The Late Miocene Colobine Monkey *Mesopithecus* (Primates, Cercopithecidae) of Greece

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ABSTRACT

The genus *Mesopithecus,* a colobine monkey, represents the earliest known cercopithecoid in Eurasia. *Mesopithecus* is very common in the Late Miocene of Greece and field work at several fossiliferous sites has provided a rich collection from the Turolian (uppermost Late Miocene). The Pikermi collection of *Mesopithecus* is the richest one. The Greek material was studied with respect to cranial, dental, and postcranial morphology using morphological and multivariate approaches. The results support the presence of at least three and possibly four species—*M. pentelicus* (type species), *M. delsoni*, *M. monspessulanus*, and a possible morph having characteristics of the first two species, mentioned as *Mesopithecus* sp. There is also an additional possible species from the Siwaliks (Indo-Pakistan), mentioned as *M. sivalensis*. The comparison of the Greek material with that from other countries indicated a close relationship, suggesting that it was a widespread taxon. *Mesopithecus* has a paleogeographic distribution extending from the Iberian Peninsula to southwestern China. Its main presence occurs in the southern Balkans (i.e., Greece, Bulgaria, North Macedonia). Its great paleogeographic distribution together with its well-known stratigraphical context and age, as well as its specific differentiation, allow one to use the taxon as a biostratigraphic indicator for the uppermost Late Miocene (Turolian). The study of the dietary and locomotor behavior of *Mesopithecus* suggests that it was a semi-terrestrial monkey living in open habitats, such as savannah-bushlands or savannah-grasslands with some trees, shrubs, and grass. In conclusion, the Greek record, due to its richness and stratigraphic context, provides a critical framework for reassessing the taxonomy, biostratigraphy, paleobiogeography, and paleoecology of *Mesopithecus*.

INTRODUCTION

Mesopithecus is the most prevalent Late Miocene cercopithecid in Eurasia and has been known to paleontologists since the early 19th century. The genus was first identified based on material from Pikermi, Greece, and has since been discovered in numerous Late Miocene and Pliocene Eurasian localities (Figure 1). Its discovery led to several opinions being formed by researchers regarding its relations to recent monkeys, apes, and hominids. Numerous publications on *Mesopithecus* exist, with many articles detailing the material discovered across Eurasia. Recently a significant quantity of new remains of *Mesopithecus* was discovered and studied from the Late Miocene-Pliocene in various Eurasian countries, augmenting the previously known sample of the taxon and changing our knowledge of its taxonomy, evolution, and paleoecology, as well as its geographic and stratigraphic distribution (Alba et al. 2015; Arambourg and Piveteau 1929; Ataabadi et al. 2016; Bakalov 1934; Bonis et al. 1990a; 1997; Costeur and Malvesy 2010; Delson 1973; Delson et al. 2005; de Mequenem 1924–25; Gaudry 1862–67; Gentili et al. 1998; Harrison and Delson 2007; Heintz and Brunet 1982; Heintz et al. 1981; Jablonski et al. 2020; Kelley et al. 2025; Khan et al. 2020; Koufos 2006a, 2016a; Koufos et al. 2004; Kullmer and Doukas 1995; Lazaridis et al. 2018; Mottura and Ardito 1992; Pradella and Rook 2007; Radovic et al. 2013; Ridolfi et al. 2023; Rook 1999, 2009; Roth and Wagner 1854; Spassov et al. 2018, 2019; Tsoukala et al. 2024; Zapfe 1991). Furthermore, several opinions have been formed by researchers regarding its relations to recent monkeys, apes, and hominids (Delson 1975, 1994; Frost 2017; Frost et al. 2015; Stevens et al. 2013; Szalay and Delson 1979).

The primary objective of the present article is to provide a comprehensive overview of *Mesopithecus* from Greece, utilizing all available data, as the Greek collection is the most extensive one known in Eurasia. Fourteen fossiliferous sites including *Mesopithecus* have been formally recognized in Greece (Figure 2), including three distinct species,

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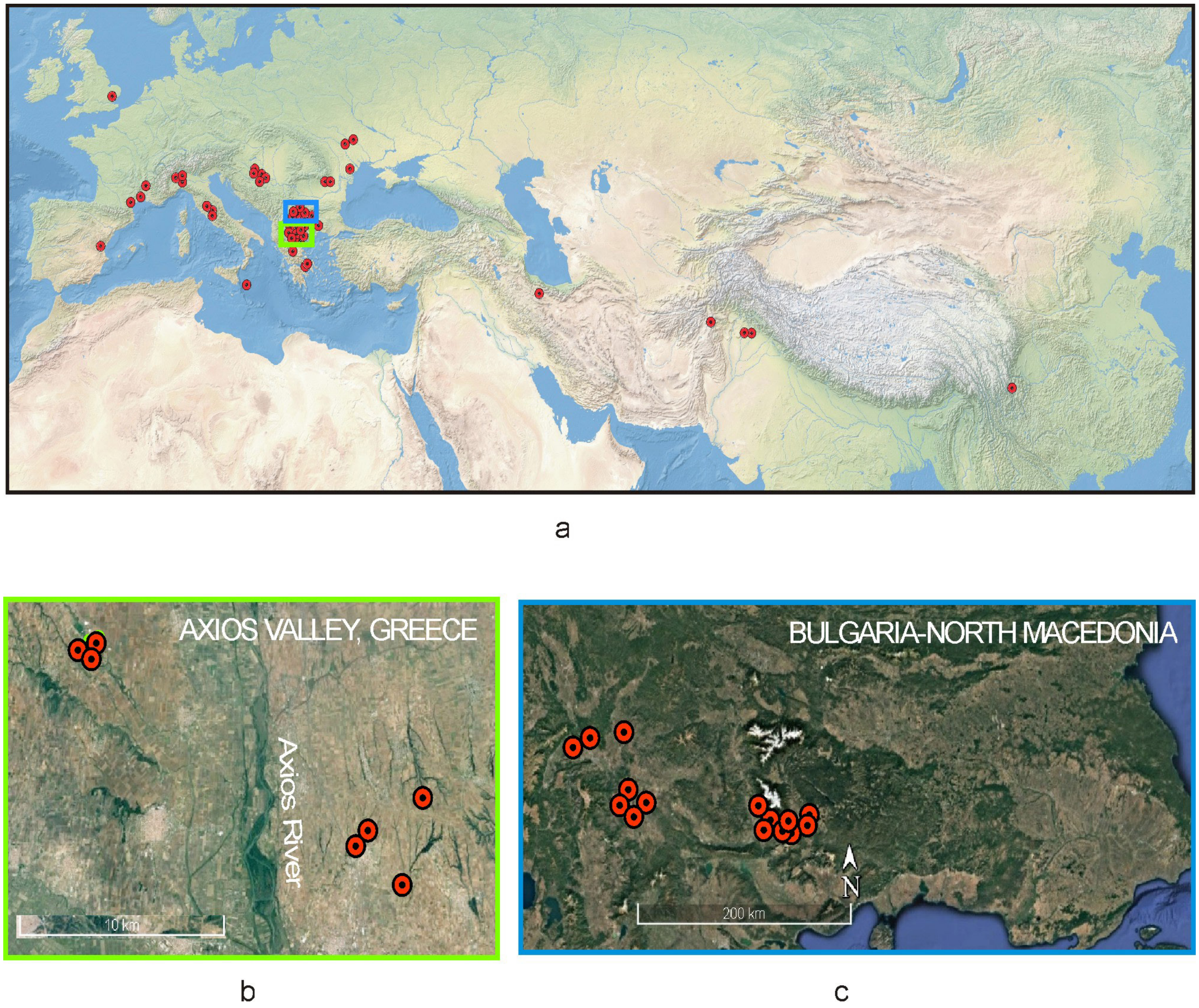

Figure 1. Geographic distribution of Mesopithecus *in Eurasia, a) Eurasia, b) Axios Valley, Greece, and c) Bulgaria and North Macedonia (Map taken from Google Earth).*

with the potential inclusion of an additional species. The majority of the material originates from well-known localities, which are characterized by certain stratigraphy and age. Their rich fauna allows biostratigraphic results and geological ages; moreover, magnetostratigraphic studies provided absolute ages for several localities. The present study offers the following information:

- some historical and geological data for the different *Mesopithecus* bearing mammal localities of Greece,
- the systematic classification of *Mesopithecus*,
- a comparison with other known *Mesopithecus* samples from Greece and Eurasia with the type species *M. pentelicus*.
- the biostratigraphy and correlation of the Greek and Eurasian localities,
- the paleoecological conditions in which *Mesopithecus* lived,
- the paleogeography of *Mesopithecus*,
- metric data collected from the Greek sample of *Mesopithecus*, and illustrations of most material from each Greek locality as supplementary material.

MATERIAL AND METHODS

The Late Miocene mammalian fossil record of Greece contains several collections with *Mesopithecus*. These are stored in the following museums and institutes: a) Athens Museum of Palaeontology and Geology, Greece (AMPG), collections from Pikermi and Maramena; b) Laboratory of Geology and Palaeontology, University of Thessaloniki (LGPUT), collections from Axios Valley (new collection), Kryopigi, and Thermopigi; c) Muséum National d'Histoire Naturelle, Paris, France (MNHNP), collections from Pikermi (Gaudry collection), Axios Valley (old Arambourg collection), Iran and Afganistan; d) Natural History Museum, London, England (NHML), collection from Pikermi; e) Naturhistorisches Museum, Vienna (NHMW), collections from Pikermi and Chomateres f) Staatliche Naturwissensaftische Sammlungen Bayerns-Bayerische Staatssammlung für Paläontologie

Figure 2. Map indicating the position of Mesopithecus*-bearing mammal localities of Greece. CHO: Chomateres; DYTI: Dytiko localities (Dytiko 1, 2, 3); KRY: Kryopigi; MAR: Maramena; NIK: Nikiti 2; PER: Perivolaki; PIK: Pikermi, R.X.: Ravin X; RZO: Ravin des Zouaves 5; SIT: Thermopigi; VATHY: Vathylakkos localities (Vathylakkos 2, 3).*

und Geologie, München, Germany (SNSB-BSPGM), collection from Pikermi; g) Paläontologisches Institut, Universität Wien, Austria (PIUW), collection from Pikermi; h) National Museum of Natural History, Sofia, Bulgaria (NMNHS), collections from Gorna Susitsa, Kromidovo 1, and Kalimantsi; and i) Palaeontological Museum of Assenovgrad, Bulgaria (PMA), collections from Kalimantsi and Hadjidimovo. Additionally, comparative data were collected from various articles on *Mesopithecus* from Spain, France, Italy, Romania, Hungary, North Macedonia, Iran, Ukraine, Afghanistan, Pakistan, and China. The number of crania and mandibles for each Greek locality and species is given in Table 1.

Measurements and dental terminology follow Delson (1973). The measurements were taken with a digital caliper and given to the nearest 0.1mm. If a measurement is significantly different than the measurements taken from the better-preserved specimens, it was omitted during the comparison; if estimated, it is given between brackets. Upper- and lower-case letters denote the upper and lower teeth, respectively (e.g., M2, upper second molar; p4, lower fourth premolar). Juvenile specimens were excluded from the analysis and referred separately. The number of a specimens consists of three parts. The first part is the museum or institute abbreviation (e.g. **MNHNP**: Museum National d'Histoire Naturelle of Paris), the second is the abbreviation of the locality (e.g. **PIK**= Pikermi) and the third is the catalogue number of the specimen. e.g. **MNHNP-PIK-134**. The multivariate analysis, and scatter diagrams were constructed using PAST 4.04 software (Hammer et al. 2001). The Pikermi collection was used as the standard for comparison in all diagrams. Specimens with complete measurements or missing 2–4 measurements were used to create

TABLE 1. NUMBER OF THE STUDIED SPECIMENS OF *MESOPITHECUS* FROM THE GREEK LOCALITIES AND THEIR AGE.*

Species	Locality	MN zone	Age Ma	Specimens
M. pentelicus	Pikermi	MN 12	7.25-7.10	94
M. pentelicus	Chomateres	MN 12	7.23-7.11	4
M. pentelicus	Dytiko 1	MN13	6.0-7.0*	1
M. pentelicus	Dytiko 2	MN13	6.0-7.0*	2
M. pentelicus	Dytiko 3	MN13	6.0-7.0*	1
M. pentelicus	Thermopigi	MN 11-12	-	3 bones
M. pentelicus	Kryopigi	MN 11-13	7.3-6.4*	3
M. pentelicus	Maramena	MN 13/14	5.40-5.23*	26
M. delsoni	Ravin des Zouaves 5	MN 11	~8.2	3
M. cf. *delsoni*	Ravin X	MN 10/11	-	1
Mesopithecus sp. (*M. delsoni?*)	Nikiti 2	early MN 11	8.7-8.2*	2 metapodials
Mesopithecus sp.	Vathylakkos 2	MN 12	~7.4	8
Mesopithecus sp.	Vathylakkos 3	MN 12	~7.3	4
Mesopithecus sp.	Perivolaki	MN 12	7.3-7.1	4
M. monspessulanus	Dytiko 1	MN 13	6.0-7.0*	3
M. monspessulanus	Dytiko 2	MN 13	6.0-7.0*	1

*The ages marked with an asterisk are estimated based on biochronological data; the rest are based on magnetostratigraphic data.

a comparative sample. Missing values were estimated by applying iterative imputation. To normalize the values of the various measurements, Mosiman's transformation using logarithms was applied. Principal Component Analysis was used to compare the different faunas with the comparative sample from Pikeimi, as well as with material from other localities. Correspondence analysis (CA) was used to determine the paleoenvironment based on the fauna from each locality in comparison to modern faunas from known environments. The term "closed" is used for forestrial conditions (woodland, open woodland, forest) with high humidity, while the term "open" is used for savannah-like environments (savannah woodland, savannah bushland, savannah grassland) with high temperatures and low humidity. In the CA diagrams, the number of taxa for each group of mammals (primates, proboscideans, bovids, giraffids, cervids, equids, and rhinocerotids) is analysed in comparison with modern faunas.

ABBREVIATIONS

Museums and Institutes: **AMPG**: Athens Museum of Palaeontology and Geology, University of Athens; **LGPUT**: Laboratory of Geology and Palaeontology, University of Thessaloniki; **MNHNP**: Museum National d'Histoire Naturelle of Paris; **NHMBEO**: Natural History Museum of Beograd; **NHML**: Natural History Museum of London; **NHMS**: Natural History Museum of Skopia; **NHMW**: Naturhistorishes Museum, Vienna; **NMNHS**: National Museum of Natural History, Sofia, Bulgaria **PIUW**: Paläontologisches Institut, Universität Vienna. **PMA**: Palaeontological Museum of Assenovgrad, Bulgaria; **PVH**: Laboratoire Paléontologie desVertébrés et Humaine Paris; **SMNHS**: Swedish Musem of Natural History, Stockholm; **SNSB-BSPGM**: Staatlische Naturwissensaftische Sammlungen Bayerns- Bayerische Staatssamlung für Paläontologie und Geologie, München.

Localities: **AKK**: Akkasdagi; **BAL**: Baltavar; **BEL**: Beluska; **BV3**: Baccinello V3; **CAP**: Capeni; **CAS**: Casino; **CEL**: Celleneuve; **CHO**: Chomateres; **DIT**: Dytiko 2; **DKO**: Dytiko 3; **DRK**: Dorkovo; **DTK**: Dytiko 1; **DYTI**: Dytiko 1, 2, 3; **GOS**: Gorna Sushitsa; **GRA**: Gravitelli; **HAJ**: Hasnácka; **HAT**: Hatvan; **HD**: Hadjidimovo; **HST**: Hasnot; **IVA**: Ivanovce; **KAL 1**: Kalimantsi 1; **KALI**: Kalimantsi (1, 2, petsata); **KAR**: Karaslari; **KIC**: Kiro Kucuk; **KRO**: Kromidovo 2; **KRY**: Kryopigi; **KTA-B:** Kemiklitepe- A, B; **MAL**: Malusteni; **MAR**: Maramena; **MLN**: Mytilinii 4; **MMR**: Middle Maragheh; **MNP**: Montpellier; **MNT**: Monticino Quarry, Brisighella; **MOL**: Molayan; **MON**: Moncucco; **MTL**: Mytilinii 1; **MYT**: Mytilinii 3; **NIK**: Nikiti 2; **PER**: Perivolaki; **PERG**: Perpignan; **PIK**: Pikermi; **PNT**: Pentalophos 1; **POL**: Polgardi; **PXM**: Prochoma 1; **Q5**: Samos Quary 5; **R.Ar**: Ravin Ar; **R.C:** Ravin C; **R.G:** Ravin G or Ravin de Vatilük; **R.X**: Ravin X; **RZO**: Ravin des Zouaves

5; **R.Z**: Ravin des Zouaves**;** **RZ1**: Ravin des Zouaves 1; **SIT**: Thermopigi; **VATHY**: Vathylakkos 2, 3. **SUT**: Shuitangba; **VAT**: Vathylakkos 3; **VLO**: Vathylakkos 1; **VTK**: Vathylakkos 2; **VDM**: Venta del Moro; **VEL**: Veles; **VLA**: Villafranca d'Asti; **WOL**: Wolfersheim; **XIR**: Xirochori 1.

Teeth: **a**: Anterior**;** **B**: Breadth; **CA**: Correspondence Analysis; **DAP**: Anteroposterior diameter; **dex**: Right; **dist**: Distal.; **DT**: Transverse diameter; **L**: Length; **p**: Posterior; **PCA**: Principal Component Analysis; **prox**: Proximal; **sin**: Left.

THE GENUS *MESOPITHECUS*

The first indication of monkeys existing in the Late Miocene of Eurasia was recognized at Pikermi, situated close to Athens, Greece, in the first half of the 19th century (see Figure 2). Among the initially collected material from Pikermi Prof. Andreas Wagner from Munich recognized a cercopithecid, which he identified as a new genus and species, named *Mesopithecus pentelicus* Wagner, 1839 (Wagner 1839, 1840).

Mesopithecus has been included in the subfamily Colobinae *incertae sedis* (Strasser and Delson 1987). The authors analyzed a set of characters, and they found that *Mesopithecus* shared several derived characters with the subfamily Colobinae. These include the high molar cusps, and the reduced proximal articular facet between the ectocuneiform and cuboid. The colobine morphotype presents secondarily reduced molar flare, shortened trigonid, mandible with expanded gonial region, reduction of the thumb, and shallow medial groove for the flexor tibialis on the astragalus (Strasser and Delson 1987; Szalay and Delson 1979). In *Mesopithecus*, thumb flare and the thumb reduction are present while there is a shallow medial groove for flexor tibialis in the astragalus. Although there are similarities, *Mesopithecus* is classified as Colobinae *incertae sedis* because it presents a derived feature that is absent in its putative descendant *Dolichopithecus* (Strasser and Delson 1987). Frost et al. (2015) hypothesized that there has been no reduction of the thumb in *Mesopithecus*. This absence could be indicative of either an independent reduction of the thumb in African and Eurasian colobines, or of several dispersal events of colobines in Eurasia. Jablonski et al. (2020), based on the developmental biology of the limb skeleton, consider that *Mesopithecus* is a stem presbytinan rather than a stem colobine Recently, Arenson (2025) considered *Mesopithecus* to be a stem colobine, and its comparison with other stem colobines indicates a more modern-colobine facial morphology. A proposed diagnosis for the genus *Mesopithecus* is: medium- to small-sized colobine, with pronounced sexual dimorphism, short face, elongated nasal bones relative to the most colobine genera, nasal cavity above the lower margin of the orbit in frontal view, low orbits on the face, weak to moderate supraorbital torus and weaker in females, ascending ramus vertical, shallow mandibular corpus with constant height between p4 and m3, rounded gonial area, steeply inclined planum alveolare, relatively small protocone (lingual cusp) in the upper premolars, variable size of the hypoconulid in the m3, elbow joint indicating terrestrial-semiterrestrial way of life, relatively long thumb, and short colobine-like tarsus (Bonis et al. 1990; Delson 1973; Koufos 2003, 2019a, b; Koufos et al. 2004; Szalay and Delson 1979). *Mesopithecus* includes three species. The best known is the typical one, *Mesopithecus pentelicus*, from the Late Miocene of Eurasia. Two other species are also referred to the same genus, the Latest Miocene-Pliocene *Mesopithecus monspessulanus* Gervais, 1849 and the early Turolian *Mesopithecus delsoni* Bonis, Bouvrain, Geraads, Koufos, 1990. One more species, *M. sivalensis*, is also mentioned from Indo-Pakistan but it is not fully documented (Harrison and Delson 2007; Kelley et al. 2025; Lydekker 1878).

MESOPITHECUS IN GREECE

Apart from the rich collection of *Mesopithecus* from Pikermi, this taxon has been recorded from several other localities in Greece (see Figure 2), which also yielded interesting specimens. The Axios Valley localities near Thessaloniki (see Figure 2) yielded a substantial collection of *Mesopithecus* in the early 20th century (Arambourg and Piveteau 1929). More material from the Axios Valley has been collected during extensive excavations in the valley since 1972 (Koufos 2009a, b). Except Pikermi *Mesopithecus* remains were discovered in several localities, including Chomateres near Pikermi (Symeonidis et al. 1973), Maramena in Serres Basin, Northern Greece (Kullmer and Doukas 1995), Nikiti 2, Kryopigi, and Thermopigi in Chalkidiki, Northern Greece, as well as at Perivolaki in Thessaly (see Figure 2) (Koufos 2006a, 2009a, b, 2016a; Lazaridis et al. 2018; Tsoukala et al. 2024). Further details regarding these localities will be provided in the corresponding sections and supplementary material.

SEXUAL DIMORPHISM IN *MESOPITHECUS*

Several authors have discussed the sex determination of *Mesopithecus* and proposed different indicators for it (e.g., Delson 1973; Szalay and Delson 1979; Zapfe 1991). The *Mesopithecus* sample from Pikermi is quite rich and its study can provide clear results for the sexual determination of the specimens. Additionally, it can serve as a comparative sample for determining the sex of *Mesopithecus* from other localities or for specimens lacking the canine.

Mesopithecus exhibits a clear sexual dimorphism in the size and shape of its upper and lower canines, with the male canines being significantly larger than those of the females (e.g., Delson 1975; Strasser and Delson 1987; Szalay and Delson 1979). Additionally, there is a slight difference in the size of the postcanine teeth, although this is less pronounced than in the canines. In addition to the sexual dimorphism of the canines, there are other characteristics that can be used to distinguish between male and female *Mesopithecus*. The development of the sagittal crest and sutures may indicate sexual dimorphism (Bonis et al. 1997; Delson 1973; Szalay and Delson 1979). In male *Mesopithecus* crania from Pikermi, the temporal lines start from the upper buccal border of the orbit, run posteriorly, and join at the posterior end of the frontals near bregma. Then they either run parallel or are joined in a sagittal crest up to the nuchal crest. This feature is clear or partially preserved in the crania AMPG-PIK-44 (Supplement 5: Figure 4), MNHNP-PIK-013, 014, 035, (Supplement 6: Figures 11, 12, 18), NHMW-PIK-A. 4693 (Supplement 9: Figure 2). The height of the sagittal crest is less than 4mm in males. In female crania, the temporal lines are not as clearly marked. As they are going backwards, they gradually weaken and disappear at the end of the frontals near bregma. The studied female Pikermi crania have no sagittal crest. This morphological difference should be considered in adult crania. It should be noted that the sagittal sutures and crest are not strongly observable in young individuals, such as in the young male cranium LGPUT-VTK-78 (Supplement 10: Figure 7), where the sutures and sagittal crest are not distinguished (Koufos et al. 2004). This suggests that both sutures and crests appear during the ontogenetic development of the animal and get their final configuration and size in the adult individuals.

The development of the supraorbital torus is a distinguishing feature for sexual separation in *Mesopithecus*. Males have a strong, thick, and protruding supraorbital torus, while females have a weaker, thinner, and less developed one, a difference clearly illustrated in the Pikermi material. In the Pikermi sample the thickness of the supraorbital torus varies from 3.5–5.8mm in males and from 2.7–3.2mm in females. It is worth noting that the ontogenetic stage of the individual influences this characteristic. In the young male cranium (LGPUT-VTK-78; see Supplement 10: Figure 7), the supraorbital torus is weak and like that of a female (Koufos et al. 2004). The canine/premolar complex is also referred to as a feature that can be used to distinguish the sexes of *Mesopithecus*. In many primates, the distal face of the upper canine is in contact with the mesial face of the p3, forming a distinctive feature. Therefore, there is a honing facet on the mesial surface of the p3. This facet is significantly larger in males than in females. This article does not refer to the postcranial skeleton, but it is important to note that there is a clear sexual dimorphism. Typically, the male skeleton is larger than the female skeleton (Delson 1973; Koufos et al. 2003; 2004; Szalay and Delson 1979; Zapfe 1991).

Sex determination of a complete specimen is relatively straightforward, especially if the canines are present. However, it can be difficult, if not impossible, to determine the sex of a fragment that lacks most of the distinguishing features mentioned above. I have tried to separate the males and females using various methods, such as comparing the length of molars to premolars, or the length of the tooth row, as well as the length to width ratio of various teeth, but unfortunately there is often considerable overlap, making it difficult to get a clear and certain determination, except in the case of canines. The sex of the Pikermi sample was primarily determined by canine size, which is the most reliable indicator of sexual dimorphism. Samples of upper and lower teeth of *M. pentelicus* preserving the canines and most of the postcanine teeth from Pikermi were analyzed using principal component analysis to determine whether they could be distinguished in separate size groups. The question is whether dental dimensions should be used instead of cranial or mandibular dimensions. In contrast to crania and mandibles, teeth are numerous, providing more reliable and precise measurements. The crania and mandibles are often deformed, distorted, and/or broken and their dimensions are limited and not accurate.

To check the sexual distinction of the *M. pentelicus* sample from Pikermi, the material was analyzed using principal component analysis. The available material of upper and lower teeth, except incisors, preserving the canines and most of the postcanine teeth were included in the analysis. The analysis of both upper and lower teeth revealed a clear separation into two size groups by PC1 matching 66.8% and 73.4% of the total variance respectively (Figure 3a, b). A small-sized group is situated in the left part of PC1, corresponding to the females, while a large-sized one is in the right part of PC1, including the males. The primary factor responsible for the differentiation of both samples is the size of the canine, with the size of the molars serving as a secondary influence (see Figure 3). The Pikermi sample of *M. pentelicus* encompasses a number of crania and mandibles that lack the canine yet retain the majority or entirety of the postcanine dentition. The sex determination of this sample is based on the comparison with the Pikermi sample, retaining the canines (Figure 4a, b). The PC1, which matches 73.8% and 72.5% of the total variance for the upper and lower teeth, respectively, separates the sample into two groups. The specimens with small size match with the specific females, whereas those of large size align with the specific males of *M. pentelicus* (see Figure 4a, b). However, there are a few specimens situated near the boundary between the two groups (see Figure 4b), which may be included either in the male or female group; this is possibly due to the lack of several postcanine teeth in these specimens.

SYSTEMATICS

Order Primates Linneaus, 1758
Suborder Anthropoidea Mivart, 1864
Infraorder Catarrhini Geoffrey, 1812
Superfamily Cercopithecoidea Gray, 1821
Family Cercopithecidae Gray, 1821
Subfamily Colobinae Jerdon, 1867
Genus *Mesopithecus* Wagner, 1839

MESOPITHECUS PENTELICUS WAGNER, 1839

Synonyms

Mesopithecus pentelicus Wagner, 1840
Mesopithecus major Roth and Wagner, 1854
Semnopithecus pentelicus Gaudry and Lartet, 1856
Semnopithecus (Mesopithecus) pentelicus Wagner, 1857
Mesopithecus pentelici Gaudry, 1862-67

Type Locality

Pikermi, Attica, Greece. Its age is Late Miocene, middle Turolian, MN 12; GPTM. 7.25–7.10 Ma (Böhme et al. 2017).

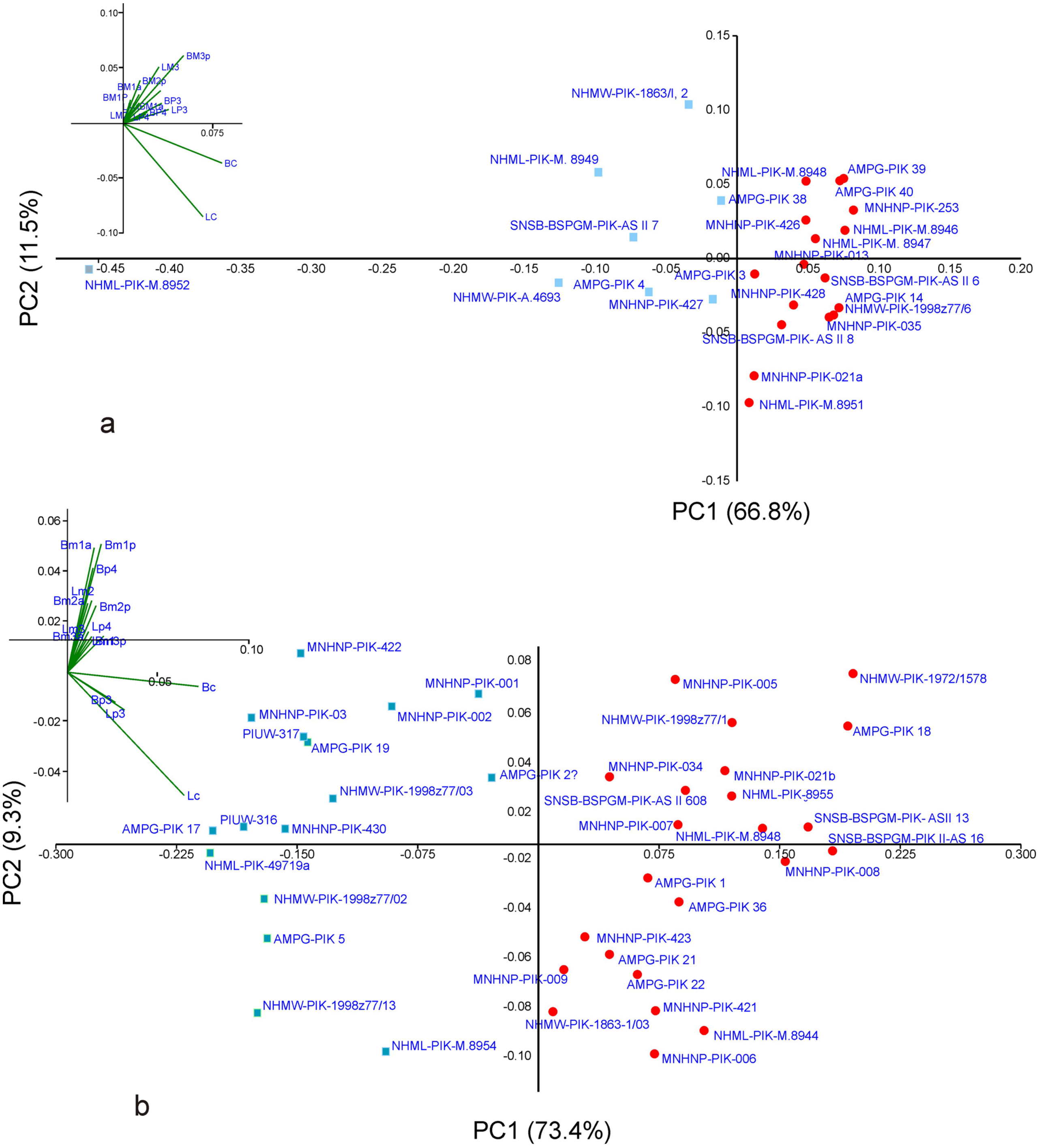

Figure 3. Principal component analysis using the upper (a) and lower (b) dental dimensions of the sample of M. pentelicus *from Pikermi preserving the canines for sexual distinction. Abbreviations.* ***L****: Length;* ***B****: Breadth;* **a**: *anterior;* ***p****: posterior;* ***DAP****: Antero-posterior diameter;* ***DT****: Transverse diameter;* ***prox****: Proximal;* ***dist****: Distal. Symbols: dot (red): males; filled square (cyan): females.*

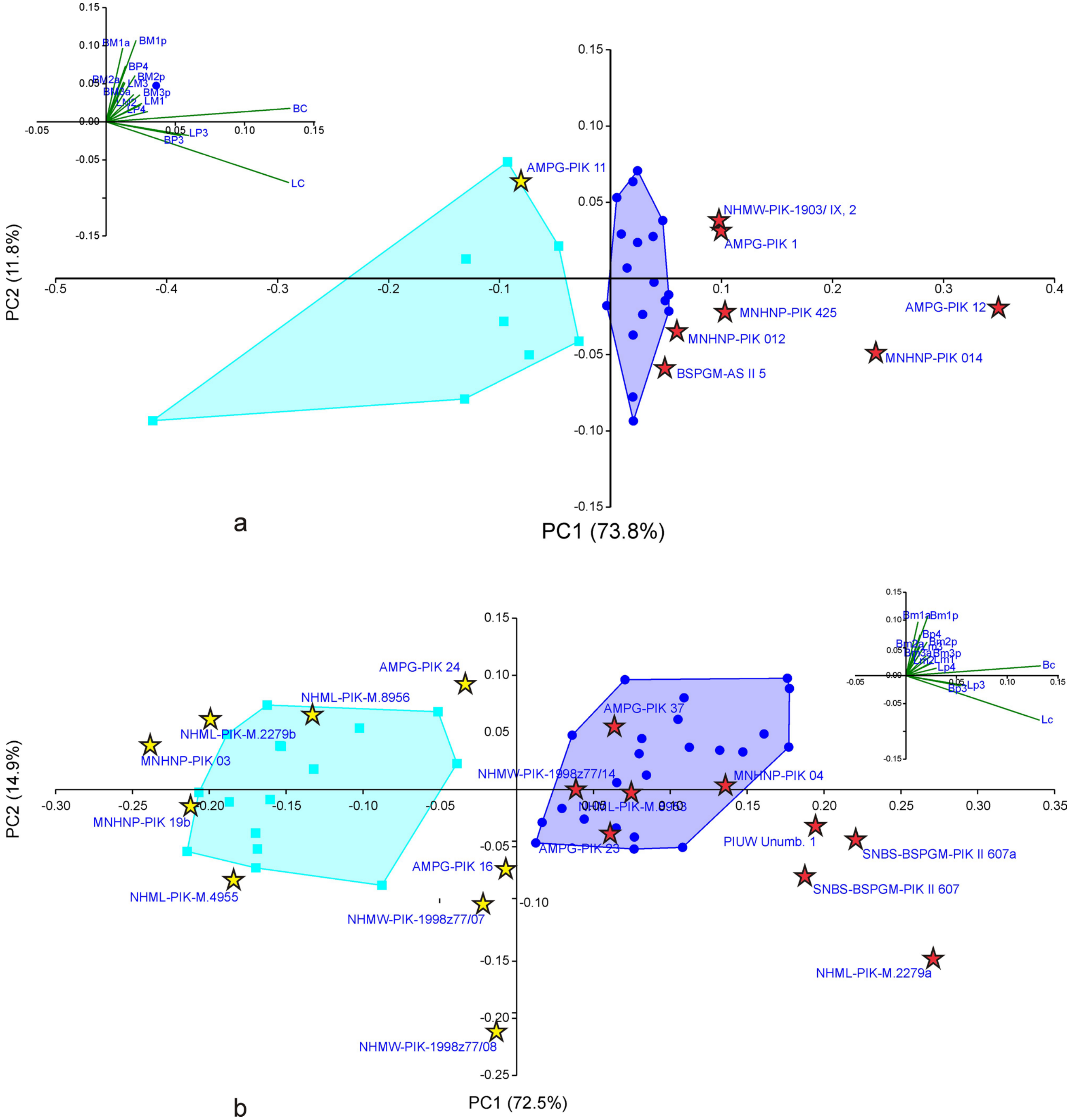

Figure 4. Principal component analysis using the upper (a) and lower (b) dental dimensions of the sample of M. pentelicus *from Pikermi lacking the canines and preserving several postcanine teeth. Symbols: dot (blue):* M. pentelicus *preserving the canines, male; filled square (cyan):* M. pentelicus *preserving the canines, female; asterisk (red): males without canines; asterisk (yellow): females without canines. Abbreviations as in Figure 3.*

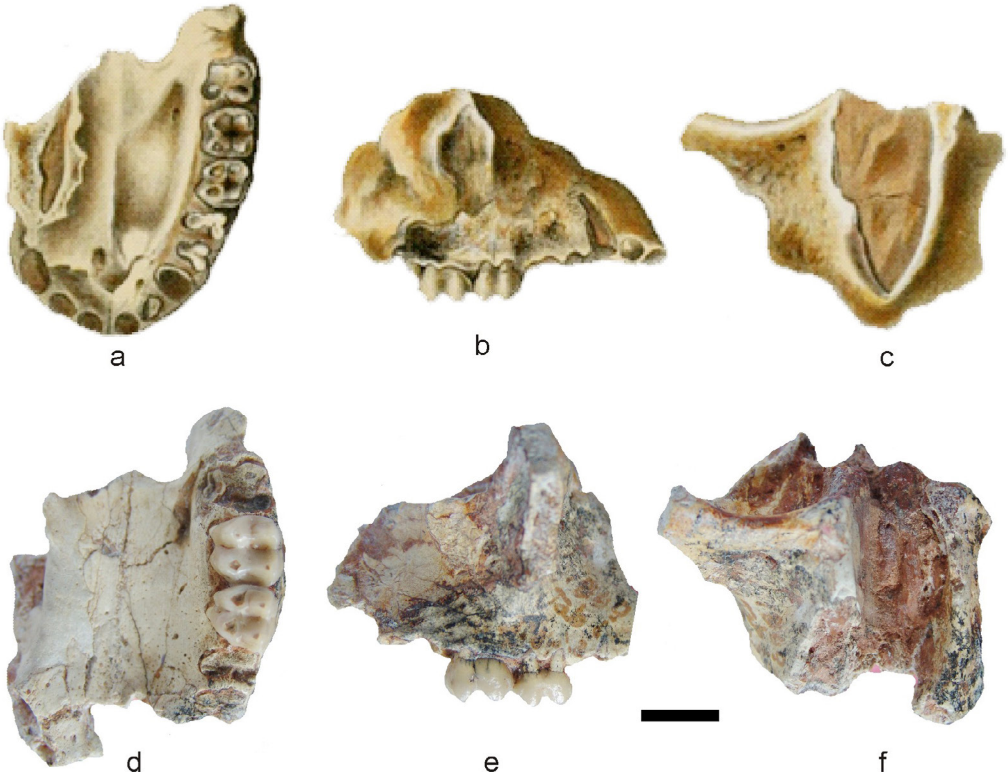

Figure 5. Mesopithecus pentelicus, *Pikermi, Attica, Greece; middle Turolian, MN 12, Late Miocene; GPTS=7.25–7.10 Ma. a-f) Right maxillary fragment with M1-M2, holotype, SNSB-BSPGM- AS II 11; a-c) original condition (Wagner, 1840) and d-f) present condition of the holotype. a, d) occlusal; b, e) lateral; c, f) dorsal view (scale bar 10mm).*

Holotype

It is a maxillary fragment preserving the right alveoli of I1-P4 and the teeth M1-M3 dex, as well as the alveoli of I1-C sin (Figure 5a-c), (Wagner (1840). During the Second World War the holotype was partially destroyed in the bombing of Munich. Currently, only a preserved maxillary fragment with M1-M2 dex of the holotype remains (Figure 5d-f). The genus name is derived from the Greek words μέσος= middle and πίθηκος= monkey; the species name comes from the mountain Pentelikon, in the foothills of which is situated the Pikermi ravine with the fossiliferous deposits. Later, the Pikermi *Mesopithecus* was referred to under the specific name *pentelici*, (Gaudry 1862-67). However, the name *pentelicus* has priority and it is currently used. In addition, *pentelicus* (= πεντελικός) means ''from Pentelikon,"and it is grammatically correct in Greek. Moreover, the generic name *Semnopithecus* has also been used (Delson 1973; Gaudry 1862-67).

Other Localities

Chomateres, Attica, Greece; Dytiko 1, 2, 3, Axios Valley; Kryopigi, Chalkidiki Peninsula; Maramena, Serres Basin (see Figure 2) (Koufos 2024).

Diagnosis

Medium-sized colobine monkey; short upright face; sexual dimorphism in the cranium, canines, and postcranials (usually the males are larger than females); well-developed sagittal crest in the males and absent or smaller in the females; shallow mandibular corpus with straight inferior border from p4 to m3; convex external symphysis; absence of symphyseal constriction; small and deeply inclined planum alveolare; weak or absent fossa genioglossa; small lingual cusp (protocone) on the P3,4; small honing facet in the p3; small or sometimes absent hypoconulid in the m3.

Morphological Characters

Cranium. The cranial material from Pikermi is abundant, consisting of over 20 crania and cranial fragments, often accompanied by the mandible. Most of the crania exhibit varying degrees of deformation, distortion, and damage resulting from fossilization and/or excavation and preparation processes. In some cases, damage is due to carnivoran predation activity (Supplement 7: Figure 1; red arrows). Usually, the braincase is filled with mud, which subsequently dried during diagenesis, causing a reduction in volume, and leaving empty spaces in the braincase. The sediment overlying the cranium and the diagenetic process can cause damage, distortions, and breakages in these areas. In some cases, the weight of the sediment and resulting pressure caused a flattening of the cranium; see crania LGPUT-VTK- 56, 61 from the Axios Valley (Supplement 10: Figures 4, 5). Additionally, carnivoran predation can result in antemortem bone breakage, as evidenced by the bite marks found on *Mesopithecus* crania. Deformation of the crania or mandibles can affect the morphological characteristics of the cranium, making precise recognition difficult. Therefore, measurements taken may not correspond to the actual size, resulting in discrepancies.

The cranial characters of the Pikermi *Mesopithecus* were given in various articles; the most important works are those of Delson (1973) and Zapfe (1991). In this article are given the main morphological characteristics of the cranium based on the known material from Pikermi. The cranium has a strong prognathism. The nasals are narrow and triangular shaped with their caudal margin terminating at the mid-height of the orbit. In addition, the rostral margin of the nasals forms two small processes, resembling small spikes, which protrude from the center of the superior margin of the nasal cavity. This is clearly visible in cranium MNHNP-PIK-013 (see Supplement 6: Figure 11; red arrow). The nasal cavity is ovoid in shape and varies in size depending on the cranial deformation (see Supplement 6: Figure 11; Figure 26; Supplement 7: Figure 2). The nasal cavity becomes narrower and more elliptical in laterally deformed crania. In the less-deformed crania, the anterior end of the nasal cavity is located above the small diastema between the C and the P3. The shape of the orbits is strongly influenced by any lateral or dorsoventral deformation. However, some crania with less deformation still retain their original shape. For instance, in the crania MNHNP-PIK-014, 428, NHML-PIK-M.8945 and NHML-PIK-M.8947 (see Supplement 6: Figure 11; see Supplement 7: Figures 1–2; Figure 3), the orbits are well-preserved and have a rounded shape. The observable orbit shape in the other crania is usually elliptical, depending on the degree of deformation. The orbit's margin is continuous in all studied crania. The interorbital distance is relatively large, but its size may vary depending on the degree of deformation of the cranium. The supraorbital torus is continuous with the glabella; it is divided into two parts by a depression in the middle. The development of the supraorbital torus depends on the sex and the ontogenetical stage of the studied specimen. In the adult males it is large and thick (see Supplement 6: Figures 11, 26; see Supplement 7: Figures 2–3; Figure 4) while in the females it is weaker (Supplement 5: Figure 2, 5; Supplement 8: Figure 4). Behind the supraorbital torus there is a slight depression which in the deformed crania is not distinguished easily. The lacrimal sulcus is well distinguished and extends onto the maxilla. The braincase is usually deformed and fractured, but in the better-preserved crania it is almost sphaerical. Temporal lines originate from the upper outer border of the orbit and are directed inwards and posteriorly. They are fused at the end of the frontals forming the sagittal crest, which is directed caudally and joins the nuchal crest (see Supplement 5: Figure 4; Supplement 8: Figure 2). The zygomatic arches are robust and originate above the contact between M1 and M2. However, it is difficult to determine their degree of lateral projection as they are often fractured and/or distorted. The basicranium is flattened, and the foramen magnum is large and tends to move forwards (Supplement 5: Figure 1; see Figure 2; Supplement 8: Figure 2). It is subcircular and has two relatively large occipital condyles. The palate is elliptical, deep and relatively wide. The posterior margin of the palate is located at the distal end of the M3. The choanae are deep, and their anterior margin is rounded. (see Supplement 5: Figure 1; see Supplement 7: Figure 4; Supplement 8: Figure 5).

Upper dentition. The upper incisors are buccolingually flattened, and I1 is larger than I2. On their distal surface there is a marginal ridge around the crown, which connected with the distal cingular projection (Figure 6a, e). This morphology forms a basin on the lingual surface of the tooth. In the unworn or little worn teeth, the basin is almost triangular in I1 and sub-elliptical in I2 (see Figure 6a, e). The basin gradually reduces, as attrition increases and finally disappears in very worn teeth (Figure 6d, h). Attrition of the incisors starts at the incisive apex of the tooth, forming a narrow mesiodistal dentine pit (see Figure 6a). As the attrition progresses, this pit gradually widens and, in heavily worn teeth, covers the entire occlusal surface, while the enamel is limited around the tooth as a thin lamella (see Figure 6d). The incisors that are worn have a triangular-shaped occlusal surface and retain the lower part of the basin as a narrow semilunar groove (Figure 6c). The upper canine of *Mesopithecus* has a triangular cross-section and is relatively robust and high-crowned, especially in the males (see Figure 6c, d, Figure 6g). It is situated laterally to the tooth row. In unworn or slightly worn teeth, there is a strong crest on the distal surface. There is also a small cingular projection on the distal surface of the canine. The upper canine is in contact with the mesial surface of p3 and thus a large wear facet is developed along its distolingual surface. In addition to the previous facet, there is another one at the base of the worn canines vertical to the previous (see Figure 6c, d, g, Figure 6f). This facet is formed by the grinding of the distal cingular projection of the upper canine with the tip of p3. There is a small diastema between the upper canine and I2. The premolars of *M. pentelicus* from Pikermi have a similar morphology, with a buccal cusp (paracone) and a smaller lingual one (protocone), the latter being less high; a basin lies between them (see Figure 6b, c, f, g). As attrition progresses, the protocone disappears, the paracone decreases in height and in the very worn teeth the entire occlusal surface becomes a dentine pit (see Figure 6d, h); however, the paracone can still be distinguished as a small peripheral cusp. The upper molars are square shaped and have four main cusps separated by deep valleys. The cusps are of almost equal size, with the buccal cusps being slightly higher than the lingual ones. There is a well-developed mesial fovea and distal fovea, although the distal fovea is slightly more pronounced in M3.

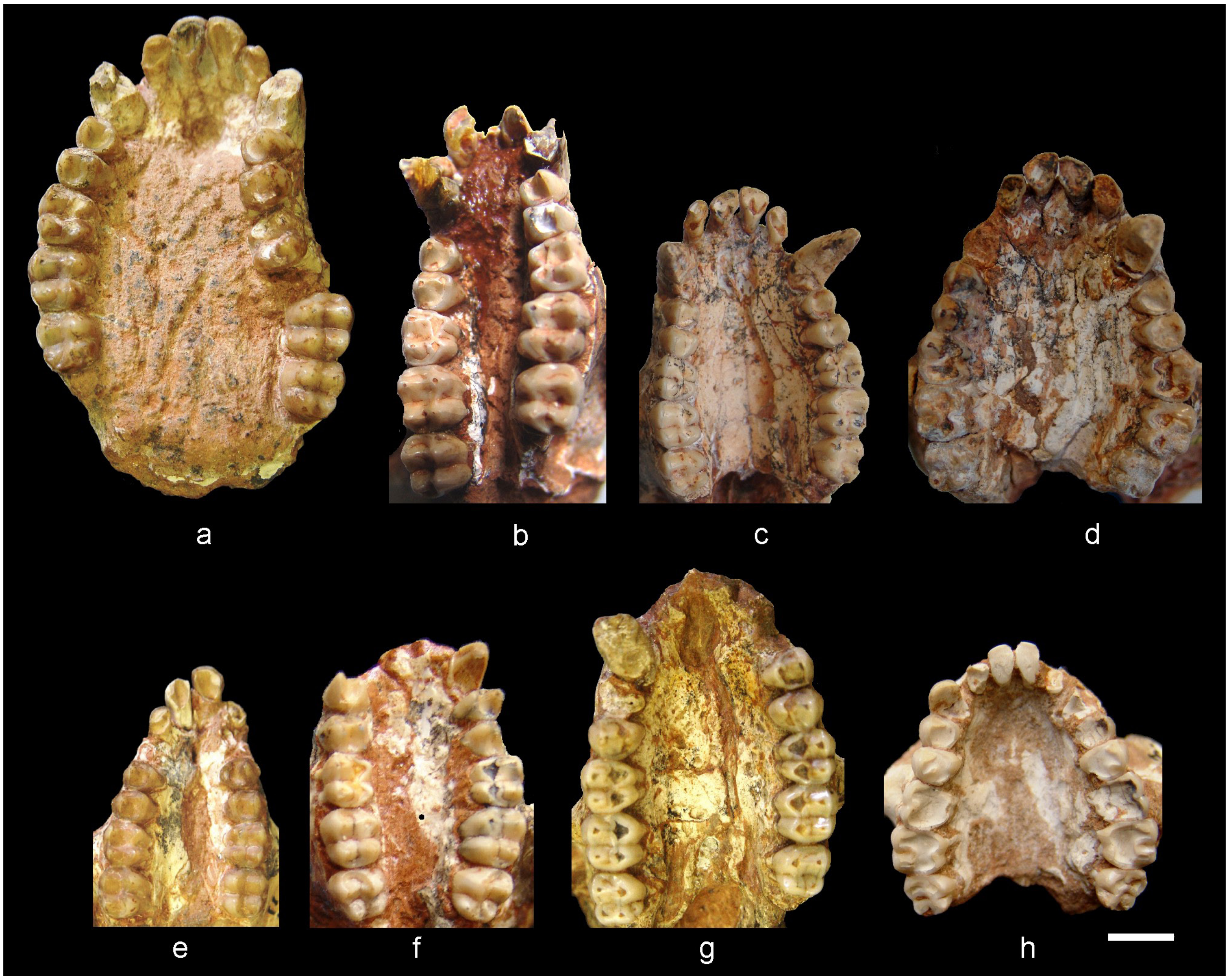

Figure 6. Mesopithecus pentelicus, *Pikermi, Attica, Greece. Upper dentition in various wearing stages. Male individuals: a) MNHNP-PIK- 427, b) NHMW-PIK-1863/I-2, c) NHML-BMNH-M.8947, d) NHML-BMNH-M.8946; Female individuals: e) MNHNP-PIK-429, f) AMPG-PIK-2, g) MNHNP-PIK-34, h) AMPG-PIK-13 (scale bar 10mm).*

The wear of the molars begins at the tips of the cusps with the formation of small, rounded dentine pits and gradually extends to the entire cusp. The wear is greater on the lingual cusps (see Figure 6c, f, g, Figure 6b). The dentine pits of the lingual cusps connect first, followed by the hypocone with the metacone. The paracone's dentine pit is the last one to remain isolated and only in extremely worn teeth joins the others (see Figure 6d, h).

Accessory cusps were observed early in the molars of *M. pentelicus* from Pikermi (Figure 7). (Bakalov 1934; Delson 1973; Gaudry 1862-67; Voruz 1968). These are common in males and appears to be restricted to the Pikermi sample of *M. pentelicus*, as they are absent in material from other localities. No accessory cusps were found in material from the Axios Valley, Maramena, and Kryopigi (Macedonia, Greece), or from Kalimantsi, Kromidovo, and Gorna Sucica (Bulgaria). There is no reference to the presence of accessory cusps in the old collection from North Macedonia (Radovic et al. 2013; Spassov et al. 2018). Accessory cusps are not present in the recently described material from Spain (Alba et al. 2015) and Pakistan (Khan et al. 2020). Nevertheless, the available specimens of *Mesopithecus* from other localities are very few in comparison to the Pikermi sample (in some cases only one specimen). The accessory cusps are usually situated in the buccal valley between the paracone and metacone and are more frequently observed in M2 (see Figure 7a, b, d, e, g; red arrows). An accessory cusp is present on the M1 of AMPG-PIK-12 and MNHNP-PIK-013, 429 (see Figure 7a, b, e). The M3s of the specimens MNHNP-PIK-035 and AMPG-PIK-4 bear an accessory cusp on the lingual side of the tooth, aligned with the paracone and metacone (see Figure 7c, f). Based on the material I have seen, I calculated the percentage of the teeth preserving accessory cusps for definitive males and females. Thus, the percentage for the male is 4.0% for M1, 3.8% for M2, and 1.3% for M3; for the female is 0% for M1, 2.1% for M2, and 2.5% for M3. Pikermi *Mesopithecus* has long been known to possess accessory cusps, but no explanation has yet been

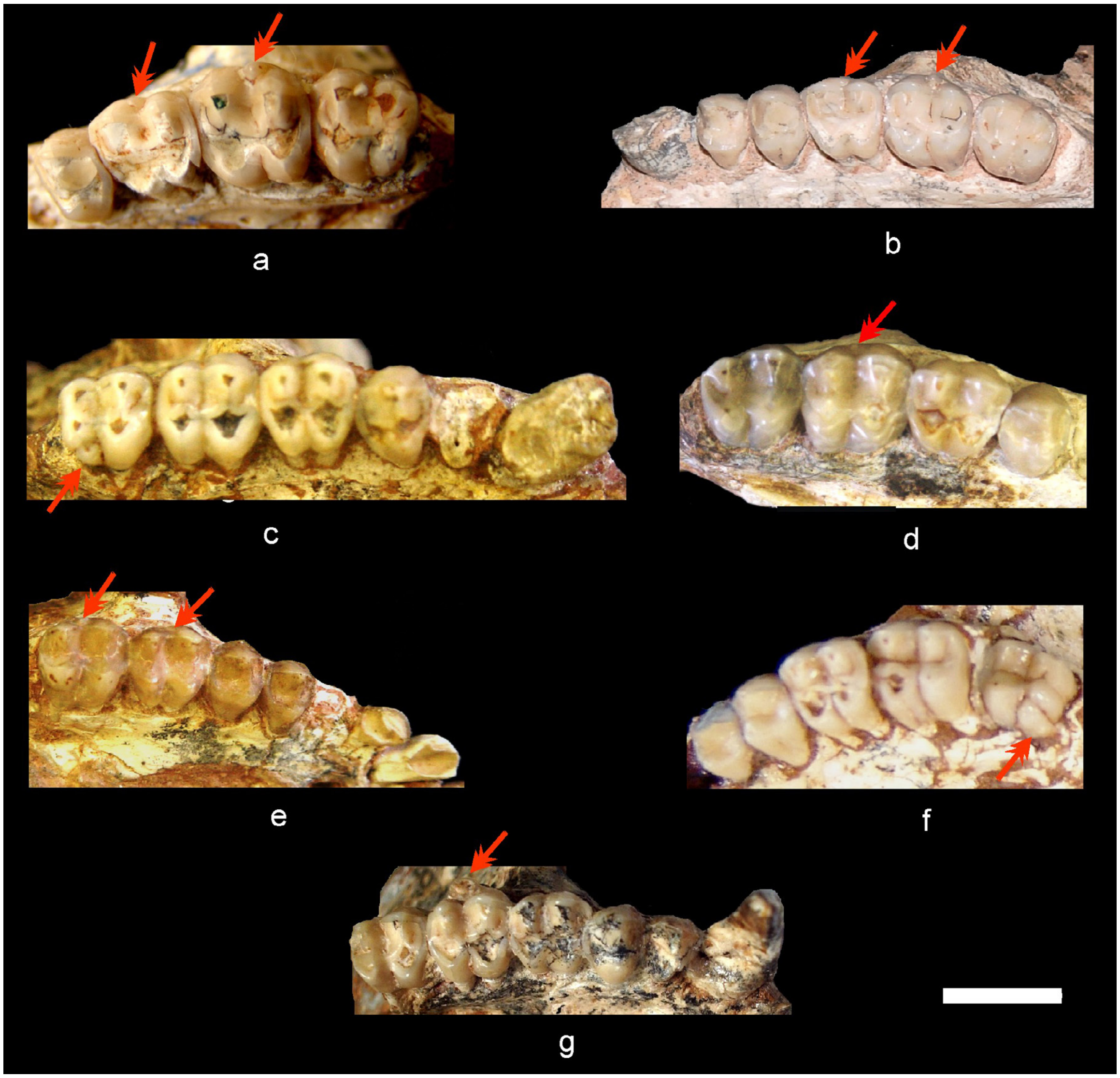

Figure 7. Mesopithecus pentelicus*, Pikermi, Attica, Greece. Specimens with accessory cusps in the upper dentition. a) AMPG-PIK-012, b) MNHNP-PIK-013, c) MNHNP-PIK-035, d) MNHNP-PIK-425, e) MNHNP-PIK-429, f) AMPG-PIK-4, g) NHML-PIK-M.8945. The red arrows indicate the accessory cusps (scale bar 10mm).*

found for its occurrence. The study of the modern Asian colobines suggests that *Presbytis* shows changes in the upper and lower M3 for better occlusion. These changes may reflect variation in body size, diet, and phylogeny (Willis and Sindler 2004).

Mandible. Most of the studied mandibles lack the ascending ramus, but a few specimens preserve a large part of it. The ascending ramus is high with a straight posterior margin and perpendicular to the mandibular corpus. The gonial angle of the lower jaw is better preserved in the male specimens MNHNP-PIK-034, 430, and NHML-PIK-M.4955 (Supplement 6: Figures 17, 28; Supplement 7: Figure 10e); it is rounded and thickened, as is common for extant colobines, and protrudes strongly in the gonial area. The mandibular corpus is straight with a straight lower border between p3-m3. The mandibular corpus is infero-superiorly deep and mediolaterally thick, but shallower and slenderer in females. The symphysis is well preserved in several specimens. The external symphysis is mesiodistally curved without lateral symphysial constriction. The internal symphysis has a relatively small planum alveolare that is abruptly inclined downwards. The fossa genioglossa, present in some specimens but absent in others, is small. The superior transverse torus is thick, and the inferior transverse torus is small and slightly protruding posteriorly. In some specimens the tooth rows are slightly divergent. Delson (1973) suggests that there may be sexual dimorphism in the divergence of the lower tooth row, being parallel in females and slightly divergent in males. However, it can be difficult to get a conclusive result as even a slight deformation of the mandible can lead to an inaccurate impression of the position of the tooth rows.

Lower dentition. The lower incisors are flattened buccolingually and mesiodistally narrower than the upper ones;

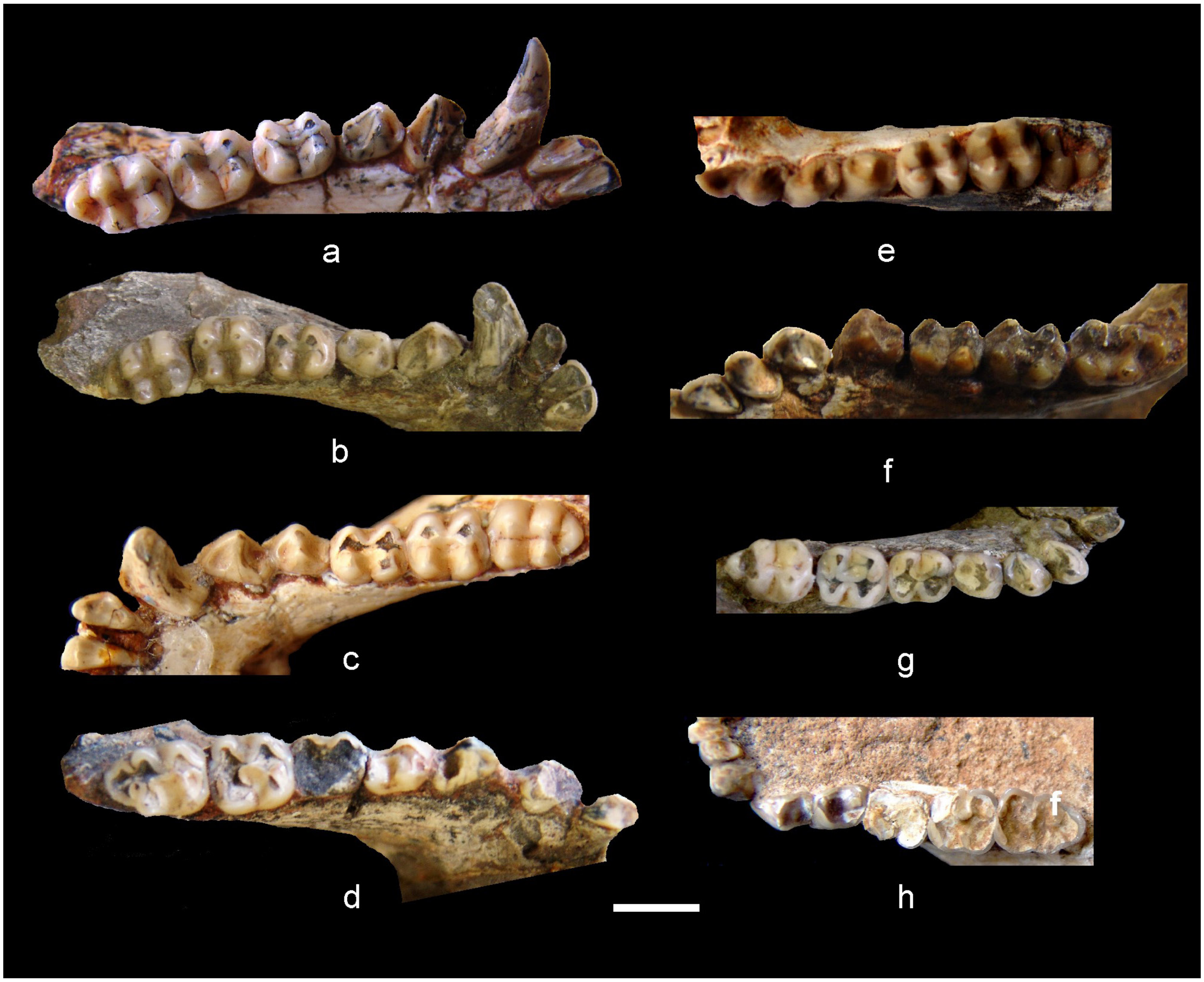

Figure 8. Mesopithecus pentelicus, *Pikermi, Attica, Greece. Lower dentition in various wearing stages. Male individuals: a) NHMW-PIK-1998z77/1, b) MNHNP-PIK-421, c) AMPG-PIK-22, d) MNHNP-PIK-021; Female individuals: e) NHMW-PIK-1998z77/3, f) PIUW-PIK-316, g) MNHNP-PIK-02, h) NHMW-PIK-1998z77/13 (scale bar 10mm).*

the i2 has elliptical occlusal shape. Their lingual surface bears a marginal ridge, which is more evident in the unworn or slightly worn teeth (Figure 8a, e). Additionally, there is a prominent projection of the lingual cingulum. Wear begins at the apex of the incisors and is initially confined to this area, appearing as a mesiodistally elongated and narrow dentine pit. The tooth gradually wears on the lingual surface, resulting in a shorter tooth with a triangular occlusal crown outline (Figures 8b, d, f-h). At this stage of wear, the enamel is limited at the edge of the tooth. In extreme wear, the occlusal surface becomes elliptical-rounded. Similar wear of the incisors occurs in both males and females. In the males there is a short diastema between i2 and lower canine (Figure 8c, see Figure 8d). The canine of the males is long, slightly curved backwards, and situated somewhat laterally. It has an elliptical cross-section and presents a large and strong distal cingular projection. Its mesiodistal axis forms an angle of ~45° with the tooth row axis. Between the canine and p3 there is a small diastema in males. In females the i2 and p3 are in contact with the canine without any diastema (see Figure 8e-h). The canine has a mesial and distolingual crest running from the tip to the base of the tooth. The female canine has similar morphology, but it is significantly smaller; its height is more or less similar to that of the p3. The distal surface of the lower canine is in functional contact with the mesial surface of the upper canine forming a wear facet on the distal surface of the lower canine. The p3 is asymmetric and lies laterally to the tooth row axis (see Figure 8). Its mesial part extends mesiobucally, providing an elongated surface that is in functional contact with the distal surface of the upper canine. The result of this continuous contact is the formation of a honing facet. The p3 bears a large buccal cuspid, from the apex of which a pronounced lingual crest begins and ends at the base of the tooth (see Figure 8). The crest divides the lingual part of p3 into two foveae, the mesial one being smaller than the distal one. The attrition of p3 begins at the apex of the cuspid with a rounded dentine pit, which is visible in teeth that

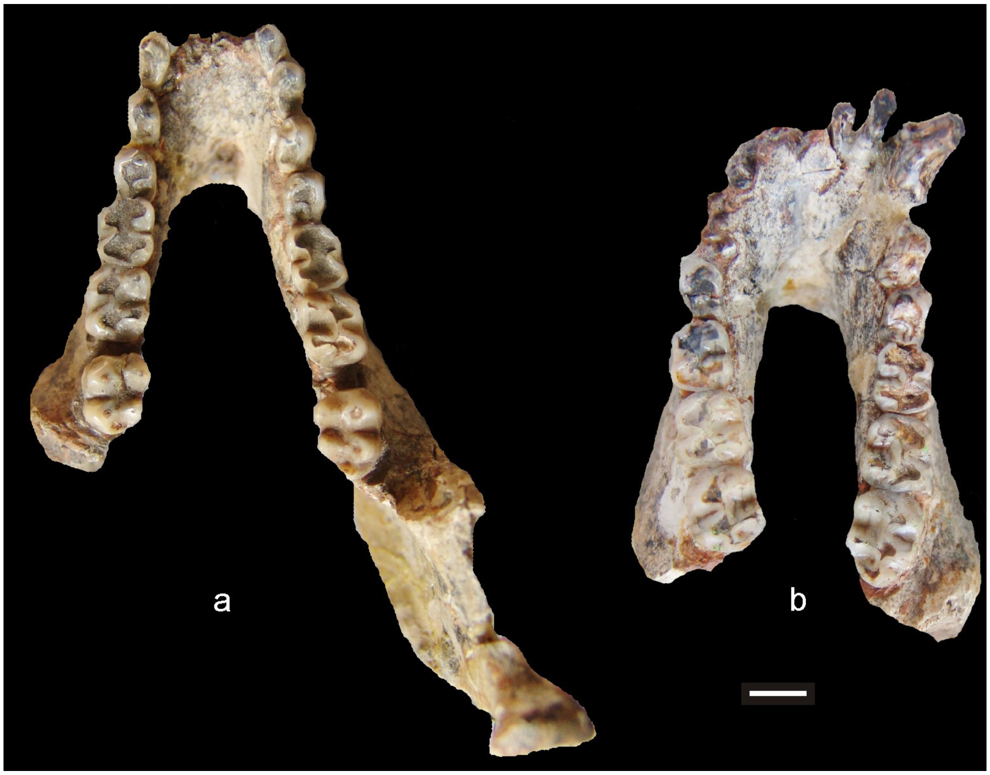

Figure 9. Mesopithecus pentelicus, *Pikermi, Attica, Greece. Specimens without or with weak hypoconulid in the m3. a) MNHNP-PIK-430, b) SNSB-BSPGM-AS II 13 (scale bar 10mm).*

are less worn, and which gradually extends to the mesial and distal surfaces. In heavily worn teeth, the mesial wall is worn (honing facet), while a dentine pit covers the entire distal surface of the cuspid, including the distal fovea (see Figure 8d, h). The p4 is more symmetrical than p3, with a large buccal cuspid and a smaller lingual one. It also has a well-developed mesial fovea and a stronger distal one. Attrition begins from the apex of the buccal cuspids as a small and rounded dentine pit and gradually extends to the lingual ones as a small and rounded dentine pit. These pits gradually increase as attrition progresses and eventually connect to each other in worn teeth (see Figure 8c, g). In the heavily worn p4, the dentine pits of the cuspids are joined to the dentine pit of the distal fovea to form a single large pit, like a basin (see Figure 8d, h). The molars are elongated and narrow with four main cuspids, while the m3 has an additional fifth cuspid, the hypoconulid (Delson 1973). The cuspids are distinguished by deep valleys and are almost equal in size, with the lingual ones slightly higher than the buccal ones. There are well-developed mesial and distal foveae. The m2 is wider than the other molars, and the m3 has a small hypoconulid located in the middle of its distal lobe. Molar attrition begins at the tip of the buccal cuspids, specifically at the protoconid (see Figure 8a, b, e, f). It then progresses to the hypoconulid (see Figure 8c, g) and finally to the entoconid. The dentine pits gradually enlarge and connect, starting with the entoconid and hypoconid, and then connecting the entoconid to the protoconid, as illustrated in Figure 8b, c. In the case of extremely worn teeth, all the dentine pits are connected, forming a large dentine pit on the occlusal surface (see Figure 8d, h). In the latter case, there is only a small lingual and buccal sinus, indicating the valley between the mesial and distal lobes. The hypoconulid of m3 is also connected to the other dentine pits, forming a uniform and large pit.

It should be noted that in some specimens of *M. pentelicus* from Pikermi the hypoconulid of m3 is either missing or it is very small. The available sample of the male and female specimens with canines gave a frequency of 2.9% for the hypoconulid absence or reduction. The male mandible SNSB-BSPGM-AS II 13 and the female MNHNP-PIK-430 have a very small hypoconulid on the right m3, whereas the left one lacks this cuspid (Figure 9). Both specimens have been examined and there is no evidence of a fracture. Roth and Wagner (1854) recognized this morphological feature early on and considered it sufficient to create the new species, *M. major*, which has not been widely accepted. Gaudry (1862-67) included these specimens in *M. pentelicus*. Apart from the Pikermi collection, the absence of a hypoconulid has also been observed in material from Baltavar, Hungary (Delson 1973).

Deciduous dentition. Among the Pikermi material there are a few remains with deciduous dentition. The lack of juvenile individuals is strange as young animals are more vulnerable to drought conditions or to carnivoran predation. Their absence means that either their bones were very

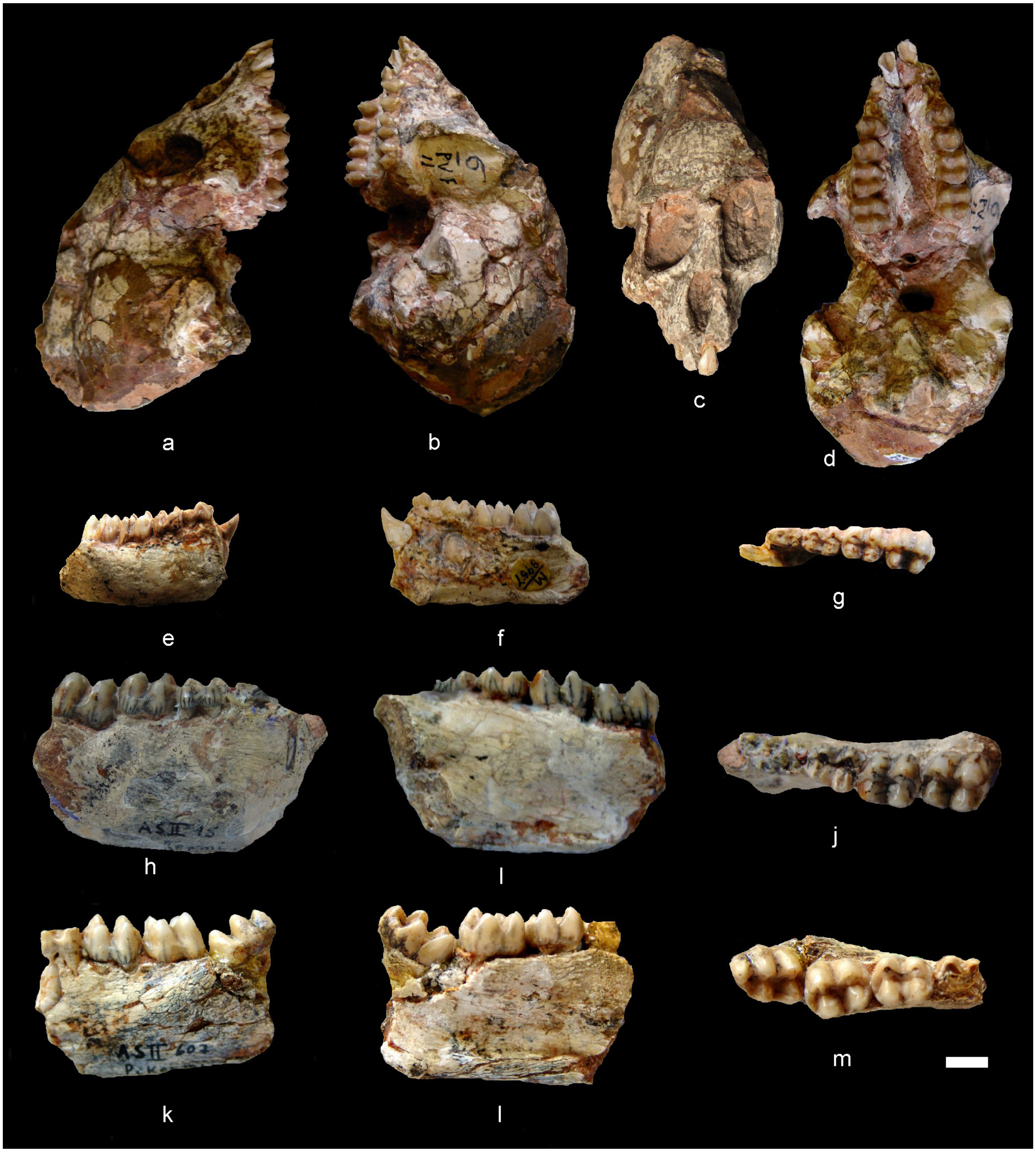

Figure 10. Mesopithecus pentelicus, *Pikermi, Attica, Greece. Upper and lower deciduous dentition. a-d) MNHNP-PIK-429, cranium of a subadult individual in which the m3 is emerging; e-g) NHML-PIK-M.8957, right mandibular fragment with c-dp3-m2; h-j) SNBS-BSPGM-PIK-AS II 15, right mandibular fragment with dp3-m2; k-m) SNBS-BSPGM-PIK-AS II 607, right mandibular fragment with dp4-m3; the dp4 is broken mesially (scale bar 10mm).*

fragile and destroyed during fluvial transportation or they were eaten by carnivores. There are no upper deciduous teeth in the material from Pikermi. Nevertheless Delson (1973) mentions two specimens from Pikermi that are subadults. One is the cranium MNHNP-PIK-429 (Figure 10a-d) with the canine and M3 erupting; the size of the teeth indicates a female individual. The other is the cranium SMNS-BSPGM-1839/3939, stored in Stuttgart, which preserves milk canine on both sides (Delson 1973). The material also includes three mandibular fragments with deciduous teeth. NHML-PIK-M.8957 is a right mandibular fragment with c, dp3-m2 (Figure 10e-g). The permanent canine is still emerging, and the broken bone allows for its measurement. Its size indicates a female individual. The dp3 has an elongated shape with a slightly triangular occlusal crown outline. Its distal lobe is wider than the mesial one. It bears four cuspids and a strong mesial projection. The cuspids are weak compared to those of dp4. A weak cingulid can be seen around the base of the tooth. The dp4 is more symmetrical than the dp3, with four cuspids. The distal lobe is wider than the mesial one, and a weak cingulid is present (see Figure 10e-g). The second specimen, SMSB-BSPGM-AS II 15, is part of a mandibular corpus that preserves the series dp3-m2, but unfortunately, the dp3 is broken, and only a small part of it is preserved. The dp4 is similar to the one described above (Figure 10h-j). The third specimen is SMNS-BSPGM-As II 607 preserving the dp4, which has similar morphology to the others (Figure 10k-m).

Material From Pikermi Housed in Other Museums

As previously mentioned, Pikermi material is dispersed throughout Europe, and it is possible that undescribed *Mesopithecus* material exists elsewhere in museums and institutes. In recent decades, three distinct cases of "new material" have been brought to light (Costeur and Malvessy 2010; Mottura and Ardito 1992; Ridolfi et al. 2023; Rook 1997).

In 2008, a "new specimen" of *Mesopithecus* from Pikermi was rediscovered in the natural history collections of the Cuvier Museum in Montbeliard, France, labelled Pg 4-1 (Figure 11a, b). The specimen was donated to the museum along with other specimens from Pikermi in honor of Georges Cuvier, a French paleontologist who was a native of the village. It is the face of a *Mesopithecus*, preserving both P3-M2 tooth rows (Costeur and Malvessy 2010). The specimen's morphological features, including its thin and unprojected supraorbital torus, rounded orbits, large interorbital distance, nasal cavity shape, and dental morphology, as well as its dimensions, are similar to those of the Pikemi sample of *M. pentelicus*, therefore it can be attributed to this species. In principal component analysis based on the upper dental dimensions, Pg 4-1 corresponds to Pikermi females of *M. pentelicus* (Figure 12a).

Two right mandibular fragments of *M. pentelicus* from Pikermi are stored in the Museo di Storia Naturale of the University of Florence. These specimens were exchanged with A. Gaudry, one (IGF-11572; Figure 11c-e) in 1861 and the other (IGF11572; Figure 11f-h) in 1870 (Rook 1997). Both specimens lack canines; however, based on the dimensions of the postcanine teeth, they correspond to those of male *M. pentelicus* from Pikermi (Figure 12b). The mandibular corpus morphology and dimensions, as well as the dentition are consistent with those of *M. pentelicus*, thus allowing their inclusion in this species.

A fossil collection from Pikermi previously housed in the Museum of Geology and Palaeontology of Turin, Italy is now housed in the Museum Regionale di Scienze Naturali, Torino. The collection was given to the Savoy family by a Greek diplomat in 1853. The collection consists of 320 specimens representing various taxa, which were studied by A. Gaudry (Ridolfi et al. 2023). The collection comprises a left mandibular fragment with c-p3 (MGPT-PU42890) and the proximal part of an ulna (MGPT-PU42891) of *Mesopithecus*. The mandibular fragment was attributed to the species *M. pentelici* by Mottura and Ardito (1992). The specimen has been mentioned and illustrated by Ridolfi et al. (2023: Figure 10). Based on the latter author's description and photographic documentation, these specimens exhibit a rounded external symphysis, an abruptly inclined planum alveolare, and a dental morphology consistent with that of *M. pentelicus*. Furthermore, a congruence is observed between this specimen and the males of *M. pentelicus* in the principal components analysis based on the lower dental dimensions (see Figure 12b).

MESOPITHECUS DELSONI BONIS ET AL., 1990

Synonyms

Mesopithecus pentelicus Zapfe, 1991
Mesopithecus pentelicus delsoni Alba et al., 2015

Type Localitiy

Ravin des Zouaves 5 (RZO), Macedonia, Greece (Figure 13). The locality is situated to the west of the village Nea Messimvria, within the lower horizons of the Vathylakkos Formation; the fossiliferous bed is a yellowish marl with calcitic concretions (more details for the geological context are available in Supplement 2).

Age

Late Miocene, early Turolian, MN 11; GPTS. ~ 8.2 Ma (Koufos 2013, 2024 and references therein; Sen et al. 2000).

Holotype

Mandible of an adult male individual, which preserves both tooth rows and lacks the ascending rami, LGPUT-RZO-159 (Figure 14; Supplement 10: Figures 1–3).

Other Localities

Thermopigi, Serres Basin, Macedonia, Greece (see Figure 2).

Diagnosis

Large size colobine monkey; deep mandibular corpus; flattened external symphysis; strong symphysial constriction; roughly inclined posteriorly planum alveolare; large fossa genioglossa; thick inferior transverse torus; strong lingual

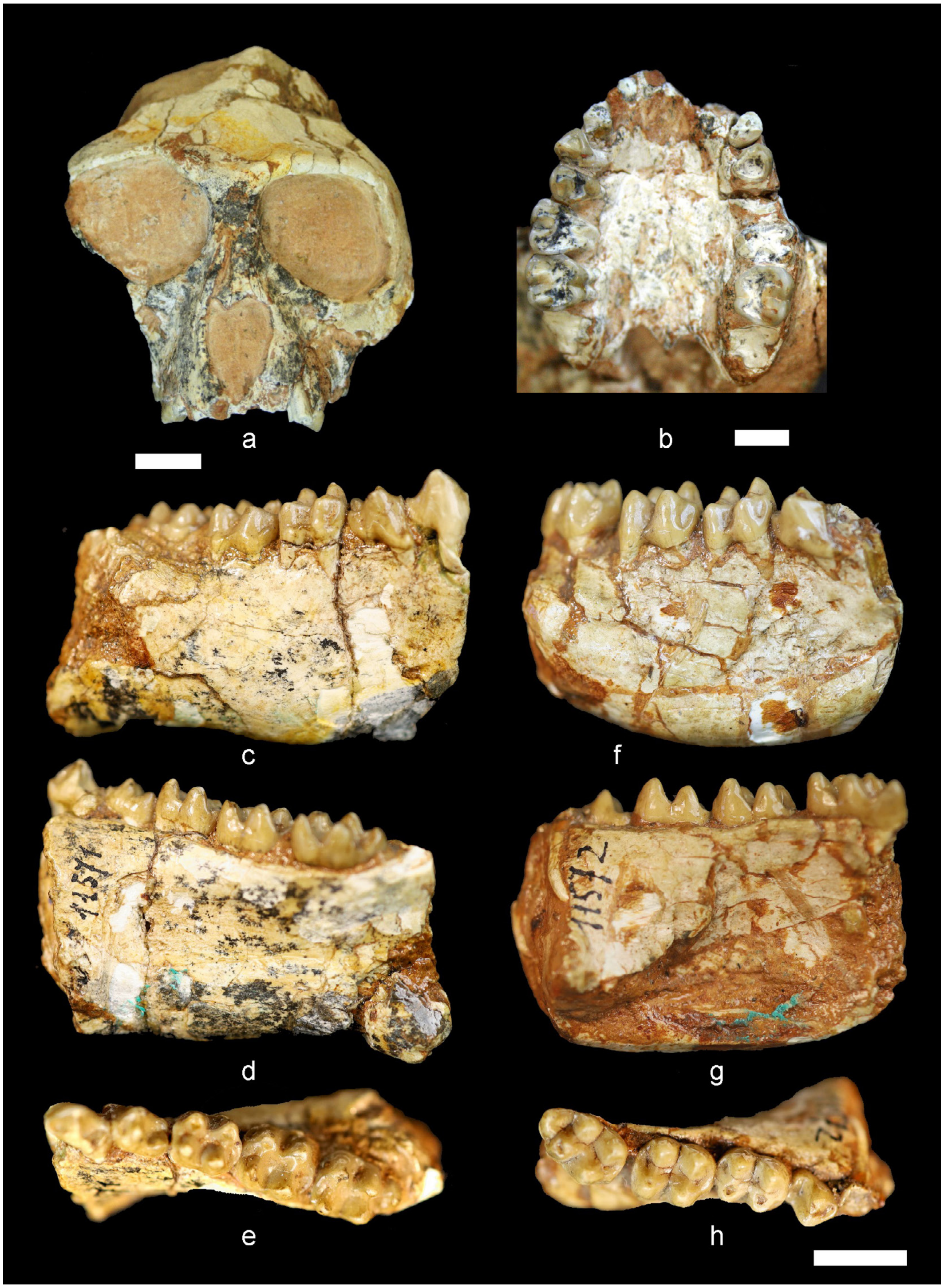

Figure 11. Mesopithecus pentelicus, *Pikermi, Attica, Greece. Some specimens from Pikermi, which are housed in other museums and described much later. a-b) Pg 4-1, partial cranium with the face and the maxilla, preserving the toothrows P3-M2 dex and C-P2, M2 sin, which is stored at the Museum of Cuvier, Montbeliard, France; photos kindly provided by Dr. L. Costeur); c-e) IGF-11571, right mandibular fragment with p3-m3, Museum of Florence, Italy; f-h) IGF-11572, right mandibular fragment with p4-m3, Museo Regionale di Scienze Naturali, Torino, Italy; photos kindly provided by Dr. L. Rook (scale bar 10mm).*

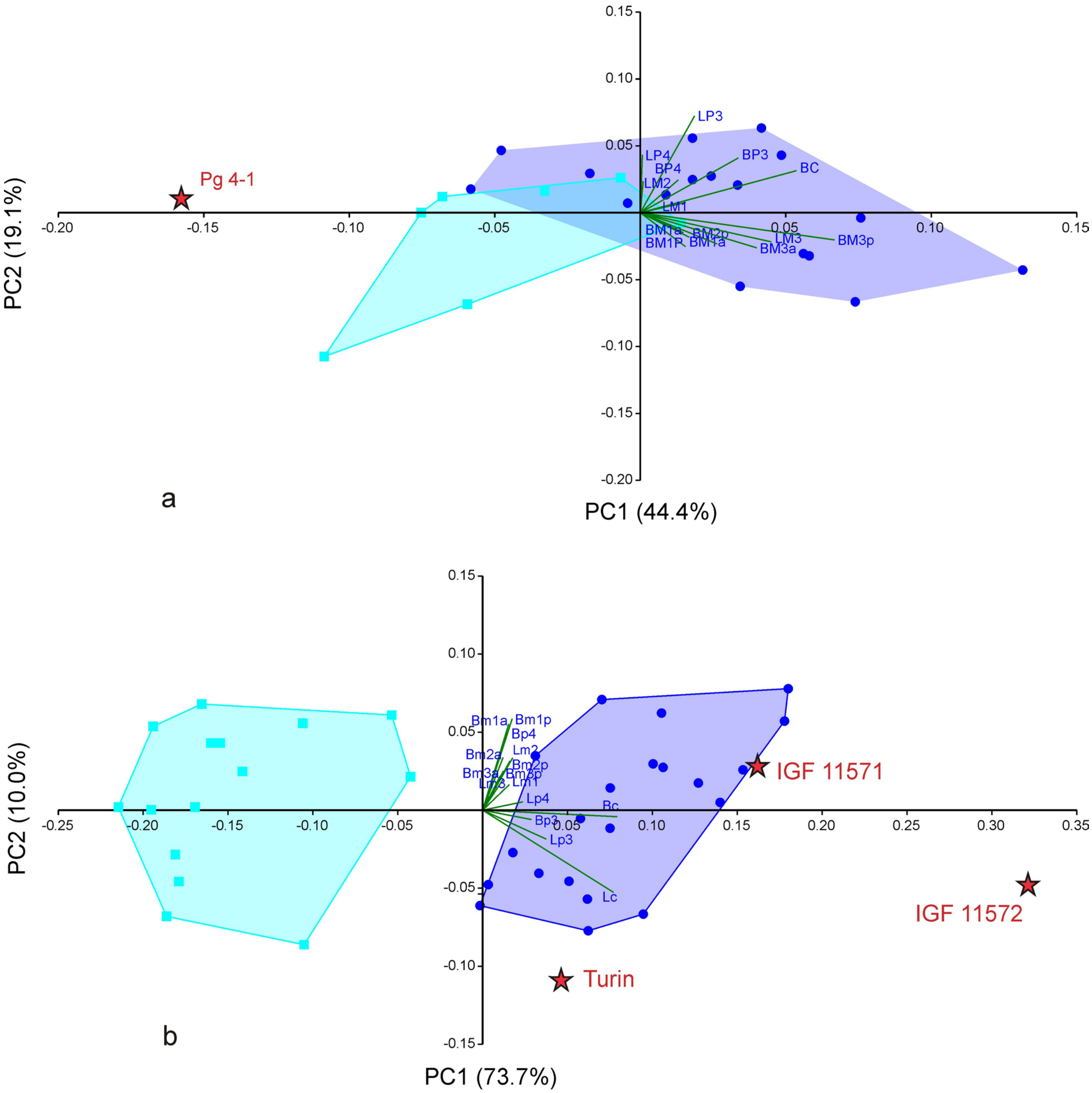

Figure 12. Principal component analysis, using the upper (a) and lower (b) dental dimensions for the comparison of the specimens from Pikermi, housed in the Museum of Cuvier Montbeliard, France, as well as in the Museo Regionale di Scienze Naturali, Turin, Italy. The dental measurements for these specimens are taken from Mottura and Ardito (1992), Rook (1999), and Costeur and Malvesy (2010). Symbols: dot (blue): M. pentelicus, *male; filled square (cyan):* M. pentelicus, *female; asterisk (red): other specimens of* M. pentelicus *from Pikermi. Abbreviations as in Figure 3.*

cusp (protocone) in the premolars; large honing facet in the p3; well-developed and biscupid hypoconulid on the m3 (see Figure 14a).

Material

Mandible of an adult male individual, which preserves both tooth rows and lacks the ascending rami, LGPUT-RZO-159, holotype; mandible of an adult male individual with both tooth rows and without the ascending rami, LGPUT-RZO-160; right mandibular fragment of an adult female individual with m1-m3, LGPUT-RZO-161 (see Figure 14; see Supplement 10: Figures 1–3).

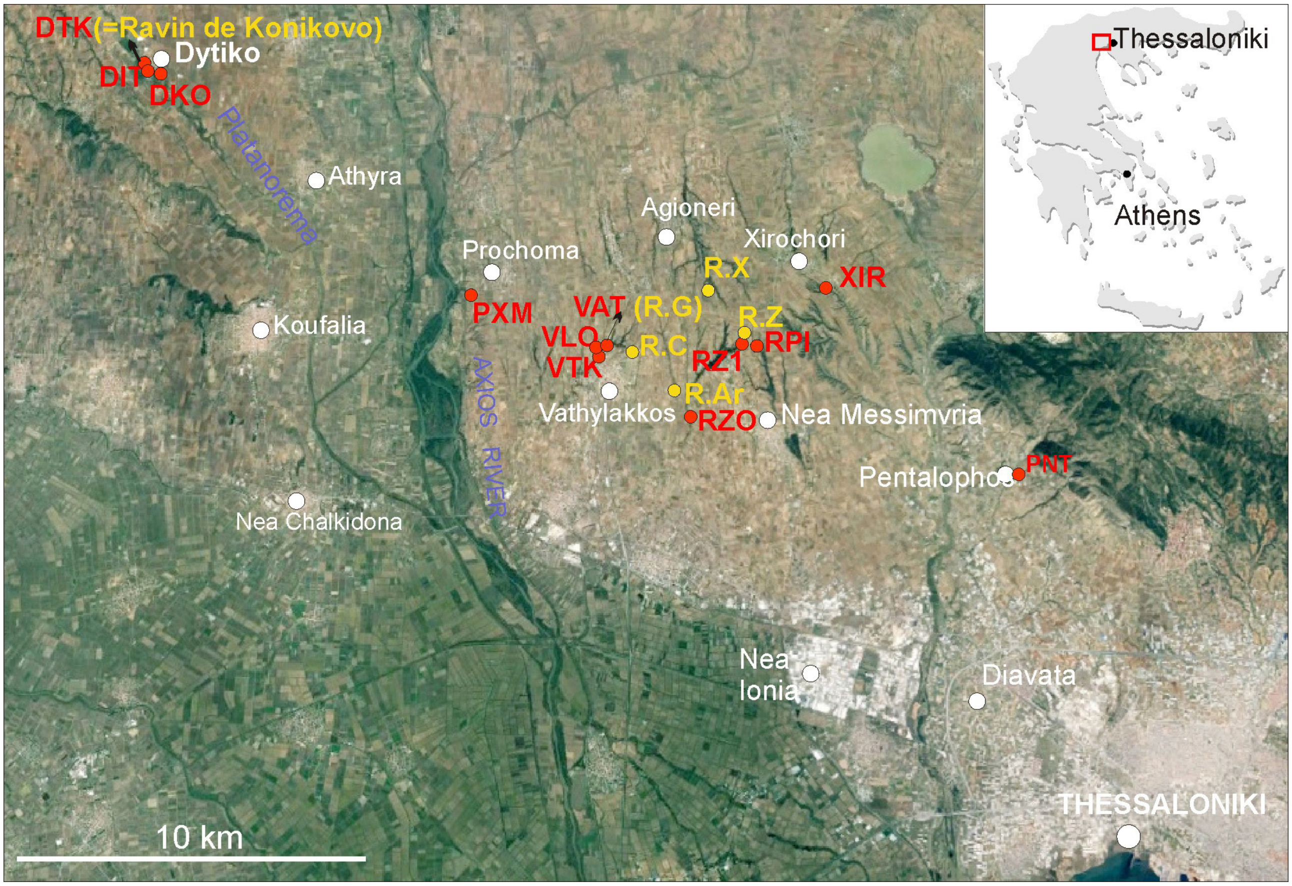

Figure 13. Map indicating the position of the different fossiliferous sites of the Axios Valley. The old localities of C. Arambourg are given in yellow and the new ones in red. (Map from Google Earth. Data SIO, NOAA, U.S. Navy, NGA, GEBCO, Image Landsat/ Copernicus, Image © 2025 Airbus).

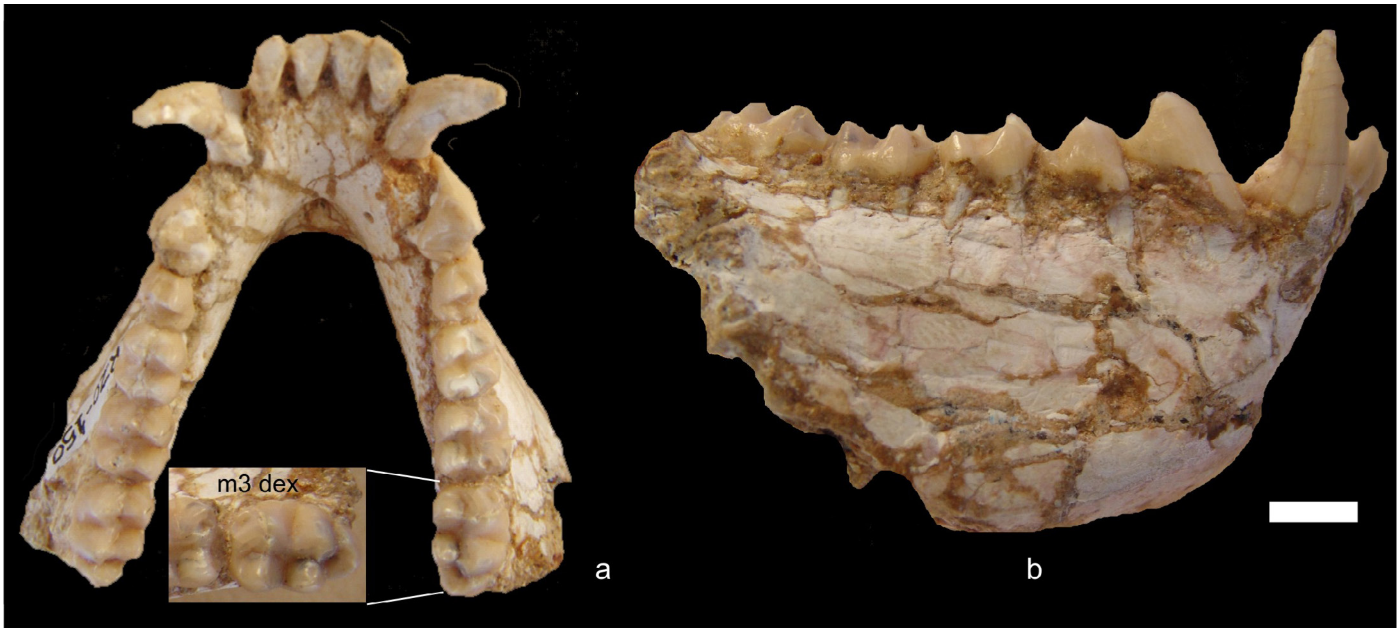

Figure 14. Mesopithecus delsoni, *Ravin des Zouaves 5 (RZO), Axios Valley (Macedonia, Greece); early Turolian, MN 11; GPTS= ~8.2 Ma. Mandible with both tooth rows, holotype, RZO-159; a) occlusal and b) right lateral view (scale bar 10mm).*

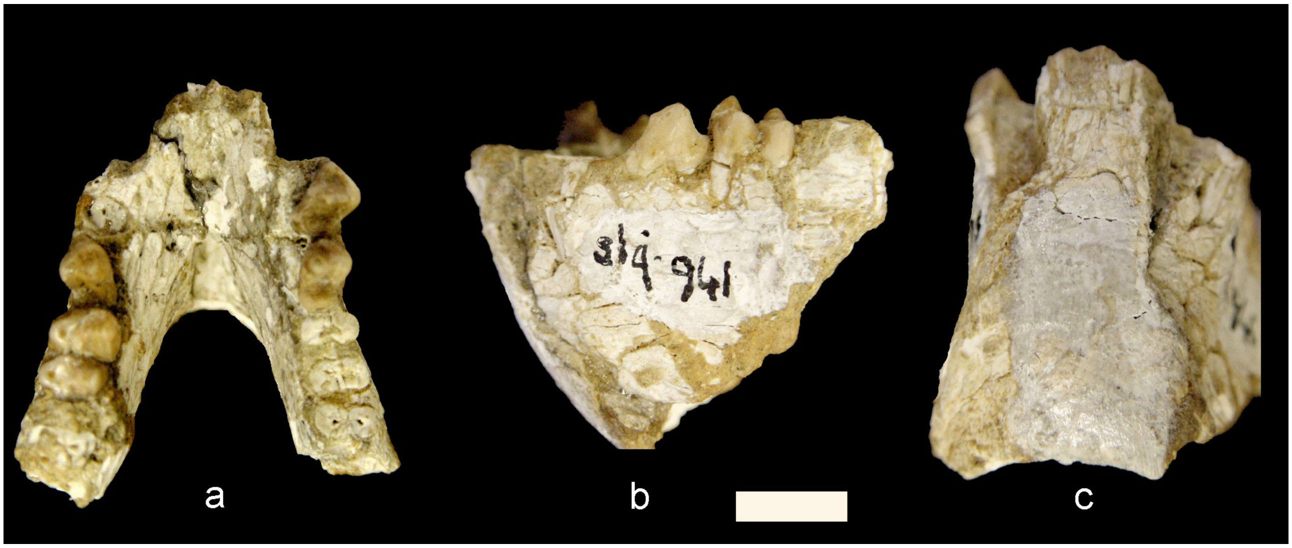

Figure 15. Mesopithecus *cf.* M. delsoni*, Ravin X (R.X), Axios Valley, Macedonia, Greece; latest Vallesian/earliest Turolian MN 10/11. Mandibular fragment with p3-p4 dex and p4-m1 sin, MNHNP-R.X-940+941; a) occlusal, b) lateral, and c) anterior symphysial view (scale bar 10mm).*

Description

The material has been extensively described in Bonis et al. (1990).

MESOPITHECUS CF. *M. DELSONI*

Synonyms

Mesopithecus pentelici Arambourg and Piveteau, 1929
Mesopithecus cf. *M. delsoni* Koufos, 2009a, b.

Locality

Ravin X (R.X), Axios Valley, Macedonia, Greece. Ravin X is an old site located by C. Arambourg to the south of the village of Agioneri (see Figure 13). Attempts to relocate Ravin X have been unsuccessful. Arambourg and Piveteau (1929) mention that the locality is situated within a grey marl intercalated in reddish sands and silts. This suggests that the fossils may be situated in a transitional horizon from the Nea Messimvria Fm to Vathylakkos Fm (more details for the geological context of the Axios Valley are available in Supplement 2).

Age

Late Miocene, Vallesian/Turolian, MN 10/11 (Koufos 2022, 2024).

Material

Anterior mandibular fragment with p3-p4 dex and p4-m1sin; MNHNP-R.X-940+941 (Figure 15; Supplement 10: Figure 15).

Description

The specimen is almost undescribed as Arambourg and Pivetau (1929) gave little information about any of the Axios Valley material. The specimen was probably broken into two pieces, each numbered separately. During the study of the material at the MNHNP, it became evident that the two fragments fit well to each other and belong to the same individual. The external symphysis is flattened with strong lateral symphysial constriction (see Figure 15c). The internal symphysis has a planum alveolare that is slightly inclined downwards, a large fossa genioglossa and a strong inferior transverse torus. The symphysis is long and high (Figure 16a), and the corpus is deep below p4 with a depth of approximately 26.1mm versus 22.7–26.5mm in *M. delsoni*. Although the p3 is not very worn, it bears a large honing facet which reaches the root of the tooth; its length is 10.6mm. The p3 resembles that of LGPUT-RZO-160 but is slightly smaller. The p4 and m1 exhibit a morphology that is like that of *M. delsoni* from Ravin des Zouaves 5.

MESOPITHECUS SP.

Synonyms

Mesopithecus pentelici Arambourg and Piveteau, 1929
Mesopithecus cf. *M. pentelicus* Bonis et al., 1997
Mesopithecus delsoni/pentelicus Koufos, 2009a, b

Localities

Vathylakkos 2, 3 (VTK, VAT), Axios Valley, Macedonia Greece (see Figure 13).

Age

Late Miocene, middle Turolian, MN 12; GPTS. VTK= ~7.4 Ma, and VAT= ~7.3 Ma (Koufos 2013, 2024 and references therein).

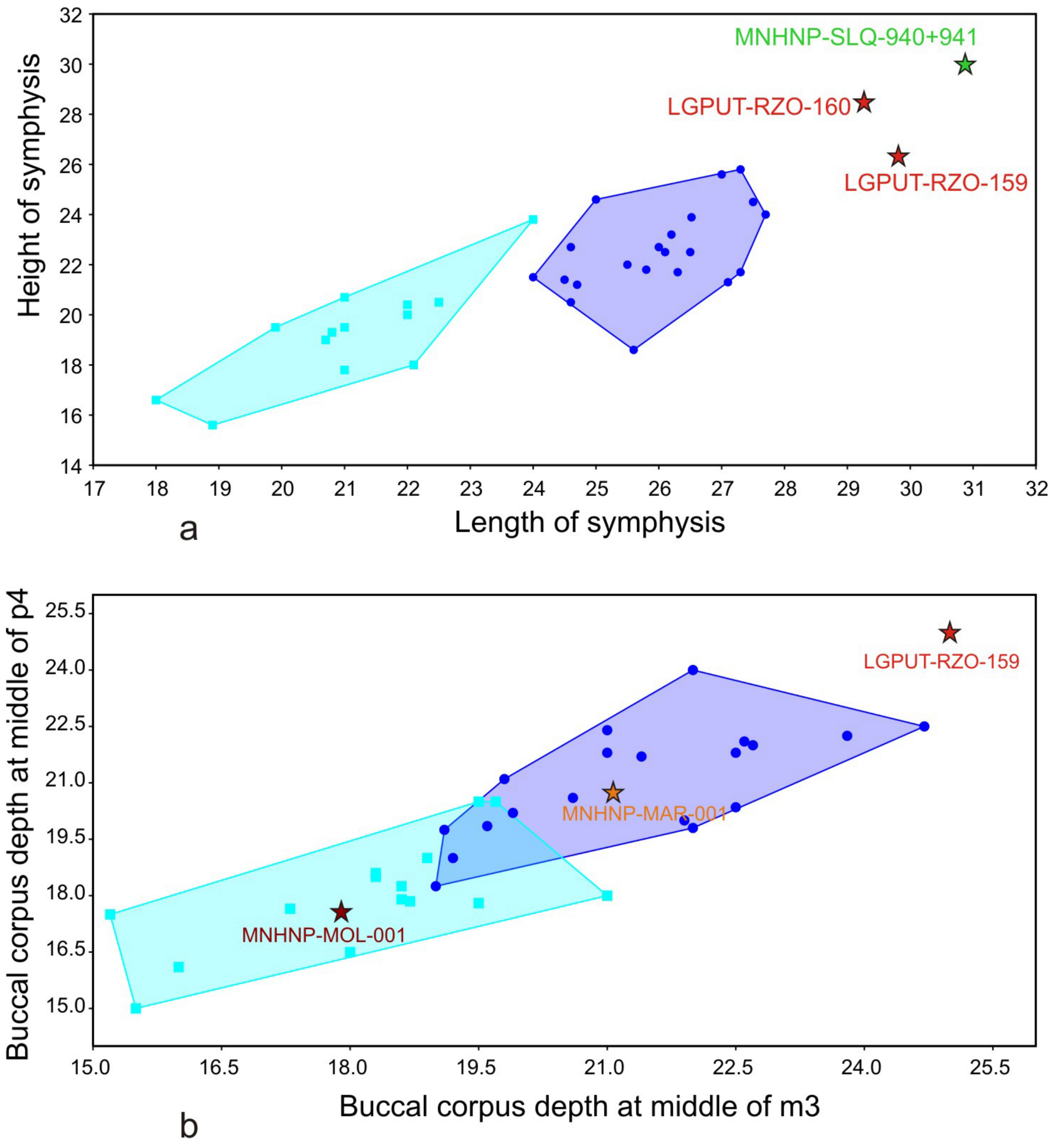

Figure 16. a) Biplot comparing the symphysis length and height of M. delsoni *and* Mesopithecus *sp. with* M. pentelicus*; b) Biplot comparing the depth of the corpus below p4 and m3 of* M. delsoni *and* Mesopithecus *from Maragheh and Molayan with* M. pentelicus *from Pikermi. Symbols: dot (blue):* M. pentelicus, *male; filled square (cyan):* M. pentelicus, *female.*

Diagnosis

Size intermediate between *M. delsoni* and *M. pentelicus*; shallow mandibular corpus; high lingual cusp (protocone) in the premolars; flattened external symphysis; presence of symphysial constriction; roughly inclined posteriorly planum alveolare; large fossa genioglossa; thick inferior transverse torus; small lingual cusp in P3; large honing facet in the p3; small hypoconulid in the m3.

Material

MNHNP (Arambourg collection): Mandibular fragment with c-m2 dex and c-p3 sin, MNHNP-SLQ-939; right mandibular fragment with p4, m2-m3, MNHNP-SLQ-942; left mandibular fragment with p3-m1, MNHNP-SLQ-943 (Supplement 10: Figures 14, 16, 17). The type of fossilization and sedimentary remains of this material are similar to those of Vathylakkos 3 (VAT).

MNHNP (Braillon collection): Partial cranium without maxilla, MNHNP-SLQ-1134; right maxillary fragment with M1-M3, MNHNP-SLQ-1126; four isolated teeth, MNHNP-SLQ-1128, 1129, 1130, 1131 (Supplement 10: Figures 18, 19). The two cranial remains are probably from the same individual. The type of fossilization and sediments of this sample correspond to those of Vathylakkos 2 (VTK).

Description

A description of the new *Mesopithecus* collection from the Vathylakkos localities, as well as the Braillon collection,

Figure 17. Mesopithecus *sp., Vathylakkos 2, 3 (VTK, VAT), Axios Valley, Macedonia, Greece; middle Turolian, MN 12. a-c) female cranium, LGPUT-VTK-56, a) lateral, b) frontal, and c) occlusal view; d-f) male cranium, LGPUT-VTK-61, d) lateral, e) frontal, and f) occlusal view; g-j) female mandible, LGPUT-VTK-62, g) occlusal, h) right lateral, and j) external symphysial view; i-l) cranium of young individual LGPUT-VTK-78, i) right lateral, k) dorsal, and l) frontal view; m) mandibular fragment with c-m2 dex and c-p3 sin, MNHNP-SLQ-939, occlusal view; n-p) right mandibular fragment with p4, m2-m3, MNHNP-SLQ-942, n) buccal, o) lingual, and p) occlusal view (scale bar 10mm).*

was provided in previous studies (Bonis et al. 1997; Koufos et al. 2004). Therefore, a brief description of the specimens from the Arambourg collection only will be given here.

MNHNP-SLQ-939 (Figure 17m; see Supplement 10: Figure 14). This is the most complete specimen from Vathylakkos 3 in the Arambourg collection, preserving the tooth rows c-m2 dex and c-p3 sin; however, the symphysis and the ventral part of the corpus are not preserved. The canine is relatively small. The p3 bears a clear and well-developed honing facet, but its size cannot be measured as it is partially broken. The m2 is also broken. The position of this specimen in the diagram of the principal component analysis of the dental dimensions indicates a male individual, but its determination is ambiguous; it is very close to *M. delsoni*,

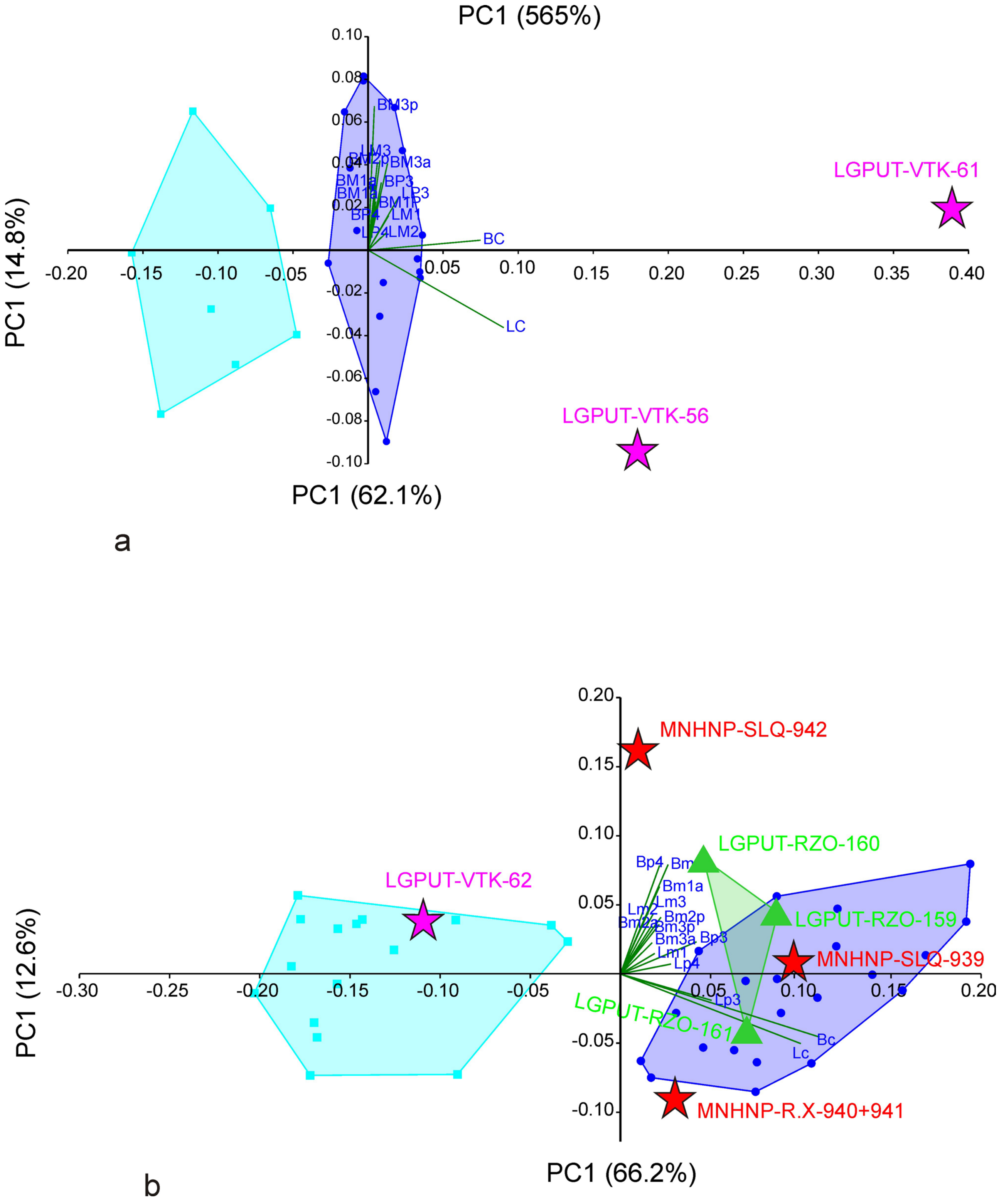

Figure 18. Principal component analysis comparing the mandible (a), upper teeth (b), and lower teeth (c) of Mesopithecus *sp. from Axios Valley with* M. delsoni *and* M. pentelicus*. Symbols: dot (blue):* M. pentelicus*, male; filled square (cyan):* M. pentelicus*, female; filled triangle (green):* M. delsoni*; diamond (purple):* Mesopithecus *sp., Vathylakkos 2; asterisk (red):* Mesopithecus *sp., Vathylakkos 3 (Arambourg collection). Abbreviations as in Figure 3.*

but also into the the convex hull of *M. pentelicus* (Figure 18b).

MNHNP-SLQ-942 (Figure 17n-p; see Supplement 10: Figure 16). It consists of a mandibular fragment preserving p4, m2-m3. The m3 hypoconulid is relatively large with a groove in its distal wall, giving it a bicuspid character. In this character, the specimen is closer to *M. delsoni*. However, the depth of the corpus below p4 is 22.0mm, which falls within the range of variation for *M. pentelicus* from Pikermi (24.0–18.3mm; mean 21.1mm for the males and 20.5–15.0mm; mean 18mm for the females). The dental dimension of this specimen indicates a male *Mesopithecus* with larger size than *M. pentelicus* and closer to *M. delsoni* (see Figure 25b below).

MNHNP-SLQ-943 (see Supplement 10: Figure 17). The specimen preserves a small portion of the left mandibular corpus with p3-m1. The morphology of the teeth is consistent with that of *Mesopithecus*. The buccal depth of the corpus is relatively shallow (21.8mm below p4 and 21.5mm below m1), which is indicative of similarities with *M. pentelicus*. The fossilization, color, and attrition of the teeth are comparable to those observed in MNHNP-SLQ-942, suggesting that they may belong to the same individual.

Distinctive Characteristics

Size intermediate between *M. delsoni* and *M. pentelicus*; shallow mandibular corpus, similar to *M. pentelicus*; higher lingual cusp (protocone) than *M. pentelicus* in the P3 and P4; flattened anterior symphysis with symphysial constriction; slightly inclined backwards planum alveolare; large fossa genioglossa; long honing facet in the p3; large hypoconulid with distal groove in the m3; similar dental dimensions to *M. pentelicus*; longer limb bones than *M. pentelicus* (Koufos 2009a; Koufos et al. 2003; 2004).

MESOPITHECUS MONSPESSULANUS GERVAIS, 1849

Synonyms

Mesopithecus cf. *monspessulanus* Bonis et al., 1990

Type Locality

Montpellier, southern France. It is in the freshwater marls of the Palais de Justice (Delson 1973). Its age is early Pliocene, Ruscinian, MN 14 (Bonis et al. 1990).

Localities

Dytiko 1 (DTK) and Dytiko 2 (DIT), Axios Valley, Macedonia, Greece (see Figures 2, 13).

Age

Late Miocene, late Turolian, MN 13; based on biochronological data, the age is estimated to be late Turolian, pre-Messinian, 7.0–6.0 Ma (Koufos and Vasileiadou 2015 and references therein).

Diagnosis

Moderate to small size colobine monkey, smaller than *M. delsoni* and *M. pentelicus*; shallow mandibular ramus; steeply inclined posteriorly planum alveolare; weak lower transverse torus; small orbits relative to *M. pentelicus*; narrow lower teeth; perhaps less posterior reflection of the humeral medial epicondyle (Bonis et al. 1990; Delson 1973; Zapfe 1991).

Material

Male maxillary and associated mandibular fragments, LG-PUT-DTK-276; male mandibular fragment with i1-m2, LG-PUT- DIT-22 (Supplement 10: Figures 9, 11).

Description

The material was described in Bonis et al. (1990a) and Koufos (2019a, b).

COMPARISONS AND DISCUSSION FOR THE GREEK *MESOPITHECUS*

In this section is given a comparison of the *Mesopithecus* material from the different Greek localities with a discussion about their relationships. The material from each locality is compared morphometrically with *M. pentelicus* from Pikermi. In most cases the comparison is restricted to the mandibles and teeth as the well-preserved crania are few.

CHOMATERES

The Chomateres fossil site, also known as Chomateri or Kisdari, is located approximately 2.6km east of the classical Pikermi ravine in the Mesogea Basin (see Figure 2; Figure 19). The fossils were discovered in a clay pit during excavation work. Between 1972 and 1980, the Laboratory of Geology and Palaeontology at the University of Athens excavated the site in collaboration with the NHMW and provided geological, sedimentary, and stratigraphical information for Chomateres (Bachmayer et al. 1982; Marinos and Symeonidis 1972, 1974; Symeonidis et al. 1973). Recent data on the stratigraphy of the wider Pikermi area indicates that Chomateres is located within the Chomateres Mb of the Pikermi Fm. The fossiliferous site of Chomateres is slightly younger than the classical Pikermi, as well as the new PV 1, 3 sites (Böhme et al. 2017). Despite the preliminary identification of the material, there has been no extensive description or comparison of the fauna, except in the case of the *Metailurus* and *Mesopithecus* specimens (Symeonidis 1978; Zapfe 1991). A revised list of the Chomateres fauna can be found in Koufos (2024: Supplement 2). Biochronological data indicate a correlation with the European mammal zone MN 12, middle Turolian. Magnetostratigraphic data suggest an age ranging between 7.23–7.11 Ma (Böhme et al. 2017).

The two mandibles from Chomateres, housed in NHMW, have been described by Zapfe (1991) as a subspecies under the name *M. p. microdon* (Figure 20). The speci-

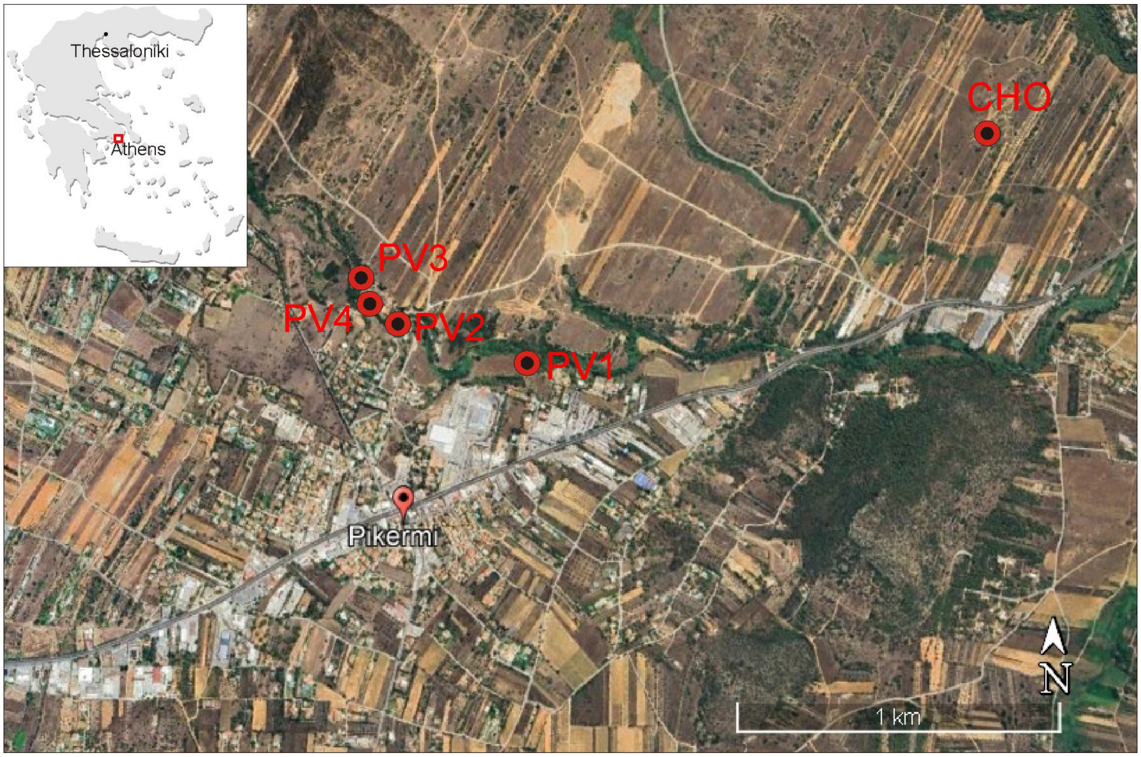

Figure 19. Map indicating the position of the localities Pikermi and Chomateres. Abbreviations: CHO: Chomateres; PV 1: Pikermi Valley 1; PV 2: Pikermi Valley 2; PV 3: Pikermi Valley 3; PV 4: Pikermi Valley 4. Thanks to Dr. A. Athanassiou for the position of the new excavations at Pikermi (Map from Google Earth. Image © 2025, Airbus. Data SIO, NOAA, U.S. Navy, NGA, GEBCO).

mens display morphological characteristics consistent with those of *M. pentelicus* from Pikermi, including a rounded external symphysis without lateral constriction, an abruptly inclined downwards planum alveolare, a thick superior transverse torus, a thick and deep mandibular corpus, and similar dental morphology and dimensions.

The establishment of the new subspecies was based on the specimen NHMW-GHO1623/la, which is considered as male, and on its smaller dimensions in comparison to the rest of the material (Zapfe 1991). In the present study, a principal component analysis was employed to compare the dental dimensions of the two specimens under investigation with those of the typical *M. pentelicus* from the classical Pikermi site (Figure 21). The results of the study indicated that NHMW-GHO-1613/1 matched with the female specimens and NHMW-GHO- 1613/1b with the male ones of *M. pentelicus* (see Figure 21). Consequently, the small size of NHMW-GHO-1613/1a is within the bounds of normal variation for the females of *M. pentelicus*.

In addition to the two previously described mandibles, a right maxillary fragment with Ml-M3 (AMPG-CHO-2211/1972) is mentioned without description (Marinos and Symeonidis 1972); however, this specimen could not be found in AMPG or NHMW. Furthermore, a left mandibular fragment of a young adult male individual numbered NHMW-1972/1578 is stored at NHMW (Figure 22). A small label in its case indicated that the specimen originated from "Pikermi, Ortsteil Chomateri", while a newer label only indicated "Pikermi." The color of the sedimentary matrix adhering to this specimen suggests that it originated from the classical site of Pikermi. This opinion is also shared by S. Roussiakis from Athens, who has been engaged in the study of Pikermi material for many years (Roussiakis 2024, personal communication).

AXIOS VALLEY LOCALITIES

The mammal localities of the Axios Valley are situated west of Thessaloniki area, near the villages of Pentalophos, Vathylakkos, Nea Messimvria, Prochoma, and Dytiko (see Figures 2, 13). They were discovered by C. Arambourg during the First World War, when he arrived there as an army officer in 1915–16. His first collection from this area was taken to France and today it is housed at MNHNP. During the last 50 years a Greek French team has been excavating in the area and has unearthed a great number of fossils, housed at LGPUT. The age of the fauna covers the entire Late Miocene from early Vallesian to the end of the Miocene. More information about the history and the geological background of the Axios Valley is given in Supplement 2. *Mesopithecus* is relatively common in the Axios Valley Late Miocene fauna, with different forms identified in several localities and different stratigraphic horizons.

RAVIN DES ZOUAVES 5 (RZO)

Mesopithecus from Ravin des Zouaves 5 has been described and identified as a new species under the name *Mesopithe-*

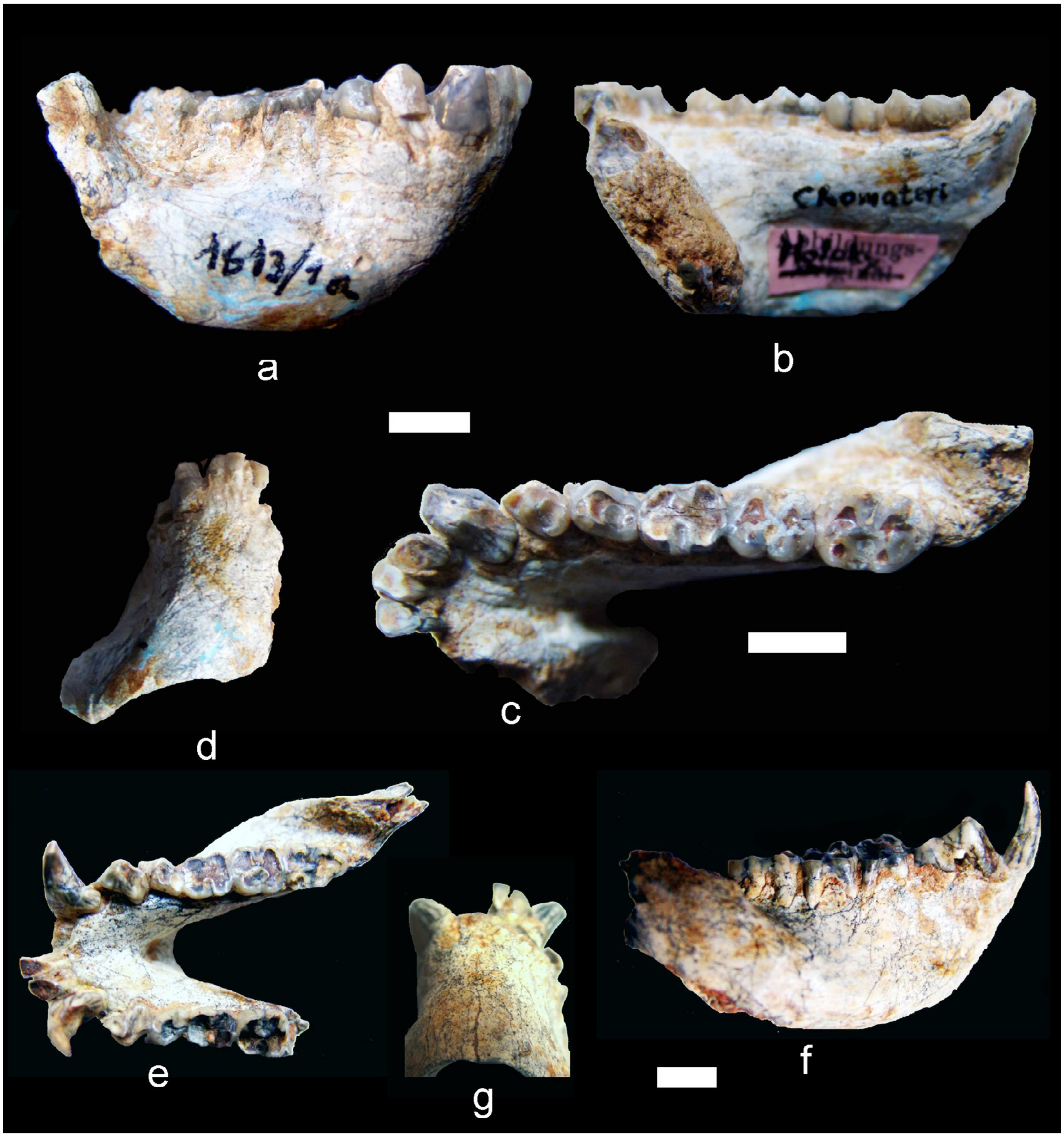

Figure 20. Mesopithecus pentelicus, *Chomateres, Attica, Greece; middle Turolian, MN 12, Late Miocene; GPTS=7.2–7.11 Ma (Böhme et al. 2017). a-d) Mandible of an adult female individual with i1-m3 dex and i1 sin NHMW-CHO-1613/1a; a) right buccal, b) right labial, c) occlusal, and d) external symphysial view. e-g) Mandible of a very old male individual with c-m3 dex and i1-m2 sin, NHMW-CHO-1613/1b; e) occlusal, f) right buccal, and g) external symphysial view.*

cus delsoni. As the description of the material is given earlier (Bonis et al. 1990), only the main diagnostic features and a discussion of the new species will be given. The diagnostic characters of the species are large size *Mesopithecus*, larger than *M. pentelicus*, deep mandibular corpus, flattened anterior symphysis, strong lateral symphysial constriction, large fossa genioglossa, slightly inclined downwards planum alveolare, thick inferior transverse torus, higher lingual (protocone) cusp in the upper premolars than *M. pentelicus*, large honing facet in the p3, and large m3 with large and bicuspid hypoconulid (Bonis et al. 1990a; Koufos 2009a; Koufos et al. 2003).

Though *M. delsoni* was created in 1990 and several articles have been written about the taxon, its systematic position is still the subject of debate. The species was synonymized with *M. pentelicus* because the mentioned distinctive characters are not enough, and its dimensions are within the ranges of variation for *M. pentelicus*. It is also reported that a compression probably affected the depth of the mandibular corpus and/or the larger size is a male character (Andrews et al. 1996; Delson 1994; Zapfe 1991). Andrews et al. (1996) used for comparisons a sample of *Mesopithecus*, named "Macedonian," including specimens from the Axios Valley (Arambourg collection), Veles area

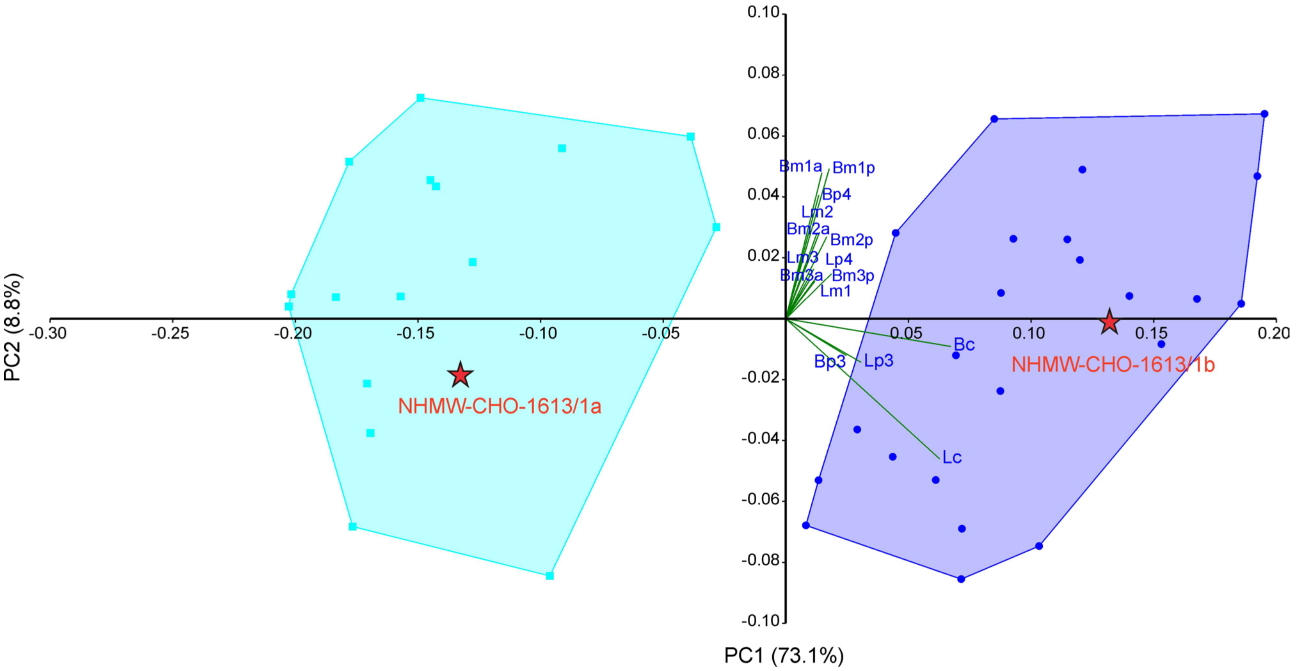

Figure 21. Principal component analysis comparing the Chomateres mandibles of Mesopithtecus *with the typical* M. pentelicus *from Pikermi, using the lower dental dimensions. Symbols: dot (blue):* M. pentelicus, *male; filled square (cyan):* M. pentelicus, *female; asterisk (red):* M. pentelicus *from Chomaters (abbreviations as in Figure 3).*

Figure 22. Mesopithecus pentelicus, *Pikermi, Attica, Greece; middle Turolian, MN 12, Late Miocene; GPTS=7.2–7.11 Ma (Böhme et al. 2017). Mandibular fragment with i1-m3 sin and i1-c dex, NHMW-PIK- 1972/1578; occlusal view (scale bar 10mm).*

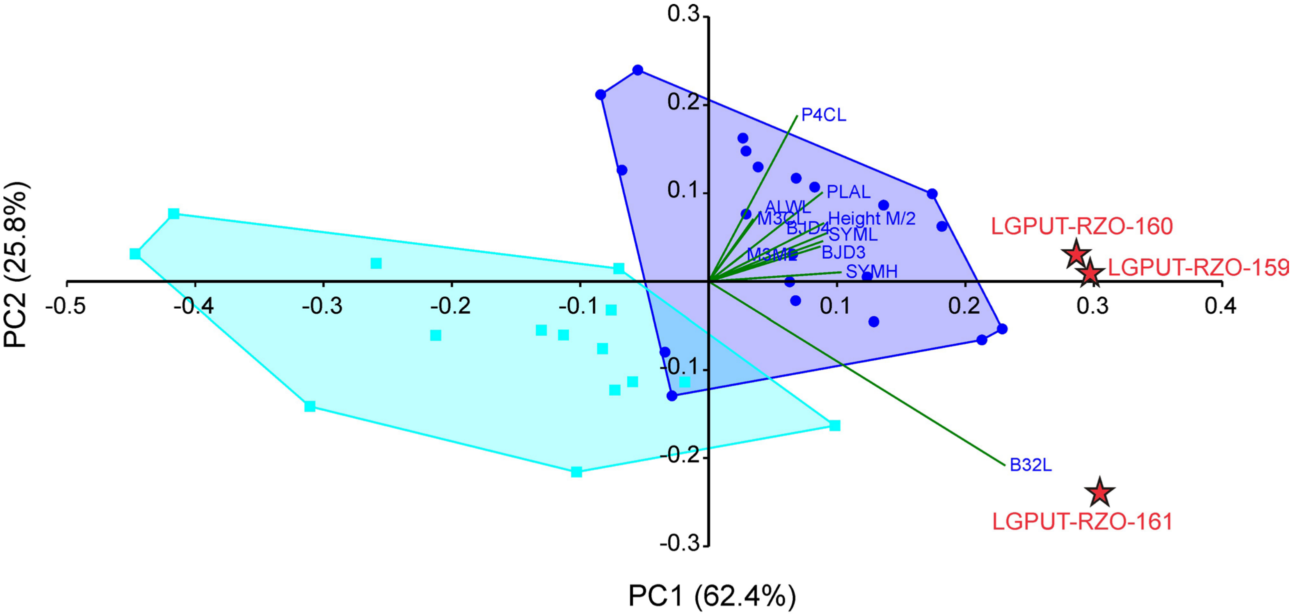

Figure 23. Principal component analysis comparing the mandible of M. delsoni *with* M. pentelicus. *Symbols: dot (blue):* M. pentelicus *male; filled square (cyan):* M. pentelicus *female; asterisk (red):* M. delsoni. *Abbreviations:* ***SYML****: Symphysial length;* ***SYMH****: Symphysial height;* ***PLAL****: Length of planum alveolare (internal distance from infradentale to slope change);* ***GNPL****: Gnathion-slope change point of PLAL;* ***BJD3****: Buccal corpus depth at middle of m3;* ***BJD4****: Buccal corpus depth at middle of p4;* ***ALWL****: Maximum width of alveolar body at middle of m2;* ***M3CL****: Tooth row length c-m3;* ***M3ML****: Tooth row length m1-m3;* ***P4CL****: Tooth row length c-p4;* ***B32L****: Transverse breadth across mandible between contact points of m2 and m3;* ***BP3L****: Transverse breadth across mandible between most lingual points of m3;* ***I1AL****: Breadth across both i1 at alveolar margin.*

(North Macedonia), and some localities from Bulgaria. The comparative sample is a composite one and the age of the different localities is open to question; for instance, in the Veles area there are localities of different age (Radovic et al. 2003; Spassov et al. 2018), and those of the Arambourg collection from Vathyakkos and Ravin X are larger than the typical *M. pentelicus* from Pikermi (present article). Furthermore, the measurements of the Ravin des Zouaves 5 sample were taken on the casts of the material. Moreover, the species was recognized at the locality of Hadjidimovo, Bulgaria (Spassov 2018 and this article) and possibly at Thermopigi, Serres Basin (Tsoukala et al. 2025). The synonymy is mentioned by others (Jablonski et al. 2020; Pradella and Rook 2007; Rook 1999), without further discussion. Later, two possibilities have been proposed for the classification of *Mesopithecus*, either with three different species (*M. delsoni*, *M. pentelicus*, and *M. monspessulanus*) including transitional forms, or with one species (*M. pentelicus*) comprising three subspecies and transitional forms. In both cases, the issue arises as to where the boundary lies between different species or subspecies (Koufos et al. 2003). A recent study proposed to reclassify the Ravin des Zouaves 5 sample as a subspecies, with the designation *M. pentelicus delsoni*, due to the lack of sufficient distinguishing characteristics (Alba et al. 2015).

To evaluate these arguments, the sample of *M. delsoni* is compared with the homogeneous and well-dated sample of *M. pentelicus* from Pikermi. The available mandibular dimensions of *M. delsoni* are analyzed in comparison with *M. pentelicus* using principal component analysis (Figure 23). PC1, which accounts for 62.4% of the original variance, effectively separates the two samples by size. It is likely that PC2, which accounts for 25.8% of the original variance, also contributes to the separation of the two samples. The mandibles of *M. delsoni* are situated outside and far from the convex hulls for males and females of *M. pentelicus*, indicating that they are larger. Even the female mandibular fragment, LGPUT-RZO-161, which lacks measurements because it is broken, exhibits larger dimensions than both male and female mandibles of *M. pentelicus*. It can be concluded from the preceding analysis that *M. delsoni* exhibits a greater size than typical *M. pentelicus*. Additionally, the upper premolars of *M. delsoni* have higher lingual cusp (protocone) and a distal secondary small cusp in the molars (Koufos et al. 2003).

The external symphysis of *M. delsoni* exhibits a distinct flattening of the anterior wall transversely, whereas that of *M. pentelicus* is rounded (Figure 24b, c, e; white arrows). A lateral constriction can be observed at the external symphysis of *M. delsoni*, which is absent in *M. pentelicus* (see Figure 24b, c, e; green arrows). Therefore, the transverse section of the symphysis has a different shape in the two species (see Figure 24b, e; yellow sketches). Additionally, the internal symphysis of *M. delsoni* displays a distinct morphology compared to that of *M. pentelicus*. The planum alveolare in *M. delsoni* is smoothly inclined downwards, in

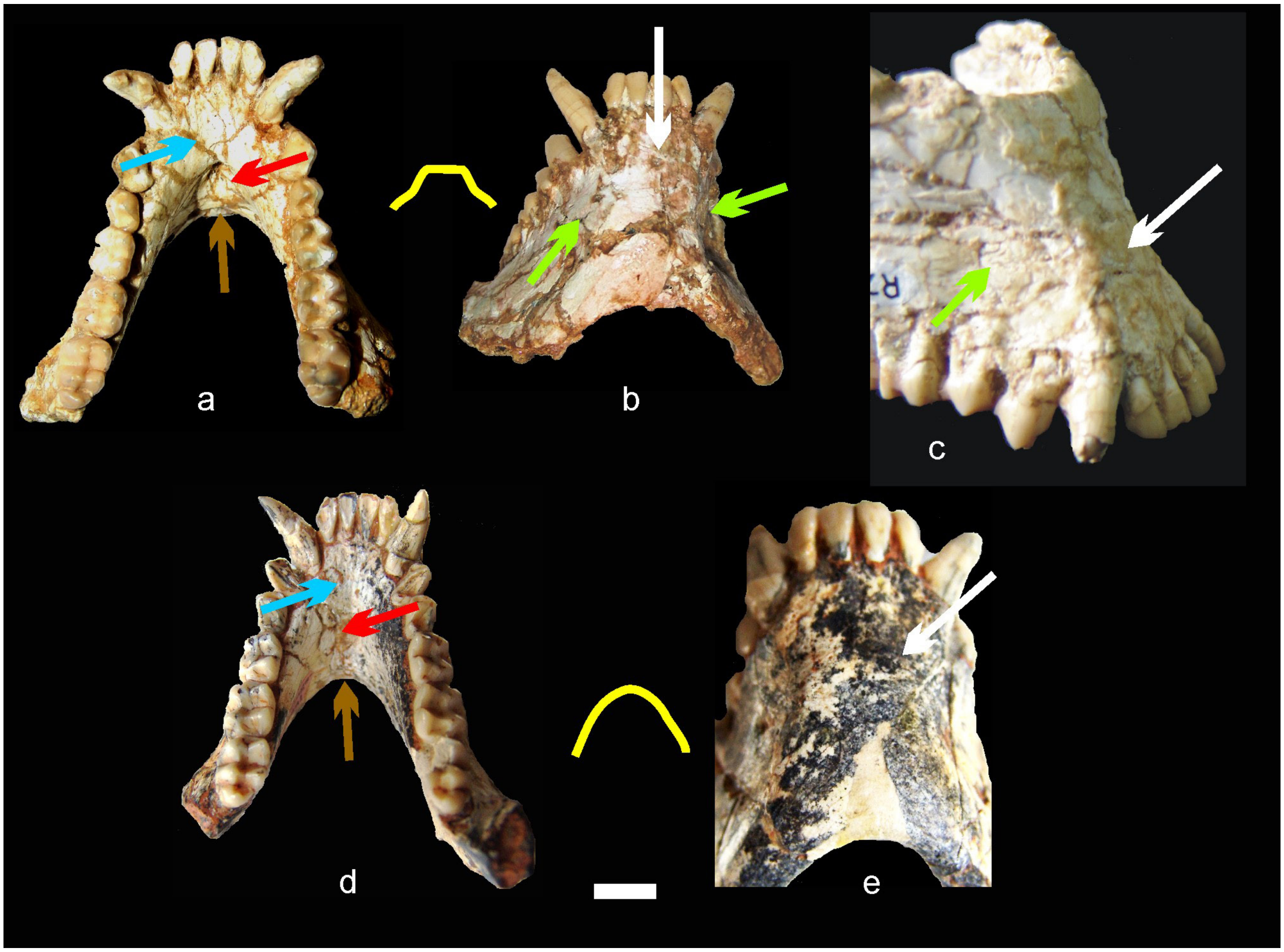

Figure 24. Distinctive morphological characteristics in the mandible of M. delsoni *and* M. pentelicus. *a-b) LGPUT-RZO-159; c) LGPUT-RZO-160), and d-e) NHMW-PIK-1998z77/1) (scale bar 10mm).*

contrast to an abrupt inclination observed in *M. pentelicus* (Figure 24a, d; blue arrows). The fossa genioglossa is notably larger in size in *M. delsoni*, while it is relatively small or absent in *M. pentelicus* (see Figure 24a, d; red arrows). The inferior transverse torus is thick in *M. delsoni*, in contrast to the thin structure observed in *M. pentelicus* (see Figure 24a, d; brown arrows). Furthermore, the length and height of the symphysis are greater in *M. delsoni* than in *M. pentelicus* from Pikermi, as both specimens are far from the convex hulls of male and female *M. pentelicus* (see Figure 16a). Additionally, the mandibular corpus is deeper below p4 and m3 in *M. delsoni* than *M. pentelicus*. This is clear from the biplot diagram (Figure 16b) in which the holotype LGPUT-RZO-159 is far from the convex hulls of male *M. pentelicus*. Concerning the argument of a possible compression and/or deformation, the mandibles from Ravin des Zouaves 5 did not present any preservational factors that would have changed significantly their shape and size.

The morphology of the teeth is similar in both species, although some differences can be observed. The honing facet of the p3 is notably larger in *M. delsoni* than that of *M. pentelicus*. In *M. delsoni*, the m3 hypoconulid is relatively larger, presenting a bicuspid morphology, whereas in *M. pentelicus*, it is smaller and monocuspid (Figure 25a). The m3 of *M. delsoni* is larger than that of *M. pentelicus*, situated outside of the convex hulls for males and females of this species, while the female specimen, LGPUT-RPl- 161 is within the convex hull for the male *M. pentelicus* (Figure 25b). In their arguments in favor of synonymizing *M. delsoni*, all the aforementioned authors concur that there are insufficient distinctive characters for the establishment of a new species. Conversely, all concur that *M. monspessulanus* is a discrete species. According to Delson (1973), this taxon differs from *M. pentelicus* in its slightly reduced size, narrower lower molars, less terrestrially adapted elbow joint and, empirically, from its Pliocene age. Such discrepancies are relatively few when compared to the differences observed between *M. delsoni* and *M. pentelicus*. This begs the question: why is *M. delsoni* recognized at the subspecies level and *M. monspessulanus* at the species level?

It is suggested that some populations of *M. pentelicus*, which adapted to a more arboreal habitat, gave rise to *M. monspessulanus* in the Pliocene (Alba et al. 2015; Andrews et al. 1996; Delson 1973; Szalay and Delson 1979). Further-

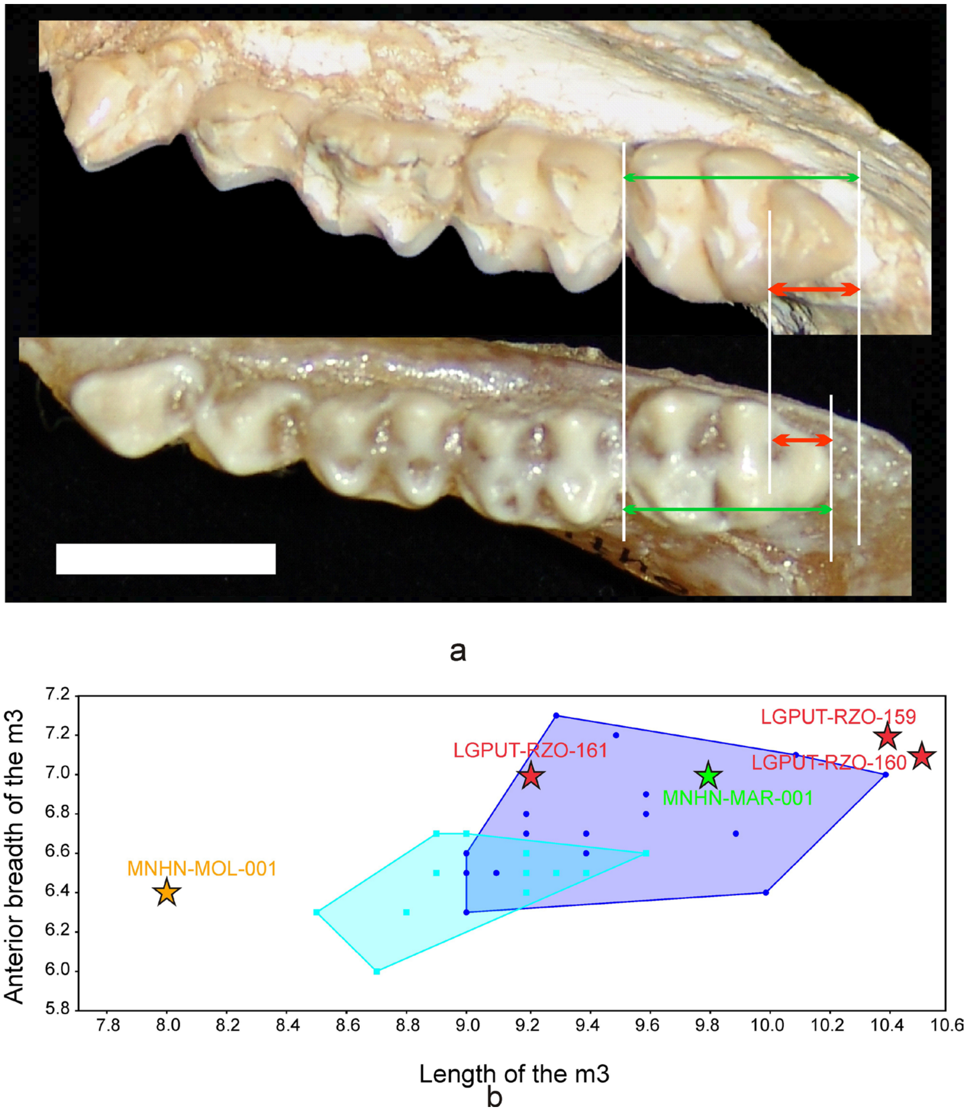

Figure 25. a) Comparison of the m3 and its hypoconulid length of M. delsoni *(upper) and* M. pentelicus *(low); b) Biplot comparing the m3 dimensions of* M. delsoni *and* M. pentelicus*. Symbols: dot (blue):* M. pentelicus *male; filled square (cyan):* M. pentelicus *female; asterisk (red):* M. delsoni*; asterisk (green):* Mesopithecus *sp. Maragheh, Iran; asterisk (yellow):* M. pentelisus*, Molayan, Afganistan (scale bar 10mm).*

more, Alba et al. (2015) suggest that the two species coexisted for a short time. The coexistence of the two species has been definitively identified in the latest Miocene (late Turolian, MN 13; 7.0–6.0 Ma) localities of Dytiko 1 (DTK) and Dytiko 2 (DIT) of the Axios Valley (Macedonia, Greece) (Koufos 2019a, b). Moreover, *M. monspessulanus* from Dytiko is larger than the typical sample from Montpellier, France, occupying a position between *M. pentelicus* and the typical Pliocene *M. monspessulanus*. Furthermore, it is worth noting that the *M. pentelicus* specimen from Dytiko is also smaller than that from Pikermi (Bonis et al. 1990a; Koufos 2019a, b). It seems plausible to suggest that a similar coexistence may have occurred at the early/middle Turolian boundary between *M. pentelicus* and its possible ancestor, *M. delsoni*. This is why intermediate forms of *Mesopithecus* are found in sites dated to the lower Middle Turolian, such as Vathylakkos, Perivolaki, Greece, and Kalimantsi, Bulgaria (Bonis et al. 1997; Koufos 2006a; Koufos et al. 2003; 2004). In consideration of the preceding comparisons and discussion, it is reasonable to conclude that *M. delsoni* should be regarded as a distinct species, along with *M. pentelicus* and *M. monspessulanus*.

LOCALITY RAVIN X

The single mandibular fragment from Ravin X has been described above. It has morphological and metrical similarities with *M. delsoni*. Based on these similarities as well as on the information of Arambourg and Piveteau (1929) for the horizon in which it was found, it can be concluded that it is closer to *M. delsoni*. However, the single specimen, as well

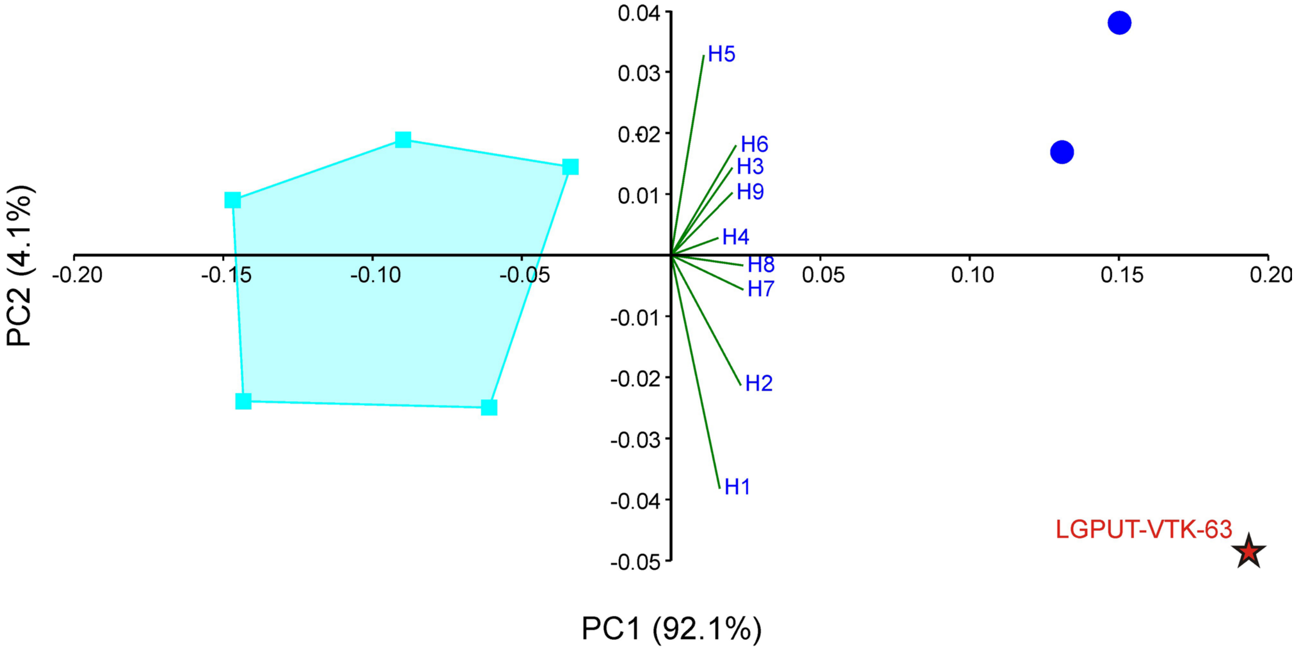

Figure 26. a) Principal component analysis comparing the humerus of Mesopithecus *sp. with* M. pentelicus*. Symbols: dot (blue):* M. pentelicus *male; filled square (cyan):* M. pentelicus *female; asterisk (red):* Mesopithecus *sp. Abbreviations:* ***H1****: Caput-Capitulum length;* ***H2****: Maximal proximal breadth;* ***H3****: Diameter of caput;* ***H4****: Breadth of fossa olecrani;* ***H5****: DAP of fossa olecrani;* ***H6****: Distal epicondylar breadth;* ***H7****: Breadth of trochlea and capitulum;* ***H8****: Breadth of trochlea;* ***H9****: Breadth of capitulum.*

as the unknown exact locality, do not permit a definitive decision, and it is designated as *Mesopithecus* cf. *M. delsoni*.

VATHYLAKKOS 2, 3

The material from the Axios Valley was initially described as *M. pentelici* (Arambourg and Piveteau 1929; Delson 1973). The preliminary study of the new *Mesopithecus* material from the Vathylakkos localities revealed differences from *M. pentelicus*. Consequently, the new material from the Axios Valley, Arambourg material, and Braillon collection were designated as *M.* cf. *pentelicus* or M. *delsoni/pentelicus*, given that they exhibit characteristics of both species (Bonis et al. 1997; Koufos 2009a, b; Koufos et al. 2004).

This morphotype of *Mesopithecus* is characterized by a flattened anteriorly external symphysis, a strong lateral constriction, a roughly inclined downwards planum alveolare, and a relatively strong fossa genioglossa. Two crania (LGPUT-VTK-56, LGPUT-VTK-61) have been discovered in Vathylakkos 2, exhibiting pronounced dorsoventral compression (see Supplement 10: Figures 4, 5). The considerable distortion precludes precise measurement and comparison with *M. pentelicus* is thus limited to dental dimensions (Figure 18a). The PC1 accounts for 62.1% of the original variance and separates males and females of *M. pentelicus*. The two crania from Vathylakkos 2 exhibit a similar pattern of separation. LGPUT-VTK-61 is assigned to a male, while LGPUT-VTK-56 is identified as a female (see Figure 18a). Both crania have larger dental dimensions than those of *M. pentelicus* from Pikermi, suggesting the presence of a *Mesopithecus* morphotype that is larger than the typical *M. pentelicus*. In the principal component analysis of the lower teeth dimensions, PC1, which accounts for 66.2% of the original variance, effectively differentiates between males and females of *M. pentelicus* (see Figure 18b); the position of the Vathylakkos 2 specimens on the diagram confirms their size and attribution.

The forelimb remains from Vathylakkos are also worthy of further investigation. The morphological features of the specimens are similar to those of *Mesopithecus pentelicus* (Koufos et al. 2004), however, there is a notable discrepancy in size. The humerus LGPUT-VTK-63 is compared with a small sample of *M. pentelicus* humeri from Pikermi using principal component analysis. The sample of *M. pentelicus* is clearly delineated into two size groups by PC1, which accounts for 92.1% of the total variance. The position of the studied humerus indicates that it belongs to a male individual and that it is longer than *M. pentelicus* from Pikermi (Figure 26). Based on the above mentioned, a *Mesopithecus* morphotype can be identified which exhibits morphometric characters of *M. delsoni* and *M. pentelicus*. This morphotype has been identified as *Mesopithecus* sp. and is thought to represent a transitional form between the *M. delsoni* and *M. pentelicus* morphotypes. *Mesopithecus* sp. is estimated to have existed from the upper early Turolian to the lower middle Turolian (MN 11 to MN 12), leading to *M. pentelicus*.

DYTIKO, 1, 2, 3

A detailed account of the Dytiko *Mesopithecus* sample can be found in the existing literature, especially in more recent papers (Bonis et al. 1990; Koufos 2019a, b), and it is therefore unnecessary to repeat this description here. The Dytiko localities yielded a variety of *Mesopithecus* fossils, including

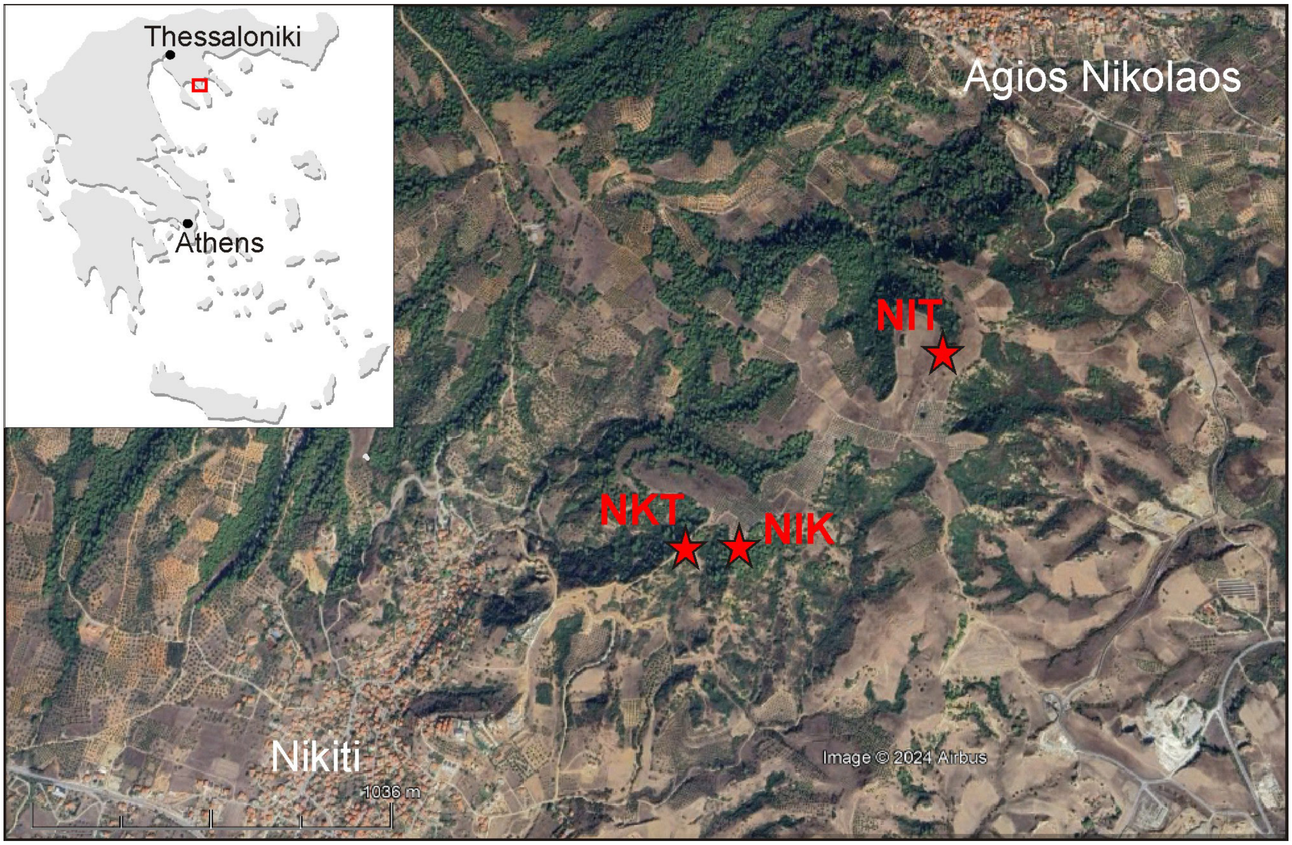

Figure 27. Map indicating the position of the Nikiti localities. NKT: Nikiti 1, NIK: Nikiti 2, NIT: Nikiti 4 (The map was taken from Google Earth. Data SIO, NOAA, U.S. Navy, NGA, GEBCO, Image Landsat/Copernicus, Image © 2025 Airbus).

cranial and mandibular remains (Supplement 10: Figures 8–13). This material was originally described by Bonis et al. (1990), who distinguished two forms in Dytiko—*M.* cf. *pentelicus* and *M.* cf. *monspessulanus*. A more thorough preparation and a revision of this material were conducted recently. This reconsideration of the material confirmed the presence of these two species in the Dytiko fauna, *M. pentelicus* and *M. monspessulanus*. The former is slightly smaller than the typical *M. pentelicus* from Pikermi and the latter is larger than the Pliocene *M. monspessulanus*.

Despite the presentation of several hypotheses regarding the potential coexistence of *M. pentelicus* and *M. monspessulanus* at the end of the Turolian (Delson 1973; Gentilli et al. 1998; Rook 1999; Szalay and Delson 1979), the co-occurrence of these species in the Dytiko fauna provides definitive evidence for their coexistence at the end of the Miocene (Koufos 2019a, b). Furthermore, this coexistence is consistant with the older hypothesis that *M. monspessulanus* originated from a population of *M. pentelicus* residing in a transitional zone between savannah-like and arboreal habutats (Delson 1973; Szalay and Delson 1979). Additionally, it is noteworthy that the size of *M. pentelicus* exhibits a gradual reduction during Late Miocene, ultimately giving rise to the Pliocene *M. monspessulanus* (Bonis et al. 1990; Koufos 2019a, b)

OTHER LOCALITIES WITH *MESOPITHECUS* IN GREECE

NIKITI 2

The Nikiti localities were discovered in 1989. They are located near the village of Nikiti (Chalkidiki Peninsula), approximately 100km from the city of Thessaloniki. The localities are situated to the northeast of the homonymous village of the same name at the Vetrino Hill (see Figure 2; Figure 27). Two principal fossiliferous sites have been identified—Nikiti 1 (NKT) and Nikiti 2 (NIK). A third site, situated near the summit of Vetrino Hill, has also been documented, although it yielded only a small number of bone fragments. The excavations carried out by a team from the LGPUT were led by the author in 1990–1998 and 2004–2009. The Late Miocene deposits of the area have been divided in two formations, Nikiti Fm and Nikolaos Fm (Koufos et al. 1991; Syrides 1991). The first recognized fossiliferous site, Nikiti 1, is situated on the southern slopes of Vetrino Hill within the upper levels of the Nikiti Formation. One year later, the Nikiti 2 locality was discovered on the eastern slopes of the Vetrino Hill within a sandy-clay layer. It is situated approximately 20m stratigraphically above the locality Nikiti 1 in the upper levels of the Nikiti Formation. The third locality, designated Nikiti 4 (NIT), is located within the marly lime-

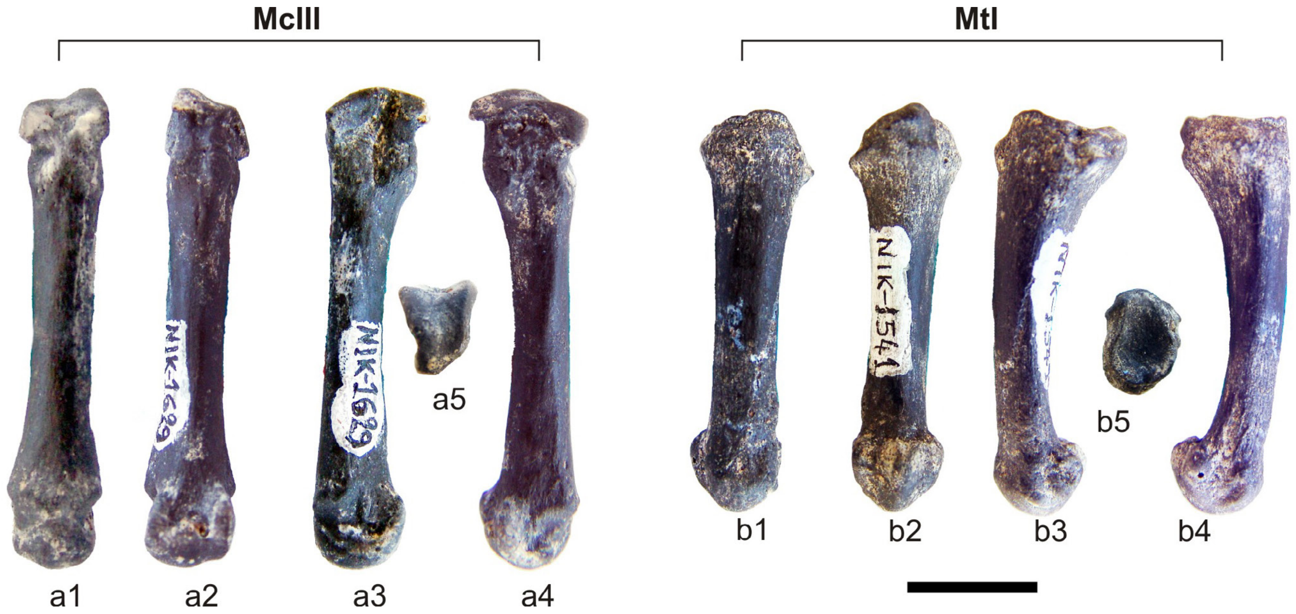

Figure 28. Mesopithecus *sp. (*M. delsoni*?), Nikiti 2 (NIK), Chalkidiki Peninsula, Macedonia, Greece; Late Miocene, early Turolian, MN 11. a) left third metacarpal, LGPUT-NIK- 1629; a1) ventral, a2) dorsal, a3) lateral, a4) medial view, and a5) proximal articular facet. b) left first metatarsal, LGPUT-NIK-154, b1) ventral, b2) dorsal, b3) lateral, b4) medial view, and b5) proximal articular facet.*

stones of the Nikolaos Formation (Koufos 2016a; Koufos et al. 1991). The fossiliferous deposits of Nikiti 1 and Nikiti 2 yielded several mammalian taxa, including the hominoid *Ouranopithecus macedoniensis* in Nikiti 1 and the cercopithecid *Mesopithecus* sp. (*M. delsoni* ?) in Nikiti 2 (Koufos and Kostopoulos 2016). The rich fauna and associated study yielded several biochronological markers, enabling the dating of the sites. The fauna of Nikiti 1 is more primitive than that of Nikiti 2, with a terminal Vallesian (terminal MN 10) age, while Nikiti 2 correlates with the early Turolian (MN 11), (Koufos et al. 2016a). More details for the stratigraphy, fauna, age, and paleoecology are given in Koufos and Kostopoulos (2016).

The material from Nikit 2 includes two metapodials (Figure 28), which were described earlier and determined as a left third metacarpal (LGPUT-NIK-1629) and a left first metatarsal (LGPUT-NIK-1541). The metapodials are compared with some known metapodials of *M. pentelicus* from Pikermi, housed in MNHNP, using principal component analysis (Figure 29). The results demonstrate that PC1, representing 91.9% of the original variance, distinguishes the Pikermi third metacarpals into two size groups (see Figure 29a). Considering the pronounced sexual dimorphism in size of *M. pentelicus*, it may be hypothesized that the smaller size group could represent female and the larger one male individuals. The third metacarpal from Nikiti 2 is larger in size than that of both male and female *M. pentelicus*. It can be reasonably deduced from the principal component analysis of the first metatarsal that it is larger than that of *M. pentelicus* (see Figure 29b). Two *Mesopithecus* morphotypes (*M. delsoni* from Ravin des Zouaves 5 and *Mesopithecus* sp. from the Vathylakkos Fm of the Axios Valley) exhibit larger dimensions than the typical *M. pentelicus*. This leads to the conclusion that the metapodials from Nikiti 2 could belong to either *M. delsoni* or to *Mesopithecus* sp. The biochronological data indicate that the Nikiti 2 faunal assemblage can be correlated with the lower early Turolian, MN 11 (Koufos et al. 2016b). The type locality of *M. delsoni* is Ravin des Zouaves 5 of the Axios Valley, which is correlated with the lower early Turolian (MN 11) (GPTS. ~8.2 Ma; Sen et al. 2000). This age similarity reinforces the attribution of the metapodials to *M. delsoni*. However, the available material is insufficient for definitive determination, and thus, these specimens are reported here as *Mesopithecus* sp. (*M. delsoni*?).

PERIVOLAKI

Perivolaki is a relatively new locality, discovered in 1996 and situated in Thessaly, Central Greece (see Figure 2). The fossiliferous site is located in proximity to the village of Mikro Perivolaki, situated approximately 12km northwest of Velestino (Figure 30). The excavations were initiated in 1996 by a team from the Laboratory of Geology and Palaeontology at Aristotle University of Thessaloniki, led by the author, and concluded in 2004. The locality has yielded a significant number of fossils belonging to several taxa, including *Mesopithecus*. The initial research on the stratigraphy and fauna of Perivolaki was published (Koufos et al. 1999). The Perivolaki collection was studied by various authors and published in a separate volume of *Palaeontographica* (Koufos 2006a). The biochronological and paleomagnetic data indicate a correlation with the middle Turolian (MN 12). The paleomagnetic data suggested an estimated age ranging between 7.3–7.1 Ma (Koufos et al.

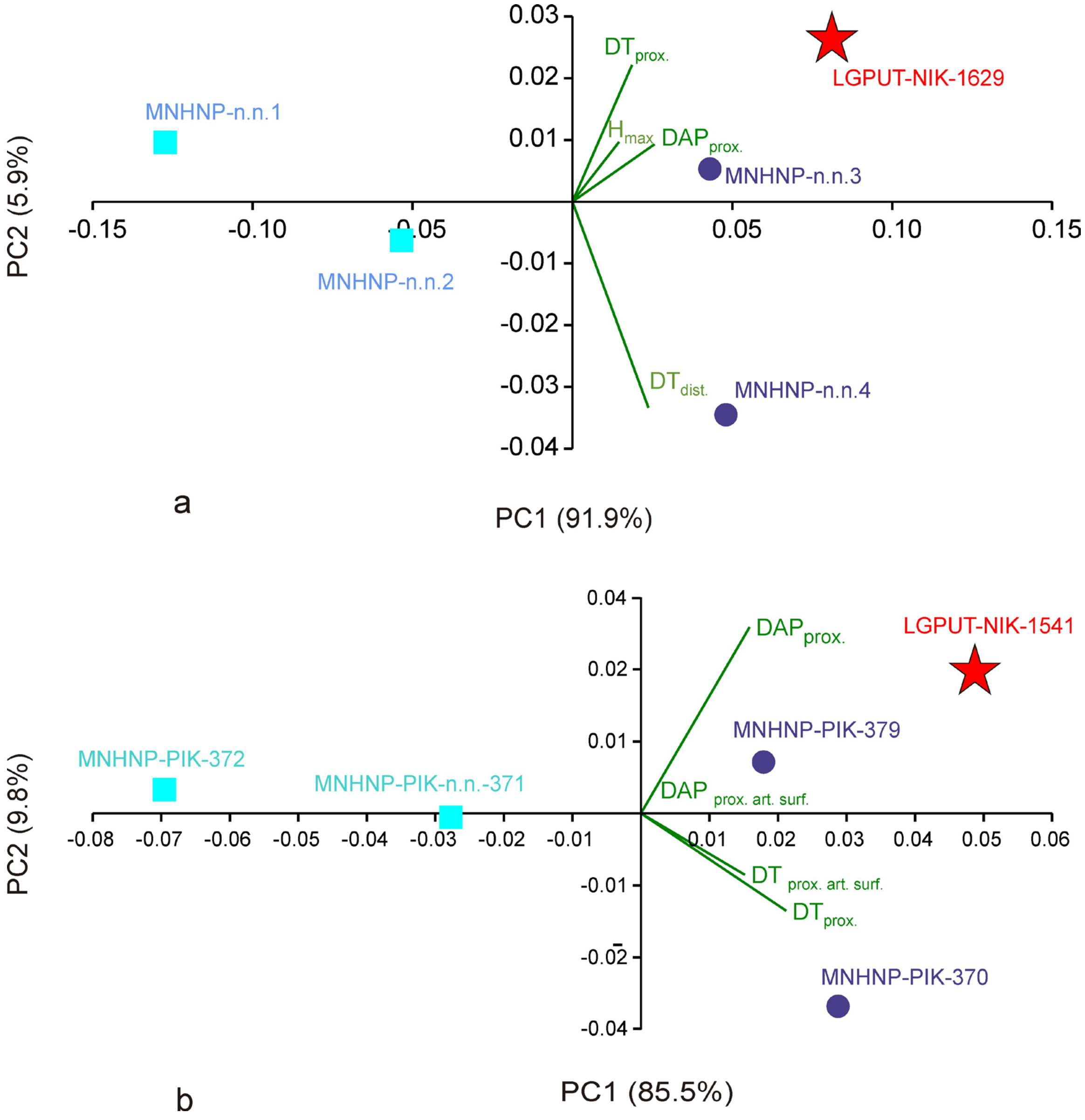

Figure 29. Principal component analysis comparing the third metacarpal (McIII) and first metatarsal (MtI) of Mesopithecus *sp. (*M. delsoni*?) from Nikiti with those of* M. pentelicus *from Pikermi; dot (blue):* M. pentelicus, *Pikermi, male; square (cyan):* M. pentelicus, *Pikermi, female; asterisk (red):* Mesopithecus *sp. (*M. delsoni*?), Nikiti 2. Data source: Zapfe (1991) for the third metacarpal and personal dataset for the MtI. Abbreviations:* $\mathbf{H}_{max}$*.: Maximal height;* $\mathbf{DAP}_{prox}$*.: Proximal anteroposterior diameter;* $\mathbf{DT}_{prox}$*.: Proximal transverse diameter;* $\mathbf{DAP}_{dist}$*.: Distal anteroposterior diameter;* $\mathbf{DT}_{dist}$*.: Distal transverse diameter.*

2006a). The paleoecological conditions of the Perivolaki fauna were analysed employing diverse methods, which collectively indicated an open, bushy-woodland and grassland environment (Koufos et al. 2006b).

A detailed description of the *Mesopithecus* sample from Perivolaki has already been published (Koufos 2006a), and therefore no further description will be included in this article. However, the Perivolaki material of *Mesopithecus* is compared with *M. pentelicus* from Pikermi, as well as *M. delsoni* and *Mesopithecus* sp. from the Axios Valley, using principal component analysis. The mandibular and lower dental dimensions of the two well-preserved mandibles LGPUT-PER-200 and LGPUT-PER-1284 (Figure 31) are included in the analysis. The other two mandibles are excluded from the analysis because they lack canines, they are deformed, and their measurements are questionable. PC1, which accounts for 57.4% of the original variance, effectively separates the two mandibles, which belong to a female and male individual, respectively (Figure 32a). The female mandible LGPUT-PER-200 exhibits a size that is marginally larger than that of *M. pentelicus*, whereas the male mandible LGPUT-PER-1284 is larger than the largest documented specimens of *M. pentelicus*, approaching the dimensions of the two mandibles of *M. delsoni* (see Figure

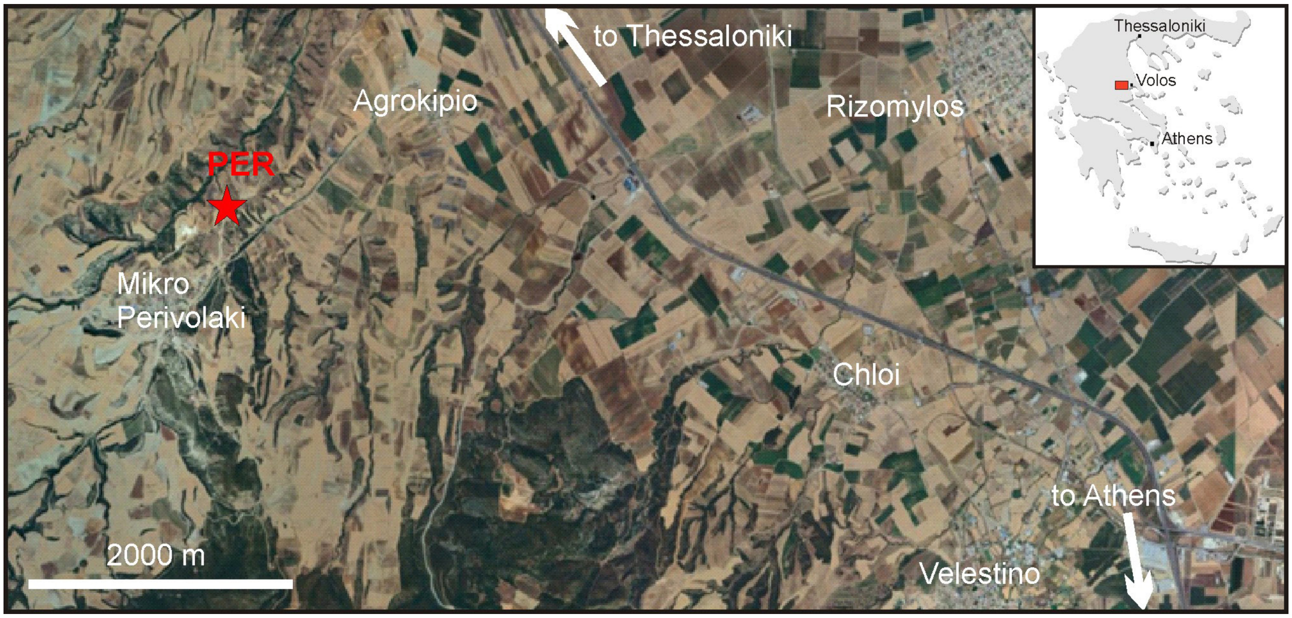

Figure 30. Map indicating the position of the locality of Perivolaki (PER), Thessaly, Greece (The map was taken from Google Earth. Data SIO, NOAA, U.S. Navy, NGA, GEBCO, Image Landsat/Copernicus, Image © 2025 Airbus).

32a).The results of the principal component analysis of the lower dental dimensions confirm the sexual distinction of the two mandibles and suggest that both have larger size than those of *M. pentelicus* from Pikermi (Figure 32b). The mandible LGPUT-PER-200 is also very close to the mandible LGPUT-VTK-62 in both PCA analyses (see Figure 32), indicating that they are morphologically similar. The comparison of the Perivolaki *Mesopithecus* suggests that its size is larger than that of *M. pentelicus* (the female has similar mandibular dimensions to *M. pentelicus* but its dental dimensions are larger) and it is more closely related to *M. delsoni*. Nevertheless, the observed morphological characteristics of the sample are heterogeneous, exhibiting characteristics of both species. The elongated and high symphysis, the flattened anterior surface of the external symphysis, the presence of symphysial constriction, the slightly inclined planum alveolare, and the large fossa genioglossa, are more consistent with that of *M. delsoni* (see Figure 31) Conversely, the less deep mandibular corpus indicates a resemblance to *M. pentelicus*. This morphology is comparable to that of *Mesopithecus* sp. from the Vathylakkos localities of the Axios Valley. This similarity is confirmed by their similar morphology and age, with the estimated magnetostratigraphic age of both localities, Perivolaki (7.3–7.1 Ma) and Vathylakkos 2 (~7.3 Ma) (Koufos et al. 2006a; Sen et al. 2000). Summarizing the above mentioned, the Perivolaki *Mesopithecus* is closer to the morphotype of *Mesopithecus* sp., found in the middle Turolian of the Axios Valley.

KRYOPIGI

Kryopigi was discovered in the 1990s. Excavations started in 1998 and continued for the next 15 years by a team from the University of Thessaloniki (directed by Prof. E. Tsoukala). The fossiliferous site is located near the village of the same name in the Kassandra Peninsula (Chalkidiki, Greece), approximately 95km east of the city of Thessaloniki (see Figure 2; Figure 33). The excavations yielded many fossils, including a variety of mammals, as well as some reptiles and birds. A comparison of the faunal data from Kryopigi with those from the Axios Valley (Macedonia, Greece) and Perivolaki (Thessaly, Greece) suggests that it is younger in age than Ravin des Zouaves 5 (~8.2 Ma) and Prochoma 1 (~7.4 Ma), (Koufos et al. 2006a). Furthermore, it is potentially younger than the Perivolaki fauna (7.3–7.1 Ma; Koufos et al. 2006a; Sen et al. 2000;) and closer in age to the Dytiko fauna (6.0–7.0 Ma; Koufos and Vasileiadou 2015). Based on these comparisons, Lazaridis (2015) proposed a time frame for the age of Kryopigi fauna, ranging from 7.3 to 6.4 Ma, which corresponds with the upper part of the middleTurolian to the lower part of the late Turolian (upper MN 12 to lower MN 13). More details about the stratigraphy, fauna, age, and paleocology of the Kryopigi fauna are given in Lazaridis (2015). The studied material includes a female cranium and associated mandible, LGPUT-KRY5600 (Figures 34, 35), a right maxillary fragment with C-M2, LGPUT-KRY2042, and two M2, LGPUT-KRY1000 and LGPUT-KRY5000.

The *Mesopithecus* specimens from Kryopigi have been previously described (Lazaridis 2015; Lazaridis et al. 2018; Tsoukala and Bartziokas 2008). Consequently, the following discussion will focus on the principal morphological characteristics and comparisons of the material. LGPUT-KRY5600 is among the most well-preserved skulls of *Mesopithecus*. It exhibits slight deformation of the braincase, likely resulting from an attack by a carnivoran (the traces of this attack are indicated by the red arrows in Figure 34b,

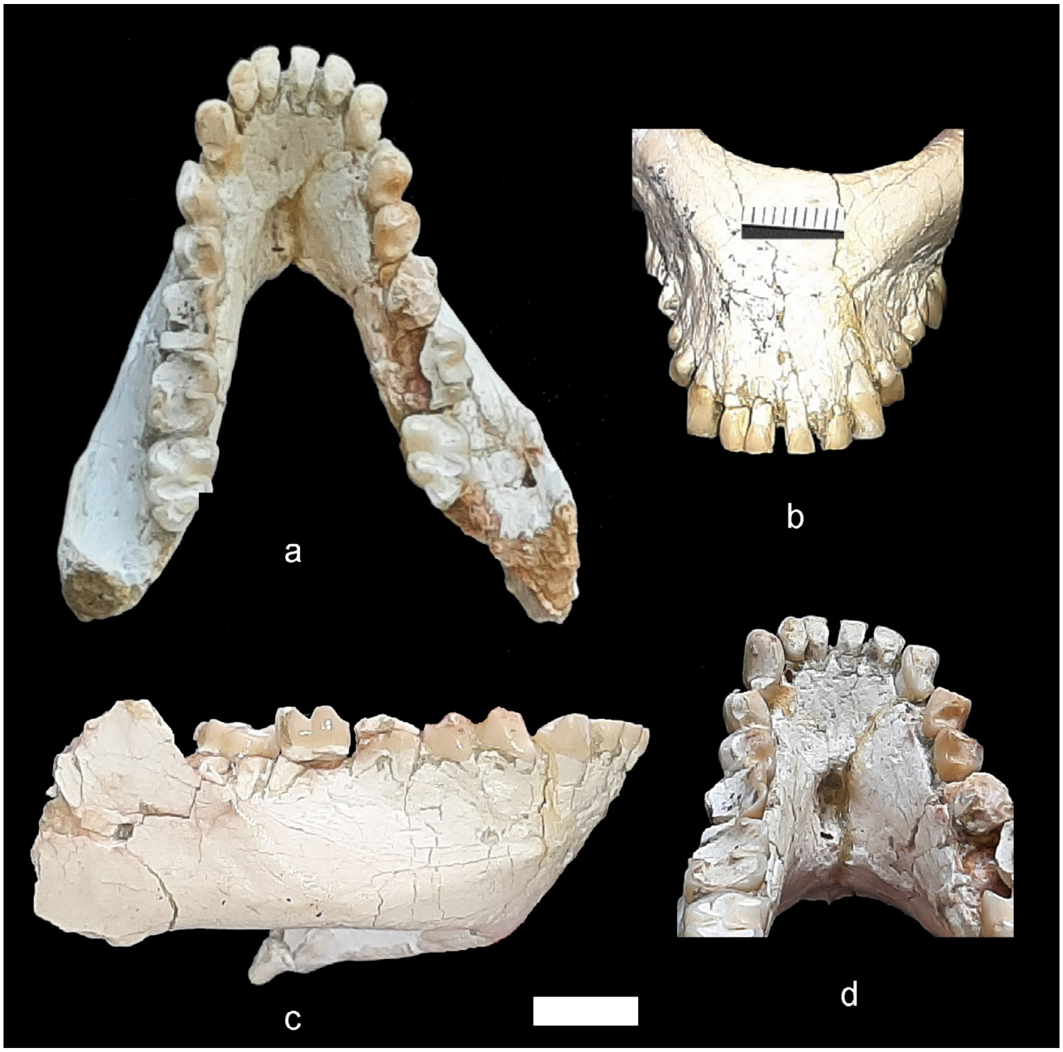

Figure 31. Mesopithecus *sp., Perivolaki (PER), Velestino, Thessaly, Greece; Late Miocene, middle Turolian, MN 12, GPTS. 7.3–7.1 Ma. a, d) Mandible with both tooth rows of an old female individual, a) occlusal, b) buccal, c) external symphysial, and d) internal symphysial view.*

c), and retains a complete dentition (see Figures 34, 35). The specimen is attributed to a young adult individual based on the observation of minimal wear on the teeth and incomplete eruption of the upper and lower canines. The following characteristics are consistent with those of *M. pentelicus*: nearly rounded orbits, elliptical and narrow nasal opening, large interorbital distance, presence of a supraorbital torus, elongated and high canines with a groove across the lingual wall, bicuspid upper premolars, and four main cusps in the molars. However, the presence of a weak and thin supraorbital torus, the absence of a prominent sagittal crest, and less pronounced sagittal lines could be indicative of a female individual. Conversely, the strong and high canines suggest a male individual. This contradiction is likely explained by the individual's youth. As discussed, the supraorbital torus, sagittal crest, and temporal lines, are weaker in young individuals and undergo progressive development during adulthood. In the only studied young cranium of *Mesopithecus* sp. from the locality Vathylakkos 2 of the Axios Valley, all the mentioned characters are absent (see Supplement 10: Figure 7). The LGPUT-KRY5600 cranium, which is from a young adult individual, is not fully developed, giving the impression that it is a female.

The mandible LGPUT-KRY5600 (see Figure 35) exhibits several characteristics that are consistent with those observed in *M. pentelicus* from Pikermi, including the rounded anterior symphysis, the absence of lateral symphysial constriction, the strongly inclined downwards planum alveolare, the reduced fossa genioglossa, the short mandibular corpus, the dental morphology, and the small hypoconulid on m3 (see Figure 35a-d).

The comparison of LGPUT-KRY5600 with *Mesopithecus* from Pikermi and the Axios Valley provides several data points that confirm the systematic position and the sex of this cranium. The mandibular and dental dimensions are compared using principal component analysis to facilitate

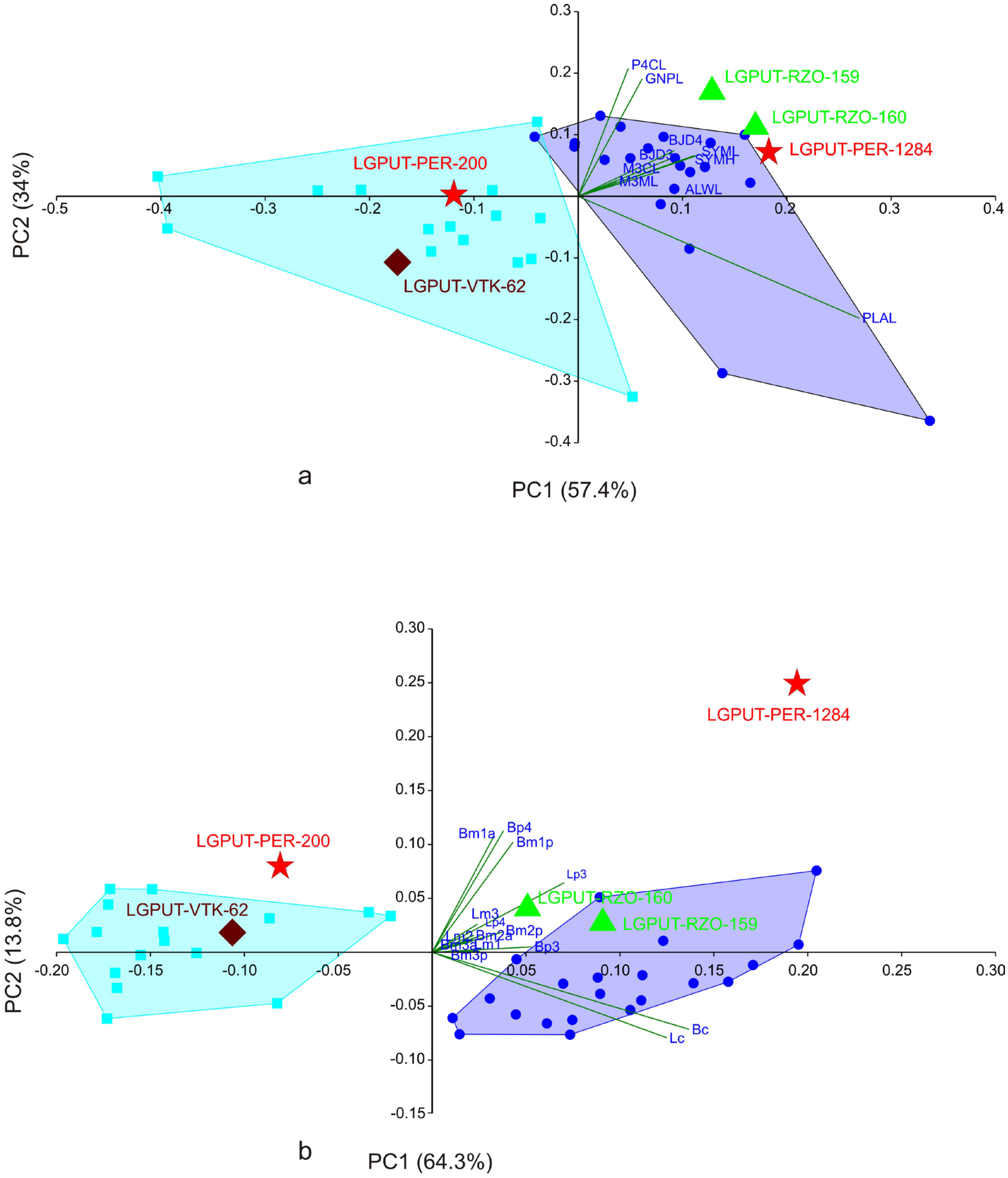

Figure 32. Principal component analysis comparing the mandibular (a) and lower dental (b) dimensions of Mesopithecus *sp. from Perivolaki with those of* M. pentelicus, M. delsoni, *and* Mesopithecus *sp. from Vathylakkos 2; dot (blue):* M. pentelicus, *Pikermi, male; square (cyan):* M. pentelicus, *Pikermi, female; filled triangle (green):* M. delsoni, *Ravin des Zouaves 5; diamond (brown):* Mesopithecus *sp., Vathylakkos 2; asterisk (red):* Mesopithecus *sp., Perivolaki (Data source. personal dataset). Abbreviations as in Figures 3 and 23.*

Figure 33. Map indicating the position of the locality of Kryopigi (KRY) (The map was taken from Google Earth. Data SIO, NOAA, U.S. Navy, NGA, GEBCO, Image Landsat/Copernicus, Image © 2025 Airbus).

the comparison. The analysis of the mandibular dimensions indicates that PC1 matching 54.7% of the original variance and, secondarily, PC2 matching 31.6% of the original variance separate the males and females of *M. pentelicus* from Pikermi (Figure 36a). LGPUT-KRY5600 corresponds to *M. pentelicus* from Pikermi, which is located within the convex hull of the males. LGPUT-KRY5600 and the mandible LGPUT-DKO-38 from Dytiko 3 in the Axios Valley are located near the smallest specimens from Pikermi. Furthermore, it was found to be smaller and different from the two mandibles of *M. delsoni* (LGPUT-RZO-159, 160) from the Axios Valley (see Figure 36a). The sole specimen of *M. monspessulanus* (LGPUT DIT-22) from Dytiko 2, although male, is notably smaller than LGPUT-KRY5600. The mandibles LGPUT-PER-200 and LGPUT-VTK-62 of *Mesopithecus* sp. are female and are smaller than the mandible from Kryopigi.

The PCA analysis of the upper dental dimensions suggests that PC1, which accounts for 62.5% of the original variance, successfully separates males and females of *M. pentelicus* (Figure 36b). The two specimens from Kryopigi occupy a position between the males and females of *M. pentelicus* from Pikermi and Dytiko 3 (LGPUT-DKO-38). LGPUT-KRY5600 is smaller than *Mesopithecus* sp. from Vathylakkos 2; their dental size is close to that of the female cranium LGPUT-VTK-56 of *Mesopithecus* sp. (see Figure 36b). Similar results are also taken from the PCA diagram comparing the lower dental dimensions. PC1, which accounts for 54.8% of the original variance, differentiates it from the males of *M. pentelicus* (Figure 36c). The Kryopigi specimen occupies a position between males and females of *M. pentelicus* indicating that it is smaller than the male *M. pentelicus* from Pikermi. In conclusion, based on the above-mentioned comparisons, the Kryopigi material can be attributed to a male *M. pentelicus*. Moreover, it is clearly smaller than *M. delsoni* and *Mesopithecus* sp., as well as larger than *M. monspessulanus* from Dytiko 1 and 2. On the other hand, it is closer to *M. pentelicus* from Dytiko 2 and 3 (LGPUT-DIT-21 and LGPUT-DKO-38), taking a position between males and females (see Figure 36c). The similarity of Kryopigi and Dytiko *Mesopithecus* agrees with the age of these localities (7.3–6.4 Ma and 7.0–6.0 Ma respectively (Koufos and Vasileiadou 2015; Lazaridis 2015). In summary, the Kryopigi *Mesopithecus* is male and belongs to a late Turolian morph of *M. pentelicus*, which is smaller than the typical one from Pikermi and leads to *M. monspessulanus* in the Pliocene. This *Mesopithecus* morphotype is also present in Dytiko localities (Koufos 2019a, b).

MARAMENA

Maramena is in the Serres Basin (Macedonia, Greece) (see Figure 2; Figure 37). As there are many publications on the stratigraphy of the Serres Basin scattered throughout various sources (some of which are in Greek), it is considered necessary to provide a summary of the stratigraphy of the Maramena fossiliferous site, as well as some historical data, in Supplement 3. The material from Maramena includes both small and large mammals, which were extensively studied (Schmidt-Kittler 1995). The biochronological data suggests a Turolian/Ruscninian age, MN 13/14 (Koufos and Vasileiadou 2015; Schmidt-Kittler et al. 1995).

The Maramena sample of *Mesopithecus* is predominantly composed of isolated teeth, which were found during the process of washing and sorting the sediments for micromammals. Among the known material there are two mandibular fragments, numbered AMPG-MA 021 and AMPG-MA 040 (Kullmer and Doukas 1995). A notable characteristic of this collection is the significant number of *Mesopithecus* deciduous teeth, which is the largest known.

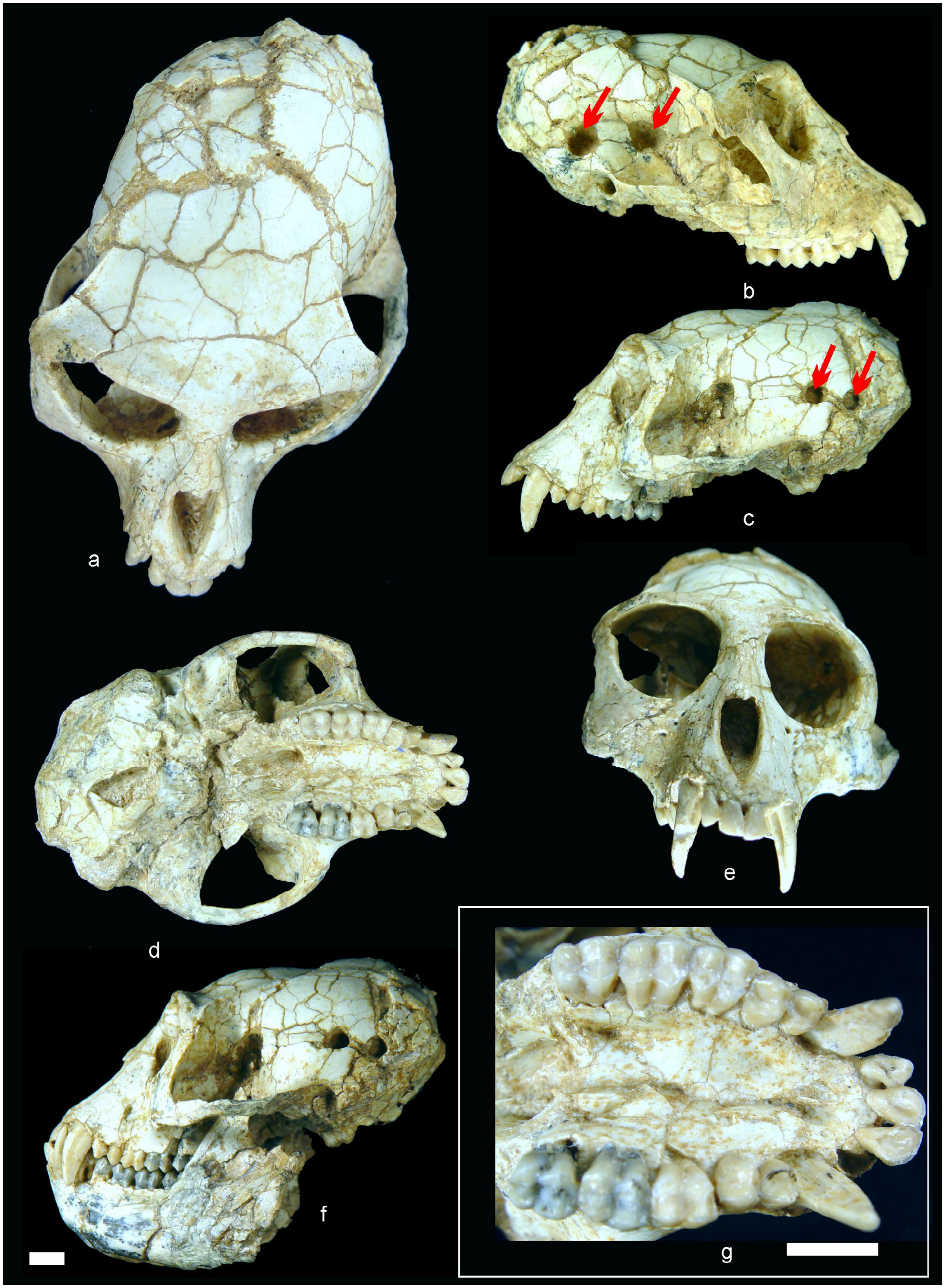

Figure 34. Mesopithecus pentelicus, *Kryopigi (KRY), Chalkidiki, Macedonia, Greece; Late Miocene, upper middle to lower late Turolian, upper MN 12-lower MN 13. a-e) Cranium and associated mandible, LGPUT-KRY5600; a) dorsal, b) right lateral, c) left lateral, d) ventral, e) facial view, f) cranium and mandible in lateral view, and g) upper dentition, occlusal view (scale bar 10mm). The photos are kindly provided by Dr. G. Lazaridis.*

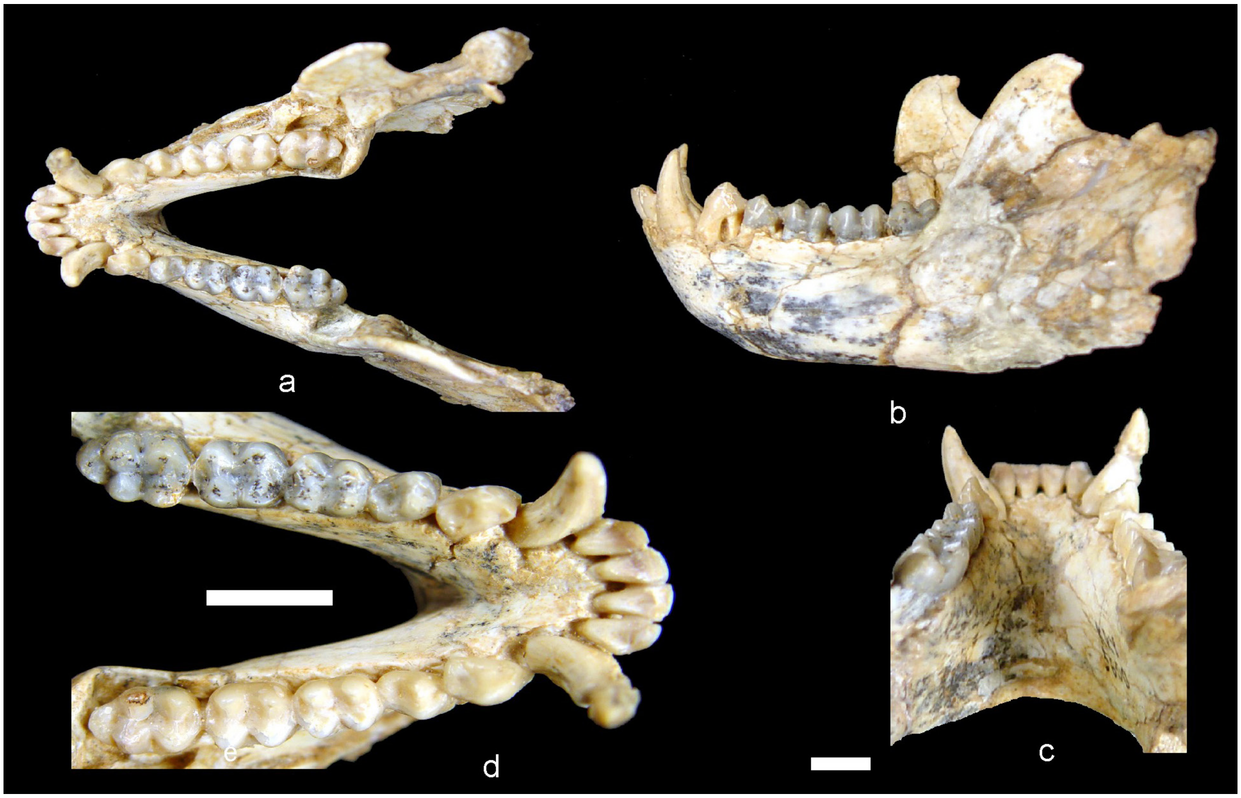

Figure 35. Mesopithecus pentelicus, *Kryopigi (KRY), Chalkidiki, Macedonia, Greece; Late Miocene, upper middle to lower late Turolian, upper MN 12-lower MN 13. a-d) Mandible, LGPUT-KRY5600; a) occlusal, b) left lateral, c) internal symphysis, and d) lower dentition (scale bar 10mm). The photos are kindly provided by Dr. G. Lazaridis.*

In contrast, the Pikermi collection, which is the richest, includes few young individuals, precluding a detailed comparison with the Maramena sample. A comprehensive study of the deciduous teeth from Maramena has been conducted by Kullmer and Doukas (1995), and it is not necessary to repeat it.

The upper teeth of Maramena are isolated. The molars have four main cusps arranged in two transverse rows separated by a valley (Figure 38a-c), a morphology similar to *Mesopithecus* while their dimensions are close to those of *M. pentelicus* from Pikermi. As already mentioned, the sexual dimorphism of *M. pentelicus* is better expressed in the canines, which are larger in the males. In the plots for M1 and M2 (Figure 39), the Maramena sample is divided into two groups, raising the question of whether it represents sexual dimorphism or the existence of two species. This question arises from the recognition of two different species *M. pentelicus* and *M. monspessulanus* in the Late Turolian localities of Dytiko 1, 2 in the Axios Valley (Koufos 2019a, b). Considering the age similarity between the Maramena and Dytiko localities (Axios Valley, Greece), the hypothesis of a second *Mesopithecus* species is plausible. However, such a distinction is not observed in the lower teeth. On the other hand, the size of the Maramena teeth is larger than that of *M. monspessulanus* from Dytiko, being more similar to *M. pentelicus* (see Figure 39). Therefore, the available material from Maramena cannot support recognition of a distinct species.

The lower teeth are best represented by the specimen AMPG-MA 058, which preserves both p3-m3 tooth rows (Figure 40; Supplement 11: Figure 6). The morphology and size of the lower teeth are consistent with those of *M. pentelicus* from Pikermi (see Figure 39) and can be attributed to this species. The lower canines AMPG-MA 053 (Figure 38d) and AMPG-MA 040 (Supplement 11: Figure 5) have similar morphology and dimensions to *Mesopithecus*, while their size indicates a male and female individual respectively (see Figure 39). In conclusion, the morphological and metrical similarity observed in the material indicates that Maramena *Mesopithecus* can be attributed to *M. pentelicus* more probably to a smaller form, like that found in the Axios Valley Dytiko localities.

MESOPITHECUS IN THE GRECO-IRANIAN PROVINCE AND ASIA

MESOPITHECUS IN BULGARIA

A substantial assemblage of *Mesopithecus* fossils has been recovered from southwestern Bulgaria with the majority originating from the Struma (Strymon) and Mesta (Nestos) Valleys. In the Mesta Valley and around the town of Hadjidimovo three mammal localities have been found,

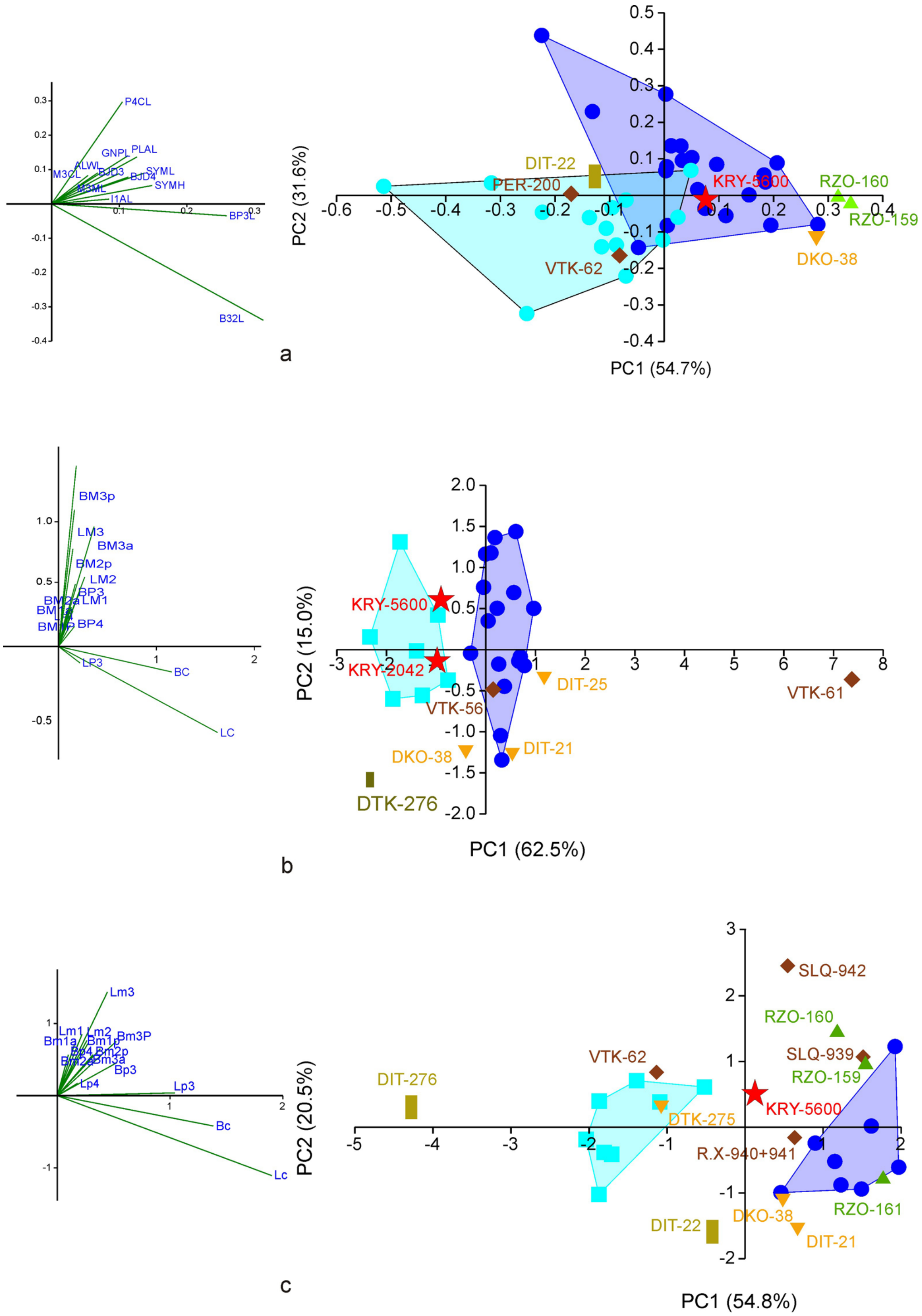

Figure 36. Principal component analysis comparing the mandibular (a), upper dental (b) and lower dental (c) dimensions of Mesopithecus *from Kryopigi with those of* M. pentelicus *from Pikermi and the Axios Valley, as well as* M. delsoni *and* M. monspessulanus *from the Axios Valley; dot (blue):* M. pentelicus, *Pikermi, male; square (cyan):* M. pentelicus, *Pikermi, female; inverse triangle (orange):* M. pentelicus, *Dytiko, Axios Valley; filled triangle (green):* M. delsoni, *Ravin des Zouaves 5, Axios Valley; diamond (brown):* Mesopithecus *sp., Ravin-X, Vathylakkos 2, Perivolaki; rectangular (olive green):* M. monspessulanus, *Dytiko, Axios Valley; asterisk (red):* M. pentelicus, *Kryopigi. Data source Tsoukala and Bartziokas (2008) and Lazaridis et al. (2018) for Kryopigi and personal dataset for other localities. Abbreviations as in Figures 3 and 23.*

Figure 37. Map indicating the position of the Maramena locality. MAR: Maramena 1, 2 (The map was taken from Google Earth. Data SIO, NOAA, U.S. Navy, NGA, GEBCO, Image Landsat/Copernicus, Image © 2025 Airbus).

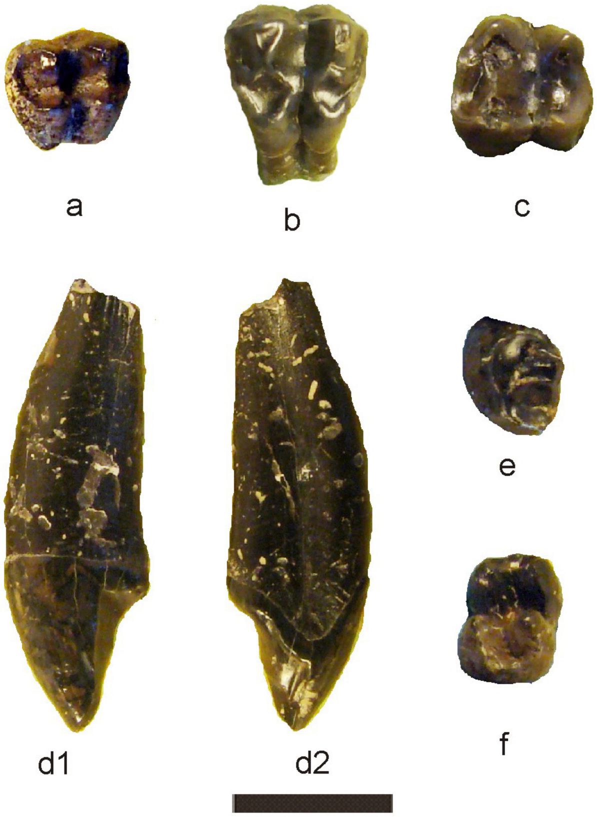

Figure 38. Mesopithecus pentelicus, *Maramena (MAR), Serres Basin, Macedonia, Greece; Late Miocene, transition Turolian/Ruscinian, MN 13/14. a) AMPG-MAR 050, right M1; b) AMPG-MAR 020, right M2; c) AMPG-MAR 049, right M3; d) AMPG-MA 053, left C1, d1) buccal and d2) lingual view; e) AMPG-MA 012, right p4; f) AMPG-MA 013, right m1 (scale bar 10mm).*

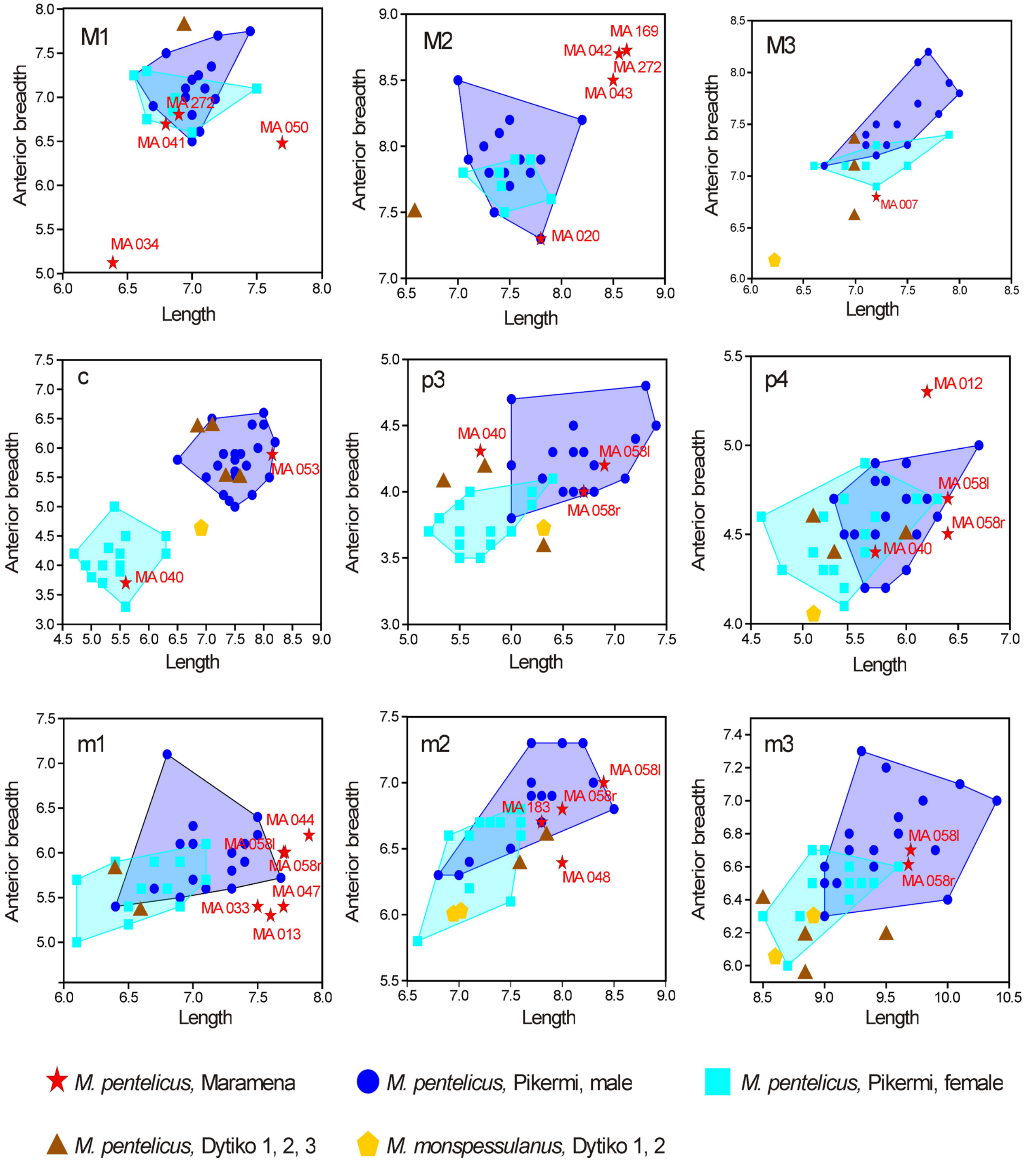

Figure 39. Scatter plots, comparing the dental dimensions of the Maramena Mesopithecus *with* M. pentelicus *from Pikermi and* M. monspessulanus *from Dytiko 1, 2, Axios Valley. Data source Kullmer and Doukas (1995) for Maramena and personal dataset for the rest.*

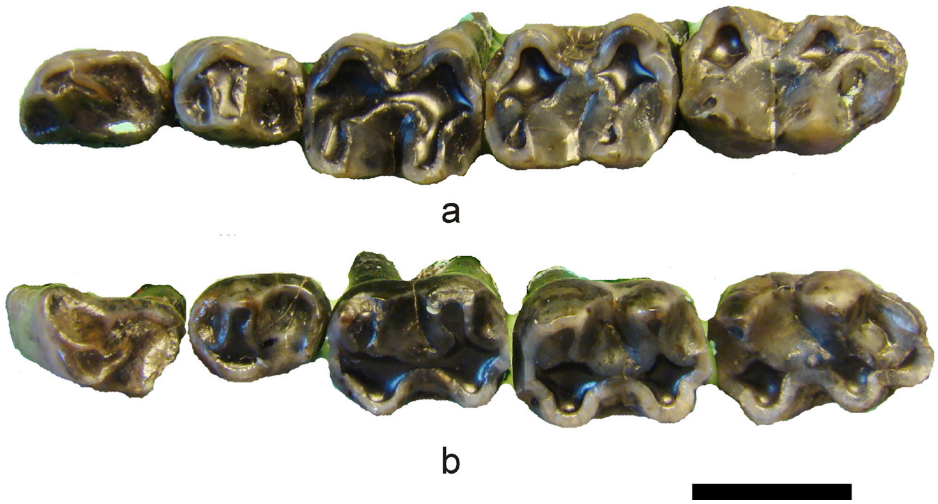

Figure 40. Mesopithecus pentelicus, *Maramena (MAR), Serres Basin, Macedonia, Greece; Late Miocene, transition Turolian/Ruscinian, MN 13/14. a-b) lower p3-m3 tooth rows, AMPG-MAR-058 (scale bar 10mm).*

Hadjidimovo 1, Hadjidimovo 2, and Hadjidimovo Tumbichkite; the first and last yielded *Mesopithecus* (Koufos et al. 2003). Most of the material originated from Hadjidimovo 1, including two almost complete skeletons. The collection is housed at PMA (Bulgaria). The Hadjidimovo fauna is dated to the lower part of the middle Turolian, MN 12 (Spassov 2002). The Hadjidimovo sample exhibits a number of distinctive morphological features, including a deep mandibular corpus, an elongated and high symphysis, a flattened anterior symphysis with lateral symphysial constriction, a gently inclined planum alveolare, a large fossa genioglossa, a thick inferior transverse torus, a large honing facet in the p3, a large m3 with large and bilobate talonid, a high lingual cusp (protocone) in the P3-P4, and elongated tooth rows (Koufos et al. 2003). All these characteristics are consistent with those observed in *M. delsoni* from the Axios Valley, Macedonia, Greece. The mandibular remains of the Hadjidimovo sample are compared with *M. pentelicus* from

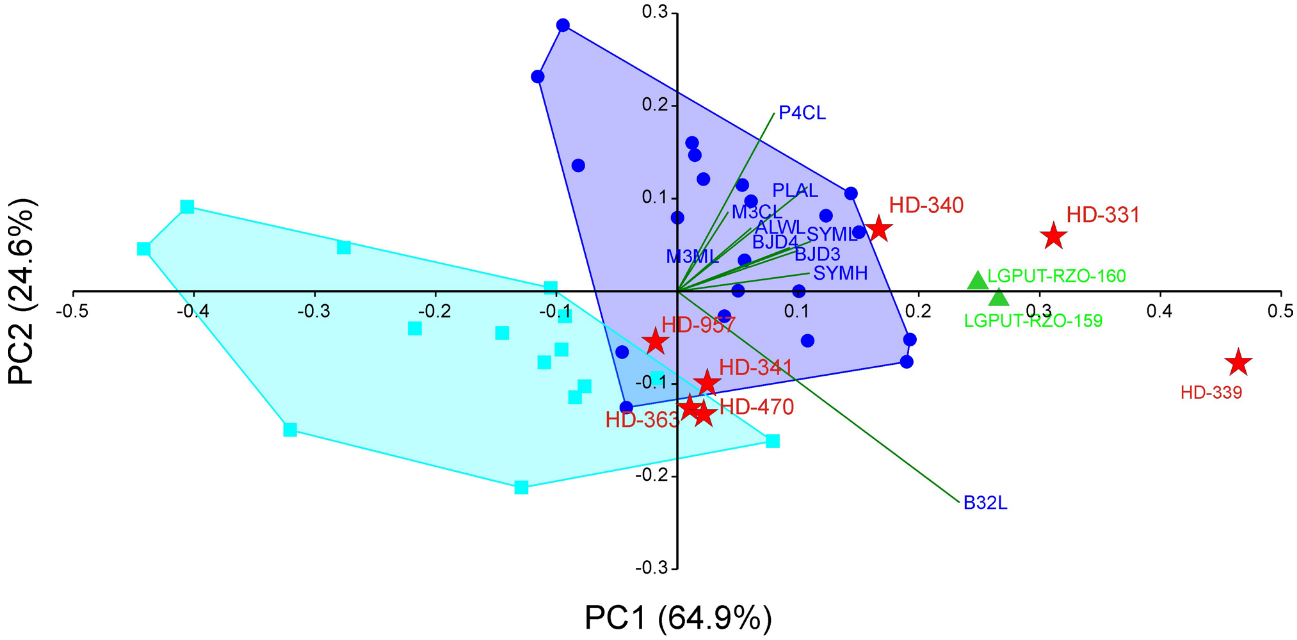

Figure 41. Principal component analysis comparing the mandibular dimensions of Mesopithecus *from Hadjidimovo (Bulgaria) with those of* M. pentelicus *from Pikermi and* M. delsoni *from Axios Valley; dot(blue):* M. pentelicus, *Pikermi, male; square (cyan):* M. pentelicus, *Pikermi, female; filled triangle (green):* M. delsoni, *Ravin des Zouaves 5, Axios Valley, Greece; asterisk (red):* Mesopithecus, *Hadjidimovo. Data source. personal dataset. Abbreviations as in Figure 23.*

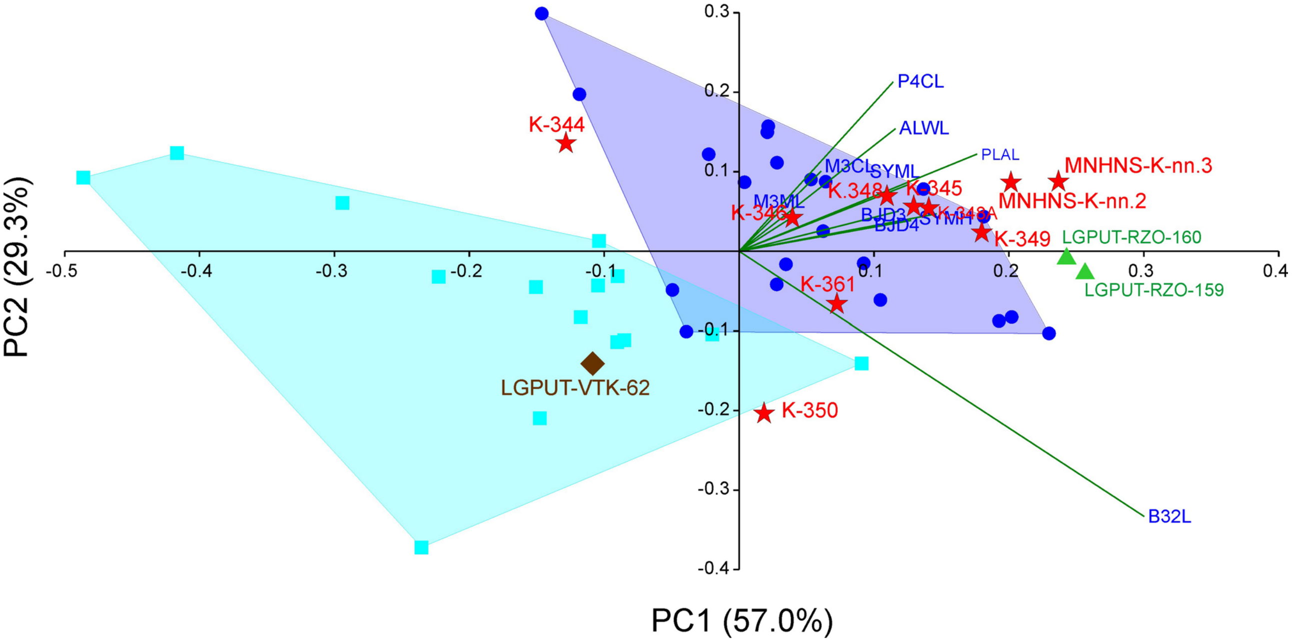

Figure 42. Principal component analysis comparing the mandibular dimensions of Mesopithecus *from Kalimantsi (Bulgaria) with those of* M. pentelicus *from Pikermi, and* M. delsoni *and* Mesopithecus *sp. from the Axios Valley. Symbols: dot (blue):* M. pentelicus*, Pikermi, male; filled square (cyan):* M. pentelicus*, Pikermi, female; filled triangle (green):* M. delsoni*, Ravin des Zouaves 5, Axios Valley, Greece; diamond (brown):* Mesopithecus *sp., Vathylakkos 2, Axios Valley, Greece; asterisk (red):* Mesopithecus*, Kalimantsi. Data source personal dataset. Abbreviations as in Figure 23.*

Pikermi and the type material of *M. delsoni*, using principal component analysis (Figure 41). The Hadjidimovo mandibles are separated into two size groups primarily by PC1, which accounts for 64.9% of the total variance, and secondarily by PC2, explaining 24.6% of the total variance; the size groups correspond to the males (large size) and females (small size) like those of *M. pentelicus*. The male Hadjidimovo mandibles are larger than *M. pentelicus* and match with those of *M. delsoni*, indicating that they have similar size. The females also match with the largest females and the smallest males of *M. pentelicus*, suggesting a mean size larger than the typical *M. pentelicus* (see Figure 41). The upper and lower dental dimensions of the Hadjidimovo material are also analyzed, but not reported, as the results obtained are like those above. The Hadjidimovo sample of *Mesopithecus* was attributed to *M.* cf. *delsoni* in its original description (Koufos et al. 2003) and later to *M. delsoni* (Spassov et al. 2018). The new analysis confirms this and thus can be attributed to *M. delsoni*.

The richest collection of *Mesopithecus* in Bulgaria comes from the region of Kalimantsi in the Struma Valley. More than ten fossil sites have been found in this area, yielding a large number of fossils. The *Mesopithecus* collection from Kalimantsi is mainly stored at the PMA, while a few specimens are housed at the NMNHS. The collection lacks detailed stratigraphic information. All localities are dated to the middle Turolian, MN 12, except Kalimantsi 1, which is correlated to the early Turolian, MN 11 (Spassov et al. 2006). The Kalimantsi material was originally described as *M. pentelicus* and *M.* cf. *delsoni* (Koufos et al. 2003). The Kalimantsi mandibular remains are analyzed with those of *M. pentelicus* from Pikermi, as well as with *M. delsoni* and *Mesopithecus* sp. from Axios Valley (Macedonia, Greece), using principal component analysis (Figure 42). The analysis shows that most of the mandibles correspond to *M. pentelicus* and are located within the convex hulls of the males and females of this species. However, two specimens (NMNHS-K-nn.2 and NMNHS-K-nn.3) are located outside the convex hulls, having larger size than *M. pentelicus*. The exact locality and therefore the age of these specimens is unknown, and they could belong to the earlier morphotype *Mesopithecus* sp. from the Axios Valley (Greece). The upper and lower dental dimensions of the Kalimantsi material were also analyzed, but not reported, as the results obtained are similar to those above.

Besides the Hadjidimovo and Kalimantsi localities, *Mesopithecus* is known from four other localities in Bulgaria; the material from these localities is stored at NMNHS. Kromidovo 2 is an old locality, situated in Struma (Strymon) Valley, which yielded two mandibular corpora with right c-m3 and left m2-m3 (NMNHS - FM 1525) and two upper tooth rows with right P4-M3 and left M1-M2 of the same individual (NMNHS -FM-15230) of *Mesopithecus*. The morphology and size of both specimens are like *M. pentelicus* and thus they were attributed to this species (Koufos et al. 2003). The Kromidovo 2 fauna is dated to the middle Turolian, MN 12 (Spassov et al. 2006). Furthermore, *Mesopithecus* is present in the locality of Gorna Sushitsa (Struma

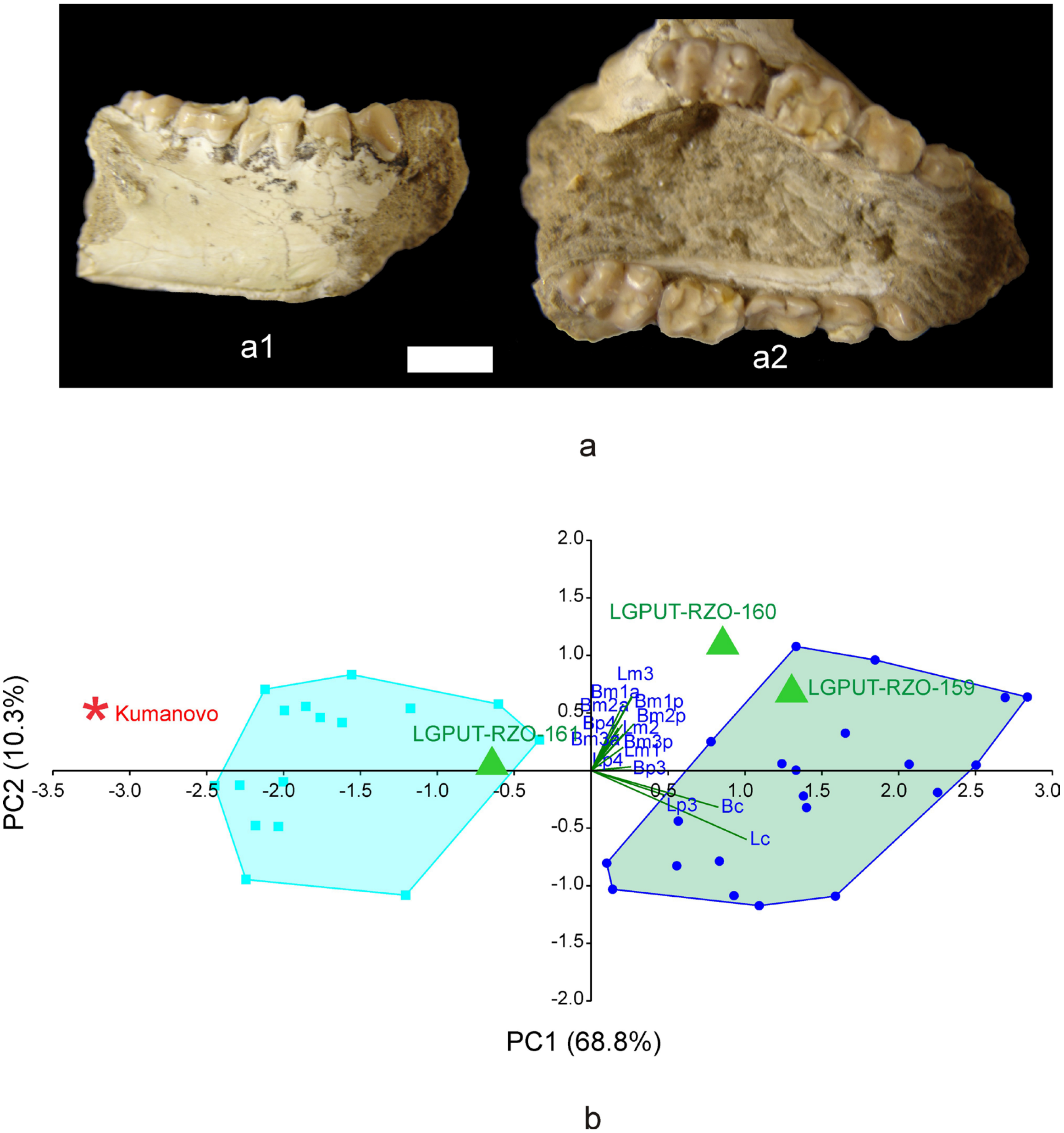

Figure 43. a) Mesopithecus pentelicus, *Kumanovo, North Macedonia; Late Miocene, Turolian, MN 11–13 (Spassov et al. 2018). Mandible with p3-m3 dex and p4-m3 sin, n.n. stored in NHMW; a1) lateral and a2) occlusal view; b) Principal component analysis comparing the lower dental dimensions of* Mesopithecus *from Kumanovo (N. Macedonia) with those of* M. pentelicus *from Pikermi and* M. delsoni *from the Axios Valley, Macedonia, Greece. Symbols: dot (blue):* M. pentelicus, *Pikermi, male; square (cyan):* M. pentelicus, *Pikermi, female; filled triangle (green):* M. delsoni, *Axios Valley ; asterisk (red):* M. pentelicus, *Kumanovo, NHMW n.n.*

Valley) with a maxillary fragment preserving the left C-M2 row. The morphology and size of the teeth allow its designation to *M. pentelicus*. The fauna suggest an early-middle Turolian age, MN 11-12 (Spassov et al. 2006).

Additionally, two isolated teeth, one p4 and one M3?, are known from the Pliocene locality of Dorkovo (southern Bulgaria); they were attributed to *M. monspessulanus* (Delson et al. 2005). Recently some remains of *Mesopithecus* were found in the Bulgarian locality of Azmaka 6, which are not yet published (Spassov 2025 personal communication). The faunal data provided a middle Turolian (MN 12) age; the paleomagnetic data suggest an age ranging from 7.28–7.20 Ma (Böhme et al. 2017).

MESOPITHECUS IN NORTH MACEDONIA

Several Late Miocene mammal localities are known from North Macedonia (the southern part of former Yugoslavia) that have yielded a relatively rich fauna. These localities are situated across the northern part of the Axios (Vardar) Valley, and their faunas are closely related to those of the lower Axios Valley in Greece. The collections are currently housed in the NHMSK and NHMBEO. A recent reconsideration of the NHMBEO collection revealed the presence of *M. pentelicus*, while *M. delsoni* was recognized at the locality of Prevalec (Radović et al. 2013: Figure 4). Based on the photographic evidence and the published measurements, the Prevalec mandibular fragment appears to exhibit certain characteristics reminiscent of *M. delsoni*. However, a definitive attribution remains uncertain due to the absence of personal study of the collection. In contrast, re-examination of the NHMSK collection from these localities showed only the presence of *M. pentelicus* (Spassov et al. 2018).

In the collections of NHMW there is a partial mandible (Figure 43a), which has been labelled "Kumanidorf," Samos, Greece. It is peculiar because such a locality name is unknown from Samos. Delson (1973) referred to this specimen being found at the southern part of the former Yugoslavia and had classified it as a female *M. pentelicus*, proposing a Meotian (early Turolian) age. Subsequently, the specimen was cited by Zapfe (1991), who suggested its probable origins as Samos or Bulgaria and assigned it to *M. pentelicus*. In a subsequent discussion with N. Spassov, it was revealed that the name of this locality is Kumanovo, a former Bulgarian territory. Spassov et al. (2018) attributed the Kumanovo mandible to *M. pentelicus* and suggested an age for it corresponding to the Turolian period. The Kumanovo mandible is poorly preserved and partially prepared (see Figure 43a). The mandible belongs to an older individual and preserves the right p3-m3 and left p4-m3 rows, which are close to the female *M. pentelicus*. The depth below m3 for the Kumanovo mandible is 20.5mm, versus 21.4mm (range 19.0–24.7mm) for males and 18.24mm (range 15.2–21.0mm) for females of *M. pentelicus*. The depth below p4 for the Kumanovo mandible is 18.90mm, in comparison to 21.07mm (range 18.3–24.0mm) for males and 18.09mm (range 15–21.5mm) for females of *M. pentelicus*. The principal component analysis of the dental dimensions of the Kumanovo specimen and *M. pentelicus* indicates a high degree of similarity between them (Figure 43b). Consequently, the Kumanovo specimen can be identified as a female of *M. pentelicus*.

MESOPITHECUS IN ROMANIA

Several species of cercopithecids are known from Romania. They are present from the beginning of the Pliocene to the end of early Villafranchian. *Mesopithecus* has been identified in the following localities: a) Malusteni with *M. monspessulanus* and cf. *Paradolichopithecus*), and b) Baraolt-Capeni with *M. monspessulanus*. The former is correlated with the early Ruscinian (MN14) and the latter with the upper part of the late Ruscinian (MN 15) (Delson 1973; Radulescu and Samson 2001; Radulescu et al. 2003; Stan et al. 2024; Szalay and Delson 1979). The *Mesopithecus* collection from Romania is limited, including a left mandibular fragment bearing m3 and a male right upper canine from an older specimen (Delson 1973).

MESOPITHECUS IN IRAN

Mesopithecus has been known from Iran since the beginning of the 20th century, when de Mequenem (1924-25) described a mammalian fauna from Maragheh. According to the author, the material of *Mesopithecus* includes a mandible (MNHNP-MAR-001; Figure 44a-e), a fragment of a femur and one phalanx; he also mentions that the *Mesopithecus* material is being studied by A. Gaudry. However, the mandible was described much later (Voruz 1968) and attributed to *M. pentelicus*; MNHNP-MAR-001 is from the Middle Maragheh interval (Bernor et al. 1996). Recent collections from Site II, Middle Maragheh interval, Dareh Gorg, yielded a right mandibular fragment of *Mesopithecus* preserving p4-m1, which has not yet been described. The site is correlated with MN 11 or possibly early MN 12 (Ataabadi et al. 2016: Figure 3c, d).

MNHNP-MAR-001 is a partially preserved mandible that lacks the ascending rami and displays both p3-m3 tooth rows (see Figure 44a-e). The external symphysis has been fractured, but the anterior symphysis, which has been preserved, is flattened and bears a lateral symphysial constriction (see Figure 44d). The internal symphysis has been found to be better preserved, exhibiting a prominent, deep, and gently sloping posteriorly planum alveolare, as well as a large fossa genioglossa. These features have been observed in *M. delsoni*. The mandibular corpus is comparatively shallow, approaching the depth of the male *M. pentelicus*. Both canines are fractured; however, the remaining portions of their roots indicate that they were robust, suggesting a probable male individual. The p3 is large and displays a large honing facet, comparable to that observed in *M. delsoni* (see Figure 44c, red arrows). The morphology and dimensions of the remaining teeth are comparable to those of *M. pentelicus*. However, the m3 is larger, exhibiting a well-developed and bilobed hypoconulid, as seen in *M. delsoni* (see Figure 44e, red arrows). Despite the observed similarities between the Maragheh mandible and the mandible of *M. delsoni*, the height of the mandibular corpus is more closely aligned with that of the male *M. pentelicus* (see Figure 16b). A comparable *Mesopithecus* morphotype has been identified in the Axios Valley (Macedonia, Greece), at Vathylakkos 2, and Vathylakkos 3. PCA analysis of the lower dental dimensions of the Maragheh mandible compared with those of *M. pentelicus* shows that PC1 (which accounts for 72.6% of the original variance) successfully separates males from females (see Figure 44b). Morphologically, the Maragheh mandible is larger than *M. pentelicus* and closer to *Mesopithecus* sp. from sites such as Vathylakkos 2 and 3 (7.4–7.3 Ma) and Perivolaki (7.3–7.1 Ma) from the Axios Valley, and Perivolaki (7.3–7.1 Ma), Greece. As the probable age of the Maragheh mandible is MN 11/12 (Ataabadi et al. 2016a), it could belong to *Mesopithecus* sp., a morphotype known from Greece. However, it cannot be ruled out that it belongs to *M. delsoni* (large honing facet in the p3, bicuspid hypoconulid in m3; see Figure 44c, e), as the single specimen and the ambiguous age of the locality do not allow for a definite conclusion.

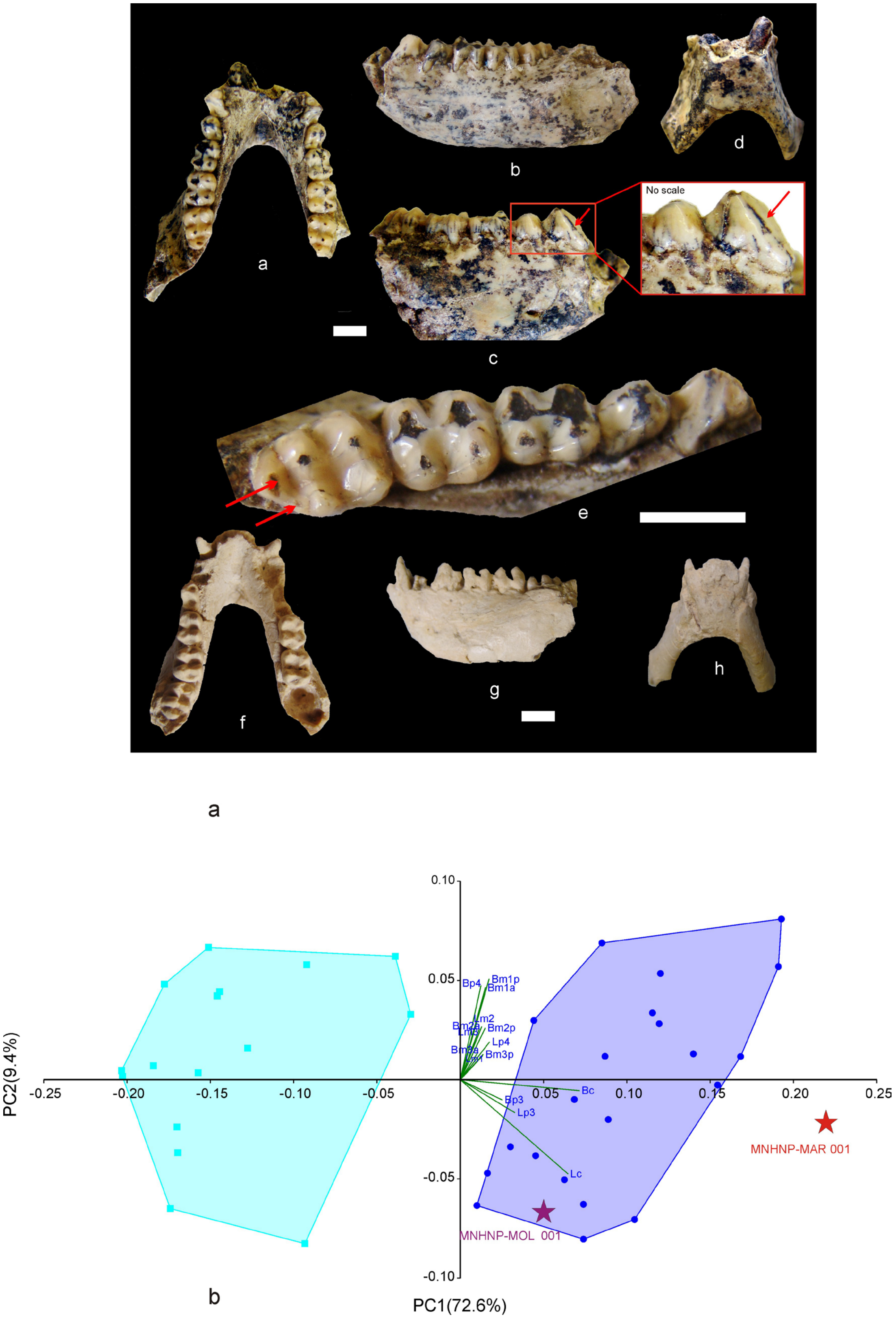

Figure 44. a-e) Mesopithecus *sp., Middle Maragheh, Iran; Late Miocene; early Turolian MN 11 or early middle Turolian MN 12. Mandible with p3-m3 dex and sin, MNHNP-MAR-001. a) occlusal; b) left lateral, c) right lateral view, d) external symphysis, and e) left tooth row. f-h)* Mesopithecus pentelicus, *Molayan, Afghanistan; Late Miocene, middle Turolian, MN 12. Mandible with c, m1-m2 dex and c, p4-m3 sin, MNHNP-MOL-001 (cast), f) occlusal, g) left lateral view, and h) external symphysis; b) Principal component analysis comparing the lower dental dimensions of* Mesopithecus *from Maragheh (Iran) and Molayan (Afghanistan) with those of* M. pentelicus *from Pikermi. Symbols: dot (blue):* M. pentelicus, *Pikermi, male; square (cyan):* M. pentelicus, *Pikermi, female; asterisk (red):* Mesopithecus, *Maragheh; asterisk (violet):* Mesopithecus, *Molayan.*

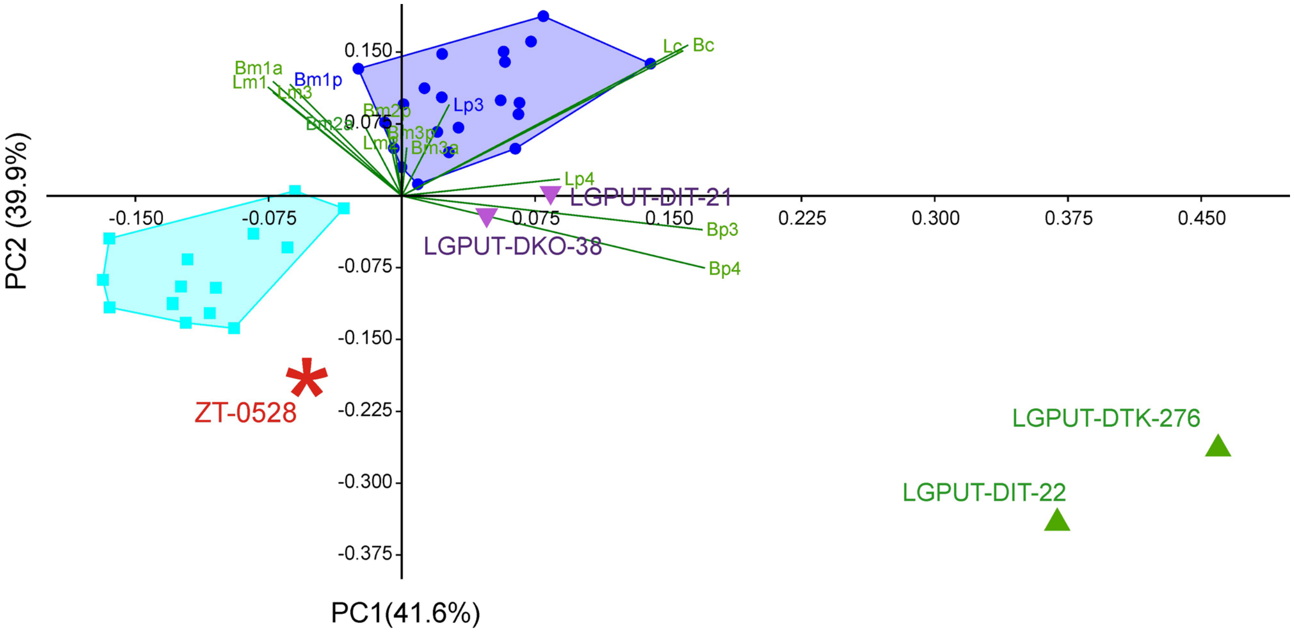

Figure 45. Principal component analysis comparing the lower dental dimensions of M*esopithecus from Suitangba (China) with those of* M. pentelicus *from Pikermi and Dytiko,* M. monspessulanus *from the Axios Valley Greece. Symbols: dot (blue):* M. pentelicus*, Pikermi, male; square (cyan):* M. pentelicus*, Pikermi, female; inverse triangle:* M. pentelicus *from Dytiko; filled tringle:* M. monspessulanus *from Dytiko; asterisk (red):* M. pentelicus*, Suitangba, China, ZT-0528. Data for ZT-0528 are from Jablonski et al. (2020).*

MESOPITHECUS IN AFGHANISTAN

A partial mandible (lacking the ascending rami) and an isolated p3 are known from Molayan, Afghanistan (Figure 44f-h); they are housed in MNHNP (MOL-001 and MOL-002; Heintz et al. 1981). The present study is based on a cast of the mandible MNHNP-MOL-001. The specimen is consistent with a subadult individual, as the canines and m3 are not yet fully erupted. The anterior wall of the symphysis is curved, the planum alveolare inclines abruptly downwards, and the fossa genioglossa is relatively small. The mandibular corpus is characterized by a shallow depth, a feature that is exemplified by *M. pentelicus* from Pikermi (see Figure 16b). The size of the m3 (see Figure 25b) and the monocuspid hypoconulid are comparable to those of *M. pentelicus*. Preliminary analysis of the Molayan fauna has indicated an early-middle Turolian age (Brunet et al. 1984; Heintz and Brunet 1982; Heintz et al. 1981; Sen et al. 1997). Nevertheless, a more thorough investigation and its subsequent comparison with the Aegean and Siwalik faunas indicated that it can be dated to the middle Turolian, MN 12 (Sen 1998). PCA analysis of the dental dimensions of the Molayan mandible, compared with *M. pentelicus*, indicates that the specimen is male (it lacks a canine) and situated within the convex hull of *M. pentelicus* (see Figure 44b). Given its similar morphology and dimensions to the Pikermi sample, it is attributed to *M. pentelicus*.

MESOPITHECUS IN CHINA

In China, *Mesopithecus* is known from the fossiliferous site of Shuitangba, near Zhaotong (southeastern China). Shuitangba is a lignite mine and yielded a rich vertebrate fauna, including several mammals. The mammals suggest a latest Miocene age. Magnetostratigraphic data suggest an age of ~6.4 for the mandible, and proximal femur, while the single calcaneus is slightly older (Jablonski et al. 2011). The age of the Chinese material corresponds to the late Turolian, MN 13 of the European Miocene. More exactly, the deposits can be correlated with the Dytiko deposits of the Axios Valley (Greece), dated to late Turolian between 7.0–6.0 Ma (Koufos and Vasileiadou 2015).

Two species of *Mesopithecus* have been identified at the Dytiko sites—*M. pentelicus* and *M. monspessulanus* (Bonis et al. 1990a; Koufos 2019a, b). PCA analysis was used to compare the dental dimensions of the Chinese mandible with those of *M. pentelicus* from Pikermi and Dytiko, as well as with *M. monspessulanus* from Dytiko (Figure 45). The Chinese mandible belongs to a female individual and has smaller dimensions than *M. pentelicus* from Pikermi. This size difference is also evident in the male specimens from Dytiko. The two *M. monspessulanus* specimens are smaller than the Chinese mandible. Considering the similarities and the similar age of the two localities, the Shuitangba *M. pentelicus* has similarities to that found in Dytiko, Greece.

DISCUSSION-CONCLUSIONS

PALEOGEOGRAHY

The divergence between Old World monkeys and apes is considered as late Oligogene (25.2 Ma) and was traced in the Rukwa Valley, Tanzania (Stevens et al. 2013). Another

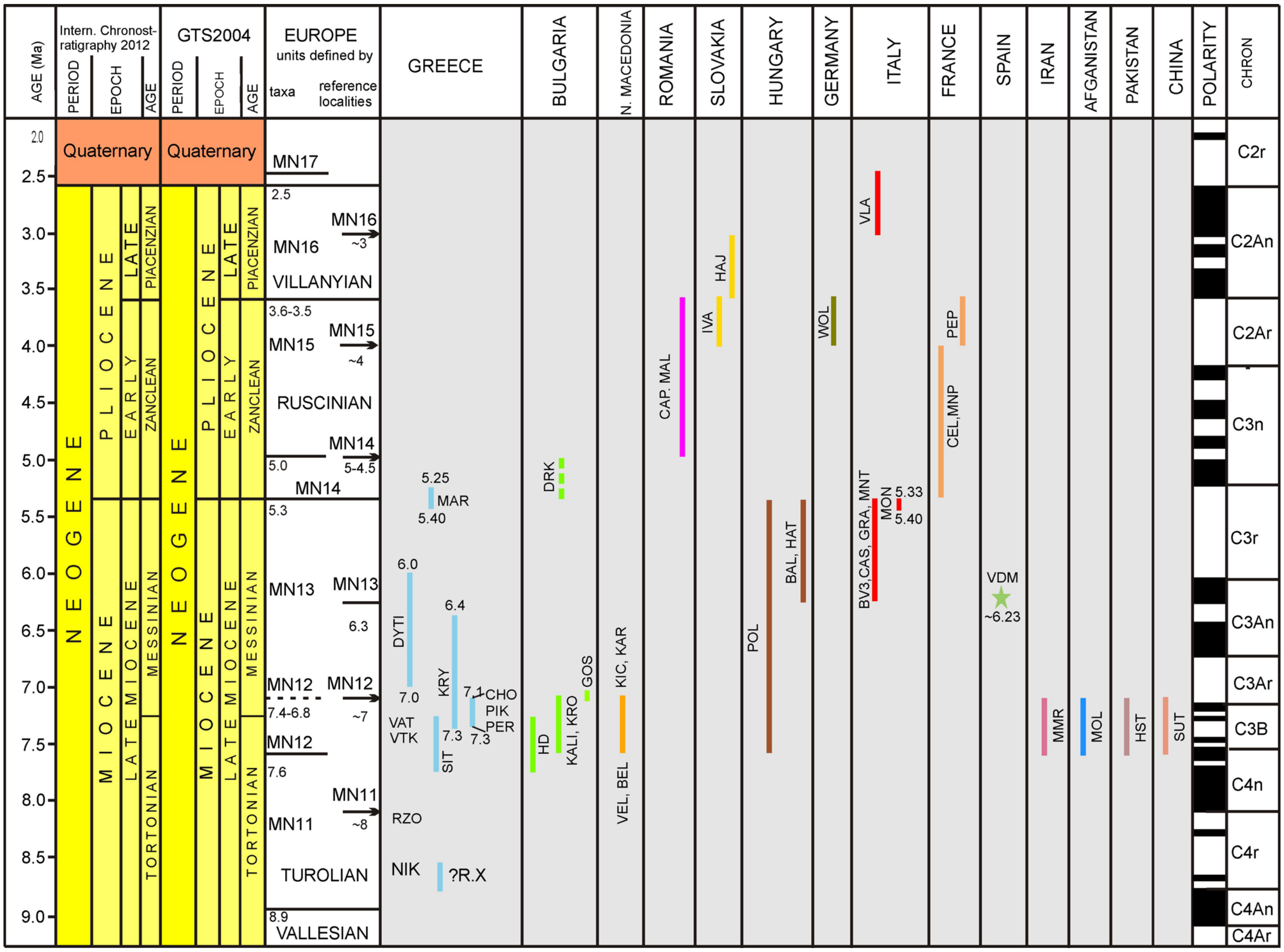

Figure 46. Biostratigraphic table with Mesopithecus*-bearing mammal localities in various Eurasian countries. Abbreviations:* ***BAL****: Baltavar;* ***BEL****: Beluska;* ***BV3****: Baccinello V3;* ***CAP****: Capeni;* ***CAS****: Casino;* ***CEL****: Celleneuve;* ***CHO****: Chomateres;* ***DRK****: Dorkovo;* ***DYTI****: Dytiko localities (DTK, DIT, DKO);* ***GRA****: Gravitelli;* ***GOS****: Gorna Sushitsa;* ***HAJ****: Hasnácka;* ***HAT****: Hatvan;* ***HD****: Hadjidimovo;* ***HST****: Hasnot;* ***IVA****: Ivanovce;* ***KALI****: Kalimantsi (KAL 1, 2, KAL petsata);* ***KAR****: Karaslari;* ***KIC****: Kiro Kucuk;* ***KRO****: Kromidovo 2;* ***KRY****: Kryopigi;* ***MAL****: Malusteni;* ***MAR****: Maramena;* ***MMR****: Middle Maragheh;* ***MNP****: Montpellier;* ***MOL****: Molayan;* ***MON****: Moncucco;* ***MNT****: Monticino Quarry, Brishigella;* ***NIK****: Nikiti 2;* ***PER****: Perpignan;* ***PER****: Perivolaki; PIK. Pikermi;* ***POL****: Polgardi;* ***R.X.****: Ravin X;* ***RZO****: Ravin des Zouaves 5;* ***SUT****: Shuitangba;* ***VAT****: Vathylakkos 3;* ***VTK****: Vathylakkos 2;* ***SIT****: Thermopigi;* ***VDM****: Venta del moro;* ***VEL****: Veles;* ***VLA****: Villafranca d'Asti;* ***WOL****: Wolfersheim. Data sourcesAlba et al. (2015), Delson (1973), Delson et al. (2005), Eronen and Rook (2004), Harisson and Delson (2007), Jablonski et al. (2020), Kelley et al. (2025), Khan et al. (2020), Koufos (2024), NOW (2025), Rook (1999), Sen (1998), and Spassov et al. (2006; 2018; 2019). Chronostratigraphic division from Hilgen et al. (2012).*

recent opinion suggests that the Old World monkeys first appeared in Kenya, Africa, at ~ 22 Ma, early Miocene (Rasmussen et al. 2019), and subsequently migrated to Eurasia during the Late Miocene. Three different migration routes have been hypothesized based on the Late Miocene fossil record of Africa. Route 1 through the Arabia-Sinai Peninsula, Route 2 through the Arabian Peninsula, and Route 3 through Gibraltar and Spain (Gilbert et al. 2014 and references therein). The main representative of the family in the Mediterranean region, *Mesopithecus*, is documented in Eurasia at the beginning of the Turolian. The presence of *Mesopithecus* is also mentioned from the early Vallesian (MN 9) locality of Wissberg (Germany), but it is probably the result of mixing with younger fossils (Andrews et al. 1996). The earliest unequivocal occurrence of the genus in Eurasia is recorded at the locality of Ravin des Zouaves 5 (RZO) in the Axios Valley (Macedonia, Greece) with *M. delsoni* and dated to early Turolian, MN 11; GPTS. ~8.2 Ma (Bonis et al. 1990a; Sen et al. 2000). Furthermore, two metapodials of a size greater than that of *M. pentelicus* have been identified in Nikiti 2 (Greece), which is dated to the beginning of the early Turolian, MN 11 (Koufos et al. 2016a). Based on these data, *Mesopithecus* is present in Europe at least by the beginning of the Turolian. *Mesopithecus* sp., a new morphotype of the genus, appeared at the end of the early Turolian in the Axios Valley. A similar morph also has been found

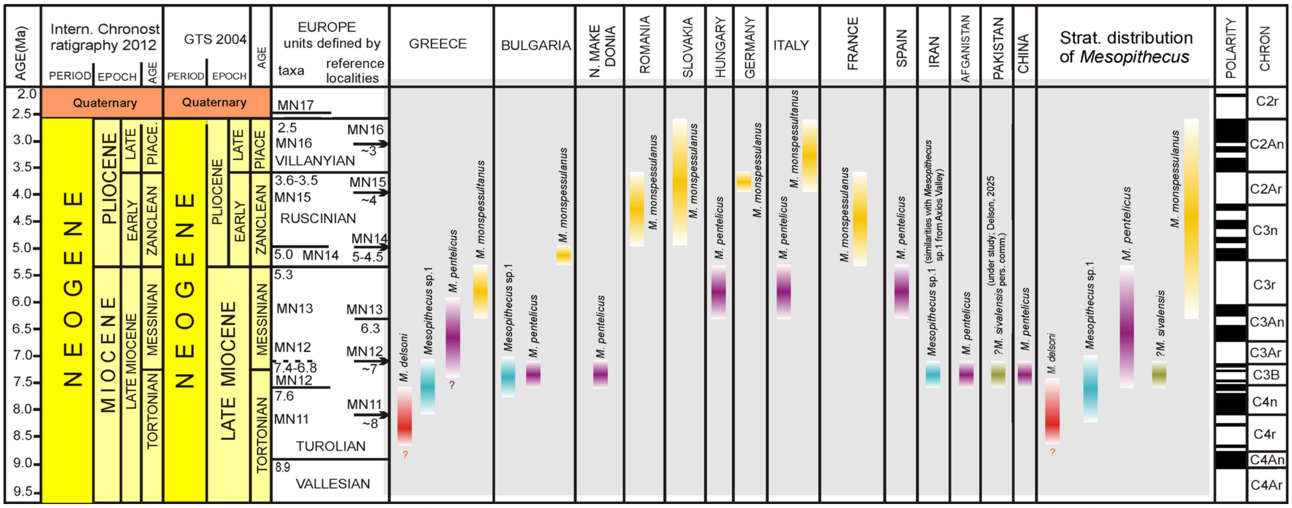

Figure 47. Biostratigraphic distribution of Mesopithecus *species in the different Eurasian countries. Data sources as in Figure 46.*

at the Middle Maragheh, Iran, dated to the early-middle Turolian, MN 11- MN 12; GPTS= 8.2–7.3 Ma (Ataabadi et al. 2016; de Mequenem 1924-25). Considering the above mentioned, *Mesopithecus* arrived in Asia, probably slightly later than in Europe, with a morphotype like *M. delsoni* or *Mesopithecus* sp.

Mesopithecus pentelicus was recognized in the locality Molayan, Afghanistan, dated to the middle Turolian, MN 12 (Heintz et al. 1981; Sen 1998). *Mesopithecus* is also known from the Middle Siwaliks (Indo-Pakistan) since the 19th century (Lydekker 1878). Several scientific expeditions work in the Maragheh collected material since the 19th century, which also includes monkeys (Ataabadi and Foretelius 2016). Later the Maragheh monkey was synomized with *M. pentelicus* (Harrison and Delson 2007), while recently it is referred to as *Mesopithecus* sp. (Kelley et al. 2025). Recently, some isolated teeth were described from Hasnot on the Potwar Plateau of Pakistan as cf. *Mesopithecus* sp.; their age ranges from 7.9 to 7.1 Ma (Khan et al. 2020). The presence of *Mesopithecus* sp. is also mentioned from the Middle Margheh, dated to Upper MN 11- early MN 12 (Ataabadi et al. 2016). The most eastern occurrence of *Mesopithecus* is known from the locality of Shuitangba (Yunan Province, China), (Figure 46) dated back to ~6.4 Ma, corresponding to the late Turolian, MN 13. The Shuitangba *Mesopithecus* was attributed to *M. pentelicus*, but it was a more arboreal form than the typical one from Pikermi as indicated from its postcranial bones (Jablonski et al. 2020).

The westward dispersal of *Mesopithecus* followed a path through Central and Western Europe. The species is known from the middle-late Turolian Hungarian locality of Polgardi (MN 12–13) with *M.* cf. *pentelicus* and the late Turolian ones of Baltavar and Hatvan (Delson 1973; Eronen and Rook 2004; Jablonski et al. 2020). In western Europe, *M. pentelicus* is recorded in the late Turolian, MN 13, of Italy, at the localities of Baccinello V3, Casino, Gravitelli, Moncucco Quarry, and Brishigella (Eronen and Rook 2004; Rook 2009). The youngest species of *Mesopithecus* is *M. monspessulanus*, which appeared in the lower late Turolian, MN 13 (6.0–7.0 Ma) in the Dytiko localities of the Axios Valley, Greece. The Dytiko *M. pentelicus* is a larger form than the typical *M. monspessulanus* from Montpellier, France (Koufos 2019a, b). *Mesopithecus monspessulanus* has been identified in the Ruscinian-early Villafranchian (MN 14-MN 16) in Central and Western Europe (Bulgaria, Slovakia, Romania, Germany, Italy, France, and Spain; see Figure 46) (Alba et al. 2015; Delson et al. 2005; Eronen and Rook 2004). The genus has also been documented in the Red Crag locality of England (Pickford et al. 2023), where the only known M3 was found to be reworked within the Red Crag Formation, derived from a pre-existing layer, and has been identified as *Mesopithecus* sp. by Pickford et al. (2023), while Delson et al. (2005) have designated it as *M.* cf. *monspessulanus.* There is not a certain age for the Red Crag fauna, but Pickford et al. (2023) suggest a possible latest Miocene to Early Pliocene age. Although *Mesopithecus* is mentioned in the Black Sea region from the localities of Grossulovo (southern Ukraine) and Taraklia (Moldova), their determination and age are debated (Koufos 2003). Jablonski et al. (2020) challenged the attribution of the Ukrainian material, i.e., that they might not be primates. The biostratigraphic table (see Figure 46) lists the Eurasian countries, the known localities with *Mesopithecus*, and their age. The total stratigraphic distribution of the different species in each country is given in Figure 47.

The paleogeographic distribution of *Mesopithecus* extends from the Iberian Peninsula to southeastern China but its presence in Asia is rare (see Figure 1a). Although the genus is very common in the southern Balkans (Greece, Bulgaria, North Macedonia), it is absent in Asia Minor and the seashores of the Black Sea except maybe Ukraine and Moldova where its presence is debated. Besides the numerous and rich Turolian faunas of Asia Minor as well as its proximity to the Balkans, *Mesopithecus* is not present in this region. *Mesopithecus* is also absent in the rich Turolian mammal fauna of Samos Island, Greece (Forsyth Major 1894; Koufos and Nagel 2009; Solounias 1981). The possible hypothesis as to the reasons for its absence are mainly paleogeographic and /or climatic. A thorough analysis and comparison of the Turolian faunas from the southern Balkans, Samos Island, and Asia Minor has indicated that they are different, thus constituting two distinct biogeographic sub-provinces (southern Balkans and West Aegean+Asia Minor) within the greater Greco-Iranian or Balkano-Iranian Province (Kostopoulos 2009; Koufos et al. 2009; Vlachou 2013). During the Turolian, the two sub-provinces remained isolated, except for a short period of interaction during the lower part of the middle Turolian, spanning from 7.5 to 7.3 Ma years ago (Kostopoulos 2009). This connection facilitated the exchange of fauna between the two sub-provinces, which likely resulted in the migration of *Mesopithecus* into Asia Minor. The notable similarity between *Mesopithecus* sp. from the Axios Valley and the Maragheh *Mesopithecus* lends substantial credence to the hypothesis that the genus entered Asia Minor. This hypothesis is further substantiated by the observation that *Mesopithecus* sp. emerged in the Axios Valley during the upper early Turolian-lower middle Turolian (upper MN 11-lower MN 12), while the age of the Middle Maragheh *Mesopithecus* ranges between 8.2–7.3 Ma (upper MN 11- lower MN 12) (Ataabadi et al. 2016); this age is in agreement to that of *M. delsoni* and *Mesopithecus* sp. from the Axios Valley, Greece. In contrast, there is no indication that *Mesopithecus* followed a migration path through the northern and eastern shores of the Black Sea, as the presence of *Mesopithecus* in Grossulovo, Ukraine, and Taraklia, Moldova, is debated. The presence of *Mesopithecus* in Molayan (Afghanistan, MN 12) and its similarity to *M. pentelicus* is another piece of evidence that the genus was present in Asia during the Middle Turolian. In the neighbouring area of Indo-Pakistan there is some material of *Mesopithecus* from Hasnot, Dhok-Pathan, which was preliminarily named *Macacus silvalensis* (Lydekker 1878). Later *Macacus sivalensis* was referred to as *?Presbytis sivalensis* with few differences from the European *Mesopithecus* (Szalay and Delson 1979). Furthermore, it is designated as *M. pentelicus* (Harrison and Delson 2007), while recently it is referred to as *Mesopithecus* sp. (Kelley et al. 2025). The material is fragmentary, and it is not possible to check its relationships with European material. The last and youngest presence of *Mesopithecus* is known from the late Turolian of southern China and has been attributed as a more arboreal form of *M. pentelicus* (Jablonski et al. 2020). A similar *Mesopithecus* morphotype is also known from the late Turolian localities of Dytiko, (Axios Valley, Greece (Bogdanova et al. 2023; Koufos 2019b)). The significant similarity of the known Asian *Mesopithecus* with the European species indicates that they originate from Europe, as the older European *Mesopithecus* is dated to the beginning of the Turolian (~8.7 Ma) and the oldest Asian *Mesopithecus* is Maragheh (8.2–7.3 Ma). The hypothesis advanced by Gilbert et al. (2014) concerning the potential migratory route 2 (through the Arabian Peninsula) appears to be unconvincing, due to the paucity of extant data. Despite the discovery of two isolated teeth of cercopithecids in Abu Dhabi (Gilbert et al. 2014; Hill and Gundling 1999), no further evidence has been found to suggest that the route continued to Asia. It is possible that further data may be obtained through a comprehensive study of the Middle Maragheh material.

BIOSTRATIGRAPHY

The extensive geographic distribution of the genus *Mesopithecus* throughout Eurasia during the Late Miocene-early Pleistocene can be utilized for the biostratigraphy of the continental deposits in this region. Based on the data available at that time, the genus appeared in Eurasia at the beginning of Turolian, approximately at ~8.7 Ma ago (see Figure 47). The earliest identified species is *M. delsoni*, known from the Axios Valley locality Ravin des Zouave 5 (early Turolian, MN 11; GPTS= ~8.2 Ma) and possibly from Nikiti 2 dated to the beginning of Turolian. A new morphotype *Mesopithecus* sp. emerged in the upper part of the early Turolian. It exhibited a mixed morphology, sharing characteristics of both *M. delsoni* and *M. pentelicus* and persisted until the upper middle Turolian, MN 12. The type species, *M. pentelicus*, appeared in the middle Turolian, MN 12, and survived to the end of Miocene MN 13. The last representative of the genus is *M. monspessulanus*, known from the late Turolian, MN 13, to the end of the Pliocene (see Figure 47).

PALEOHABITAT

The habitat of *Mesopithecus* has been a subject of investigations since its discovery at Pikermi in the 18th century. Several publications have attempted to infer its way of life, locomotion, and food preferences. Gaudry (1862-67) reported *Mesopithecus* as being more terrestrial than arboreal, but there was a paucity of data to support this conclusion. Gabis (1961) suggested a terrestrial way of life for *Mesopithecus*, based on the hind limb proportions of this species. However, subsequent comprehensive research on *Mesopithecus* has indicated that certain morphological characteristics and proportional indices of the hind limb suggest a semiterrestrial lifeway (Delson 1973; Szalay and Delson 1979). Notably, these authors excluded *M. monspessulanus* and the latest *M. pentelicus*, for which they proposed a more arboreal lifeway. The term ''semiterrestrial'' denotes an animal that spends a significant part of its day on the ground in pursuit of sustenance but also utilizes arboreal habitats for finding food and refuge from predators. This behaviour suggests a dynamic relationship between terrestriality and arborealism in *Mesopithecus*, underscoring the need for a comprehensive examination of the paleoenvironmental conditions that once characterized its habitat.

Mesopithecus is mainly a Turolian taxon, and a comparison of the Turolian faunas with contemporary faunas from specific environments, using multivariate methods can furnish some evidence to determine the paleoecology (e.g., Bonis et al. 1992a, b; Geraads 2003; Kostopoulos 2009; Koufos 2006b; Koufos et al. 2006b; Sen et al. 1994). For this comparison, Correspondence Analysis was employed, utilizing

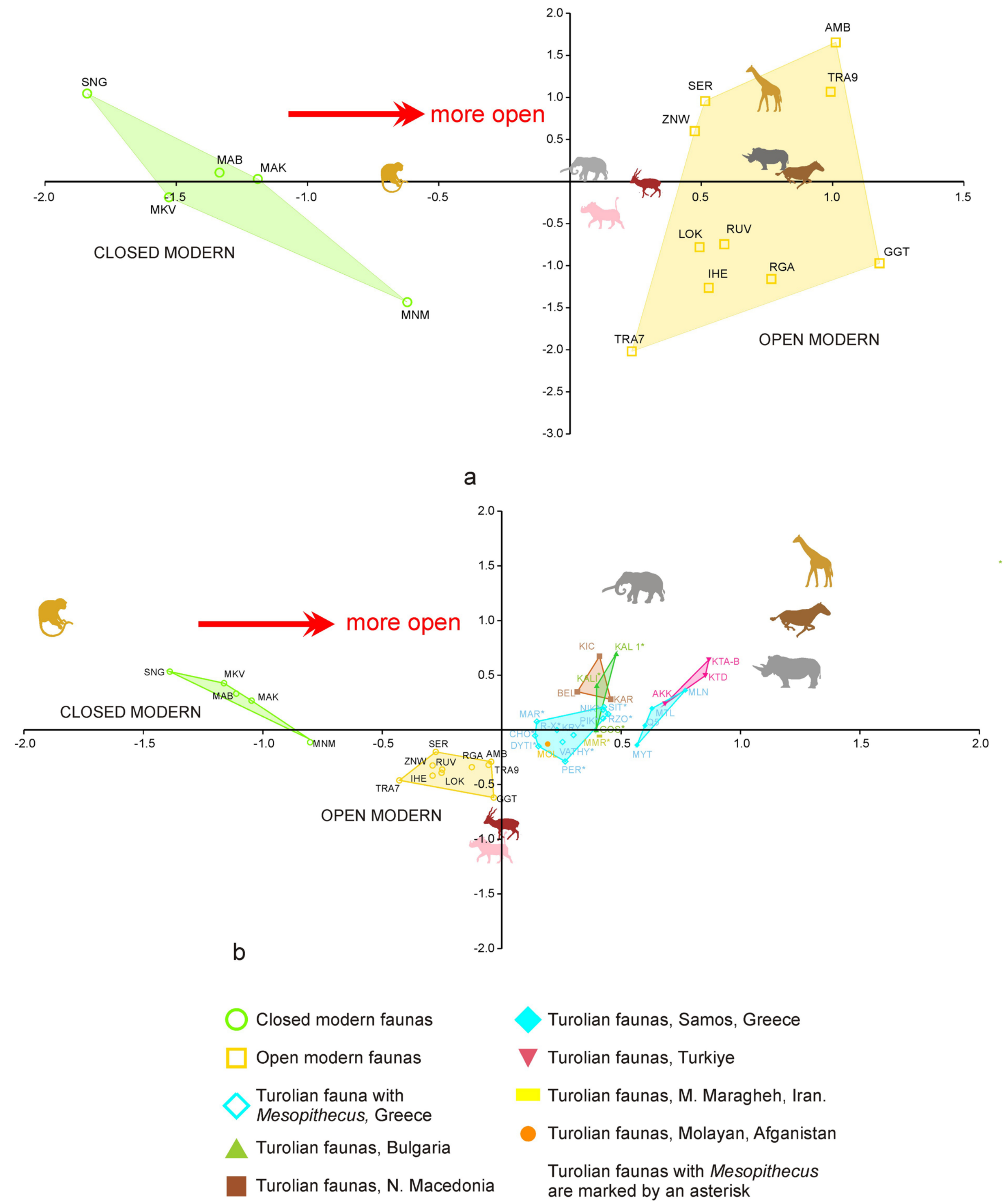

Figure 48. Correspondence Analysis of the Turolian mammal faunas from Eurasia with and without Mesopithecus *in comparison with modern faunas from known environments. Modern faunas: AMB: Amboseli; GGT: Golden Gate: IHE: Ihema; LOK: Lokori; MAB: La Maboke; MAK: Makokou; MKV: Mont Kiwu; MNM: Mont Nimba; RGA: Region Gabiro; RUV: Rukwa Valley; SER: Serengeti; SNG: Sangmellina; TRA7: Transvaal-7; TRA9: Transvaal-9; ZNW: Zinawe. Data source Legendre (1989). Fossil faunas:* ***AKK****: Akkasdagi;* ***BEL****: Beluska;* ***CHO****: Chomateres;* ***DYTI****: Dutiko 1, 2, 3;* ***GOS****: Gorna Sushitsa;* ***KAL 1****: Kalimantsi 1;* ***KALI****: Kalimantsi (1, 2, petsata);* ***KAR****: Karaslari;* ***KIC****: Kiro Kucuk;* ***KRY****: Kryopigi;* ***KTA-B****: Kemiklitepe- A, B;* ***MAR****: Maramena;* ***MMR****: Middle Maragheh;* ***MLN****: Mytilinii 4;* ***MOL****: Molayan;* ***MTL****: Mytilinii 1;* ***MYT****: Mytilinii 3;* ***NIK****: Nikiti 2;* ***PER****: Perivolaki;* ***PIK****: Pikermi;* ***Q5****: Samos Quarry 5;* ***R.X.****: Ravin X;* ***RZO****: Ravin des Zouaves 5;* ***SIT****: Thermopigi;* ***VATHY****: Vathylakkos 2, 3. Data sources Kostopoulos and Bernor (2011), Koufos (2024), Sen (1998), Spassov et al. (2006; 2018; 2019).*

the number of taxa in each mammal group (families and classes). The employed groups are the most prevalent ones in the Turolian faunas. The comparative material includes five modern faunas inhabiting arboreal habitats (′′closed′′ faunas) and nine faunas inhabiting open savannah-type areas (′′open faunas′′). The fossil faunas are divided into two groups, based on the presence or absence of *Mesopithecus*. Most of the fossil faunas containing *Mesopithecus* originate from the Southern Balkans, Iran, and Afghanistan, while the remainder are from Greece (Samos Island) and Turkey.

The modern faunas were analyzed separately to ascertain whether the method can distinguish between ′′closed′′ and ′′open′′ faunas. The results indicate that axis 1 can separate the ′′closed′′ and ′′open′′ modern faunas on the left and right parts of axis 1, respectively. This position of the faunas indicates an increase in the open character from the left to the right (Figure 48a). The incorporation of fossil faunas into the analysis yielded a plot that effectively differentiates the modern (left) from the fossil (right) faunas. The fossil faunas were positioned on the right side of axis 1, parallel to the modern open faunas, suggesting an open paleoenvironment during the Turolian (Figure 48b). The faunas containing *Mesopithecus* were distinctly separated from those devoid of *Mesopithecus* and situated to the right of them. This suggests a drier and more open environment in the western Aegean region and Asia Minor (see Figure 48b). This may be the reason for the absence of *Mesopithecus* from the known Turolian localities of Samos Island (Greece) and Asia Minor (see Figure 47). The faunas of the Middle Maragheh and Molayan are like those including *Mesopithecus*, indicating an open and dry paleoenvironment. Recent studies on the microwear of *Mesopithecus* teeth suggest that this species was a widespread opportunistic feeder living in savannah-like habitats (Merceron et al. 2009). Recent morphometric analyses of known postcranial material from Greece and Bulgaria suggest semiterrestrial activities that became more arboreal towards the end of the Miocene (Bogdanova et al. 2023; Youlatos 2003; Youlatos et al. 2010; 2012). Considering all the above, *Mesopithecus* lived in open and dry environments such as savannah grasslands or savannah bushlands with grass and scattered small trees.

The body mass of *Mesopithecus* is subject to variation depending on the method employed. A comprehensive analysis of the body mass of cercopithecidae was conducted by Delson et al. (2000). The mean body mass of *M. pentelicus* from Pikermi has been estimated to be 11.0kg for males and 8.0kg for females, based on the postcranium. Using the dentition, the same values are recorded as 14.0kg and 11.0kg for males and females, respectively. This suggest that *Mesopithecus* was a megadont taxon like many extant colobines. The mean estimated body mass for *M. monspessulanus* is 10.5kg for males and 7.5kg for females, as determined by Delson et al. (2000) using dentition.

CONCLUSIONS

In conclusion, *Mesopithecus* was a widespread colobine that lived throughout Eurasia, from Spain to China. It possibly originated from an Early Miocene African colobine and arrived in Eurasia during the Late Miocene. It was more prevalent in Europe than in Asia, particularly in the southern Balkan Peninsula (see Figure 1). Three species of the genus have been identified—*M. pentelicus* (type species), *M. delsoni*, and *M. monspessulanus*. Another possible species, *M. sivalensis*, has been identified in the Siwaliks (Indo-Pakistan), but its specific status is unclear (Harrison and Delson 2007; Kelley et al. 2025). Additionally, another morphotype with mixed "pentelicus" and "delsoni" characteristics has been found in the Turolian deposits of the Axios Valley and is referred to as *Mesopithecus* sp. The widespread nature of *Mesopithecus* and its species found in the Axios Valley provide certain biochronological data, which helps with biostratigraphy. The genus first appeared in Eurasia at the beginning of the Turolian (latest Miocene) and survived until the end of the Pliocene (see Figure 47). During the Turolian, *Mesopithecus* lived in savannah-like environments, whereas the more arboreal *M. monspessulanus* was common in the Pliocene.

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CONFLICT OF INTEREST

I have no conflict of interest to declare.

DATA AVAILABILITY

No restrictions on data availability.

SUPPLEMENTARY MATERIAL

- Supplement 1. History and geological background of the Pikermi locality.
- Supplement 2. History and geological background of the Axios Valley localities.
- Supplement 3. History and geological background of the Maramena locality, Serres Basin.
- Supplement 4. Measurements of the Pikermi material.
- Supplement 5. Collection of *Mesopithecus pentelicus* from Pikermi, housed at the Athens Museum of Palaeontology and Geology (AMPG).
- Supplement 6. Collection of *Mesopithecus pentelicus* from Pikermi, housed at the Muséum Nationale d'Histoire Naturelle Paris (MNHNP).
- Supplement 7. Collection of *Mesopithecus pentelicus* from Pikermi, housed at the Natural History Museum

of London (NHML).

- Supplement 8. Collection of *Mesopithecus pentelicus* from Pikermi, housed at the Staatliche Naturwissensaftische Sammlungen Bayerns-Bayerische Staatssammlung für Paläontologie und Geologie, München (SNSB-BSPGM).
- Supplement 9: Collection of *Mesopithecus pentelicus* from Pikermi, housed at Naturhistorishes Museum, Wien (NHMW) and the Paläontologisches Institut, Universität Wien (PIUW).
- Supplement 10. Collection of the material from the Axios Valley, housed at the Laboratory of Geology and Palaeontology, Aristotle University of Thessaloniki (LGPUT) and the Muséum Nationale d'Histoire Naturelle Paris (MNHMP).
- Supplement 11. Collection of *Mesopithecus* sp. from from Perivolaki, housed at the Laboratory of Geology and Palaeontology Aristotle University of Thessaloniki (LGPUT) and *Mesopithecus pentelicus* from Maramena, housed at Athens Museum of Palaeontology and Geology (AMPG).

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Supplement 1 to The Late Miocene Colobine Monkey *Mesopithecus* (Primates, Cercopithecidae) of Greece

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SUPPLEMENT 1

This supplement contains: text and references for the history and geological background of the Pikermi locality.

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Supplement 1: The Late Miocene colobine monkey *Mesopithecus* (Primates, Cercopithecidae) of Greece

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SUPPLEMENT 1: HISTORY AND GEOLOGICAL BACKGROUND OF THE PIKERMI LOCALITY

This file includes: text

History

The Pikermi fossil-bearing site was discovered in 1836 by the Scottish historian G. Finlay, who was exploring the Mesogea region for archaeological evidence. He collected some bones, which were given to the newly founded Physiographic Society of Athens. Later, G. Finlay and the German A. von Lindermayer collected more material from the Pikermi ravine. During excavations in the area, a Bavarian soldier of King Otto discovered bone agglomerates with calcite crystals formed in the bone's cavities. He considered them to be diamonds, and he took the bones to Munich and gave them to Prof. A. Wagner, who studied them. Another story says that a soldier working in Finlay's group found the fossils and brought them to München. Among the fossils was the first primate found in Greece, a monkey, described under the name *Mesopithecus pentelicus* Wagner, 1839; this specimen is the holotype of the genus and species. The Greek geologists Prof. H. Mitzopoulos and Prof. Th. Skoufos, as well as the physician A. Chaeretis, excavated at Pikermi and the collected material is stored at AMPG in the University of Athens. Several foreign palaeontologists, (e.g. R. Roth, A. Chaeretis, A. Gaudry, W. Dames, A. S. Woodward, and O. Abel), excavated at Pikermi ravine in the following years and took the fossils to their countries. The last excavation was conducted by Abel in 1911, and till 2008, no one worked at the classical site of Pikermi. After a long gap, the University of Athens started in 2008 a new fieldwork campaign at the classical site of Megalo Rema, which continues till now. The preliminary results of this campaign are presented in Theodorou et al. (2010), Roussiakis et al. (2019), and Filis et al. (2019).

As previously stated, the Pikermi material is stored in various European museums and institutes, while some small collections or isolated specimens dispersed throughout. Some of these specimens are relatively unknown to the palaeontological community and are only discovered incidentally in different museums. For instance, the Museum Cuvier in Montbéliard (France) houses a partial cranium with the dentition of *Mesopithecus* that preserves the dentition, which was described recently (Costeur and Malvessy 2010). In AMPG at the University of Athens there is a large collection of *Mesopithecus* (S5) but the largest is Gaudry collection at the MNHNP, which includes several specimens (S6). Smaller collections can be found in London (NHML; S7) in München (SNSB-BSPGM; S8), Vienna (NHMW; S9), the Palaeontological Institute of the University of Vienna (PIUW; S9), the University of Cambridge in England, the Swedish Museum of Natural History in Stockholm (SMNWS), the Museum Cuvier in Montbeliard, France, and the Geo-Palaeontological Museum of Natural Sciences at the University of Turin, Italy. It is possible that there are additional specimens in other collections that were not found or require "new excavations" in the museum's collections or stores.

The Pikermi collection has been a valuable source of information on the Late Miocene fauna of southeastern Europe since the mid-19th century. Numerous new genera and species have been identified, and terms such as "Pikermian fauna", "Pikermian chronofauna", and "Pikermian biome" are commonly used in the literature. However, the main issue with the old Pikermi collections is the lack of clear information regarding the localities and their stratigraphy. Gaudry (1862-67) provides information about the excavation site, and it is possible that his collection originates from a single location. The recent excavations in Pikermi suggest that the fauna of the new collection is similar to the old one, indicating that they likely originated from the same locality (Filis et al. 1919). However, the issue of stratigraphy remains unresolved due to the presence of several fossiliferous lenses in different horizons, as shown in a photograph by Abel (1922: figure 132). Additional data for more accurate stratigraphy is expected from the new investigations at Pikermi.

Geological Background and age

Pikermi is situated in the Mesogea basin of Attica, approximately 20 km from Athens city, in a ravine called Megalo Remma, located in the foothills of Pentelikon Mountain (Figures 2, 19 in the main text). According to Gaudry (1862-67: plate 74, figure 1), the basement is composed of alternating red clays and conglomerates-agglomerates with intercalations of red clays. The conglomerates are composed of marble, limestone, and quartz pebbles from the basement. The red clays are either sandy or clayey, and sometimes they are transformed into sandstones. The fossiliferous site where A. Gaudry excavated is located into the red clays at the bottom of the ravine (Gaudry1862-67: plate 74, figures1-3). According to Marinos and Symeonidis (1974), the Neogene deposits of Pikermi uncomformably overlay the marbles and schists of the basement. The deposits consist of three lithological units, from bottom to top: a) Basal Beds, fluviatile, loose-cohesive conglomerates, sandstones, marls and clays with all intermediate lithological types; b) Fossiliferous Beds, fluvial-fluviolacustrine deposits, consisted of reddish clays with large mammals, alternated with conglomerates, sandstones and marshy clays (the latter contains micromammals and lacustrine gastropods); c) Calcareous Beds, lacustrine, white yellowish to brownish limestones and marls with conglomerates containing *Melanopsis* and *Planorbis*, which overlay all above deposits in the whole area; and d) Quaternary Conglomerates covering the Neogene deposits.

The Pikermi Upper Miocene deposits were recently studied and divided into two formations: a) the Pikermi Formation, which consists of red terrestrial alluvial sediments deposited unconformably on the basement limestones, and b) the Rafina Formation, which consists of palustrine to lacustrine clays, coals, and platy limestones. Furthermore, the Pikermi Formation is divided into two members: a) the Red Conglomeratic Member, which is composed of alternating red silts and channel deposits (conglomerates and sandstones) that are 20 m thick, and b) the Chomateri Member, which consists of alternating reddish-yellowish silts with fluvial channel and channel-fill deposits that are approximately 7m thick (Böhme et al. 2017; Roussiakis et al. 2019). All fossil collections from Pikermi are sourced from the Red Conglomeratic Member, which is currently being excavated by the University of Athens (Filis et al. 2019 and references therein).

Various opinions have been expressed regarding the formation of fossiliferous lenses at Pikermi. Neumayer (1887) argued that a prolonged drought during the Late Miocene led to the death of many animals, particularly herbivores. Then, during the rainy season, the water collected and carried the bones and red clays, which combined to form the fossiliferous lenses. Lepsius (1893) suggested that there were several small lakes in the Pikermi area, and that the red clay found there are lacustrine deposits. The animals living in the area would go to the lakes for water, and the carnivores would attack and kill them, leaving behind various fossiliferous lenses. Abel (1922) proposed that an extensive fire in the Pikermi area caused the death of several animals. As they fled in fear along the slopes of the surrounding hills, they fell into the ravines and were killed. The water carried their bones and concentrated on certain points, forming fossiliferous lenses. According to Symeonidis et al. (1979), the lenses were likely formed by the water carrying red clays and the remains of animals that died during the dry period, which were then concentrated in the lower and deeper points, forming small water spots. The animals went to these spots for water and were killed by carnivores and their remains contributed to the formation of the lenses. During rainfall's period, these seasonal basins are filled with water carrying clays and bones. The small movements of the water collected all the bones and formed the fossiliferous lenses. This perspective is supported by a well-documented dry period during the middle Turolian (Bonis et al. 1992; Koufos 2006c; Kostopoulos 2009) and can explain: a) the mixing of bones from different taxa and individuals, b) the presence of several bone fragments; the bones were broken either during the carrying process or by the carnivores, c) the presence of bite marks on the bones from the carnivore's action, d) the lenticular shape of the fossil concentrations, and e) the presence of some fish and amphibians in the fauna (Gaudry 1862-67). Various authors have compiled faunal lists of Pikermi, including taxa of mammals, fishes, reptiles, and birds. Koufos (2024) provides the most recent list of mammal taxa, which is primarily based on Gaudry's collection and recent references on the Pikermi fauna.

The dating of Pikermi has been a topic of debate among palaeontologists for a long time. Initially, Pikermi dated to the Pontian stage, which corresponds to Late Miocene-Early Pliocene timespan. Several red clay deposits in Greece and neighboring countries were considered isochronous to Pikermi. However, during the last 50 years there has been a division of the continental Mediterranean Neogene into several biozones based on mammals. Consequently, it has become necessary to place Pikermi within this system. The main problem for this concerns the mammal fauna, as it is unclear whether it represents a single or mixed chronofauna. This has led to differing opinions on the age of Pikermi.

In the initial biozonation of the continental Mediterranean Neogene, Pikermi is referred to the European mammal biozone MN 12 together with Samos Q1-4, "Salonique", Tito Veles, Kücükcekmece, Çobanpinar and Garkin (Mein 1975). This dating of Pikermi remained until the end of the 1980's when a revision of the biozones was given and Pikermi was correlated with the end of the biozone MN 12 (Mein 1975, 1989, 1999; de Bruijn et al. 1992). Another opinion correlates Pikermi to the MN 11/12 boundary, corresponding to 8.3-8.2 Ma (Bernor et al. 1996). The age of Pikermi is also discussed later and again proposed a correlation with the upper part of MN 12 (Koufos 2013 and ref. therein). Recent magnetostratigraphic study of the Pikermi Formation provided interesting results about the age of the fauna. The results imply for the Pikermi Fm an age between ~7.4 and ~7.0 Ma, while the levels including the classical fauna of Pikermi can be dated between 7.25-7.10 Ma (Böhme et al. 2017).

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Supplement 2 to The Late Miocene Colobine Monkey *Mesopithecus* (Primates, Cercopithecidae) of Greece

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SUPPLEMENT 2

This supplement contains: text and references for the history and geological background of the Axios Valley localities.

Supplement 2: The Late Miocene colobine monkey *Mesopithecus* (Primates, Cercopithecidae) of Greece

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SUPPLEMENT 2: HISTORY AND GEOLOGICAL BACKGROUND OF AXIOS VALLEY LOCALITIES

This file includes: text

History

The mammal localities of Axios Valley were discovered by the French geologist Camille Arambourg in 1915-16. C. Arambourg arrived in the area as an army officer during the First World War. The French army camped around the village of Vathylakkos (formerly Vatilük) and during excavations to make trenches for protection, they found some mammal fossils. Subsequently, C. Arambourg conducted further exploration and identified several fossil-bearing sites. He undertook excavations and collected fossils from six different localities in Axios Valley, in addition to one locality designated as Falaise de Karabouroun (it is known as Megalo Emvolon today) in the vicinity of the eastern end of the Thermaikos Gulf (Koufos et al. 1991), situated approximately 32 km from Thessaloniki City. The Arambourg localities were as follows: Ravin X (R.X), Ravin des Zouaves (R.Z), Ravin Ar (R.Ar), Ravin C (R.C), Ravin de Vatilük or Ravin G (R.G), and Ravin de Konikovo (Figure 13 in the main text; yellow circles). The last locality is situated in the vicinity of the village of Dytiko (formerly known as Konikovo), with the rest located around the villages of Vathylakkos, Nea Messimvria and Agioneri (Arambourg and Piveteau 1929). Further details regarding the Arambourg localities and their age are given in Koufos (2022). The "Arambourg collection" was initially transported to Algeria and then via Marseille to Paris, where it is currently housed at the MNHNP. The collection was studied later and published in the monograph "Les Vertébrés du Pontien de Salonique" (Arambourg and Piveteau 1929).

The primates are represented in the "Arambourg collection" by the genus *Mesopithecus*. Among the available material, there are some mandibular remains (S10, Figures 14-17), which were partially described but not figured by Arambourg and Piveteau (1929) as *M. pentelici*. Addiotionally the collection of MNHNP contains a cranial fragment, a right maxillary fragment, and some isolated teeth, which are mentioned as the "Braillon collection" (S10, Figures 18-19). The specimens in question appear to have been collected relatively recently by an unskilled person. Its fossilization type indicates that the material originated from the new locality of Axios Valley Vathylakkos 2 (VTK).

Since 1972, no further excavations have been conducted in the localities of Axios Valley. Some sporadic fragments of bones, discovered by villagers, have been deposited at the University of Thessaloniki. In 1972, the Laboratory of Geology and Palaeontology of the University of Thessaloniki (Prof. J. K. Melentis) and the Laboratoire de Paléontologie des Vertébrés et Paléontologie Humaine, Université Paris VI and later Université Poitiers (Prof. L. de Bonis) initiated a field campaign in the Axios Valley, which was subsequently continued. The author was included to this team in 1976, assuming responsibility for the excavations and study of fossils. Following the retirement of Prof. Melentis, he continued the collaboration with L. de Bonis. During the new excavations in the Axios Valley, several localities were discovered (Figure 13 in the main text; red circles), and a great number of fossils were collected. The primates included in this collection comprise several specimens of *Mesopithecus*, which were recovered from the different localities of the Axios Valley (S10, Figures 1-13). In addition to *Mesopithecus*, the hominoid *Ouranopithecus macedoniensis* was also found at two Axios Valley localities: Xirochori 1 and Ravin de la Pluie (Bonis et al. 1974, 1990b).

Geological background and localities

The Axios Valley belongs geotectonically to the Axios Zone and more precisely to the Peonias subzone. The basement consists of ophiolites, ophiolitic conglomerates, schists, marbles, and granitic intrusions (Mercier 1966). During Eocene-Oligocene started the filling of the basin with marine deposits and continued till the beginning of Early Miocene. The deposition continued with brackish deposits during the Middle-Late Miocene and followed by fluvio-terrestrial deposits in the Late Miocene-Early Pleistocene (Christodoulou 1965; Kalkreuth et al. 1991).

Three different formations have been distinguished in the Late Miocene deposits of the lower Axios Valley:

a) Nea Messimvria Fm, comprising of reddish-brownish sands, gravels, compact to lose conglomerates, and clays. This formation is thick, more than 1km according to Mercier (1966). Four different mammalian localities have been found in the upper part of Mea Messimvria Fm, named Pentalophos 1 (PNT), Xirochori 1 (XIR), Ravin de la Pluie (RPl) and Ravin des Zouaves 1 (RZ1), (Figure 13 in the main text). The biochronological and magnetostratigraphical data allowed us to date them. Pentalophos 1 is correlated with the upper part of the early Vallesian (MN 9), Xirochori 1 with the lower part of the late Vallesian (MN 10; GPTS= ~9.6 Ma), Ravin de la Pluie and Ravin des Zouaves 1 with the upper part of the late Vallesian (MN 10; (GPTS= ~9.3 Ma) (Koufos 2013, 2024 and ref. therein). Concerning the old localities of Arambourg, Ravin des Zouaves (R.Z) is within Nea Messimvria Fm and can be correlated with Ravin de la Pluie. The locality Ravin X (R.X) could be within the Nea Messimvria Fm or to the younger Vathylakkos Fm (Koufos 2022), (Figure 13 in the main text).

b) Vathylakkos Fm, normally overlain Nea Messimvria Fm and consists mainly of yellowish marls at the base followed by whitish-grey sands, sandy marls, gravels and clays with crossbedding in some parts. Five mammal fossiliferous sites have been found in Vathylakkos Fm: Ravin des Zouaves 5 (RZO), Prochoma 1 (PXM), and Vathylakkos 1, 2, 3 (VLO, VTK, VAT) (Figure 13 in the main text). The faunal data and the magnetostratigraphy suggested that Ravin des Zouaves 5 is correlated with the early Turolian (MN 11; ~8.2 Ma), Prochoma 1 with the middle Turolian (MN 12; GPTS= ~7.4 Ma), and Vathylakkos 1, 2, 3 with the middle Turolian (MN 12; GPTS= ~7.3 Ma) (Koufos, 2013, 2024 and ref. therein). The localities of Arambourg belonging to Vathylakkos Fm are: Ravin Ar (R.Ar) which can be correlated with Ravin des Zouaves 5; Ravin C (R.C) is possibly correlative with Vathylakkos localities, while Ravin de Vatilük or Ravin G (R.G) is the same as Vathylakkos 3 (VAT) (Koufos 2022).

c) Dytiko Fm, it outcrops in the western bank of Axios river (Figure 16 in the main text), no evidence for the presence of the older formations in this part of the valley. In the geological map of the area, it is mentioned a large fault across the Axios river, recognized by geophysical prospecting (EAGME sheet Thessaloniki, 1:50.000). This fault probably cannot allow to follow the deposits and to see the contact between

Vathylakkos and Dytiko Fm. This formation consists mainly of whitish-yellowish and grey sands, gravels, sandy marls, clays and in the top fresh-water tuffaceous limestones. Three different localities have been found around the village of Dytiko and across the stream Platanoremma, Dytiko 1, 2, 3 (DTK, DIT, DKO) (Figure 13 in the main text). The fauna of these localities suggests that can be correlated with the late Turolian (MN 13); more precisely the fauna is post-Messinian with an age ranging between 7.0-6.0 Ma (Koufos and Vasileidadou 2015). The Arambourg's locality Ravin de Konikovo corresponds to Dytiko 1 (Figure 13 in the main text).

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Supplement 3 to The Late Miocene Colobine Monkey *Mesopithecus* (Primates, Cercopithecidae) of Greece

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SUPPLEMENT 3

This supplement contains: text and references for the history and geological background of the Maramena locality, Serres Basin.

Supplement 3: The Late Miocene colobine monkey *Mesopithecus* (Primates, Cercopithecidae) of Greece

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SUPPLEMENT 3: HISTORY AND GEOLOGICAL BACKGROUND OF MARAMENA LOCALITY, SERRES BASIN

This file includes: text

History and geological background

As there are many publications on the stratigraphy of the Serres Basin (North Greece) scattered throughout various sources (some of which are in Greeks), it is considered necessary to provide a summary of the stratigraphy of the Maramena fossiliferous site, as well as some historical data. In the 1970s, the Neogene deposits of the Serres Basin (Macedonia, Greece) were the subject of a uranium exploration project in northern Greece. The project involved the investigation of several physical and artificial sections to study the stratigraphy of the basin. Concurrent with these excavations, new fossiliferous sites were discovered within the Neogene deposits (Armour-Brown et al. 1977). The initial published results of the project documented seven fossil sites containing micromammals. Subsequent years have seen the efforts of a team of paleontologists from the University of Athens and the University of Utrecht in the area, who have conducted surface collections. During that time different faunal lists for these localities have been published (e.g. Steffens et al. 1979; de Bruijn and van der Meulen 1979; Karystineos 1984). In 1986, H. de Bruijn (Utrecht University), K. Doukas (Athens University), and N. Schmidt-Kittler (Mainz University) conducted research in the region north of Serres and discovered the locality of Maramena. In the subsequent two years (1987-1988), an extensive excavation was conducted at the site, resulting in the discovery of a remarkably diverse collection of fossil mammals. One year later de Bruijn (1989) presents the preliminary data from the study of the micromammals. Finally, the complete study of the Maramena fauna was given in a separate volume of Münchner Geowissenschaftlishe Abhandlungen (Schmidt-Kittler, Ed. 1995).

The Neogene deposits north of Serres are divided into three informal formations (Armour-Brown et al. 1977). In the following, the term "lithostratigraphic unit" will be used instead of the term "informal formation". The three recognized lithostratigraphic units of the Neogene deposits are as follows:

- Lefkon Lithostratigraphic Unit. It constitutes the basal stratum that overlies the basement. This unit is characterized by a polymict conglomerate that is poorly sorted, comprising pebbles of schist, gneiss, and granite. It is succeeded by well sorted siltstones, sandstones, and mudstones. Two breccias occur within the upper parts of the formation: the lower consists primarily of pebbles from metamorphic rocks, while the upper is composed mainly of granitic pebbles.
- Ceorgios Lithostratigraphic Unit. It overlies conformably the Lefkon one and consists of calcareous sandstones, silts and sandy limestones and includes marine and brackish faunas. A granitic breccia occurs locally within this unit.
- Spilia Lithostratigraphic Unit. It composed of sands, marls with lignites and overlied the Georgios unit. The upper part of the unit consists of poorly shorted conglomerate, fanglomerate and Vamvakofiton travertine.

Subsequent research in the area provided another more detail division of the Neogene deposits, which were divided into two formal groups and various informal formations (Karystineos 1984):

- Lefkonas Group, which was divided into four informal formations (Conglomerate Fm, Lefkonas sandstone Fm, Lignitic Fm, and Red-beds-Breccia Fm).
- Georgios Group divided into three informal formations (Georgios calcareous sandstone Fm, Spilia fine-grained sandstones Fm, Micro Strogilo conglomerate Fm and travertines at the top.

The fossiliferous site of Maramena is located within the Lefkon Unit (Armour-Brown et al. 1977) or the Perdikari Lignitic Member (Karystineos and Ioakim 1989). The locality is situated 7 km north of Christos village, in the eastern wall of a small valley that opens to the Strymon plain. The fossiliferous horizon is a sandy marl with a thickness of approximately two metres, which is exposed at the base of the Maramena pit. This bed is overlain by medium to coarse-grained sand with lignitic intercalations (Schmidt-Kittler et al. 1995). Maramena has yielded a rich mammal fauna, including mainly micromammals; additionally, invertebrates, amphibians and reptiles are also found (Schmidt-Kittler et al. 1995; Koufos 2024 and ref. therein). Furthermore, a flora comprising pollen and spores has been described in Maramena sediments, encompassing at least eleven taxa (Karystineos and Ioakim 1989).

The first reference to the age of the Lefkon lithostratigraphic unit was based on a preliminary collection from its upper part, including a small number of micromammals (determined by H. de Bruijn), giving a late Turolian (MN 13) age (Armour-Brown et al. 1977). A decade later, however, Maramena was discovered and a micromammal faunule (comprising four rodents and one lagomorph) again indicated a late Turolian age (de Bruijn 1989). Extensive excavations at Maramena in 1987-1988, together with a comprehensive study of the collection (Schmidt-Kittler, Ed. 1995), provided several biochronological evidence for a more precise age. The mammalian fauna includes certain late Turolian and early Ruscinian taxa, thus indicating an age of the Turolian/Ruscinian transition, MN 13/14 (Schmidt-Kittler et al. 1995). In northern Greece, micromammal faunas analogous to those from Maramena have been identified in the Serres Basin (Ano Metochi, Monasteri), and in the Komotini Basin (Kessani 1, 2); information for the micromammal faunas of these localities, see to Koufos (2024 and ref. therein). The comparison of the faunas with the well dated late Turolian-early Ruscinian ones from the Ptolemais Basin (Hordijk and de Bruijn 2009) suggests an age ranging from 5.40 to 5.25 Ma for them. Considering that the Miocene/Pliocene boundary is dated at 5.33 Ma, then the Maramena, Ano Metochi and Kessani 1, 2 faunas can be regarded as transitional from the Miocene to the Pliocene, MN 13/14 (Koufos and Vasileiadou 2015).

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Supplement 4 to The Late Miocene Colobine Monkey *Mesopithecus* (Primates, Cercopithecidae) of Greece

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SUPPLEMENT 4

This supplement contains: tables with measurements of the Pikermi material.

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Supplement 4: The Late Miocene colobine monkey *Mesopithecus* (Primates, Cercopithecidae) of Greece

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SUPPLEMENT 4: MEASUREMENTS OF THE PIKERMI MATERIAL

This file includes Tables with measurements

Table 1. Cranial measurements of some specimens of *Mesopithecus pentelicus* from Pikermi, which are better preserved. Measurements according to Delson (1973).

Abbreviations. **NAIN**. Nasion-Inion; **GLIN**. Glabella-Inion; **NABA**. Nasion-Basion; **GLBA**. Glabella-Basion; **BABR**. Glabella-Bregma; **NABR**. Nasion-Prosthion; **GLPR**. Glabella-Prosthion; **NARH**. Nasion-Rhinion; **BAIN**. Basion-Inion; **BABR**. Basion-Bregma; **BAVE**. Basion-Vertex; **BAPR**. Basion-Prosthion; **BAST**. Basion-Staphylion; **BAPT**. Basion-Palate rear; **PRIN**. Prosthion-Inion; **PRST**. Prosthion-Staphylion; **PRPT**. Prosthion Palate rear; **PROB**. Prosthion-Orbit base; **MAXW**. Maximum width; **FACH**. Face height; **PORB**. Minimum post-Orbital width; **BIOR**. Maximum bi-orbital width; **INOR**. Interorbital width; **ORBH**. Orbit height; **ORBW**. Orbit width; **SUPO**. Thickness of the supraorbital torus; **FORW**. Transverse width of foramen magnum; **FORL**. Antero-posterior (Dorsoventral) length of foramen magnum; **ORHA**. Perpendicular height with occlusal plane horizontal from orbit to alveolar plane; **RHNW**. Width of nasal bones at rhinion; **NASW**. Maximum width at nasal aperture; **NASL**. Maximum length of nasal aperture; **PRND**. Prosthion- Inferior end of nasal aperture; **BXEU** Maximum transverse breadth of palate between external alveolar borders; **I1AU**. Breadth across both I1 at alveolar margin; **M3CU**. Length C-M3; **M3MU**. Molar length; **P4CU**. Premolar length; **ALWU**. Transverse breadth of alveolar border at middle of M2; **PDEP**. Depth of palate midline below horizontal alveolar plane at middle of M1.

CRANIUM	SNSB-BSPM-AS II 4	SNSB-BSPM-AS II 5	NHML-PIK-M.8944	NHML-PIK-M.8946	NHML-PIK-M.8947	NHMW-PIK-A.4714	NHMW-PIK-A.4693	NHMW-PIK-1863/I,2	AMPG-PIK-01	AMPG-PIK-02	AMPG-PIK-04	AMPG-PIK-05	AMPG-PIK-08	MNHNP-PIK-013	MNHNP-PIK-016	MNHNP-PIK-035	MNHNP-PIK-303A	MNHNP-PIK-424	MNHNP-PIK-428
SEX	**?F**	***M**	**M**	**M**	**M**	**?M**	**F**	**F**	**M**	**F**	**F**	**F**	**?**	**M**	**M**	**M**	**?**	**F**	**M**
NAIN						86.2+	75.5		80.0	78.0	71.0	79.5	83.0			85.0			
GLIN		79.8				83.8+	70.1		78.5	75.5	67.5	76.7	79.8			83.4			
NABA			57.8							56.0						72.5			
GLBA			58.6							56.0						72.0			
NABR							51.4						49.0	53?					
NAPR				43.8	38.8	41.1	39.0	44.0			44.0	37.0		37.5?	36.3	48?	35.0	31.3	43.0
GLPR				52.0	48.2	48.8	48.6	52.7			47.0	41.8	33.2		44.3	56.8	42.5	40.0	53.0
NARH							14.0	13.6	15.7		17.5			15.5					
BAIN																45.6			
BABR																52.5			
BAVE																54.5			
BAPR																87.0			
BAST			36.5						36.2							42.5			
BAPT	30.2		40.9						41.0							51.7			
PRIN						111.4	112.0				109.0	105.5	105.5			114.2			
PRST					43.8						42.5			45+		44.5			
PRPT					43.2		42.5				38.0	41.8		41.5+		36.5			
PROB				37.2	36.0	34.2	34.1	35.2			31.4	30.7	29.5	34+	31.0	39.0	29.3	28.0	35.0
MAXW							46.7						65.0			50+			
FACH				48.0	40.0		43+	48.3								59.0			
PORB	33.7		39.2			41.1		34?								31.7			
BIOR		63.6	56.7		56.6	51.8	57.0						52.5						
INOR	7.0	10.7	10.5	11.2	11.5	12.0	9.7	8.9		7.5	11.0	[10]	9.0	11.5		11.6	10.0	8.0	11.5
ORBH	18.5	17.4	22.0	23.8	20.0	25.0	20.4			19.7	[13.4]		16.2						25.0
ORBW	23.6	28.1	27.6	24.1	24.7	24.2	25.8			26.8	28.8		26.0						26.7
SUPO	2.8	4.7	4.1	5.5	4.5	5.0	4.5	3.5	3.7	2.7	3.2	3.2	3.2	5.2	2.7	3.6	3.5	2.7	5.0
FORW		13.1	12.3													9.0			
FORL		12.2	13.7																
ORHA			20.0	19.8	18.7	22.3	18.0	23.2										19.3	24.2
RHNW								6.5						9.2					
NASW				12.3	9.3	12.5	10.0	8.3			8.0		11.7	15.0		11.9	10.1	10.6	14.1
NASL				21.0	16.9	21.6	21.6	23.1			21.2		12.5	21.0		25.4	21.5		
PRND						5.0	4.9	6.4					25.0			5.0			
BXEU	26.7	37.2		40.8	34.4	34.4	35.2		36.0		34.5			37.8		34.1	30.5	34.7	40.7
I1AU				9.5	8.5	11.1	11.2						16.0					16.3	
M3CU				40.4	39.0	39.2	35.3	39.2		34.6	38.0	34.0		39.3	36.2	40.2	38.7	33.6	37.4
M3MU	21.2	22.9	20.6	23.5	22.4	22.1	20.0	23.1	22.5	20.6	21.1	19.7		21.6	20.6	21.9	20.8	20.7	21.7
P4CU				19.8	17.8	17.1	16.6	17.0		15.2	17.2	14.4		18.0	15.9	18.0	19.6	14.6	16.2
ALWU	12.3	21.4		23.7	18.9		18.6		18.6		19.7			21.0			15.5+	19.8	23.5
PDEP			4.6	5.1	5.6		4.0		4.7		3.7			6.3		4.4		4.4	5.6

Table 2. Mandibular measurements of some specimens of *Mesopithecus pentelicus* from Pikermi, which are better preserved.

Abbreviations. **SYML**. Symphysis length; **SYMH**. Symphysis height; **PLAL**. Length of planum alveolare; GNPL. Gnathion-Slope point of PLAL; **GNGO**. Gnathion-Gonion; **GNCO**. Gnathion-Condylion; **RAML**. Minimum mesiodistal length of ascending ramus at a level dorsal to toothrow; **IDGO**. Infradentale-Gonion; **BJD3**. Buccal corpus depth at middle of m3; **BJD4**. Buccal corpus depth at middle of p4; **ALWL**. Maximum width of alveolar body at the middle of m2; **M3CL**.Tooth row length c-m3; **M3ML**.Tooth row length m1-m3; **P4CL**. Tooth row length c-p4; **B32L**. Transverse breadth across mandible between contact points of m2 an m3; **BP3L**. Transverse breadth across mandible between most lingual points of p3; **I1AL**. Breadth across both i1 at alveolar margin.

MANDIBLE	SEX	SYML	SYMH	PLAL	GNPL	GNGO	GNCO	RAML	IDGO	BJD3	BJD4	ALWL	M3CL	M3CL	M3ML	P4CL	B32L	BP3L	I1AL
SNSB-BSPM AS II 13	M	26.5	23.9							19.9	20.3			47.2	24.4	12.4	16.2	15.6	
NHML-PIK-M.8944	M	25.5	22.0	12.2						19.2	19.0			44.6	24.0	21.0		14.3	
NHML-PIK-M. 8948	M	25.6	18.6	13.8						20.9	20.0	9.5		47.0	24.8	22.1	15.9		
NHML-PIK-M.8953	*M	26.5	22.5	15.2						20.6	20.6	8.5			25.0		16.2	12.8	
PIUW-PIK-316	F		20.5							18.7	17.9	8.0		39.4	23.5	15.6			
PIUW-PIK-317	F	20.8	19.3							18.3	18.6			39.6	24.3	15.8	15.0	12.0	5.7
NHMW-PIK-A.4714	?M	24.5	21.4			77.2	84.4	30.0	65.6	22.5	20.4			43.5	43.3	20.5			
NHMW-PIK-1998z77/1	M	26.3	21.7	12.6	15.7					19.6	19.9	8.9		44.7	25.4	18.6	23.4	13.0	6.3
NHMW-PIK-1998z77/13	F	19.9	19.5			52.3	70.6	24.0		19.7	20.5			36.5	21.5	15.9	16.5	12.8	4.8
1863-1/03	M	24.6	22.7	10.8	14.2		9.3	31.3		21.3	22.6	7.3		42.0	23.5	19.9	19.5	15.6	5.5
AMPG-PIK- 1	M	26.2	23.2							22.7	22.0	8.3	43.6		25.7	19.0	27.0	14.5	
AMPG-PIK- 2?	F	24.0	23.8							19.5	20.5	7.8			24.0		25.0	16.6	
AMPG-PIK- 17	F	20.7	19.0	9.3	13.8					17.3	17.7	7.2	37.7		21.2	16.4	13.4	10.7	
AMPG-PIK- 19	F	22.1	18.0	11.0	12.7					18.6	17.9	7.6	38.7		22.8	15.3	18.8	12.3	
AMPG-PIK- 20	?F	22.5	20.5	11.0	13.7					18.9	19.0	8.5	39.7		23.5	16.8	14.7	14.0	
AMPG-PIK- 36	M	27.0	25.6	12.8	15.5					22.0	24.0		43.5		24.2	21.1			
MNHNP-PIK- 001	F	21.0	17.8				66.4			18.0	16.5	6.8			23.3	16.8			5.1
MNHNP-PIK- 002	F	22.0	20.0			48.5		23.0	60.0	21.0	18.0	7.5	40.0		23.8	16.6			
MNHNP-PIK- 003	F	21.0	19.5							18.6	18.3				23.1	11.9	19.0	15.0	5.6
MNHNP-PIK- 006	M	27.5	24.5	15.8	16.8					23.8	22.3	8.5	44.2		23.3	22.0			
MNHNP-PIK- 009	M	25.8	21.8	15.8	15.0					19.1	19.8	8.7	42.5		23.6	18.3	18.4	13.4	
MNHNP-PIK- 019b	F	18.0	16.6							15.2	17.5				20.7				
MNHNP-PIK- 421	M	24.7	21.2							19.0	18.3	8.9		41.5	23.2	12.9	19.0	12.0	6.2
MNHNP-PIK- 423	M	25.0	24.6	12.3	16.4						22.0	8.1		43.8	24.4	20.1	20.5		6.2
MNHNP-PIK- 430	F	21.0	20.7	11.6	10.6	57.0		24.0	66.4	19.5	17.8	6.7		38.7	21.8	15.8	18.3	11.4	

Table 3. Measurements of the male upper dentition of *Mesopithecus pentelicus* from Pikermi. A. specimens preserving canine; B. specimens with canine, plus those without canine, which were determined to be male after comparison with specimens preserving canine, using PCA.

Abbreviations. **TTL**. Total toothrow length (I1-M3); **PL**. premolar length (P3-P4); **ML**. molar length (M1-M3); **L**. length; **B**. breadth; **a**. anterior; **p**. posterior.

Upper teeth	***Mesopithecus pentelicus*, Pikermi**					***Mesopithecus pentelicus*, Pikermi**				
	A					**B**				
	n	**x̄**	**min**	**max**	**s**	**n**	**x̄**	**min**	**max**	**s**
TTL	12	47.83	45.2	50	1.50	12	47.83	45.2	50	1.50
PL	29	9.98	9.3	10.7	0.37	30	9.96	9.3	10.7	0.39
ML	32	21.91	20	23.4	0.89	37	22.00	20	24.1	0.93
LI1	13	5.09	4.7	5.9	0.46	13	5.09	4.7	5.9	0.46
BI1	13	4.77	4.3	5.2	0.27	13	4.77	4.3	5.2	0.27
LI2	11	4.52	3.8	5.2	0.47	11	4.52	3.7	5.2	0.47
BI2	10	4.12	3.7	4.8	0.36	10	4.12	3.7	4.8	0.36
LC	22	8.23	6.3	9.8	0.83	23	8.25	6.3	9.8	0.82
BC	22	6.42	5.2	7	0.50	23	6.45	5.2	7	0.51
LP3	29	4.87	4.1	5.5	0.31	30	4.87	4.1	5.5	0.31
BP3	28	5.93	5.1	6.5	0.36	29	5.94	5.1	6.5	0.35
LP4	32	5.08	4.7	5.7	0.27	38	5.09	4.7	5.7	0.27
BP4	32	6.47	5.6	6.9	0.27	38	6.51	5.6	7.1	0.30
LM1	34	7.04	6.4	7.8	0.29	41	7.08	6.4	7.8	0.30
BM1a	32	7.12	6.5	7.9	0.33	38	7.13	6.49	7.9	0.33
BM1p	31	6.86	6.3	7.5	0.35	36	6.84	6.3	7.5	0.33
LM2	34	7.46	6.8	8.2	0.33	43	7.52	6.8	8.2	0.32
BM2a	34	7.91	7.3	8.5	0.33	43	7.93	7.3	8.5	0.34
BM2p	32	7.36	6.7	8.1	0.36	40	7.40	6.7	8.1	0.37
LM3	35	7.25	6.3	8.0	0.40	43	7.25	6.3	8.0	0.40
BM3a	35	7.39	6.7	8.2	0.37	43	7.41	6.7	8.2	0.37
BM3p	34	6.39	5.3	7.8	0.57	42	6.44	5.3	7.8	0.57

Table 4. Measurements of the female upper dentition of *Mesopithecus pentelicus* from Pikermi. A. specimens preserving canine; B. specimens with canine, plus those without canine, which were determined to be female after comparison with specimens preserving canine, using PCA.

Abbreviations. **TTL**. Total toothrow length (I1-M3); **PL**. premolar length (P3-P4); **ML**. molar length (M1-M3); **L**. length; **B**. breadth; **a**. anterior; **p**. posterior.

Upper teeth	***Mesopithecus pentelicus*, Pikermi**					***Mesopithecus pentelicus*, Pikermi**				
	A					**B**				
	n	**x̄**	**min**	**max**	**s**	**n**	**x̄**	**min**	**max**	**s**
TTL	5	44.78	42.7	46.2	1.46	7	44.21	42.6	46.2	1.54
PL	17	9.46	8.3	10.1	0.46	19	9.47	8.3	10.1	0.44
ML	17	20.62	19.5	23.1	1.07	18	20.66	19.5	23.1	1.05
LI1	3	4.93	4.7	5.1	0.21	5	4.86	4.5	5.1	0.25
BI1	3	4.70	4.0	5.1	0.61	5	4.76	4.0	5.1	0.45
LI2	7	4.44	4.2	5.1	0.30	9	4.43	4.2	5.1	0.26
BI2	7	3.79	3.3	4.5	0.50	9	3.78	3.3	4.5	0.44
LC	12	5.95	4.9	7.5	0.81	14	6.17	4.9	7.7	0.94
BC	11	4.64	3.3	5.7	0.74	13	4.94	3.3	6.9	1.01
LP3	16	4.68	3.8	5.1	0.38	18	4.67	3.8	5.1	0.35
BP3	15	5.63	5.0	6.0	0.32	17	5.66	5.0	6.0	0.31
LP4	17	4.89	4.3	5.7	0.34	19	4.90	4.3	5.7	0.32
BP4	17	6.24	5.4	6.7	0.31	19	6.24	5.4	6.7	0.30
LM1	15	6.69	6.4	7.5	0.27	17	6.69	6.3	7.5	0.28
BM1a	15	6.85	6.3	7.4	0.39	17	6.84	6.3	7.4	0.37
BM1p	15	6.62	6.2	7.2	0.30	17	6.62	6.2	7.2	0.28
LM2	20	7.26	6.6	7.7	0.28	22	7.27	6.6	7.7	0.28
BM2a	20	7.58	7.0	8.0	0.22	22	7.57	7.0	8.0	0.21
BM2p	20	6.98	6.7	7.5	0.20	22	6.99	6.7	7.5	0.19
LM3	16	6.90	6.4	7.9	0.36	18	6.91	6.4	7.9	0.35
BM3a	15	7.08	6.8	7.4	0.14	17	7.09	6.8	7.4	0.13
BM3p	15	5.95	5.6	7.0	0.36	17	5.96	5.6	7.0	0.34

Table 5. Measurements of the male lower dentition of *Mesopithecus pentelicus* from Pikermi. A. specimens preserving canine; B. specimens with canine, plus those without canine, which were determined to be male after comparison with specimens preserving canine, using PCA.

Abbreviations. **TTL**. Total toothrow length (I1-M3); **PL**. premolar length (P3-P4); **ML**. molar length (M1-M3); **L**. length; **B**. breadth; **a**. anterior; **p**. posterior.

Lower teeth	***Mesopithecus pentelicus*, Pikermi**					***Mesopithecus pentelicus*, Pikermi**				
	A					**B**				
	n	**$\bar{x}$**	**min**	**max**	**s**	**n**	**$\bar{x}$**	**min**	**max**	**s**
TTL	26	48.29	43.3	52.7	2.20	26	48.29	43.3	52.7	2.20
PL	31	11.99	11.0	14.1	0.69	33	11.97	11.0	14.1	0.67
ML	30	24.19	22.7	27.3	0.97	33	24.21	22.7	27.3	0.94
Li1	25	4.32	3.3	5.4	0.44	25	4.32	3.3	5.4	0.44
Bi1	25	3.33	3.0	4.6	0.39	25	3.33	3.0	4.6	0.39
Li2	20	4.51	3.3	5.1	0.51	20	4.51	3.3	5.1	0.51
Bi2	20	3.51	2.7	4.7	0.48	20	3.51	2.7	4.7	0.48
Lc	32	7.53	6.5	8.3	0.42	32	7.53	6.5	8.3	0.42
Bc	31	5.78	5.0	6.6	0.45	30	5.80	5.1	6.6	0.44
Lp3	34	6.51	5.0	7.5	0.50	37	6.53	5.0	7.5	0.49
Bp3	34	4.19	3.7	5.2	0.31	37	4.17	3.7	5.2	0.30
Bp4	36	5.76	5.0	6.7	0.36	39	5.74	5.0	6.7	0.37
Bp4	35	4.64	4.1	6.3	0.37	38	4.64	4.1	6.3	0.36
Lm1	29	7.03	6.0	7.5	0.35	35	7.05	6.0	7.5	0.34
Bm1a	27	5.84	5.3	7.1	0.40	33	5.79	5.2	7.1	0.40
Bm1p	26	6.16	5.4	7.1	0.43	32	6.16	5.2	7.1	0.44
Lm2	35	7.61	6.8	8.5	0.41	41	7.62	6.8	8.5	0.40
Bm2a	36	6.75	6.2	7.4	0.32	41	6.74	6.2	7.4	0.30
Bm2p	34	7.03	6.4	7.8	0.39	39	7.01	6.3	7.8	0.40
Lm3	34	9.42	8.7	10.4	0.41	37	9.42	8.7	10.4	0.39
Bm3a	33	6.71	6.2	7.4	0.29	36	6.74	6.2	7.4	0.29
Bm3p	33	6.44	6.0	7.4	0.33	36	6.45	6.0	7.4	0.33

Table 6. Measurements of the female lower dentition of *Mesopithecus pentelicus* from Pikermi. A. specimens preserving canine; B. specimens with canine, plus those without canine, which were determined to be female after comparison with specimens preserving canine, using PCA.

Abbreviations. **TTL**. Total toothrow length (I1-M3); **PL**. premolar length (P3-P4); **ML**. molar length (M1-M3); **L**. length; **B**. breadth; **a**. anterior; **p**. posterior.

Lower teeth	***Mesopithecus pentelicus*, Pikermi**					***Mesopithecus pentelicus*, Pikermi**				
	A					**B**				
	n	**x**	**min**	**max**	**s**	**n**	**x**	**min**	**max**	**s**
TTL	26	48.29	43.3	52.7	2.20	16	42.44	38.7	47	2.20
PL	31	11.99	11.0	14.1	0.69	22	10.89	10.1	11.4	0.34
ML	30	24.19	22.7	27.3	0.97	18	23.01	21.3	24.5	0.89
Li1	25	4.32	3.3	5.4	0.44	12	4.19	3.8	4.4	0.20
Bi1	25	3.33	3.0	4.6	0.39	12	2.92	2	3.4	0.47
Li2	20	4.51	3.3	5.1	0.51	14	4.39	4	4.9	0.26
Bi2	20	3.51	2.7	4.7	0.48	14	3.14	2.6	3.6	0.28
Lc	32	7.53	6.5	8.3	0.42	19	5.35	4.6	6.3	0.37
Bc	31	5.78	5.0	6.6	0.45	18	4.08	3.3	5	0.37
Lp3	34	6.51	5.0	7.5	0.50	22	5.66	5.2	6.4	0.34
Bp3	34	4.19	3.7	5.2	0.31	22	3.71	3.4	4.1	0.21
Bp4	36	5.76	5.0	6.7	0.36	27	5.34	4.5	6.1	0.38
Bp4	35	4.64	4.1	6.3	0.37	27	4.45	4	5	0.23
Lm1	29	7.03	6.0	7.5	0.35	23	6.65	5.9	7.4	0.37
Bm1a	27	5.84	5.3	7.1	0.40	23	5.68	4.8	6.3	0.36
Bm1p	26	6.16	5.4	7.1	0.43	22	5.87	5	6.4	0.42
Lm2	35	7.61	6.8	8.5	0.41	23	7.28	6.4	7.8	0.35
Bm2a	36	6.75	6.2	7.4	0.32	23	6.56	5.8	7	0.28
Bm2p	34	7.03	6.4	7.8	0.39	23	6.58	6.2	7.2	0.32
Lm3	34	9.42	8.7	10.4	0.41	22	9.05	8.2	10	0.39
Bm3a	33	6.71	6.2	7.4	0.29	21	6.48	6	6.9	0.25
Bm3p	33	6.44	6.0	7.4	0.33	22	6.07	5.6	6.5	0.30

Supplement 5 to The Late Miocene Colobine Monkey *Mesopithecus* (Primates, Cercopithecidae) of Greece

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SUPPLEMENT 5

This supplement contains: illustrations of *Mesopithecus pentelicus* from Pikermi, housed at the Athens Museum of Palaeontology and Geology (AMPG).

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Supplement 5: The Late Miocene colobine monkey *Mesopithecus* (Primates, Cercopithecidae) of Greece

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SUPPLEMENT 5: COLLECTION OF *MESOPITHECUS PENTELICUS* FROM PIKERMI

This file includes: Illustrations of the material stored at the Athens Museum of Palaeontology and Geology (AMPG)

NOTE: The sex of the specimens preserving the canines are reported as male and female if it is based on the analysis of their dental dimensions (Fig. 3 in the main text); it is marked by an asterisk in the specimens lacking the canines and preserving several postcanine teeth (Fig. 4 in the main text) and by a question mark if it is estimated empirically. Scale bar in all figures 10 mm.

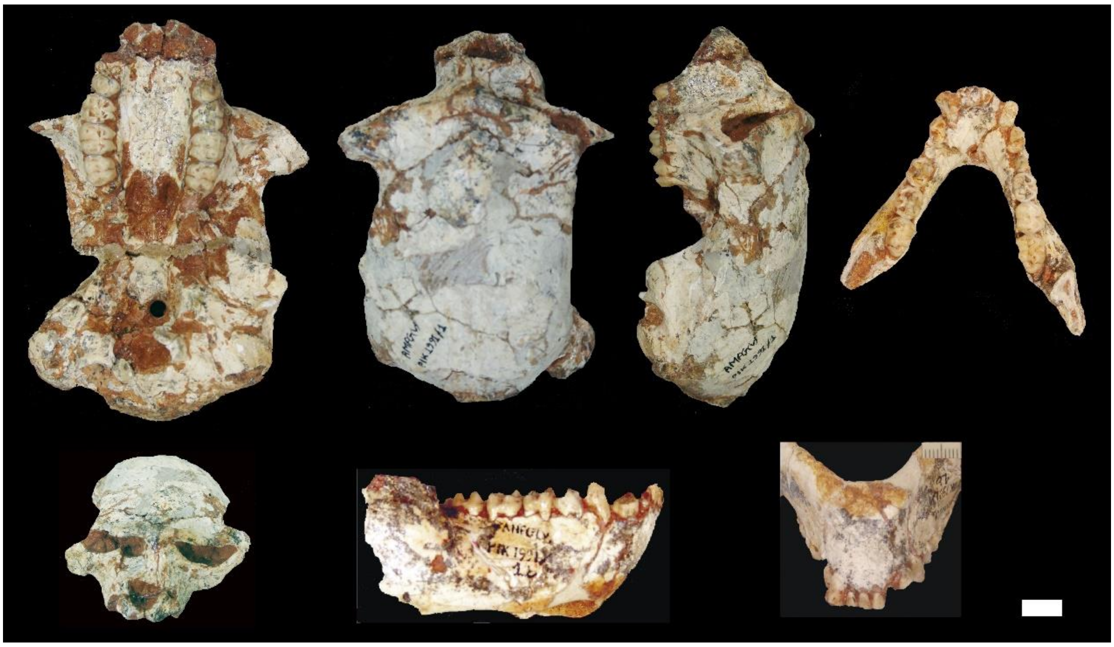

Figure 1. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. AMPG-PIK-1. Cranium and mandible of an adult female individual.

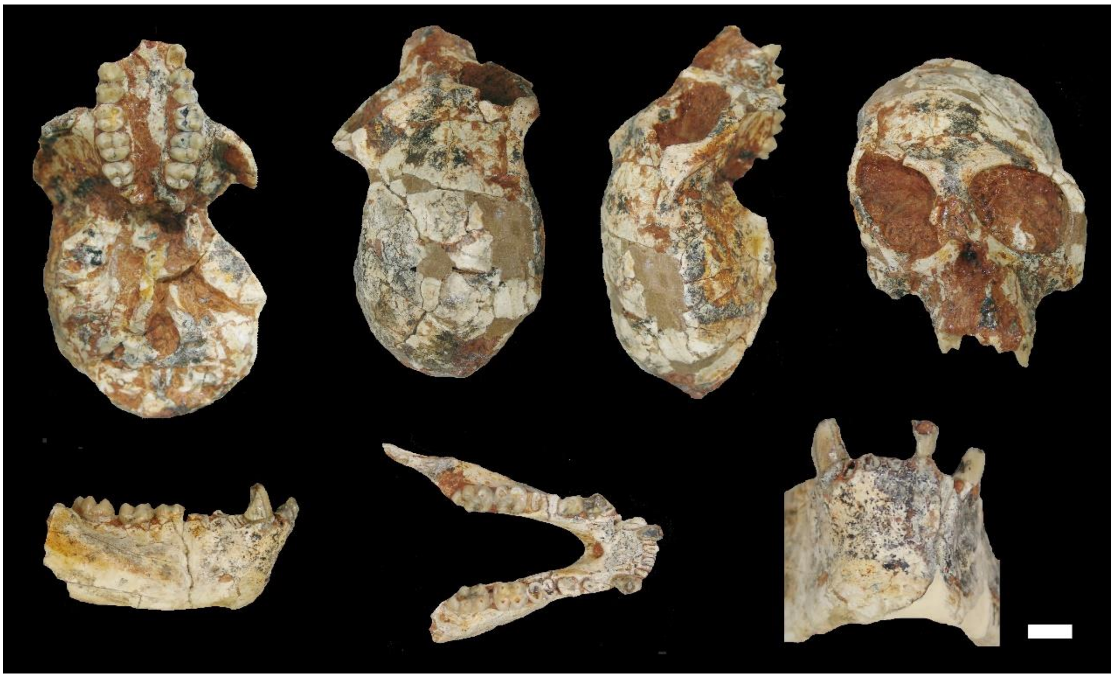

Figure 2. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. AMPG-PIK-2. Cranium and mandible of an adult female individual.

Figure 3. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. AMPG-PIK-3. Cranium of an adult male individual.

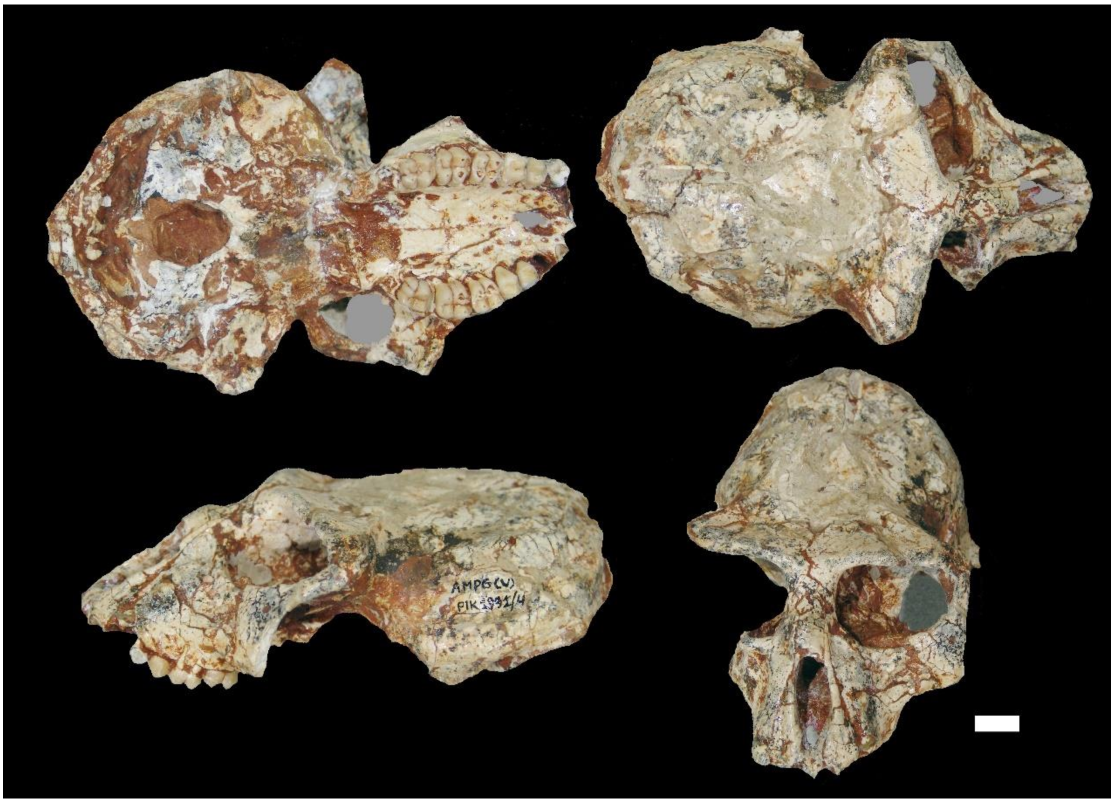

Figure 4. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. AMPG-PIK-4. Cranium of an adult female individual.

Figure 5. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. AMPG-PIK-5. Cranium and mandible of an adult female individual.

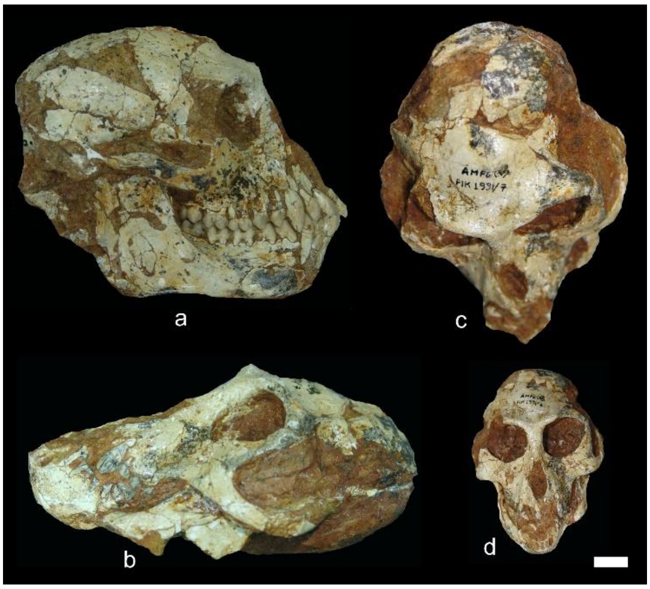

Figure 6. *Mesopithecus pentelicus*, Pikermi; Attica, Greece. a. AMPG-PIK-6, cranium and mandible in connection of an adult ?male individual, b-d. AMPG-PIK-7, cranium and mandible of an adult ?male individual

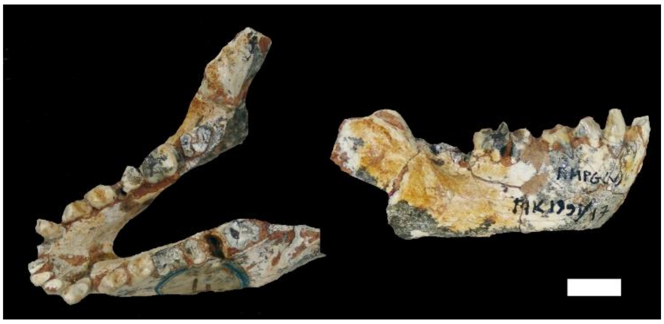

Figure 7. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. a. AMPG-PIK-17. Mandible of an adult female individual.

Figure 8. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. AMPG-PIK-18. Mandible of an adult male individual.

Figure 9. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. AMPG-PIK-19. Mandible of an adult female individual.

Figure 10. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. AMPG-PIK-20. Mandible of an adult ?female individual.

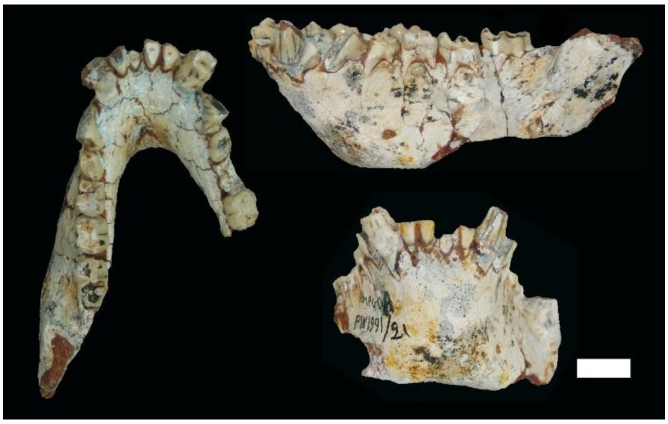

Figure 11. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. AMPG-PIK-21. Mandible of an adult male individual.

Figure 12. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. AMPG-PIK-22. Mandible of an adult male individual.

Figure 13 *Mesopithecus pentelicus*, Pikermi, Attica, Greece. AMPG-PIK-36. Mandible of an adult male individual.

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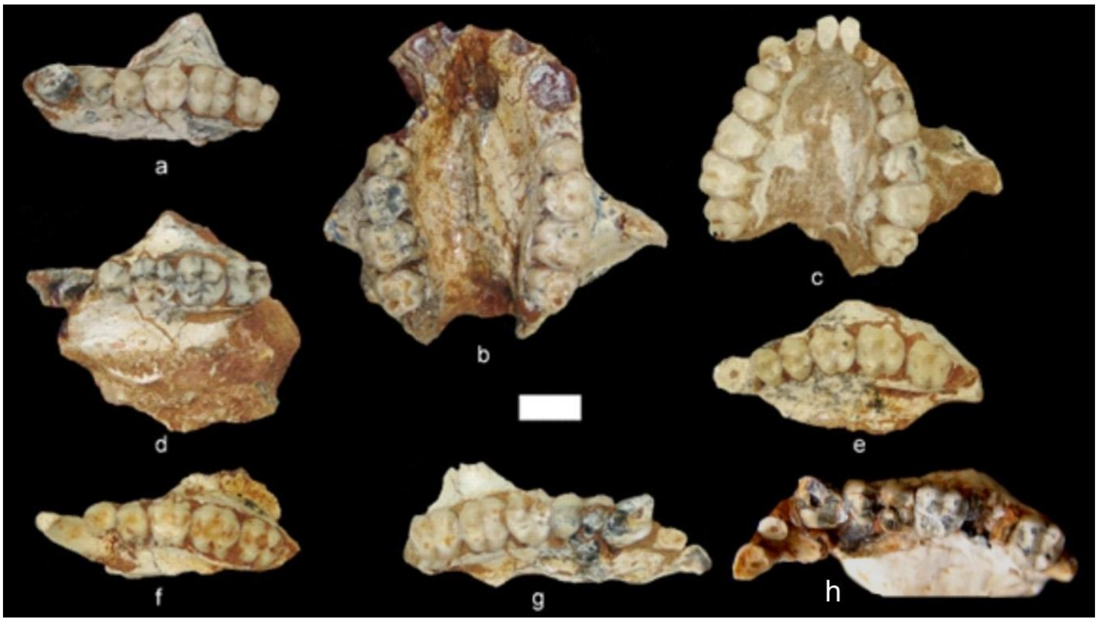

Figure 14. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. a. Left maxillary fragment with C-M3, of a male individual, AMPG-PIK-8; b. Maxilla with P4-M3 dex and sin of a *male individual, AMPG-PIK-12; c. Maxilla with I1, P3-M3 dex and I1-M3 sin, of a ?female individual, AMPG-PIK-13; d. Left maxillary fragment with P4-M3 of a *male individual, AMPG-PIK-14; e. Left maxillary fragment with C-M3 of a *female individual, AMPG-PIK-16; f. Left maxillary fragment with C-M3 of male individual, AMPG-PIK-38; g. Right maxillary fragment with I1-M3 of a male individual, AMPG-PIK-39; h. Left maxillary fragment with I1-M1, M3 of a male individual, AMPG-PIK-40.

Figure 15. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. a. Left hemimandible with i1-i2 dex and i1-m3 sin of a *female individual, AMPG-PIK-24; b. Right mandibular fragment with p3-m2 of a *male individual, AMPG-PIK-37; c. Left mandibular fragment with m2-m3, AMPG-PIK-1991-016? (possibly same individual with the maxillary fragment AMPG-PIK-16).

Supplement 6 to The Late Miocene Colobine Monkey *Mesopithecus* (Primates, Cercopithecidae) of Greece

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SUPPLEMENT 6

This supplement contains: illustrations of *Mesopithecus pentelicus* from Pikermi, housed at the Muséum Nationale d'Histoire Naturelle Paris (MNHNP).

Supplement 6: The Late Miocene colobine monkey *Mesopithecus* (Primates, Cercopithecidae) of Greece

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SUPPLEMENT 6: COLLECTION OF *MESOPITHECUS PENTELICUS* FROM PIKERMI

This file includes: Illustrations of the material stored at the Muséum Nationale d'Histoire Naturelle Paris (MNHNP)

NOTE 1: The sex of the specimens preserving the canines are reported as male and female if it is based on the analysis of their dental dimensions (Fig. 3 in the text); it is marked by an asterisk in the specimens lacking the canines and preserving several postcanine teeth (Fig. 4 in the text) and by a question mark if it is estimated empirically. Scale bar in all figures 10 mm.

NOTE 2. In the MNHNP collection of *Mesopithecus* there is a cranium numbered MNHNP-PIK-420, which belongs to a modern *Macaca*. Probably was mixed with fossils by someone who studied the collection and used it for comparisons; the illustration of this cranium is not given.

Figure 1. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. MNHNP-PIK-01. Mandible of an adult female individual.

Figure 2. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. MNHNP-PIK-02. Mandible of an adult female individual.

Figure 3. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. MNHNP-PIK-03. Mandible of an adult female individual.

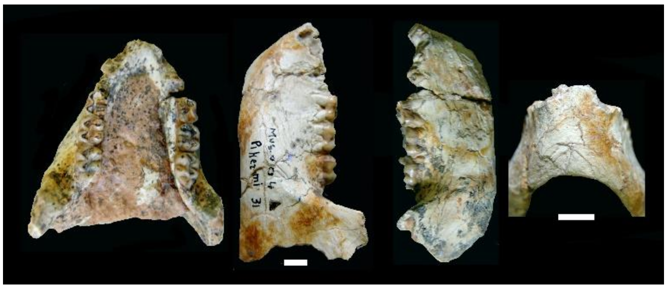

Figure 4. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. MNHNP-PIK-04. Mandible of an adult *male individual.

Figure 5. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. MNHNP-PIK-05. Mandible of an adult male individual.

Figure 6. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. MNHNP-PIK-06. Mandible of an adult male individual.

Figure 7. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. MNHNP-PIK-07. Mandible of an adult male individual.

Figure 8. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. MNHNP-PIK-08. Mandible of an adult male individual.

Figure 9. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. MNHNP-PIK-09. Mandible of an adult male individual.

Figure 10. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. MNHNP-PIK-010. Maxilla of an adult male individual.

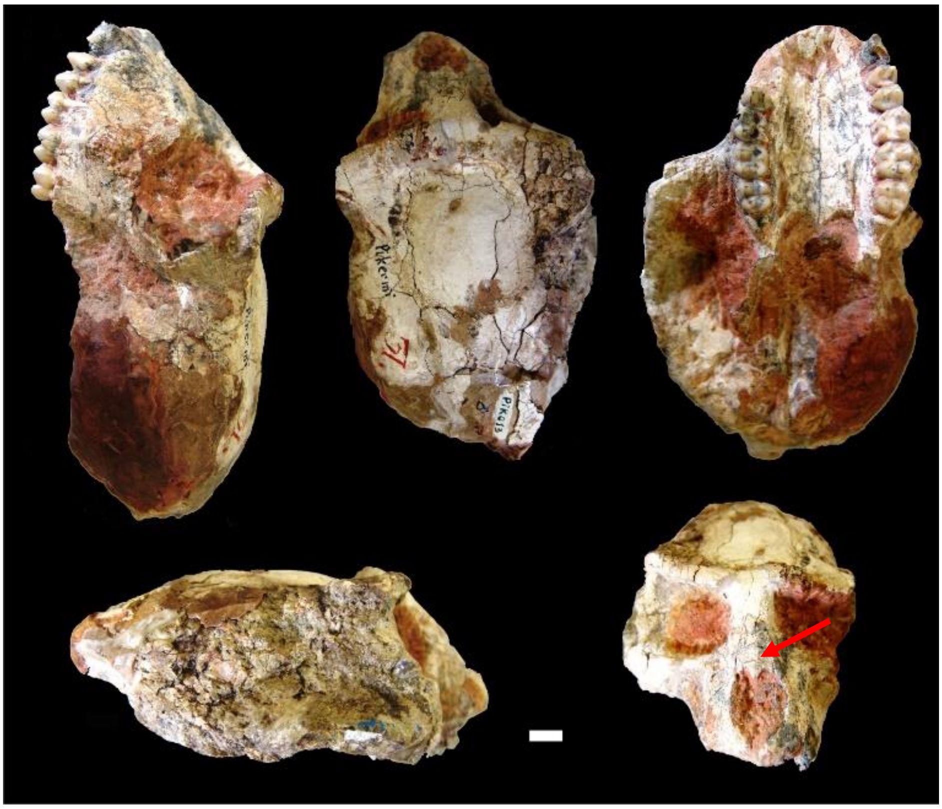

Figure 11. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. MNHNP-PIK-013. Cranium of an adult male individual.

Figure 12. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. MNHNP-PIK-014. Cranium of an adult male individual.

Figure 13. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. MNHNP-PIK-016. Cranium of an adult male individual.

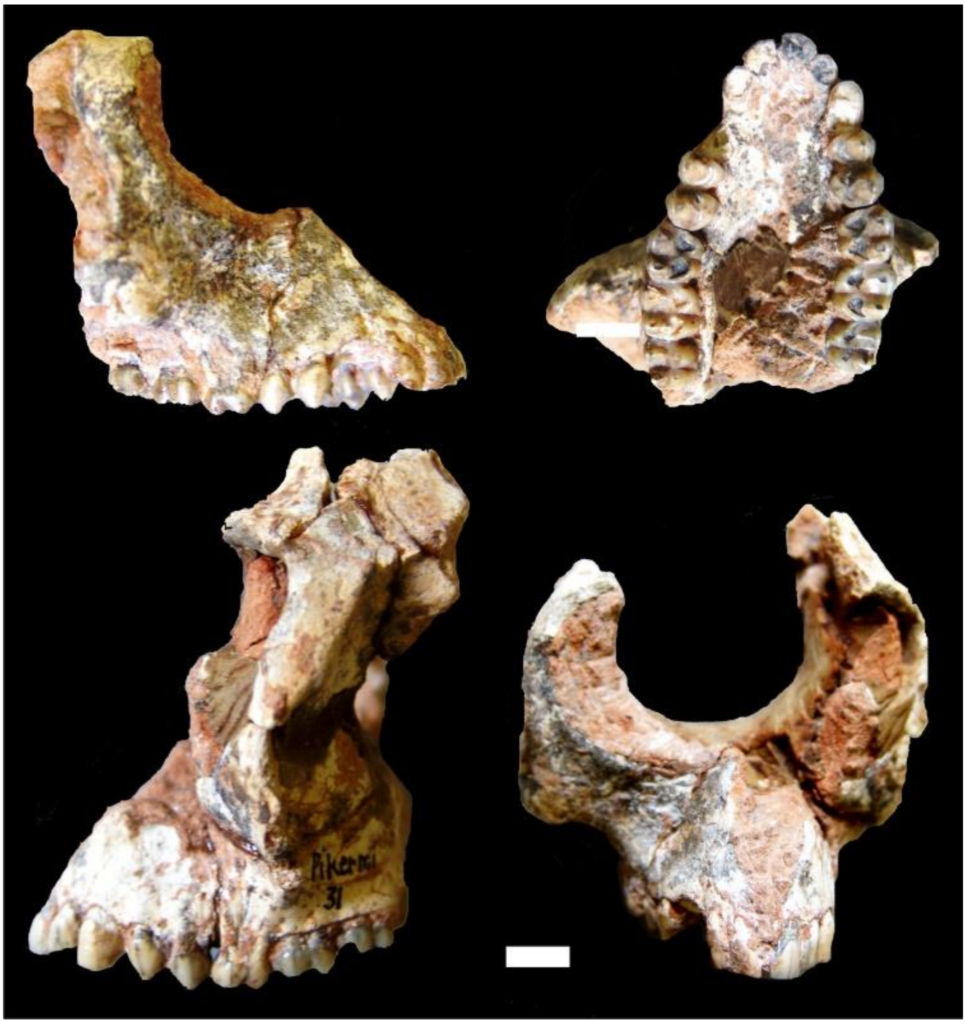

Figure 14. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. MNHNP-PIK-017. Partial cranium of an adult ?female individual.

Figure 15. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. MNHNP-PIK-019a+b. Cranium and mandible of an adult ?female individual.

Figure 16. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. MNHNP-PIK-021a+b. Partial cranium and mandible of an adult male individual.

Figure 17. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. MNHNP-PIK-034 Mandible of an adult male individual.

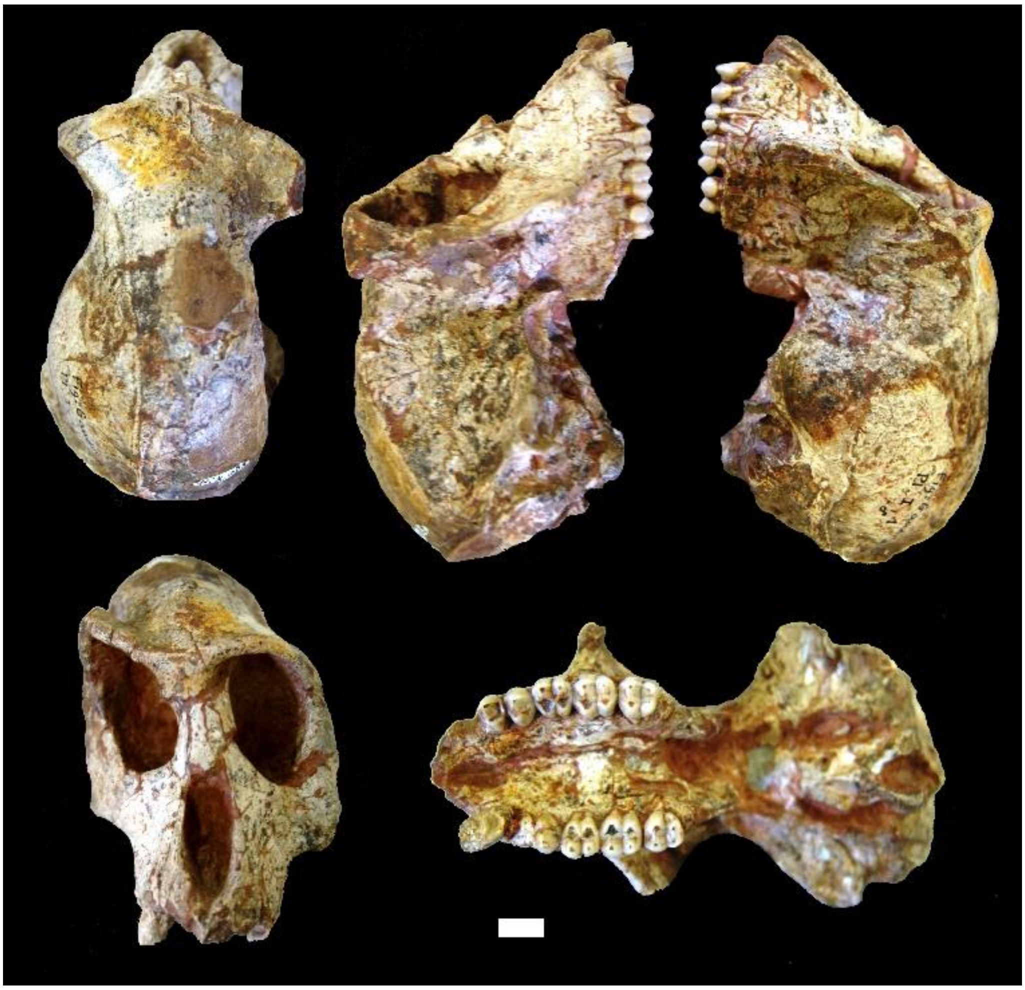

Figure 18. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. MNHNP-PIK-035. Cranium of an adult male individual.

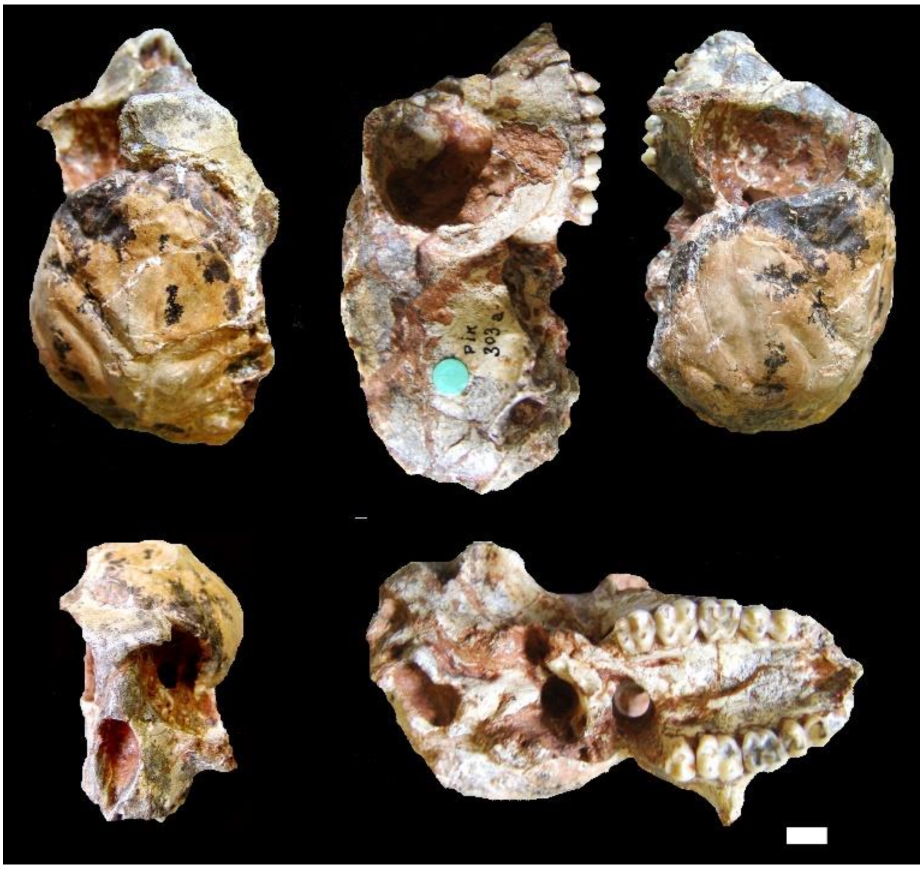

Figure 19. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. MNHNP-PIK-303a. Cranium of an adult individual.

Figure 20. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. MNHNP-PIK-421. Mandible of an adult male individual.

Figure 21. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. MNHNP-PIK-422. Mandible of an adult female individual.

Figure 22. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. MNHNP-PIK-423. Mandible of an adult male individual.

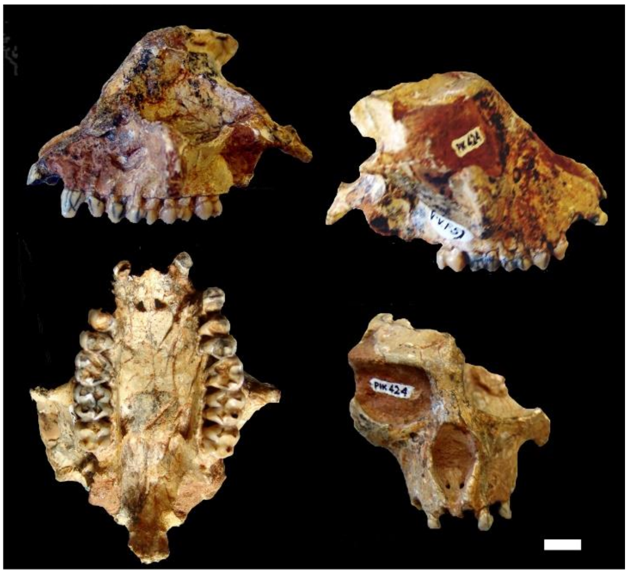

Figure 23. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. MNHNP-PIK-424. Maxillary fragment of an adult female individual.

Figure 24. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. MNHNP-PIK-426. Frontal part of the cranium of an adult male individual.

Figure 25. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. MNHNP-PIK-427. Frontal part of the cranium of an adult *female individual.

Figure 26. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. MNHNP-PIK-428. Frontal part of the cranium of an adult male individual.

Figure 27. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. MNHNP-PIK-429. Cranium of an adult ?female individual.

Figure 28. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. MNHNP-PIK-430. Mandible of an adult female individual.

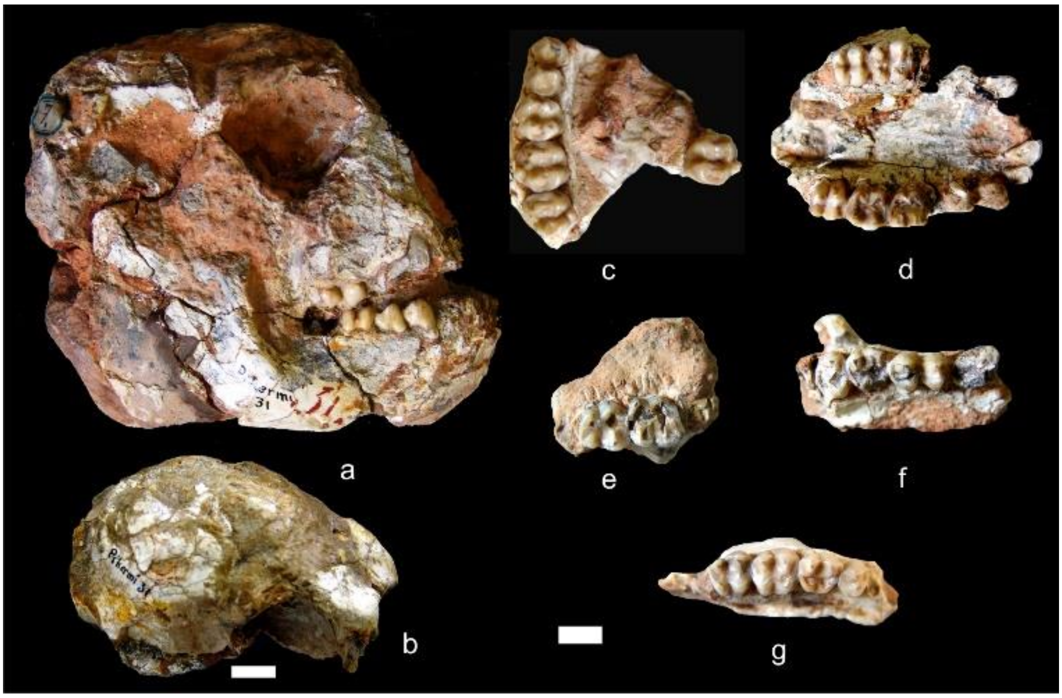

Figure 29. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. a. Cranium and associated mandible, MNHNP-PIK-015; b. Cranium without maxilla MNHNP-PIK-018; c. Maxillary fragment with P3-M3 dex and M2 sin of an adult *male individual, MNHNP-PIK-012; d. Maxillary fragment with M2-M3 dex and I1-M3 sin of an adult ?female individual, MNHNP-PIK-020; e. Left maxillary fragment with M2-M3, MHNNP-PIK-252; f. Right maxillary fragment with C-M1 of an adult male individual, MNHNP-PIK-253; g. Right maxillary fragment with P4-M3 of an adult *male individual, MNHNP-PIK-425.

Supplement 7 to The Late Miocene Colobine Monkey *Mesopithecus* (Primates, Cercopithecidae) of Greece

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SUPPLEMENT 7

This supplement contains: illustrations of *Mesopithecus pentelicus* from Pikermi, housed at the Natural History Museum of London (NHML).

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SUPPLEMENT 7: COLLECTION OF *MESOPITHECUS PENTELICUS* FROM PIKERMI

This file includes: Illustrations of the material stored at the Natural History Museum of London (NHML)

NOTE: The sex of the specimens preserving the canines are reported as male and female if it is based on the analysis of their dental dimensions (Fig. 3 in the text); it is marked by an asterisk in the specimens lacking the canines and preserving several postcanine teeth (Fig. 4 in the text) and by a question mark if it is estimated empirically. Scale bar in all figures 10 mm.

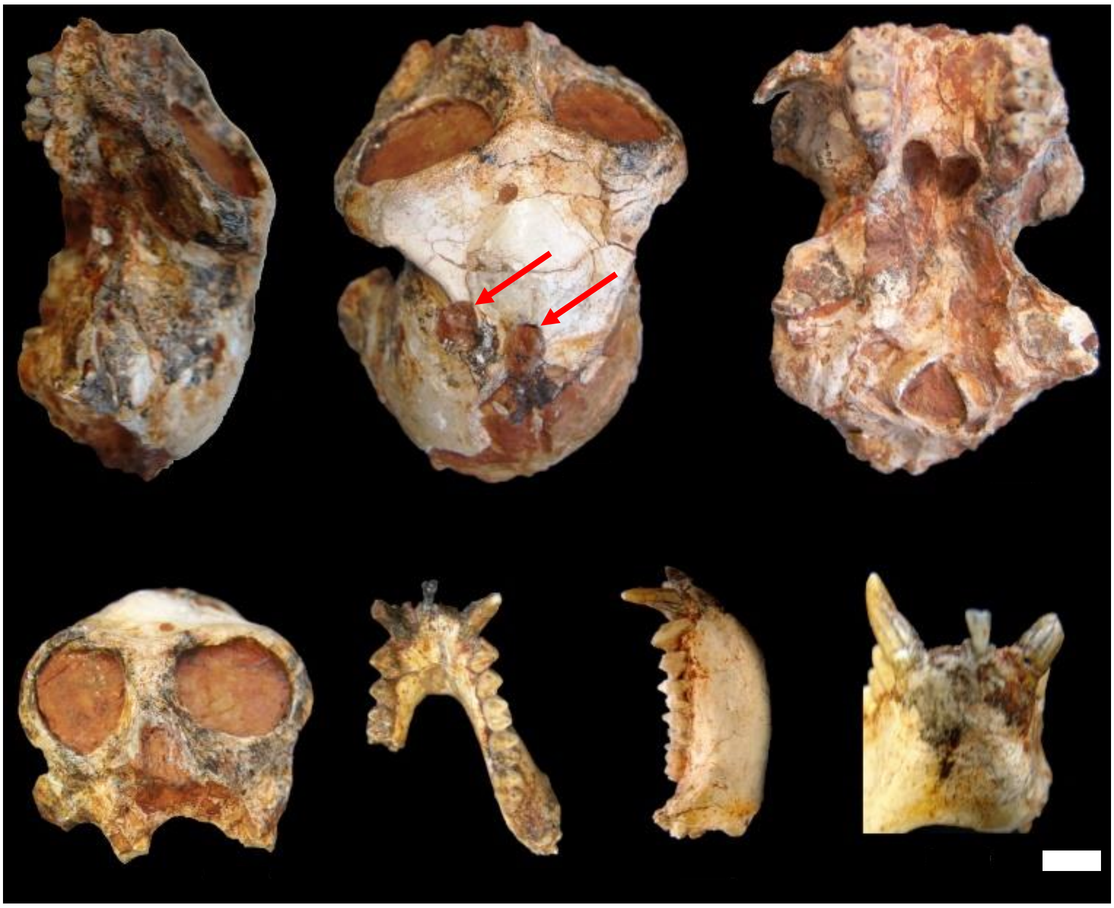

Figure1. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. Cranium and mandible of an adult male individual, NHML-PIK-M.8944. The cranium preserves hole-shaped bite-marks on the roof (red arrows), indicating the attack by a carnivoran.

Figure 2. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. Partial cranium with I1-M3 dex and sin of an adult male individual, NHML-PIK-M.8945.

Figure 3. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. Partial cranium with I1-M3 dex and sin of an adult male individual, NHML-PIK-M.8946.

Figure 4. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. Partial cranium with I1-M3 dex and sin of an adult male individual, NHML-PIK-M.8947.

Figure 5. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. Maxilla and mandible of an adult male individual, NHML-PIK-M.8948.

Figure 6. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. Cranium of an adult female individual, NHML-PIK-M.8949.

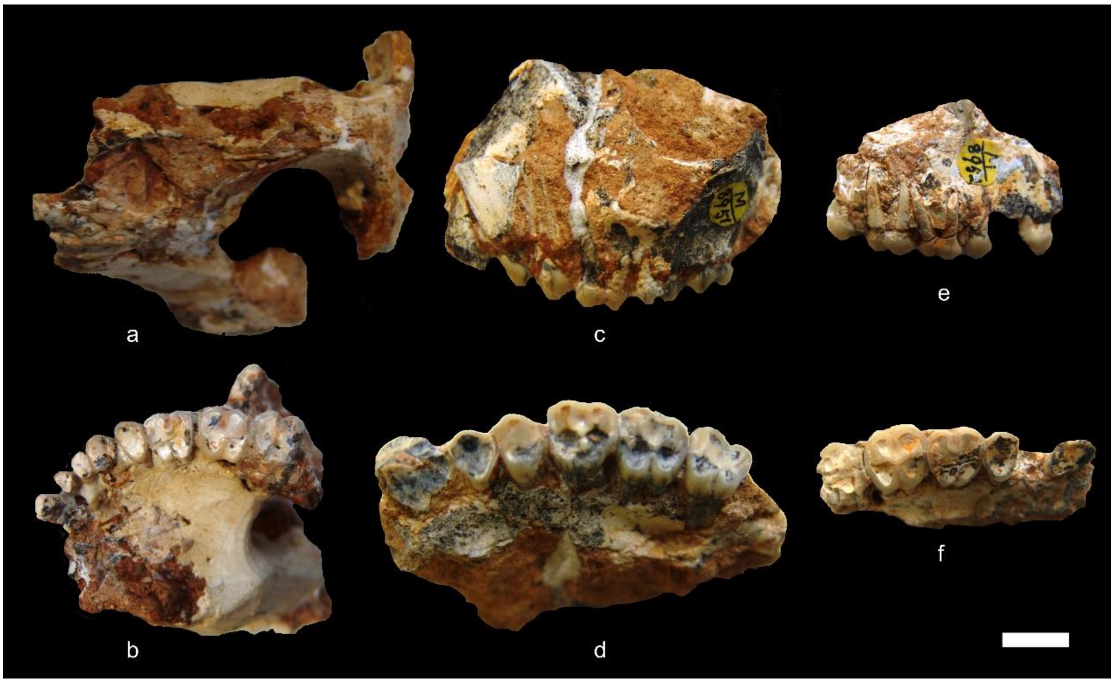

Figure 7. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. a-b. Maxilla with M1-M3 of an old ?female individual, NHML-PIK-M.8950; c-d. Left maxillary fragment with C-M3 of an adult male individual, NHML-PIK-M.8951; e-f. Right maxillary fragment with C, P4-M3 of an old adult female individual, NHML-PIK-M.8951.

Figure 8. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. Mandible of an adult *male individual, NHML-PIK-M.8953.

Figure 9. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. Mandible of an adult male individual, NHML-PIK-M.8955.

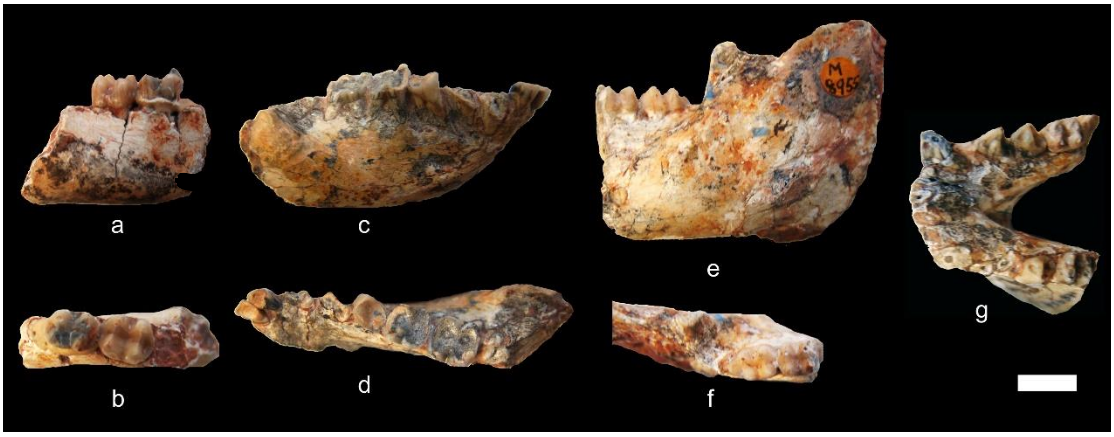

Figure 10. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. a-b. Right mandibular fragment with m1-m3 of an adult *male individual, NHML-PIK-M.2279a; c-d. Left mandibular fragment with i1, p4-m2 of an adult *female individual, NHML-PIK-M.2279b; e-f. Left mandibular fragment of an adult *female individual, NHML-PIK-M.4955; g. Mandibular fragment with c-m1 dex and p4-m1 sin of an adult female individual, NHML-PIK-M.4954.

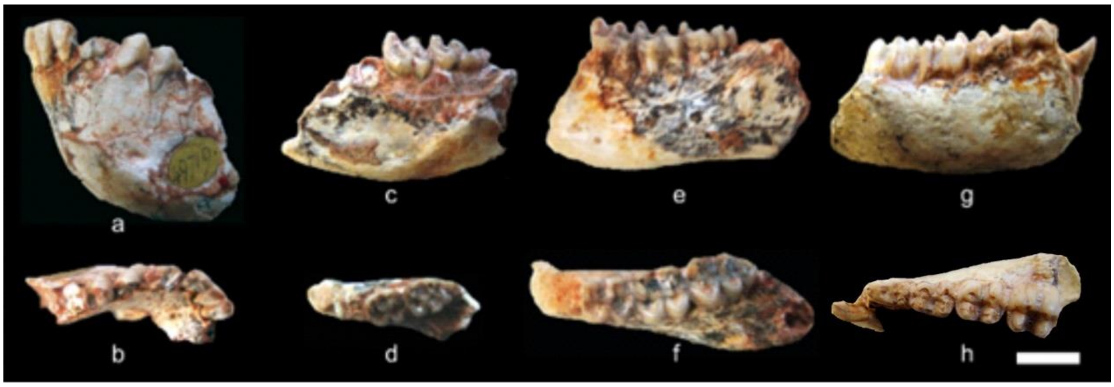

Figure 11. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. a-b. Mandibular fragment with i1-p4 sin and i1 dex of an adult female individual, NHML-PIK-M.49719a; c-d. Left mandibular fragment of an adult ?female individual, NHML-PIK-M.49719b; e-f. Left mandibular fragment with m1-m3 of an adult *female individual, NHML-PIK-M.8956; g-h. Right mandibular fragment with c, dp3-dp4m m1-m2 of a young individual, NHML-PIK-M.8957.

Supplement 8 to The Late Miocene Colobine Monkey *Mesopithecus* (Primates, Cercopithecidae) of Greece

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SUPPLEMENT 8

This supplement contains: illustrations of *Mesopithecus pentelicus* from Pikermi, housed at the Staatliche Naturwissensaftische Sammlungen Bayerns-Bayerische Staatssammlung für Paläontologie und Geologie, München (SNSB-BSPGM).

Supplement 8: The Late Miocene colobine monkey *Mesopithecus* (Primates, Cercopithecidae) of Greece

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SUPPLEMENT 8: COLLECTION OF *MESOPITHECUS PENTELICUS* FROM PIKERMI

This file includes: Illustrations of the material stored at the Staatliche Naturwissensaftische Sammlungen Bayerns-Bayerische Staatssammlung für Paläontologie und Geologie, München (SNSB-BSPGM)

NOTE: The sex of the specimens preserving the canines are reported as male and female if it is based on the analysis of their dental dimensions (Fig. 3 in the text); it is marked by an asterisk in the specimens lacking the canines and preserving several postcanine teeth (Fig. 4 in the text) and by a question mark if it is estimated empirically. Scale bar in all figures 10 mm.

Figure 1. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. Cranium of an adult ?female individual, SNSB-BSPG-PIK-AS II 4.

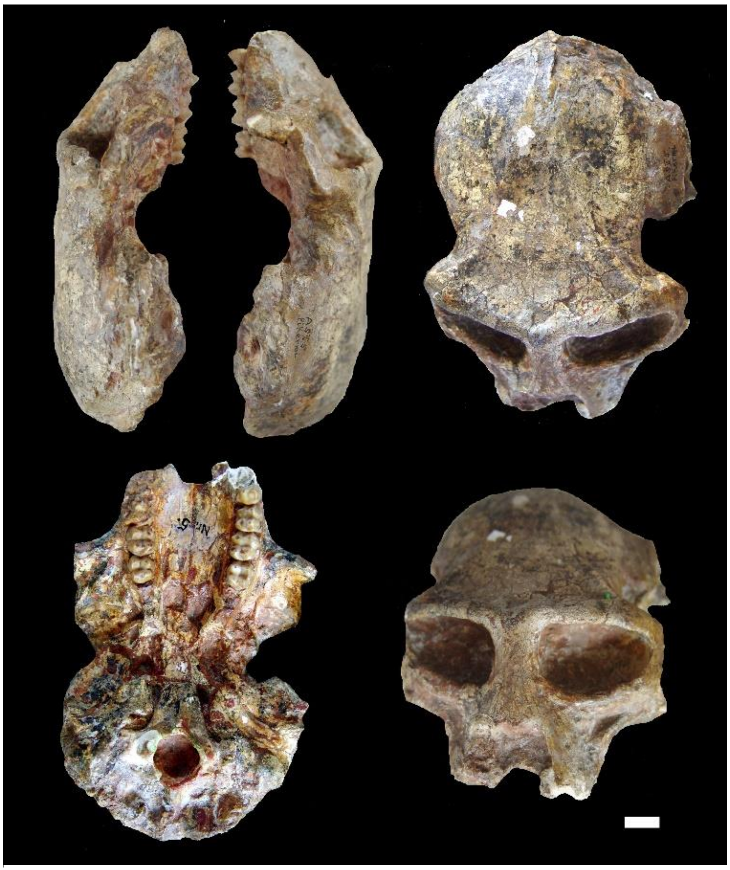

Figure 2. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. Cranium with M1-M3 dex and P4-M3 sin of an adult *male individual, SNSB-BSPG-PIK-AS AS II 5.

Figure 3. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. Left maxillary fragment with C-M3 of an adult male individual, SNSB-BSPG-PIK-AS II 6.

Figure 4. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. Cranial fragment with C-M3 dex and M2-M3 sin of an adult female individual, SNSB-BSPG-PIK-AS II 7.

Figure 5. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. Frontal part of the cranium with complete maxilla and both toothrows of an adult male individual, SNSB-BSPG-PIK-AS II 8,

Figure 6. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. Mandible with i1-m3 dex and p4-m3 sin of an adult male individual, SNSB-BSPG-PIK-AS II 13.

Figure 7. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. Right mandibular fragment with dp3-m2 of a young individual, SNSB-BSPG-PIK-AS II 15.

Figure 8. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. Right mandibular fragment with m1-m3, SNSB-BSPG-PIK-AS II 607.

Figure 9. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. Right upper canine of an adult male individual, SNSB-BSPG-PIK-AS II 16.

Supplement 9 to The Late Miocene Colobine Monkey *Mesopithecus* (Primates, Cercopithecidae) of Greece

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SUPPLEMENT 9

This supplement contains: illustrations of *Mesopithecus pentelicus* from Pikermi, housed at Naturhistorishes Museum, Wien (NHMW) and the Paläontologisches Institut, Universität Wien (PIUW).

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Supplement 9: The Late Miocene colobine monkey *Mesopithecus* (Primates, Cercopithecidae) of Greece

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SUPPLEMENT 9: COLLECTION OF *MESOPITHECUS PENTELICUS* FROM PIKERMI

This file includes: Illustrations of the material stored at Naturhistorishes Museum, Wien (NHMW) and of the Paläontologisches Institut, Universität Wien (PIUW)

NOTE: The sex of the specimens preserving the canines are reported as male and female if it is based on the analysis of their dental dimensions (Fig. 3 in the text); it is marked by an asterisk in the specimens lacking the canines and preserving several postcanine teeth (Fig. 4 in the text) and by a question mark if it is estimated empirically. Scale bar in all figures 10 mm.

Figure 1. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. Cranium and mandible of an adult ?male individual, NHMW-PIK-A.4714.

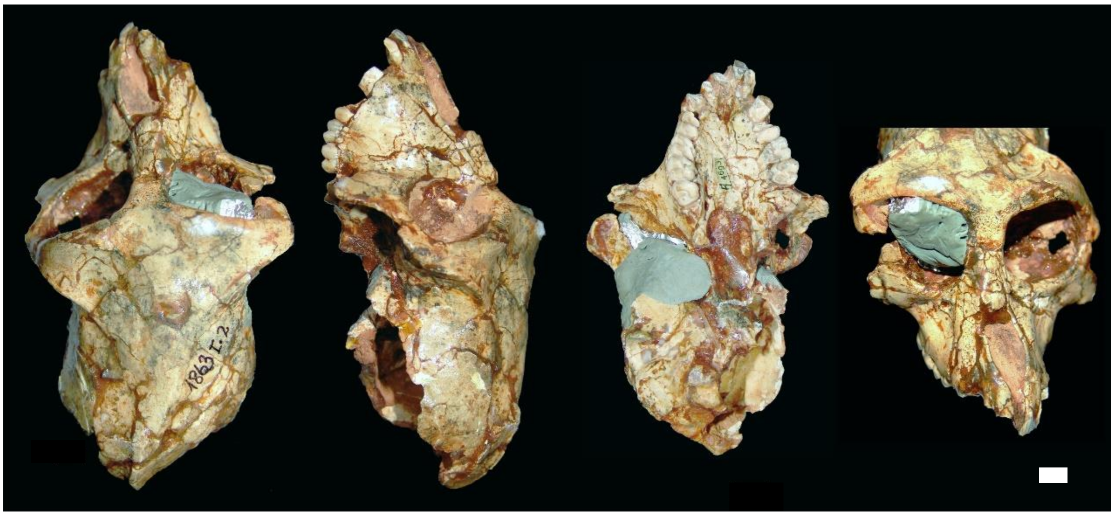

Figure 2. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. Cranium of an adult female individual, NHMW-PIK-A. 4693.

Figure 3. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. Partial cranium of an adult female individual, NHMW-PIK-1863/I, 2.

Figure 4. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. Mandible of an adult male individual, NHMW-PIK-1863/I,

Figure 5. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. Mandible of an adult male individual, NHMW-PIK-1998z

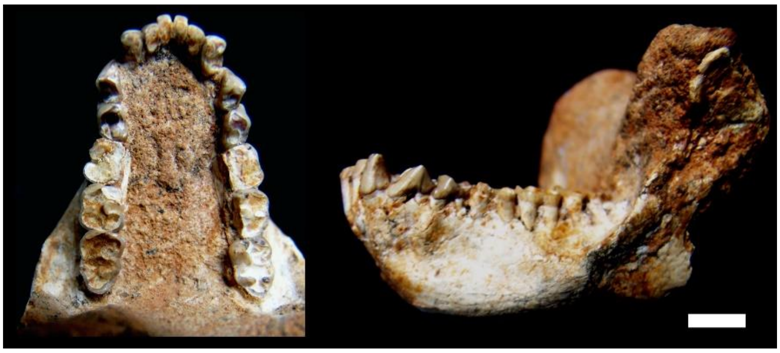

Figure 6. *Mesopithecus pentelicus*, Pikermi, Mandible of an adult female individual, NHMW-PIK-1998z77/13.

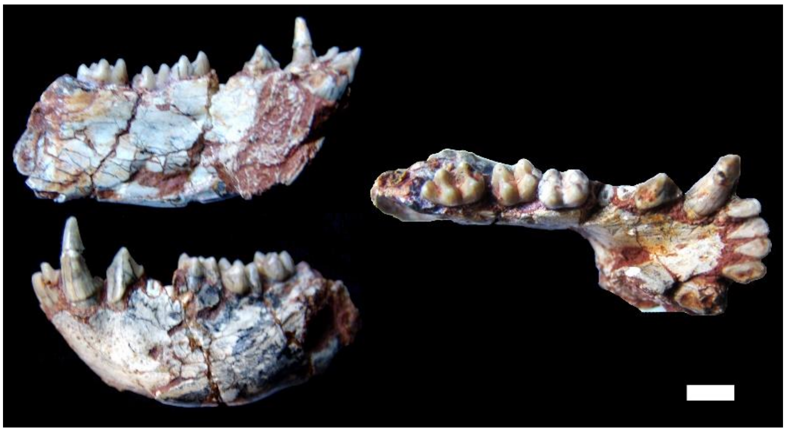

Figure 7. *Mesopithecus pentelicus*, Pikermi, Mandibular fragment of an adult male individual, NHMW-PIK-1972/1578.

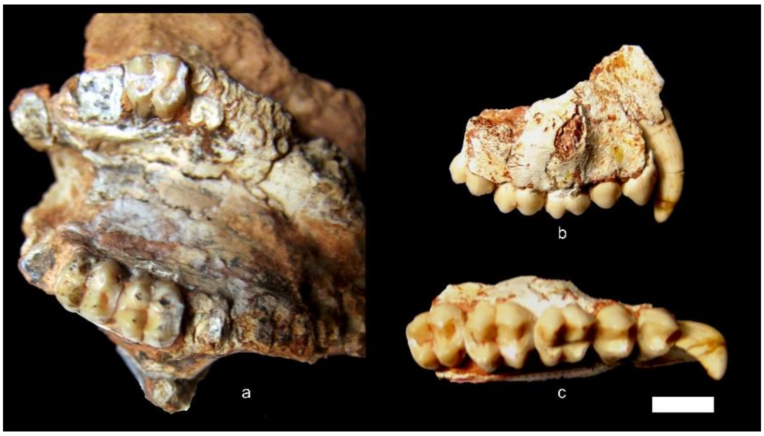

Figure 8. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. a. maxilla of an adult *male individual, NHMW-PIK-1903/IX,2. b-c. Right maxillary fragment of an adult male individual, NHMW-PIK-1998z77/6.

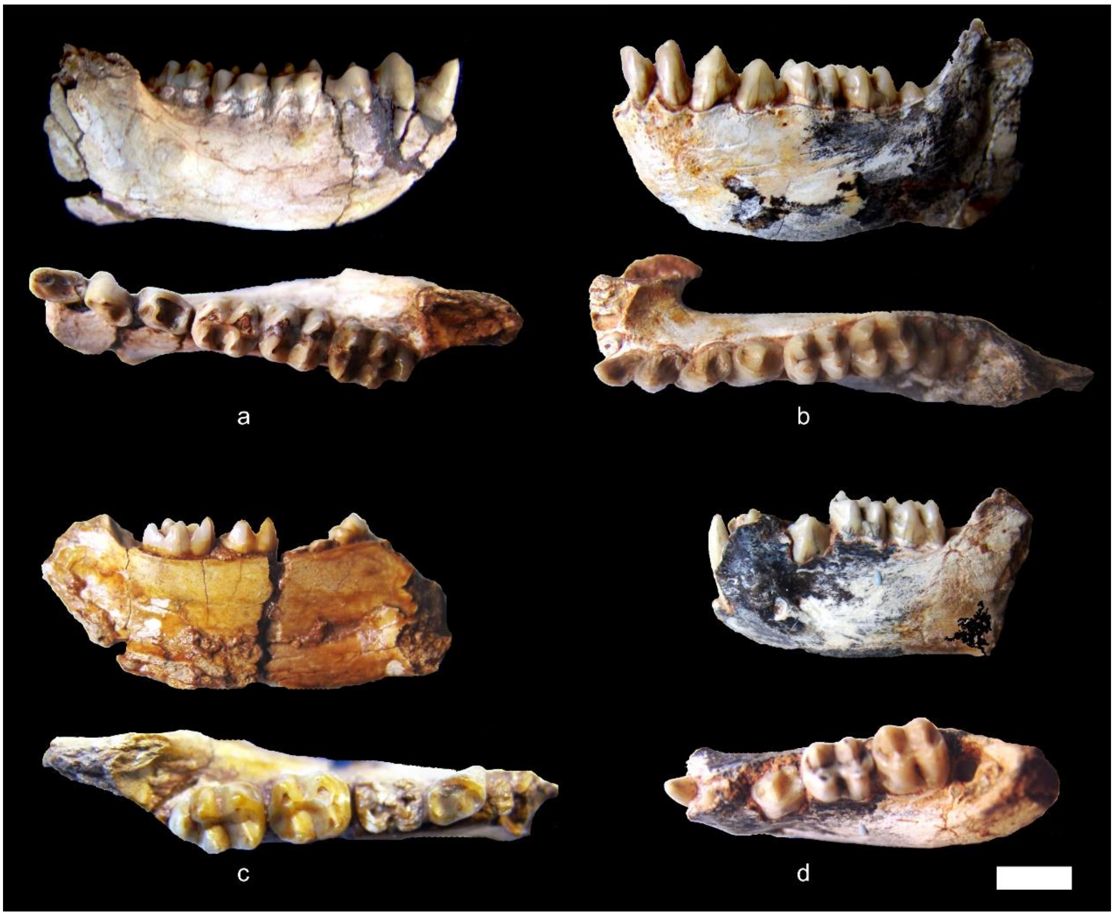

Figure 9. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. a. right mandibular fragment with c-m3 dex of an adult female individual, NHMW-PIK-1998z77/2; b. left mandibular fragment with i2-m2 sin of an adult female individual, NHMW-PIK-1998z77/3; c. left mandibular fragment with p4, m2-m3 of an adult individual, NHMW-PIK-1998z77/7; d. left mandibular fragment with c-m2 of a young adult individual, NHMW-PIK-1998z77/14.

Figure 10. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. Mandible of an adult female individual, PIUW-PIK-316.

Figure 11. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. Mandible of an adult female individual, PIUW-PIK-317.

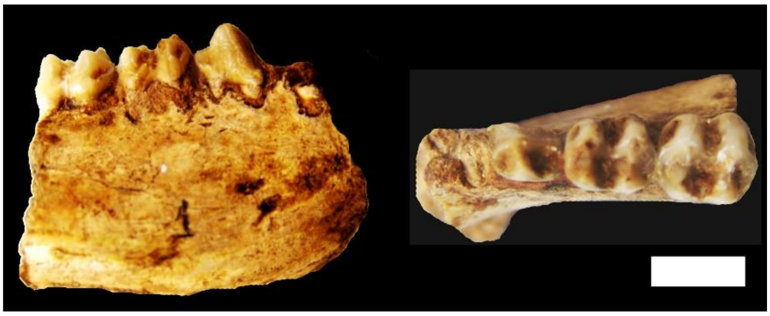

Figure 12. *Mesopithecus pentelicus*, Pikermi, Attica, Greece. Right mandibular fragment with p4-m2 of an adult ?male individual, PIUW-PIK-unumbered.

Supplement 10 to The Late Miocene Colobine Monkey *Mesopithecus* (Primates, Cercopithecidae) of Greece

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SUPPLEMENT 10

This supplement contains: illustrations of the material from the Axios Valley, housed at the Laboratory of Geology and Palaeontology, Aristotle University of Thessaloniki (LGPUT) and the Muséum Nationale d'Histoire Naturelle Paris (MNHMP).

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SUPPLEMENT 10: COLLECTION OF *MESOPITHECUS* FROM AXIOS VALLEY

This file includes: Illustrations of the material stored at the Laboratory of Geology and Palaeontology, Aristotle University of Thessaloniki (LGPUT) and the Muséum Nationale d'Histoire Naturelle Paris (MNHMP)

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Laboratory of Geology and Palaeontology, University of Thessaloniki (LGPUT)

Locality Ravin des Zouaves 5 (RZO)

Figure 1. *Mesopithecus delsoni*, Ravin des Zouaves 5, Axios Valley, Macedonia, Greece. LGPUT-RZO-159, mandible missing both ascending rami of an adult male individual, HOLOTYPE.

Figure 2. *Mesopithecus delsoni*, Ravin des Zouaves 5, Axios Valley, Macedonia, Greece. LGPUT-RZO-160, mandible lacking both ascending rami of an adult male individual.

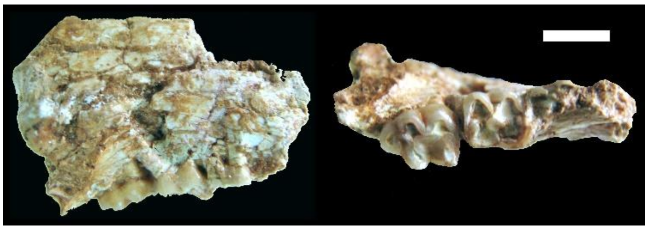

Figure 3. *Mesopithecus delsoni*, Ravin des Zouaves 5, Axios Valley, Macedonia, Greece. LGPUT-RZO-161, right mandibular fragment with m2-m3 of an adult *female individual.

Locality Vathylakkos 2 (VTK)

Figure 4. *Mesopithecus* sp, Vathylakkos 2, Axios Valley, Macedonia, Greece. LGPUT-VTK-56, partial cranium of an adult *female individual badly preserved and strongly deformed.

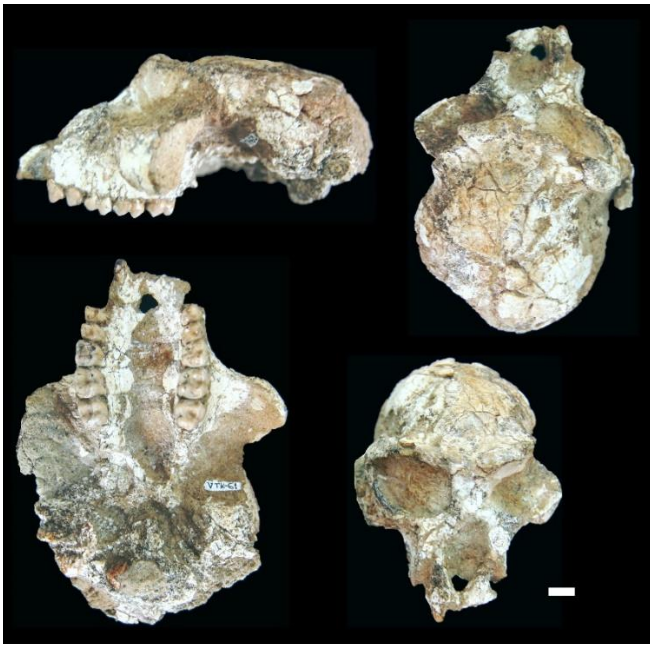

Figure 5. *Mesopithecus* sp., Vathylakkos 2, Axios Valley, Macedonia, Greece. LGPUT-VTK-61, cranium of an adult *male individual.

Figure 6. *Mesopithecus* sp., Vathylakkos 2, Axios Valley, Macedonia, Greece. LGPUT-VTK-62, mandible without ascending rami of an adult female individual.

Figure 7. *Mesopithecus* sp., Vathylakkos 2, Axios Valley, Macedonia, Greece. LGPUT-VTK-78, cranium and associated mandible of a young ?female individual.

Locality Dytiko 1 (DTK)

Figure 8. *Mesopithecus pentelicus*, Dytiko 1, Axios Valley, Macedonia, Greece. LGPUT-DTK-275, left mandibular fragment with p3-m1, m3 of an adult ?male individual.

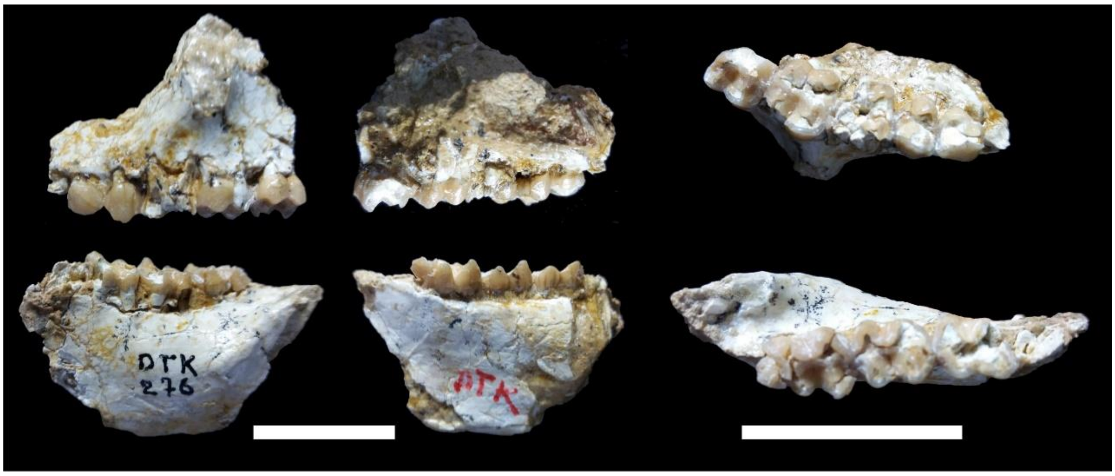

Figure 9. *Mesopithecus monspessulanus*, Dytiko 1, Axios Valley, Macedonia, Greece. LGPUT-DTK-276, right maxillary and associated mandibular fragments with P4-M3 and m1-m3 of an adult *male individual.

Locality Dytiko 2 (DIT)

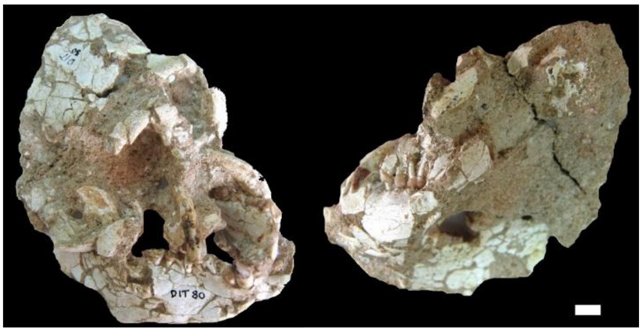

Figure 10. *Mesopithecus pentelicus*., Dytiko 2, Axios Valley, Macedonia, Greece. LGPUT-DIT-21, cranium and mandible of an adult male individual.

Figure 11. *Mesopithecus monspessulanus*, Dytiko 2, Axios Valley, Macedonia, Greece. LGPUT-DIT-22, partial mandible with i1-m2 sin of an adult *male individual.

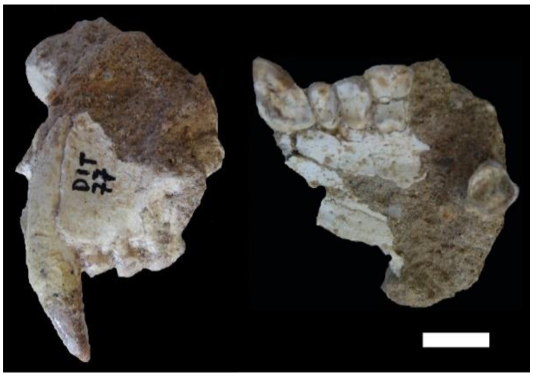

Figure 12. *Mesopithecus pentelicus*, Dytiko 2, Axios Valley, Macedonia, Greece. LGPUT-DIT-25 left maxillary fragment with C- M1 of an adult male individual.

Locality Dytiko 3 (DKO)

Figure 13. *Mesopithecus pentelicus*, Dytiko 3, Axios Valley, Macedonia, Greece. LGPUT-DKO-38, cranium and associated mandible of an adult male individual.

Muséum national d’Histoire naturelle, Paris (MNHNP)

(Arambourg collection)

Figure 14. *Mesopithecus* sp., Ravin de Vatilük (Vathylakkos 3), Axios Valley, Macedonia, Greece. MNHNP-SLQ-939 right mandibular fragment with c-m2 of an adult *male individual.

Figure 15. *Mesopithecus* cf. *delsoni*, Ravin X, Axios Valley, Macedonia, Greece. MNHNP-SLQ-940+941, mandibular fragment with p3-p4 dex and p4-m1 sin of an adult *male individual.

Figure 16. *Mesopithecus* sp., Ravin de Vatilük (Vathylakkos 3), Axios Valley, Macedonia, Greece. MNHNP-SLQ-942, right mandibular fragment with p4, m2-m3 of an adult *male individual.

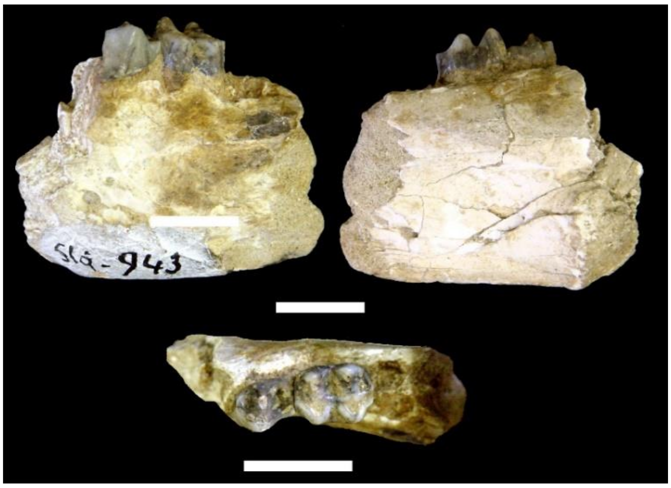

Figure 17. *Mesopithecus* sp., Ravin de Vatilük (Vathylakkos 3), Axios Valley, Macedonia, Greece. MNHNP-SLQ-943, left mandibular fragment with p3-m1 of an adult individual.

Collection Muséum national d'Histoire naturelle, Paris (MNHNP)

(Braillon collection)

Figure 18. *Mesopithecus* sp., Vathylakkos 2, Axios Valley, Macedonia, Greece. MNHNP-SLQ-1126, right maxillary fragment with M1-M3 of an adult individual.

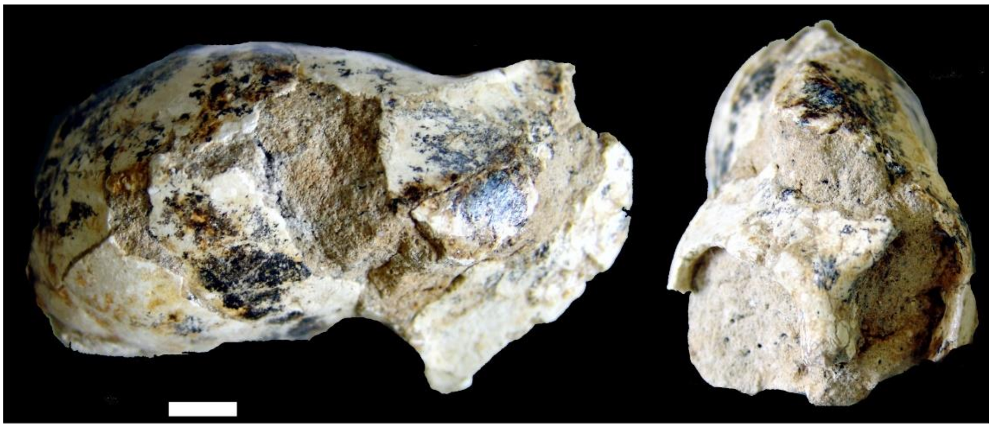

Figure 19. *Mesopithecus* sp., Vathylakkos 2, Axios Valley, Macedonia, Greece. MNHNP-SLQ-1134, partial cranium of an adult individual.

Supplement 11 to The Late Miocene Colobine Monkey *Mesopithecus* (Primates, Cercopithecidae) of Greece

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SUPPLEMENT 11

This supplement contains: illustrations of *Mesopithecus* sp. from Perivolaki, housed at the Laboratory of Geology and Palaeontology Aristotle University of Thessaloniki (LGPUT) and *Mesopithecus pentelicus* from Maramena, housed at Athens Museum of Palaeontology and Geology (AMPG).

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Supplement 11: The Late Miocene colobine monkey *Mesopithecus* (Primates, Cercopithecidae) of Greece

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SUPPLEMENTARY MATERIAL 11: COLLECTION OF *MESOPITHECUS PENTELICUS* AND *MESOPITHECUS* SP. FROM VARIOUS GREEK LOCALITIES

This file includes: Illustrations of the material stored at the Laboratory of Geology and Palaeontology Aristotle University of Thessaloniki (LGPUT) and Athens Museum of Palaeontology and Geology (AMPG).

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Laboratory of Geology and Palaeontology, University of Thessaloniki (LGPUT)

Locality Perivolaki (PER)

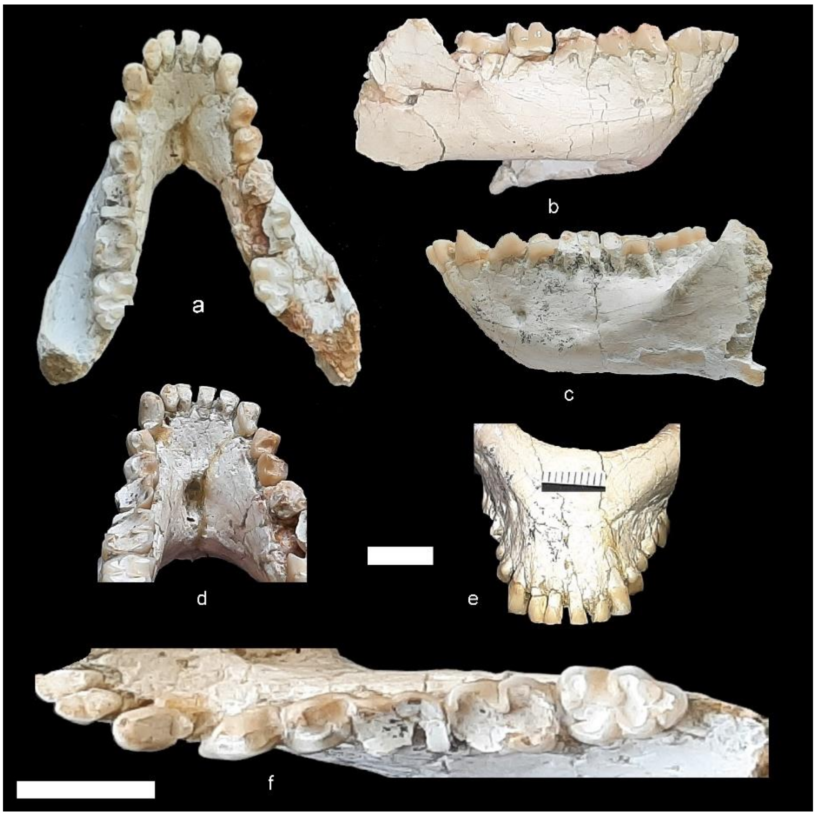

Figure 1. *Mesopithecus* sp., Perivolaki, Velestino, Greece. PER-1284, mandible missing both ascending rami of an adult female individual.

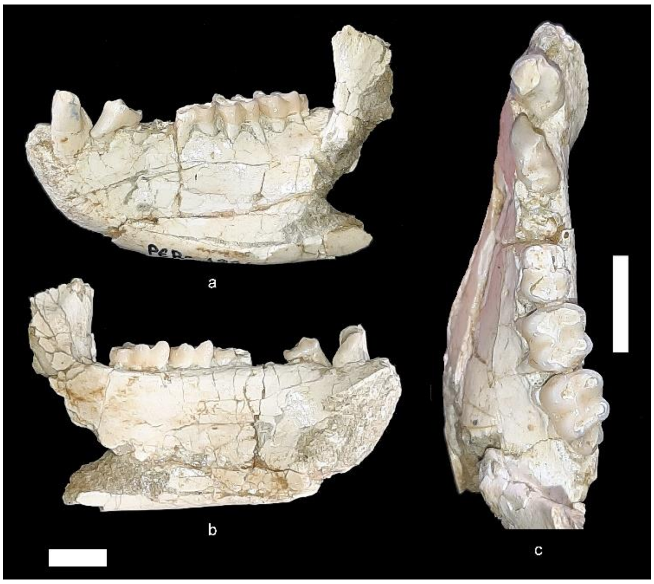

Figure 2. *Mesopithecus* sp., Perivolaki, Velestino, Greece. PER-1284, mandibular fragment with c-p3, m1-m3 of an adult male individual.

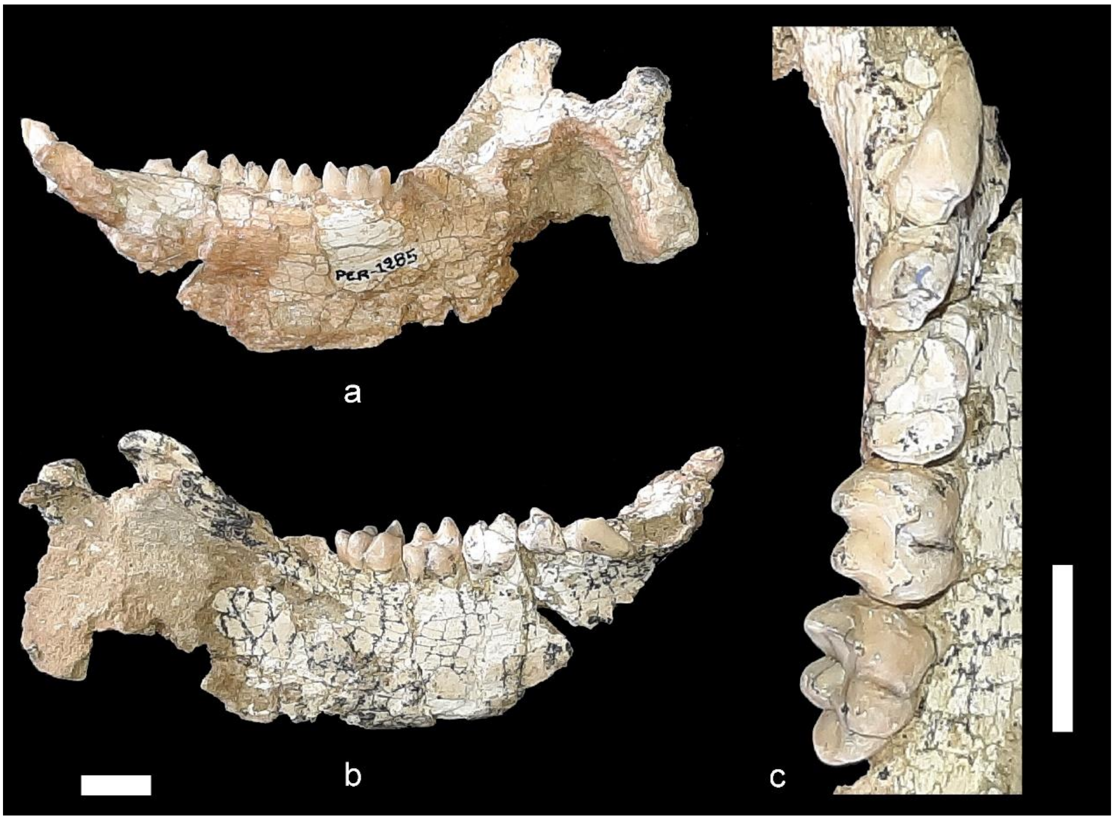

Figure 3. *Mesopithecus* sp., Perivolaki, Velestino, Greece. PER-1285, mandibular fragment with p3-m3 of an adult *male individual.

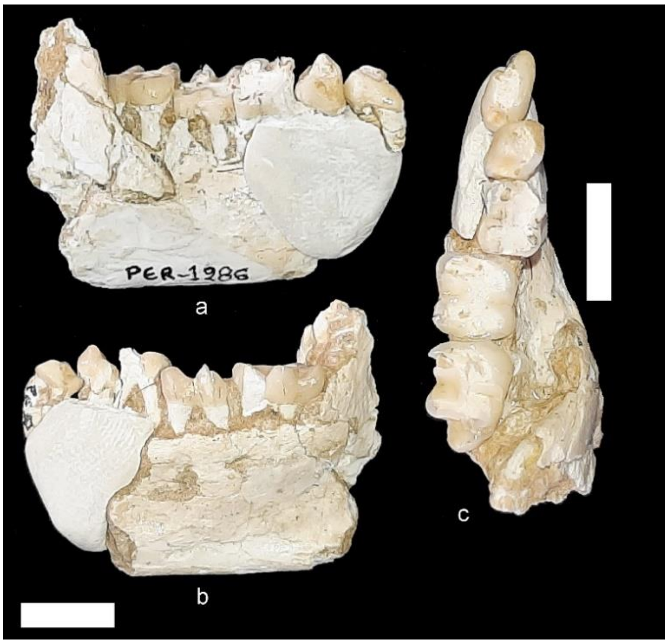

Figure 4. *Mesopithecus* sp., Perivolaki, Velestino, Greece. PER-1286, right mandibular fragment with p3-m3 of an adult *female individual.

Locality Maramena (MAR)

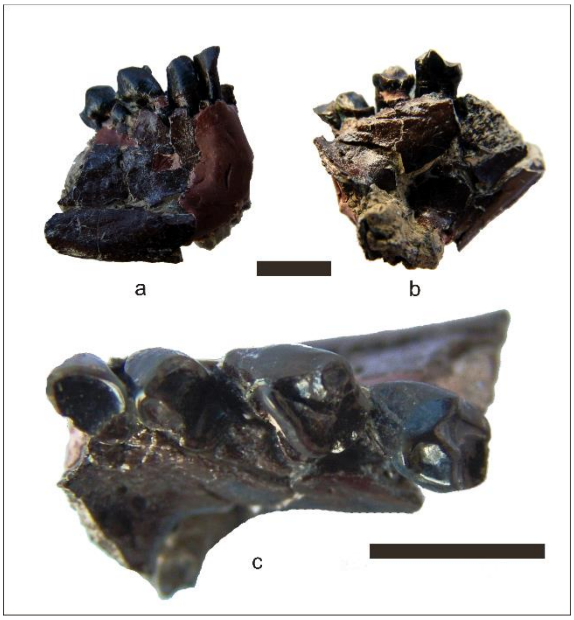

Figure 5. *Mesopithecus pentelicus*, Maramena, Serres Basin, Greece. AMPG-MAR 040, right mandibular fragment with i2-p4 of an adult female individual.

Figure 6. *Mesopithecus pentelicus*, Maramena, Serres Basin, Greece. AMPG-MAR 058, mandibular dentition with i1, p3-m3 dex and i1-12, p3-m3 sin of an adult *male individual.

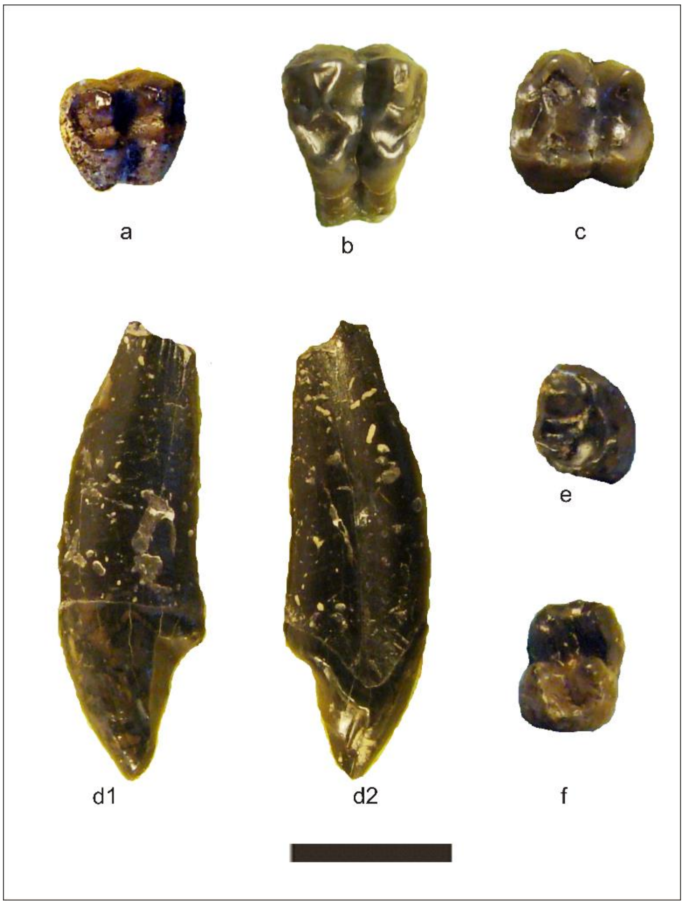

Figure 7. *Mesopithecus pentelicus*, Maramena, Serres Basin, Greece. a. AMPG-MAR 050 right M1; b. AMPG-MAR 020, right M2; c. AMPG-MAR 049, right M3; d. AMPG-MA 053, right c1, d1. buccal and d2. lingual view; e. AMPG-MA 012, right p4; f. AMPG-MA 013, right m1.