The Neogene cercopithecids (Mammalia, Primates) of Greece

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ABSTRACT
The presence of the cercopithecids in the Neogene of Greece is known since the beginning of the 19th century. The excavations of the last 20 years increase their number in Greece. The main taxon of the cercopithecids is *Mesopithecus* Wagner, 1839 found originally in the middle Turolian (MN 12) locality of Pikermi, near Athens. The Pikermi *Mesopithecus* sample is rich and belongs to a medium-sized form, *M. pentelicus* Wagner, 1839. Besides the well-known *M. pentelicus,* two other species were recognized. The new species *M. delsoni* Bonis, Bouvrain, Geraads & Koufos, 1990, a large-sized form found in the early Turolian (MN 11) locality Ravin des Zouaves-5 of Axios Valley (Macedonia, Greece) has several differences from the type species. In the middle Turolian (MN 12) localities of Vathylakkos (Axios Valley) and Perivolaki (Thessaly) a large to medium-sized *Mesopithecus* form with "*delsoni*" and "*pentelicus*" characters was found and is referred to as *M. delsoni*/*pentelicus*. A small-sized form named *M.* cf. *monspessulanus* was recognized by a mandibular fragment in the late Turolian (MN 13) locality Dytiko-2 of Axios Valley and indicates the early appearance of the taxon at the end of Miocene. The rest of the material found in the late Turolian localities of Dytiko has some differences from the typical *M. pentelicus*. Moreover, *Mesopithecus* was traced in several late Miocene localities, indicating its wide distribution in Greece. Two other cercopithecids were also found in the Pliocene of Greece. *Dolichopithecus ruscinensis* Depéret, 1889 was recognized in the locality of Megalon Emvolon and in Ptolemais Basin (Macedonia, Greece); both are dated to late Ruscinian (MN 15). The second Pliocene cercopithecid is *Paradolichopithecus arvernensis* (Depéret, 1929), found in the locality of Vatera (Lesvos Island) and dated to late Pliocene. The stratigraphic distribution and the palaeoenvironment of these cercopithecids are also discussed.

KEY WORDS
Mammalia,
Primates,
Cercopithecidae,
Mesopithecus,
Dolichopithecus,
Paradolichopithecus,
Neogene,
Greece,
systematic,
biostratigraphy,
palaeoecology.

RÉSUMÉ
Les cercopithécidés du Néogène (Mammalia, Primates) de Grèce.
La présence des cercopithécoïdes dans le Néogène de Grèce est reconnue depuis le début du XIXe siècle. Les fouilles des 20 dernières années ont permis d'enrichir considérablement l'échantillon et de nouveaux taxons ont pu être décrits. Le taxon le plus répandu est *Mesopithecus*, initialement mis au jour dans la localité Pikermi du Turolien moyen (MN 12), près d'Athènes. L'échantillon de Pikermi est riche et est reconnu comme *M. pentelicus* Wagner, 1839. Hormis cette espèce particulièrement bien décrite, deux autres taxons ont été décrits. La nouvelle espèce *M. delsoni* Bonis, Bouvrain, Geraads & Koufos, 1990, est une forme de grande taille trouvée dans la localité Ravin des Zouaves-5, dans des dépôts du Turolien inférieur (MN 11) de la vallée de l'Axios (Macédoine, Grèce). Les localités Vathylakkos (vallée de l'Axios) et Perivolaki (Thessalie) du Turolien moyen (MN 12) ont livré une forme de taille moyenne qui partage des caractères avec *M. pentelicus* et *M. delsoni* et est ici nommée *M. delsoni/pentelicus*. Un fragment de mandibule mis au jour dans le Turolien supérieur (MN 13) de Dytiko-2 (vallée de l'Axios) attribué à l'espèce de petite taille *M.* cf. *monspessulanus* accrédite une première apparition antérieure au Pliocène pour ce taxon. Le reste du matériel de Dytiko présente quelques différences avec *M. pentelicus*. Le genre *Mesopithecus* est signalé dans de nombreuses localités du Miocène supérieur confirmant sa vaste répartition en Grèce. Deux autres cercopithécoïdes ont été également décrits dans le Pliocène de Grèce. *Dolichopithecus ruscinensis* Depéret, 1889 est reconnu dans la localité de Megalon Emvolon et dans le bassin de Ptolemais (Macédoine, Grèce) ; deux localités datées du Ruscinien récent (MN 15). Le second cercopithécoïde pliocène est Paradolichopithecus arvernensis Depéret, 1929 trouvé dans la localité de Vatera (Pliocène supérieur de Lesbos, Grèce). La distribution stratigraphique et le paléoenvironnement de ces cercopithécoïdes sont également discutés.

MOTS CLÉS
Mammalia,
Primates,
Cercopithecidae,
Mesopithecus,
Dolichopithecus,
Paradolichopithecus,
Néogène,
Grèce,
systématique,
biostratigraphie,
paléoécologie.

INTRODUCTION

The cercopithecids (Mammalia, Primates) are quite common in the Neogene of Greece; the most common one is *Mesopithecus* Wagner, 1839, representing the first evidence of their presence in Greece. It was originally discovered in the late Miocene locality of Pikermi (Fig. 1) in 1835; during the years after several excavators found *Mesopithecus* in Pikermi and today its sample is the richest one (Wagner 1839; Roth & Wagner 1854; Gaudry 1862-1867; Weithofer 1888; Woodward 1901). Later, the genus was recognized in Axios Valley, Macedonia, Greece (Arambourg & Piveteau 1929). In the meantime the late Miocene fossiliferous sites of Samos had been discovered (Forsyth Major 1888, 1894) and no cercopithecids have been found there up to now. The genus is also recognized in the neighbouring area, known from the late Miocene of Italy, Hungary, FYROM, Bulgaria, and Ukraine, as well as from the Pliocene of Italy, Bulgaria and Romania (Schlosser 1921; Gentilli *et al.* 1998; Rook 1999; Kordos 2000; Koufos *et al.* 2003 and references therein; Radulescu *et al.* 2003; Delson *et al.* 2005; Pradella & Rook 2007; NOW 2008)

During the last 20 years new excavations have been carried out in various late Miocene Greek localities, providing several remains of *Mesopithecus*. The genus was discovered in Axios Valley, Serres Basin, Thessaly and Chalkidiki (Bonis *et al.* 1990, 1997; Kullmer & Doukas 1995; Koufos *et al.* 2004; Koufos 2006a; Tsoukala & Bartziokas 2008). The new findings enriched our knowledge

FIG. 1. — Map indicating the cercopithecid bearing mammal localities of Greece: **1**, Pikermi (PIK); **2**, Chomateres (CHO); **3**, Ravin des Zouaves-5 (RZO); **4**, Vathylakkos-2, 3 (VTK, VAT) and Ravin-X (R-X); **5**, Dytiko-1, 2, 3 (DTK, DIT, DKO); **6**, Perivolaki (PER); **7**, Maramena (MAR); **8**, Kryopigi (KRY); **9**, Nikiti-2 (NIK); **10**, Megalon Emvolon (MEV); **11**, Ptolemais basin; **12**, Vatera (VTR). The map was taken from http://www.shaded-relief.com/.

about the systematic and biostratigraphy of this cercopithecid. Moreover, the analysis of the *Mesopithecus* associated faunas using new methods allowed to determine its palaeoecology.

During the 1990's two other cercopithecids were discovered in the Neogene of Greece. The genus *Dolichopithecus* Depéret, 1889 was found in the Pliocene deposits of Megalon Emvolon and Ptolemais Basin, Macedonia, Greece (Koufos *et al.* 1991a; Doukas & de Bruijn 2002). The second genus is *Paradolichopithecus* Necrasov, Samson & Radulesco, 1961, discovered in the Pliocene locality of Vatera, Lesvos Island (de Vos *et al.* 2002; Van der Geer & Sondaar 2002).

The present article is an effort to summarize all available data about the Greek cercopithecids, giving information for their localities, stratigraphy, morphology, age and systematics. Some biostratigraphical and palaeoecological remarks for the Neogene cercopithecids are also given.

This article is written in honour of Prof. Louis de Bonis, University of Poitiers, and really it was a great pleasure for me to do it, as Louis is a good friend for a long time. I met Louis in 1976 when he was excavating with Prof. J. K. Melentis in Axios Valley. After that time we have been working together in the area; we also worked together in Turkey and Chad. All these 35 years we had a nice collaboration and we worked in a friendly and scientifically productive way, trying to solve all small problems by discussion and comprehension. The writing of this article is a minimum offer to the long time collaboration, the scientific discussions and the hard work I shared with Louis.

ABBREVIATIONS

AMPG	Athens Museum of Palaeontology & Geology, University of Athens;
BSPM	Bayerische Staatssammlung für Paläontologie und Historische Geologie, München;
CHO	Chomateres, Attica, Greece;
DIT	Dytiko-2, Axios Valley, Macedonia, Greece;
DKO	Dytiko-3, Axios Valley, Macedonia, Greece;
DTK	Dytiko-1, Axios Valley, Macedonia, Greece;
Fm.	Formation;
KRY	Kryopigi, Chalkidiki, Macedonia, Greece;
LGPUT	Laboratory of Geology and Palaeontology, University of Thessaloniki;
MAR	Maramena, Serres Basin, Macedonia, Greece;
MEV	Megalon Emvolon-1, Macedonia, Greece;
MNHN	Museum national d'Histoire naturelle, Paris;
NHML	Natural History Museum, London;
NHMW	Naturhistorisches Museum, Vienna;
NIK	Nikiti-2, Chalkidiki, Macedonia, Greece;
NKT	Nikiti-1, Chalkidiki, Macedonia, Greece;
NOW	Neogene Old World database;
PER	Perivolaki, Thessaly, Greece;
PIK	Pikermi, Attica, Greece;
PNT	Pentalophos-1, Axios Valley, Macedonia, Greece;
PTL	Ptolemais, Western Macedonia, Greece;
PXM	Prochoma-1, Axios Valley, Macedonia, Greece;
RPl	Ravin de la Pluie, Axios Valley, Macedonia, Greece;
R-G	Ravin-G or Ravin du Vatilük, Axios Valley, Macedonia, Greece;
R-X	Ravin-X, Axios Valley, Macedonia, Greece;
RZ1	Ravin des Zouaves-1, Axios Valley, Macedonia, Greece;
RZO	Ravin des Zouaves-5, Axios Valley, Macedonia, Greece;
VAT	Vathylakkos-3, Axios Valley, Macedonia, Greece;
VLO	Vathylakkos-1, Axios Valley, Macedonia, Greece;
VTK	Vathylakkos-2, Axios Valley, Macedonia, Greece;
VTR	Vatera, Lesvos Island, Greece;
XIR	Xirochori-1, Axios Valley, Macedonia, Greece.

LATE MIOCENE LOCALITIES

NIKITI

History

The localities of Nikiti were discovered at the beginning of the 1990's, when the villagers found some fossils during excavations for a new road. They gave the information to the author who went there and collected the fossils. This first locality was named Nikiti-1 (NKT) and it is well known by the presence of the hominoid primate *Ouranopithecus macedoniensis* Bonis & Melentis, 1977 (Koufos *et al.* 1991b). The prospection of the area gave several fossiliferous sites; most of them are poor in fossils but one named Nikiti-2 (NIK), provided a rich fauna. Among the collected material from NIK there are some remains of *Mesopithecus*, found in the summer of 2008.

Stratigraphy and localities

The localities of Nikiti are situated in the Chalkidiki Peninsula about 120 km east of Thessaloniki city (Fig. 1). The Neogene deposits of the Nikiti area overlie unconformably the granitic basement and they are divided in two formations (Syrides 1990; Koufos *et al.* 1991b; Kostopoulos & Koufos 1999).

Nikiti Fm. It outcrops around the village of Nikiti and consists of clastic sediments, mainly sands, gravels with intercalations of pebbles; in the upper part of the formation there are intercalations or lenses of red-brown sands, sandstones and sandy clays. The fossils are located in one of these lenses in the upper part of the Nikiti Fm.

– Nikolaos Fm. It is a fluvio-lacustrine formation outcropping around the village of Agios Nikolaos. It consists of marls, marly limestones, clays, sands and sandstones. Some macromammals were collected from the reddish sands of the lower part of the formation, as well as some micromammals from the clays.

Age
A quite rich mammalian fauna has been collected from NIK which allows its certain age determination to the beginning of early Turolian (MN 11); the NIK fauna is slightly younger than the NKT one, dated to latest Vallesian (MN 10) and slightly older than that of RZO, dated to early Turolian (MN 11) at ~8.2 Ma (Koufos 2006b and references therein).

Morphology
The available material from NIK is very poor including two postcranials which can confirm the presence of *Mesopithecus* in its fauna but cannot allow specific determination at the moment. Thus, it is referred to as *Mesopithecus* sp.

PIKERMI
History
As it was referred above *Mesopithecus* was originally recognized in Pikermi; its holotype is a maxilla with M1-M3 sin described by Wagner (1839) as *M. pentelicus* Wagner, 1839 and figured one year later by Wagner (1840) too. During the 1860's a significant number of *Mesopithecus* remains from Pikermi was collected by A. Gaudry, described under the name *M. pentelici*. Gaudry's collection is housed in MNHN and includes several cranial and postcranial remains (Gaudry 1862-1867). Remains of the Pikermi *Mesopithecus* are also included in Woodward's collection housed in NHML, Wagner's collection in BSPM and in the University of Athens (AMPG collection). Besides these main collections there are several remains of *Mesopithecus* from Pikermi in various institutes (Stuttgart, Berlin, Florence, Turin, Vienna). Several publications and reports on this material have been published but the first complete study of the Pikermi sample was given by Delson (1973) in his doctorat thesis. Two decades later a monograph on Pikermi *Mesopithecus* was published by Zapfe (1991), giving more significance to some undescribed material from AMPG and to the postcranial skeleton. Some *Mesopithecus* remains were also found during the preparation of several big-blocks from Pikermi, collected earlier by various excavators and which remained for many years unprepared in the University of Athens (Theodorou & Roussiakis pers. comm. 2008); this material is unpublished up to now.

Stratigraphy and locality
All the old collections originate from the classical ravine of Pikermi, where the first fossils were found and all the scientists excavated. The first description of the deposits and their stratigraphy are given by Gaudry (1862-1867: pl. 74, fig. 1). According to this description, the basement of the Neogene deposits is the Pentelikon marbles. The Neogene sediments consist of alternated red clays and conglomerates-anglomerates with intercalations of red clays. The fossils are concentrated in lenses intercalated in the red clays. The fossiliferous level, where Gaudry excavated, is situated near the bottom of the ravine and in the red clays. This level probably represents the main site where Gaudry excavated. The stratigraphy of the Pikermi Neogene deposits is given by Marinos & Symeonidis (1974). According to them, the Neogene deposits overlie the marbles and schists of the basement and consist of the following lithology from below to upwards.
– Basal Beds. They are fluvial deposits consisted of loose-cohesive conglomerates, sandstones, marls and clays with all intermediate lithological types;
– Fossiliferous Beds. They are of fluvial-fluvio-lacustrine origin, consisting of the typical reddish clays of Pikermi alternated with conglomerates, sandstones and marshy clays; the latter include micromammals and lacustrine gastropods. The red clays include the lenses with the mammal fossils;
– Calcareous Beds. They overlie all the above mentioned beds in the whole area. They consist of white-yellowish to brownish limestones and marls with conglomerates of lacustrine origin as indicated by the remains of *Melanopsis* Férussac, 1823 and *Planorbis* (Müller, 1774). All the Neogene deposits are covered by a series of Quaternary conglomerates.

Although the Pikermi collections are reported as homogeneous, this cannot be proved, as there are fossiliferous lenses across the ravine in different horizons (Abel 1927: fig. 136), while the faunal data would suggest different stratigraphic levels (Theodorou & Nicolaides 1988).

Age

The lack of stratigraphic data and the doubt about the homogeneity of the Pikermi material gave rise to long discussions about its age which, although there is a general agreement, still continue. The available data of Pikermi suggest an age at the end of middle Turolian (MN 12) at about 7.0 Ma, which is considered as the most possible (Koufos 2006b and references therein). Besides all these age determinations I strongly believe that it is necessary to have a new series of excavations and detailed stratigraphic studies in the classical Pikermi ravine to get certain data which will allow us to determine correctly its fauna and age.

Morphology

As it was referred above, the material of *Mesopithecus* from Pikermi is quite rich, the richest known for the genus. However, its dispersion in several museums and institutes makes its study difficult. Fortunately, I had the opportunity to study most of the Pikermi *Mesopithecus* sample during the last five years visiting various museums and institutes housing it. The main characters of the Pikermi *Mesopithecus* are given below.

It is a colobine monkey having medium size (between *M. delsoni* Bonis, Bouvrain, Geraads & Koufos, 1990 and *M. monspessulanus* Gervais, 1859). The skull is characterized by strong prognathism giving to it a primitive feature (Fig. 2A). The nasals are narrow and triangular-shaped with its posterior border situated at the middle of the orbits; their anterior border form two small processes in the middle of the posterior border of the nasal cavity. The nasal cavity is oval-shaped, large and their posterior border is situated above the short diastema between the canine and P3. The orbits are large, rounded, with large interorbital distance (Fig. 2B-D). The supraorbital torus is strong or weak (depending on the sex), continuous and with glabella. The braincase is rounded with sagittal sutures originating from the orbits and connected in the parietals forming a sagittal crest (Fig. 2B, C) (the sagittal crest is stronger in the males). The zygomatic arches are quite strong starting above the contact between the M1 and M2. The basicranium is flattened with large and rounded foramen magnum and large occipital condyles. The palate is elliptical, deep and its posterior end is situated at the posterior border of the M3 (Fig. 2E, F). The mandible has high ascending ramus vertical to the mandibular corpus, the inferior border of which is straight. The mandibular angle is rounded and projects strongly in the gonial area. The mandibular corpus is shallow and thick; its thickness and depth depend upon the sex, being higher in the males (Fig. 3). The anterior face of the external symphysis is rounded without symphyseal constriction, while the internal symphysis has small *planum alveolare* strongly inclined backwards and a small or absent *fossa genioglossa*. The dentition has the characters of the colobines with bunodont teeth and four cusps (-ids) in the molars except the m3 which has a clear hypoconulid (Figs 2; 3). The incisors are flattened buccolingually, the lower being narrower than the upper ones (the I2 is more triangular-shaped). In the upper ones the I1 is larger than I2. In their lingual surface there are two grooves running across them. The canines have a strong sexual dimorphism being remarkably larger in the males. The upper canine has triangular transverse section with a relatively deep groove running across its mesiolingual surface and a small distal cingular projection. The lower canine is elliptical, curved backwards in the males, with a large and strong distal angular projection and two crests running across its mesial and distolingual surface. The upper premolars are bicuspid with the buccal cusp larger than the lingual one, which is small and disappears early by the attrition. The p3 is asymmetric, situated laterally to the tooth row axis and having one large cuspid extended mesially; it has a relatively small honing facet. The p4 is more symmetrical than the p3 bearing a large buccal and a smaller lingual cuspid, as well as, a mesial and a larger distal fovea. The molars have four cusps (-ids) and the upper ones are more squarish than the lower ones. The M3 has more developed distal fovea (talon) and the m3 a relatively small hypoconulid.

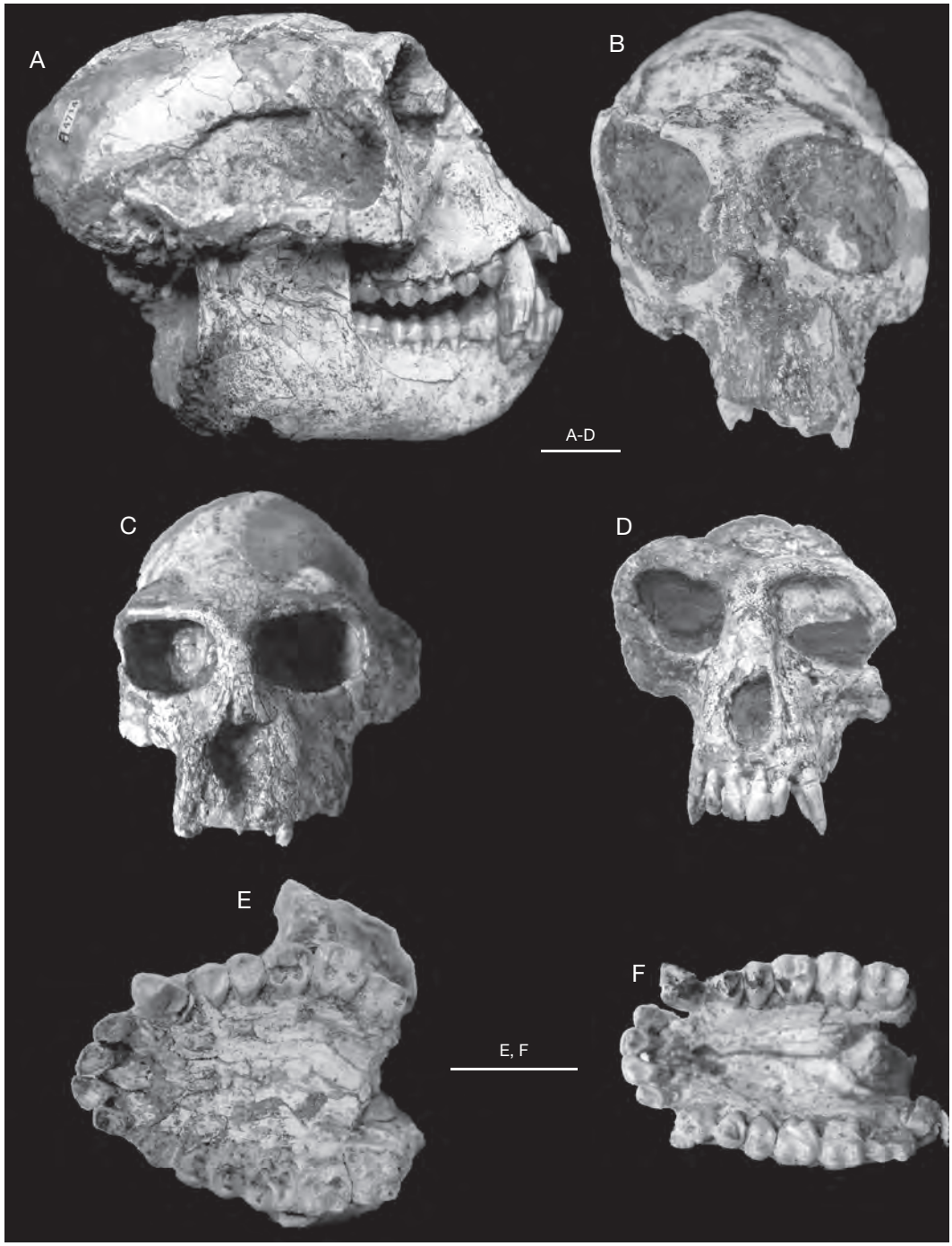

FIG. 2. — Cranial and maxillary remains of *Mesopithecus pentelicus* Wagner, 1839 from Pikermi (PIK), Attica, Greece: **A**, male skull associated with the mandible, NHMW-PIK-A.4714; **B**, female skull, AMPG-PIK-2; **C**, male skull, MNHN-PIK-14; **D**, male facial region, NHML-PIK-M.8947; **E**, male maxilla, NHML-PIK-M.8946; **F**, female maxilla, NHML-PIK-M.8948. Scale bars: 1 cm.

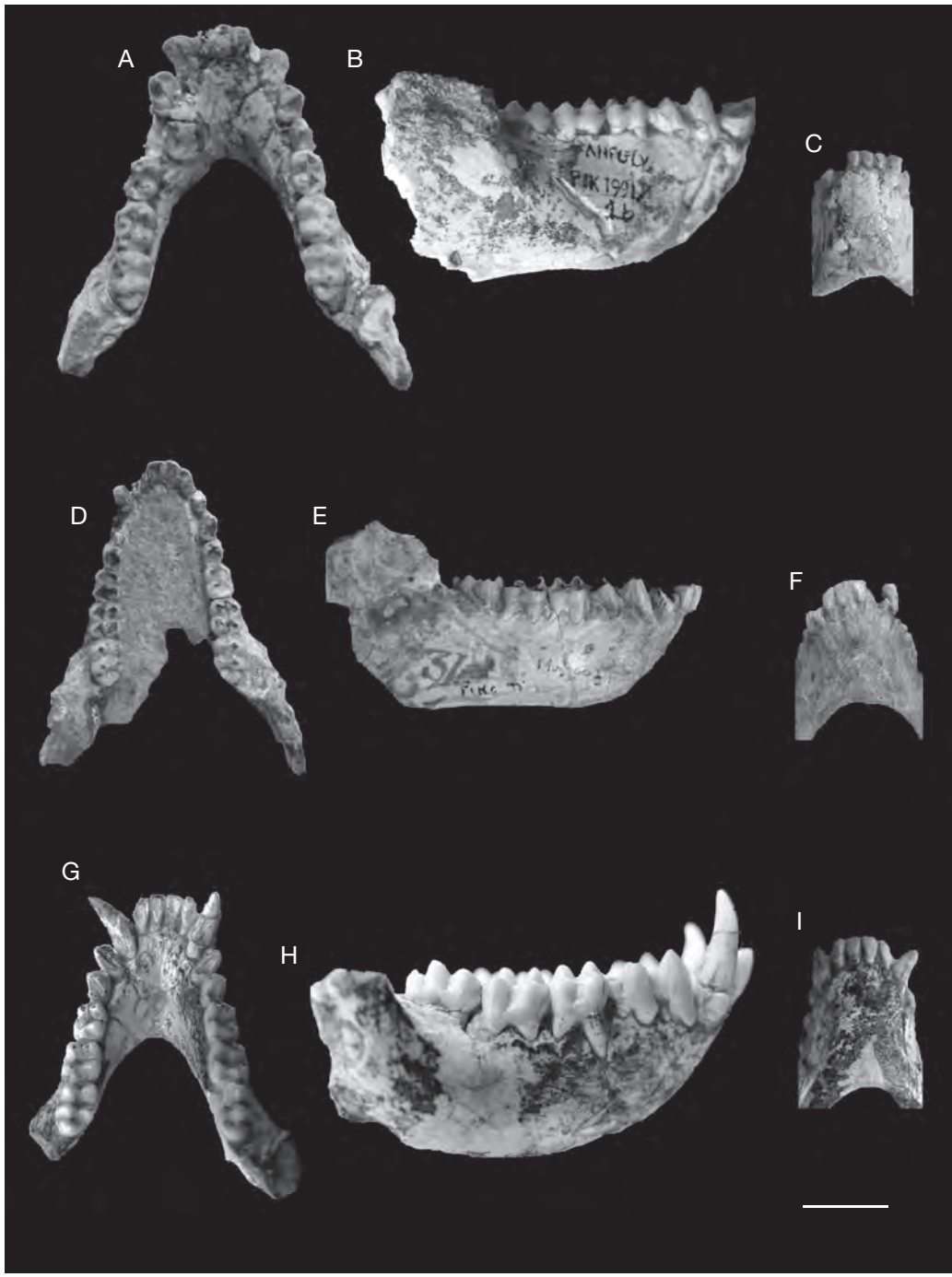

Fig. 3. — Mandibular remains of *Mesopithecus pentelicus* Wagner, 1839 from Pikermi (PIK), Attica, Greece: **A**-**C**, male mandible, AM-PG-PIK-1b; **D**-**F**, female mandible, MNHN-PIK-03; **G**-**I**, male mandible, NHMW-PIK-1998z-01; **A**, **D**, **G**, occlusal views; **B**, **E**, **H**, right ramus; **C**, **F**, **I**, external symphysis. Scale bar: 1 cm.

Axios Valley

History

The late Miocene mammal localities of Axios Valley (Macedonia, Greece) are situated across the river Axios, 25-50 km west of Thessaloniki city (Fig. 1). The first reference about their presence is that of Bourcart (1919) who reported some mammal fossils found near the village of Vathylakkos. During the First World War (1915-1916) the geologist C. Arambourg, who arrived in the area as an officer of the French Army, found some fossils around the village of Vathylakkos. Then, he investigated the area and he found several fossiliferous sites; thus he made a collection which is now stored in MNHN (Arambourg & Piveteau 1929). In 1972 the Laboratory of Geology and Palaeontology of the University of Thessaloniki (Prof. J. K. Melentis and from 1976 the author) and the Laboratoire de Paléontologie des Vertébrés et Paléontologie humaine of the University Paris 6 and after 1980 of the University of Poitiers (Prof. L. de Bonis) started a series of excavations in Axios Valley which still continue. During these field campaigns new fossiliferous sites were discovered and a great amount of fossils has been unearthed, while more than 100 articles have been published. The old Arambourg's collection includes some remains of *Mesopithecus* which come from the localities R-X and R-G (Arambourg & Piveteau 1929). It is worth mentioning that Arambourg's collection is mixed including fossils from different localities of different age; some fossils have locality indications, some others do not and, thus, cannot provide certain data for biochronology and comparisons. During the new excavations several remains of *Mesopithecus* were found in the various localities of Axios Valley, stored in LGPUT (Bonis *et al.* 1990, 1997; Koufos *et al.* 2004).

Stratigraphy and localities

The late Miocene deposits of Axios Valley are divided in three different formations (Koufos 1980, 1990).

– Nea Mesimvria Fm. It outcrops in the southern part of the eastern bank of Axios River. The formation consists of gravels, sands, conglomerates and red clays; their cohesion varies greatly from very hard and compact conglomerates to loose sands and gravels. According to Mercier (1968) the thickness of the formation exceeds 1000 m. In the upper horizons of the formation four fossiliferous localities have been recognized: Pentalophos-1 (PNT), Xirochori-1 (XIR), Ravin de la Pluie (RPl) and Ravin des Zouaves-1 (RZ1);

– Vathylakkos Fm. It overlies normally Nea Messimvria Fm., outcropping in the eastern bank of Axios River around the villages of Vathylakkos, Prochoma and Agionerion. It consists of white-grey sands and gravels, alternated with yellowish sandy clays. Several fossiliferous sites were found in this formation; the majority of Arambourg's collection comes from this formation. The main fossiliferous sites are Ravin des Zouaves-5 (RZO), Prochoma-1 (PXM), Vathylakkos-1, 2, 3 (VLO, VTK, VAT), Ravin du Vatilük or Ravin-G (R-G) and Ravin-X (R-X). The locality R-G corresponds to the new one, named VAT;

– Dytiko Fm. It outcrops in the western bank of Axios River around the village of Dytiko. It mainly consists of yellow-yellowish sands, gravels and sandy clays with intercalations of sandstones, while in the top of the formation there are yellowish fresh water marly limestones. Three fossiliferous sites Dytiko-1, 2, 3 (DTK, DIT, DKO) have been discovered in this formation.

The *Mesopithecus* bearing localities of Axios Valley are RZO, VTK, VAT and R-X of Vathylakkos Fm., as well as, all the localities of Dytiko Fm.

Age

The available fauna of the Axios Valley localities allow their certain biochronological dating. The locality RZO is dated to early Turolian, MN 11, the localities VTK, VAT and R-X to the lower middle Turolian, MN 12, and the Dytiko localities to late Turolian, MN 13 (Koufos 2006b and references therein). The magnetostratigraphic record suggests an estimated age of ~8.2 Ma for RZO and ~7.3 Ma for VTK and VAT localities (Sen *et al.* 2000; Koufos, unpubl. data).

Morphology

Locality RZO. The available material from RZO includes only mandibular remains (Fig. 4), described as a new species *M. delsoni* (Bonis *et al.* 1990).

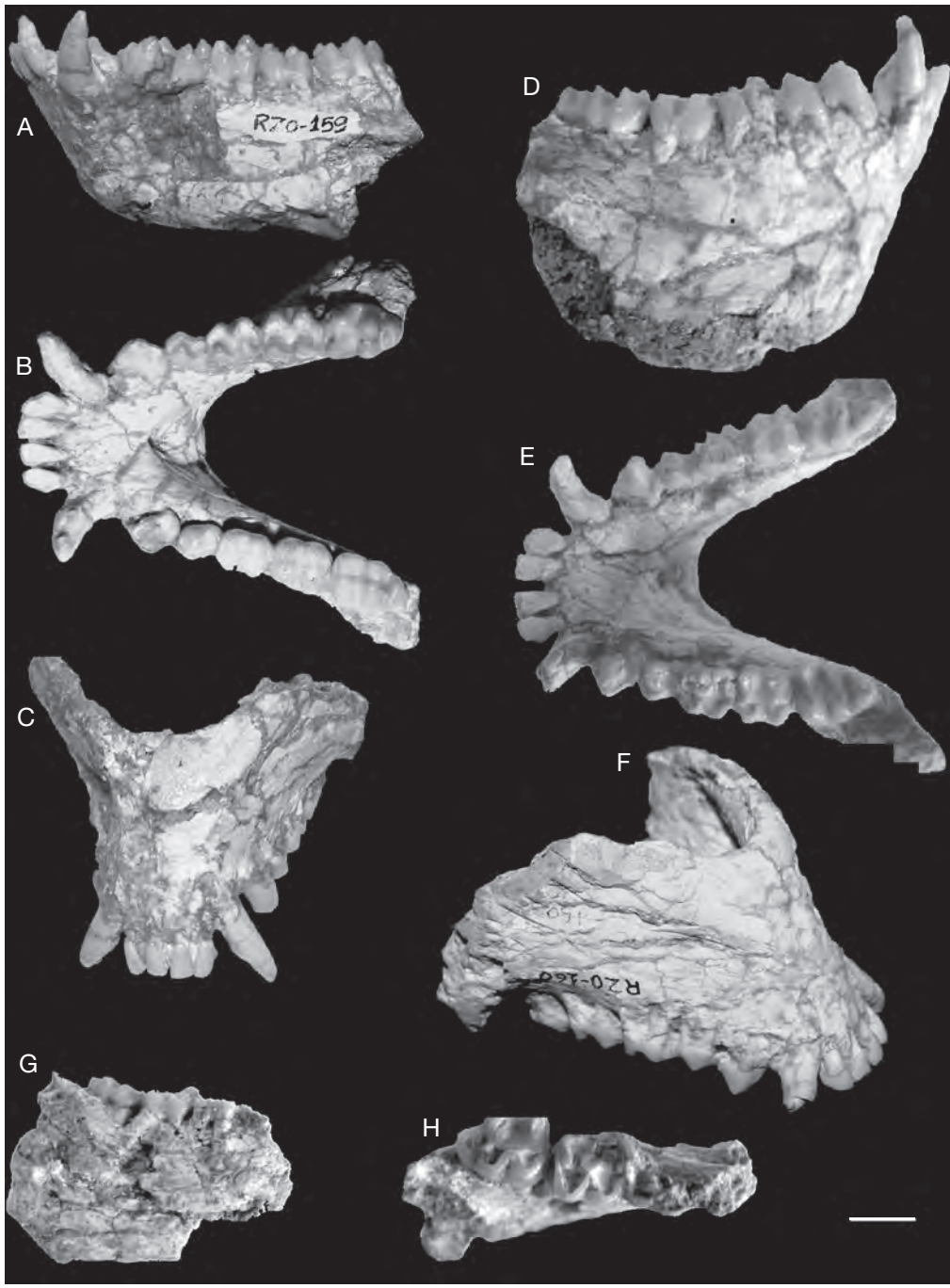

FIG. 4. — Mandibular remains of *Mesopithecus delsoni* Bonis, Bouvrain, Geraads & Koufos, 1990 from Ravin des Zouaves-5 (RZO), Axios Valley, Macedonia, Greece: **A**-**C**, male mandible, LGPUT-RZO-159; **D**-**F**, male mandible, LGPUT-RZO-160; **G, H**, mandibular fragment of a female individual, LGPUT-RZO-327; **A**, left ramus; **B**, **E**, **H**, occlusal views; **C**, **F**, external symphysis; **D**, right ramus; **G**, lateral view. Scale bar: 1 cm.

The mandibular corpus is very deep distinguishing the RZO mandibles from those of *M. pentelicus*. Contrary to *M. pentelicus,* the anterior symphysis is flattened and has lateral symphyseal constriction, while the internal symphysis has slightly inclined backwards *planum alveolare* and large *fossa genioglossa*. The inferior transverse torus is thick and prominent. The teeth are large, the p3 has large honing facet versus a small one in *M. pentelicus* and the m3 has a large hypoconulid versus a small one in *M. pentelicus*. In the distal face of the hypoconulid there is a deep groove giving to it a bicuspid aspect. The Principal Component Analysis (PCA) of the RZO and PIK samples indicates that the RZO sample is separated from *M. pentelicus* having relatively larger mandibular and dental dimensions, as well as smaller lower canine (Koufos in press). All the above mentioned morphological and metrical differences separate the RZO sample from the typical *M. pentelicus* and allowed Bonis *et al.* (1990) to erect the new species *M. delsoni*.

Locality VTK. The *Mesopithecus* sample from VTK is a recent collection and includes some cranial and mandibular remains (Figs 5; 6), housed in LGPUT and described earlier (Bonis *et al.* 1997; Koufos *et al.* 2004). Some dental remains stored in MNHN and referred to as Braillon's collection seem to originate from VTK too (Bonis *et al.* 1997). The VTK *Mesopithecus* is larger in size than the typical *M. pentelicus* from Pikermi and closer to *M. delsoni* from RZO. The orbits are more squarish with rounded corners and they have supraorbital torus which is separated in two parts by a depression in the area of the glabella. The supraorbital torus is stronger in the male skull than in the female one (Fig. 5). A sulcus is present behind the supraorbital torus. The interorbital distance is large being 10.8 mm in VTK-61 and ~10 mm in VTK-56. The nasal cavity is deep elliptical-shaped with its posterior border situated above the contact between the P4 and M1. The lacrymal fossa is well distinguished and it is extended into the maxilla. The zygomatic arches are strong and their base is situated above the first lobe of the M2. The cranial roof is damaged in VTK-61 but in the skull VTK-56 the sagittal sutures and crest are weakly developed as in the female skulls of *M. pentelicus* from Pikermi. The palate is elliptical and deep with wide and relatively shallow choanae, the anterior border of which is situated at the level of the M3. The mandible VTK-62 has flattened anterior symphysis with symphyseal constriction. The internal symphysis has slightly inclined backwards *planum alveolare* and large *fossa genioglossa* (Fig. 6E, G). The mandibular corpus is not very deep, having similar depth to that of *M. pentelicus* from Pikermi. The upper teeth of the Vathylakkos sample have the general morphology of *Mesopithecus* and similar dental size to *M. pentelicus*. The upper premolars have relatively larger lingual cusp (protocone) than that of *M. pentelicus*. The p3 has large honing facet and the m3 large hypoconulid with a groove in its distal face, like in *M. delsoni*. The PCA of the upper and lower dental dimensions of the VTK sample with those of *M. pentelicus* and *M. delsoni* indicates its separation from both taxa having intermediate characters (Koufos in press). The VTK *Mesopithecus* has characters between *M. delsoni* and *M. pentelicus* and thus is referred to as *M. delsoni/pentelicus*. In the earlier articles it is referred as *M.* aff. *M. pentelicus* (Bonis *et al.* 1997; Koufos *et al.* 2004) but it is better to refer this as *M. delsoni/pentelicus* because of its similarities to both species; it can be considered as an evolutionary stage between the two species.

Localities R-G and R-X. The material from these two localities includes that of Arambourg's collection housed in MNHN (Fig. 4). According to Arambourg & Piveteau (1929: 74), *Mesopithecus* was found in Ravin du Vatilük or Ravin-G (R-G) and in Ravin-X (R-X). However, in the faunal lists given for each locality (Arambourg & Piveteau 1929: 13, 14) *Mesopithecus* is referred only from R-X. The locality R-G corresponds to the new one referred as VAT; both VAT and R-X are located in Vathylakkos Fm. The type of fossilization and the colour of the sediments indicate that most specimens of the Arambourg's collection originated from VAT but one specimen (MNHN-SLQ-940+941) possibly comes from R-X. The specimens from VAT have similar morphology to those from VTK and must belong to the same morphotype, *M. delsoni/pentelicus*. The specimen from R-X is a small part of the anterior mandible

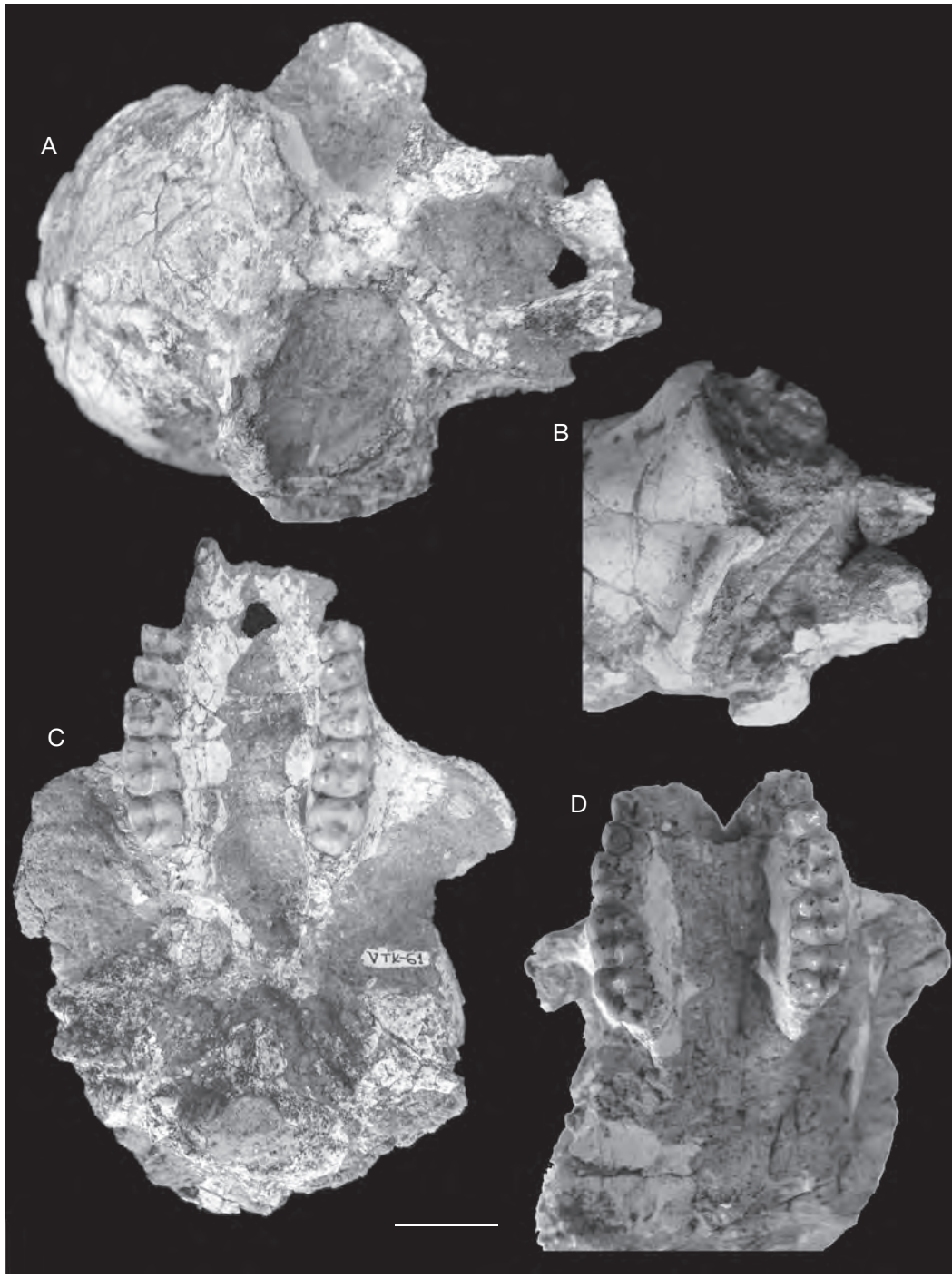

Fig. 5. — Cranial remains of *Mesopithecus delsoni/pentelicus* from Vathylakkos-2 (VTK), Axios Valley, Macedonia, Greece: **A**, **C**, male skull, LGPUT-VTK-61; **B**, **D**, female skull, LGPUT-VTK-56; **A**, **B**, facial views; **C**, **D**, occlusal views. Scale bar: 1 cm.

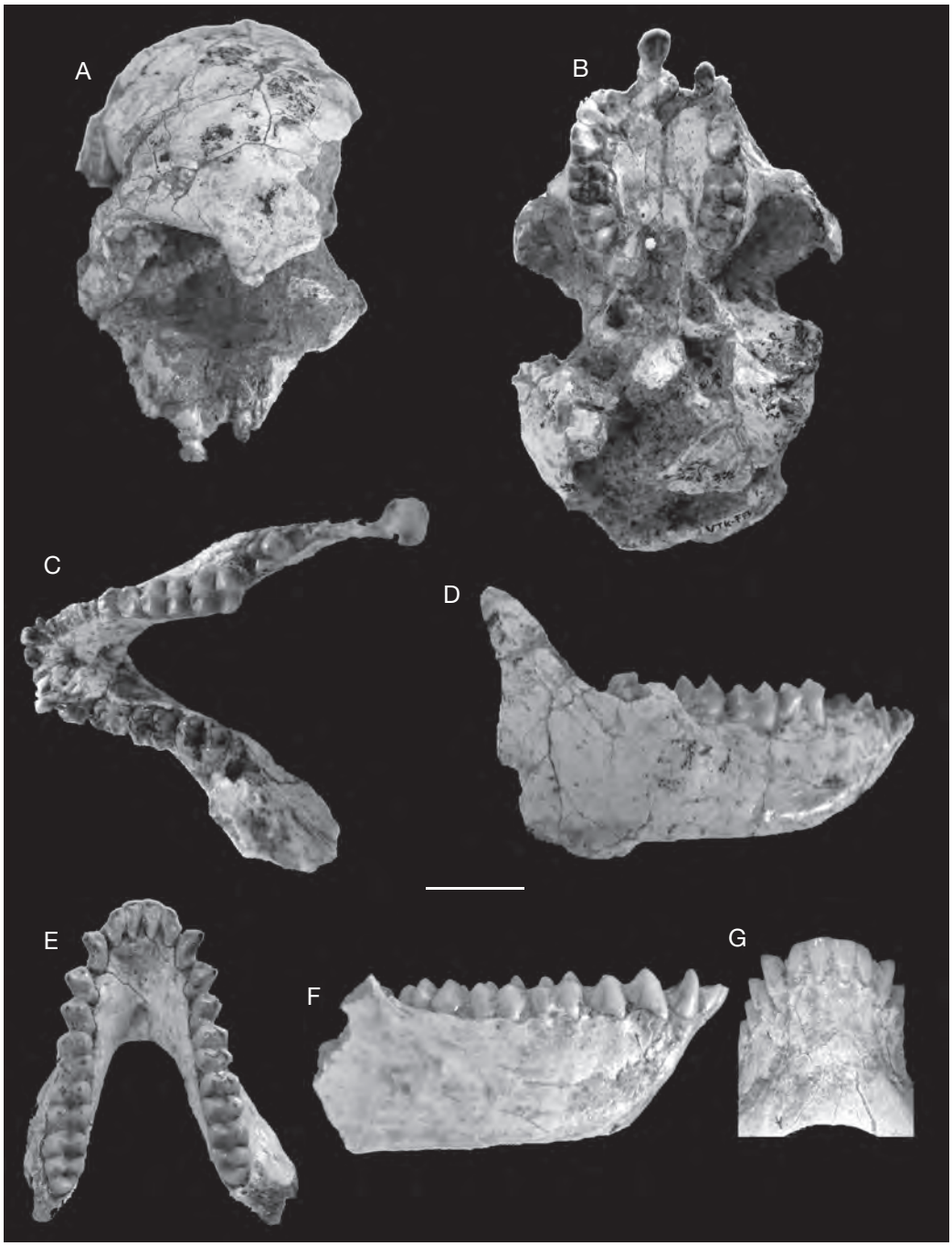

FIG. 6. — Cranial and mandibular remains of *Mesopithecus delsoni/pentelicus* from Vathylakkos-2 (VTK), Axios Valley, Macedonia, Greece: **A**, **B**, young male skull, LGPUT-VTK-78, facial (**A**) and occlusal (**B**) views; **C**, **D**, young male mandible, LGPUT-VTK-78, occlusal (**C**) and right ramus (**D**) views; **E-G**, female mandible, LGPUT-VTK-62, occlusal view (**E**), right ramus (**F**) and external symphysis (**G**). Scale bar: 1 cm.

FIG. 7. — Cranial and mandibular remains of *Mesopithecus* Wagner, 1839 from the localities of Dytiko (DTK, DIT, DKO), Axios Valley, Macedonia, Greece: **A**, **B**, *M.* aff. *pentelicus*, male skull, LGPUT-DKO-38, occlusal (**A**) and facial (**B**) views; **C**, **D**, same, partial mandible, LGPUT-DKO-38, right ramus (**C**) and occlusal views (**D**); **E**, **F**, *M.* cf. *monspessulanus*, partial mandible, LGPUT-DIT-22, occlusal view (**E**) and left ramus (**F**).

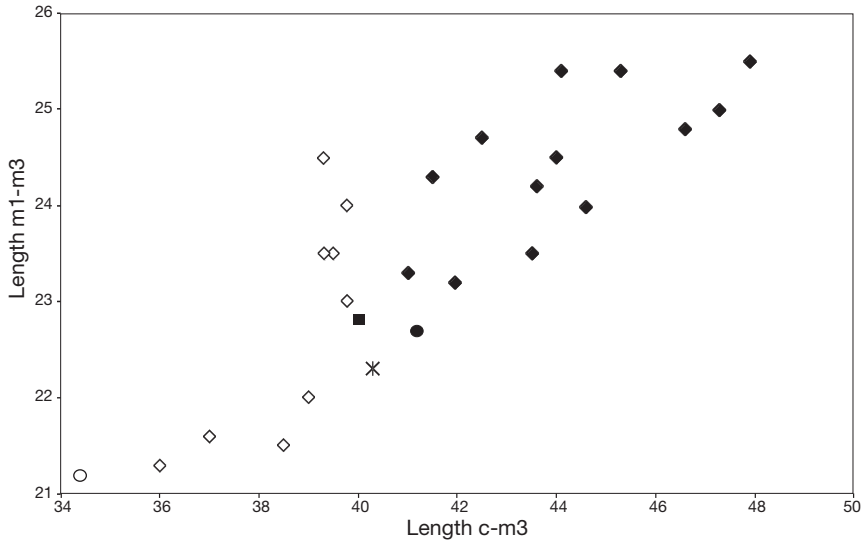

FIG. 8. — Scatter diagram comparing the length c-m3 versus molar length of *M. pentelicus* Wagner, 1839, *M. monspessulanus* Gervais, 1859 and *M.* cf. *monspessulanus* from DIT. ◆, M. pentelicus, PIK, male; ◇, same, female; ✱, *M.* cf. *monspessulanus*, DIT-22; ■, *M. monspessulanus*, Villafranca d'Asti, male (Delson 1973); ●, *M. monspessulanus*, Montpellier, male (Delson 1973); ○, same, female (Delson 1973).

which has stronger similarities (flattened external symphysis with symphyseal constriction, slightly inclined *planum alveolare*, large *fossa genioglossa*, deep mandibular corpus, strong honing facet in the p3) to the RZO *Mesopithecus* and could belong to *M. delsoni*; thus it is referred to as *Mesopithecus* cf. *M. delsoni* because of the limited material.

Dytiko localities. The Dytiko material of *Mesopithecus* is quite rich including both cranial and postcranial remains. The material from DKO includes a partial male skull associated with the mandible, DKO-38 (Fig. 7). Although it has slightly smaller size than *M. pentelicus* (Table 1), a more careful comparison indicates some morphological differences. The orbits are relatively smaller with stronger supraorbital torus and the lower incisors are smaller than those of the Pikermi *M. pentelicus*. The DKO postcranials have also some differences from those of the typical *M. pentelicus* (Bonis *et al.* 1990). The epicondylus medialis of the humerus is less reflected backwards in comparison to that of the Pikermi *M. pentelicus*. The radius has more oval section at the shaft than *M. pentelicus*, while the facet for the ulna is small in comparison to that of *M. pentelicus*. Based to these morphological differences of the DKO material from the Pikermi *M. pentelicus*, it is referred to as *Mesopithecus* aff. *M. pentelicus*. The material from DIT includes a strongly deformed skull which is similar both to Pikermi and DKO material and it is also referred to as *Mesopithecus* aff. *M. pentelicus* (Bonis *et al.* 1990). The material from DTK (Fig. 5) is similar to Pikermi and it is referred to as *Mesopithecus* cf. *M. pentelicus* (Bonis *et al.* 1990).

TABLE 1. — Comparative measurements of *Mesopithecus* Wagner, 1839 from Pikermi and Dytiko.

	DKO-231	***M. pentelicus* Wagner, 1839 (Pikermi)**	
	male	male	female
Orbit length	19.5	20.0-25.5	
Orbit breadth	24.0	24.1-30	
Li1	3.2	(3.8) 4.39 (5.4)	(3.8) 4.14 (4.4)
Bi1	2.7	(2.7) 3.21 (3.6)	(2.0) 2.84 (3.4)
Li2	4.0	(4.0) 4.60 (5.1)	(4.0) 4.40 (4.9)
Bi2	2.9	(2.7) 3.38 (3.9)	(2.6) 3.02 (3.5)

Fig. 9. — Mandibular remains of *Mesopithecus* Wagner, 1839 from the localities of Chomateres (CHO), Attica, Greece and Perivolaki (PER), Thessaly, Greece: **A**-**D**, *M. pentelicus* Wagner, 1839, male mandible, NHMW-CHO-1623/1a, right ramus (**A**), left ramus (**B**), external symphysis (**C**) and occlusal view (**D**); **E**-**G**, *M. delsoni*/*pentelicus*, female mandible, LGPUT-PER-200, occlusal view (**E**), left ramus (**F**) and external symphysis (**G**); **H**, **I**, same, left male mandibular ramus, LGPUT-PER-1284, external (**H**) and occlusal (**I**) views. Scale bar: 1 cm.

Among the material of DIT there is a male mandible (DIT-22) which is smaller than the male mandibles of the Pikermi *Mesopithecus*; its dental dimensions are remarkably smaller than those of the male *M. pentelicus* of Pikermi ranging between the latter and the male *M. monspessulanus* (Fig. 8). The multivariate comparison of its mandibular and dental dimensions with *M. pentelicus* clearly confirms its smaller size (Koufos in press). The small size of DIT-22 suggests similarities to *M. monspessulanus* but the limited material cannot allow a certain determination and thus it is referred to as *Mesopithecus* cf. *M. monspessulanus* (Bonis *et al.* 1990).

Chomateres

History

In 1971 a new fossiliferous site was discovered in Attica, named Chomateres or Kisdari (Fig. 1). During the excavating activities in a clay-pit of the area some mammal fossils were found and the University of Athens made the first collection (Marinos & Symeonidis 1972). The University of Athens in collaboration with NHMW continued the excavations in Chomateres during 1972-1973, while H. de Bruijn washed material and found some micromammals in the marshy clays of the area (Marinos & Symeonidis 1974). The collected fauna of the large mammals is similar to that of Pikermi and includes some remains of *Mesopithecus* (Fig. 7A, B). The Chomateres mammal collection is unpublished except for some general information about the locality and fauna and some few taxa, like *Mesopithecus* and *Metailurus* Zdansky, 1924 (Marinos & Symeonidis 1972, 1974; Symeonidis *et al.* 1973; Symeonidis 1978; Zapfe 1991). The CHO collection is housed in AMPG except for the *Mesopithecus* sample which is in NHMW, at the moment. The initial description of the Chomateres *Mesopithecus* is given by Zapfe (1991) who described a mandibular fragment as a new subspecies, named *M. pentelicus microdon.*

Stratigraphy and locality

The locality of Chomateres is situated about 2.5 km east of the classical Pikermi ravine. The stratigraphy of the Neogene deposits is similar to that given for Pikermi (see above).

Age

Based to the preliminary published articles about Chomateres a faunal list is given by Koufos (2006b); the fauna is similar to that of Pikermi, suggesting a middle Turolian age, MN 12. In the updating of the MN biozones (Mein 1990) Chomateres is considered as slightly older than Pikermi. A similar age is also proposed by de Bruijn *et al.* (1992), Bonis & Koufos (1999) and Koufos (2006b). However, only the study and comparison of the fauna with that of Pikermi and other Greek localities will provide certain data about the precise age of the Chomateres fauna.

Morphology

The available Chomateres sample of *Mesopithecus* includes only two mandibular fragments (Fig. 9A-D). The mandible NHMW-CHO-1613/1a is similar to that of Pikermi but it has smaller tooth rows, possibly due to the very worn dentition; its mandibular dimensions put it in the group of *M. pentelicus* (Koufos in press). The other mandible (NHMW-CHO-1613-/1b) has mandibular and dental dimensions similar to *M. pentelicus* but it has some minor morphological differences. The anterior face of the symphysis is less convex (more flattened than in *M. pentelicus*), there is a weak symphyseal constriction, a slightly larger *fossa genioglossa* and a larger honing facet in the p3. However, both CHO mandibles cannot be separated from *M. pentelicus* at the moment and they are referred to as *M. pentelicus* (Koufos in press). The presence of some "*delsoni*" characters in the CHO sample should be considered as an indication for an age slightly older than Pikermi.

Perivolaki

History

The locality of Perivolaki was discovered in 1996 by some geologists of IGME (Institute of Geological and Mineralogical Exploration, Athens). The information about the presence of the fossils was given to the author who went there and made a surface collection saving some fossils. Next year, a team of palaeontologists from the LGPUT, led by the author, started a series of excavations which continued until 2004. During these field trips a great amount of fossils have been unearthed. All Perivolaki

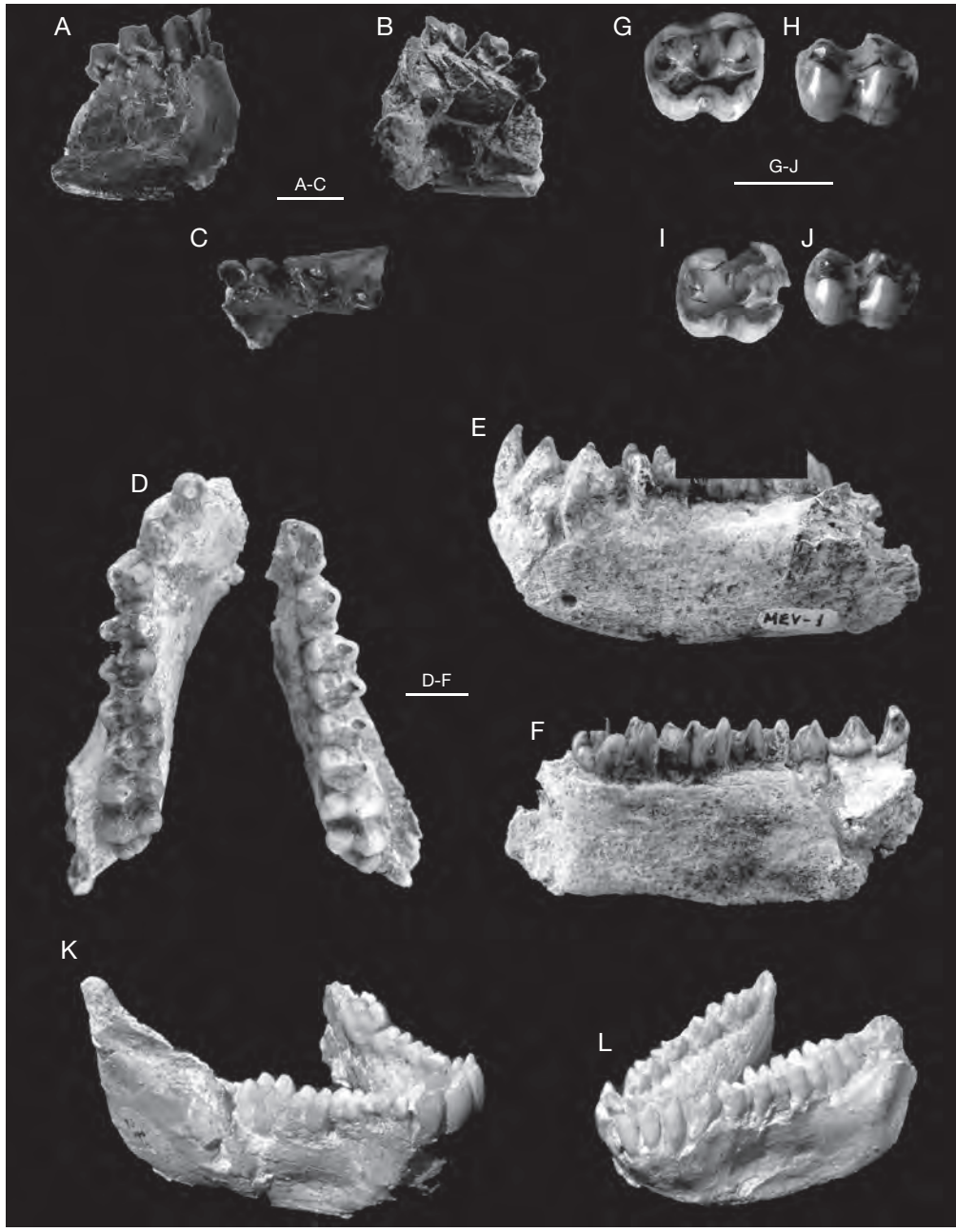

Fig. 10. — Mandibular remains of *Mesopithecus* Wagner, 1839 from Maramena (MAR), Serres Basin Macedonia, Greece, *Dolichopithecus* Depéret, 1889 from Megalon Emvolon (MEV) and Ptolemais (PTL), Macedonia, Greece and *Paradolichopithecus* Necrasov, Samson & Radulesco, 1961 from Vatera (VTR), Lesvos Island, Greece: **A**-**C**, *Mesopithecus* sp., AMPG-MAR-040, right female mandibular fragment with i2-p4, labial (**A**), lingual (**B**) and occlusal (**C**) views; **D**-**F**, *Dolichopithecus ruscinensis* Depéret, 1889, female mandible, LGPUT-MEV-1, occlusal view (**D**), left labial ramus (**E**) and left lingual ramus (**F**); **G**, **H**, same, M2, AMPG-PTL-nn1, occlusal (**G**) and labial (**H**) views; **I**, **J**, same, M2, AMPG-PTL-nn2, occlusal (**I**) and labial (**J**) views (photos kindly provided by Prof. C. Doukas); **K**, **L**, *P. arvernensis* (Depéret, 1929), two mandibles AMPG-VTR-114F (**K**) and AMPG-VTR- (**L**) (photos kindly provided by Dr G. Lyras). Scale bars: 1 cm.

collection is stored in LGPUT and it was published in a complete volume of *Palaeontographica* (Koufos ed. 2006e). The Perivolaki collection includes some remains of *Mesopithecus*, which were described by Koufos (2006a).

Stratigraphy and locality
The locality of Perivolaki is situated near Velestinon town about 40 km southwest of Volos city, Thessaly, Central Greece (Fig. 1). The Neogene stratigraphy of the Perivolaki wider region is not known but our investigations in the neighbouring area allow the distinction of four different lithostratigraphic units (Koufos *et al.* 1999; Sylvestrou & Koufos 2006):
– Unit-A consists mainly of white-grey lacustrine massive marls and marly limestones with a visible thickness of 50-60 m;
– Unit-B is characterized by interbedded, green-brown fine to coarse sediments consisting of brownish-greenish clays alternating with sands, sandstones and marly-sandy limestones with a thickness of 60-80 m. The fossiliferous site is located in the upper part of the Unit-B;
– Unit-C consists of red-brown conglomerates alternating with yellowish clays and locally with reddish clays, having a thickness of ~100 m;
– Unit-D includes the recent deposits consisting of terrestrial red clays alternating with clayey sands and silts.

Age
The biochronological data suggests a middle Turolian (MN 12) age for Perivolaki, while the palaeomagnetic record indicates a correlation to Chron C3Br.2r, suggesting an age between 7.3 and 7.1 Ma (Koufos *et al.* 2006).

Morphology
The Perivolaki *Mesopithecus* sample consists of mandibular remains only (Fig. 9E-I). The available female mandible PER-200 is well preserved and characterized by intermediate size and morphology between *M. pentelicus* (similar dental dimensions and low mandibular corpus) and *M. delsoni* (flattened anterior symphysis with symphyseal constriction, small and roughly inclined backwards *planum alveolare*, large *fossa genioglossa*, large honing facet in the p3, and large hypoconulid in the m3). All these characters suggest similarities to the Vathylakkos *Mesopithecus* and thus it is determined to as *Mesopithecus delsoni/pentelicus* (Koufos 2006a, in press).

MARAMENA
History
The locality of Maramena was discovered in an artificial outcrop made by the uranium exploration activities of "Demokritos" (now IGME) in the 1970's. A surface collection was made by some geologists of IGME and later by H. de Bruijn and C. Doukas. A preliminary list of the Maramena fauna is given by Karistineos (1984). Then the University of Athens in collaboration with the Universities of Utrecht and Mainz excavated and collected both micro- and macro-mammals. The micromammals are rich but the macromammals are relatively few and include several remains of *Mesopithecus*, mainly isolated teeth. The Maramena material is housed in AMPG and was described in a separate volume of *Münchner Geowissenschaftliche Abhandlungen* (Schmidt-Kittler 1995).

Stratigraphy and locality
The locality of Maramena is situated in Serres Basin, about 10 km north of Serres town (Fig. 1). The Neogene deposits of the area can be divided in the following formations (Armour Brown *et al.* 1977):
– Lefkon Fm. which overlies unconformably the basement and has a thickness of ~250 m. It consists of polymict conglomerates and coarse unsorted arkose with intercalations of fine grained sediments (arkosic sandstones, siltstones, mudstones, marls and lignites). The locality MAR is situated in the upper part of the formation in the ligniferous beds;
– Georgios Fm. which is ~100 m thick and consists mainly of carbonate clastic sediments and sandy limestones interfingered with a breccia composed of granitic blocks. The thin sediments include a marine and brackish fauna, well known in the southern part of the basin;
– Spilia Fm. It has a thickness of ~300 m and consists mainly of white well-sorted sandstones with sporadic lenses of well-rounded pebbles. In the center of the area the sandstones interfinger with

carbonaceous mudstones, siltstones and fine sandstones. The Spilia Fm. includes several fossiliferous levels with small mammals.

Age
The rich micromammalian fauna of Maramena allowed its age determination to the Turolian/Ruscinian boundary, MN 13/14 (Schmidt-Kittler *et al.* 1995). However, the whole fauna has more Miocene feature and thus an age to the uppermost Turolian is quite possible (Koufos 2006b).

Morphology
The *Mesopithecus* sample of Maramena includes mainly isolated teeth, as well as some mandibular fragments (Fig. 10A-C). The morphology of the teeth is similar to *Mesopithecus*. The honing facet of the p3 and the hypoconulid of the m3 are small. In AMPG-MAR-040 the horizontal ramus is broken but its small height below p3 (~18.3 mm) indicates similarities with *M. pentelicus*. The material has been determined to *M. pentelicus* (Kullmer & Doukas 1995) but after the discoveries in Axios Valley and Perivolaki (see above) needs a revision. However, the isolated teeth cannot allow a comparison with the new material as the distinctive characters are mainly recognized in the mandible and skull. Thus, it is better to refer this as *Mesopithecus* sp., at the moment.

Kryopigi
The locality of Kryopigi is situated in Chalkidiki (Macedonia Greece) and it was found during the 1990's (Fig. 1). The *Mesopithecus* sample includes a skull associated with the mandible and a maxillary fragment. The Kryopigi fauna is not studied and thus the few available data cannot allow a certain age determination except for late Miocene. Although the *Mesopithecus* material is refered to *M. pentelicus* (Tsoukala & Bartziokas 2008), detailed descriptions and comparisons with other *Mesopithecus* are necessary to assign a specific level to this sample. Keeping in mind all the above mentioned, the Kryopigi sample must be referred as *Mesopithecus* sp. at the moment, waiting for more precise morphological study, comparisons and dating which will allow a certain attribution.

PLIOCENE LOCALITIES

Megalon Emvolon
History
The locality of Megalon Emvolon was discovered by C. Arambourg at the beginning of the 20th century (see Arambourg & Piveteau 1929, chapter 3); it is referred as "Falaise de Karabouroun" (Arambourg & Piveteau 1929). The Arambourg's collection includes few specimens from Megalon Emvolon, housed in MNHN. During the 1970's several palaeontologists visited the area and collected isolated specimens which are mainly housed in Athens and Utrecht. In 1989 the author visited the area and found some small concentrations of fossils dispersed in the sediments of the area. Among them there were the two branches of a cercopithecid mandible (Koufos *et al.* 1991a). Our efforts to get more fossils in these sites, where we found the initial material, were unsuccessful. The fossils are dispersed in the sediments and there is not any fossiliferous level or large fossiliferous lenses. Thus, we go there from time to time and check if some fossils have appeared by the erosion.

Stratigraphy and locality
The locality of Megalo Emvolon is situated ~20 km south of Thessaloniki city in a cap, named Megalon Emvolon, marking the entrance of Thessaloniki Gulf. Some data about the lithology of the sediments are given by Arambourg & Piveteau (1929); they mentioned reddish marls (~3 m thick) at the bottom of the section, followed by grey marls with sands and gravels (~30 m) and gravels-pebbles at the top (~15 m). A more detailled lithostratigraphy of the section is given by Koufos *et al.* (1991a: fig. 1).
– Lower Sands. The lower part of the section consists of fluvial deposits, mainly sands and gravels with cross-bedding and with lenses or lenticular intercalations of sandstones.
– Red-brown Sands. They overlie the Lower sands and consist of red to brown sands and gravels, red-sands with red-clay and intercalations of conglomerates and calcitic concretions.
– Upper Sands. In the upper part of the section there are fluvial sands, with cross-bedding, intercalations of conglomerates and calcitic concretions. The upper part of the Upper Sands is more clayey.

As referred above there is not any fossiliferous level in Megalon Emvolon, but there are small concentrations of fossils dispersed in the outcrop. Based to our collection there are three different fossiliferous levels. The Megalon Emvolon 1 (MEV), situated at the bottom of the section (near the sea), the Megalon Emvolon 2 (MEM), situated at the bottom of the Upper Sands and the Megalon Emvolon 3 (MEL), situated in the clayey part of the Upper Sands.

Age

Based to the available faunal data of Megalon Emvolon a late Ruscinian (MN 15) age is proposed for it (Koufos 2006b and references therein).

Morphology

The sole known cercopithecid mandible (MEV-1) belongs to an aged female individual (Fig. 10D-F). The mandibular corpus is deep and thick with a single mental foramen below the anterior root of the p3. The canine is small, indicating a female individual, and characterized by a distal crest beginning from the base to the middle of the canine's height. The p3 has a large protoconid and talonid basin, as well as strong lingual and distal basal cingulum. The p4 is narrow and characterized by the approximately equal height of the metaconid and protoconid but the latter cuspid is wider; this character is quite clear in *D. ruscinensis* (Delson 1973). The m2 is larger than m1 and both have metaconid and entoconid of equal height, while they are higher than the protoconid and hypoconid. The distal breadth of the m1 is greater than the mesial one. The m3 is large with well-developed hypoconulid situated between the midline of the tooth and the line connecting the buccal cuspids. In the lingual part of the talonid there is an elevation of the distal cingulum, indicating the beginning of a sixth cuspid. The mesial breadth of the m3 is larger than the distal one and the distal breadth of the m2. The size of the teeth fits quite well to the size of those of *D. ruscinensis* (Koufos *et al.* 1991a). Keeping in mind all the above mentioned, the mandible MEV-1 is attributed to *D. ruscinensis*. This is the first evidence of the presence of *Dolichopithecus* in eastern Mediterranean. Recently a new species *D. balcanicus* has been described from Bulgaria and the MEV mandible was included to it (Spassov & Geraads 2007).

PTOLEMAIS BASIN

History

The cercopithecid material found in the Ptolemais lignitic basin was discovered at the end of the 1990's by H. de Bruijn and C. Doukas working there for micromammals. Two cercopithecid teeth were found in the ligniferous pit, named South Field and they were described by Doukas & de Bruijn (2002).

Stratigraphy and locality

Ptolemais Basin is located in western Macedonia (Greece) about 140 km west of Thessaloniki city (Fig. 1). It is part of a large tectonic depression, filled by Neogene-Quaternary deposits including lignites. The Neogene deposits of Ptolemais Basin are divided in three main formations (Koufos & Pavlides 1988; Steenbrink 2001):

– Basal Fm. consisting mainly of gravels, pebbly breccia and conglomerates. There is no outcrop of this formation;

– Vegora Fm. consisting of green sands, sand-silts, grey marls and yellowish sandy silts. The formation is characterized by the presence of lignites (xylitic type). The Vegora Fm. includes a rich megaflora which indicates a late Miocene age (Kvaček *et al.* 2002);

– Ptolemais Fm. outcroping in the whole Ptolemais area and including the main lignitic deposits of the area. The Ptolemais Fm. consists mainly of sandy-silts, silts, sands and clays with lignitic intercalations. The formation can be distinguished in a lower and upper ligniferous level, separated by an intermediate without lignites part (Koukouzas *et al.* 1979);

– the Neogene deposits overlied unconformably by Quaternary mainly lacustrine-fluviolacustrine deposits.

Age

The available faunal data of Ptolemais Fm. suggest a Ruscinian age (Koufos 2006b and references therein) for it; more precisely a late Ruscinian (MN 15) age is referred for Notio Mb where *Dolichopithecus* was found (de Bruijn pers. comm. 2008).

Morphology

The two available M2 are quite worn and their morphology is not clear (Figs 10G-J). However,

their characters indicate a colobine monkey, while their dimensions fall within the range of *Dolichopithecus ruscinensis* from Perpignan (Doukas & de Bruijn 2002). Thus, the authors identified them to this species, despite the material paucity and limited morphology.

VATERA

History

The fossiliferous site of Vatera is located in Lesvos Island (Aegean Sea) and was discovered in 1997 (Fig. 1). The fossils were found during the construction of a road at an olive yard. Subsequently, the University of Athens and the Natural History Museum of Leiden collected some fossils and the year after they started a systematic excavation of the locality. In 2000 the excavations were ended due to lack of further fossils. During these field campaigns several fossils had been collected, among them some cercopithecids remains (Van der Geer & Sondaar 2002; de Vos *et al.* 2002; Sondaar *et al.* 2006; Lyras & Van der Greer 2007).

Stratigraphy and locality

The locality of Vatera is situated in the southern part of Lesvos Island (Fig. 1) about 45 km from Mytilini town. The Neogene deposits of the Vatera region consist of a series of lacustrine-brackish deposits (lower part) which are overlied by a series of fluvial deposits (upper part). The lacustrine-brackish deposits consist of marly limestones with sandstone and tuffite's intercalations. The fluvial deposits consist of alternating sandy clays, sandy conglomerates, silts and breccia-conglomerates (Drinia *et al.* 2002). The mammal fossils were found in the upper fluvial horizons of the sequence and they are dispersed in small pockets.

Age

The Vatera Fm. includes a number of fossiliferous sites (F, DS, E, U, U, T, V) corresponding to different fossil pockets. The richest fauna including the cercopithecid is F, dated to middle Villafranchian *s.l.*, or MN 17 (late Pliocene), at ~2.0 Ma. The faunas from DS and E sites are dated to late Pliocene, while those of the U, H, T and V sites are too poor to allow a certain determination of their geological age (de Vos *et al.* 2002; Lyras & Van der Geer 2007).

Morphology

The sample of cercopithecids from Vatera includes two mandibles, some isolated teeth, including an adult upper canine, and several postcranials (Fig. 10K, L) (Van der Geer & Sondaar 2002). According to Van der Geer (pers. comm. 2008) the lower dentition of the Vatera *Paradolichopithecus* is typically papionin. The anterior teeth are large and the canine bears a clear sexual dimorphism. The incisors lack enamel on their lingual surface. The p3 is elongated with a relatively large distal fovea and rather large honing facet. The p4 is wide with a relatively larger labial (metaconid) than lingual (protoconid) cuspid. The trigonid of the m3 is long with low relief; between the hypoconulid and the entoconid there is a large sixth cuspid. The postcranials have been studied and they are morphologically and metrically similar to the type material of *P. arvernensis* (Depéret, 1929) from Senéze (France) and to that from Graunceanului, Romania (Van der Geer & Sondaar 2002; Sondaar *et al.* 2006). According to Sondaar *et al.* (2006) the postcranials of the Vatera *Paradolichopithecus* are unique as far as the degree of terrestriality is considered, indicating similarities to *Australopithecus afarensis* Johanson & White, 1978. Thus, the authors proposed that the locomotion of *Paradolichopithecus* might be similar to that of *Australopithecus* Dart, 1925 which, according to them, retained basically a chimpanzee-like locomotion. Chimpanzees can walk bipedally but also climb to the trees (Sondaar *et al.* 2006). The eruption sequence of the lower teeth of the Vatera *Paradolichopithecus* is similar to that of the recent papionins (Van der Geer & Dermitzakis in press).

SYSTEMATICS

Order PRIMATES Linnaeus, 1758
Family CERCOPITHECIDAE Gray, 1821
Subfamily COLOBINAE, Blyth, 1875

Genus *Mesopithecus* Wagner, 1839

Mesopithecus pentelicus Wagner, 1839

HOLOTYPE. — Maxillary fragment with M1-M3 described by Wagner (1839) and figured by Wagner (1840). The specimen is housed in BSPM numbered as BSPM ASII. 11.

LOCALITIES. — Classical Pikermi ravine (PIK), Attica, Greece (near Athens); Chomateres or Kisdari (CHO), Attica, Greece (near Athens).

AGE. — Middle Turolian, MN 12 (late Miocene); more precisely it is referred to the uppermost MN 12 with an age of ~7.0 Ma. The fauna of Chomateres is considered slightly older than the Pikermi one.

DIAGNOSIS. — Medium-sized colobine monkey; short, upright face; sexual dimorphism in the skull, canines and postcranials; absent or very small sagittal crest in the males; enlarged mandibular angle; shallow mandibular corpus with constant height between p4 and m3; convex anterior symphysis without symphyseal constriction; small and deeply inclined *planum alveolare*; absent or weak *fossa genioglossa*; small lingual cusp in the P3, 4; small honing facet in the p3; small hypoconulid in the m3.

Mesopithecus delsoni Bonis, Bouvrain, Geraads & Koufos, 1990

HOLOTYPE. — Mandible of male adult individual with both tooth rows, RZO-159. It is housed in the Laboratory of Geology and Palaeontology, University of Thessaloniki.

LOCALITY. — Ravin des Zouaves-5 (RZO), Axios Valley, Macedonia, Greece.

AGE. — Early Turolian, MN 11 (late Miocene); estimated magnetostratigraphic age ~8.2 Ma.

DIAGNOSIS. — Large size; deep mandibular corpus; flattened anterior symphysis; strong symphyseal constriction; slightly inclined alveolar plane; large fossa genioglossa; thick inferior transverse torus; large honing facet in the p3; well-developed and bicuspid talonid in the m3.

Mesopithecus cf. *M. delsoni*

MATERIAL EXAMINED. — Mandibular fragment with symphysis preserving p3-p4 dex and p4-m1 sin, MNHN-slq-940 + 941.

LOCALITY. — ?Ravin-X (R-X), Axios Valley, Macedonia, Greece.

AGE. — Early-middle Turolian, MN 11-12 (late Miocene).

CHARACTERISTICS. — Characters and size similar to *M. delsoni*. The sole known specimen does not allow the certain attribution to this species.

Mesopithecus delsoni/pentelicus

MATERIAL EXAMINED. — The studied material includes that referred in Bonis *et al.* (1997), Koufos *et al.* (2004) and Koufos (2006a).

LOCALITIES. — Vathylakkos-2, 3 (VTK, VAT), Axios Valley, Macedonia, Greece; Perivolaki (PER), Thessaly, Central Greece.

AGE. — Middle Turolian, MN 12 (late Miocene). More precisely the Vathylakkos localities are dated to the lower middle Turolian with an estimated age of ~7.3 Ma, while Perivolaki is younger and its magnetostratigraphic study suggests an age between 7.3-7.1 Ma.

CHARACTERISTICS. — Size intermediate between *M. delsoni* and *M. pentelicus*; relatively shallow mandibular corpus, similar to *M. pentelicus*; high internal cusp (protocone) in the P3,4; flattened anterior symphysis with symphyseal constriction; slightly inclined backwards alveolar plane; large fossa genioglossa; strong honing facet in the p3; large hypoconulid with distal groove in the m3; similar dental dimensions to *M. pentelicus*; longer bones than *M. pentelicus*.

Mesopithecus aff. *M. pentelicus*

MATERIAL EXAMINED. — See Bonis *et al.* (1990).

LOCALITIES. — Dytiko-2, 3 (DIT, DKO), Axios Valley, Macedonia, Greece.

AGE. — Late Turolian, MN 13 (late Miocene).

CHARACTERISTICS. — Relatively smaller orbits with stronger supraorbital torus than *M. pentelicus*; longer sagittal crest than *M. pentelicus*; smaller incisors; less reflected backwardly epicondylus medialis in the humerus; oval section of the radius shaft; radius with smaller facet for the ulna.

Mesopithecus cf. *M. pentelicus*

MATERIAL EXAMINED. — See Bonis *et al.* (1990).

LOCALITY. — Dytiko-1 (DTK), Axios Valley, Macedonia, Greece.

AGE. — Late Turolian, MN 13 (late Miocene).

CHARACTERISTICS. — Similar to *M. pentelicus* but as there is few material available and it is badly preserved, the certain determination is difficult.

Mesopithecus cf. *M. monspessulanus*

MATERIAL EXAMINED. — Mandibular fragment with l1-m3 sin, LGPUT-DIT-22.

LOCALITY. — Dytiko-2 (DIT), Axios Valley, Macedonia, Greece.

AGE. — Late Turolian, MN 13 (late Miocene).

CHARACTERISTICS. — Mandibular and dental dimensions smaller than *M. pentelicus* and closer to *M. monspessulanus.*

Mesopithecus sp.

MATERIAL EXAMINED. — MCIII, LGPUT-NIK-unumbered; MtI, LGPUT-1541.

LOCALITY. — Nikiti-2 (NIK), Chalkidiki, Macedonia, Greece.

AGE. — Early Turolian, MN 11 (late Miocene); more precisely it is referred to the lowermost part of early Turolian (MN 11) between 8.7 and 8.2 Ma.

CHARACTERISTICS. — The morphology and the size of the bones are close to those of *Mesopithecus*.

Mesopithecus sp.

MATERIAL EXAMINED. — See Kullmer & Doukas, 1995.

LOCALITY. — Maramena (MAR), Serres Basin, Macedonia, Greece.

AGE. — Latest Turolian, MN13/14 (late Miocene).

CHARACTERISTICS. — Similar to *M. pentelicus* according to Kullmer & Doukas (1995).

Dolichopithecus ruscinensis Depéret, 1889

LOCALITY. — Megalon Emvolon (MEV), near Thessaloniki, Macedonia, Greece; Ptolemais Basin (PTL), Notio Mb of Ptolemais Fm., Macedonia, Greece.

AGE. — Late Ruscinian, MN 15 (early Pliocene).

DIAGNOSIS. — Colobine monkey of moderate size; constant mandibular depth; strong sexual dimorphism in the canines; strong metaconid and protoconid in the relatively narrow p4; the mesial breadth of the m3 is larger than the distal one of the m2; the m3's hypoconulid is situated between the midline and the line joining the buccal cuspids of the tooth; there is no clear fifth cuspid in the m3's talonid but there is a cingular elevation indicating its development (Koufos *et al.* 1991a).

Subfamily CERCOPITHECINAE Gray, 1821
Genus *Paradolichopithecus*
Necrasov, Samson & Radulesco, 1961

Paradolichopithecus arvernensis
(Depéret, 1929)

LOCALITY. — Vatera (VTR), Lesvos Island, Greece.

AGE. — Middle Villafranchian *s.l.*, MN 17 (late Pliocene).

DIAGNOSIS. — Large-sized; clear sexual dimorphism in the canine's complex; large anterior lower teeth; lingual surface of the lower incisors without enamel; p4 with larger labial than lingual cuspid; m3 with elongated trigonid, low relief and a large sixth cuspid; eruption pattern of lower dentition typically papionin.

STRATIGRAPHIC DISTRIBUTION

The known Neogene cercopithecids of Greece belong to three taxa: *Mesopithecus, Dolichopithecus* and *Paradolichopithecus*. There is also evidence for the presence of *Macaca* sp. in the early Pleistocene locality Tourkobounia 2 (fissure filling) near Athens (Symeonidis & Zapfe 1976). The latter two Neogene genera are relatively rare, and known from one or two localities: *Dolichopithecus* is known from the localities Megalon Emvolon and Ptolemais, both dated to Pliocene (Fig. 11). The Megalon Emvolon fauna includes several species suggesting a late Ruscinian (MN 15) age (Koufos 2006b and references therein). The Ptolemais *Dolichopithecus* (two isolated teeth) comes from Notio Mb of Ptolemais Fm., dated to late Ruscinian, MN 15 (de Bruijn pers. comm. 2008). *Paradolichopithecus* is only known from the locality of Vatera (Lesvos Island) dated to

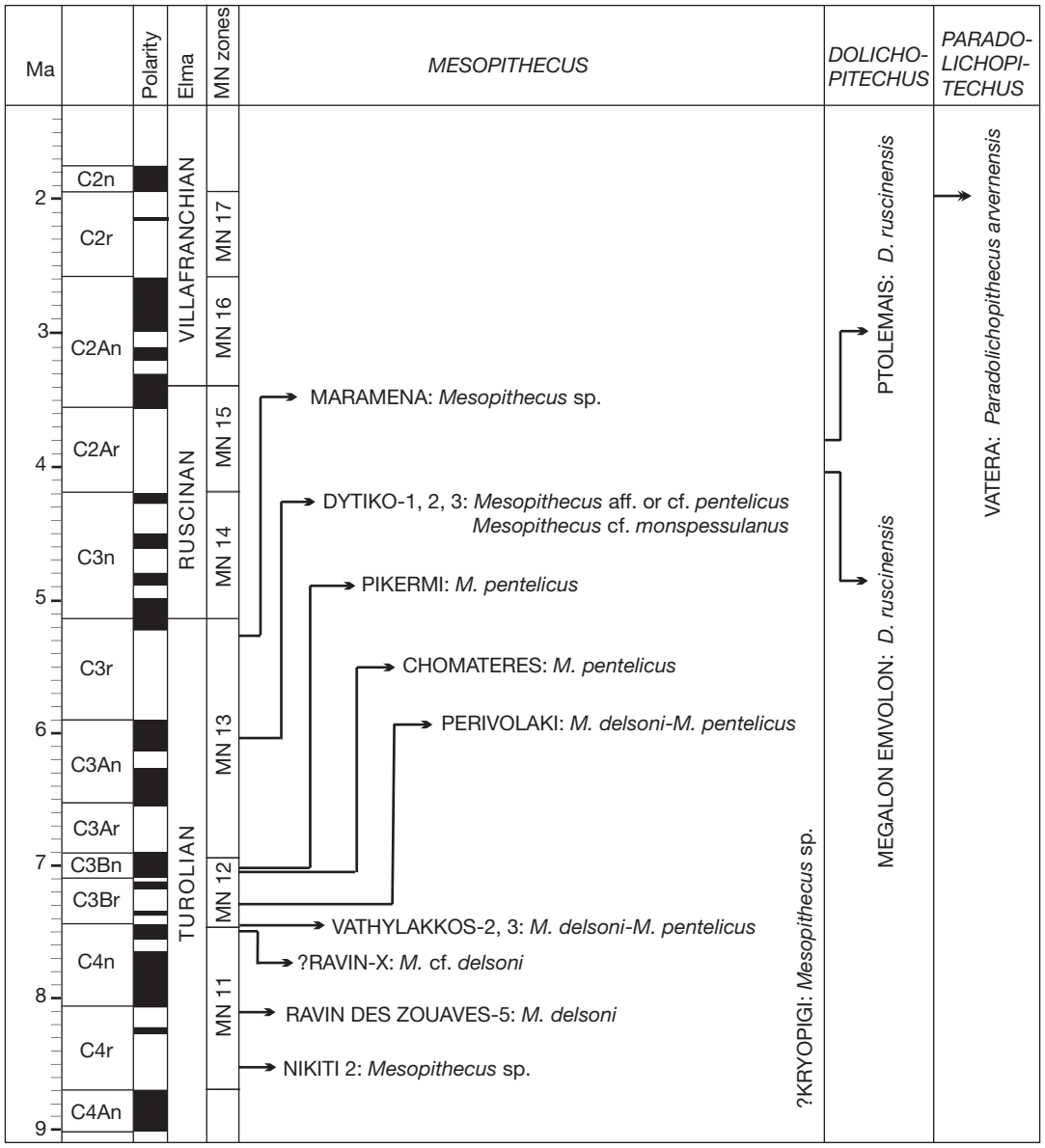

FIG. 11. — Stratigraphic distribution of the cercopithecids in the Neogene of Greece.

the latest Pliocene, MN 17 (Fig. 8) at ~2.0 Ma (de Vos *et al.* 2002; Lyras & Van der Geer 2007).

On the contrary, *Mesopithecus* is very common in Greece and except Pikermi is known from several other localities covering whole Turolian (Fig. 11). Its earliest occurrence is traced in the locality Nikiti-2 (NIK), dated biochronologically at the lowermost early Turolian, MN 11 (Koufos 2006b and references therein). The available *Mesopithecus* material from NIK includes some postcranials, which cannot allow specific determination at the moment; thus it is referred to as *Mesopithecus* sp. Another early

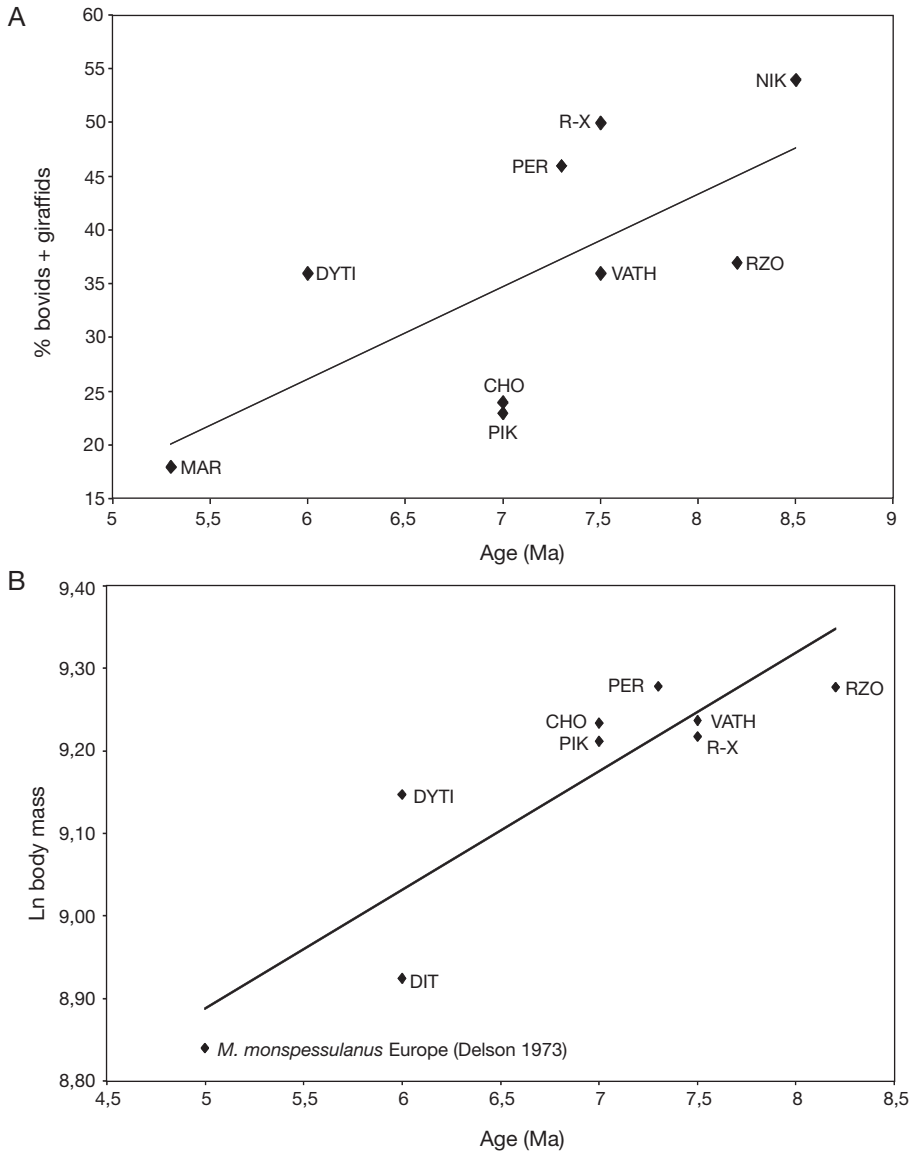

FIG. 12. — **A**, distribution of the bovids + giraffids in the *Mesopithecus* Wagner, 1839 bearing mammal localities of Greece versus their geological age; **B**, distribution of *Mesopithecus* body mass in the *Mesopithecus* bearing mammal localities of Greece versus their geological age. Abbreviations: see text.

trace of *Mesopithecus* comes from the locality RZO of Axios Valley with the large-sized taxon *M. delsoni* dated to early Turolian (MN 11); more precisely the palaeomagnetic record suggests an age of ~8.2 Ma (Koufos 2006b; Sen *et al.* 2000). During middle Turolian (MN 12), *Mesopithecus* is represented in Greece by a to medium-sized form having characters between *M. delsoni* and *M. pentelicus* and referred to as *M. delsoni/pentelicus*. It is known from the localities VAT and VTK of Axios Valley, dated to middle Turolian at ~7.3 Ma (Koufos 2006b, unpubl. data and references therein). This form is also known

TABLE 2. — Faunal composition by taxonomy (% number of species per family or group) of the *Mesopithecus* Wagner, 1839 bearing mammal localities of Greece. Abbreviations: see text.

	NIK	RZO	VATH	R-X	PER	CHO	PIK	DYTI	MAR	MEV	VTR
Rodentia	0	4	4	0	0	38	17	0	50	13	0
Primates	8	4	4	7	4	5	2	8	3	13	6
Carnivora	15	22	24	14	23	5	36	8	15	13	18
Tubulidentata	0	0	0	0	0	0	0	4	0	0	0
Hyracoidea	0	0	0	0	0	0	2	0	0	0	0
Proboscidea	8	7	4	7	4	5	7	12	3	0	12
Equidae	13	14	8	7	13	21	6	38	13	8	6
Rhinocerotidae	0	4	4	7	4	5	5	4	3	0	6
Chalicotheriidae	0	4	8	0	0	5	2	4	0	0	0
Suidae	0	7	4	7	4	5	2	4	3	13	0
Tragulidae	0	0	4	0	0	0	2	4	0	0	0
Cervidae	0	0	0	0	4	5	2	4	3	0	6
Giraffidae	15	7	8	7	8	5	5	8	3	0	6
Bovidae	38	30	28	43	38	19	17	28	15	38	41

from the locality PER, dated to middle Turolian too but older than Pikermi; the palaeomagnetic record suggests an age between 7.3-7.1 Ma (Koufos *et al.* 2006). The middle-sized *M. pentelicus* is smaller than *M. delsoni* and *M. delsoni/pentelicus* and appeared in the localities of Pikermi and Chomateres at the end of middle Turolian (Fig. 11). During late Turolian (MN 13) *Mesopithecus* was present by two forms found in the localities of Dytiko, Axios Valley (Fig. 11). The first form is slightly smaller than *M. pentelicus* with some minor differences (see above), while the other is clearly smaller and closer to the small-sized *M. monspessulanus*. The sole known and small-sized mandibular branch from DIT (Fig. 8) indicates an early appearance of *M. monspessulanus* at the end of Miocene. A similar size decrease is also observed in the late Turolian *Mesopithecus* of Italy (Rook pers. comm. 2008). The youngest Greek locality with *Mesopithecus* is Maramena dated to the end of Turolian (Schmidt-Kittler *et al.* 1995; Koufos 2006c). The majority of the Maramena sample includes isolated teeth and thus it is difficult to compare them with the rest of the Greek material. Therefore, although it was described as *M. pentelicus*, it is better to refer it as *Mesopithecus* sp. for the moment. The age of the locality Kryopigi in Chalkidiki is not certainly known, as the material is still undescribed and it is better to date it to late Miocene for the moment (Fig. 11).

Having in mind all the above mentioned we can conclude to the following:
– *Mesopithecus* appeared in Greece at the beginning of Turolian with the large-sized species *M. delsoni*;
– a large-medium size form named *M. delsoni/pentelicus* is known from middle Turolian;
– the medium-sized *M. pentelicus* appeared at the end of middle Turolian and probably exists in late Turolian;
– the small-sized *M. monspessulanus,* which is considered as Ruscinian, seems to appear earlier during the uppermost Turolian;
– there is a size decrease of *Mesopithecus* during Turolian which can be used as a biostratigraphic tool;
– *Dolichopithecus* in Greece is known from late Ruscinian (MN 15) but it is quite possible that it exists in older levels, since the Ruscinian mammal localities are very rare in Greece;
– *Paradolichopithecus* is only known from the end of Villafranchian (MN 17), but it is possible that it exists in younger levels.

PALAEOECOLOGY

The palaeoecology of *Mesopithecus* has been discussed quite earlier when Gaudry (1862-1867) described the sample from Pikermi; he proposed a more terrestrial than arboreal way of life for it. Later on,

TABLE 3. — Modern and fossil faunas used in the Correspondance Factor Analysis of Figure 11.

Locality	Abbreviation	Country	Environment
Makokou	MAK	Gabon	Tropical forest
La Maboke	MAB	Republic of Central Africa	Tropical forest
Sangmelina	SNG	Cameroon	Tropical forest
Mont Kivu	MKV	Zair	Tropical forest
Mont Nimba	MNM	Libria, Guinea	Tropical forest
Transvaal 9	TRA9	South Africa	Savannah
Amboseli	AMB	Kenya	Savannah
Region Gabiro	RGA	Rwanda	Savannah
Ihema	IHE	Rwanda	Savannah
Transvaal 7	TRA7	South Africa	Savannah
Zinawe	ZNW	Mozambuque	Savannah
Lokori	LOK	Kenya	Savannah
Golden Gate	GGT	South Africa	Savannah
Eppelsheim	EPP	Germany	Open
Hostalets	HST	Spain	Open
La Roma	LRO	Spain	Open
Los Valles de Fuentinueva	LVF	Spain	Open
Can Ponsic	PON	Spain	Open
Rudabanya	RUD	Hungary	Open
Terassa	TRS	Spain	Open
Villadecabals	VDC	Spain	Open

several authors studying *Mesopithecus,* proposed a semi-terrestrial way of life. Their results were based mainly to the postcranial proportions of the animal, as well as to their comparison with recent cercopithecoids (Gabis 1961; Szalay & Delson 1979; Zapfe 1991; Youlatos 2003; Koufos *et al.* 2003). However Escarguel (2005) does not agree that the distal part of the hindlimb is discriminative for the way of life of *Mesopithecus*. The genus *Mesopithecus* is quite well known from Greece covering the whole Turolian. Most of the *Mesopithecus* bearing localities include a rich fauna. Except Pikermi and Ravin-X faunas, the others are new collections well correlated to the stratigraphy and without any admixture. The study and comparison of these faunas can help to the determination of the landscape where *Mesopithecus* was living and consequently of its way of life.

The faunal composition (% taxa per family or taxonomic group) of the *Mesopithecus* bearing localities of Greece is given in Table 2. In all these localities the bovids + giraffids dominate; their percentage varies between 18 and 58%. The dominance of these two groups suggests a relatively open environment (wooded or bushed savannah) in which it is possible for these animals to move in large groups from one region to another in order to find food. The open character of the landscape is strengthened by the high percentage of equids (Fig. 10), the majority of which belongs to running forms (elongated and slender metapodials). The main rhino of the *Mesopithecus* bearing localities is "*Diceros*" *neumayri* (Osborn, 1900), which also characterizes open-dry environments (Giaourtsakis 2009). The suids, tragulids, tapirids and cervids are absent or very rare, confirming the above mentioned open-dry conditions.

The comparison of the bovids and giraffids percentage with the geological time suggests a linear relation, indicating a decrease of their taxa during Turolian (Fig. 12A). The decrease of the bovids and giraffids could indicate a less open and dry palaeoenvironment to the end of Miocene. A relatively more wet with closed spots environment (patchy environment) has been reported for the late Turolian of Eastern Mediterranean region (Koufos 2006c). This change of the palaeoenvironment seems to agree with the size decrease of *Mesopithecus* during Turolian, leading to the small *M. monspessulanus*, a form which is more arboreal (Szalay & Delson 1979). This size decrease of *Mesopithecus* is clear

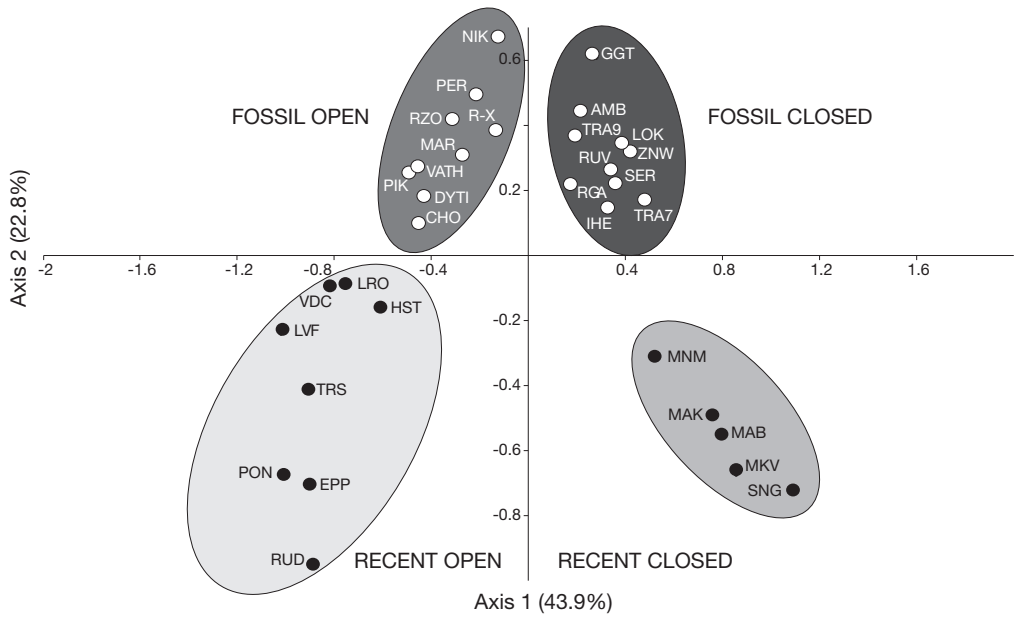

FIG. 13. — Correspondence Factor Analysis of the *Mesopithecus* Wagner, 1839 bearing Greek Turolian mammal localities with a set of Vallesian ones from Europe and a set of modern ones from certain environments (Table 2). Abbreviations: see text.

in the diagram of Figure 12B in which the linear relation between the body mass and the geological age of *Mesopithecus* is quite clear. The body mass of *Mesopithecus* was calculated using the dimensions of the m1 according to Legendre (1988: 18, 240).

The open character of the Turolian landscape is also confirmed by the Correspondence Factor Analysis (CFA) of the *Mesopithecus* including Greek mammal faunas with modern faunas from certain environments and with a set of Vallesian Western and Central European faunas (Table 3; Fig. 13). The software PAST is used for the multivariate analysis (Hammer *et al.* 2001). During Vallesian in Western and Central Europe the conditions were relatively closed and wet (Bonis *et al.* 1992, 1999; Agustí *et al.* 1999, 2003; Koufos 2006d). The analysis indicates that axis-1 distinguishes clearly the modern closed and open faunas, while axis-2 separates the modern from the fossil faunas. All the *Mesopithecus* bearing localities of Greece match together and can be clearly correlated with the modern open faunas, indicating similar palaeoenvironmental conditions. The open-dry character of the Turolian Greek and Eastern Mediterranean faunas has been reported in several recent works (Bonis *et al.* 1992, 1994, 1999; Merceron *et al.* 2004, 2005a, b; Koufos *et al.* 2006, 2009; Kostopoulos, 2009).

All the available data for the Turolian advocate to an open-dry environment where *Mesopithecus* was living. An open environment could be more or less bushy, bosky with or without gallery forests. In such an environment, a terrestrial rather than arboreal way of life is more possible for *Mesopithecus*. The open bushy or bosky areas provided enough food to *Mesopithecus*, especially during the rainfalls period. On the other hand the sparse trees protected it from the carnivores and provided a place for passing safely the night. The dental microwear of *M. pentelicus*, *M. delsoni* and *M. delsoni/pentelicus* indicates that their feeding habits are alike, including leaves, seeds, fruits or underground vegetal parts (Merceron *et al.* 2009, this volume). Such feeding preferences are in accordance with their locomotion and the determined environment.

Concerning Ruscinian, the available mammal localities of Greece and Eastern Mediterranean are

very scarce with limited data. The fauna of Megalon Emvolon is very poor to allow certain comparisons and results. However, there are some indications for a significant faunal change at the Miocene/Pliocene boundary with the extinction of several Miocene faunal elements. This faunal change could be related to climatic reasons. A change to more wet and closed conditions was observed from late Turolian (Koufos 2006c) which probably extended to Ruscinian. Although the faunal elements from Greece are few, the extended Ruscinian lignitic deposits of northern Greece (Koukouzas *et al.* 1979) and neighbouring countries indicate closed and wet conditions. Thus one can suppose that *Dolichopithecus* could probably live in a relatively closed and wet environment. However, such conclusion is doubtful and only the discovery of more fossils from that period and their study will provide the available data for a certain determination of the environment.

The sole known occurrence of *Paradolichopithecus* is traced in the latest Pliocene locality of Vatera, Lesvos Island. The fauna of Vatera includes elements of open habitats (savannah-like) (Van der Geer & Sondaar 2002). In fact the faunal composition of the known Vatera fauna with a lot of bovids and giraffids (Table 3) indicates a relatively open environment. The analysis of the Villafranchian faunas of southern Europe and western Asia with those of Greece suggests a relatively open/mixed character for the late Villafranchian faunas (Kostopoulos & Koufos 2000). Considering this interpretation, a similar environment must be referred for *Paradolichopithecus*. Such an environment fits quite well with the terrestrial way of life proposed for *Paradolichopithecus* (Szalay & Delson 1979).

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