The genus *Mesopithecus* (Primates, Cercopithecidae) in the late Miocene of Greece

George D. Koufos

G.D. Koufos, Aristotle University of Thessaloniki, Department of Geology, Laboratory of Geology and Palaeontology, 54124 Thessaloniki, Greece; koufos@geo.auth.gr

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**ABSTRACT** - The genus *Mesopithecus* is quite common in the late Miocene of Greece being recognized in various localities. After its first discovery in Pikermi, near Athens, it was found in Axios Valley, Serres Basin, Thessaly and Chalkidiki Peninsula. In the present article the Greek sample of *Mesopithecus* is compared and analyzed by multivariate methods. The following taxa can be recognized. The type species *M. pentelicus* was recorded in Pikermi and Chomateres both dated to the uppermost middle Turonian (MN 12). A large-sized species named *M. delsoni* was recognized in the locality Ravin des Zouaves-5 of Axios Valley, dated to early Turonian (MN 11) at ~8.2 Ma. A form intermediate between the above mentioned species, named *M. delsoni/pentelicus* was found in the localities Vathylakkos-2, 3 of Axios Valley and in the locality of Perivolaki in Thessaly; both localities are dated to middle Turonian (MN 12) at ~7.5 Ma and 7.3-7.1 Ma respectively. Two forms similar to *M. pentelicus* but with some minor differences are known from the late Turonian (MN 13) localities Dytiko-1, 2, 3 of Axios Valley; they are referred to as *M. cf.*, or aff. *M. pentelicus*. A small-sized form is also known from the late Turonian locality Dytiko-2 of Axios Valley, which is similar to *M. monspessulanus* and it is referred to as *M. cf.* *M. monspessulanus*. The *Mesopithecus* from the localities Maramena (Serres Basin) and Kryopigi (Chalkidiki Peninsula) cannot be certainly determined and they are referred to as *Mesopithecus* sp.

**INTRODUCTION**

The Miocene cercopithecids of Greece are known since the beginning of the 19th Century, when the well-known mammal locality of Pikermi (Attica, near Athens) was discovered. Among the initially found material there was a cranial fragment of a monkey, named *Mesopithecus pentelicus* Wagner, 1839. During the years after several
researchers excavated in Pikermi and a great amount of Mesopithecus remains has been unearthed. All this material is now housed in various European museums or institutions, as Athens Museum of Palaeontology and Geology (AMPG), Museum Nationale d’Histoire Naturelle Paris (MNHN), Natural History Museum of London (NHML), Naturhistorisches Museum Wien (NHMW), Bayerische Staatsammlung für Paläontologie und Historische Geologie, München (BSPM), etc. Except for the well-known Pikermi collections, it is quite possible that unknown or unpublished material exists in some small collections.

Mesopithecus is also known from Axios Valley (Macedonia, Greece), where some remains were discovered at the beginning of the 20th Century (Arambourg & Piveteau, 1929). During the new campaign of excavations in Axios Valley Mesopithecus was recorded in several fossiliferous sites (Bonis et al., 1990, 1997; Koufos et al., 2004). The genus was also recognized in Serres Basin (Macedonia, Greece), (Kullmer & Doukas, 1995). Recently, Mesopithecus was discovered in Thessaly, Central Greece (Koufos, 2006a), as well as in Chalkidiki Peninsula (Tsoukala & Bartziokas, 2008). Some postcranials of Mesopithecus were discovered near the village of Nikiti (Chalkidiki Peninsula) last summer (Koufos, in press). The genus is widely distributed in Greece but it is also well known in a wider area. It is recorded from the Miocene and/or Pliocene of Bulgaria with a quite rich sample (Koufos et al., 2003 and references therein; Delson et al., 2005), Former Yugoslavian Republic of Macedonia (Schlosser, 1921). Romania (Radulescu et al., 2003). Ukraine (Delson, 1973 and references therein). It is also known from Italy (Gentili et al., 1998; Rook, 1999; Pradella & Rook, 2007), Germany (Andrews et al., 1996) and Hungary (Kordos, 2000). It is unknown in the Miocene of Turkey but it is present in Iran, Afghanistan and the Siwaliks, Pakistan (Mecquenem, 1925; Heintz et al., 1981; Harrison & Delson, 2007).

In the present article the late Miocene Greek sample of Mesopithecus is studied, compared and analyzed with multivariate methods in order to determine its similarities and differences and to give its systematic. Some data about the Greek Mesopithecus bearing mammal localities and their age are also given; more information about them is provided by Koufos (2006b, in press). All the used measurements in the text and the diagrams are original taken by the author; the measurements are in mm.

SYSTEMATIC PALAEOONTOLOGY

Order Primates Linné, 1758
Family Cercopithecidae Gray, 1821
Subfamily Colobinae Blyth, 1875

Genus Mesopithecus Wagner, 1839

Mesopithecus delsoni Bonis et al., 1990

Type locality - Ravin des Zouaves-5 (RZO), Axios Valley, Macedonia, Greece.

Age - Early Turolian, MN 11 (late Miocene); magnetostratigraphic age ~8.2 Ma (Sen et al., 2000; Koufos, 2006b).

Diagnosis - Large size; deep mandibular corpus; flattened anterior symphysis; strong symphysal 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.

Discussion - The species was originally recognized in the locality RZO of Axios Valley (Fig. 1). The biochronological data allow the dating of RZO to early Turolian or MN 11 (Koufos, 2006b and references therein), while the magnetostratigraphy suggests an estimated age of ~8.2 Ma (Sen et al., 2000). The available material from RZO includes two male mandibles (RZO-159, 160) and a female mandibular fragment (Figs. 2d, e). The material has been originally described by Bonis et al. (1990) as a new species, M. delsoni.

The RZO sample of Mesopithecus has larger size than M. pentelicus from Pikermi as it is shown by the comparison of some dental dimensions (Bonis et al., 1991, figs. 2, 5). The various dimensions of the lower dentition of the RZO and PIK samples are analyzed using Principal Component Analysis (PCA) in Fig. 3; the software PAST-2008 is used for the PCA (Hammer et al., 2001). The PIK sample includes 8 male and 8 female specimens and that from RZO two male ones. The first
principal component (PC1) distinguishes the males and females of *M. pentelicus* by their size; all used variables have positive influence to PC1, indicating a size increase across horizontal axis from left to right. Looking at the loadings of the second principal component (PC2), the majority of the variables especially the molar length have
negative influence to it; however, the canine’s dimensions (Lc, Bc) have positive influence and this means that across vertical axis there is an increase of the canine size from below to upwards and relatively a decrease of the molar row from up to down. The position of the RZO mandibles at the most right extreme of the horizontal axis is due to their larger size, while its position below the horizontal axis would be attributable to the relatively longer molar row and smaller canine. However, the specimen NHMW-PIK-1998z77/1 from Pikermi has dental dimensions very close to RZO sample (Fig. 3).

Besides the similarity in dental size, the remaining mandibular dimensions and the morphology of NHMW-PIK-1998z77/1 are close to \textit{M. pentelicus} (Figs. 4-5).

The mandibular corpus of the RZO sample is deeper than that of \textit{M. pentelicus}, a character which distinguishes clearly the two samples. The comparison of the depth below p4 versus that below m3 (Fig. 4a) distinguishes the males and females of \textit{M. pentelicus} (30 specimens), although there is some overlap. The male RZO mandible is clearly separated being very far from the males of \textit{M. pentelicus} (Figs. 4-5).

The most important differences between the RZO mandible and \textit{M. pentelicus}, as the depth of the mandibular corpus (D\textsubscript{corpus}), the symphysis length (L\textsubscript{symph}) and height (H\textsubscript{symph}), the tooth rows length (L\textsubscript{t}, L\textsubscript{p}, L\textsubscript{m}) and the m3 size (L\textsubscript{m3}, B\textsubscript{m3}), are analyzed by PCA (Fig. 5). All the variables have positive influence to the PC1, which distinguishes very well the males (right) from females (left) of \textit{M. pentelicus} indicating a size increase across the horizontal axis from left to right. The mandible RZO-160 is situated in the most right part of the PC1 far from the males of \textit{M. pentelicus} because of its larger size than the latter taxon.

A significant morphological character that distinguishes the RZO sample from \textit{M. pentelicus} is its larger honing facet in the p3. The RZO molars are larger than those of \textit{M. pentelicus} and the m3 has a large hypoconulid. The latter bears a groove to its distal surface giving to it a bicuspid feature. All the above-mentioned characters distinguish the RZO sample from \textit{M. pentelicus} and allowed Bonis et al. (1990) to erect the new species \textit{M. delsoni}.  

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**Fig. 3 - Principal Component Analysis (PCA) of the Greek \textit{Mesopithecus} sample based on their lower dental dimensions. The variables are:**

- \text{Lt}=\text{length} i1-m3
- \text{Lp}=\text{premolar length}
- \text{Lm}=\text{molar length}
- L, B= the length and the breadth of the teeth c-m3
- \text{$\varphi$}= male; \text{$\circ$}= female

The studied specimens are given with the abbreviation of the museum and locality as well as the catalogue number.
Mesopithecus cf. M. delsoni

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

Age - Early/middle Turolian, MN 11/12 (late Miocene); the age of R-X is based to the old Arambourg’s collection in MNHN and indicates an age of early/middle Turolian (Koufos, 2006b and references therein).

Discussion - There is a mandibular fragment with right p3-p4 and left p4-m1 (MNHN-SLQ-940+941) probably from the locality Ravin-X (R-X) of Axios valley (Arambourg & Piveteau, 1929). The morphology of the symphysis (flattened anterior face, symphyseal constriction, slightly inclined backwards alveolar plane), as well as the symphysis dimensions (Fig. 4b) are similar to M. delsoni. The preserved mandibular corpus seems to be deep and the p3 has a large honing facet, both characters of M. delsoni. The sole known fragmentary specimen and its doubtful stratigraphic position cannot allow its certain determination and thus it is referred to as M. cf. delsoni.

Mesopithecus delsoni/pentelicus

Localities - Vathylakkos-2 (VTK), Ravin du Vatilük (=Vathylakkos-3, VAT), Axios Valley, Macedonia, Greece; Perivolaki (PER), Thessaly, Greece.
Age - Middle Turolian, MN 12, (late Miocene); magnetostratigraphic age ~7.5 Ma for VTK and 7.3-7.1 Ma for PER (Koufos, 2006b and references therein; Koufos et al., 2006).

Morphological characters - Large-medium size; shallow mandibular corpus; flattened anterior symphysis; strong symphyseal constriction; slightly inclined backwards alveolar plane; large fossa genioglossa; high lingual cusp (protocone) in the P3 and P4; large hypoconulid in the m3; similar dental size, except m3, to M. pentelicus; longer bones than M. pentelicus.

Discussion - Among the studied material of Mesopithecus from Greece there are some specimens having characters of both M. pentelicus and M. delsoni. This Mesopithecus morphotype was originally recognized in the locality VTK (Fig. 1) and described as M. cf. M. pentelicus (Bonis et al., 1997). Later on, it was recognized in the Bulgarian localities of Kalimantsi and Hadjidimovo and it was referred to as M. aff. M. delsoni (Koufos et al., 2003). Later, the old and new material from VTK was described as M. aff. M. pentelicus (Koufos et al., 2004). Recently a similar form was described from PER (Koufos, 2006a) as M. cf. M. delsoni (Koufos, 2006a). As this Mesopithecus morphotype has similarities with both M. delsoni and M. pentelicus, the name M. delsonii pentelicus could be better for it, indicating an evolutionary stage between the two species.

The RZO material of M. delsoni includes only mandibular remains and a direct comparison with the female mandibles LGPUT-VTK-62 and LGPUT-PER-200 (Figs. 2h, j) is possible. Both are morphologically similar to those of M. delsoni having flattened anterior symphysis, strong symphyseal constriction, slightly inclined backwards alveolar plane, large fossa genioglossa, large honing facet in the p3, and large hypoconulid in the m3. The female m3 from VTK and PER are larger or very close to the maximum for the female m3s of M. pentelicus (Koufos, 2006a, fig. 2). Although the VTK and PER mandibles are morphologically different from M. pentelicus, they have similar size (Figs. 4-5). Both mandibles match together with the M. pentelicus female group (Figs. 4a-b). The PCA of their mandibular dimensions (Fig. 5) indicates that both clustered with the typical M. pentelicus, while their position in the PCA diagram of Fig. 3 is due to their intermediate tooth row size between M. delsoni and M. pentelicus.

The lack of cranial remains from M. delsoni does not allow a comparison with M. pentelicus. The two available skulls from VTK (LGPUT-VTK-56, 61) have some differences from M. pentelicus including larger size, stronger lingual cusp (protocone) in the P3 and P4 and larger upper dentition (Koufos et al., 2004). The dental dimensions of the two samples (PIK and VTK) are analyzed by PCA (Fig. 6). The variables of molar size (LM, LM1, LM2, LM3) have positive influence to the PC1, which distinguishes the males and females of M. pentelicus, indicating a size increase across the horizontal axis from left to right. The female skull LGPUT-VTK-56 is quite far from the male group of M. pentelicus (Fig. 6); this is due to the larger dental
dimensions of the VTK skulls from the typical *M. pentelicus*. Some postcranials from VTK are larger from both males and females of *M. pentelicus* from PIK (Koufos et al., 2004, fig. 13). Taking in mind all the above mentioned there is a *Mesopithecus* morphotype, having characters of both *M. delsoni* and *M. pentelicus*, which probably represents a transitional form between the two species. This morphotype is referred to as *M. delsoni/pentelicus*.

*Mesopithecus pentelicus* Wagner, 1839

*Type locality* - Classical Pikermi ravine, PIK, Attica, Greece.

*Referred locality* - Chomateres, CHO, Attica, Greece.

*Holotype* - Maxillary fragment with the right M1-M3 described by Wagner (1839) and figured by Wagner (1840); the specimen is numbered as BSPM ASII 11.

*Age* - Middle Turolian, MN 12 (late Miocene); more precisely it is referred to the uppermost MN 12 with an age of ~ 7.0 Ma (Koufos, 2006b and references therein).

*Diagnosis* - Medium-sized colobine monkey; short flattened 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 the p4 and m3; rounded anterior symphysis without symphyseal constriction; small and deeply inclined backwards alveolar plane; absent or weak fossa genioglossa; small lingual cusp in the P3 and P4; small honing facet in the p3; small hypoconulid in the m3.

*Discussion* - The Pikermi material of *Mesopithecus* is described or referred in several articles, where someone can find useful information about its morphology. A more complete study of the known material was given by Delson (1973) in his doctoral thesis; later a monograph focused mainly on the bones of the Pikermi *Mesopithecus* was published by Zapfe (1991). *M. pentelicus* is a medium-sized colobine monkey, smaller than *M. delsoni* and *M. delsoni/pentelicus* (Figs. 3, 6) with a relatively shallower mandibular corpus than *M. delsoni* (Fig. 4a). The anterior face of the symphysis is convex and lacks symphyseal constriction; both features separate it from *M. delsoni*. The alveolar plane inclines strongly backwards and fossa genioglossa is weak or absent. The skull (Fig. 2a) has strong pronathism, oval nasal cavity, narrow and triangular shaped nasals, large-rounded orbits, large interorbital distance, as well as strong supraorbital torus in the males and weak in the females, clear sagittal lines which are connected in the males and give a sagittal crest. The dentition is typically colobine like. The P3 and P4 are characterized by small lingual cusp (protocone). There is clear sexual dimorphism in the canines. The p3 has a small honing facet versus one in *M. delsoni*. The hypoconulid of the m3 is small, without a groove on its distal face.

The species *M. pentelicus* is also referred from the locality Chomateres, CHO (situated near PIK) by a
mandible (Zapfe, 1991, Abb. 131). The mandible (NHMW-CHO-1613/1a) was described as a new subspecies under the name *M. pentelicus microdon* Zapfe, 1991. The CHO mandible is distinguished by its slightly smaller size, deeper mandibular corpus and longer p4 in comparison to p3 and m1. In fact the specimen NHMW-CHO-1613/1a has smaller dental dimensions (Fig. 3) than the typical *M. pentelicus* but this is probably due to the extremely worn dentition. Its mandibular dimensions overlap with those of male *M. pentelicus* (Figs. 4-5) indicating its similarity to this taxon. There is another male mandible from CHO (NHMW-CHO-1613/1b), which is always clustered with *M. pentelicus* (Figs. 3-5). The deeper mandibular corpus of NHMW-CHO-1613/1a, mentioned by Zapfe (1991), indicates similarities to *M. delsoni* and I tried to check if there are other characters of *M. delsoni* in the second CHO mandible, which is more complete. In fact the anterior face of the symphysis is less convex and bears a weak symphyseal constriction, the fossa genioglossa is more pronounced than that of *M. pentelicus*, and the honing facet of the p3 is slightly larger than that of *M. pentelicus* (Koufos, in press). Based to these features the CHO material retains some, even weak, characters of *M. delsoni*. However, it is difficult to distinguish the CHO sample from *M. pentelicus* and must be referred to this.

**Mesopithecus cf. M. pentelicus**

**Locality** - Dytiko-2 (DIT), Axios Valley, Macedonia, Greece.

**Age** - Late Turolian, MN 13 (late Miocene), (Koufos, 2006b and references therein).

**Diagnosis** - Similar to *M. pentelicus* but since the available material is scarce and badly preserved the certain determination is difficult.

**Discussion** - The DTK material includes some dental and postcranial remains that are neither similar to *M. pentelicus* nor to the DKO material; for this reason they are referred to as *M. cf. M. pentelicus* (Bonis et al., 1990).

**Mesopithecus cf. M. monspessulanus**

**Locality** - Dytiko-2 (DIT), Axios Valley, Macedonia, Greece.

**Age** - Late Turolian, MN 13 (late Miocene), (Koufos, 2006b and references therein).

**Diagnosis** - Mandibular and dental size smaller than *M. pentelicus* and close to *M. monspessulanus*.

**Discussion** - There is a male mandibular fragment (LGPUT-DIT-22), (Fig. 2l) which is significantly smaller than those from the Dytiko localities, as well as from *M. pentelicus* (Figs. 3-5). Although it is male, it is smaller than all male mandibles of *M. pentelicus*, being very close to the female ones. Its size resembles to that of *M. monspessulanus* and thus it is referred to as *M. cf. M. monspessulanus*.

**Mesopithecus sp.**

**Locality** - Maramena (MAR), Serres Basin, Macedonia, Greece; Kryopigi (KRY), Chalkidiki, Macedonia, Greece.

**Age** - Maramena, latest Turolian MN 13/14 (Schmidt-Kittler, 1995).

**Discussion** - A fragmentary sample, including mainly isolated teeth of a colobine, is known from the latest Turolian locality MAR (Fig. 1) (Kullmer & Doukas, 1995). The kind of the material cannot allow a certain comparison with the samples from Axios and Pikermi; thus a detailed taxonomic determination is impossible and the material must be referred to as *Mesopithecus sp.*

The presence of *M. pentelicus* is also reported from the locality KRY (Fig. 1), but its description and...
comparison is not detailed enough (Tsoukala & Bartziokas, 2008) and cannot allow a certain specific
determination at the moment. On the other hand, the
associated fauna is not studied and the precise age of the
locality is unknown; thus it is better to refer this to as
Mesopithecus sp., at the moment.

CONCLUSIONS

The Mesopithecus sample from Greece is quite rich
and its study allows the recognition of several
morphotypes. The older one is M. delsoni, a large-sized
form originated from the locality RZO of Axios Valley
and dated to early Turolian at ~8.2 Ma (Koufos, 2006b
and references therein). Last summer, Mesopithecus was
recovered from the locality of Vathylakkos, VTK, VAT (Fig. 1),
which is dated to the lowermost early Turolian, MN 11
(Koufos, 2006b, in press). A mandibular fragment of
Arambourg's collection (MNHN-SLQ-940+941) possibly from the locality Ravin-X (R-X) of Axios Valley
could belong to this taxon; based to Arambourg's
collection the R-X fauna should be referred to early
Turolian or to the beginning of middle Turolian (Koufos,
2006b and references therein). A Mesopithecus morphotype, named M. delsonipentelicus, has size and
characters between M. delsoni and M. pentelicus; it is
known from the Vathylakkos localities (VTK, VAT) of
 Axios Valley dated to the earliest middle Turolian at ~7.5
Ma, as well as from Perivolaki (PER) dated to middle
Turolian with an age between 7.3-7.1 Ma (Koufos, 2006b;
Koufos et al., 2006). A third form of
Mesopithecus is the medium-sized M. pentelicus known from PIK and
CHO, both dated to the end of middle Turolian. The
Chomateres fauna seems to be slightly older than that of
Pikermi (Koufos, 2006b and references therein); the weak presence of some characters of M. delsoni in the
CHO sample strengthens the slightly older age hypothesis
for Chomateres fauna. Two forms similar to M. pentelicus, but with some minor differences, are known
from the late Turolian localities of Dytiko; they are referred to as M. aff. or cf. M. pentelicus; the previous
one should correspond to a form slightly smaller than Pikermi. Finally a small-sized Mesopithecus was traced in the late Turolian locality of Dytiko-2 (DIT), which is
very close to M. monspessulanus; however, the limited
material cannot allow a certain determination, so it is
referred to as M. cf. M. monspessulanus. The
Mesopithecus from the latest Turolian locality of
Maramea cannot be certainly determined to one of these
forms because of the limited material. The Kryopigi
Mesopithecus needs a detailed study for its certain
determination and also a study of the associated fauna
for its dating. The material from the two above mentioned
localities must be referred to as Mesopithecus sp., at the moment.

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