

A “new” *Mesopithecus pentelicus* (Primates, Cercopithecidae) skull from Pikermi (Late Miocene, Greece)*

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ABSTRACT: An unpublished face of the colobine monkey *Mesopithecus pentelicus* from Pikermi is described. In 1866 Albert Gaudry donated this specimen together with 31 other bones from Pikermi to the Museum Cuvier in Montbéliard, France. The specimens remained unknown to the scientific community for 144 years. This paper describes the newly rediscovered face of the cercopithecoid and compares it to others stored in different Museums in Europe. Because it is only slightly deformed, several important parameters can be measured. This “new” face, that of a female, fits perfectly into the population of the published *Mesopithecus pentelicus* from Pikermi.

Key-words: *Mesopithecus*, *Primates*, *Cercopithecidae*, *Pikermi*, *Late Miocene*, *Greece*.

ΠΕΡΙΛΗΨΗ: Στην παρούσα εργασία περιγράφεται ένα αδημοσίευτο τμήμα κρανίου του πιθήκου *Mesopithecus pentelicus* από το Πικέρμι. Το 1866, ο Albert Gaudry κατέθεσε το δείγμα μαζί με άλλα 31 τεμάχια οστών από το Πικέρμι στο Μουσείο Cuvier in Montbéliard της Γαλλίας. Τα δείγματα παρέμειναν άγνωστα στην επιστημονική κοινότητα για 144 χρόνια. Το “νέο” τμήμα του κρανίου που περιγράφεται σε αυτή την εργασία συγκρίνεται με παρόμοια δείγματα που βρίσκονται σε διάφορα Μουσεία της Ευρώπης. Το δείγμα παρουσιάζει μικρή παραμόρφωση, επιτρέποντας την ανάλυση και την αξιολόγηση πολλών σημαντικών παραμέτρων. Το “νέο” τμήμα κρανίου, που ανήκει σε θηλυκό άτομο, ταιριάζει απόλυτα στον πληθυσμό που έχει δημοσιευθεί για τον *Mesopithecus pentelicus* από το Πικέρμι.

Λέξεις-κλειδιά: *Mesopithecus*, *Primates*, *Cercopithecidae*, *Πικέρμι*, *Ανώτερο Μειόκαινο*, *Ελλάδα*.

INTRODUCTION

Pikermi is a classic locality of the Late Miocene of Greece. It is biochronologically ascribed to the European Land Mammal Zone MN12 (BONIS & KOUFOS, 1999; MEIN, 1975) and dated at ~7.0 My (KOUFOS, 2009a). It is a famous example of the Greek woodland faunas (SOLOUNIAS *et al.*, 1999) recording several tens of mammal species, including gazelles, giraffes, rhinos, horses, carnivores and primates (BERNOR *et al.*, 1996; BONIS & KOUFOS, 1999; GAUDRY, 1862-1867; SOLOUNIAS *et al.*, 1999; ZAPFE, 1991). Other palaeoenvironmental interpretations indicate a more open savanna-like landscape (BONIS *et al.*, 1992; KOSTOPOULOS, 2009; KOUFOS SPASSOV & KOVACHEV, 2003; KOUFOS, 2009a). Perhaps the most characteristic fossil species from Pikermi is the cercopithecoid colobine monkey *Mesopithecus pentelicus* first described by WAGNER in 1839 and then extensively documented by later excavations. ZAPFE (1991) indicates that at least 60 individuals of the species were uncovered at Pikermi which makes it the best recorded monkey in the Neogene fossil record. *Mesopithecus*, either as *M. pentelicus*, *M. monspessulanus* or possibly *M. delsoni*, was also discovered in more than 30 European and South-West Asian localities spanning the early Late Miocene to the Early Pliocene (ANDREWS *et al.*, 1996; ERONEN & ROOK, 2004; KOUFOS, 2009a, 2009b).

In his monograph of the fossil cercopithecoid primate from

Pikermi, ZAPFE (1991) mentioned 21 skulls that could be measured. Yet in 1866, Gaudry, one of the first to excavate the site, briefly noted that he had uncovered 22 skulls of the primate. Later on in the same year, Gaudry offered a present to the “Société d’Emulation de Montbéliard”, an association of naturalists that initiated the city’s Natural History Museum with the aim of developing the natural sciences in the home city of the famous French palaeontologist Georges Cuvier. In this gift, Gaudry donated a number of fossils from the locality of Pikermi that he extensively described in 1862; reports of the Society (DUVERNOY, 1866, 1867) state that he kindly offered “doubles” to Montbéliard.

In 2008, we rediscovered this material. Among 31 other bones of *Hipparion* sp., *Gazella capricornis*, *Helladotherium duvernoyi*, *Tragoportax amalthea*, *Rhinocerotidae* indet. and *Palaeoreas lindermayeri* (see Table 1), we found a *Mesopithecus* skull; actually a face rather than a complete skull. If this skull is the 22nd mentioned by Gaudry, it has not been lost but stored for 144 years in the Museum’s collections. However tempting, it is impossible to verify if this “new” skull is the missing specimen. In the 1970’s, the curator of the Museum Cuvier at Montbéliard did indicate in her journal the presence of the colobine in the collection but did not describe it, neither did she measure or compare it to the pikermian population (SALMON, 1973).

Although no complete skeleton in connection was ever

* Ένα “νέο” κρανίο *Mesopithecus pentelicus* (Primates, Cercopithecidae) από το Πικέρμι (Ανώτερο Μειόκαινο, Ελλάδα)

found in Pikermi, *M. pentelicus* is particularly well known from isolated cranial and post-cranial material from males and females so that the body of the primate has been entirely reconstructed (GAUDRY, 1862-1867). New material recently published from Bulgaria (KOUFOS *et al.*, 2003) yielded partially complete skeletons and helped better understand the colobine monkey. It seems that not much has to be added to the species description. However it is always interesting to add unknown material to existing collections in order to better grasp the morphological and size variability of a species. In addition, the publication of a specimen stored in public collections makes it available for future studies. With the growing importance of non-destructive methods used to reconstruct ecology (e.g., dental microwear) or internal skeletal morphology (e.g., CT-scan) of fossil species, every new specimen might prove useful.

Unlike many of the known specimens, the face of the Montbéliard fossil is only slightly deformed making reliable measurements and precise descriptions possible.

Here we describe this new specimen of *Mesopithecus pentelicus* in the context of all present knowledge of this

species in the Late Miocene of Europe and especially of Pikermi. We add a number of skull measurements and characteristics to the variability already described in a large number of samples of this primate and briefly address the question of sexual dimorphism.

MATERIAL & METHODS

Here we describe a partial skull represented by a face, numbered Pg 4-1 (Plate 1) and hosted in the collections of natural history of the Museum Cuvier in Montbéliard. A cast is also stored in the collections of the Naturhistorisches Museum Basel where a number of fossils from Pikermi including a *Mesopithecus* skull have already been deposited. We collected the skull and teeth measurements already published for the other specimens of *Mesopithecus pentelicus* from Pikermi and we compare them to those of the re-discovered face. The measurements can be seen in Table 2 and 3. The already published measurements are taken from BONIS *et al.* (1990) and ZAPFE (1991). To investigate sexual dimorphism and population variability, we analysed the measurements we

TABLE 1

List of the material donated to the Museum Cuvier by Albert Gaudry in 1866. In bold letters the face of *Mesopithecus pentelicus*.

Collection number	Species	Material
Pg 4-1	<i>Mesopithecus pentelicus</i>	Face
Pg 5-1	<i>Hipparion</i> sp.	Left mandible
Pg 5-10	<i>Hipparion</i> sp.	Right femur
Pg 5-2	<i>Hipparion</i> sp.	Distal part of right humerus
Pg 5-3	<i>Hipparion</i> sp.	Distal part of right radius
Pg 5-4	<i>Hipparion</i> sp.	Right metatarsal with cuneiform and navicular
Pg 5-5	<i>Hipparion</i> sp.	Left maxillary with P2-M3
Pg 5-6	<i>Hipparion</i> sp.	Metacarpal
Pg 5-7	<i>Hipparion</i> sp.	Right calcaneum
Pg 5-7, 8, 9	<i>Hipparion</i> sp.	Distal part of right tibia with astragalus and calcaneum
Pg 5-8	<i>Hipparion</i> sp.	Right astragalus
Pg 5-9	<i>Hipparion</i> sp.	Distal part of right tibia
Pg 6-1	Rhinocerotidae indet. 1	Left radius
Pg 6-2	Rhinocerotidae indet. 1	Mandible, broken teeth
Pg 6-3	Rhinocerotidae indet. 1	Left astragalus
Pg 6-3, 4, 5	Rhinocerotidae indet. 1	Distal part of left tibia with astragalus and calcaneum
Pg 6-4	Rhinocerotidae indet. 1	Left calcaneum
Pg 6-5	Rhinocerotidae indet. 1	Distal part of left tibia
Pg 6-6	Rhinocerotidae indet. 1	Proximal part of left femur
Pg 6-7	Rhinocerotidae indet. 1	Upper left premolar
Pg 7-1	<i>Gazella capricornis</i>	Right mandible with d2-m2
Pg 7-2	<i>Gazella capricornis</i>	Horn core
Pg 8-1	<i>Helladotherium duvernoyi</i>	Right astragalus
Pg 8-2	<i>Helladotherium duvernoyi</i>	Left maxillary with P4-M3 - Cast
Pg 9-1	<i>Tragoportax amalthea</i>	Left maxillary with P2-M2
Pg 9-2	<i>Tragoportax amalthea</i>	Horn core
Pg 9-3	<i>Tragoportax amalthea</i>	Left mandible with p2-m3
Pg 10-1	<i>Palaeoreas lindermayeri</i>	Horn core
Pg 11-1	Rhinocerotidae indet. 2	Right metacarpal II
Pg 11-2	Rhinocerotidae indet. 2	Right metacarpal III
Pg 11-3	Rhinocerotidae indet. 2	Right metacarpal IV

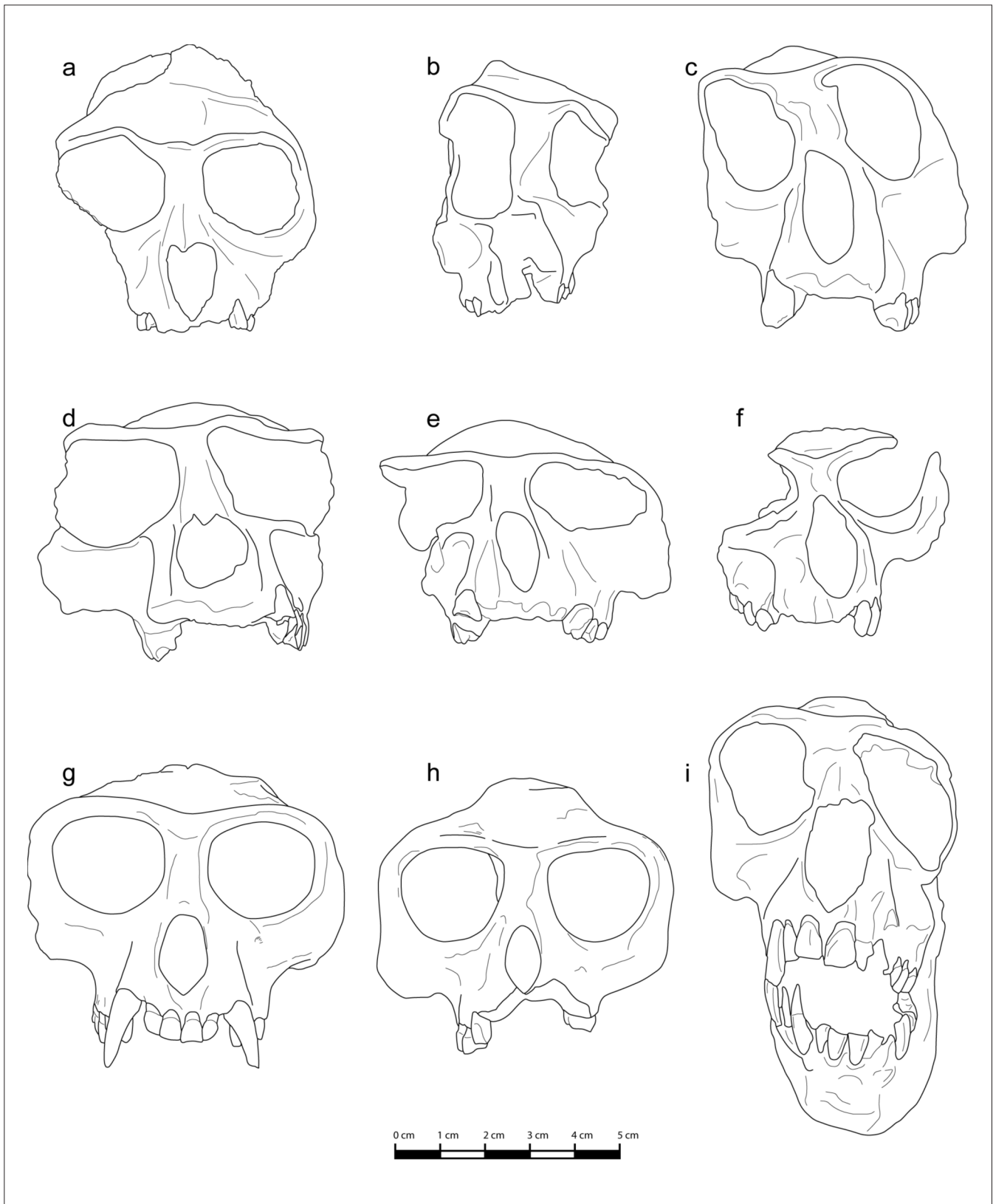


Fig. 1. 8 skulls of *Mesopithecus pentelicus* from Pikermi including Pg 4-1. a. Pg 4-1, Museum Cuvier Montbéliard; b. Pk 120, Museum of Palaeontology and Geology Athens; c. Pk 119, Museum of Palaeontology and Geology Athens; d. Pk 121, Museum of Palaeontology and Geology Athens; e. Pk 118, Museum of Palaeontology and Geology Athens; Pk 91, Naturhistorisches Museum Basel; f. BNHM M8945, Natural History Museum London; g. AS II 7, Bayerische Staatssammlung für Paläontologie und Geologie Munich; h. A4714, Naturhistorisches Museum Vienna. Note the good condition of Pg 4-1 in comparison with most of the other skulls.

took on Pg 4-1 together with the published material through a bivariate plot of interorbital width vs. palatine breadth and through a Principal Component Analysis (PCA, using software PAST, HAMMER *et al.*, 1998) of all the cranial measurements except the rarely available facial angles. Other bivariate plots with the other parameters are not shown here but give essentially the same results.

The 31 other specimens donated by Gaudry to Montbéliard in 1866 are included in Table 1.

RESULTS

Systematic Palaeontology

Order Primates LINNAEUS, 1758

Infraorder Catarrhini E. GEOFFROY, 1912

Family Cercopithecidae GRAY 1821

Subfamily Colobinae BLYTH, 1875

Mesopithecus pentelicus WAGNER, 1839

The species was described by WAGNER (1839) but the holotype stored in Munich is a badly preserved skull. Skull Pg 4-1 is partly preserved consisting of the face with its frontal region. The posterior part of the skull is broken. The palatine region with the choanae is very well-preserved. The upper teeth are also present but the mandibles are not preserved.

The face is typical for a *Mesopithecus pentelicus* from Pikermi. It is worth noting that it is only slightly deformed with the roof slightly elevated. Most of the other skulls of *Mesopithecus pentelicus* from Pikermi show a greater amount of deformation (see Fig. 1 where 8 other skulls are drawn, only BNHM M8945, Fig. 1g, and AS II 7, Fig. 1h, are virtually uncrushed).

The upper teeth are largely worn preventing any precise description (Plate 1b). The right upper P3, P4, M1 and M2 are preserved together with the broken roots of I1, I2, C and M3. The left P3 and M2 are preserved together with the broken roots of C, M1 and M3.

We measured the non-broken teeth to plot them in comparison to the other specimens from Pikermi (Table 3 and Fig. 2). The absence of large upper canines or large canine roots most probably indicates that the individual was a female.

The skull is typical for a colobine monkey; with a short and upright face (facial angle of approx. 65°). The orbits are rather quadrangular and also show no sign of deep deformation (Plate 1). The supraorbital tori are marked but not strongly developed. This condition is also found in the other known female skulls (DELSON, 1973; KOUFOS *et al.*, 2004). The interorbital region is rather narrow but affected by a fracture preventing any precise measure. The nasal bones together with the maxilla are slightly crushed. As described by Delson (1973) for the best preserved *Mesopithecus pentelicus* skull (BNHM M8945, see Fig. 1g), the supraorbital torus is

not very pronounced and there's here only a very slight depression behind it, just like a skull stored at the Paris University (LPVP 11 in DELSON, 1973 or PVH 11 in BONIS *et al.*, 1990). The lacrimal fossae are slight depressions extending onto the maxilla. Again exactly as on BNHM M8945, the well preserved palate does not extend beyond the level of the upper third molar. It ends in a characteristic W shape also partly preserved on NMB Pk.91 (Fig. 1f, pers obs. and ZAPFE, 1991), fully preserved on BSM AS II 8 (figured in DELSON, 1973) and to a lesser extent on the holotype BSM AS II 11 and on BNHM M8945 (figured in DELSON, 1973). The choanae are wide and not preserved in their posterior part.

Overall the shape of the skull is very close to the face of

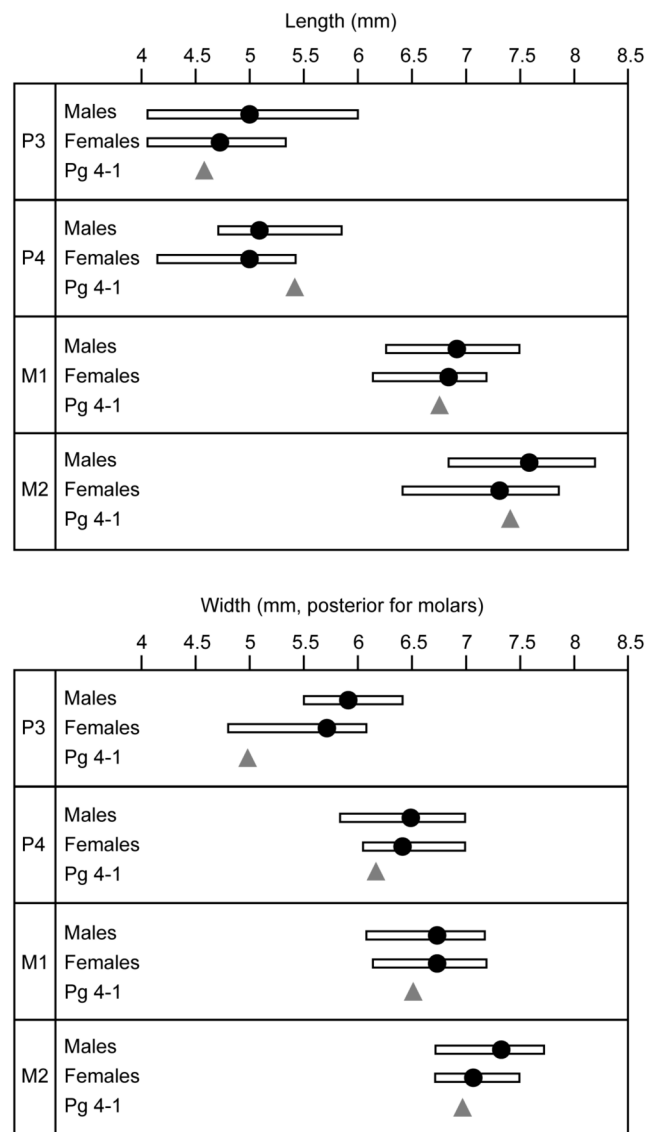


Fig. 2. Diagrams of length and width (posterior for molars) of the upper teeth of *Mesopithecus pentelicus* from Pikermi. Note that Pg 4-1 described here fits in the population of the other *M. pentelicus* from Pikermi (data from BONIS *et al.*, 1990 and ZAPFE, 1991). Bars show the size distribution, filled black circles show the mean for males and females, respectively and gray triangle is Pg 4-1.

the female from Munich BSM AS II 7, the orbit being slightly lower than in the males (especially male BNHM M8945 figured in ZAPFE, 1991).

DISCUSSION

The dimensions of the skull and teeth fit into the variability pattern of the already published material from Pikermi. Table 2 shows the parameters that could be measured on the skull, following ZAPFE (1991). A comparison with other skulls (ZAPFE, 1991) shows that the female from Montbéliard fits perfectly into the *Mesopithecus* population. As far as teeth

are concerned (Table 3 and Fig. 2), the specimen proves to be a rather small individual but fits into the variability pattern of the population. These data also show that there is no sexual size difference in the teeth. However, cranial metrics do show that females tend to be slightly smaller than males. Our bi-variate plot and PCA (Figs 3 and 4) both show that females cluster together, while males exhibit a large size variability. Skull Pg 4-1 fits well into the females from Pikermi. There seems to be a clear tendency towards sexual dimorphism as mean values of the different parameters are systematically higher in males than in females (Table 2). A non-parametric Mann-Whitney significance test comparing males to females

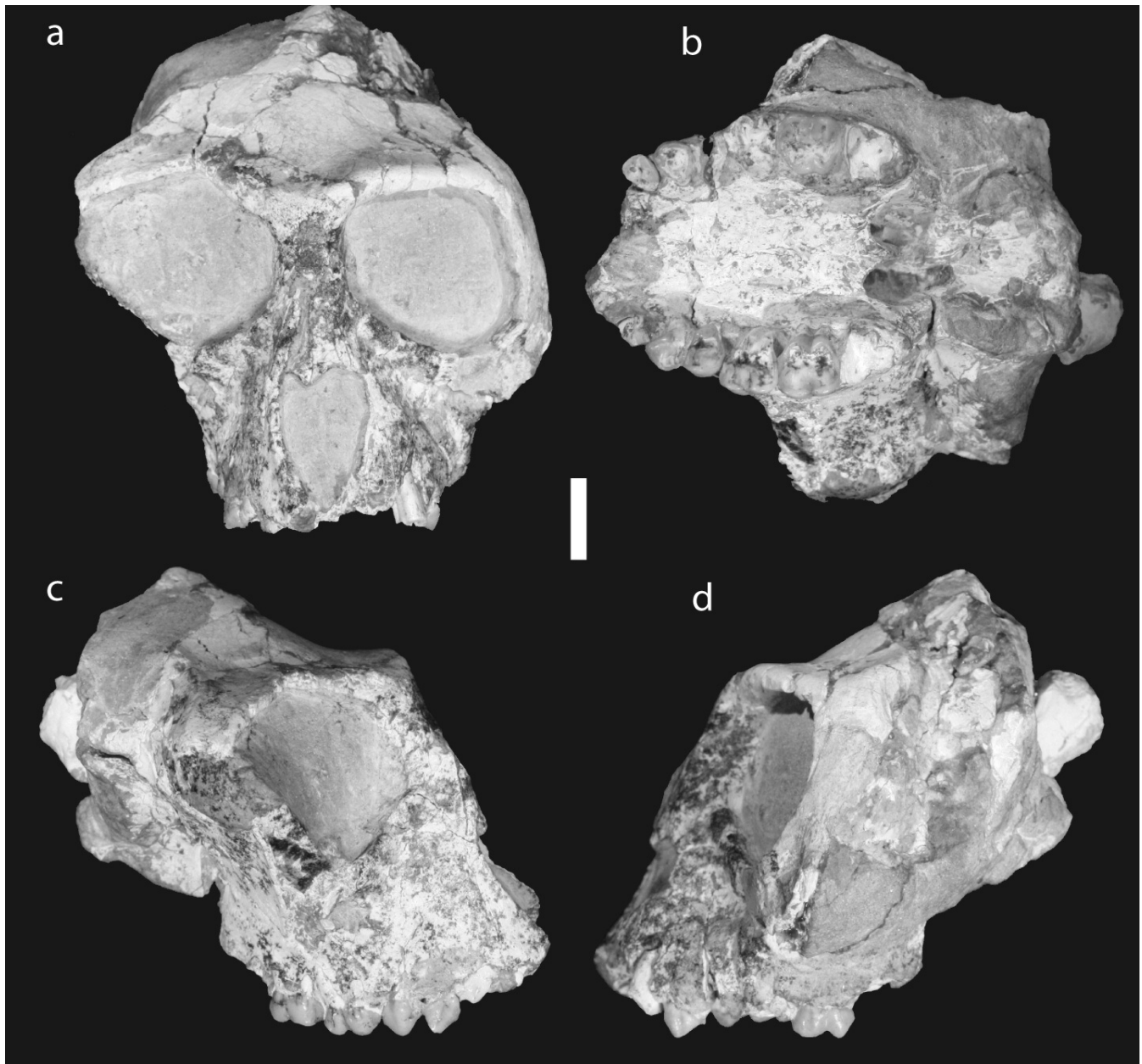


PLATE 1

Skull Pg 4-1 of *Mesopithecus pentelicus* from the Museum Cuvier, Montbéliard.
a. frontal view; b. palatal view; c. right lateral view; d. left lateral view. Scale bar: 1 cm.

TABLE 2

Skull parameters for males and females of the *Mesopithecus pentelicus* population from Pikermi (from ZAPFE, 1991).
The skull Pg 4-1 from Montbéliard is marked in bold letters. All measurements in mm.

Specimens	Interorbital Width 1	Palatine Breadth 2	Thickness of the orbital edge	Nasal Width	Facial angle (°)	1/2
MALES						
London M 8945	9.7	37.3	4.5	12	68	26.0
London M 8946	11	40.3	5	12.5		27.3
London M 8947	10	34.2	4.1	9.6		29.2
London M 8944	10.5	36	4.3			29.2
Paris Pik. 014	8.7		5	13.3		
Paris Pik. 035	11		4.3	11*		
Paris Pik. 013	11.5	37.8	4.1	14		30.4
Paris-Univ. 11	12	39.8	5	14.7		30.2
Paris-Univ. 9	10.8	37.5		11		28.8
Berlin MB 1882/83 . 216 . 1	10	36.5	4	10.5	50	27.4
Stuttgart	9		4		60	
Wien 4693	10	35.5	4.7	9*		28.2
Wien 4714	12	35	5	12*	65	34.3
N	13	10	12	11	4	10
Mean	10.5	37.0	4.5	11.8	60.8	29.1
FEMALES						
Pg 4-1 - Montbéliard	8.7*	32.6	4.5	8.5*	65	26.7*
Paris Pik. 119a	8.2		4			
Paris Pik. 016	8.3		2.7			
Paris-Univ. 5	8.2	34.5	3	10.2		23.8
Berlin MB 1857 . 1	8		5	10.5	57	
München AS II 7	9.6	32.7	4	8.3	62	29.4
Basel Pik. 91	9	34	3	10.5		26.5
Athen 7	8.5	38	3.7			22.4
Athen 8	9.5	33.7	4	9.5	64	28.2
N	8	6	9	5	4	5
Mean	8.7	34.3	3.8	9.8	62.0	26.0
N population	21	16	21	16	8	15
Mean population	10.2	36.0	4.2	11.7	61.4	29.9

was applied to four of the parameters and yielded low p values but often non-significant (interorbital width, $p < 0.001$; palatine breadth, $p = 0.026$; thickness of the orbital edge, $p = 0.014$; nasal width, $p = 0.013$). Sexual dimorphism is thus not statistically supported for most of the parameters, but this might also be an artifact resulting from the low number of skull parameters available. Despite this, the size of the upper canines and possibly the thickness of the supraorbital tori are significant characteristics allowing differentiation between the sexes (ZAPFE, 1991).

New specimens of *Mesopithecus*, sometimes excellently preserved, are continuously being found in other places of Eastern Europe (DELSON *et al.*, 2005; KOUFOS *et al.*, 2004; KOUFOS, 2006; TSOUKALA & BARTSIOKAS, 2008) testifying to

the abundance of this genus in the Late Miocene and Early Pliocene. Knowledge of its taxonomy, variability, geographic distribution and its palaeoecological preferences is thus steadily growing. Despite the abundance of specimens and localities where they occur, most of this knowledge is quite recent and taxonomical questions still persist.

It long looked as though only 2 species of *Mesopithecus* existed in the Late Miocene and Early Pliocene, *M. pentelicus* and *M. monspessulanus*. To DELSON (1994) and later ANDREWS *et al.* (1996) the species *M. delsoni* described by BONIS *et al.* (1990) seemed to be within the range of *M. pentelicus*' variability and they rejected a separation. New material from Bulgaria relaunched the debate (KOUFOS *et al.*, 2003) and very recent publications reaffirm the identity of

TABLE 3

Length and width of the upper teeth of skulls of *Mesopithecus pentelicus* from Pikermi (from BONIS *et al.*, 1990 and ZAPFE, 1991).

The teeth of Pg 4-1 from Montbéliard are in bold letters. Ant W and Post W: anterior width and posterior width, respectively.

All measurements in mm. See Fig. 2 for a graphical representation.

PIKERMI			P3		P4		M1			M2		
			L	W	L	W	L	Ant. W	Post. W	L	Ant. W	Post. W
Paris PIK 13	Male		4.6	6.4	5.1	6.7	6.9	7	6.7	7.4	7.5	7.2
Paris Pik 014	Male		5.1	6	5	6.2	6.7	7.2	6.7	8.1	8.1	7.4
Paris Pik 035	Male		5	6.1	5.4	6.4	6.3	7	6.4	7.5	7.5	7.2
Paris PIK 21A	Male		4.5	6.1	4.8	6.6	6.7	7.1	6.7	7.2	7.7	7.2
PVH 09 (Paris Univ)	Male		4.7	5.9	4.7	6.6	6.3	7.1	6.8	7.5	7.8	7.3
Paris Univ. 10	Male		4.4	5.6	4.8	6.2	6.8	6.8	6.7	7.3	7.5	7.1
Berlin MB 1882/83.216.1	Male		5.6	5.6	5	7	7			8	8.2	7.5
London M 8946	Male		5.5	6.4	5.4	7	7.5	7.2	7.2	8.2	8.1	7.7
London M 8947	Male		5.2	5.7	5.2	6.6	7.3	7.2	6.7	8.2	7.9	7.6
London M 8945	Male		5	5.6	5.2	6.6	7.3	7	6.7	7.5	7.9	7.1
London M 8951	Male		6	5.8	5.7	6.3	6.8	7.1	7	7.7	8.3	7.5
Wien A 4714 (Abb. 50)	Male		5.5		5.8	6	7.5	6.8	6.5	8	7.3	6.7
Wien A 4693	Male		4.1	5.5	4.8	6.6	6.6	7.1	7.1	7.2	7.2	7.1
Wien o. Nr.	Male		5.1	5.7	5.1	6.3	7.2	7.6	6.6	8	8	7.4
München AS II 8	Male		5.6	6	5.2	6.5	7.2	6.5	6.5	7.6	7.4	7
Athen 38	Male		5.6		5.8	5.8	7	6.6	6.8	7.8	7.7	7.7
Paris PIK 12	Male		4.8	6.3	5.2	6.6	6.9	7.1	6.9	7.8	7.8	7.1
Paris PIK 253	Male		4.5	6.4	4.8	6.6	6.6	6.9	7.2			
PVH 07 (Paris Univ)	Male		4.8	5.9	5.2	6.4	6.8	7	6.1	7.4	7.8	7.1
PVH 08 (Paris Univ)	Male		4.8	5.8	4.8	6.6	6.3	6.8	6.7	6.8	7.8	7.3
Paris Univ. 11	Male		4.6	5.8	5	6.7	7	7	6.7	7.7	8.2	7.3
Paris PIK 010	Female		5.2	6	5.3	6.7	7.2	7.2	7.2	7.8	7.8	7.2
Paris Pik 16	Female		4.6	5.5	5.2	6.1	6.6	7	6.3	6.8	7.5	6.7
Paris PIK 17	Female		4.1	5.7	4.8	6.5	6.7	6.6	6.8	7	7.4	7.2
Paris Pik 20	Female?		4.1	4.8			6.3	6.9	6.3	7	7.8	7.4
PVH 05 (Paris Univ)	Female		4.2	5.9	4.2	6.6	6.2	7.1	6.9	6.7	7.5	7.3
PVH 06 (Paris Univ)	Female				4.9	7	6.7	6.9	6.7	7.4	7.8	7.5
Paris Pik 016	Female		5	6.6	5.4	6.2	6.9	6.7	6.2	7.6	7.4	6.8
Berlin MB 1857.1	Female		5.1	5.5	5.2	6.5	7.2	7	7	7.5	7.9	7.4
München AS II 7	Female		4.5	5.8	5	6.4	6.6	7	7	7.2	7.5	7.1
London M 8949	Female		4.9	6	5	6.7	7	7.4	7	7.4	7.8	7.2
Basel Pk 91	Female		5.3	5.4	5	6.3	6.9	6.5	6.5	7.7	7.3	6.8
Athen 5	Female		5.1	5.3	5	6.1				7.4	7.8	7
Athen 2	Female		4.8	5.9	4.9	6.4	7.2	6.7	6.2	7.5	7.8	7
Athen 8 (Abb. 51)	Female		4.7		4.8		6.9			7.5		
Paris PIK 303A	Female		4.5	5.1	4.9	6.1	6.7	6.6	6.6	6.4	7.2	6.9
Pg 41 - montbéliard	Female	Right	4.6	4.9	5.4	6.2	6.7		6.5	7.7	7.4	7
Pg 41 - montbéliard	Female	Left	4.5	5						7.1	7.1	6.9
	N population		37	34	36	35	36	33	34	37	36	36
	Mean population		4.87	5.76	5.08	6.46	6.85	6.96	6.70	7.48	7.69	7.19

this species and describe an intermediate form between *M. pentelicus* and *M. delsoni* from Greece (KOUFOS *et al.*, 2004). Further material is now required to improve the taxonomy of

the Miocene species. Concerning the palaeoecology of the genus, its diet was until very recently not particularly well-known. A recent analysis suggests an opportunistic diet com-

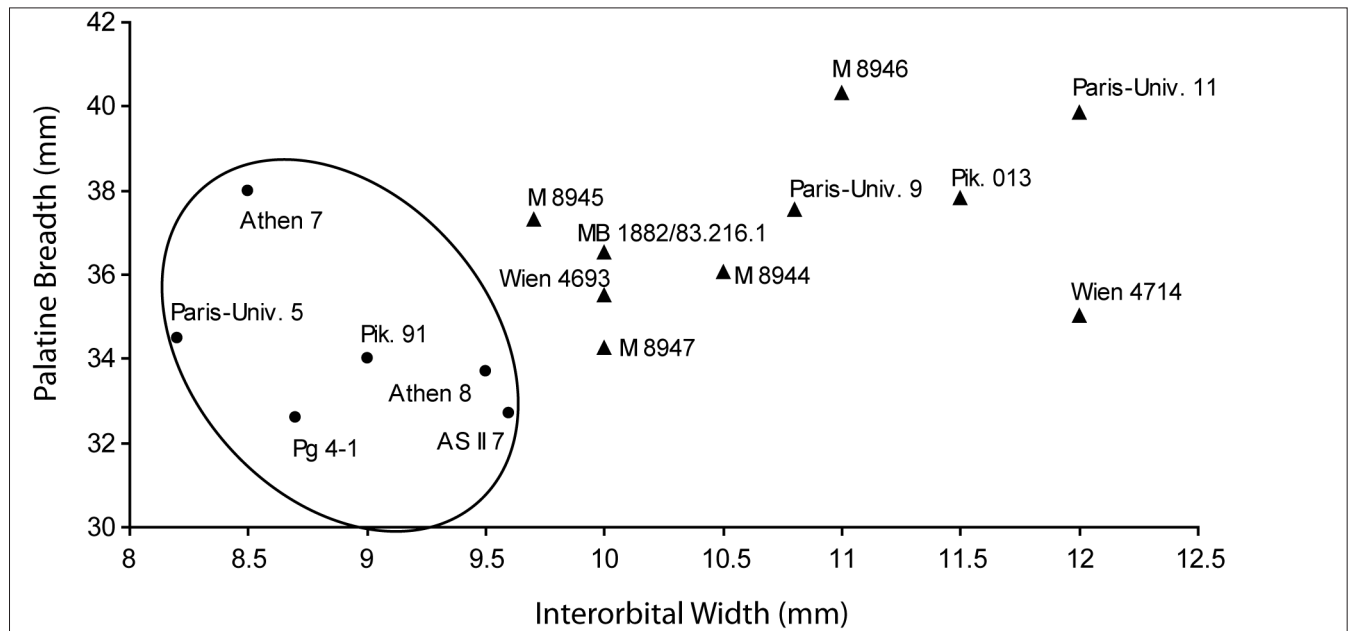


Fig. 3. Bivariate plot of interorbital width vs. palatine breadth; females are in the circle. Black circles: females; black triangles: males. Names refer to Table 2.

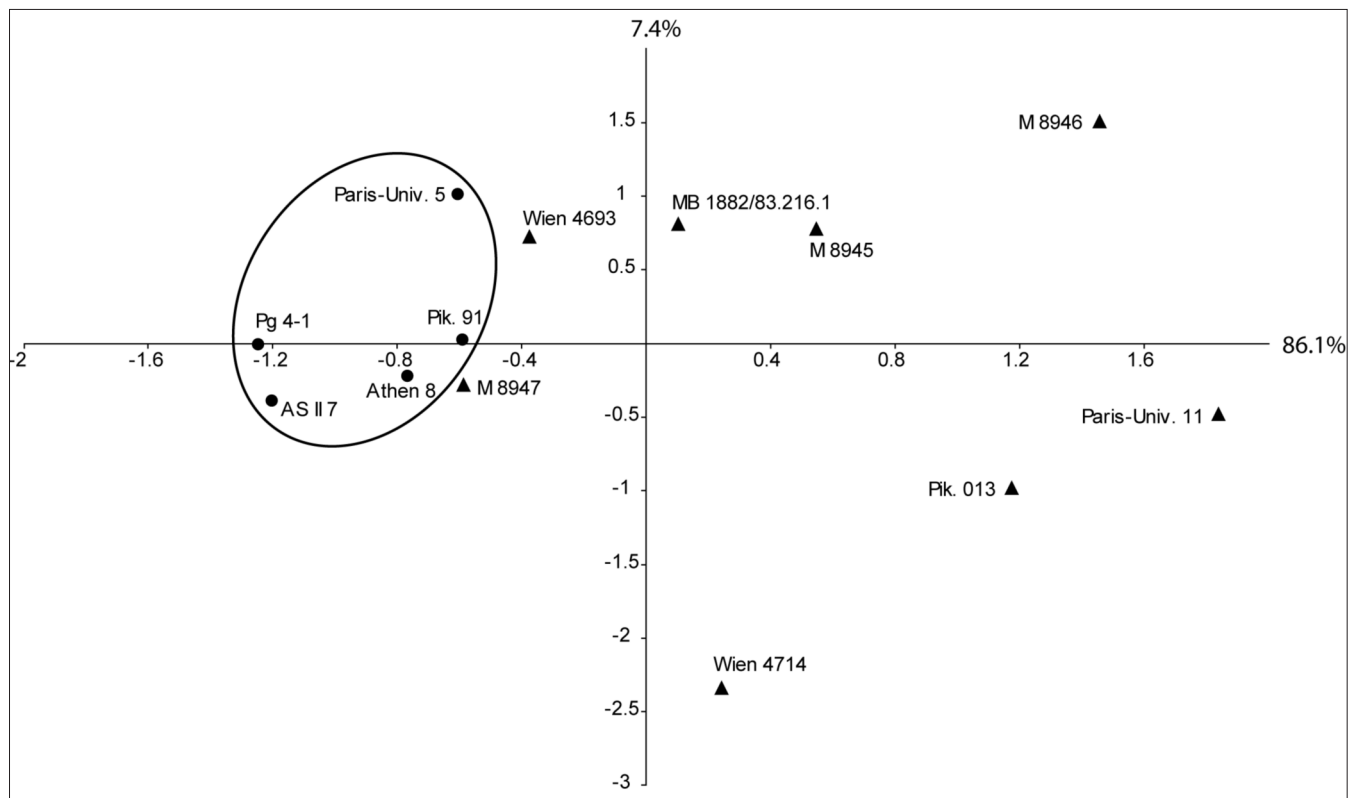


Fig. 4. Principal Component Analysis of cranial parameters (interorbital width, palatine breadth, thickness of the orbital edge and nasal width). Females are in the circle, note that they cluster together. Black circles: females; black triangles: males. Names refer to table 2.

posed of leaves, fruits and seeds (MERCERON *et al.*, 2009) and its locomotor adaptations indicate a semiterrestrial mode of life (YOULATOS, 2003; YOULATOS & KOUFOS, 2010). This is consistent with the environmental interpretations for Pikermi. The genus was found across a large geographic area from

France to the Siwaliks (ERONEN & ROOK, 2004; HARRISON & DELSON, 2007; TSOUKALA & BARTSIOKAS, 2008) and as far North as Germany where only a single tooth was discovered in the early Late Miocene of Weissberg (DELSON, 1973; although the age is debated, see ANDREWS *et al.*, 1996). De-

spite the abundance of the material, *Mesopithecus* still requires attention to answer these remaining taxonomical questions and to improve its geographic range.

CONCLUSIONS

This “new” skull of *Mesopithecus pentelicus* was rediscovered in the public collection of the Museum Cuvier of the French city of Montbéliard after 144 years. Gaudry donated it to the Museum together with a number of fossils from Pikermi in 1866; it was then forgotten and thus never published, not even in Zapfe’s comprehensive monograph on the species in 1991 (ZAPFE, 1991). The species itself is already well-known through a rather large number of skulls and post-cranial material, but the good condition of this specimen allows several parameters to be measured. Comparison with other published skulls shows that this female fits precisely into the population of the Pikermian *Mesopithecus* and adds new data to the variability of the species present in Pikermi. It confirms the sexual dimorphism of the species.

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REFERENCES

- ANDREWS, P., HARRISON, T., DELSON, E., BERNOR, R.L. & L. MARTIN (1996). Distribution and Biochronology of European and Southwest Asian Miocene Catarrhines. In: BERNOR, R.L., FAHLBUSCH, V. & H.-W. MITTMANN (Eds), *The Evolution of Western Eurasian Neogene Mammal Faunas*. Columbia University Press, New York, 168-207.
- BERNOR, R.L., SOLOUNIAS, N., SWISHER III, C.C. & J.A. VAN COUVERING (1996). The correlation of three classical “Pikermian” mammal faunas - Maragheh, Samos, and Pikermi - with the European MN Unit system. In: BERNOR, R.L., FAHLBUSCH, V. & H.-W. MITTMANN (Eds), *The Evolution of Western Eurasian Neogene Mammal Faunas*. Columbia University Press, New York, 137-154.
- BONIS, L. DE & G.D. KOUFOS (1999). The Miocene large mammal succession in Greece. In: AGUSTI, J., ROOK, L. & P. ANDREWS (Eds), *Hominoid evolution and climatic change in Europe, Volume 1. The evolution of Neogene terrestrial ecosystem in Europe*. Cambridge University Press, Cambridge, 205-237.
- BONIS, L. DE, BOUVRAIN, G., GERAADS, D. & G.D. KOUFOS (1992). Diversity and paleoecology of Greek late Miocene mammalian faunas. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 91, 99-121.
- BONIS, L. DE, BOUVRAIN, G., GERAADS, D. & G.D. KOUFOS (1990). New remains of *Mesopithecus* (Primates, Cercopithecoidea) from the Late Miocene of Macedonia (Greece), with the description of a new species. *Journal of Vertebrate Paleontology*, 10, 473-483.
- DELSON, E. (1973). Fossil Colobine Monkeys of the Circum-Mediterranean Region and the Evolutionary History of the Cercopithecidae (Primates, Mammalia). *Unpublished PhD. dissertation*. Columbia University, New York, 856 p.
- DELSON, E. (1994). Evolutionary history of the colobine monkeys in palaeoenvironmental perspective. In: DAVIES, A.G. & J.F. OATES (Eds), *Colobine Monkeys: Their Ecology, Behaviour and Evolution*. Cambridge University Press, Cambridge, 11-43.
- DELSON, E., HERBERT, T. & N. SPASSOV (2005). Fossil Old World monkeys (Primates, Cercopithecidae) from the Pliocene of Dorkovo, Bulgaria. *Geodiversitas*, 27(1), 159-166.
- DUVERNOY, M. (1866). Discours de la séance du 3 Mai 1866. *Mémoires de la Société d'Emulation de Montbéliard*, 2e série, 2e volume, 12.
- DUVERNOY, M. (1867). Discours de la séance du 2 Mai 1867. *Mémoires de la Société d'Emulation de Montbéliard*, 2e série, 2e volume, 21.
- ERONEN, J. & L. ROOK (2004). The Mio-Pliocene European fossil primate record: dynamics and habitat-tracking. *Journal of Human Evolution*, 47, 323-341.
- GAUDRY, A. (1862-1867). *Animaux Fossiles et Géologie de l'Attique. D'après les recherches faites en 1855-1856 et en 1860 sous les auspices de l'Académie des Sciences*. Savoy F., Paris.
- HAMMER, O., HARPER, D.A.T. & P.D. RYAN (2001). PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica*, 4, art. 4, 9pp.
- HARRISON, T. & E. DELSON (2007). *Mesopithecus sivalensis* from the Late Miocene of the Siwaliks. *American Journal of Physical Anthropology*, Supp. 44, 126.
- KOSTOPOULOS, D.S. (2009). The Pikermian Event: Temporal and spatial resolution of the Turolian large mammal fauna in SE Europe. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 274, 82-95.
- KOUFOS, G.D., SPASSOV, N. & D. KOVATCHEV (2003). Study of *Mesopithecus* (Primates, Cercopithecidae) from the Late Miocene of Bulgaria. *Palaeontographica*, A269, 39-91.
- KOUFOS, G.D., BONIS, L. DE, KOSTOPOULOS, D.S., VIRIOT, L. & T.D. VLACHOU (2004). *Mesopithecus* (Primates, Cercopithecidae) from the Turolian locality of Vathyakkos 2 (Macedonia, Greece). *Paläontologische Zeitschrift*, 78(1), 213-228.
- KOUFOS, G.D. (2006). The Late Miocene vertebrate locality of Perivoli, Thessaly, Greece – 3 Primates. *Palaeontographica*, A276, 23-37.
- KOUFOS, G.D. (2009a). The Neogene cercopithecids (Mammalia, Primates) of Greece. *Geodiversitas*, 31(4), 817-850.
- KOUFOS, G.D. (2009b). The genus *Mesopithecus* (Primates, Cercopithecidae) in the late Miocene of Greece. *Bollettino della Società Paleontologica Italiana*, 48(2), 157-166.
- MEIN, P. (1975). Proposition de biozonation du Néogène méditerranéen à partir des Mammifères. *Actas i coloquio internacional sobre biostratigrafia continental del Neogeno superior y cuaternario inferior*, 12.
- MERCERON, G., KOUFOS, G.D. & X. VALENTIN (2009). Feeding habits of the first European colobine, *Mesopithecus* (Mammalia, Primates): evidence from a comparative dental microwear analysis with modern cercopithecids. *Geodiversitas*, 31(4), 865-878.
- SALMON, E. (1973). Les collections de Géologie du Musée de Montbéliard. *Annales Scientifiques de l'Université de Besançon*, 18, 283-285.
- SOLOUNIAS, N., PLAVCAN, J.M., QUADRE J. & L. WITMER

- (1999). The paleoecology of the pikermian biome and the savanna myth. In: AGUSTI, J., ROOK, L. & P. ANDREWS (Eds), *Hominoid evolution and climatic change in Europe. Volume 1. The evolution of Neogene terrestrial ecosystem in Europe*. Cambridge University Press, Cambridge, 436-453.
- TSOUKALA, E. & A. BARTSIOKAS (2008). New *Mesopithecus pentelicus* from Kryopigi, Macedonia, Greece. *Journal of Human Evolution*, 54, 448-451.
- WAGNER, A. (1839). Fossile Überreste von einem Affenschädel und einigen andern Säugethierreste aus Griechenland. *Gelehrte Anzeiger der Bayerische Akademie der Wissenschaften*, 38, 301-312.
- YOULATOS, D. (2003). Calcaneal features of the Greek Miocene primate *Mesopithecus pentelicus* (Cercopithecoidea: Colobinae). *Geobios*, 36, 229-239.
- YOULATOS, D. & G.D. KOUFOS (2010). Locomotor evolution of *Mesopithecus* (Primates: Colobinae) from Greece: evidence from selected astragalar characters. *Primates*, 51(1), 23-35.
- ZAPFE, H. (1991). *Mesopithecus pentelicus* WAGNER aus dem Turolien von Pikermi bei Athen, Odontologie und Osteologie (eine Dokumentation). *Neue Denk-Schriften des Naturhistorischen Museums in Wien*, 5, 203 p.