



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

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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 Turolian (MN 12). A large-sized species named *M. delsoni* was recognized in the locality Ravin des Zouaves-5 of Axios Valley, dated to early Turolian (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 Turolian (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 Turolian (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 Turolian 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.*

RIASSUNTO - [Il genere *Mesopithecus* (Primates, Cercopithecidae) nel Miocene superiore della Grecia] - *Cercopitecidi miocenici sono noti in Grecia sin dall'inizio del XIX secolo, quando fu scoperto a Pikermi Mesopithecus pentelicus. Per molto tempo questo rappresentò l'unica presenza del taxon miocenico proveniente dalla Grecia e dai paesi limitrofi. In seguito, il genere fu rinvenuto in molte località greche (Axios Valley, Maramena, Perivolaki, Nikiti e Kryopigi). Lo studio dei fossili di Mesopithecus provenienti dalla Grecia indica la presenza dei seguenti morfotipi:*

Mesopithecus delsoni - proveniente dalla località Ravin des Zouaves-5 (RZO), valle di Axios, Macedonia (Grecia), è riferito al Turoliano inferiore (MN 11), circa 8,2 Ma. È caratterizzato da grandi dimensioni, corpo mandibolare spesso, sinfisi anteriore appiattita e con marcata costrizione, piano alveolare leggermente inclinato, robusto toro inferiore trasverso, p3 con faccetta occlusale ampia, talonide sviluppato e bicuspidato in m3.

Mesopithecus delsoni/pentelicus - rinvenuto nelle località greche di Vathylakkos-2 (VTK), Ravin du Vatiliük (=Vathylakkos-3, VAT) e ?Ravin-X (R-X), valle di Axios, in Macedonia, e Perivolaki (PER), Tessaglia. Tutti questi siti sono riferibili al Turoliano medio (MN 12); più precisamente VTK ha un'età stimata di ~7,3 Ma e PER di 7,3-7,1 Ma. I caratteri principali della specie sono: dimensioni medio-grandi, corpo mandibolare basso, sinfisi appiattita anteriormente, con marcata costrizione, piano alveolare leggermente inclinato posteriormente, ampia fossa genioglossa, cuspidi linguale (protocono) in P3 alta, 4; m3 con grande ipoconulide, misure dentarie (eccetto m3) simili a *M. pentelicus*, ma con ossa più lunghe rispetto a quest'ultimo taxon.

Mesopithecus pentelicus - proveniente dalle località greche di Pikermi (PIK), Chomateres (CHO), in Attica, and forse anche da Kryopigi (KRY), in Macedonia. Questa specie è presente nel Turoliano medio (MN 12) (ma l'età di Kryopigi non è chiara) ed è caratterizzata da medie dimensioni, muso corto e subverticale, marcato dimorfismo sessuale nel cranio, nei canini e nel postcraniale, cresta sagittale poco evidente o assente nei maschi, angolo mandibolare allargato, corpo mandibolare basso, con altezza costante tra p4 e m3, sinfisi anteriore arrotondata senza restringimento, piano alveolare piccolo e poco inclinato posteriormente, fossa genioglossa debole o assente, piccola cuspidi linguale in P3 e P4, piccola faccetta occlusale in p3, ipoconulide ridotto in m3.

Mesopithecus cf. o aff. pentelicus - proveniente dalle località di Dytiko-1, 2, 3 (DTK, DIT, DKO), valle di Axios (Macedonia, Grecia), ascrivibile al Turoliano superiore (MN 13). I fossili hanno dimensioni simili a *M. pentelicus*, ma orbite più piccole, toro sopraorbitale più sviluppato, cresta sagittale più lunga, incisivi inferiori più piccoli, epicondylus medialis meno orientato posteriormente nell'omero, colonnina radiale a sezione ovale, faccetta radiale dell'ulna piccola e denti di dimensioni simili. La determinazione *M. aff. pentelicus* è usata in quanto la morfologia del cranio potrebbe indicare un taxon differente. I fossili di DTK differiscono da DKO e da Pikermi e sono riferiti a *M. cf. pentelicus*. Parte del materiale di DIT è simile a DKO e Pikermi ed è pertanto attribuito a *M. aff. pentelicus*.

Mesopithecus cf. monspessulanus - proveniente da Dytiko-2 (DIT), valle di Axios (Macedonia, Grecia) e attribuito al Turoliano superiore (MN 13). L'unico reperto rinvenuto a DIT è un frammento mandibolare di un esemplare di sesso maschile, più piccolo di tutte le mandibole maschili di Pikermi e assai prossimo alle mandibole femminili provenienti sempre da Pikermi. Il piano alveolare è molto corto e fortemente inclinato, gli incisivi e i molari sono più piccoli di quelli di *M. pentelicus*, più simili a quelli di *M. monspessulanus*.

Mesopithecus sp. - alcuni resti di *Mesopithecus* provengono dai siti greci di Maramena (MAR), bacino di Serres, (Macedonia) e Kryopigi (KRY) (Calcidica) e sono stati descritti come *M. pentelicus*. Il sito MAR è riferito al Turoliano superiore (MN 13/14). La tipologia del materiale di MAR non permette un confronto certo con i campioni di Axios e Pikermi; pertanto una dettagliata analisi tassonomica è impossibile e qui si fa riferimento a *Mesopithecus sp.* La descrizione e il confronto del *Mesopithecus* di KRY non sono ancora completi, inoltre la fauna associata non è ancora stata studiata; per questo motivo al momento non è possibile dare una determinazione specifica e un'età certe.

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

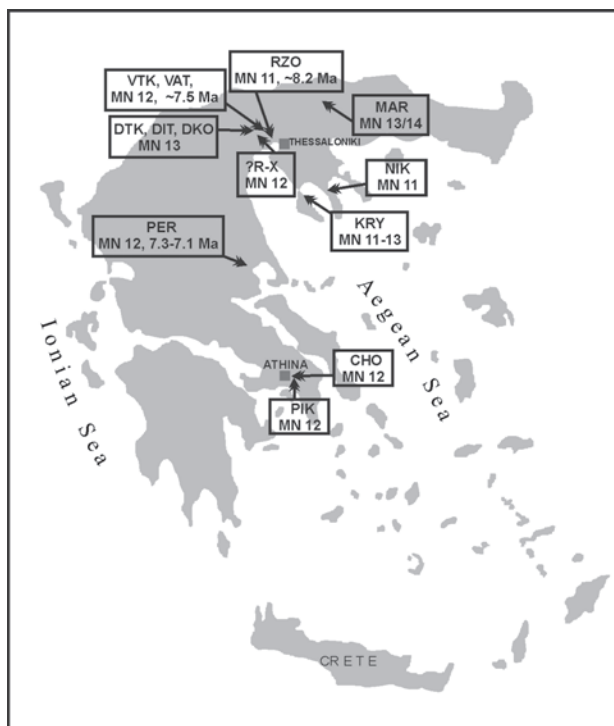


Fig. 1 - Map of Greece indicating the geographic position of the *Mesopithecus* bearing mammal localities. CHO = Chomateres; DTK, DIT, DKO = Dytiko-1, 2, 3; KRY = Kryopigi; MAR = Maramena; NIK = Nikiti-2; PER = Perivolaki; PIK = Pikermi; R-X = Ravin-X; RZO = Ravin des Zouaves-5; VTK, VAT = Vathylakkos-2, 3.

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 Staatssammlung 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 PALAEONTOLOGY

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 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.

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

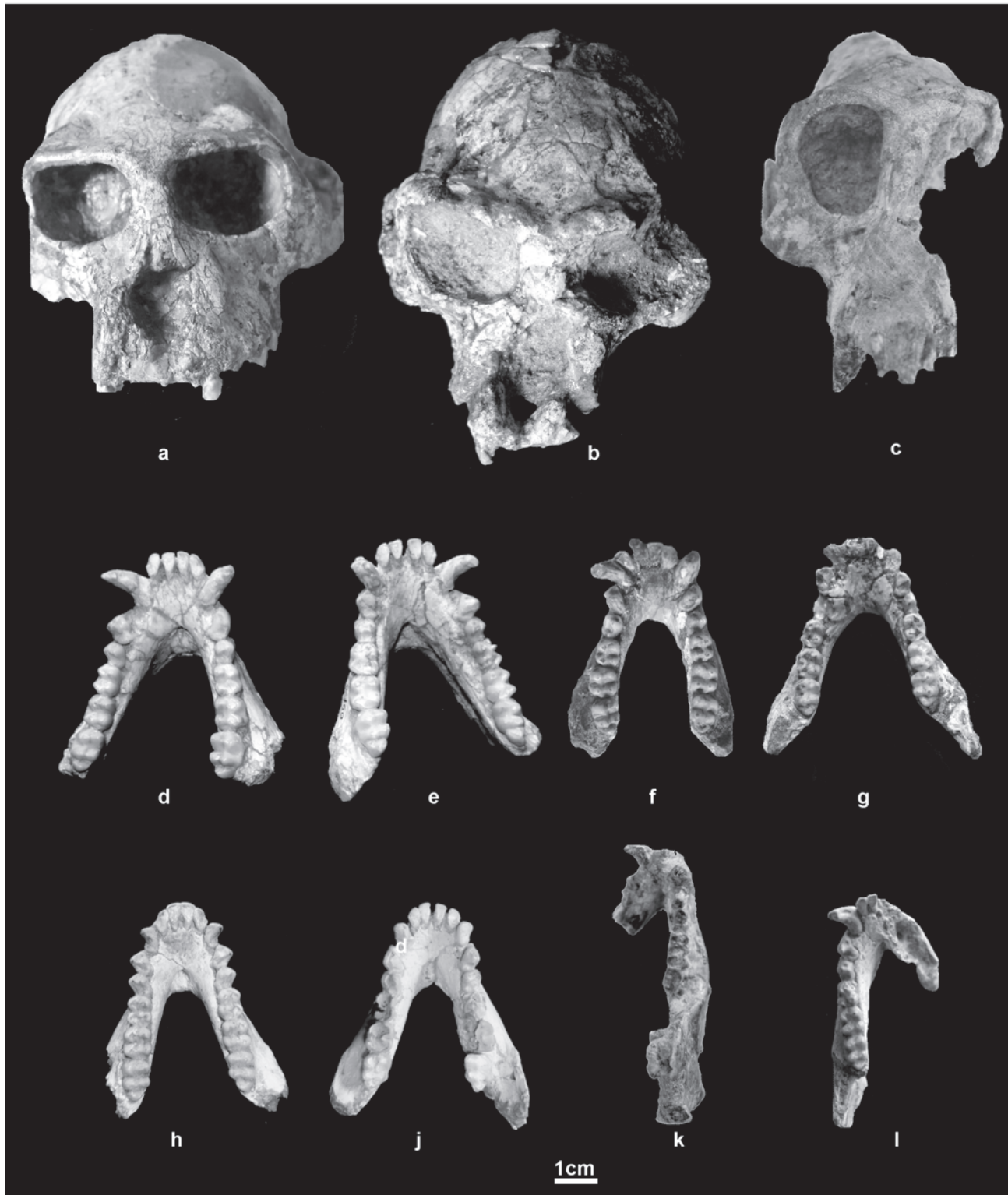


Fig. 2 - Remains of *Mesopithecus* from various Greek localities. a) *M. pentelicus*, male skull MNHN-PIK-14, Pikermi; b) *M. delsoni/pentelicus*, male skull, LGPUT-VTK-61, Vathylakkos-2, Axios Valley; c) *M. aff. pentelicus*, male partial skull, associated with the mandible, LGPUT-PIK-DKO-38; d-e) *M. delsoni*, male mandible, LGPUT-RZO-159, 160; f-g) *M. pentelicus*, male (NHML-PIK-M.8948) and female (AMPG-PIK-1) mandible, Pikermi; h) *M. delsoni/pentelicus*, female mandible, LGPUT-VTK-62, Vathylakkos-2, Axios Valley; j) *M. delsoni/pentelicus*, female mandible, LGPUT-PER-200, Perivolaki, Thessaly; k) *M. aff. pentelicus*, male mandibular fragment, LGPUT-DKO-38, Dytiko-3, Axios Valley; l) *M. cf. monspessulanus*, male mandibular fragment, LGPUT-DIT-22, Dytiko-2, Axios Valley.

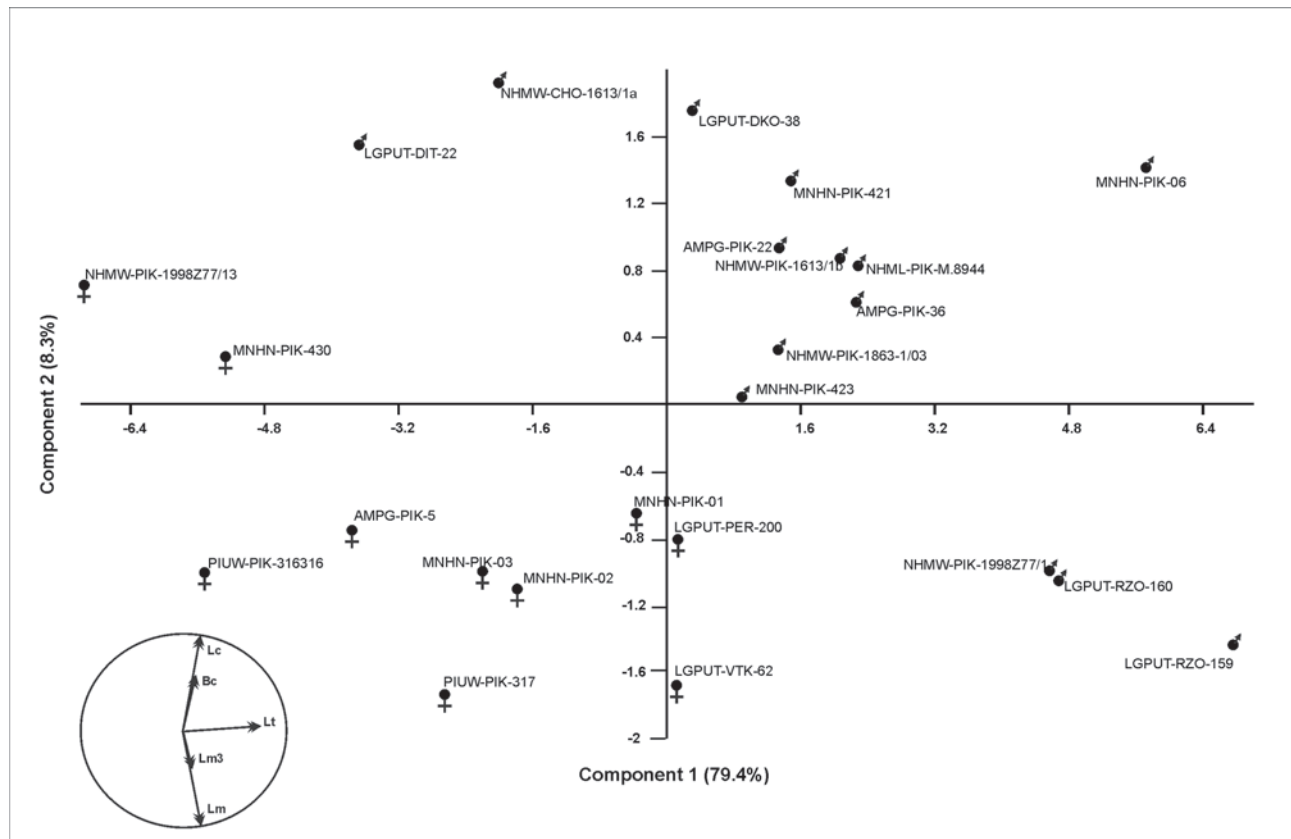


Fig. 3 - Principal Component Analysis (PCA) of the Greek *Mesopithecus* sample based on their lower dental dimensions. The variables are: Lt=length i1-m3; Lp=premolar length; Lm=molar length; L, B= the length and the breadth of the teeth c-m3; ♂ = male; ♀ = female. The studied specimens are given with the abbreviation of the museum and locality as well as the catalogue number.

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 NHMH-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 NHMH-PIK-1998z77/1 are close to *M. pentelicus* (Figs. 4-5).

The mandibular corpus of the RZO sample is deeper than that of *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 *M. pentelicus* (30 specimens), although there is some overlap. The male RZO mandible is clearly separated being very far from the males of *M. pentelicus*. The morphology of the symphysis in the two samples is also different. In the RZO sample there is a relatively large and slightly inclined backwards alveolar plane, as well as a large fossa genioglossa. On the contrary in *M. pentelicus* the alveolar plane is more inclined and the fossa genioglossa is either absent or weak. The

anterior face of the symphysis is flattened with symphyseal constriction in the RZO sample, while it is convex without constriction in *M. pentelicus*. The symphysis is longer and higher in the RZO sample; both RZO male mandibles are very far from the male group of *M. pentelicus* (Fig. 4b).

The most important differences between the RZO mandible and *M. pentelicus*, as the depth of the mandibular corpus (D_{p4}), the symphysis length (L_{symp}) and height (H_{symp}), the tooth rows length (L_i, L_p, L_m) and the m3 size (L_{m3}, B_{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 *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 *M. pentelicus* (Fig. 5) because of its larger size than the latter taxon.

A significant morphological character that distinguishes the RZO sample from *M. pentelicus* is its larger honing facet in the p3. The RZO molars are larger than those of *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 *M. pentelicus* and allowed Bonis et al. (1990) to erect the new species *M. delsoni*.

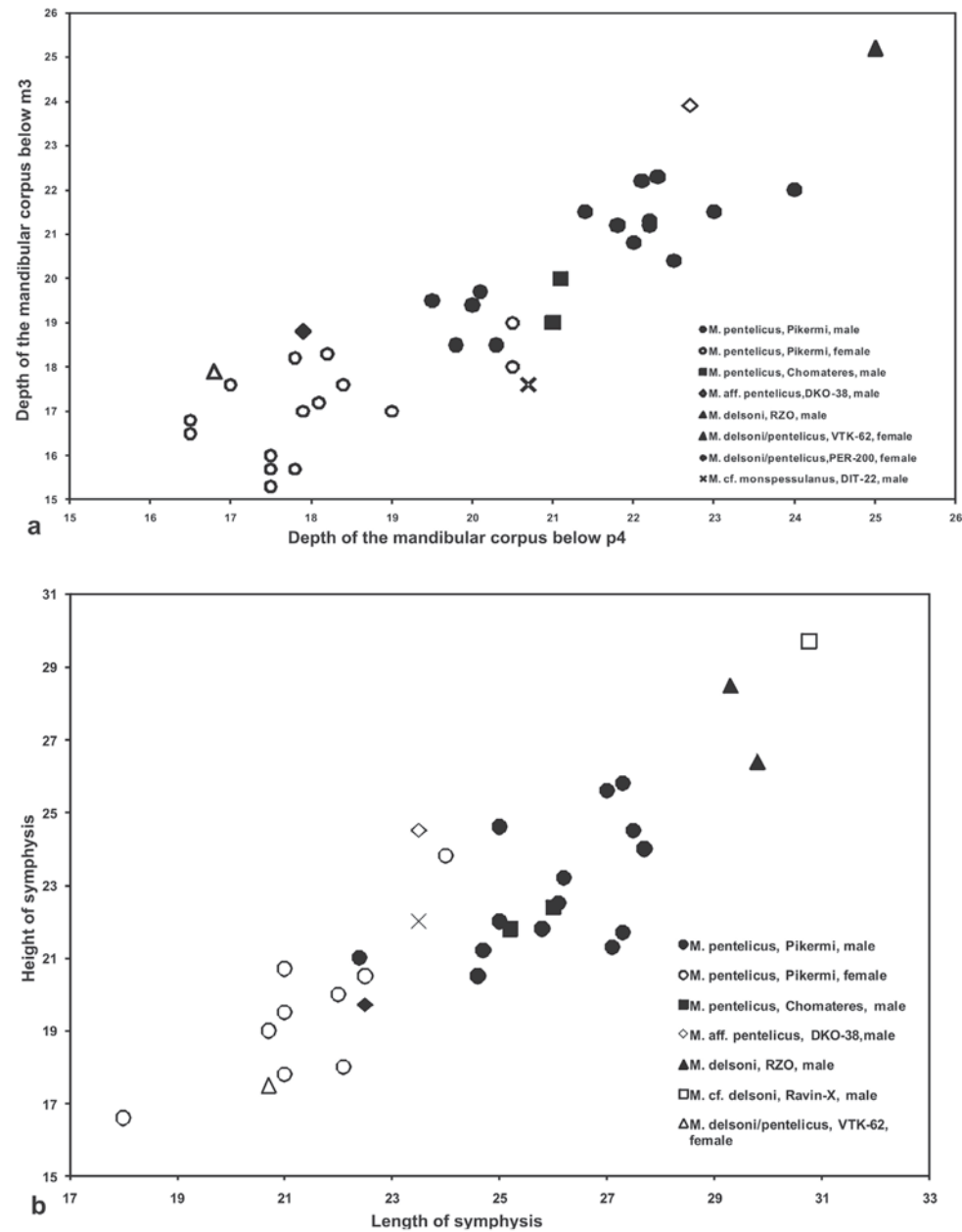


Fig. 4 - a) Scatter diagram comparing the mandibular depth below p4 versus that behind m3 in *Mesopithecus*. b) Scatter diagram comparing the symphysis length versus symphysis height in *Mesopithecus*.

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 Vatilik (=Vathylakkos-3, VAT), Axios Valley, Macedonia, Greece; Perivolaki (PER), Thessaly, Greece.

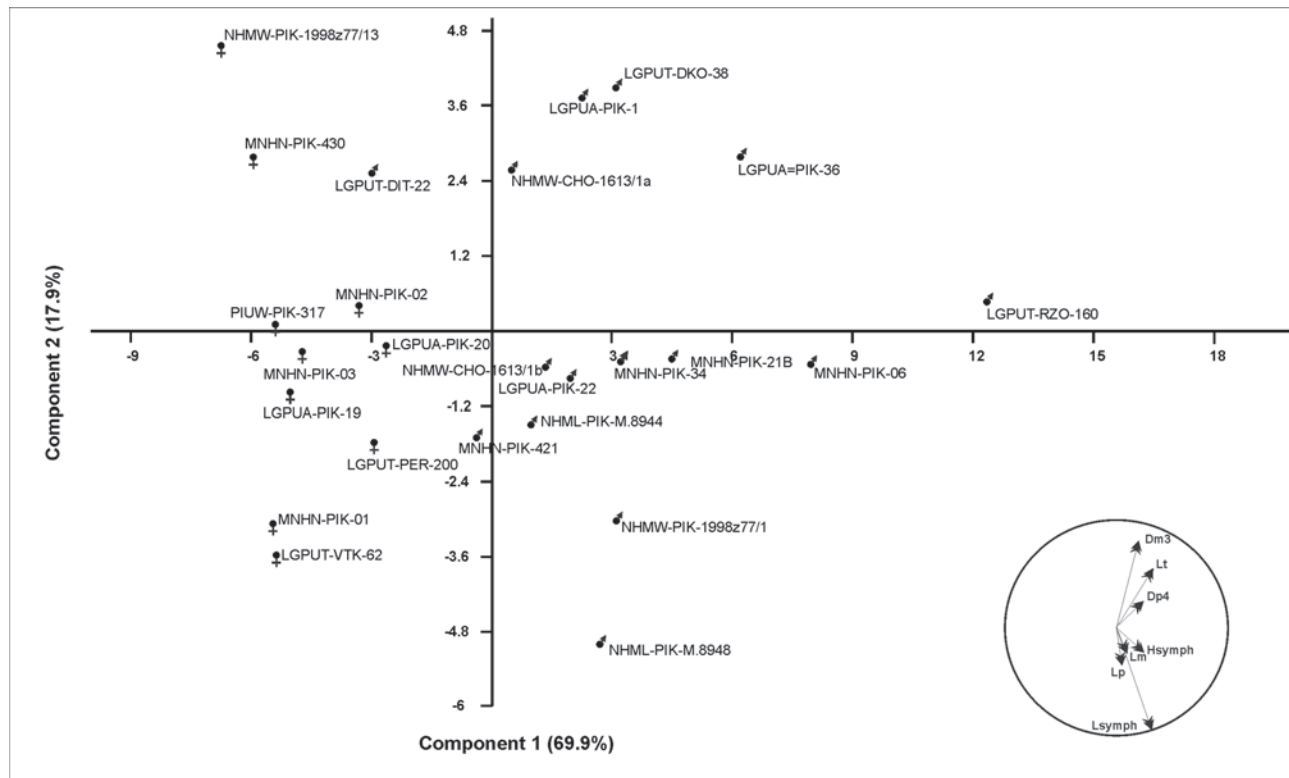


Fig. 5 - Principal Component Analysis (PCA) of the Greek *Mesopithecus* sample, based on some mandibular dimensions. The variables are: L_{symp} = symphysis length; H_{symp} = symphysis breadth; $Dp4$ = depth below p4; $Dm3$ = depth behind the m3; L_t = length i1-m3; L_p = premolar length; L_m = molar length; L_{m3} = Length of m3; $B_{m3\text{ant}}$ = anterior breadth of the m3; $B_{m3\text{post}}$ = posterior breadth of the m3.

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).

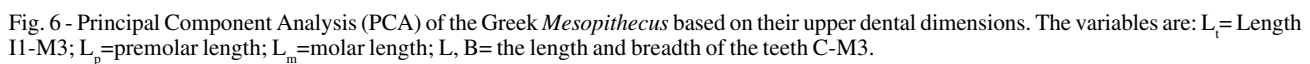
Morphological characters - Large-medium size; shallow mandibular corpus; flattened anterior symphysis; strong symphyseal constriction; slightly inclined backwards alveolar plane; large fossa genioglossa; high lingual cusp (protocone) in the P3 and P4; large hypoconulid in the m3; similar dental size, 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, 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 on, 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 (Fig. 1) as *M. cf. M. delsoni* (Koufos, 2006a). As this *Mesopithecus* morphotype has similarities with both *M. delsoni* and *M. pentelicus*, the name *M. delsoni/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 far from the female group of *M. pentelicus*, being near the minimum for the male skulls of PIK, while the male skull LGPUT-VTK-61 is quite far from the male group of *M. pentelicus* (Fig. 6); this is due to the larger dental



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.

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

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 aff. *M. pentelicus*

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

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

Diagnosis - Relatively smaller orbits with stronger supraorbital torus than *M. pentelicus*; longer sagittal crest than *M. pentelicus*; smaller incisors; less reflected backwardly medial epicondyle in the humerus; oval section of the radial shaft; radius with smaller facet for the ulna (Bonis et al., 1990).

Discussion - The material includes some cranial and postcranial elements originally described by Bonis et al. (1990). The two male skulls (LGPU-DKO-38, LGPU-DIT-21) and several postcranials, although similar in size to *M. pentelicus*, display some differences from the latter. The orbits are smaller, the supraorbital torus is stronger, the sagittal crest is longer, the lower incisors are smaller, the medial epicondyle of the humerus is less reflected backwards, and the radial shaft has an oval section and a small facet for the ulna (Bonis et al., 1990). The dental dimensions of the skull and mandible LGPU-DKO-38 suggest that it is quite smaller than the typical *M. pentelicus* from Pikermi (Figs. 3, 6), but this is partially due to the extremely worn dentition. The mandibular dimensions of LGPU-DKO-38 are also close to *M. pentelicus*, but again near the specimens with the smaller tooth rows (Fig. 5). Although the dentition of LGPU-DKO-38 is extremely worn, it cannot support its size difference from *M. pentelicus*. The DKO skull and mandible have smaller size than the typical *M. pentelicus*, as well as some morphological differences; for this

reason it is referred to as *M. aff. M. pentelicus*. The skull LGPU-DIT-21 is very deformed and thus difficult to be measured and compared.

Mesopithecus cf. *M. pentelicus*

Locality - Dytiko-1 (DTK), 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 (LGPU-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.

Localities - 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 Nikiti-2, NIK (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 Maramena 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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