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Late Turolian *Mesopithecus* (Mammalia: Cercopithecidae) from Axios Valley (Macedonia, Greece): earliest presence of *M. monspessulanus* in Europe

Mesopithecus *du Turolien final (Mammalia : Cercopithecidae) de la vallée d'Axios (Macédoine, Grèce) : présence du plus ancien* M. monspessulanus *en Europe*

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ABSTRACT

The fossil mammal localities of the Axios Valley (Macedonia, Greece) yielded a rich collection of *Mesopithecus* remains, which were first described at the beginning of the 1990s. The late Turolian Dytiko localities include several specimens of *Mesopithecus*, which were originally separated in two size-related forms: the relatively larger-sized *M.* cf. or aff. *pentelicus*, and the relatively smaller-sized *M.* cf. *monspessulanus*. However, some Dytiko specimens were only partially described, or remained even undescribed because the cranium either was still in connection with the mandible or was markedly deformed. Later, careful cleaning of the materials and their revision based on larger comparative samples indicate that they represent two distinct species: the relatively larger-sized specimens belong to *M. pentelicus*, while the relatively smaller-sized ones to *M. monspessulanus*. The Dytiko *M. pentelicus* has slightly smaller dental dimensions compared to *M. pentelicus* from Pikermi, indicating a possible trend for size decrease. The Dytiko *M. monspessulanus*, although close to the typical form of this species, has somewhat larger dimensions. The semi-terrestrial *M. pentelicus* disappeared at the end of the Miocene, while some of its populations adapted to the wetter and more woody Pliocene habitats, finally giving origin to *M. monspessulanus*, whose elbow-joint indicates an arboreal lifestyle. *M. monspessulanus* was widely distributed in Europe, but its remains are very scarce and are all from the Pliocene. Some questionable indications for the presence of *M. monspessulanus* in the latest Miocene come from some Italian Messinian sites (Gravitelli, Baccinello V3), but this scenario still needs verification. However, even if its presence in some Italian localities was confirmed, the Dytiko *M. monspessulanus* nonetheless represents the earliest known occurrence of this species in Europe, as the Dytiko fauna is considered as latest Turolian (pre-Messinian, 7.0–6.0 Ma).

RÉSUMÉ

Les gisements à mammifères fossiles de la vallée d'Axios (Macédoine, Grèce) offrent une collection assez riche de restes de *Mesopithecus* qui ont été décrits au début des années 1990. Les localités de Dytiko, du Turolien final, comprennent plusieurs spécimens de

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Mesopithecus
Turolien final
Grèce

Mesopithecus, originellement distingués sous deux formes, en fonction de leur taille: *M.* cf. ou aff. *pentelicus*, de taille relativement plus grande, et *M.* cf. *monspessulanus*, de taille relativement plus petite. Toutefois, certains spécimens de Dytiko ont été seulement partiellement décrits, alors que d'autres sont même restés inédits, parce que les crânes étaient encore en connexion avec la mandibule, ou parce qu'ils étaient fortement déformés. Depuis, une préparation minutieuse du matériel, ainsi qu'une révision basée sur des échantillons de comparaison plus grands, permettent désormais d'identifier deux espèces distinctes : l'ensemble des spécimens de taille relativement plus grande appartient à *M. pentelicus* et celui des spécimens de taille plus petite à *M. monspessulanus*. *M. pentelicus* de Dytiko a des dimensions dentaires légèrement plus petites que *M. pentelicus* de Pikermi, ce qui indique un possible processus de diminution de taille. *M. monspessulanus* de Dytiko, bien qu'il soit proche de la forme typique de cette espèce, a des dimensions un peu plus grandes. Le semi-terrestre *M. pentelicus* a disparu à la fin du Miocène, tandis que certaines populations vivant dans des micro-habitats progressivement plus humides et fermés se sont adaptées aux nouvelles conditions du Pliocène et sont à l'origine de *M. monspessulanus*, dont l'articulation du coude indique un mode de vie arboricole. *M. monspessulanus*, bien qu'il soit largement répandu en Europe, reste très rare au Miocène terminal et la majorité des spécimens provient du Pliocène. Même s'il existe quelques indications douteuses de la présence de *M. monspessulanus* dans le Miocène terminal d'Italie (sites de Gravitelli et Baccinello V3), les fossiles de Dytiko sont les plus anciens restes attribués à cette espèce, car ce site est daté du Turolien final (antérieur au Messinien, 7,0–6,0 Ma).

1. Introduction

The Dytiko fossiliferous sites are located in the upper Miocene continental deposits of the lower Axios Valley (Macedonia, Greece), about 40 km northwest of the city of Thessaloniki. They are included in the Dytiko Formation, alternating yellowish–grey marls, sandy marls, gravels, and freshwater massive marly limestones at the top (Koufos, 1990). Three fossiliferous sites have been found in the Dytiko area: Dytiko 1 (DTK), Dytiko 2 (DIT) and Dytiko 3 (DKO), all situated along the ravine Platanoremma, a tributary of the Axios River. The Dytiko localities provided a rich fauna of large mammals, including many taxa. The biochronological data suggest a correlation with the late Turolian, MN 13 (Koufos, 2006a, 2013 and references therein). The faunal comparisons with the well-dated latest Miocene–earliest Pliocene mammal localities of the Ptolemais Basin (Western Macedonia, Greece) suggest a latest Turolian (pre-Messinian) age, between 7.0 and 6.0 Ma (Koufos and Vasileiadou, 2015).

Cercopithecids are present in all Dytiko localities and their fossil remains have been earlier described as belonging to the genus *Mesopithecus*. Two forms were mentioned: one slightly smaller than *M. pentelicus* from Pikermi, described as *M.* cf. or aff. *pentelicus*, and another closer to *M. monspessulanus* from the Pliocene of Montpellier (France), described as *M.* cf. *monspessulanus*. Their identification is mainly based on the specimens DTK-275, DTK-276, DIT-21, DIT-22 and DKO-38 (de Bonis et al., 1990). In the original description of the Dytiko *Mesopithecus*, the specimens DTK-276 and DIT-21 were not detailed, while DKO-38 was described before the cranium and the mandible went separated (de Bonis et al., 1990). Since then, these specimens were cleaned and separated, while this did not occur for DIT-21. A photographic record of the separated cranium and mandible of DKO-38 was provided by Koufos (2009: figure 7A–D), but a full description is not yet available. Accordingly, the present article concerns the revision and the revised identification of the materials cited above following their last preparation and, for some specimens, their cranium–mandible separation, as well as the description and identification of the still unreported remains.

2. Materials and methods

Abbreviations: AMPG = Athens Museum of Palaeontology and Geology; BSPM = Bayerische Staatssammlung für Paläontologie und Historische Geologie München; LGPUT = Laboratory of Geology and PalaeontologyUniversity of Thessaloniki; MNHNP = Muséum national d'histoire naturelle Paris; NHMB = Naturhistorisches Museum Basel; NHMUK = Natural History Museum United Kingdom; NHMW = Naturhistorisches MuseumWien; PIUW = Paläontologische InstitutUniversity of Wien; UM = Université de Montpellier.

The studied *Mesopithecus* material is housed at the LGPUT. The comparative material of *M. pentelicus* includes the Pikermi collections curated at AMPG, MNHNP, NHMUK, BSPM, NHMW, and PIUW. All measurements of the Axios Valley and Pikermi materials are original and have been taken with a digital calliper with 0.1-mm accuracy. The metrical data of *M. monspessulanus* are from the PRIMO database PRIMO, 2019). The software PAST-2019 has been used for PCA calculations. Stefania Veldemiri separated the cranium from the mandible of the specimens DTK-276 and DKO-38.

3. The genus *Mesopithecus*

The genus *Mesopithecus* was originally erected as *M. pentelicus* from Pikermi on the base of the cranial

fragment no. BSPM-AS II housed in Munich (Wagner, 1839), and later it was recognized in several late Miocene and Pliocene Eurasian localities. *Mesopithecus* belongs to the family Cercopithecidae, the ancestry of which is to be found among the Victoriapithecidae (in the past, the victoriapithecids were a subfamily of the Cercopithecidae). Although there is an indication of the presence of victoriapithecids in the latest Oligocene (25.0 Ma), the earliest certain members of the family are known from the Miocene of Africa (Frost, 2017). The victoriapithecids possess a mixture of the characters of the two Cercopithecidae subfamilies, Cercopithecinae and Colobinae, but also share characters with the earliest Hominoidea (Benefit, 1999; Benefit and McCrossin, 2002). Divergent date estimates suggest that the colobines and cercopithecines went separated by 14.7 Ma (13.2–16.2 Ma) (Sterner et al., 2006).

The first Cercopithecidae are known from the Tugen Hills, Kenya, and are dated to 12.5 Ma (Rossi et al., 2013). According to Szalay and Delson (1979), the first cercopithecids were similar to the modern macaques, with elongated extremities, arboreal or semi-arboreal way of life, feeding mainly on fruits and supplementing their diet with leaves. The cercopithecids dispersed into Europe from Africa at the beginning of the Turolian. The earliest evidence is from the early Turolian Greek localities Nikiti 2 (NIK) (8.7–8.2 Ma) and Ravin des Zouaves 5 (RZO) (~8.2 Ma) (Koufos, 2009, 2016). However, there is an isolated tooth from the Vallesian locality of Wissberg (Germany), which has been attributed to *Mesopithecus*, but its origin has been questioned (Andrews et al., 1996). The presence of *Mesopithecus* in the Vallesian of Grossulovo (Ukraine) is also questionable (see Koufos, 2003). *Mesopithecus* is also reported from the Ukrainian locality Grebeniki 1 (or Grebeniki; Gremyatskii, 1961), whose age is debated. Indeed, while it was originally dated to the Meotian (early Turolian), it is currently correlated with the late Vallesian, MN 10 (Vangengeim and Tesakov, 2013). All other European evidences of *Mesopithecus* (Bulgaria, FYROM, Romania and Hungary) are correlated with the Turolian and the Pliocene (Andrews et al., 1996). The mandible of *Mesopithecus* from Maragheh (Iran), included in the Middle Maragheh fauna (~8.24 Ma, i.e. early Turolian), displays differences with the typical *Mesopithecus* from Pikermi (Bernor et al., 1996; de Bonis et al., 1990; Delson, 1973) and has similarities with the early Turolian *M. delsoni* from the penecontemporaneous Ravin des Zouaves 5 locality (de Bonis et al., 1990; Sen et al., 2000). The Molayan (Afghanistan) *Mesopithecus* mandible is similar to the Pikermi ones and it is dated to the middle Turolian, MN 12 (Heintz et al., 1981; Sen, 1998). Since the end of the 19th century, fossil cercopithecids are also mentioned from the Siwaliks (Pakistan). The revision of the "Dhok Pathan" cercopithecids suggests they belong to a ~7.5 Ma-old single species, *Mesopithecus sivalensis* (Harrison and Delson, 2007). *Mesopithecus* was recently recognized in the Chinese site of Shuitangba (Yunnan Province), whose palaeomagnetic record suggests an age of 6.5–6.0 Ma (Jablonski et al., 2014). Based on the currently available fossil record, *Mesopithecus* certainly appeared in Eurasia at the beginning of the Turolian, although there are indications for an earlier arrival of this taxon still needing for verification and further support.

Mesopithecus is the common late Miocene–Pliocene colobine of Eurasia with four known species: *M. delsoni, M. pentelicus, M. monspessulanus,* and *M. sivalensis*. As reported above, fossil remains of these taxa have been found in Europe and Asia but, remarkably, they are absent in Samos and Turkey (Alba et al., 2015; Andrews et al., 1996; Delson, 1973; Delson et al., 2005; Jablonski et al., 2014; Koufos, 2009; Pradella and Rook, 2007; Radović et al., 2013; Radulescu et al., 2003; Tobien, 1986). Close relationships of *Mesopithecus* with the Asian colobines (Tribe Presbytini) were first suggested on palaeobiogeographical grounds (Delson, 1973; Szalay and Delson, 1979). Later, cladistic analyses based on morphological characters suggested very close relationships with the Asian odd-nosed colobines, especially with *Pygathrix* (Jablonski, 1998; Pan et al., 2004).

Mesopithecus appeared in the Turolian, a period of warm and dry climatic conditions in the Mediterranean area. Its semi-terrestrial habits (Delson, 1973; Szalay and Delson, 1979; Youlatos et al., 2012 and references therein) granted its survival in the more open and/or mixed habitats of that period. Later, at the end of Miocene, appeared a smaller form of *Mesopithecus* that adapted to wetter conditions and woody habitats and had a more arboreal life style (Szalay and Delson, 1979). During the Turolian, a decrease in the body size of *Mesopithecus* clearly occurred, from the larger *M. delsoni* to the smaller *M. monspessulanus* through a series of intermediate forms (de Bonis et al., 1990; Koufos, 2009a). Unlike its modern closest relatives, the dental microwear analysis of the Greek and Bulgarian *M. pentelicus* sample indicates a non-leaf eater, but a semi-terrestrial opportunistic feeder that often consumed hard seeds (Merceron et al., 2009a, b).

4. Systematic palaeontology

Order Primates Linnaeus, 1758
Superfamily Cercopithecoidea Gray, 1821
Family Cercopithecidae Gray, 1821
Subfamily Colobinae Blyth, 1863
Genus *Mesopithecus* Wagner, 1839

4.1. *Mesopithecus pentelicus* Wagner, 1839

Synonyms. *Mesopithecus* cf. *pentelicus* in de Bonis et al., 1990 (DTK material); *Mesopithecus* aff. *pentelicus* in de Bonis et al., 1990 (DIT and DKO material); *Mesopithecus* cf. M. *pentelicus* in Koufos, 2009 (DTK material); *Mesopithecus* aff. *M. pentelicus* in Koufos, 2009 (DIT and DKO material).

Locality. Dytiko 1 (DTK), Dytiko 2 (DIT) and Dytiko 3 (DKO); Axios Valley, Macedonia, Greece.

Age. Late Turolian, MN 13, late Miocene; based on the available biochronological data, the age is estimated as latest Turolian (pre-Messinian), between 7.0 and 6.0 Ma (Koufos and Vasileiadou, 2015 and references therein).

Material. Male cranium and associated mandible DKO-38; male cranium and associated mandible DIT-21; left male maxillary fragment DIT-25 with C–M1 and M3; left mandibular fragment DTK-275, possibly male, with p3–m1 and m3.

Table 1
Dental measurements (in mm) of the Dytiko *Mesopithecus* sample.
Tableau 1
Mesures dentaires (en mm) de l'échantillon *Mesopithecus* de Dytiko.

Upper teeth	DTK-276	DIT-25	DIT-21		DKO-38		Lower teeth	DTK-275	DTK-276	DIT-21		DIT-22	DKO-38	
	sin	sin	dex	sin	dex	sin		sin	sin	dex	sin	sin	dex	sin
SEX	?	male	male		male		SEX	?	?	male		male	male	
Premolar length	9.7	9.3	–	9.4	9.9	–	Premolar length	12	–	–	–	10.9	9.7	–
Molar length	19.9	–	22.9	–	19.9	–	Molar length	[24.2]	23.1	24.1	–	22.3	22.7	–
LI1	–	–	–	–	–	4.3	Li1	–	–	–	–	2.5	–	–
BI1	–	–	–	–	–	4.8	Bi1	–	–	–	–	3.2	–	–
LI2	–	–	–	–	–	–	Li2	–	–	–	–	3.0	–	–
BI2	–	–	–	–	–	–	Bi2	–	–	–	–	3.9	–	–
LC	–	9	9.1	9.3	7.6	–	Lc	–	–	7.6	7.3	6.9	6.8	7.1
BC	–	7.5	6.7	6.7	7.3	–	Bc	–	–	5.5	5.5	4.6	6.4	6.4
LP3	4.3	4.6	5.1	5.5	5.5	–	Lp3	5.7	–	–	6.3	6.3	5.3	–
BP3	5.2	6.3	4.5	–	6.1	–	Bp3	4.2	–	–	3.6	3.7	4.1	–
LP4	4.2	5.6	4.8	4.8	4.8	4.4	Lp4	6	–	–	5.6	5.1	5.3	5.1
BP4	5.5	7.3	6.3	–	6.5	6.5	Bp4	4.5	–	–	–	4.0	4.4	4.6
LM1	6.4	6.8	–	6.7	6.9	–	Lm1	–	7.0	–	6	6.7	6.6	6.4
BM1A	–	–	–	–	7.8	–	Bm1A	–	–	–	–	–	5.3	5.8
BM1P	–	–	–	–	7.7	–	Bm1P	–	5.6	–	–	5.4	6.4	6.2
LM2	7.4	–	–	–	6.2	–	Lm2	–	7	7.8	6.4	7.0	7.6	7.0
BM2A	7.9	–	–	–	7.5	–	Bm2A	–	6.0	6.6	–	6.0	6.4	–
BM2P	7.2	–	–	–	7.1	–	Bm2P	–	6.0	6.8	–	6.2	6.7	6.4
LM3	6.1	7	7	–	7	–	Lm3	9.5	8.9	8.5	8.7	8.6	8.8	8.8
BM3A	6.1	7.4	7.1	–	6.6	–	Bm3A	6.2	6.3	6.4	–	6.1	6.2	5.9
BM3P	–	6.1	6	–	5.3	–	Bm3P	5.8	5.3	6.2	–	5.6	5.8	5.7

Table 2
Mandibular measurements (in mm) of the *Mesopithecus* samples from Dytiko, Villafranca d'Asti and Pikermi.
Tableau 2
Mesures mandibulaires (en mm) des échantillons de *Mesopithecus* de Dytiko, Villafranca d'Asti et Pikermi.

Mandible	DTK-276 ?	DIT-21 Male	DIT-22 Male	DKO-38 Male	*M. monspessulanus* UM 4043 Female	VJ 87 Male	VJ 130 Male	*M. pentelicus*, Pikermi Mean Male	Mean Female
	Original measurements					Pradella & Rook, 2007		Original measurements	
Labial height below p3	–	–	20.5	22	–	–	–	21.44 (19.0–24.7)	18.24 (15.2–21.0)
Idem below p4	–	–	20.5	21.8	17.0	19.3	19.8	21.07 (18.3–24.0)	18.09 (15.0–21.5)
Idem below m1	18.9	22.3	[19.0]	22.5	17.0	19.6	20.4		
Idem below m2	< 19.8	23.7	18.1	21.7	16.1	–	–	20.86 (18.5–22.8)	17.56 (15.2–22.0)
Mandibular thickness below m1	7	?8.0	7.3	9.4	7.5	6.5	7.1		
Mandibular thickness below m2	7.8	?7.6	8.2	8.9	8.2	–	–		
					Cast				

Measurements. The measurements are given in Tables 1 and 2.

4.1.1. Description

Cranium and associated mandible DKO-38. This laterally compressed specimen was originally described when cranium and mandible were still joined (de Bonis et al., 1990). It belongs to an aged individual lacking the left facial part and part of the cranial roof (Fig. 1A). The large and sharp upper and lower canines, the strong, thickened and projected supraorbital torus, and the well-defined sagittal crests indicate a male individual (Koufos et al., 2003; Szalay and Delson, 1979). The right orbit is well preserved, but it is deformed by lateral compression of the skull and became egg-shaped (Fig. 1A_4). The zygomatic bone lies deep below the orbit. The upper dentition preserves the right tooth row, the left broken canine, and the P4 (Fig. 1A_3, $_5$). The upper canine, although worn, is large, sharp, with large lingual wear surface, strong distal projection and triangular basal occlusal outline. The occlusal surface of the molars is extremely worn. The mandible preserves the right mandibular ramus and part of the left one, the latter lacking the ascending portion (Fig. 1B_1). The external aspect of the symphysis is slightly distorted but, as in *M. pentelicus*, it is rounded, without lateral constriction. The mandibular corpus is relatively deep (Table 2), with straight ventral margin. The ascending ramus is not high, the distance from the coronoid process to the ventral margin of the corpus corresponding to 51.0 mm. The condyle is small (length = 11.3 mm; breadth = 6.1 mm) and the coronoid process is low. The height measured from the coronoid process to the condyle is 10.3 mm. The lower dentition preserves both series, lacking only the incisors (Fig. 1$B_{1,2}$). The lower canine, bearing a large wearing facet on the distal

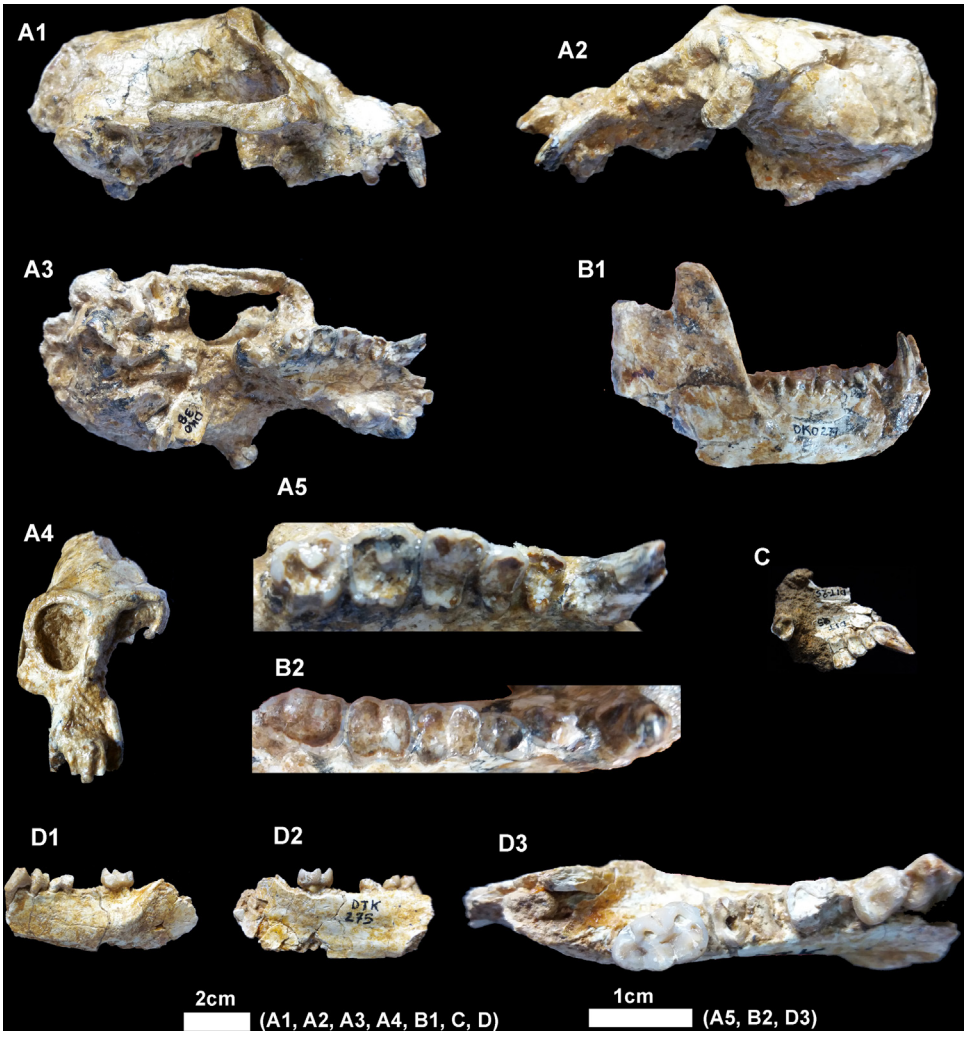

Fig. 1. *Mesopithecus pentelicus*, Dytiko 3 (DTK). A: Cranium and associated mandible of DKO-38. A1: right lateral view; A2: left lateral view; A3: ventral view; A4: frontal view; A5: upper dentition in occlusal view. B: right mandibular branch DKO-38. B1: lateral view; B2: occlusal view. C: left maxillary fragment with C–M1 and M3 DIT-25 in occlusal view. D: left mandibular fragment with p3–m1 and m3 DTK-275. D1: labial view; D2: lingual view: D3: occlusal view.

Fig. 1. *Mesopithecus pentelicus*, Dytiko 3 (DTK). A : crâne et mandibule associés de DKO-38. A1 : vue latérale droite ; A2 : vue latérale gauche ; A3 : vue ventrale ; A4 : vue frontale ; A5 : série dentaire supérieure en vue occlusale. B : fragment de mandibule DKO-38. B1 : vue latérale ; B2 : vue occlusale. C : fragment de mandibule gauche avec C–M1 et M3 DIT-25 en vue occlusale. D : fragment de mandibule gauche avec p3–m1 et m3 DTK-275. D1 : vue labiale ; D2 ; vue linguale ; D3 : vue occlusale.

surface and a large distal projection, is strong and sharp. The p3 has a clear honing facet extending to its mesiolingual root. The molars are markedly worn.

Cranium and associated mandible DIT-21. The specimen, crushed and strongly compressed laterally, was originally numbered as DIT-80 (de Bonis et al., 1990: appendix 1). It belongs to a rather old individual bearing a markedly worn dentition (Fig. 2). Attempts to separate the mandible from the cranium were unsuccessful. During our intervention, a small part from the right maxilla went broken and thus it was possible to photograph and measure the teeth. The right orbit is partially preserved, but it is deformed. The right mandibular ramus, although crushed, is better preserved than its counterpart. It is relatively high and likely thick, as its measured thickness is slightly smaller than the real one due to crushing and compression (Table 2). The upper dentition preserves the right C–P4 and M3 and the left C–M3. The well-preserved left upper canine is large, worn and sharp, with a triangular basal outline in occlusal view. The right P3 and P4 are nearly entirely worn and their occlusal surface consists of a large dentine pit surrounded by thin enamel. The preserved M3 is also worn and has an almost rounded occlusal outline. The lower dentition is nearly complete, lacking the left i1 and i2, as well as the right p3 (Fig. 2F). The lower canines are strong and sharp, with developed distal projections and strongly worn distal surfaces. The well-preserved left p3 is elongated and narrow; its wear resulted into a large distal fovea and a honing facet extending to its mesial root, as well as into an entirely worn labial cuspid. The p4 and m1

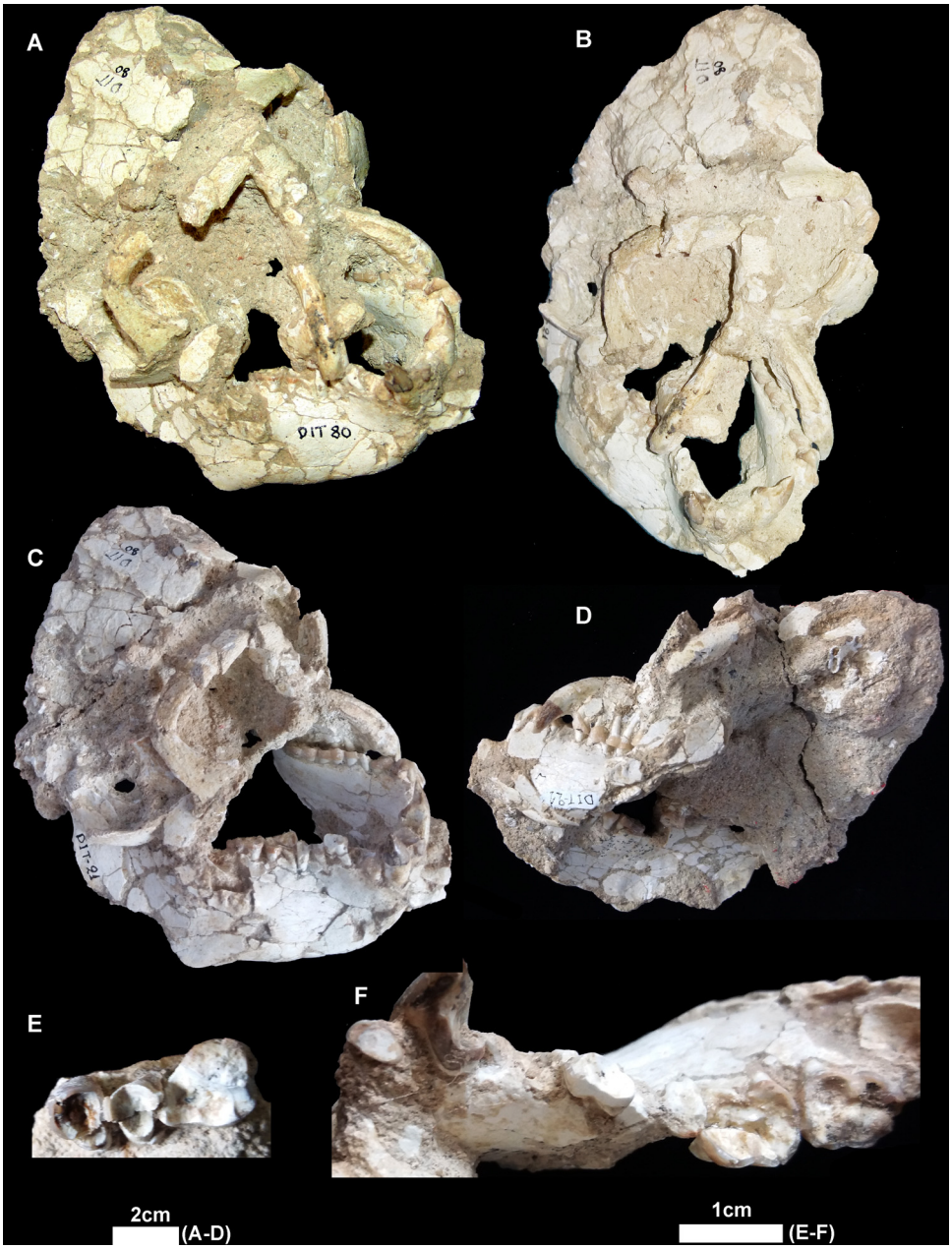

Fig. 2. *Mesopithecus pentelicus*, Dytiko 2 (DIT). A–F: Cranium and associated mandible DIT-21. A: The specimen before the last cleaning. B: frontal view. C: right lateral view. D: left lateral view. E: left upper tooth row C–P3 in occlusal view. F: right lower tooth row c, p4–m3 in occlusal view.
Fig. 2. *Mesopithecus pentelicus*, Dytiko 2 (DIT). A–F : crâne et mandibule associés DIT-21. A : le spécimen avant sa préparation. B : vue frontale. C : vue latérale droite. D : vue latérale gauche. E : rangée dentaire supérieure gauche C–P3 en vue occlusale. F : rangée dentaire inférieure droite c, p4–m3 en vue occlusale.

are either entirely worn (what remains of the right m1 is just a root), or indiscernible/unreadable. However, the m3 is less worn than the other molars and preserves a small hypoconulid.

Left maxillary fragment with C–M1 and M3 DIT-25. It is a small maxillary fragment with extremely worn teeth (Fig. 1C). The canine is large and similar to the other specimens. A clear groove, extending to the root, can be seen on its mesial surface. The canine root is long and strong (mesial height of the root = 26.8 mm).

Left mandibular fragment with p3–m1 and m3 DTK-275. The specimen is erroneously mentioned as DTK-235 (de Bonis et al., 1990: fig. 7; appendix 1). It lacks the ventral margin of the mandibular corpus, the ascending ramus and the m2 (Fig. 1D). The p3 bears two cuspids, a large labial (protoconid) and a small lingual one (metaconid); its mesial fovea is small, while the distal one is large. The honing facet is well-developed, extending to the mesial root of the tooth. The p4 is more symmetric than the p3, with a rectangular occlusal outline. It bears two mesial

cuspids, a small mesial fovea and a larger distal one. The m3 has the typical form for *Mesopithecus*, with four cuspids and a small and monocuspid hypoconulid.

4.1.2. Discussion

DKO-38 has been originally described as *M.* aff. *pentelicus* based on some differences with respect to the typical *M. pentelicus* from Pikermi (comparisons limited to the MNHNP collection) (de Bonis et al., 1990) and this attribution was later reported in all articles referred to the Axios Valley *Mesopithecus*. The original determination mostly relies on the smaller and higher orbits, the thicker supraorbital torus, the zygomatic bone higher under the orbit, and the slightly deeper canine fossa. In the initial description, the comparison of the dentition was not possible because cranium and mandible were still in connection. Their recent separation and new comparisons with a larger sample of *M. pentelicus* from Pikermi (collections of the MPGA, MNHNP, NHMUK, BSPM, NHMW and PIW) currently allow a revised identification of this specimen.

Most of the *M. pentelicus* skulls from Pikermi have a deformed face, the best-preserved specimen being NHMUK-M. 8945. The shape of the orbit of DKO-38 differs from that of M. 8945. In DKO-38, the maximal orbital height and breadth correspond to 24.2 mm and 21.4 mm, respectively, while in the Pikermi sample they range between 19.7–25.5 mm and 23.0–30.0 mm, respectively. However, the difference for the orbital breadth clearly results from the lateral compression and deformation suffered by DKO-38. The thickness of the supraorbital torus of DKO-38 is 4.8 mm, which is well within the range of variation of *M. pentelicus* fromPikermi (3.6–5.5 mm) and Kalimantsi (4.2–5.0 mm; Koufos et al., 2003). At first glance, DKO-38 seems to have a deeper zygomatic bone than *M. pentelicus*; however, the distance from the lowermost point of the orbit to the zygomaxillary suture of DKO-38 is 16.8 mm, which is within the range of variation of the *M. pentelicus* from Pikermi (13.2–18.0 mm; Delson, 1973). The canine fossa (= suborbital fossa) looks slightly deeper than in *M. pentelicus*, but again this is likely due to cranial deformation. According to de Bonis et al. (1990), the dental size of DKO-38 fits better the estimates of *M. pentelicus*. Indeed, most dental dimensions of DKO-38 support this interpretation, but some measurements are smaller, even when compared to those of the mean female *M. pentelicus* (Fig. 3A, B). Such differences could indicate a slight dental size decrease in the late Turolian forms of *M. pentelicus*.

Principal Component Analysis (PCA) of the upper and lower cheek teeth dimensions of DKO-38 and of the large dental samples of *M. pentelicus* from Pikermi and Kryopigi (Greece) and Kalimantsi (Bulgaria) provides distinct comparative evidence (Fig. 4). The upper dentition of *M. monspessulanus* is not included in the PCA because the known material is scarce (see Section 4.2.2). The PC1 for the upper teeth (Fig. 4A), which accounts for 67.9% of the total variance, well separates *M. pentelicus* males and females, respectively located within its positive and negative spaces. In this comparative context, the upper dentition of DKO-38 is closer to that of the *M. pentelicus* males, but the dimensions of the upper postcanine teeth are slightly smaller than those typical of this taxon. Concerning the lower teeth, the PC1 (62% of variance) again separates males and females of *M. pentelicus* (Fig. 4B). However, the PC2 (19.4% of variance) separates *M. pentelicus* from *M. monspessulanus*, located at its positive and negative parts, respectively. DKO-38 falls within the convex hull of the *M. pentelicus* males, suggesting size similarities with this species (Fig. 4B). Besides their morphological similarity with those of the *M. pentelicus* males, the upper and lower canines of DKO-38 are also included within the male size variation of this species, thus supporting most likely attribution of DKO-38 to a male individual (Fig. 5).

The strong deformation and the extreme dental wear of DIT-21 inhibit some morphological comparisons; accordingly, its comparison with *M. pentelicus* is mainly based on the dental size. The upper dental dimensions of DIT-21 are close to the mean of the estimates of female *M. pentelicus*, except those of the canine and the P3 length. The P3 breadth is remarkably smaller than measured in female *M. pentelicus* individuals, but this is likely due to its extreme wear (Fig. 3A). However, the upper canine morphology and size are similar to those of the male *M. pentelicus* specimens (Figs. 4A). The lower teeth of DIT-21, except the canine, are generally shorter than those of *M. pentelicus*, but their breadth fits with those of this species (Fig. 3B). In the PCA diagram for the lower teeth, DIT-21 falls within the convex hull for the male *M. pentelicus* (Fig. 4B). Moreover, its lower canine has large size and matches the values reported for the male *M. pentelicus* (Fig. 5B).

The specimen DIT-25 does not display maxillary and dental morphological characters suitable for taxonomic assessment, and its determination is uniquely based on dental dimensions, which are close to the estimates for the male *M. pentelicus* (Fig. 3A). Its canine morphology and its size (Fig. 5A) suggest that it represents a male individual. In the PCA diagram, DIT-25 plots near the convex hull of the male *M. pentelicus* individuals (Fig. 4A), which confirms its specific and sexual attribution.

The mandibular fragment DTK-275, possibly erroneously reported as *M. monspessulanus* by Jablonski (2002), preserves the m3. Except for the m3 breadth, the dental dimensions in this specimen are similar to the mean of those recorded for the male *M. pentelicus* (Fig. 3B). In the PCA diagram, DTK-275 plots together with *M. pentelicus* within the PC2 positive space, but its sex attribution is uncertain as it is situated in an intermediate position between *M. pentelicus* males and females (Fig. 4B). Although DTK-275 has only modestly worn teeth, some of its dental dimensions are smaller than those of *M. pentelicus*, especially the breadth of the molars (Fig. 3B). The narrow lower molars are the main distinctive character separating *M. monspessulanus* from *M. pentelicus* (Delson, 1973), thus indicating that some *monspessulanus*-like features appeared in the late Turolian forms of *M. pentelicus.*

In conclusion, the relatively large-sized Dytiko *Mesopithecus* is similar in size and morphology to *M. pentelicus* and can be attributed to this species. However, the Dytiko *M. pentelicus* preserves some characters (e.g., narrow lower molars, slightly smaller dental dimensions) similar to those of *M. monspessulanus,* thus suggesting relationships between the two taxa.

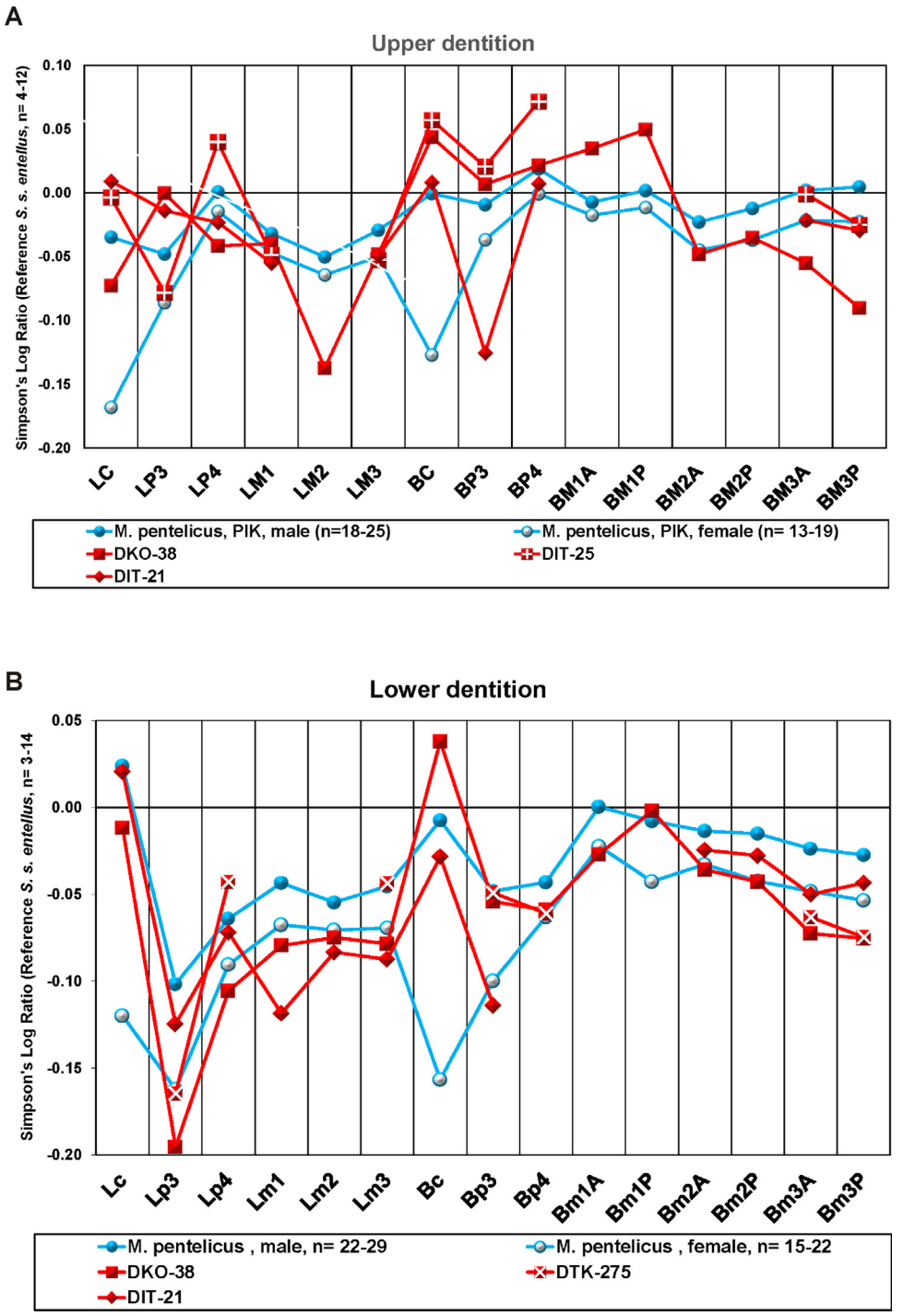

Fig. 3. Simpson's Log-ratio diagram based on the upper (A) and lower (B) dental dimensions of *M. pentelicus* from Dytiko and Pikermi (Attica, Greece). Reference: *Semnopithecus entellus*, recent. Data source: PRIMO database (Primo, 2019) for *S. e. entellus* and personal data for *M. pentelicus*.
Fig. 3. Diagramme de Log-ratio de Simpson basé sur les dimensions dentaires supérieures (A) et inférieures (B) de *M. pentelicus* de Dytiko et Pikermi (Attique, Grèce). Référence : *Semnopithecus entellus*, récent. Source : PRIMO database (Primo, 2019) pour *S. e. entellus* et données personnelles pour *M. pentelicus*.

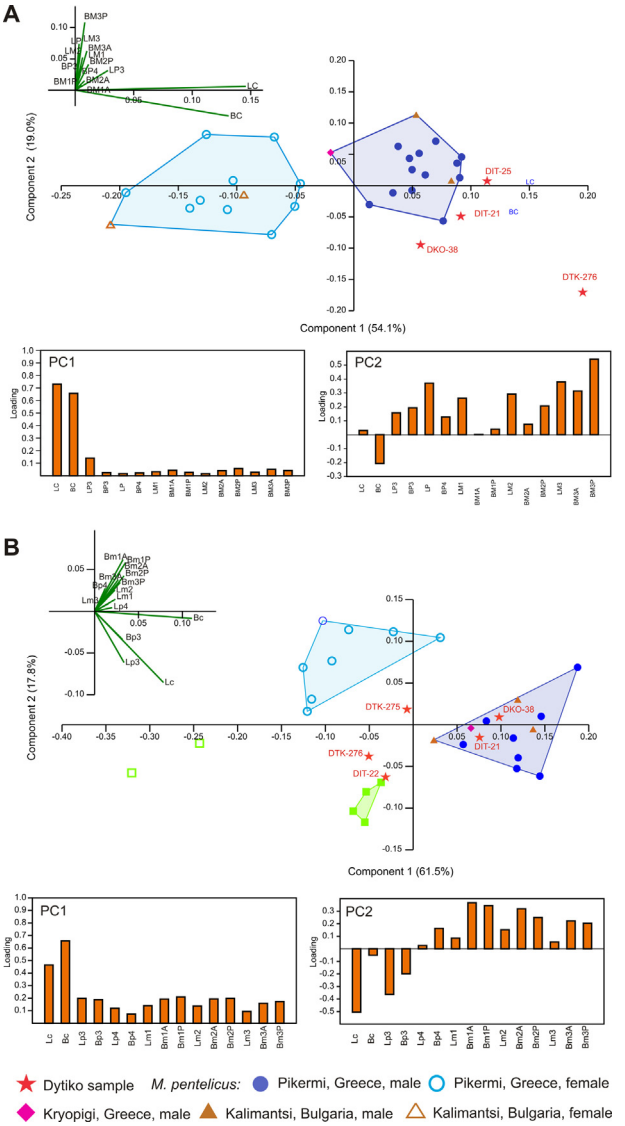

Fig. 4. Principal Component Analysis (PCA) loading dental dimensions (mesio-distal and bucco-lingual diameters) of the Dytiko material representing *M. pentelicus* from Pikermi and Kryopigi (Greece) and Kalimantsi (Bulgaria) and *M. monspessulanus* from various European sites, using Mosiman's log-ratio transformation. The principal component loadings are also given. Data source: PRIMO database (Primo, 2019) for *M. monspessulanus*, Lazaridis et al. (2018) and personal data for *M. pentelicus*. Filled circle (cyan): *M. pentelicus*, Pikermi, male; open circle (cyan): *M. pentelicus*, Pikermi, female; filled diamond (fuchsia): *M. pentelicus,* Kryopigi, male; filled triangle (brown): *M. pentelicus,* Kalimantsi, male; open triangle (brown): *M. pentelicus,* Kalimantsi, female; filled square (green): *M. monspessulanus*, Europe, male; square (green): *M. monspessulanus*, Europe, female.

Fig. 4. Analyse en composantes principales (ACP) avec les dimensions dentaires (diamètres mésio-distal et bucco-lingual) du matériel de Dytiko représentant *M. pentelicus* de Pikermi et Kryopigi (Grèce) et Kalimantsi (Bulgarie) et *M. monspessulanus* de plusieurs sites européens, en utilisant la transformation log-ratio de Mosiman. Les charges principales des composants sont également données. Source : PRIMO database (Primo, 2019) pour *M. monspessulanus,* Lazaridis et al. (2018) et données personnelles pour *M. pentelicus*. Cercle plein (bleu) : *M. pentelicus*, Pikermi, mâle ; cercle vide (bleu) : *M. pentelicus*, Pikermi, femelle ; losange plein (fuchsia) : *M. pentelicus,* Kryopigi, mâle ; triangle plein (marron) : *M. pentelicus,* Kalimantsi, mâle ; triangle vide (marron) : *M. pentelicus,* Kalimantsi, femelle ; carré plein (vert) : *M. monspessulanus*, Europe, mâle ; carré vide (vert) : *M. monspessulanus*, Europe, femelle.

4.2. Mesopithecus monspessulanus Gervais, 1849

Synonyms. *Mesopithecus* cf. *monspessulanus* in de Bonis et al. (1990); *Mesopithecus* cf. *M. monspessulanus* in Koufos (2009).

Locality. Dytiko 1 (DTK), Dytiko 2 (DIT), Axios Valley, Macedonia, Greece.

Age. Late Turolian, MN 13, late Miocene; based on the available biochronological data, the age is estimated as latest Turolian (pre-Messinian), between 7.0 and 6.0 Ma (Koufos and Vasileiadou, 2015 and references therein).

Material. Male maxillary and associated mandibular fragments DTK-276, possibly male; male mandible DIT-22 with i1-m2.

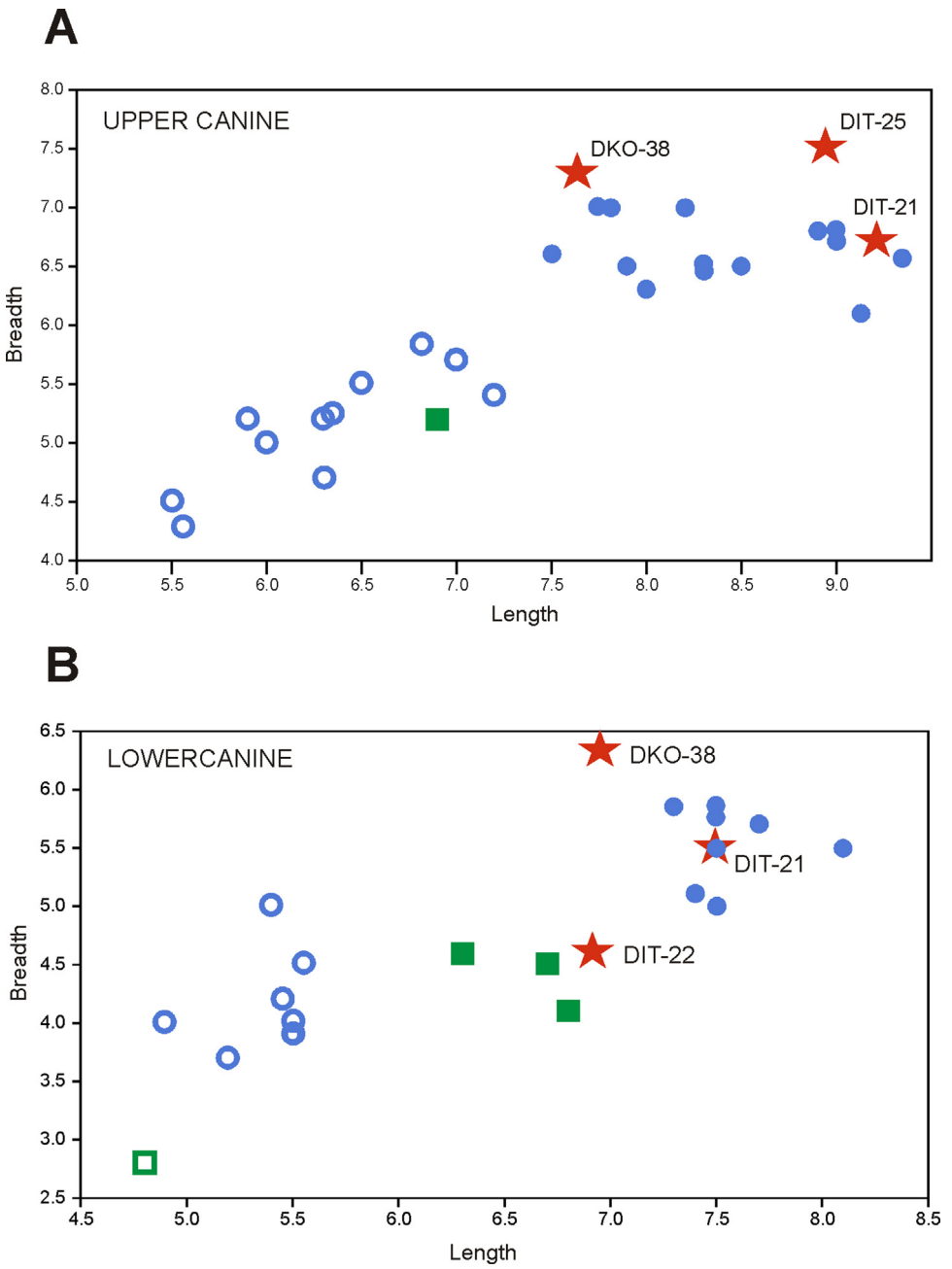

Fig. 5. Scatter plots comparing the upper (A) and lower (B) canine dimensions of the Dytiko material representing *M. pentelicus* from Pikermi and *M. monspessulanus* from various European sites. Data source: PRIMO (primo.nycep.org, 2019) for *M. monspessulanus* and personal data for *M. pentelicus*. Abbreviations as in Fig. 4.

Fig. 5. Diagrammes comparant les dimensions des canines supérieures (A) et inférieures (B) du matériel de Dytiko représentant *M. pentelicus* de Pikermi et *M. monspessulanus* de plusieurs sites européens. Source : PRIMO database (Primo, 2019) pour *M. monspessulanus* et données personnelles pour *M. pentelicus*. Abréviations : voir Fig. 4.

Measurements. The measurements are given in Tables 1 and 2.

4.2.1. Description

Male mandible with i1–m2 DIT-22. The specimen (Fig. 6A) has been described earlier (de Bonis et al., 1990: fig. 7B).

Maxillary and associated mandibular fragments DTK-276. The specimen is reported as DTK-240 in the original publication (de Bonis et al., 1990: appendix 1). It belongs to an adult individual and preserves the P4–M3 tooth row (Fig. 6B). The base of the zygomatic arch is well distinct, and its anterior margin is situated above the M1/M2 contact (Fig. 6B_1). The P3 has an almost triangular

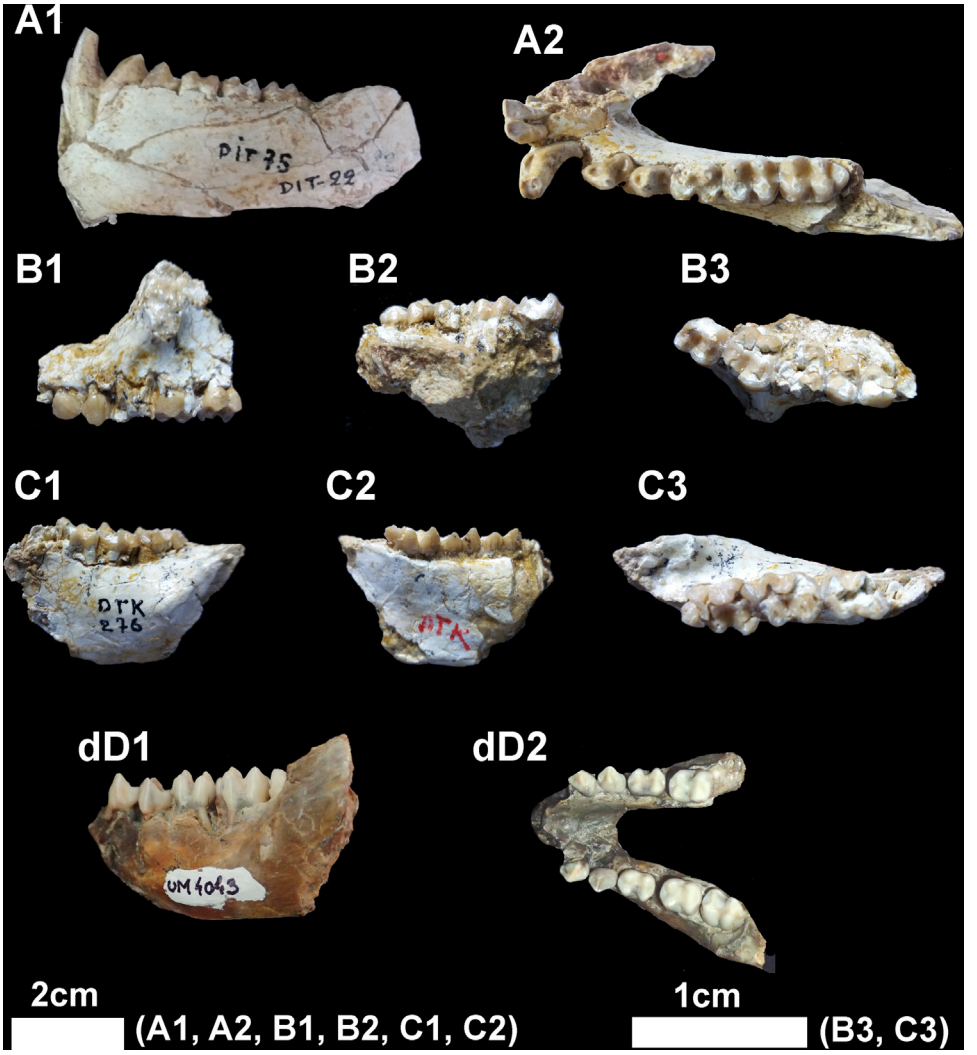

Fig. 6. A–C: *Mesopithecus monspessulanus*, Dytiko 1, 2 (DTK, DIT). A: Male partial mandible with i1-m2 DIT-22. A1: left lateral view; A2: occlusal view. B–C: Maxillary and associated mandibular fragments DTK-276, unknown sex. B1–C1: labial view; B2–C2: lingual view; B3–C3: occlusal view. D. *Mesopithecus monspessulanus*: UM 4043 mandible (Montpellier, France; Ruscinian, MN 14). D1: left lateral view; D2: occlusal view.
Fig. 6. A–C. *Mesopithecus monspessulanus*, Dytiko 1, 2 (DTK, DIT). A : fragment de mandibule avec i1-m2 DIT-22, male. A1 : vue latérale gauche ; A2 : vue occlusale. B–C. Fragments de maxillaire et de mandibule associés DTK-276, sexe inconnu. B1–C1 : vue labiale ; B2–C2 : vue linguale : B3–C3 : vue occlusale. D. *Mesopithecus monspessulanus* : mandibule UM 4043 (Montpellier, France ; Ruscinien, MN 14). D1 : vue latérale gauche ; D2 : vue occlusale.

shape; the mesio-labial corner projects mesially, giving a triangularly-shaped occlusal outline. It bears two main cusps, the labial one being higher than the more worn lingual cusp. The occlusal surface is worn, forming a large dentine pit originating from the connection of the corresponding pits on the cusps and the foveae (Fig. 6B_3). The P4 is also bicuspid, but more symmetric and less worn than the P3, with a more rounded occlusal outline. The M1 is badly preserved, having been partially damaged during the separation of the maxilla from the mandible. The M2 lacks the buccal part of the metacone; the paracone is the largest cusp and the metacone is the smallest one. The M3, lacking the lingual part of the hypocone, is similar in shape to the M2, but smaller.

The mandibular fragment DTK-276 preserves the molars and the p4 root (Fig. 6C). The corpus is shallower than typical in *M. pentelicus* (Table 2). The molars are well preserved, except the mesio-labial part of the m1. The m1 is worn, bearing a large dentine pit almost covering the entire occlusal surface; the protoconid and hypoconid are more worn than the paraconid and the metaconid. The well-preserved m2 is similar in morphology to the m1. The less worn m3 is elongated and bears a fifth cuspid (hypoconulid) (Fig. 6C_3).

4.2.2. Discussion

Mesopithecus monspessulanus was originally found in Montpellier, France, in the middle Ruscinian freshwater marls of the foundations of the Palais de Justice (Delson, 1973). The known European material of *M. monspessulanus* is scarce and fragmentary, one of the best known specimens being the female mandible UM 4043 from the Pliocene site

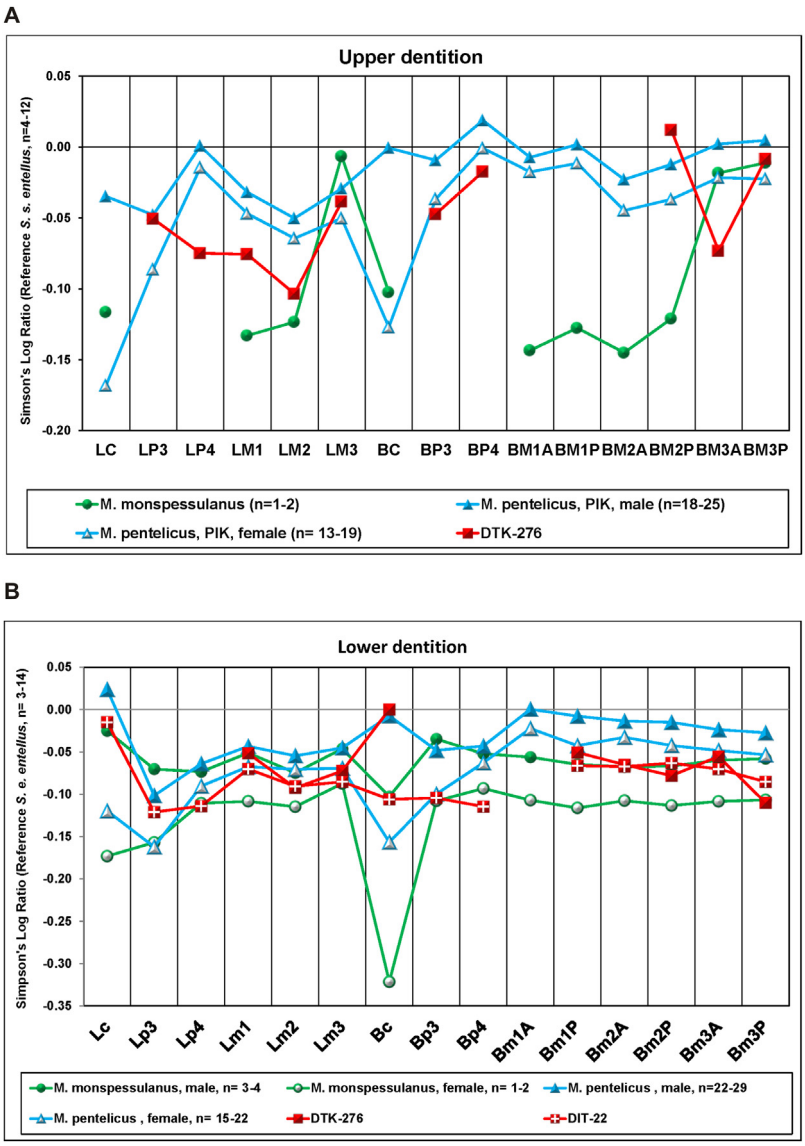

Fig. 7. Simpson's log-ratio diagrams based on the upper (A) and lower (B) dental dimensions of *M. monspessulanus* from Dytiko and other European sites and of *M. pentelicus* from Pikermi (Attica, Greece). Reference: *Semnopithecus entellus*, recent. Data source: PRIMO database (Primo, 2019) for *S. e. entellus* and *M. monspessulanus* and personal data for *M. pentelicus*.

Fig. 7. Diagrammes de log-ratio de Simpson basés sur les dimensions dentaires supérieures (A) et inférieures (B) de *M. monspessulanus* de Dytiko et d'autres gisements européens et de *M. pentelicus* de Pikermi (Attique, Grèce). Référence : *Semnopithecus entellus*, récent. Source : PRIMO database (Primo, 2019) pour *S. e. entellus* et *M. monspessulanus* et données personnelles pour *M. pentelicus.*

of Montpellier described and figured by Mauche (1906: pl. VII, fig. 5–6), as well as two male fragmentary mandibles (NHMB-VJ 87 and NHMB-VJ 130) and a male left hemimandible from Villafranca d'Asti (Italy), dated to the upper Pliocene, MN 16, 3.3–3.0 Ma (Gentili et al., 1998; Hürzeler, 1967; Pradella and Rook, 2007; Rook et al., 2001). The comparison of DTK-276 and DIT-22 with a cast of UM 4043, housed at the LGPUT, shows that the height and thickness of the mandibular corpus are similar (Table 2). The mandibular dimensions of the Greek material are also similar to those of the Italian specimens of *M. monspessulanus* (Table 2). The main difference of *M. monspessulanus* with *M. pentelicus* is its smaller and narrower lower teeth (Delson, 1973). The Simpson logarithmic ratio diagrams comparing the mean dental dimensions of DTK-276 and DIT-22 show that they are closer to *M. monspessulanus*, more precisely to the males of this species (Fig. 7B). In the PCA diagram for the lower teeth (Fig. 4B), DTK-276 and DIT-22 are close to the convex hull defined by the male *M. monspessulanus* representatives. In DIT-22, the presence of the canine tooth confirms its sexual attribution, as it distinctly matches with the male canines of *M. monspessulanus* (Fig. 5B). Conversely, DTK-276 lacks the canine and it is thus difficult to certify its sex. Nonetheless, its location

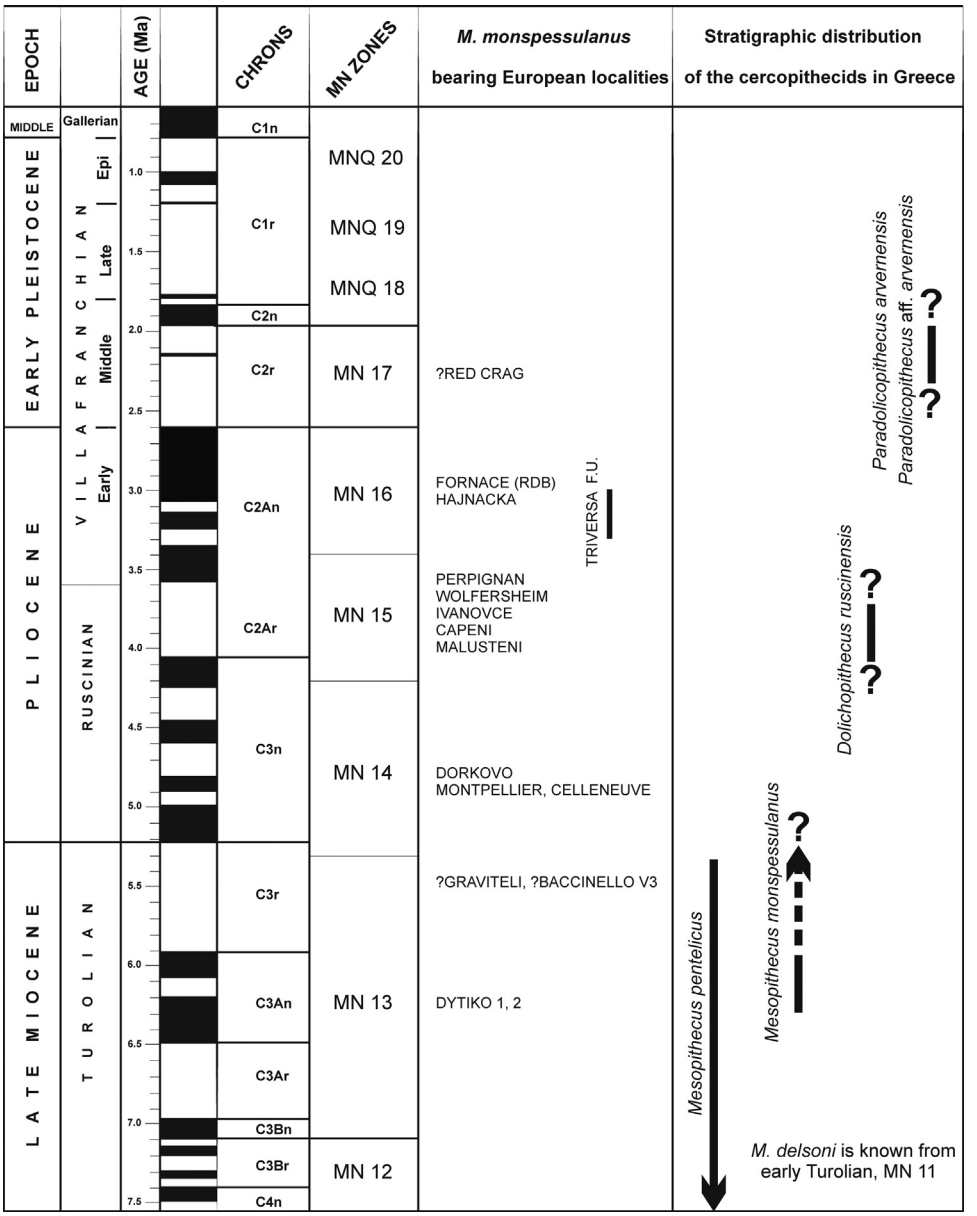

Fig. 8. Biostratigraphic distribution of *M. monspessulanus* in Europe and that of the cercopithecids in Greece.
Fig. 8. Répartition biostratigraphique de *M. monspessulanus* en Europe et celle des Cercopithecidae en Grèce.

within the PCA diagram suggests a slightly larger size than typically measured in the Pliocene representatives of this species.

The available European *M. monspessulanus* remains bearing upper teeth are scanty and consist of a few isolated teeth of unknown sex. In the PRIMO database (Primo, 2019), one male upper canine, as well as one m1, one m2 and two m3s of unknown sex, are included, and we used them in a Simpson diagram comparing the upper dentition (Fig. 7A). The maxillary fragment DTK-276 has generally smaller dental dimensions than measured in *M. pentelicus*, although some are close to this species. It is also interesting that the M3 size (mean of two specimens one from Dorkovo, Bulgaria, and another from Red Grag, England) are very close to *M. pentelicus*, which suggests that their attribution may deserve revision.

Based on the currently available morphological and dimensional record, the relatively small-sized Dytiko sample of *Mesopithecus* (DTK-276 and DIT-22) can be more confidently attributed to *M. monspessulanus*. However, its absolute dental dimensions are slightly larger than those measured in the typical Pliocene *M. monspessulanus* representatives.

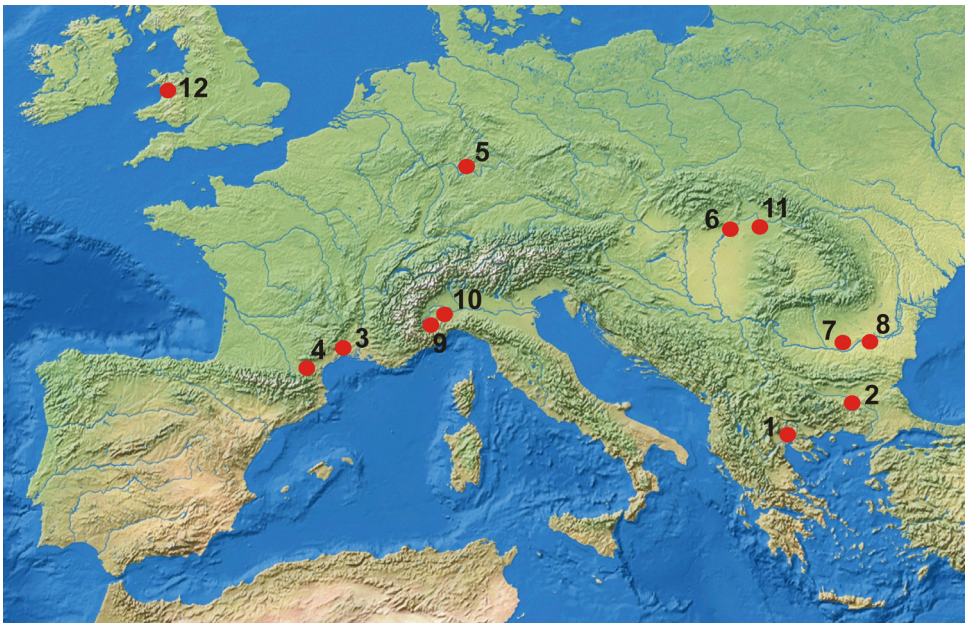

Fig. 9. Geographic distribution of *M. monspessulanus* in Europe. 1: Dytiko (DTK, DIT), Greece, MN 13 (c. 7.0–6.0 Ma, latest Turolian [pre–Messinian]); 2: Dorkovo, Bulgaria, MN 14 (5.3–4.2 Ma); 3: Montpellier (type locality and Celleneuve), France, MN 14 (5.3–4.2 Ma); 4: Perpignan, France, MN 15 (4.2–3.4 Ma); 5: Wolfersheim, Germany, MN 15 (4.2–3.2 Ma); 6: Ivanovce, Slovakia, MN 15 (4.2–3.4 Ma); 7: Capeni, Romania, MN 15 (4.2–3.4 Ma); 8: Malusteni, Romania (MN 15 (4.2–3.4 Ma); 9: Villafranca d'Asti (Fornace RDB), Italy, MN 16 (3.4–2.6 Ma); 10: Villafranca d'Asti (Triversa F.U.), Italy, MN 16–17 (3.4–1.95); 11: Hajnácka, Slovakia, MN 16 (3.4–2.6 Ma); 12: Red Crag (?), England, MN 17 (?) (ca. 2.3 Ma?). The age of the localities is taken from NOW (2019), except for Dytiko (from Koufos and Vasileiadou, 2015).

Fig. 9. Répartition géographique de *M monspessulanus* en Europe. 1 : Dytiko (DTK, DIT), Grèce, MN 13 (environ 7,0–6,0 Ma, Turolien final [pré–Messinien]) ; 2 : Dorkovo, Bulgarie, MN 14 (5,3–4,2 Ma) ; 3. Montpellier (localité type et Celleneuve), France, MN 14 (5,3–4,2 Ma) ; 4 : Perpignan, France, MN 15 (4,2–3,4 Ma) ; 5 : Wolfersheim, Allemagne, MN 15 (4,2–3,2 Ma) ; 6 : Ivanovce, Slovaquie, MN 15 (4,2–3,4 Ma) ; 7 : Capeni, Roumanie, MN 15 (4,2–3,4 Ma) ; 8 : Malusteni, Roumanie (MN 15 (4.2–3.4 Ma) ; 9. Villafranca d'Asti (Fornace RDB), Italie, MN 16 (3.4–2.6 Ma) ; 10 : Villafranca d'Asti (Triversa F.U.), Italie, MN 16–17 (3,4–1,95) ; 11 : Hajnácka, Slovaquie, MN 16 (3,4–2,6 Ma) ; 12 : Red Crag (?), Angleterre, MN 17 (?) (environ 2,3 Ma?). L'âge des localités est issu de NOW (2019), à l'exception de celui de Dytiko (d'après Koufos et Vasileiadou, 2015).

5. Conclusions

Mesopithecus is present in the fossil record from the early Turolian to the beginning of the Pleistocene (but its presence in the Vallesian is doubtful; see Section 3). Its presence in the late Turolian is rare but interesting, as it probably includes more than one species. Late Turolian *Mesopithecus* specimens had been reported under various specific names (e.g., Ardito and Mottura, 1987; Delson, 1973; Gentili et al., 1998; Szalay and Delson, 1979). In Italy, Seguenza (1902, 1907) described some cercopithecid teeth from Gravitelli (Sicily) under the name of *M. monspessulanum*. Later, the Gravitelli material underwent destruction and all younger references to this assemblage are based on the descriptions and illustrations provided by Seguenza (1902, 1907). Delson (1973) refers the Gravitelli material as?*M. monspessulanus*, and later Andrews et al. (1996) and Rook (1999) referred it as *Mesopithecus* sp. Because of its small size, an m2 tooth (IGF 7507V) from the latest Turolian (latest Messinian) site of Baccinello V3 (Italy) was described as close to *M. monspessulanus* (Rook, 1999). The same author also described another m1 tooth (IGF 7508V) from Paganico, Italy (sediments equivalent in age to Baccinello V3), as slightly larger and closer in size to *M. pentelicus*, thus supposing that these two teeth could belong to two morphs attributable based on the dental size to *M. monspessulanus* and *M. pentelicus*, respectively. However, the material is very limited to support such a conclusion, the reason why it is referred to as *Mesopithecus* sp. (Rook, 1999). Moreover, *M.* cf. *pentelicus* was recognized in the Monticino gypsum quarry of Brishigella (Faenza) and *M. pentelicus* in the Casino Basin, both Italian localities dated to the latest Turolian (Rook, 1999). Some *Mesopithecus* remains, mainly consisting of isolated deciduous teeth, are known from the locality of Maramena in the Serres Basin (Macedonia, Greece), which is dated to the Turolian/Ruscinian (MN 13/14, ~5.4–5.2 Ma, end of the Messinian salinity crisis; Koufos and Vasileiadou, 2015 and references therein). This material has been assigned to *M. pentelicus* (Kullmer and Doukas, 1995). However, as the known deciduous teeth of both *M. pentelicus* and *M. monspessulanus* are rare, their features and dimensions are still poorly documented, thus preventing reliable determinations. Accordingly, until its revision, it is preferable to refer the Maramena sample as *Mesopithecus* sp.

The appearance of *M. monspessulanus* at the end of Miocene is very likely related to some palaeoenvironmental changes. Such changes can be traced in the faunas of Pikermi and Dytiko, including taxa living in a relatively wetter and woody habitat, as well as in some younger faunas of the wider area (de Bonis et al., 1992; Kostopoulos, 2009; Koufos, 2006b; Merceron et al., 2005, 2006). The

new environmental conditions were less favourable for the more terrestrial *M. pentelicus* (Merceron et al., 2009a, b; Youlatos, 2003; Youlatos et al., 2012), which went extinct at the end of the Miocene. On the other hand, some populations of *M. pentelicus*, like that represented at Dytiko, show some adaptations to the new environmental conditions. Based on the humeral characters, the Dytiko *M. pentelicus* shows affinities to arboreal and walking monkeys with terrestrial activities (Youlatos et al., 2012). Moreover, the Dytiko *M. pentelicus* seems to have some *monspessulanus*-like characters (e.g., narrow lower canines, slightly smaller size compared to the average of the typical *M. pentelicus* from Pikermi; see Section 4.1.2), and we can thus figure an adaptive trend to face the new environmental constraints. According to Delson et al. (2005), *M. pentelicus* may have given rise to *M. monspessulanus* and have co-existed for a short time with its descendant before it went extinct at the end of the Miocene. The coexistence of the two species in Dytiko, as well as their late Turolian age, supports this interpretation. Another possibility is that *M. monspessulanus* could be an immigrant from Eurasia or Africa, but at the moment there is not cogent evidence for this scenario.

Mesopithecus pentelicus disappeared at the end of the Miocene and only *M. monspessulanus* existed in Europe during the Pliocene (Fig. 8). In the eastern Mediterranean regions, the Pliocene mammal fossiliferous sites are rare. In the Balkans, although *M. pentelicus* is very common, *M. monspessulanus* is rarely present, but recognized in Romania (Capeni and Malusteni; Delson, 1973; Radulescu et al., 2003) and in Bulgaria (Dorkovo; Delson et al., 2005). Conversely, the presence of this taxon is still unreported from Turkey and from Asian sites (Fig. 9).

The most recent evidence of *M. monspessulanus* in Europe, dated to the late early Villafranchian, MN 17, is from the Red Crag site (England), but the material available so far uniquely consists of an isolated M3 crown. Because of its dimensional affinities with the M3 of a male mandible from Montpellier (France), it was attributed to this species (Delson, 1973). However, the author himself does not exclude the possibility of sampling problems or of an erroneous association of the specimen with the Red Crag fossil assemblage (Delson, 1973). Crown size of the Red Crag M3 specimen ($7.6 \times 7.0 \times 6.5$ mm) is close to that of the likely male specimen DTK-276 ($- \times 6.3 \times 6.4$ mm). On the other hand, as shown by the Simpson log-diagram (Fig. 7A), the dimensions of the Red Crag's tooth fall within the range of variation of the *M. pentelicus* M3s from Pikermi [$(6.3–8.1) \times (6.4–7.9) \times (5.3–7.1$ mm)]. By taking into account such comparative evidence and accepting as reliable the age of the Red Crag fauna, it appears that Delson's concern (Delson, 1973) is well substantiated and that the presence of this species in the early Pleistocene, MN 17, is questionable (Fig. 8).

In conclusion, the revision of the *Mesopithecus* remains from Dytiko (Macedonia, Greece) allowed the recognition of the two species *M. pentelicus* and *M. monspessulanus*. *M. pentelicus* is represented by a form slightly smaller than that typically represented at Pikermi, while *M. monspessulanus* is somewhat larger than the Pliocene form of the taxon. The semi-terrestrial *M. pentelicus* went gradually extinct at the end of Miocene, while *M. monspessulanus* lasted until the Pliocene. The presence of *M. monspessulanus* in the latest Miocene fauna of Dytiko represents the first and earliest occurrence of this taxon in Europe, even if the possible presence of this species is signalled in the Italian localities of Gravitelli and Baccinello V3, whose age is nonetheless younger than Dytiko (Fig. 8). *M. monspessulanus* is widely distributed in Europe, except in the Iberian Peninsula. However, compared to the relatively rich assemblages of *M. pentelicus* from various Eurasian sites, especially from the Balkan Peninsula, so far, the *M. monspessulanus* fossil record remains quantitatively poor.

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