**NEW VIEW ON THE OLD COLLECTION – ‘PIKERMIAN FAUNA’
FROM THE VICINITY OF VELES (REPUBLIC OF MACEDONIA).
PART 1 – PRIMATES**

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The paper presents the first detailed description and the first analysis of the fossil colobine monkey *Mesopithecus* housed in the collections of the Natural History Museum in Belgrade, Serbia. The material is described using the standard methodology and analyzed in a comparative context of specimens from the published literature (n=45), by using bivariate and multivariate statistical methods (principal component analysis). We determined several species: *M. pentelicus*, *M. delsoni*, *M. cf. pentelicus*, *M. cf. delsoni*. The associated fauna suggests MN11 to MN12 (Turolian) age, and a relatively open landscape - bushy or sparsely wooded savannah. However, further research into the associated collection will allow us to discuss biostratigraphic and paleoecological characteristics in more detail.

Key words: *Mesopithecus*, Cercopithecidae, Veles, Pikermi

INTRODUCTION

The first vertebrate fossil remains from the vicinity of Veles (Republic of Macedonia) were discovered at the fossil site of Prevelec during World

War I, by a group of German soldiers. The material was taken to Munich and published by Schlosser (1921). Subsequently, two scientific expeditions in the Veles area, each spanning a period of several years, recorded numerous fossiliferous sites represented by lenses (bony breccia and lumachelle), with rich *Hipparion* fauna. Two fossiliferous sites - Beluška and Prevalec - were excavated in the course of the first expedition (1921-1929). Laskarev (1923) published a report on geomorphological conditions and a preliminary list of fossil fauna. The second expedition took place after World War II (1948-1952) and the excavations continued in the two previously known localities and the new site of Brce; Ćirić (1957) published a complete list of the fauna from all three sites as a part of his doctoral dissertation. The associated fauna (Tab. 1) suggests MN11 to MN12 (Turolian) age, which is in accordance with the ages of these species in other European sites (Koufos 2009b). Pavlović & Marković (1990) examined the sediments that covered the large vertebrate bones in the collection and identified the numerous specimens of the small vertebrates: *Parapodemus gaudryi*, *Progonomys cathalai*, *Occitanomys neutrum*, *Kowalskia* cf. *lavocati*, *Cricetus* sp., *Soriculus* sp. and *Ophisaurus panonicus*.

Table 1. - The list of fauna from the localities in the vicinity of Veles (Schlosser 1921, Ćirić 1957, Forsten & Garevski 1989).

Locality	Fauna
Beluška	<i>"Hyaena eximia"</i> , <i>"Mastodon pentelicus"</i> , <i>"Hipparion gracile"</i> , <i>Hipparion matthewi</i> , <i>Hipparion verae</i> , <i>"Rhinoceros schleiermacheri"</i> , <i>"Sus erimanthius"</i> , <i>Helladotherium duvernoyi</i> , <i>Palaeoreas lindermayeri</i> , <i>"Tragocerus amaltheus"</i> , <i>Palaeoryx pallasii</i> , <i>"Protragelaphus</i> cf. <i>zitteli"</i> , <i>Gazella brevicornis</i> .
Prevalec	<i>"Ictitherium robustum"</i> , <i>"Palhyaena hipparionum"</i> , <i>"Machairodus orientalis"</i> , <i>"Mastodon longirostris"</i> , <i>Dinotherium giganteum</i> , <i>Hipparion matthewi</i> , <i>"Rhinoceros schleiermacheri"</i> , <i>"Nestoriterium pentelica"</i> , <i>"Sus erimanthius"</i> , <i>"Camelopardalis parva"</i> <i>Palaeotragus rouenii</i> , <i>Helladotherium duvernoyi</i> , <i>Palaeoreas lindermayeri</i> , <i>"Tragocerus amaltheus"</i> , <i>Protragelaphus skouzesi</i> , <i>Gazella brevicornis</i> , <i>"Gazella deperdita"</i> .
Brce	<i>Hipparion</i> sp.

All of the abovementioned remains are stored at the Natural History Museum in Belgrade and represent an important part of the Collection of Tertiary Vertebrates. With the discovery of the similar faunas in the Balkans (Koufos 2006), the accumulation of the comparative fossil material and the application of the modern methods of systematics, we questioned

the original taxonomic identifications and re-examined the material in this collection.

MATERIAL AND METHODS

The first find of a primate in the Central Balkans, represented by a proximal femur joint and later identified by Schlosser (1921) as *Mesopithecus pentelicus* (Wagner 1839), was among the fossil material collected by German soldiers in WWI. In the two subsequent scientific expeditions seven *Mesopithecus* specimens were recorded at three sites: Beluška, Prevalec and Brce. Ćirić (1957) provided a brief description of *Mesopithecus* specimens, along with the rest of the fauna. Since no modern descriptions and no comparative analysis of this material have been provided to date, we decided to re-assess the morphology and taxonomic status of *Mesopithecus* from the Veles vicinity. Few fossil primates are recovered from the Central Balkans in general, which is surprising given that numerous species of both monkeys and apes were recovered from adjacent areas: in the Pannonian plane to the north (Begun 2007) and in Greece to the south (Koufos 2009a). This paper describes and compares seven cranial and gnathic specimens of the genus *Mesopithecus* discovered at three Macedonian localities in the vicinity of Veles – Prevalec, Beluška and Brce (Tab. 2), which form part of the collection of the Natural History Museum in Belgrade (Figs. 1-7).

Table 2. - The list of investigated specimens.

Specimen	Locality	Year of the discovery	Discovery made by
NHMBEO-0332652	Beluška, Macedonia	1950	Ćirić, A.
NHMBEO-0332653	Beluška, Macedonia	1950	Ćirić, A.
NHMBEO-0332654	Beluška, Macedonia	1949	Ćirić, A.
NHMBEO-0332655	Brce, Macedonia	1948	Ćirić, A.
NHMBEO-0332656	Prevalec, Macedonia	1921	Laskarev, V.
NHMBEO-0332657	Prevalec, Macedonia	1922	Laskarev, V.
NHMBEO-0332658	Prevalec, Macedonia	1923	Laskarev, V.

Our comparative sample (n=45) was taken from the published literature and it comprises the fossil remains from eight localities (Tab. 3). We conducted principal component analysis (PCA) and bivariate comparisons using PAST software (Hammer *et al.* 1998).

Table 3. - The list of fauna from the localities in the vicinity of Veles (Schlosser 1921, Ćirić 1957, Forsten & Garevski 1989).

Locality	Specimens	Country	Taxon	Age	References
Ravin des Zouaves 5	RZO159, RZO160, RZO161	Greece	<i>Mesopithecus delsoni</i>	MN12	Bonis <i>et al.</i> (1990)
Dytiko 1	DTK235	Greece	<i>Mesopithecus</i> cf. <i>pentelicus</i>	MN13	Bonis <i>et al.</i> (1990)
Dytiko 3	DKO38	Greece	<i>Mesopithecus</i> aff. <i>pentelicus</i>	MN13	Bonis <i>et al.</i> (1990)
Dytiko 2	DIT22	Greece	<i>Mesopithecus</i> cf. <i>monspessulanus</i>	MN13	Bonis <i>et al.</i> (1990)
Maragha	MRG	Iran	<i>Mesopithecus</i> aff. <i>delsoni</i>	MN11	Bonis <i>et al.</i> (1990)
Montpellier	MPL uncat.	France	<i>Mesopithecus</i> <i>monspessulanus</i>	MN14	Bonis <i>et al.</i> (1990)
Villafranca d'Asti	VJ87, VJ130	Italy	<i>Mesopithecus</i> <i>monspessulanus</i>	MN16a	Pradella & Rook (2007)
Pikermi	PIK01, PIK02, PIK03, PIK06, PIK07, PIK08, PIK09, PIK10, PIK12, PIK13, PIK16, PIK17, PIK20, PIK21, PIK21A, PIK34, PIK35, PIK94, PIK253, PIK303A, PVH02, PVH03, PVH04, PVH05, PVH06, PVH07, PVH08, PVH09, PVH11, PVH12	Greece	<i>Mesopithecus pentelicus</i>	MN12	Bonis <i>et al.</i> (1990), Costeur & Malvesy (2010)

RESULTS

Systematic paleontology

Order PRIMATES Linnaeus 1758

Family CERCOPITHECIDAE Gray 1821

Subfamily COLOBINAE, Blyth 1875

Genus *Mesopithecus* Wagner 1839

Mesopithecus is a Late Miocene and Pliocene (8.7 - 3 Ma [millions of years ago]) genus of monkey known from western Europe to China (Youlatos *et al.* 2012). These fossil monkeys resemble living colobines in most dental features, and they are found to be particularly close to the Asian odd-nosed colobine species (*Rhinopithecus*, *Nasalis*, *Pygathrix*, and *Simias*), which is in contrast to previous studies, which proposed that *Mesopithecus* is more closely related to the African colobus and the gray langur (*Semnopithecus*) (Zapfe 1991, Jablonski 1998, 2002, Pan *et al.* 2004). Unlike their modern relatives, *Mesopithecus* species were not exclusively folivorous, but rather they were opportunistic feeders, often consuming hard seeds (Merceron *et al.* 2009). All species were langur-sized and sexually dimorphic and presumably lived in multi-female social groups (Fleagle 1998). *Mesopithecus* was a semi-terrestrial quadruped found in a wide range of conditions, from more wooded to more open landscapes (Merceron *et al.* 2009, Youlatos *et al.* 2012). Two species were traditionally recognized within the genus: the large-bodied (around 8 kg) Late Miocene *M. pentelicus* (Wagner 1839) and the smaller-bodied (around 5 kg) Pliocene *M. monspessulanus* (Gervais 1849). A third species, the Late Miocene *M. delsoni* (Bonis *et al.* 1990), defined on the basis of large mandibular specimens from the fossil site of Ravin des Zouaves 5 (Greece), was added later. Although the taxonomic validity of this species has been questioned (Delson 1994, Andrews *et al.* 1996, Rook 1999), fossils from Bulgaria (Hadjidimovo-1 and Kalimantsi), Iran (Maragha), and possibly others from Greece (Ravin X) give this species additional support (Bonis *et al.* 1990, Koufos *et al.* 2003, Koufos 2009a). Following this, we consider *M. delsoni* a valid taxon.

MESOPITHECUS PENTELICUS, Wagner 1839**Locality:** Brce, Republic of Macedonia.**Material:** Mandible fragment with i1-m1 dex. and i1-p4 sin. NHMBEO-0332655 (Fig. 1).**Characteristics:** Mandibular and dental characters and metrics similar to *M. pentelicus*.**Diagnosis:** See Koufos (2009a).**Description:** The specimen is strongly damaged. The mandibular corpus is shallow and the symphysis is short. The external symphysis is not

flattened and lacks symphyseal constriction. The inferior transverse torus is not particularly thick, and there is only a hint of the genioglossal fossa. All the teeth show an advanced stage of dental attrition, indicating an older individual. Compared to the premolars, the right canine is relatively gracile, suggesting a female individual. Both p3s show the presence of a metaconid and a deep fovea. On the p4s, metaconids are higher than protoconids; the entoconid is small. Heavily worn m1 shows a typical bilophodont pattern. Measurements for the specimen are given in Table 4.

Fig. 1 - Fragmented mandible from Brce (NHMBEO-0332655): occlusal view (top left), lateral view (bottom left) and the view of external symphysis (right).

Table 4. - *Mesopithecus pentelicus*: Measurements for the mandibular specimens. Values marked with the star (*) are not certain, due to the bad preservation of the specimen.

Specimen	Side	c		p3		p4		m1			m2			m3			p3-p4	m1-m3	p3-m3	Mand. depth at p4	Mand. depth at m2	Length of symphysis
		AP	ML	L	B1	L	B1	B2	L	B1	B2	L	B1	B2	L	B1						
NHMBEO-0332654	L	—	—	—	—	—	—	—	7.5	7.3	6.9	10.1	7.4	6.8	—	—	—	—	—	—		
	R	—	—	—	—	—	—	—	6.6	—	—	—	—	—	—	—	—	19.8*	19.5*	—		
NHMBEO-0332655	L	—	—	6.3	3.8	6.5	4.7	—	—	—	—	—	—	—	11.4	—	—	18.8	—	19.1		
	R	5.5	4	6.2	3.9	5.6	4.9	6.6	5.8	6.2	—	—	—	—	11.1	—	—	—	—			
NHMBEO-0332657	L	—	—	5.9	5.1	6	4.9	7.5	5.7	5.9	8.3	6.6	7.1	10.6	6.6	6.3	12.4	27.3	33.4	22.6	22.7	28.7
	R	—	—	—	—	5.8	4.6	7.4	5.7	6.1	8.1	6.5	6.8	10.2	6.7	6.3	—	25.9	32.3	22.5	23.2	
NHMBEO-0332658	L	8.4	5.1	—	—	6.2	4.7	—	—	—	—	—	—	—	—	—	—	—	—	—	28.3	
	R	8.4	5	—	—	6.2	4.5	—	—	—	—	—	—	—	—	—	—	—	22.4	—		

MESOPITHECUS* CF. *PENTELICUS, Wagner 1839

Locality: Prevalec, Republic of Macedonia.

Material: Front portion of the skull NHMBEO-0332656 (Fig. 2).

Fig. 2. - Fragmentary cranium from Prevalec (NHMBEO-0332656): frontal (left), occlusal (right) and right lateral (bottom) views.

Characteristics: Splanchnocranial, palatal and dental morphologies and metrics similar to *M. pentelicus*, but the fragmentary nature of the specimen does not allow its certain identification.

Description: The fragmentary cranium consists of splanchnocranium: frontal (with the lateral portions of the supraorbital region missing), anterior portions of the parietals, the portion of the right temporal squama, the maxilla (the frontal processes, the palatine processes), lacrimals, the palatine - with teeth - left M1-M3 and fragments of left M3. The facial portion of the skull is minimally deformed, and it is quite possible that additional cleaning could reveal more anatomical details. The crowns of the right M1 and M2 are missing, with only a small part of the right M3 crown present. The teeth on the left side are in a better state of preservation, although M1 is missing a large portion of a crown; M1-3 show characteristic biolophodont morphology which is attenuated by heavy wear. The hypocone is present on the M3, but its relative size is difficult to determine due to the wear. Measurements for the specimen are given in Table 5.

Locality: Beluška, Republic of Macedonia.

Material: Maxilla NHMBEO-0332652 (Fig. 3).

Fig. 3. - Maxillary fragment from Beluška (NHMBEO-0332652) in occlusal view.

Characteristics: Metrics of the maxilla and dentition are similar to *M. pentelicus*, but the fragmentary nature of the specimen does not allow certain identification.

Description: The specimen consists of the palatal portion of the maxilla with damaged nasal septum, attached to the palatal bones. The fossil preserves M1-M3 on the right and P4-M3 on the left; the teeth display a moderate level of attrition, especially on cusps on the lingual side of the tooth, with the M3s showing only minimum wear. It is difficult to determine the relative size of the cusps on the preserved P4 but it seems that protocone was not high. Molars show bilophodont pattern; both M3s show small entocone. The left M3 shows a small additional cusp at the base of the median lingual cleft (absent on the right). Measurements for the specimen are given in Table 5.

Table 5. - *Mesopithecus* cf. *pentelicus*: Measurements for the partial crania.

Specimen	Side	P3		P4		M1			M2			M3			M1-M3	Inter-orbital breadth	Palatal breadth	Orbital torus thickness
		L	B1	L	B1	L	B1	B2	L	B1	B2	L	B1	B2				
NHMBEO-0332652	L	–	–	5.3	6.3	7	6.8	7	7.8	8.2	7.9	7.5	7.1	6	21.7	–	35.6	–
	R	–	–	–	–	7	7.1	6.9	7.8	8.2	7.7	7.7	7.2	6.3	21.9			
NHMBEO-0332656	L	–	–	–	–	–	–	–	7.4	8.1	7.3	6.8	7	6	–	10.9	37.2	3.9
	R	–	–	–	–	–	–	–	–	–	–	–	–	–	–			

MESOPITHECUS DELSONI, Bonis, Bouvrain, Geraads & Koufos 1990

Locality: Prevalec, Republic of Macedonia.

Material: Front mandibular fragment NHMBEO-0332658 (Fig. 4).

Fig. 4 - Fragmented mandible from Prevalec (NHMBEO-0332658): occlusal view (top left), lateral view (bottom left) and the view of external symphysis (right).

Characteristics: mandibular and dental characters and metrics similar to *M. delsoni*.

Diagnosis: See Bonis *et al.* (1990).

Description: The mandible preserves i1, i2, c and p4 on both sides; post-p4 portions of the bone are missing. Although the canine crowns are broken off, their relatively large size and robustness are evident, indicating that the individual was likely a male. The mandibular corpus

is robust and deep. The external symphysis is flattened and there is a well-marked symphyseal constriction. The alveolar plane is slightly inclined. A large genioglossal fossa is present, which is emphasized by the presence of a strong inferior transverse torus. The teeth are not too heavily worn, making the cusp patterns on p4s evident. The metaconid in p4 seems to be higher than the protoconid, the metalophid (protocristid) is short and blunt; two small cusps (entoconid and hypoconid) are present; fovea are well-marked - the anterior (trigonid basin) is small, compared to the larger and lower posterior fovea (talonid basin); the mesiobuccal flare is strongly expressed. Measurements for the specimen are given in Table 4.

Locality: Prevalec, Republic of Macedonia.

Material: Mandible NHMBEO-0332657 (Fig. 5).

Fig. 5. - Fragmented mandible from Prevalec (NHMBEO-0332657): occlusal view (top left), lateral view (bottom left) and the view of external symphysis (right).

Characteristics: Mandibular and dental characters and metrics similar to *M. delsoni*.

Description: This is the most complete mandibular specimen in the collection, consisting of the entire mandibular corpus, with the fragment of the right ramus preserved. The anterior aspect shows flattening of the symphysis and a slight constriction. The mandibular corpus is deep. The alveolar plane is not steeply inclined; there is a

moderately large genioglossal fossa and inferior transverse torus. The crowns of the anterior dentition are missing (with the exception of the part of the left canine), but the posterior teeth are completely preserved (with the exception of the right p3). The teeth do not show much attrition, indicating a young adult individual. The left p3 displays the large honing facet, with a large mesiobuccal projection, no metaconid, and well-defined metalophid. The diastema is not large, and the canines seem to be relatively small. Both p4s show significantly higher metaconid than protoconid, blunt metalophid and marked fovea. All molars show bilophodont pattern. The first and second molars display wear, but it is not significant. The third molars show less attrition and the presence of the large bicuspid hypoconulid. Measurements for the specimen are given in Table 4.

MESOPITHECUS* CF. *DELSONI, Bonis, Bouvrain, Geraads & Koufos 1990

Locality: Beluška, Republic of Macedonia.

Material: Partially preserved mandible NHMBEO-0332654 (Fig. 6).

Fig. 6. - Fragmented mandible from Beluška (NHMBEO-0332654) still embedded in rock matrix: occlusal view (top left), lateral (bottom left) and the view of external symphysis (right).

Characteristics: Characters and m3 measurements similar to *M. delsoni*, but the specimen is badly preserved, so certain determination is difficult.

Description: The posterior portion of the partially preserved mandibular corpus is still embedded in the matrix. Although the superior-anterior aspect of the corpus is damaged, the preserved portion of the symphysis suggests a rather flat surface; on the interior aspect, there is a clear transverse torus and a large genioglossal fossa (partially filled with matrix). The mandibular corpus looks closer in depth to *M. delsoni* according to our measurements, but there is significant damage which precludes certain assessment of the trait. On the right side, p3, p4, fragmentary m1 and m2 are preserved; on the left, m2 and m3 are present. All teeth show marked attrition, especially teeth of the right portion of the corpus; this suggests an older individual. The m3 shows the presence of a large hypoconulid. Measurements for the specimen are given in Table 4.

MESOPITHECUS SP. INDET.

Locality: Beluška, Republic of Macedonia.

Material: Fragmentary neurocranium NHMBEO-0332653 (Fig. 7).

Characteristics: Characters generally fit with *Mesopithecus* morphology, but there is no basis for the determination at the species level.

Description: The specimen consists of the partial brain endocast and very fragmentary neurocranial bones - small portion of the frontal squama along the coronal suture, the right parietal fragment along the sagittal suture, almost complete left parietal, the superior and the nuchal portions of the occipital. The supratemporal ridge (temporal crest) is evident on the left parietal. There is the nuchal crest on the occipital, but the sagittal crest is completely absent.

Comparative metric analysis

Bivariate comparisons of the teeth measurements are given in Figure 8. Figure 8a shows a bivariate plot of m3 length and trigonid breadth; both NHMBEO-0332654 and NHMBEO-0332657 specimens present long m3 that group most closely with *Mesopithecus delsoni* (Ravin des Zouaves 5, Greece) material. This is especially important because m3 is larger in *M. delsoni* compared to the other species of the genus. Figure 8b shows a bivariate plot of lower cheek teeth lengths – p3-p4 and m1-m3 lengths. NHMBEO-0332657 plots far from the most comparative specimens, but most closely with Ravin des Zouaves specimens, as in Figure 8a. Bivariate plot of mandibular depth at p4 and symphysis length, with NHMBEO-0332655, NHMBEO-0332657 and NHMBEO-0332658, is shown in Figure

Fig. 7. - Fragmentary cranium with the endocranium from Beluška (NHMBEO-0332653) in vertical (top) and left lateral (bottom) views.

in Figure 9a. The first principal component (PC1) accounts for 66.671% and the second (PC2) accounts for 17.092% of the total variance. Loadings for PC1 are positive for all molar measurements; loadings for PC2 are negative for m1 and m3 lengths (Tab. 6). *M. monspessulanus* specimens (Montpellier and Villafranca d'Asti) are clearly separated from *M. pentelicus* (Pikermi). *M. delsoni* (Ravin des Zouaves 5) specimens group at the bottom right part of the plot, together with NHMBEO-0332657 specimen.

The second PCA was based on 4 measurements – p4 length, p4 trigonid breadth, mandibular depth at p4 and symphysis length. There were no missing values. Two specimens from the Veles collection were included (NHMBEO-0332657, NHMBEO-0332658). PC1 accounts for 90.279% and

8c. NHMBEO-0332657 and NHMBEO-0332658 present deep mandibles and group with Ravin des Zouaves 5 specimens, outside the Pikermi range (although close). NHMBEO-0332655 is also positioned outside the Pikermi range, but far from Ravin des Zouaves.

We conducted a principal component analysis (PCA) of the variance-covariance matrix based on raw mandibular molar measurements – lengths, trigonid and talonid breadths for m1, m2 and m3. The sample was chosen to include only those specimens for which all nine variables were available; only one specimen from the Veles collection (NHMBEO-0332657) was included in the analysis. Results are presented

Fig. 8. - Bivariate scatter plots: a) m3 length and trigonid breadths (n=23); b) p3-p4 and m1-m3 lengths (n=20); c) mandibular depth at p4 and symphysis length (n=15). Veles (cross), *M. delsoni* from Ravin des Zouaves 5 (diamond), *M. pentelicus* from Pikermi (square), *M. cf. pentelicus* from Dytiko 1 (star), *M. cf. monspessulanus* from Dytiko 2 (X), *Mesopithecus aff. pentelicus* from Dytiko 3 (circle), *M. aff. delsoni* from Maragha (filled inverted triangle), *M. monspessulanus* from Montpellier (filled diamond) and Villafranca d'Asti (triangle). Collection numbers for Veles specimens are shown on plots.

Table 6. - Principal components for the first PCA.

Measurement	Axis 1	Axis 2
m1 length	0.2679	-0.02180
m1 trigonid breadth	0.2671	0.21170
m1 talonid breadth	0.3306	0.19750
m2 length	0.2478	0.08790
m2 trigonid breadth	0.3756	0.39140
m2 talonid breadth	0.3926	0.18130
m3 length	0.4585	-0.84580
m3 trigonid breadth	0.2867	0.02903
m3 talonid breadth	0.3140	0.07476

Fig. 9. - Principal component analysis: a) PCA based on 9 raw mandibular molar measurements (n=17); b) PCA based on four mandibular measurements (p4 length, p4 trigonid breadth, mandibular depth at p4 and symphysis length) (n=13); c) PCA based on 6 maxillary molar measurements (n=14); d) PCA based on interorbital and palatal breadths and orbital torus thickness (n=15). For a, b and c: Veles (cross), *M. delsoni* from Ravin des Zouaves 5 (diamond), *M. pentelicus* from Pikermi (square), *M. aff. delsoni* from Maragha (filled inverted triangle), *M. monspessulanus* from Montpellier (filled diamond) and Villafranca d'Asti (triangle). For d: Veles (cross), *M. pentelicus* Pikermi males (square), *M. pentelicus* Pikermi females (filled square). Collection numbers for Veles specimens are shown on plots.

PC2 accounts for 6.9962% of the total variance. Loadings for PC1 are positive for all measurements; loadings for PC2 are negative for all measurements, except for mandibular depth at p4 (Tab. 7). As shown in Figure 9b, both NHMBEO-0332657 and NHMBEO-0332658 group together with *M. delsoni* (Ravin des Zouaves 5), and outside of the range of Pikermi *M. pentelicus* material.

Table 7. - Principal components for the second PCA.

Measurement	Axis 1	Axis 2
p4 length	0.11940	-0.08294
p4 trigonid breadth	0.02096	-0.03219
mandibular depth at p4	0.61110	0.79140
Symphysis length	0.78220	-0.60470

The third PCA was based on 6 maxillary molar measurements – length, trigon and talon breadths of M2 and M3. We compared NHMBEO-0332652 and NHMBEO-0332656 with Pikermi material, with no missing values. Loadings for PC1 are positive for all measurements; loadings for PC2 are negative for all measurements, except for M3 length (Tab. 8). PC1 accounts for 41.831% and PC2 accounts for 38.171% of the total variance. The plot (Fig. 9c) shows that both specimens fit within the range of Pikermi specimens.

Table 8. - Principal components for the third PCA.

Measurement	Axis 1	Axis 2
M2 length	0.3473	-0.226700
M2 trigon breadth	0.1886	-0.144900
M2 talon breadth	0.172	-0.087510
M3 length	0.1807	0.952200
M3b1	0.4294	-0.115400
M3b2	0.7728	-0.001808

Table 9. - Principal components for the fourth PCA.

Measurement	Axis 1	Axis 2
Interorbital breadth	0.3110	0.8691
Palatal breadth	0.9423	-0.3347
Orbital torus thickness	0.1236	0.3642

The fourth PCA was based on three cranial measurements – interorbital and palatal breadths and orbital torus thickness; we compared the NHMBEO-0332656 with Pikermi male and female samples. PC1 accounts

for 83.197% and PC2 accounts for 14.359% of the total variance; loadings for PC1 are positive for all measurements (strongly positive for palatal breadth), while the loadings for PC2 are positive for interorbital breadth (strongly positive), orbital torus thickness, and negative for palatal breadth (Tab. 9). As shown in Figure 9d, the NHMBEO-0332656 cranium plots right in the middle of the Pikermi male range, far from Pikermi females.

DISCUSSION

Our re-assessment of the primate material from the vicinity of Veles suggests substantial size and morphological variation, which indicates the presence of a minimum two different taxa (contra Ćirić, 1957). Both morphological description and statistical analyses show that the two best preserved mandibular specimens (NHMBEO-0332657, NHMBEO-0332658) fit most closely with *M. delsoni*. These specimens show diagnostic features (Koufos 2009a, Bonis *et al.* 1990) such as large size, flattened anterior symphysis, symphyseal constriction, slight inclination of the alveolar plane, the presence of a large genioglossal fossa and of a thick inferior transverse torus, deep mandibular corpus (Tab. 3; Fig. 8c), large cheek teeth (especially m3; see Figs. 8a, b), large p3 honing facet, well developed and bicuspid m3 hypoconulid. On this basis, NHMBEO-0332657 and NHMBEO-0332658 should be identified as *M. delsoni*. The bad preservation of NHMBEO-0332654 precludes certain identification on the species level; however, the mandible seems to suggest some features diagnostic for *M. delsoni*: flat symphysis, transverse torus, genioglossal fossa, large hypoconulid, large m3 (Fig. 8a). On this basis, NHMBEO-0332654 could be referred to as *M. cf. delsoni*. NHMBEO-0332655 differs from the other mandibular specimens and fits more closely with *M. pentelicus*; it shows a relatively shallow corpus and short symphyseal length (Fig. 8c), no constriction of the symphysis, short p3-p4 length, strongly inclined alveolar plane, relatively thin inferior transverse torus and a relatively small genioglossal fossa. Therefore, NHMBEO-0332655 would be best referred to as *M. pentelicus*. Since the holotype material for *M. delsoni* consists only of mandibular specimens, diagnostic features on the other cranial regions are not known for this species. However, NHMBEO-0332652 and NHMBEO-0332656 show a close resemblance to Pikermi material in molar dimensions (Fig. 9c). The small protocone on P4 of NHMBEO-0332652 also supports this similarity with *M. pentelicus*. Cranial measurements (palatal and interorbital breadths, orbital torus thickness) for NHMBEO-0332656 are also similar to *M. pentelicus* male range (Fig. 9d). On this basis, NHMBEO-0332652 and NHMBEO-0332656 specimens could be identified as *M. cf. pentelicus*. Since

specimen NHMBEO-0332653 has not preserved enough morphological characters, certain identification is difficult; therefore, we can only identify the specimen as *Mesopithecus* sp. indet. However, there is the possibility that NHMBEO-0332652 and NHMBEO-0332653 could belong to the same individual; if this is the case, we would also regard NHMBEO-0332653 as *M. cf. pentelicus*.

The cercopithecoid genus *Mesopithecus* does not appear in the European fossil records until the late Miocene; a short land bridge was formed between Africa and Eurasia, allowing faunal exchanges and the arrival of *Mesopithecus* (Koufos *et al.* 2005). The *M. delsoni* species is older than the best known species of the genus, *M. pentelicus*; type material of *M. delsoni* (Ravin des Zouaves 5, Greece) dates to the early Turolian, MN11 (~8.2 Ma), while *M. pentelicus* dates to the middle Turolian, MN12 (~7 Ma) at the Pikermi site (Greece). *M. pentelicus* is also known from a number of other European and Asian localities, where it also dates to the middle Turolian (Szalay & Delson 1979, Bonis *et al.* 1990, Jablonski 2002, Koufos 2009a, Youlatos *et al.* 2012). The third species, *M. monspessulanus*, is later and dates to MN14 at Montpellier (France), and to MN16a at Villafranca d'Asti (Italy), where it is conspecific with *Macaca* (Pradela & Rook 2007); the species could also briefly coexist with *M. pentelicus* during the latest Turolian (MN13) (Rook & Alba 2012). There are also numerous other intermediate morphotypes identified at Greek sites: *M. cf. delsoni* (Ravin-X) dates to MN11/12, *M. delsoni/pentelicus* (Vathylakkos-2,3; Perivolaki) dates to MN12; *M. aff. pentelicus* (Dytiko-2,3), *M. cf. pentelicus* (Dytiko-1), *M. cf. monspessulanus* (Dytiko-2), dates to late Turolian, MN13 (Koufos 2009a, 2009b). The Bulgarian specimens from Hadjidimovo-1 and Kalimantsi assigned to *M. aff. delsoni* date to late MN11 and MN12 (Koufos *et al.* 2003). Maragha mandible from Iran, also referred to as *M. aff. delsoni*, probably dates somewhere between the age of Ravin des Zouaves 5 and Pikermi (Bonis *et al.* 1990). Since the information on the exact stratigraphical location of *Mesopithecus* specimens from the vicinity of Veles is lacking, we cannot provide precise dating. However, the associated fauna (see the list of fauna in the first section), suggest late MN11 to MN12 (early/middle Turolian) age. More information will certainly be available when the revision study of the whole Veles fauna collection is finished.

The presence of the particular herbivorous mammal species (*Palaeoreas lindermayeri*, *Palaeoryx pallasii*, *Gazella brevicornis*, *G. capricornis*, *Palaeotragus rouenii*, *Ictitherium robustum*, *Kowalskia cf. lavocati*, *Parapodemus gauryi*, *Progonomys cathalai*, *Occitanomys neutrum*) at the sites in the vicinity of Veles at the end of the Miocene indicates a relatively open landscape - bushy or sparsely wooded savannah,

similar to some recent African habitats. The study of the small vertebrate remains from Beluška and Prevelec by Pavlović & Marković (1990) confirmed this picture. This is in accordance with all the available data for the Turolian (see Koufos 2009a). While *M. delsoni* and *M. pentelicus* were more terrestrial, the smaller *M. monspessulanus* was probably also arboreal, with specific postcranial adaptations (Delson 1975). The occurrence of *Mesopithecus* in Eurasia seems to coincide with the disappearance of the Miocene hominoids (Andrews *et al.* 1996), which has been correlated with the competition between these groups under the conditions of the more seasonal climate (Agustí *et al.* 2003, Jiménez-Moreno *et al.* 2007, Clavel *et al.* 2012). However, the discovery of a hominoid premolar in the same fossil association as *M. pentelicus* in the middle Turolian (ca. 7 Ma) Bulgarian locality of Azmaka seems to contradict this notion. This find either shows that some hominoid groups persisted into the second half of the Turolian in the Balkans, or alternatively, it documents a new westward dispersal via Anatolia (Spassov *et al.* 2011). Considering the absence of hominoid finds in the Veles collection, and in other Balkan Turolian sites, the latter seems more likely.

CONCLUSION

The morphological characters and the dimensions of the primate fossil specimens from the vicinity of Veles suggest the presence of several *Mesopithecus* taxa. *M. pentelicus* has been identified at Brce (NHMBEO-0332655), and forms similar to *M. pentelicus* have been identified both at Prevelec (NHMBEO-0332656) and Beluška (NHMBEO-0332652). The large-sized specimens from Prevelec (NHMBEO-0332658, NHMBEO-0332657) and Beluška (NHMBEO-0332654) have been identified as *M. delsoni* and *M. cf. delsoni*. The specimen NHMBEO-0332653 is not allocated specifically at present, but identified only as *Mesopithecus* sp. indet. It must be remembered, however, that these taxonomical designations are purely phenetic, mostly based on the size differences; there are no apomorphies which would separate different species in the cladistic sense. So, the case may be that we are simply dealing with a single morphologically variable species. The morphological variability of the primate material from the vicinity of Veles is comparable to the diversity observed in the Greek part of the Vardar (Axios) River valley, where species *M. delsoni* and forms similar to *M. delsoni* and *M. pentelicus* have also been identified (Koufos 2009b). On the basis of the ages of the Greek sites, it has become evident that *M. delsoni* morph is older than *M. pentelicus*. At present, this cannot be tested at Veles, since the precise ages for the primate specimens from Prevelec, Brce and Beluška are lacking.

The only available information on the age and the paleoecology of *Mesopithecus* comes from the associated fauna, which is consistent with the early to middle Turolian (MN11-12), and a bushy or a sparsely wooded savannah habitat.

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НОВИ ПОГЛЕД НА СТАРУ КОЛЕКЦИЈУ – „ПИКЕРМИЈСКА ФАУНА“ ИЗ ОКОЛИНЕ ВЕЛЕСА (РЕПУБЛИКА МАКЕДОНИЈА)

ПРЕДРАГ РАДОВИЋ, САЊА АЛАБУРИЋ,
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Р Е З И М Е

Остаци фосилизованих примата који се чувају у збиркама Природњачког Музеја у Београду, сакупљени су током две вишегодишње теренске експедиције на локалитетима у околини Велеса (БЈР Македонија). То су богата фосилоносна налазишта, која у карактеристичним асоцијацијама животиња садрже и колобине, претходно одређене као *Mesopithecus pentelicus* (Ћирић, 1957). Током прве експедиције 1921-1929, остаци примата констатовани су у Белушки и у Превалецу док су у оквиру друге експедиције 1948-1952 истраживања обављена на Белушки и на новооткривеном локалитету Брце. Целокупна фоси-

лизована фауна у којој се налази и *Mesopithecus* публикована је у докторској дисертацији А. Ћирића (Ћирић 1957).

У раду су дати описи седам кранијалних фрагмената примата рода *Mesopithecus*, каталошки заведени под NHMBEO-0332652, NHMBEO-0332654, NHMBEO-0332655, NHMBEO-0332656, NHMBEO-0332657, NHMBEO-0332658. Поређењем примерака из збирке Музеја са примерцима из публиковане литературе, утврђено је да примати из околине Велеса показују значајна одступања у величини и у морфолошким карактеристикама. Идентификовани су представници *M. pentelicus*, *M. delsoni*, *M. cf. pentelicus*, *M. cf. delsoni*. Припадници врсте *Mesopithecus delsoni* први пут су констатовани на локалитету Превалец што представља први налаз за околину Велеса.

Присуство колобина у палеоасоцијацији индикатор је високо развијене биоценозе. Појава ове врсте примата у Евроазији, која се поклопила са нестанком хоминоида, може се објаснити већим сезонским климатским варијацијама крајем миоцена. На основу присуства одређених представника хербиворних врста, околина Велеса је крајем миоцена вероватно представљала савану односно делимично пошумљен биотоп, који су колобини користили као склониште од предатора. Више података о палеоекологији очекују се након ревизије целокупне фауне.