO is dated from the early Turolian or perhaps late Vallesian and is thus earlier than Pikermi; the localities of Dytiko are younger than Pikermi (Bonis et al., 1986). The evolution of *Mesopithecus* is in agreement with these dates. *M. delsoni* is older and larger than *M. pentelicus*. One may suppose that during the Turolian the size decreased from *M. delsoni* to *M.*, aff. *M. pentelicus*. During the late Turolian a new lineage may have appeared and evolved into the Pliocene with *M. monspessulanus*. This framework can help to

identify the other specimens of *Mesopithecus* and be used as a biostratigraphic tool.

Mesopithecus has been found in several localities out of Greece. The earliest one would be Wissberg (Vallesian of Germany) if the remains are correctly identified. But the bulk of the Miocene finds come from Turolian localities in Yugoslavia (Titov Veles), Bulgaria (Kalamanci), and the southern U.S.S.R. (Grebeniki). However, these fossils have not been described recently, and we cannot identify them at the species level. A male mandible from Maragha (Iran) was found by Mecquenem (1925) but never described (Fig. 7A, E). Delson (1973:448) referred it to *M. pentelicus* "with more doubt than the other populations . . .," whereas Heintz et al. (1981) stated "the anterior side of the symphysis is flattened on the Maragha mandible, whereas it is rounded on the Molayan and Pikermi mandibles. On account of these differences, it seems that the primate mandible from Maragha is perhaps not assignable to *Mesopithecus pentelicus*, but might be referred to another taxon, perhaps new." Most of the characters of the mandible of Maragha fit pretty well the mandibles of RZO, i.e., *Mesopithecus delsoni*: general size, size of the honing facet of P_3 , and size of the hypoconulid of M_3 . But the corpus of the Maragha specimen is shallow and more *pentelicus*-like. Therefore the mandible of Maragha must be considered as *M.*, aff. *M. delsoni*. We can hypothesize that these mixed morphological features indicate that the horizon of Maragha where this mandible has been found is younger than RZO but older than Pikermi, i.e., it can be dated to the early Turolian. Another mandible of a young male *Mesopithecus* has been found in the locality of Molayan in Afghanistan (Heintz et al., 1981). Its characters, size, and proportions allow us to refer it to *M. pentelicus*. This identification fits the age of the locality, which is early middle Turolian (S. Sen, pers. comm.). No *Mesopithecus* remains have ever been found in Samos or in Turkey despite the numerous fossils collected.

Mesopithecus is associated in each locality with a savannah fauna. But, as noted by Delson (1975), its adaptations to terrestrial life are not strongly marked (see, for example, the radius shorter than the femur, the ulna shaft not straighter than in *Colobus*, and the humeral epicondyle little reflected), and a part of its time was probably devoted to tree dwelling.

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- Appendix. *Mesopithecus* fossils from the new localities of Macedonia (Greece).
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- a. Dytiko 1: DTK
- DTK 235: lower jaw of P₃–M₁ and M₃.
- DTK 240: lower jaw with incomplete M_{1–3}, associated with upper jaw with incomplete P³–M³.
- DTK 241: incomplete foot with calcaneus, astragalus, navicular, cuboid, and fragmentary metatarsals.
- DTK 242: distal femur.
- DTK 243: distal femur and associated patella and proximal tibia.
- DTK 237: metatarsals I to IV and entocuneiform.
- DTK 236: incomplete foot with distal tibia, astragalus, calcaneus, navicular, cuboid, cuneiforms, and fragmentary metatarsals.
- b. Dytiko 2: DIT
- DIT 21: crushed old male cranium.
- DIT 25: fragment of male maxilla, old.
- DIT 22: male lower jaw, with I₁–M₃.
- DIT 23: distal humerus.
- DIT 26: astragalus.
- DIT 27: distal Mt IV.
- DIT 28: phalanx.
- DIT 24: incomplete hind limb with distal tibia and fibula, astragalus, calcaneus, fragments of other tarsals, metatarsals, fragments of phalanges.
- c. Dytiko 3: DKO
- DKO 38: old male skull, with mandible.
- DKO 39: distal humerus.
- DKO 40: forearm (radius, ulna, and 2 carpals).
- DKO 41: incomplete femur.
- DKO 42: femur and fragment of pelvis.
- DKO 43: femur.
- DKO 44: incomplete hindlimb with distal tibia, sub-complete tarsus, fragments of metatarsals.
- DKO 45: astragalus and calcaneus.
- DKO 46: navicular.
- DKO 47: proximal Mt II.
- DKO 48: fragment of phalanx.
- d. Ravin des Zouaves 5: RZO
- RZO 159: almost complete adult male mandible.
- RZO 160: almost complete old male mandible.
- RZO 161: fragmentary right mandible with worn teeth.
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