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36

37 ABSTRACT This study represents the first extensive systematic investigation of the Miocene
38 mammalian faunas of the Republic of Macedonia (FYROM), stored in the Macedonian
39 Museum of Natural History, Skopje. They range in age from perhaps the early Miocene to the
40 early Ruscinian, but the bulk of the fossils represent middle Turolian mammals. At least 57
41 taxa have been identified, from 25 different paleontological sites, mostly from the Vardar and
42 Strumitsa river basins, but also from the Morievo and Delchevo regions. The richest localities
43 are the middle Turolian localities of Karaslari (with 22 species) and Kiro Kuchuk (17
44 species). The rich fossil material greatly improves our knowledge of the Turolian Hipparion
45 faunas of the Balkan-Iranian zoogeographic paleo-province, whose westernmost part was
46 mostly documented in Greece and Bulgaria. The fauna displays the typical faunal features of
47 the Balkan Pikermian biome, with dominance of hipparions (especially *H. brachypus*, but our
48 revision does not confirm the presence of *Hipparion verae* in the Turolian faunas) and bovids
49 such as *Gazella*, *Tragoptax*, and spiral-horned antelopes. Other forms usually found in the
50 area, such as *Microstonyx erymanthius*, *Dihoplus pikermiensis*, chalicotheres,

51 *Choerolophodon pentelici*, *Mesopithecus pentelicus*, or *Adcrocuta eximia* are also common.
52 Several new forms have been identified among the carnivores, the giraffids and the bovids.
53 The Macedonian material contributes to reconstructing the history of several taxa such as
54 *Simocyon*, *Metailurus*, several hipparion species, *Propotamochoerus*, *Bohlinia*, *Sivatherium*.
55 The most noticeable features of these Turolian faunas are: the abundance of spiral-horned
56 antelopes, and rarity of antelopes of the *Protoryx-Pachytragus* group, as in Bulgaria; the co-
57 existence of chalicotheriins and schizotheriins; the frequency of *Dihoplus* compared to
58 *Ceratotherium*; the presence of *Chilotherium*, which reaches its westernmost longitude; and
59 the presence of *Anancus* sp. in some localities, considered here as post-Pikermian.

60

61 **KEYWORDS:** Republic of Macedonia; FYROM; late Miocene; Mammalia; Pikermian fauna;
62 biochronology

63

64 **I. INTRODUCTION**

65 The first late Miocene faunas were discovered in the country during World War I and
66 were published by SCHLOSSER (1921). They probably come from the region around Prevalets
67 near Veles. Simultaneously, LASKAREV (1921) published a description of the Pikermian fauna
68 from the region of Veles. Until the 1960s, only a few papers dealing with late Miocene faunas
69 of the country were published, by BRUNNER (1939), PAPP (1939), and ĆIRIĆ (1957; 1964).
70 More recent publications on these faunas bear the signature of one of us (GAREVSKI 1956;
71 1960a,b; 1974a,b; 1976a,b; 1985; 1989a,b; 1991; 1992; 1997; GAREVSKI & ZAPFE 1983;
72 FORSTEN & GAREVSKI 1989; GAREVSKI & MLADENOVSKI 2006), but were mostly published
73 in local journals with limited distribution into the scientific world, some of the articles being
74 even written in native language making all these works of limited use. Some publications of
75 broader diffusion appeared recently (GERAADS et al. 2008; GERAADS, 2009; GAREVSKI &

76 MARKOV 2011; SPASSOV & GERAADS 2011, 2015; GAREVSKI et al. 2012; RADOVIĆ et al.
77 2013), but they focused on specific elements of the assemblages, so that the composition,
78 biochronology, and zoogeographical affinities of these late Miocene faunas remain poorly
79 documented compared to other areas of the Balkano-Iranian zoogeographic province (BONIS
80 et al. 1992; GERAADS et al. 2003; SPASSOV et al. 2006; KOUFOS 2013).

81 The purpose of this paper is to provide a taxonomic revision of the rich collections
82 stored in the Macedonian Museum of Natural History in Skopje. They were accumulated
83 during the last decades by the excavations of the late R. GAREVSKI but remain largely
84 unpublished. Together with new interpretations of old publications and the revision of some
85 additional material stored in other institutions, this will form the basis of revised faunal lists
86 of a number of (mostly upper) Miocene sites from the Republic of Macedonia, and of their
87 preliminary biochronological estimates. Thus we try to offer a picture of the richness of the
88 “Pikermian” fauna of this region, which is very promising for future investigations, as many
89 localities remain virtually unexploited.

90 The geographic regions (fossiliferous areas) in the text are mentioned from north to
91 south and from west to east and the localities in each region are given in alphabetic order.
92 (Text-fig. 1).

93

94

95 **Abbreviations**

96 LGPUT: Laboratory of Geology and Paleontology, Aristotle University of Thessaloniki;
97 MNHNP: Muséum National d’Histoire Naturelle, Paris; MMNH-Sk: Macedonian Museum of
98 Natural History, Skopje; NHMB: Natural History Museum, Belgrade; NHMUK: Natural
99 History Museum, London; NHMW: Naturhistorisches Museum Wien; NMNHS: National

100 Museum of Natural History at the Bulgarian Academy of Sciences, Sofia; PMA: Kovachev
 101 Paleontological Museum, Assenovgrad (Branch of the NMNHS).

102 Locality names in Republic of Macedonia [Originally spelt in Cyrillic, some of the
 103 names have been published in older (Yugoslav) literature following the Cyrillic to Latin
 104 transcription rules of Serbo-Croatian (but sometimes omitting diacritics). In this text, we
 105 provide these forms together with spellings that are closer to the actual pronunciation of the
 106 place names.]: BB: Bashibos; BEL: Belushka (Beluska); CHA: Chashka (Caska); CHD:
 107 Choloshevski Dol; DD: Dolni Disan; GRA: Gradeshnitsa (Gradesnica); KLN: Kalnitsa
 108 (Kalnica); KAR: Karaslari; KK: Kiro Kuchuk; KUM: Kumanovo; MOR: Morievo area; NRZ:
 109 Nerezi; PRE: Prevalets (Prevalec); PRS: Prsten; RAP: Rashtanski Pat; STM: Stamer; TRE:
 110 Tremnik; UD: Umin Dol; VOZ: Vozartsi (Vozarci); VSH: Veshie (Vesje); ZM1: Zmiovets 1
 111 (Zmijovec 1); ZM2: Zmiovets 2 (Zmijovec 2); ZVE: Zvegor.

112 Other localities: AKK: Akkaşdağı (Turkey); AZM: Azmaka (Bulgaria); DTK: Dytiko
 113 (Greece); GR: Grebeniki (Ukraine); HD: Hadjidimovo (Bulgaria); KAL: Kalimantsi
 114 (Bulgaria); KCH-1, KCH-2, KCH-3: Kocherinovo 1, 2 and 3 (Bulgaria); MAR: Maragha
 115 (Iran); MTL: Mytilini (Greece); NKT: Nikiti 1; NIK: Nikiti 2; PER: Perivolaki (Greece); PIK:
 116 Pikermi (Greece); PNT: Pentalophos (Greece); RPL: Ravin de la Pluie (Greece); RZO: Ravin
 117 des Zouaves-5 (Greece); STR 2: Strumyani 2 (Bulgaria); VTH: Vathylakkos; YLF: Yulafli.

118 Other abbreviations: FM: Fossil Mammal collection, NMNHS; APD: anteroposterior
 119 diameter; ET: enamel thickness; H: height; L: length; Lfr: length of fragment; max.:
 120 maximum; TD: transverse diameter; *H.*: *Hipparion*.

121

122 **II. THE LATE MIOCENE LOCALITIES AND THEIR FAUNAS**

123

124 **II.1 KUMANOVO AREA**

125 DELSON (1973: fig.55K-M) reported "an unregistered mandible of *Mesopithecus*
 126 *pentelicus* – M/02, badly eroded and damaged" stored in the collections of the University of
 127 Vienna, labelled as "Kumanidorf", i.e. Kumanovo, indicating a Turolian age. There is no
 128 fossil material from this area in the NMNH-Sk.

129

130 **II.2. SKOPJE REGION**

131 **II.2.1. Nerezi**

132 Proboscidea. This locality has yielded two elephantoid taxa. A right M3, misidentified
 133 as m3 and referred by LASKAREV (1936, pl. 3, Fig. 4) to "*Mastodon angustidens* f.
 134 *subtapiroidea*" actually belongs to *Zygodolophodon turicensis* (as well as probably the
 135 unfigured "m3 sin" from the same locality and possibly from the same individual described
 136 by LASKAREV, 1936, p. 112: see GAREVSKI et al. 2012). A mandible referred by LASKAREV
 137 (1936, pl. 1 and 2) to "*Mastodon angustidens* f. *typica* var. *skopljensis*" cannot be
 138 unequivocally determined on morphological grounds. It could indeed belong to
 139 *G. angustidens* but also to the amebelodontid *Archaeobelodon filholi* – while these two taxa
 140 are readily set apart by a number of cranio-mandibular characters, their dental morphology
 141 (especially the m3s which are preserved with the Nerezi specimen) can be very similar
 142 (TASSY 1985). The symphysis of the mandible is unfortunately not preserved, and
 143 LASKAREV's description does not mention the shape of the alveoli. Measurements of the third
 144 molars provided by LASKAREV (1936) fit with the size observed in male *G. angustidens* (see
 145 TASSY 1996, figs. 11.12 and 11.14) – the same size, however, would correspond to female
 146 individuals of *A. filholi* (see TASSY 1985). As far as mandibular measurements are concerned,
 147 the maximum height of the mandible (dental age XXII of TASSY 1996) plots closer to the
 148 *A. filholi* values for XXI (TASSY 1985, fig. 171) but does not surpass the *G. angustidens*
 149 values in such a way as to preclude affinities with the latter, and plots very close to the value

150 for *G. angustidens* from Villefranche d’Astarac (see TASSY 1985, fig. 178; TASSY 2013, fig.
 151 40). Results from the other measurements provided by LASKAREV (1936) (and comparable to
 152 those in TASSY 1985) are also equivocal. Thus, the identification of the Nerezi mandible
 153 remains uncertain, but in any case the two elephantoids at the locality point at a pre-Turolian
 154 age – quite rare for Republic of Macedonia, where most fossil vertebrates localities are
 155 Turolian or later. Among the exceptions are two other closely situated localities: Dolno Sonje
 156 (Donje Solnje in LASKAREV 1936) has yielded a molar fragment, referred by LASKAREV
 157 (1936, pl. 4, fig. 1) to “*Mastodon* aff. *angustidens* f. *subtapiroidea*”; while precise
 158 identification is impossible, the figured fragment apparently belongs to a pre-Turolian
 159 elephantoid, judging from its primitive morphology. Similarly, fragmentary remains from
 160 Skopje, Zhelezara neighbourhood (GAREVSKI 1985) cannot be determined with precision but
 161 indicate a pre-Turolian age: the figured tusk fragment has a well pronounced lateral enamel
 162 band, a character absent in all Turolian elephantoids.

163 The two Nerezi elephantoids are insufficient for a determination of the locality’s age –
 164 *Z. turicensis* is known from MN3b to MN10 and *G. angustidens* from MN6 to MN9 (TASSY
 165 1985; 1990). *A. filholi* (as an alternative identification for the Nerezi mandible) occurs from
 166 MN4 to MN7/8 (TASSY 1984, 1985), so the age of Nerezi could in theory be from early
 167 Miocene to Vallesian (but not later than MN9).

168

169 **II.3. DELCHEVO FOSSILIFEROUS AREA**

170 **II.3.1. Stamer**

171 The main locality is situated just at the vicinity of the village Stamer in brown-yellowish
 172 clay sands (coordinates: 41°57’21” N, 22°49’12” E; elev. 796 m); it yielded the following
 173 fauna:

174 Artiodactyla. Cervidae. Cf. *Cervavitus* sp. The basal part of a cervid antler has its first
175 bifurcation low above the burr, and is thus certainly distinct from *Pliocervus* and
176 *Procapreolus*; it is more like *Cervavitus* from the Northern Black Sea region and China, but is
177 too incomplete for definitive identification. Measurements: diameters of the burr = 24 x 20,
178 length of first segment = 61. A second specimen has a slightly higher first fork (105 mm), but
179 is probably of the same species. The genus is typical for the late Miocene of Central Asia and
180 Eastern Europe but probably exists there until the early Pliocene (VISLOBOKOVA 1990). Some
181 other very fragmentary, slender antler fragments with a high fork suggest another genus,
182 perhaps *Procapreolus*.

183 Giraffidae. *Sivatherium garevskii*. This gigantic giraffid was defined upon fragmentary
184 cranial remains from this locality, including a relatively complete cranial appendage that was
185 central in determining its affinities (GERAADS 2009). It is related both to the African
186 *S. maurusium* and to the Upper Siwalik *S. giganteum* but closer to the latter. It is only the
187 second known representative of this species in Europe, after a horn piece described by Abel
188 more than a century ago (ABEL 1904). New additional materials in the private coll. of LUBE
189 MITEVSKI from Stamer, probably from the same individual as the holotype, include a talus
190 (max. height = 117mm, distal width = 73 mm) and a distal humerus (distal articular breadth =
191 140 mm). The genus is not known before the Pliocene.

192 Perissodactyla. Equidae. *Hipparion* indet. (sp. 1): Three molars (M1–M3) discovered 2–
193 3 meters above the *Sivatherium* remains are from a medium to large sized hipparion. They are
194 moderately plicated, the pli caballin is single on M3 and absent on the other molars. The
195 hypoconal sinus is of medium depth, the lingual one is well developed on M3. The protocone
196 is lingually rounded and labially flattened, subtriangular in outline. These teeth are larger than
197 in the small *H. macedonicum*, *H. matthewi*, *H. periafricanum*, but the molar length (65.4 mm)
198 is within the range of variation of all medium to large late Miocene hipparions of the Balkans,

199 *Hippotherium brachypus*, *H. dietrichi*, *Cremohipparion proboscideum* and *C. mediterraneum*.
200 They differ from the Pliocene *H. crassum* in their less plicated enamel and less open
201 hypoconal sinus.

202 *Hipparion* indet. (sp. 2): A single fragment of P2 is of a large hipparion. Its enamel
203 plication looks moderately complex, with deep folds, the pli caballin looks complex, the
204 protocone is lingually rounded and labially flattened. Unfortunately it is at an early stage of
205 wear and not all features are visible on the occlusal surface.

206 From the green clays of the village of Stamer, we have seen:

207 Artiodactyla. Suidae indet (in the private coll. of L. MITEVSKI in Stamer). A maxillary
208 fragment with P3-M2 was discovered during the digging of a well in the center of the village
209 (at a lower stratigraphic and topographic position than the main locality). The same clays
210 outcrop in the vicinity of the village, overlain by the brown yellowish clay sands of the main
211 locality. The teeth are intermediate in size between *Microstonyx* and *Propotamochoerus* (P2 =
212 16.5 x 9.8; P4 = 14.5 x 16.5; WM2 = 23.7) but are not diagnostic, especially given the present
213 state of confusion regarding the taxonomy of Pliocene European suids. The premolars are less
214 bunodont than those from Montpellier assigned to *Dasychoerus strozzii* by PICKFORD (2013),
215 and the protocone of P4 is less shifted mesially, and in these two features they are more like
216 *Sus scrofa*, but in the absence of M3 and front teeth, an identification would be premature.

217 Bovidae. Cf. *Parabos cordieri*. A pair of horn-cores from the same individual, very
218 similar to those of *Parabos cordieri* (approx. restored anteroposterior diameter at the base =
219 47 – 48 mm; transversal diameter = 45 – 46 mm) indicate the presence of this bovid in the
220 area, but the fossilization of these horn-cores is different from the other fossils mentioned, and
221 they were found far from them (not in the main locality). *Parabos cordieri* is best known from
222 the Ruscinian but was reported from the uppermost Miocene of Venta del Moro, Spain
223 (MORALES 1984).

224 Biochronology: The Neogene beds of Stamer may include different fossiliferous levels.
 225 The green clays in the village (lowest beds) could be upper Miocene. *Sivatherium* in the main
 226 fossiliferous spot suggests a Ruscinian age, in agreement with the presence of *Parabos* cf.
 227 *cordieri* but the hipparions from the same fossiliferous spot suggest a Turolian age.

228

229 **II.3.2. Zvegor** (41°57'32" N, 22°48'14" E; elev. 736 m)

230 Proboscidea. *Anancus* sp. The locality, of late Turolian or early Ruscinian age, has
 231 yielded a palate with tusks and a mandible of *Anancus* sp., not described yet.

232

233 **II.4. VELES FOSSILIFEROUS AREA**

234 It is from the region of Veles (formerly Titov Veles) that the first late Miocene faunas
 235 were reported (SCHLOSSER 1921; LASKAREV 1921) and they are still often lumped under this
 236 name. In fact at least nine localities are known in the vicinity of the town of Veles, in the
 237 Vardar basin. Fossils from eight of them are stored in the MMNH-Sk, namely: Belushka,
 238 Chashka, Choloshevski Dol, Karaslari, Kiro Kuchuk, Prevalets, Rashtanski Pat, and Umin
 239 Dol. In addition, RADOVIĆ et al. (2013), following ĆIRIĆ (1957) noted *Mesopithecus*
 240 *pentelicus* and *Hipparion* sp. in the locality of Brce, also in the Veles area; these finds are
 241 discussed below, but there is no material from Brce in MMNH-Sk. From the area of Veles,
 242 but without precise provenance, *Ch. pentelici* and *D. gigantissimum* were also reported (ĆIRIĆ
 243 1957; LASKAREV 1948).

244

245 **II.4.1. Belushka (Beluska)** (41°39'35" N, 21°44'03" E; elev. 311 m)

246 ĆIRIĆ collected in 1949-1950 and described (1957) a number of fossils from this site,
 247 but most of them are not in the MMNH-Sk, and we have not seen them.

248 Proboscidea. A juvenile skull with mandible belonging to *Ch. pentelici* was described
249 by GAREVSKI (1997).

250 Primates. *Mesopithecus* cf. *pentelicus*. ČIRIĆ's material was re-described by RADOVIĆ et
251 al. (2013). They identified the maxillary NHMB-EO-0332652 as *M. pentelicus*. The lack of
252 canines forbids gender identification, and consequently size comparisons with samples from
253 well-known localities. However, the P4 protocone is low according to the description and
254 photo, so the identification is acceptable (see discussion below). NHMBEO-0332654 was
255 identified by RADOVIĆ et al. (2013) as *M. cf. delsoni*, but the preservation of the material is
256 too bad for taxonomic conclusions and the co-occurrence of both taxa is unlikely.

257 Artiodactyla. Giraffidae. Cf. *Helladotherium duvernoyi*. An upper tooth-row of large
258 size (P2-M3 = c. 210 mm), poorly figured by ČIRIĆ (1957, pl. 17) displays the broad
259 premolars of this species defined at Pikermi and reported from several other Turolian sites.

260 Bovidae. ČIRIĆ (1957, pl. 18-19) figured a cranium as *Palaeoreas lindermayeri* but the
261 concave lateral part of the horn-cores does not fit this species. Other taxa that can very
262 tentatively be identified from ČIRIĆ's plates are *Majoreas woodwardi* (pl. 25-26) and *Gazella*
263 sp. (pl. 29).

264 Perissodactyla. Equidae. *Hippotherium brachypus*. The description by ČIRIĆ (1957) of
265 materials from this locality is insufficient for an identification. We found only one cranium,
266 MMNH-Sk B 2708 (Plate 1, Fig. 4; Table 1 [all equid measurements follow EISENMANN et al.
267 1988]). It is of a sub-adult individual, with M3 erupting. The orbit is above M3. The
268 preorbital bar is long (42 mm) and the lacrimal bone occupies more than half of its width. The
269 preorbital fossa is moderately deep, egg-shaped, anteroposteriorly oriented and well
270 delineated all around, with a weak pocket (about 5 mm). Judging by the premolar length (P2–
271 P4 = 86 mm), the tooth row appears to be long. The enamel plication on M1 is moderate (19
272 folds). The pli caballin is single. The protocone is oval. The single, relatively deep preorbital

273 fossa located far from the orbit is similar to that of *Hippotherium*. As the preorbital fossa in
 274 *Hippotherium primigenium* is deeper and better outlined, and the tooth plication richer, we
 275 can exclude it from the comparison. The other species with close features are *Hippotherium*
 276 *giganteum* and *Hippotherium brachypus*. The species *Hippotherium giganteum* was erected
 277 by GROMOVA (1952) for the large sized specimens from Grebeniki on the basis of only one
 278 adult specimen. GABUNIA (1959) extended the diagnosis of the species with several adult
 279 skulls from the same locality. After the more precise description of *Hippotherium brachypus*
 280 from Pikermi by KOUFOS (1987b) and the discovery of new samples of this species (HD,
 281 KAL, AKK, KHC 2) (HRISTOVA et al. 2003, HRISTOVA & KOVACHEV, 2005, KOUFOS &
 282 VLACHOU 2005, HRISTOVA et al. 2013,) it is now obvious that the two species are quite
 283 similar and characterized by: large size, elongated skull, long and wide muzzle, simple and
 284 oval preorbital fossa, elongate preorbital bar, rich enamel plication in the upper cheek teeth,
 285 and elliptical protocone. A possible difference between them could be a slightly shorter nasal
 286 notch in the sample from Grebeniki, but the ranges of variation of this feature also overlap.
 287 Pending a revision of the Grebeniki hipparions we can accept *Hippotherium giganteum* as a
 288 synonym of *Hippotherium brachypus* (HENSEL, 1862), and MMNH-Sk B2708 falls within its
 289 range of variation, as also shown by the Simpson diagrams (Text-fig 2).

290 Rhinocerotidae. Cf. *Dihoplus pikermiensis*. The skull poorly sketched in ĆIRIĆ (1957,
 291 pl. 13-14) as *Rhinoceros schleiermacheri* could represent this Turolian species.

292 Biochronology: The fauna clearly indicates a Turolian age; the presence of
 293 *Hippotherium brachypus* and the morphology of *Mesopithecus* fit better the middle Turolian.

294

295 **II.4.2. Chashka (Čaška or Caska)**

296 Proboscidea. *Anancus ? arvernensis*. The locality has yielded only anancine remains –
 297 isolated molars and a tusk described by GAREVSKI (1960b). Identification at the species level
 298 (i.e. Pliocene *Anancus arvernensis* or Turolian *Anancus* sp.) is not possible.

299 Artiodactyla. Cervidae indet. Two basal pieces of antlers are still attached to the pedicle.
 300 One is much weathered (diameters of pedicle 24 x 25, diameter of the burr ca. 35), but
 301 another specimen (Chashka-2648) is better preserved (diameter of the burr 31, diameters of
 302 the beam 21.2 x 22.4). The divergence of the beam increases upwards, and at about 5 cm
 303 above the burr, there is still no indication of the first fork. This would fit *Procapreolus* or
 304 *Pliocervus* (some additional antler fragments are too large for *Procapreolus*), but the material
 305 is too incomplete for a better identification. More cervid remains from this locality are stored
 306 at the Belgrade Museum.

307 Biochronology: The large number of cervid remains suggests a Ruscinian age, and the
 308 Proboscideans do not contradict this hypothesis, but the stratigraphy is unclear.

309

310 **II.4.3. Choloshevski Dol** (4.5 km from Veles on the road Veles – Štip)

311 Rodentia. *Hystrix primigenia*. A skull fragment with upper molars was described by
 312 GAREVSKI (1956).

313 Carnivora. Hyaenidae. *Adcrocuta eximia*: A right rostral mandible fragment (MMNH-
 314 Sk CHD 27) of a young adult (measurements: Table 2). The p2 is pyriform, enlarged distally.
 315 The premolar morphology resembles the Turolian stage of the species (see below under
 316 Karaslari).

317 Biochronology: Middle Turolian ?

318

319 **II.4.4. Karaslari** (41°41'21" N, 21°49'31" E; elev. 168 m)

320 The locality was discovered in the 1970s during the construction of the highway
321 Skopje-Negotino, and excavated by R. GAREVSKI. With 22 mammal species, Karaslari is the
322 richest upper Miocene mammalian locality of the R. of Macedonia.

323 Proboscidea. There are two Proboscideans at Karaslari: *Choerolophodon pentelici*,
324 represented by a sub-adult skull and mandibles, and an unidentified tetralophodont
325 elephantoid: a breccia at the MMNH-Sk exhibition contains a DP4 with a broken crown.
326 Three Turolian elephantoids co-occurring with *Ch. pentelici* ("*Mastodon*" *grandincisivus*,
327 *Tetralophodon atticus*, and *Anancus* sp.; see MARKOV 2008) have tetralophodont intermediate
328 teeth, and the DP4 could belong to any of them.

329 Primates. *Mesopithecus pentelicus*. The material includes an unnumbered male skull
330 with rather worn left and right P4-M3, and two unnumbered male mandibular fragments with
331 p3-m3 (Tables 3-5, Plate 2, Fig. 1). Most of the left side of the neurocranium of this skull is
332 missing, and a natural endocranial cast is visible. Teeth are worn in some extent, but it seems
333 that the upper premolars had a small protocone. The *Mesopithecus pentelicus* skull (NMNH-
334 Sk 68) on display with moderately worn P3-M3 and somewhat crushed vault (Plate 2, Fig. 2)
335 could also be from Karaslari, after unpublished notes of the late R. GAREVSKI. The teeth are
336 small (Table 3). Two fragments of male semimandibles No. 0332657 and 0332658 of small
337 size (Table 4) are probably also from Karaslari.

338 RADOVIĆ et al. (2013) published the *Mesopithecus* material collected by ĆIRIĆ and
339 LASKAREV from three localities in the vicinity of Veles and stored in the NHMB. Following
340 KOUFOS (2009a, b) they identified *M. pentelicus*, *M. cf. pentelicus*, *M. delsoni*, and *M. cf.*
341 *delsoni*. The M3 size of NHMB-EO-0332656, identified as *M. cf. pentelicus*, is similar to that
342 of a female *M. pentelicus* from the middle Turolian of Kalimantsi, thus confirming the
343 presence of this species. By contrast, RADOVIĆ et al. (2013) identified the mandibles NHMB-
344 EO-0332657 and NHMB-EO-0332658 as *Mesopithecus delsoni*. The presence of two

345 different *Mesopithecus* species in the same locality is unlikely, especially if they are
346 chronospecies. In fact, on the basis of the mandible dimensions and symphysis shape (judging
347 from the published photos), we are not convinced of the presence of *M. delsoni* in this
348 locality.

349 The genus *Mesopithecus* has been recorded from the late Miocene and Pliocene of
350 Eurasia, where three species have been distinguished: *M. delsoni*, *M. pentelicus* (early and
351 Middle Turolian) and the smaller *Mesopithecus monspessulanus* (latest Turolian [?] and
352 Pliocene) (DELSON 1973, 1974; BONIS et al. 1990; DELSON et al. 2005; ALBA et al. 2014, and
353 references therein). Its occurrence in the Vallesian (Wissberg) (DELSON 1973, 1974) is
354 questionable (ANDREWS et al. 1996); it may result from stratigraphic mixture. The taxonomic
355 status of the earliest form, *M. delsoni* BONIS et al., 1990, from Ravin des Zouaves n°5 is
356 debated, as the differences between the late Miocene samples are rather subtle. They may be
357 regarded as two species, *M. delsoni* and *M. pentelicus* (BONIS et al. 1990; KOUFOS et al.
358 2003), one species, *M. pentelicus* (ANDREWS et al. 1996; DELSON et al. 2000), one species
359 with two subspecies *M. p. delsoni* and *M. p. pentelicus* (ALBA et al. 2014) or two species and
360 intermediate stages with possible specific status (KOUFOS 2006a, 2009a, b). In any case,
361 several differences usually separate the earlier form *M. delsoni* from *M. pentelicus* (best
362 represented at Pikermi): longer tooth-row, little inclined planum alveolare, deeper mandibular
363 corpus (see also Table 4), and larger m3 hypoconulid (BONIS et al. 1990), a list to which
364 KOUFOS et al. (2003) added a larger protocone on the upper premolars. One of us (N.S.
365 unpublished results) confirms this last difference in the late early Miocene population of
366 Hadjidimovo (Text-fig. 3), and adds the presence of a crista connecting the protocone to the
367 labial cone in upper premolars. It is clear, however, that transitional forms exist in localities
368 that are intermediate in age between RZO/ Hadjidimovo, and Pikermi. Overall, dental size
369 decreases (with some exceptions) from the early Turolian *M. delsoni* to the late Turolian form

370 from Dytiko, this trend being especially clear in m3, while it may be that the relative premolar
371 length slightly increases in relation to the molar length (Table 5). This change could be related
372 to a change in diet towards consumption of less abrasive/more arboreal food with time
373 (SPASSOV & GERAADS 2007; MERCERON et al. 2009). In its overall size, and the probable
374 small size of the premolar protocone, the Karaslari *Mesopithecus* is intermediate between the
375 populations from the early/middle Turolian transition and that of Pikermi.

376 Artiodactyla. Suidae. *Microstonyx erymanthius* . (Plate 3, Fig. 2, 5). The best specimen
377 is the skull NMNH-Sk KAR-1542/73 (Plate 3, Fig. 5). This species is well represented in the
378 Republic of Macedonia by several specimens, including more or less complete skulls; some of
379 them were illustrated by GAREVSKI (1956). Measurements are given in Tables 6 and 7. Their
380 morphology and dimensions leave no doubt as to their belonging to *Microstonyx*, a genus
381 common in the Turolian of Europe, but whose systematics has been much debated. Some
382 authors (BONIS & BOUVRAIN 1996) recognize an evolution from the early Turolian (with the
383 species or subspecies *erymanthius* to the middle-late Turolian (*Microstonyx major* s. str.),
384 while others reject this distinction; by contrast, VAN DER MADE & MOYÀ-SOLÀ (1989) and
385 VAN DER MADE et al. (1992) distinguished the late Vallesian and early Turolian forms as *M.*
386 *major major*, whereas VAN DER MADE (1997) preferred to regard them as two distinct co-
387 existing lineages. LIU et al. (2004) argued that differences in skull morphology could be
388 related to the environment rather than to geological age. In any case, it is certainly true that
389 there is no simple relationship between size (especially that of the third molars) and age. In
390 the localities that have yielded enough material, the range of variation of M3/m3 length
391 covers a large part of the variation of all other sites combined, and Karaslari is no exception.
392 Like most other authors (VAN DER MADE et al. 1992; KOSTOPOULOS 1994; VAN DER MADE
393 1997; KOSTOPOULOS et al. 2001; GERAADS 2013), we failed to find any significant difference
394 in the morphology of the cheek-teeth of *M. major/erymanthius* from the various localities. LIU

395 et al. (2004) stated that the Akkaşdağı population has "a somewhat complicated M3/m3
396 occlusal pattern", but the lack of detailed illustrations makes comparisons difficult; they also
397 stated that "the main lingual cusp of P4 [is] placed as far forward as the labial one"; none of
398 the specimens that we have seen, from the R. of Macedonia or elsewhere, has such a mesially
399 shifted protocone.

400 Most *Microstonyx* lack a p1 (except probably the one from Dorn-Dürkheim: VAN DER
401 MADE, 1997), but the occurrence of P1 is more variable. VAN DER MADE & MOYÀ-SOLÀ
402 (1989) suggested that this tooth tends to disappear during the evolution of this lineage, and
403 KOSTOPOULOS (1994) and KOSTOPOULOS et al (2001) agreed that early forms are more likely
404 to preserve a P1 close to P2. This is the case in the skull from the earliest Turolian of Nikiti-1,
405 and in a maxilla from Kalimantsi K-5268 suspected by KOSTOPOULOS et al. (2001) to come
406 from a lower level than the main Kalimantsi fauna, and this is also true for an unpublished
407 maxilla in the RODLER collection of the NHMW, found at Kopran, where the lowermost
408 layers of the Maragheh Fm crop out. Therefore, there is little doubt that this feature is really
409 indicative of an early age. Unfortunately, most specimens from the R. of Macedonia lack this
410 part of the maxilla, and the material shows that this feature is variable even within a single
411 site.

412 PICKFORD (2015) reviewed these forms, and considered *Microstonyx* as a synonym of
413 *Hippopotamodon* Lydekker, whose type-species is *H. sivalense*. However, the latter species is
414 large, and has a large upper canine and a short snout (PICKFORD 1988), in contrast to
415 *M. erymanthius*, so that the synonymy is not obvious. In addition, PICKFORD (2015) assumed
416 that "*H.*" *major* (type-locality: Cucuron) and "*H.*" *erymanthius* (type-locality: Pikermi) belong
417 to different lineages, the former (his "group A") having shorter snout, bigger canines, P1 and
418 p1 present, and broader cheek-teeth than in group B (in which P1/p1 are often shed) that
419 includes "*H.*" *erymanthius*. He also noted, as a major distinctive feature, that M3 is as long as

420 m3 in "*H.*" *major* from Cucuron, whereas it is shorter in "*H.*" *erymanthius*. We are not
421 convinced that this distinction is valid, because:

422 - m3 is always distinctly longer than M3 in a suid, so that the sample from Cucuron
423 must be biased; indeed, it is clear that the partial skull in MNHN is from a larger individual
424 than the mandibles (as already noticed by GAUDRY). According to PICKFORD himself (2015),
425 the range of m3 length for "*H.*" *major* (38.1 – 57.4) is above that of M3 (34.5 – 49.5) so that
426 their relative proportions are in fact normal;

427 - several maxillae from Pikermi in MNHNP and one in the Paleontological Museum,
428 University of Athens, bear a P1, but not the Cucuron maxilla;

429 - there is no evidence that the canines were larger, nor the snout shorter, at Cucuron than
430 at Pikermi.

431 Pending conclusive evidence of the existence of two species in the European Turolian,
432 we keep the oldest name *M. erymanthius*.

433 "*Propotamochoerus*" sp. A maxilla fragment with dP3-M2, not mentioned in GERAADS
434 et al. (2008) is the only remain of *Propotamochoerus* from Karaslari. PICKFORD (2013, fig.16)
435 assigned the material from the Republic of Macedonia to *Dasychoerus*, mostly on a size-
436 based comparison with Pliocene forms, but we are unsure that this can be extended to the
437 upper Miocene; we acknowledge, however, that *Propotamochoerus* is hard to characterize.

438 Giraffidae. *Bohlinia attica*. Some long, slender limb bones belong to this close relative
439 of the modern giraffe (GERAADS 2009). There is also a piece of maxilla, MMNH-Sk KAR
440 2603, with P4, M2 and M3. The teeth are brachyodont, with strong labial styles and pillars;
441 P4 has the bifid parastyle characteristic of this species (GERAADS 2009).

442 *Helladotherium* sp. A maxilla MMNH-Sk KAR 2752 (Table 8) was described
443 elsewhere (GERAADS 2009). A metacarpal is slightly larger than most of those from Pikermi,

444 and matches better those from Bulgaria or Gülpınar, but some specimens from Maragha and
 445 Ravin des Zouaves 5 are still larger.

446 Bovidae. *Gazella* sp. A few fragmentary horn-cores belong to this genus.

447 *Palaeoreas lindermayeri*. A frontal with complete right horn-core (MMNH-Sk KAR
 448 2610, Plate 4, Fig. 6; Table 9) shows the main characters of the species: horn-core large
 449 compared to skull size, very upright on the fronto-parietal region, not spiralled but strongly
 450 twisted, with a strong posterolateral keel and a tendency towards an anterior one, frontal
 451 sutures closed. Another horn-core (MMNH-Sk KAR 2613, Table 9) is slightly spiralled, with
 452 accessory small keels and grooves parallel to the main one. This specimen is larger than the
 453 other, and compares best with the Hadjidimovo ones (GERAADS et al. 2003).

454 *Tragoportax rugosifrons*. A partial skull MMNH-Sk KAR 1564/73 and two
 455 unnumbered male partial skulls on display as well as an incomplete skull (MMNH-Sk KAR
 456 1593/13, Tables 9, 10) with only the base of the right horn-core preserved can be referred to
 457 this species (SPASSOV & GERAADS 2004). (max. oblique APD of the horn core = 84 mm,
 458 perpendicular APD = 76.4).

459 *Pikermicetus gaudryi*. This species is represented by a frontlet (MMNH-Sk KAR 145)
 460 on display that has the typical horn core features of this species (sensu SPASSOV & GERAADS
 461 2004).

462 Perissodactyla. Equidae. The hipparions from Karaslari were studied by FORSTEN &
 463 GAREVSKI (1989). These authors designated three species in the locality: *Hipparion schlosseri*
 464 ANTONIUS - *dietrichi* WEHRLI, *Hipparion verae* GABUNIA and *Hipparion proboscideum*
 465 STUDER. Our analysis of the main skull material leads to somewhat different taxonomic
 466 conclusions.

467 *Hippotherium brachypus*. Skulls: adult - MMNH-Sk Kar 20/75 MMNH-Sk Kar 24/73,
 468 MMNH-Sk Kar 26/73, MMNH-Sk Kar 75/73, MMNH-Sk Kar 204/73; subadult - MMNH-Sk

469 Kar 76/73; juvenile - MMNH-Sk Kar 82/73, MMNH-Sk Kar 94/73, MMNH-Sk Kar 409/73,
470 MMNH-Sk Kar 1552/73, MMNH-Sk Kar 2704 (Plate 1, Figs 2, 3; Text-fig. 4; Measurements:
471 Table 1. The specimens of this species have deep, well delineated, subtriangular, and antero-
472 posteriorly oriented preorbital fossa. The posterior pocketing is reduced, moderately deep to
473 shallow or even not pocketed but with a posterior rim. The preorbital bar is long (42 to 49
474 mm). The anterior edge of the lacrimal bone is closer to the posterior rim of the fossa than to
475 the anterior orbital rim. The nasal notch ends above P2. The tooth-row lengths of the two
476 skulls with preserved teeth are 144 and 147 mm. The enamel plication is rich, with 15 to 22
477 folds. The pli caballin is usually double to complex. The protocone is oval, but triangular in
478 slightly worn teeth.

479 In their description of *Hipparion verae*, FORSTEN & GAREVSKI (1989) mentioned some
480 skulls (MMNH-Sk KAR 24/73, MMNH-Sk KAR 26/73, MMNH-Sk KAR 20/75, MMNH-Sk
481 KAR 75/73, MMNH-Sk KAR 204/73, MMNH-Sk KAR 76/73, MMNH-Sk KAR 407/73; and
482 the juvenile skulls MMNH-Sk KAR 409/73, MMNH-Sk KAR 94/73) with anterior
483 (=subnasal) fossa. Almost all of these skulls are included here in *Hippotherium brachypus*.
484 Between the preorbital and buccinator fossae, they have a depression that takes the place of
485 the subnasal fossa of *Cremohipparion*, but there are several differences between them. The
486 subnasal fossa ends above P3-P4, its borders are well defined (at least the posterior one), and
487 its bottom is more or less flat. The bar between the two fossae is well developed, about 20–30
488 mm long. It represents a semi-cylindrical structure, which could be observed in most cases
489 even when the skull is crushed. The depression on the *Hippotherium brachypus* skulls is
490 elliptical, ends above P2 or the anteriormost part of P3 and its long axis is parallel to the
491 suture between premaxilla and maxilla. Its borders are not clear. We observed this depression
492 in some other *Hippotherium* skulls (*Hippotherium primigenium*, Nesebar; *Hippotherium*
493 *brachypus*, Hadjidimovo, Pikermi), but the bar is short (with X outlines), not so pronounced.

494 In some skulls there is a groove at the same place, connecting the preorbital fossa with the
495 buccinator one. The groove was described in the type skull of *H. giganteum* GROMOVA, 1952
496 from Grebeniki and was observed also in some skulls from Hadjidimovo and Karaslari.

497 The species name *Hipparion verae* GABUNIA, 1979 was intended to replace
498 *H. gromovae* GABUNIA, 1959 from Grebeniki, preoccupied by *H. gromovae* VILLALTA &
499 CRUSAFONT, 1957. The species *H. verae* needs revision. It shares many similarities with
500 *Hipparion* and possibly belongs to this genus. Its only definite occurrence is Grebeniki, other
501 records being dubious. Comparisons of the above described KAR specimens with *H. verae*
502 (Grebeniki) reveal several differences. The skulls from Karaslari (*Hippotherium brachypus*)
503 have a bar that is longer (between 42–50 mm) and wider than in *H. verae*. The preorbital fossa
504 in *H. verae* is shallow, with well-developed posterior border only, whereas in *Hippotherium*
505 *brachypus* it is of medium depth to deep, with well outlined borders. Despite the smaller size
506 of the Karaslari specimens, the distance from the most anterior point of P2 to the most
507 anterior point of orbit is larger (157–167mm) whereas it varies from 146 to 159 mm for
508 *H. verae*. Another difference is the more plicated tooth enamel.

509 All skull features of the above-mentioned Karaslari specimens allow their assignment to
510 *Hippotherium brachypus*. The SIMPSON diagram (Text-fig. 2) shows that the Karaslari sample
511 has slightly shorter tooth row and palate length than the samples from HD, PIK and AKK
512 (KOUFOS 1987a, b; HRISTOVA et al. 2003; KOUFOS & VLAHOU 2005). The distance from the
513 most anterior point of P2 to the anterior point of the orbit is close to the lower end of the
514 range of the Hadjidimovo sample. The KAR sample share similarities with *Hippotherium*
515 *primigenium*, but the preorbital fossa and posterior pocket are less developed, the nasal notch
516 is deeper (above P2 instead of before P2 in *Hippotherium primigenium*) and the enamel
517 plication is less complex.

518 *Cremohipparion mediterraneum*: Skulls: adult - MMNH-Sk Kar 23/73, MMNH-Sk Kar
519 81/73, MMNH-Sk Kar 86/73; subadult - MMNH-Sk Kar 28/73, MMNH-Sk Kar 78/73,
520 MMNH-Sk Kar 209/73; juvenile - MMNH-Sk Kar 25/73, MMNH-Sk Kar 83/73a, MMNH-
521 Sk Kar 86/73b, MMNH-Sk Kar 88/73 (Plate 5, Figs. 1, 2, Text-fig. 5). Most of the listed
522 above skulls have been described by FORSTEN & GAREVSKI (1989) as *Hipparion verae*, while
523 the specimen MMNH-Sk KAR 23/73 has been described as *Hipparion proboscideum*.

524 The preorbital fossa is deep, subtriangular, and anteroventrally oriented, with weak
525 dorsal rim. The preorbital bar is short (24–29 mm). The lacrimal is reduced in size, usually
526 reaching or at most slightly invading the posterior border of the preorbital fossa. The suture of
527 the lacrimal bone is not visible in one out of three specimens, while in the other two the
528 lacrimal reaches the posterior border of the preorbital fossa but does not invade it; out of 8
529 juvenile skulls, four have the same lacrimal features and one has a lacrimal reaching about 6
530 mm forward of the preorbital fossa rim (the preorbital bar on this specimen is 24.5 mm wide).
531 The posterior pocketing is reduced, moderate in depth to shallow. Some of the specimens
532 have a faint subnasal fossa (less expressed than at Hadjidimovo). The tooth row length varies
533 from 142 to 153 mm. The enamel plication is usually moderate with 12–15 plis, the pli
534 caballin is single. In the specimen MMNH-Sk Kar 24/73 enamel plication is rich (18–21 plis)
535 and the pli caballin is complex. The protocone is oval to slightly flattened lingually.
536 Measurements are given in Table 11.

537 The comparison with the diagnosis of *Hipparion verae* shows differences in the
538 preorbital bar length and the preorbital fossa morphology and dimensions. The preorbital bar
539 in *H. verae* is wider and the fossa is shallow, with only the posterior border well developed,
540 whereas in *C. mediterraneum* the preorbital bar is narrow; the fossa is larger, deeper and the
541 borders are well developed; there is a subnasal fossa on some of the specimens. Intraspecific
542 variability cannot explain these differences between the Karaslari sample and *H. verae*.

543 Instead, the skull features of the Karaslari sample bring it close to *Cremohipparion*
544 *mediterraneum*, especially the Pikermi population (KOUFOS 1987 a, b).

545 Another species with subnasal fossa is *C. forstenae*. This name was created by
546 ZHEGALO (1971) on the basis of the materials collected by SEFVE from Locality 30, Baode
547 County, China. He did not provide detailed description of the cheek region, but BERNOR et al.
548 (1990) expanded the species description and provided a precise diagnosis. The species is
549 medium-sized, with short preorbital bar, lacrimal closely approaching or invading the
550 posterior rim of the preorbital fossa, which is subtriangular, anteroventrally oriented, with
551 posterior pocketing slight, posterior rim distinctly thickened, lacking anterior rim and distinct
552 peripheral border outline. There is a distinct but shallow subnasal fossa (BERNOR et al. 1990).
553 Despite the similarities in some features, the well delineated preorbital fossa of the Karaslari
554 specimens differs from that of *C. forstenae*.

555 *Cremohipparion moldavicum* is another species with short preorbital bar and large
556 preorbital fossa. It was described from Taraklia (Moldova) (GROMOVA 1952) and several
557 other localities from and Ukraine (GABUNIA 1959; FORSTEN 1980, KRAKHMALNAYA 1996 a,
558 b; FORSTÉN, A.-M. & KRAKHMALNAYA, T. 1997), as well as from Maragheh (BERNOR 1985,
559 WATABE & NAKAYA 1991, BERNOR et al. 2016) and Akkaşdağı (KOUFOS & VLACHOU 2005).
560 Its features are close to those of *C. mediterraneum*, but there are several differences: slightly
561 smaller skull size, shape (rhomboidal) and size (absolutely and relatively larger) of the
562 preorbital fossa, slightly shallower nasal slit and absence of subnasal fossa. The Simpson log-
563 ratio diagrams shows the similarity of the Karaslari *C. mediterraneum* sample with the samples
564 of the species from other localities. (Text-fig. 8).

565 *Hipparion dietrichi*: cranials: adult - MMNH-Sk KAR 79/73, MMNH-Sk KAR 92/73,
566 MMNH-Sk KAR 93/73, MMNH-Sk KAR 158, MMNH-Sk KAR 203/73; juvenile - MMNH-
567 Sk KAR 95/73, MMNH-Sk KAR 159 (Plate 5, Figs. 5, 6; Text-fig. 7). The preorbital bar is

568 slightly reduced in length (36–41 mm) but the anterior edge of the lacrimal reaches farther
569 anteriorly than its mid-length. The preorbital fossa is moderately deep to shallow,
570 subtriangular, anteroventrally oriented and moderately to weakly delineated. Posteriorly the
571 fossa is not pocketed but with a posterior rim. The nasal slit ends above anterior part of P2 or
572 just before it. Tooth row length is about 142–150 mm. The enamel plication is moderate to
573 rich with 10–24 plis, the pli caballin is single, the protocone is lingually flattened, and labially
574 rounded. The muzzle is short (110–111 mm) and wide (57–65 mm). Measurements are given
575 in Table 12.

576 There are several species with shallow preorbital fossa and more or less reduced
577 preorbital bar, assigned to the genus *Hipparion* (BERNOR et al. 1996). The above described
578 sample shows greatest similarity with the species *Hipparion dietrichi* (Text-fig. 6), well
579 known from several Greek Turolian localities – RZO, Vathylakkos, NIK, PER, and Samos
580 (WEHRLI 1941; SONDAAR 1971; KOUFOS 1987a, b, c, 1988a, 2006c; VLACHOU & KOUFOS
581 2002, 2006, 2009; KOUFOS & VLACHOU 2005) and from Strumyani, SW Bulgaria (GERAADS
582 et al. 2011). *Hipparion prostylum* has a similar morphology, but in the Maragheh sample the
583 reduced preorbital fossa is slightly pocketed, with stronger preorbital and we can exclude it
584 from the comparison; BERNOR et al. (2016) called it aff. *Hippotherium brachypus*.

585 Recently, KOUFOS & VLACHOU (2016) erected a new *Hipparion* species, *H. philippus*.
586 They unite under this name all samples described until now as *H. dietrichi* from the Balkan
587 Peninsula, leaving only in *H. dietrichi* s.s. the samples from AKK and Samos. Their
588 arguments about this splitting of *H. dietrichi* are the different size of the hipparions from both
589 area: larger and more robust at AKK and Samos, smaller in continental Greece, Bulgaria and
590 Republic of Macedonia. In their description of the new species they state: “...differs from
591 *H. dietrichi* in having a smaller size, shorter muzzle, shorter POB, shorter snout and
592 symphysis, and relatively more elongated and slenderer metapodials.” In fact, the size

593 difference between the skulls of *H. dietrichi* from Samos and AKK on the one side and those
594 from Bulgaria and R. of Macedonia on the other side, is not big, just a few millimetres. The
595 skull length at Samos varies from 385 to 411 mm, and from 380 to 420 mm at STR2. The
596 distance anterior rim of the orbit – anterior end of P2 is also very similar: 136 –146,6 mm at
597 Samos *H. dietrichi*, and 145 – 149 mm for STR 2, 146 – 163 mm for the specimens from the
598 R. of Macedonia. The preorbital bar length of STR2 and R. of Macedonia samples are in the
599 range of variation of the AKK sample. The tooth row length varies from 133 to 155 mm at
600 Samos, 152 – 158 mm at AKK, 137 – 150 mm in the R. of Macedonia, and 136 to 155 mm at
601 STR2. The muzzle length varies from 106 to 117 mm at AKK, from 96 to 111 mm in the R.
602 of Macedonia, and from 112 to 115 mm at STR2. Thus, these skull size differences are
603 minute. Body size (reflected in the metapodial proportions) is highly sensitive to climate and
604 to the quality and quantity of food resources, and differences are not necessarily of genetic
605 origin. Its variations across the populations of *H. dietrichi* could be explained by the
606 differences in paleoecological conditions between the Balkan Peninsula and the
607 Samos/Turkey area during the Late Miocene, as well as by slight differences in age between
608 the localities; they do not imply species distinction, and we prefer to keep the name
609 *H. dietrichi* for the populations from Bulgaria and R. of Macedonia.

610 Rhinocerotidae. *Acerorhinus* sp. A skull and attached mandible MMNH-Sk KAR 30/73
611 on display resembles a skull from Kalimantsi in Bulgaria (GERAADS & SPASSOV 2009) in that
612 the lower incisors are quite long and upturned. This shape might have been exaggerated by
613 reconstruction, but they were certainly larger than at Pentalophos (GERAADS & KOUFOS
614 1990), or in the holotype of *A. neleus* (ATHANASSIOU et al. 2014), from Kerassia but not that
615 in the Pikermi specimen that these authors assign to the same species. Measurements are
616 given in Table 13. Systematics of the Balkano-Turkish *Acerorhinus* is still confused (HEISSIG

617 1999; FORTELIUS et al. 2003; GERAADS & SPASSOV 2009; ATHANASSIOU et al. 2014),
618 although detailed study of the Sinap material could clarify the issue.

619 *Dihoplus pikermiensis*. A complete skull with attached mandible, also on display, is the
620 most complete known specimen of this species, although it is somewhat crushed transversally.
621 Measurements are given in Table 13. Like the specimens from Bashibos mentioned below, it
622 shows the typical features listed by GERAADS (1988) and GERAADS & SPASSOV (2009). The
623 nasals are long and only gently convex dorsally, the nasal notch reaches only the anterior root
624 of P2, and the infra-orbital foramen is above the posterior root of P3; both are more posterior
625 in *Ceratotherium neumayri*, and in contrast to the latter species, the lower orbital border is not
626 sloping ventrally. The premaxillae are well-preserved, and it is almost certain that there were
627 no upper incisors, in contrast to some other specimens referred to this species (GERAADS &
628 SPASSOV 2009). The i2s are rather uprightly inserted in the mandible, and have a flat
629 horizontal wear. Their diameter is ca. 13.5 mm, and they are thus definitely smaller than in
630 the specimen from Strumyani in Bulgaria (GERAADS & SPASSOV 2009).

631 Chalicotheriidae. *Anisodon* sp. An unnumbered mandible, described in detail and
632 illustrated by GAREVSKI & ZAPFE (1983), has also been discussed by BONIS et al. (1995) and
633 ANQUETIN et al. (2007) (plate 6, fig. 2). Not much can be added to the already published
634 descriptions, but it must be made clear that a p2 was certainly present, albeit small and single-
635 rooted, as GAREVSKI & ZAPFE (1983) had correctly noted in their text, although their figure is
636 imperfect. State (0) of character (48) of ANQUETIN et al. (2007) is therefore incorrect. These
637 latter authors included this mandible in their *Anisodon* group because of its symphysis
638 extending more posteriorly than in *Chalicotherium*, and because of the ventral tubercle on the
639 symphysis, also present in the Dytiko (*Anisodon macedonicus*) mandible. Although we
640 believe that the number of known specimens is too low to provide a satisfactory support to

641 this conclusion (the occurrence of the ventral tubercle is unknown in *C. goldfussi*, and no
642 mandible of *Kalimantsia* has been found yet), we provisionally follow their conclusions.

643 *Ancylotherium pentelicum*. A skull on display was described by GAREVSKI (1974b) (T
644 6, Figs. 3, 4). It is worth mentioning that cracks on the cranial roof strongly suggest that a
645 frontal boss was present, as on the skull from Thermopigi (GERAADS et al. 2007). A lower jaw
646 from the same site was described by GAREVSKI & ZAPFE (1983); as already mentioned
647 (COOMBS 1989; GERAADS et al. 2006b), these authors misinterpreted the mental foramen as
648 the bottom of a canine alveolus, and this tooth is probably absent. The p2 is quite small, as at
649 Hadjidimovo (GERAADS et al. 2006a), so that the premolar series is short (71.3 mm) whereas
650 it is larger at Kiro Kuchuk (see below) and at Pikermi, but we do not know the meaning of
651 these differences. Two associated metapodials, MT III and Mt IV, are also of this species, but
652 their precise origin is doubtful, although they are certainly from the area of Veles.

653 Carnivora. Ailuridae. *Simocyon primigenius*. An unnumbered, relatively complete skull
654 was briefly described by GAREVSKI (1974a) and re-described by SPASSOV & GERAADS (2011).
655 The latter authors concluded that the skull of the middle Turolian *Simocyon primigenius* from
656 South-Eastern Europe has unique derived characteristics, related to a high morphofunctional
657 specialisation: strongly domed and enlarged frontal region, correlated with large frontal
658 sinuses. It differs not only from earlier European *Simocyon* species, but also from the Chinese
659 samples previously accepted as eastern populations of *S. primigenius*. SPASSOV & GERAADS
660 (2011) concluded that the Chinese material of *Simocyon* from Baode (ZDANSKY 1924) should
661 be called *S. zdanskyi* KRETZOI, 1927, of which the Fugu skull (WANG 1997) is probably an
662 early representative. *Simocyon primigenius* is restricted to the Aegean – Pontian region,
663 mostly in the middle Turolian.

664 Mustelidae. *Eomellivora* cf. *wimani*. We assign to this large species a virtually complete
665 skull, slightly compressed dorsally, and poorly preserved in its rostral and ventral parts. Most

666 teeth are missing, except for the left M1 (Plate 7, Fig. 6). In dorsal view the skull and
667 zygomatic arches have *Mustela*-like outline. The muzzle is short. The nasal region is concave.
668 The frontal region is relatively broad and flat, with weak postorbital processes. The
669 postorbital constriction is moderate, located far from the postorbital processes. The
670 neurocranium is piriform in outline. The temporal crests are well marked but low and short;
671 the sagittal one is rather strong (but damaged) and long, starting rostrally at the level of the
672 postorbital constriction. The external occipital protuberance is not protruding, as in the
673 Batallones-1 skulls (VALENCIANO et al. 2015). The orbits are small and rounded; the
674 zygomatic arches are long but robust (significantly more robust than in the similar-sized
675 *Simocyon* skull), with well pronounced zygomatic process. The preserved right infraorbital
676 foramen is large. M1 is short and wide, pyriform, and constricted in its central portion. It is
677 short labially, but enlarged in its lingual part, which is circled by a cingulum. The paracone
678 and metacone are not quite distinct in the slightly damaged labial tooth surface, but the
679 paracone looks larger. Measurements: max. skull length = 185? mm (restored); zygomatic
680 width = c. 123 mm; skull width over postorbital processes = c. 63; width at postorbital
681 constriction = 47; W max. of the neurocranium = c. 72- ; M1 lingual L = 9.3, W = 19. The
682 Karaslari skull is similar in size to *Plesiogulo* ZDANSKY, but differs from this genus in the
683 much less enlarged lingual part of M1 and the more rounded lingual contour of this tooth as
684 well as by the weaker zygomatic process of the frontal bone, stronger postorbital constriction,
685 and the more robust zygomatic arches (ZDANSKY 1924, pl. 8; KOUFOS 2006b, pl. 1).

686 We follow here the taxonomic concept of VALENCIANO et al. (2015) who recognizes
687 *E. piveteaui* OZANSOY for the Vallesian of Europe and Turkey, *E. ursogulo* ORLOV for the
688 early Turolian of Eastern Europe (Grebeniki), *E. wimani* ZDANSKY for the middle and late
689 Turolian of Europe, Central Asia and N. America and *E. hungarica* KRETZOI for the late
690 Turolian of Central Europe (Polgárdi). The M1, the only tooth that can be compared, is

691 slightly more slender than the known Eurasian specimens (WOLSAN & SEMENOV 1996, fig. 1;
 692 VALENCIANO et al. 2015, fig. 4) but matches the dimensions of *E. piveteaui* and *E. wimani*.
 693 The size difference between its paracone and metacone seems larger than in *E. piveteaui* and
 694 *E. ursogulo*. The M1 of the Karaslari skull differs from that of the latter form in the mesio-
 695 distally shorter lingual part of the tooth. It fits better with *E. wimani*, which is acceptable from
 696 a chronostratigraphic point of view. We tentatively assign it to the latter species, of which
 697 Karaslari would document the only occurrence in the Balkans, and the last record of the genus
 698 there.

699 Hyaenidae: *Adcrocuta eximia*. Material: skull MMNH-Sk KAR 2602 with P1-P2 (Plate
 700 8, Fig. 3); damaged mandible with both c-m1 (MMNH-Sk KAR 68, of uncertain but likely
 701 provenance)(Tables 2, 14). According to one of us (N.S.) some evolutionary trends can be
 702 recognized in the species:

703 1. Morphometric trends:

704 - lengthening of the carnassials (P4 and m1) from the Vallesian to the second half of the
 705 Turolian (especially from the early to the middle Turolian) (Text-figs. 11-14) .

706 - size increase of p3 and especially p2 (mainly in width) of the Turolian populations in
 707 relation to the Vallesian ones (RPL, RZO) (Text-fig. 15). BONIS & KOUFOS (1981) note the
 708 slender upper and lower premolars (except P4) of the RPL specimen, *A. eximia leptoryncha*.

709 2. Morphological trends:

710 - secondary enlargement (probably related to improved bone-breaking efficiency) of the
 711 P4 protocone, from the early Turolian to the middle Turolian (from Hadjidimovo - end of
 712 MN11 - to Kalimantsi and Pikermi - MN12).

713 - reduction to disappearance of the anterior accessory cuspid of p2 and P3 and of the
 714 lingual cingula of upper teeth;

715 - changes in p2, p3 and P3 shapes from the Vallesian and early Turolian to the middle
 716 Turolian: p2 changes from ellipsoid to piriform (in occlusal view), broadening distally; p3
 717 from elongate to quadrangular with enlarged main cusp and broadening of the mesial part; P3
 718 from rectangular to piriform, with enlargement of the mesial part;

719 - the mandibular corpus of the relatively small in size (?) post-Pikermian/late Turolian
 720 representatives of the species becomes more twisted and robust, and the tooth row more
 721 arched but the material is limited for certain judgement.

722 The above mentioned trends may provide a basis for biochronological estimates of the
 723 different *Adcrocuta* samples, especially those from the R. of Macedonia.

724 The m1 size of MMNH-Sk KAR 68 matches the samples from Maragha and
 725 Hadjidimovo (lower Turolian), but is also comparable to the lower values of the MN12
 726 samples. The p3 is broad as in the MN12 samples and the skull MMNH-Sk KAR 2602 is as
 727 large as the complete skull from Hadjidimovo, HD 9309 (maximal length of 276 mm vs. 268
 728 mm) (Table 14), and its oblique length from orbit to rostrum (about 107 mm) is almost
 729 identical with the complete skull PIK-3000 from Pikermi. Thus, it best corresponds to early
 730 MN12 specimens, but the data are insufficient for firm biochronological conclusions.

731 Felidae. *Yoshi garevskii*. A complete, undistorted skull and mandible, MMNH-Sk KAR
 732 69 (Table 15) is the type of this species, characterized by a round, short, and deep skull with
 733 domed frontals, and short canines that are somewhat transversely compressed but are not
 734 serrated. SPASSOV & GERAADS (2015) assigned to the same genus the poorly preserved skulls
 735 from the Aegean region described as *Metailurus parvulus* (HENSEL, 1862), the Chinese type
 736 of "*Metailurus*" *minor* ZDANSKY, as well as some other skulls from China, and a partial skull
 737 from the middle Turolian of Kalimantsi (Bulgaria). The latter name thus becomes *Y. minor*
 738 (ZDANSKY, 1924), but *M. parvulus* is a nomen dubium. *Metailurus* ZDANSKY, 1924, is
 739 represented by the type-species *M. major* ZDANSKY, 1924, and *M. ultimus* (see LI, 2014) and

740 perhaps also by *M. hengduanshanensis*, *M. mongoliensis* and *M. teilhardi* (see also
 741 ANDERSON & WERDELIN 2005). The new genus *Yoshi* was distributed from South Europe to
 742 Central Asia. Although plesiomorphic in dental features, *Yoshi* (which is assigned to the
 743 Pantherini), especially *Y. garevskii*, reaches a high specialization in its skull shape, parallel to
 744 that of the cheetah, suggesting that it represents the first attempt towards the
 745 morphofunctional model of this modern felid.

746 *Machairodus* sp. This machairodont is represented by an unnumbered juvenile half-
 747 mandible with broken canine, incomplete p4 still embedded in bone, and incomplete m1
 748 (Plate 9, Fig. 2). It is of moderate size (restored length of c–m1 > 108 mm; L p4 = 29.6 mm, L
 749 m1 = c. 30 mm). The post-canine teeth lack crenulations, a feature that SOTNIKOVA (1991)
 750 observed mostly in pre-Turolian forms. On the other hand there is probably a mesial cingular
 751 cuspid on p4 and the m1-talonid looks vestigial, as in the middle Turolian
 752 *M. (Amphimachairodus) giganteus*. The morphology of the Karaslari mandible corresponds to
 753 the *M. (Neomachairodus)* stage sensu SOTNIKOVA & NOSKOVA (2004) or the
 754 *M. (Neomachairodus) / M. (Amphimachairodus)* transition which probably correspond to the
 755 middle/late Turolian transition. Given the controversies with the taxonomy of the genus, we
 756 prefer not to attempt species identification.

757 Biochronology: *Tragoportax rugosifrons* is mostly a MN11 species but reaches MN12.
 758 The *Mesopithecus* stage suggests the first half of MN12, *Simocyon* is mostly known in MN12
 759 and the hipparions suggest the first half of MN12. The best fit for the Karaslari fauna is the
 760 first half of the middle Turolian (MN12), i.e. pre-Pikermi middle Turolian.

761

762 **II.4.5. Kiro Kuchuk (Kiro Kucuk)** (41°42'20" N, 21°45'21" E)

763 With at least 17 species of mammals Kiro Kuchuk is the second richest locality of
 764 Republic of Macedonia after Karaslari.

765 Proboscidea. *Deinotherium gigantissimum*. MMNH-Sk KK 2740, a palate with left and
766 right DP2–DP4 and partially preserved erupting first molars, was described and discussed in
767 detail by GAREVSKI & MARKOV (2011).

768 “*Mammut*” *obliquelophus* (on the adopted systematics for the Turolian mammutids of
769 Europe see MARKOV 2008). The material includes MMNH 2743, right M3 (Plate 10, Fig. 2; L
770 = 182; W = 87/91/87/78; H = 52 [on 4th pretrite]; ET = 5–6) and MMNH Sk KK 2773, a
771 partially preserved juvenile skull (Plate 10, Fig. 1; Tables 16, 17) with right DP4 and left
772 DP4–M1. Both DP4s are in use, the first molar is erupting, and the anterior deciduous
773 premolars (traces of which are still visible) were apparently lost postmortem. The facial skull
774 is mostly intact, showing a relatively short and high face; the orbit is situated above the tooth
775 row. Premaxillaries, bearing the two tusks (the right tusk is broken and a fragment is curated
776 separately at MMNH) diverge at the level of the infraorbital foramina (some matrix has been
777 left on the specimen between the two tusks). The nasal aperture is transversally enlarged, with
778 a straight border: a plesiomorphic condition typical for mammutids (TASSY 1994a). Both
779 zygomatic arches are broken. MMNH-Sk KK 2773 is the fourth known juvenile skull of
780 “*Mammut*” *obliquelophus*, the other three coming from Pikermi and RZO in Greece and
781 Belka in Ukraine (MARKOV 2008:160, and references therein). Interestingly, all four are of
782 similar individual age, with MMNH-Sk KK 2773 slightly older than the rest, judging from the
783 wear of the DP4s.

784 *Choerolophodon pentelici*. MMNH-Sk KK 2811 is a right DP3 (Plate 10, Fig. 3).
785 Measurements: L = 57; Wmax. = 44.5; ET = 1.5. Size and derived morphology of the
786 specimen (second entoflexus present: see TASSY 1994b) correspond to the typical, later
787 (MN12) morph of *Ch. pentelici*. MMNH-Sk KK2684 is a right m1 (L = 91e; W =
788 46e/54e/53e; H = 52; ET = 2.5).

789 Primates. *Mesopithecus pentelicus* is represented by the rostral fragment of a skull and a
 790 fragment of a male mandible. Mandible measurements indicate a relatively small specimen,
 791 similar to the middle Turolian *M. pentelicus* s. str. L p4 = 5.8; L p3 (occl.) = 6.4; L m2 = 8.2,
 792 W mes. m2 = 6.8, W dist. m2 = 6.6, L m1 = 9.6.

793 Rodentia. *Hystrix primigenia*. The species is represented by a mandible MMNH-Sk KK
 794 2745.

795 Artiodactyla. Suidae. *Microstonyx erymanthius*. A poorly preserved unnumbered skull
 796 is associated with a piece of mandible (measurements: Table 6); the P1 was absent. This
 797 species is discussed under 'Karaslari'.

798 Giraffidae. *Bohlinia attica*. Two skulls have been described elsewhere (GERAADS 2009).
 799 The most complete one is the best preserved cranium of this species, whose limb bones are
 800 rather common in the Eastern Mediterranean Upper Miocene.

801 Bovidae. *Nisidorcas* sp.? A skull fragment (MMNH-Sk KK 2772) with part of left horn-
 802 core differs from *Palaeoreas* in that the sutures are visible, the horn-cores are small, have
 803 only a weak posterolateral keel but no anterior keel; they are twisted on their axis but not
 804 spiralled. This specimen may belong to the group of small antelopes from Greece and Turkey
 805 centred on *Nisidorcas*, but is too incomplete for contributing to the definition of this genus
 806 that persists in the Aegean region until the Middle Turolian (BOUVRAIN 1979; KOSTOPOULOS
 807 & KOUFOS 1999; KOSTOPOULOS 2006).

808 Perissodactyla. Equidae. *Hippotherium brachypus*. There is only one unnumbered skull
 809 (Plate 1, Fig. 1). It has a deep, subtriangular, and anteroposteriorly oriented preorbital fossa
 810 with well delineated borders. The preorbital bar is long (43 mm). The posterior pocketing is
 811 reduced, and moderately deep. The nasal notch ends above the anterior portion of P3 and it is
 812 deeper than in the most crania of the species. Only one other specimen (HD) has such a deep
 813 nasal notch; usually its end is above the P2 or just before it. The tooth row length is long

814 (164.3 mm). The enamel plication is rich, from 21 to 29 folds. The pli caballin is complex, the
815 protocone is oval. The hypocone is rounded, the hypoconal sinus is deep, the lingual sinus
816 well developed on M3 and rudimentary on the premolars. The features of the specimen are
817 close to the rest samples of *H. brachypus* from the other localities. The specimen lacks its
818 muzzle, which does not allow better comparison.

819 Rhinocerotidae. *Dihoplus pikermiensis*. There are four virtually complete rhino skulls
820 from Kiro Kuchuk, and they all display the typical features of this species, by comparison
821 with *Ceratotherium neumayri*, of which there is no evidence at Kiro Kuchuk: elongated nasals
822 and horizontal ventral orbital surface, short cranial basis, post-tympanic process stretched well
823 forwards and overlapping the postglenoid process, steep caudal edge of the pterygoid wings
824 (Plate 11, Figs. 1-4; Table 13). The well-preserved tooth-rows also show the characteristics of
825 this species (GERAADS 1988; GIAOURTSAKIS 2009; GERAADS & SPASSOV 2009).

826 Chalicotheriidae. Chalicotheriinae gen. et sp. indet. A chalicotheriine M3 MMNH-Sk
827 KK 2810 has a continuous mesial cingulum, a metacone distinctly more labial than the
828 paracone, a mesiodistally oriented labial wall of the metacone, a broad postfossette, and a
829 hypocone distinct from the distal cingulum. This tooth is not so long ($L = 43.6$, $W = 38.4$) as
830 that of *Kalimantsia* (GERAADS et al. 2001), but its other features do not match those of other
831 late Miocene forms (ANQUETIN et al. 2007). In *Chalicotherium goldfussi*, the metacone is
832 more transverse and the postfossette is narrower; in *Anisodon* the metacone is less labial, and
833 the distal crest reaches the summit of the hypocone.

834 *Ancylotherium pentelicum*. Jaw fragments with partial upper tooth rows, MMNH-Sk
835 KK 2770 (M1–M2), MMNH-Sk KK 2805 (P3–DP4–M1), and MMNH-Sk KK 2812 (DP4–
836 M1) fall into the variation range of this species (Plate 6, Fig. 6; Table 18), which varies
837 mostly in the size of P2 and especially M3; unfortunately, none of these teeth is represented in
838 the R. of Macedonia.

839 A partial mandible (MMNH-Sk KK 2748) bears the left p2–p4 and right p2. Holes in
840 the poorly preserved symphysis could represent incisor alveoli. The premolars are almost
841 completely circled by a cingulum, except in the middle of the lingual side. Measurements:
842 mandible depth under p2 = 49.5, under p4 = ca. 55 x 30. Left teeth: p2= 19.1 x 12.4; p3 = 28
843 x 16.3; p4 = 33.5 x 20.5; length p2–p4 = ca. 80.

844 MMNH-Sk KK 2733 is an exceptionally complete sub-adult posterior limb, including
845 all associated elements from tibia to third phalanges (Pl. 6, Fig. 5). Unfortunately, it is still
846 partly included in matrix, so that detailed study is impossible. The tibia much differs from that
847 of *Anisodon grande* in its larger size and more normal proportions, with a proximal epiphysis
848 not much broader than the distal one (see also ROUSSIAKIS & THEODOROU 2001). Some
849 measurements are: Tibia: overall length = 465; proximal width = 165; min. width of shaft =
850 80; distal width = 140. Calcaneus: max. length = 166. Talus: max. width = 113. Mt II: max.
851 length = 136. Mt III: max. length = 162; max. transverse distal W = 56; min. W shaft = 40. Mt
852 IV: max. length = 148; APD proximal articulation = 53.

853 Carnivora. “Ictitheres”: The large ictithere group was widespread in the late Miocene
854 and includes numerous taxa of the Pikermian fauna. Paradoxically, although discussed and
855 described in a large number of works, its taxonomy remains controversial (for discussion see
856 WERDELIN & SOLOUNIAS 1991; ANDERSON & WERDELIN 2005; SEMENOV 1989, 2008).

857 *Plioviverrops cf. orbignyi*. We refer to this species a left half-mandible NMNH-Sk
858 KK2803 with p2–m1 and a large m2 alveolus (Plate 12, Fig. 2; Table 19). The rostral part and
859 the mandibular ramus are broken off. The corpus is slender, the masseteric fossa hardly
860 reaches the distal border of the m2 alveolus. Two mental foramina are present, under p2 and
861 p3. The labial cingulum is present mainly on the mesiolabial and distolabial parts of the
862 premolars. The p2 and p3 are low and long, with distal edges much longer than the mesial
863 ones and bearing small but clear cuspids. The anterior cingula are also cuspid-like, so that the

864 mesial edges of the teeth bear small but clear additional cuspids at their bases. The distal
 865 cingula are strong. A small but salient lingual protuberance is visible at mid-length of the
 866 crown base of p3, probably above an extra-root. The p4 is molariform, with a strong anterior
 867 cuspid and a very large talonid (much broader than the rest of the tooth). In spite of heavy
 868 wear, a large posterior additional cuspid is visible on the labial border of the talonid, whose
 869 lingual cingulum is well developed and bears a small, worn cusplet on its top. The m1 is much
 870 worn, so the relative heights of the conids can only be estimated. The metaconid and
 871 paraconid are of similar height. The protoconid was at most as high as the metaconid. The
 872 talonid is very large. The hypoconid was much lower than the entoconid. The latter is very
 873 tall, its apex is worn but it could have been only a little lower than the metaconid.

874 Five species of *Plioviverrops* are known in the Miocene. *Plioviverrops gervaisi* and
 875 *P. gaudryi* are successive species from the early to middle Miocene of France. The other three
 876 species are Turolian: *P. orbigny* (early to middle Turolian of the Eastern Mediterranean),
 877 *P. guerini* (early to middle Turolian of Spain) and *P. faventinus* (late Turolian of Brisighella,
 878 Italy) (BEAUMONT & MEIN 1972; KOUFOS 2006b, 2011 and references therein). The type
 879 species *P. orbigny* from Pikermi was reported from several Turolian localities: Ravin des
 880 Zouaves 5, Vathylakkos-2 and 3, Prochoma, Mytilinii-1B on Samos Island (Greece)
 881 (SOLOUNIAS 1981; BONIS & KOUFOS 1991; KOUFOS 2000, 2006b, 2011). BAKALOV (1934)
 882 and BAKALOV & NIKOLOV (1962) also reported this species from Kalimantsi, Bulgaria; only
 883 the skull from Kalimantsi-Peshternik (early middle Turolian) is correctly identified, but three
 884 additional skulls from Kalimantsi are stored in the PMA.

885 NMNH-Sk KK 2803 clearly differs from *P. gervaisi* and *P. gaudryi* in the large talonid,
 886 tall paraconid and low protoconid of m1; in these hypocarnivorous features as well as in its
 887 smaller size it also differs from *Protictitherium*. *Plioviverrops guerini* was described as
 888 lacking p2-p3 accessory cuspids and having a relatively small m1 talonid (VILLALTA &

889 CRUSAFONT 1945; CRUSAFONT & PETTER 1969) and a protoconid taller than the other cuspids
890 on this tooth (TORRE 1989), but accessory cuspids have been reported on p3 in later
891 publications (ALCALA 1994). NMNH-Sk KK 2803 has stronger accessory cuspids on the
892 premolars, a larger m1 talonid, a lower m1 protoconid, and a shorter m1. BONIS & KOUFOS
893 (1991) describe some material from Vathylakkos-3 as *P. cf. guerini* but later KOUFOS (2006b)
894 questioned this identification and the existence of *P. guerini* as a distinct taxon, and we agree
895 with him. The various specimens described as *P. orbigny* from Pikermi, Samos, Vathylakkos
896 and Perivolaki (as well as the mandibles from Kalimantsi, Bulgaria) display a large dental
897 polymorphism (especially in the premolars) that also includes morphotypes said to be
898 characteristic for *P. guerini* (as shown by the comparison between the Perivolaki mandible
899 PER-1 and the Kalimantsi sample in PMA). The development of accessory cuspids has been
900 shown to be variable in modern mustelids (WOLSAN 1989). It is unlikely that two different
901 species (*P. orbigny* and *P. guerini*) co-occurred during the early to middle Turolian at either
902 ends of the Northern Mediterranean. Alternatively, all remains from S-W Europe and the
903 Balkans, virtually lacking additional cuspids could represent *P. guerini*. Still another
904 possibility, which we favour, is that only one species ranged throughout the Northern
905 Mediterranean during the Turolian, *P. guerini* being a synonym of *P. orbigny*, but more
906 material would be welcome.

907 *Plioviverrops faventinus* from Brisighella differs from KK-2803 in its stronger, very
908 massive anterior accessory cuspids on p3-4, probably larger m1 entoconid, and larger size.
909 However, MMNH-Sk KK 2803 is more like this species than other specimens of *P. orbigny*
910 in the strong accessory cuspids (especially the anterior ones) of its premolars and in the
911 development of the talonid (especially the entoconid).

912 Hyaenidae. Hyaenotheriini indet. A right mandible fragment (MMNH-Sk KK 2768)
913 with c and p2–m1, and a fragment of a maxilla (MMNH-Sk KK 2769) are probably from the

914 same individual (Plate 12, Fig. 1). The ventral mandibular border under p3 is concave. A
 915 small additional cuspid is present on the lingual edge of the distal cingulum as in
 916 *Hyaenotherium wongii* whose teeth are of similar size and which is present in the late
 917 Miocene of Greece (SOLOUNIAS 1981; WERDELIN & SOLOUNIAS 1991). The P3 is broad
 918 distally and its lingual border is concave. The mesial border of the protocone of P4 is at the
 919 level of the mesial border of the minute parastyle. Tooth measurements (length x width): c =
 920 8.8 x 6.3; p3 = 13.5 x 5.9; p4 = 15.3 x 6.6; m1 = 18.3 x 7.6; C = 8.5 x 6.9; P1 = 4.2 x 3.8; P2
 921 = 11.7 x 4.0; P3 = 14.5 x 7.7; P4 = 23.6 x 13.5.

922 Cf. *Lycyaena chaeretis*. A rostral fragment of a cranium (MMNH-Sk KK 2808) with the
 923 canine (diameters = 14 x 12.3) and poorly preserved left P4 can be referred to this hyaenid,
 924 the canine being too broad for an ictithere; its dimensions are small for an *Adcrocuta* and
 925 close to those of the canine (14.9 x 11.2) of an undescribed partial skull of *L. chaeretis* from
 926 the middle Turolian of Kalimantsi, Bulgaria, collected by D. KOVACHEV (PMA).

927 *Adcrocuta eximia*. The material consists of three mandibular fragments (MMNH-Sk KK
 928 2799, left and right from the same individual, and MMNH-Sk KK 2775, with c, p2–m1; p2–
 929 p3 inverted in the jaw during its restoration), and three partial skulls (MMNH-Sk KK 2806
 930 right rostral part; MMNH-Sk KK 2771 with I3–M1; and unnumbered skull) (Plate 8, Figs. 1,
 931 2, 4, 5). The morphologies of P3 and P4, as well as those of p2 and p3 indicate a relatively
 932 evolved stage (current research by N.S. – see the discussion of *Adcrocuta* under Karaslari).
 933 However, the carnassial teeth are small (Table 2, 14). On the whole, the *Adcrocuta* from Kiro
 934 Kuchuk best fits the early middle Turolian but all indicators are not fully consistent.

935 Felidae. *Paramachaerodus* sp. Material: MMNH-Sk KK 2813, male (?) cranial rostrum,
 936 restored with plaster with I1–3 and left canine; MMNH-Sk KK-2807, female (?) cranium with
 937 most teeth preserved but strongly crushed dorsoventrally (Plate. 9, Figs. 3,4; Table 20). The
 938 canine of MMNH-Sk KK 2813 is strongly compressed transversally. Its mesial edge is

939 damaged, but clear crenulations are visible along its distal edge. On MMNH-Sk KK 2807 the
940 sagittal crest is damaged, but was probably weak. It has an elongated rostral part and well
941 developed zygomatic processes of the frontal. The canines are also machairodont: elongated
942 and transversally compressed, with a flattened lingual surface; the tooth edges are damaged
943 and coated with glue, but thin crenulations are present at least on the mesial edges, and
944 probably also on the metacone of P4. The C–P3 diastema is long. I3 is distinctly larger than
945 I1–2, conical, and caniniform. The diastema is damaged, but no trace of P1 or P2 is visible.
946 P3 is elongated, broad distally because of a clear distolingual expansion; there is only a
947 minute mesial accessory cusp but a large distal one. P4 is much longer, with a small
948 protocone located between the levels of the paracone and parastyle, a minute preparastyle and
949 an almost straight buccal border, slightly concave distally. P3 and P4 are almost in line with
950 each other.

951 The Kiro Kuchuk material differs from the earlier *Promegantereon ogygia* in the
952 crenulated teeth (although they are weak), strongly flattened and larger canines, elongated P3
953 and straight P4 buccal border. It has the crenulated teeth and the P3 and P4 morphology of
954 *Paramachaerodus*, but differs from the type of *Pa. orientalis* (Upper Maragheh) in the clear
955 distolingual expansion of P3, aligned P3 and P4, rudimentary preparastyle of P4, and larger
956 C–P3 diastema (although the individual variability of this feature is not very clear). It also
957 differs from the Chinese *Pa. maximiliani* in the weak crenulations, virtual lack of P4
958 preparastyle (very large in *Pa. maximiliani*), protocone of P4 located more mesially, and
959 weaker canines (SALESA et al. 2010). Thus the KK material combines features of
960 *Paramachaerodus* (tooth crenulations and elongated P3) and of *Promegantereon* (virtual lack
961 of P4 preparastyle and aligned P3-P4), bridging the gap between these genera (diagnosed in
962 SALESA et al. 2010).

963 Biochronology: The *Paramachaerodus* features look less derived than the typical
 964 *Pa. orientalis* from the middle Turolian, and the *Adcrocuta* stage might also indicate early
 965 MN12, so that we very tentatively suggest pre-Pikermian middle Turolian age for Kiro
 966 Kuchuk.

967

968 **II.4.6. Prevalets (Prevalec)** (41°42'03" N, 21°45'17" E, elev. 263 m)

969 According to GAREVSKI (1956), the fauna described by SCHLOSSER (1921) originates
 970 from the region of Prevalets. SCHLOSSER (1921) obtained the following list from the locality
 971 near Köprülü (an * indicates a likely identification from Schlosser's descriptions and figures;
 972 updated taxonomy in brackets; other species are discussed below):

973 **Mesopithecus pentelici*; *Ictitherium robustum* [*Thalassictis robusta* ?]; **Machairodus*
 974 *orientalis*; *Mastodon longirostris*; ? *Deinotherium giganteum*; *Rhinoceros schleiermachersi*
 975 [*Dihoplus orientalis* ?]; *Nestoritherium pentelici* [*Ancylotherium pentelicum*]; *Hipparion*
 976 *gracile*; **Sus* [*Microstonyx*] *erymanthius*; *Camelopardalis parva*; *Palaeotragus rouenii*;
 977 **Helladotherium* cf. *duvernoyi*; *Tragocerus* [*Tragoportax*] *amaltheus*; ? *Tragocerus* sp.;
 978 *Palaeoreas lindermayeri*; *Protragelaphus* cf. *skouzesi*; *Gazella brevicornis*; *Gazella*
 979 *deperdita*. His *Hipparion gracile* probably belongs to two different species: a small one
 980 (upper tooth row length 124 mm), and a medium-sized one (tooth row length about 143 mm,
 981 and relatively robust metapodials) that could be a *Hippotherium*. His *Camelopardalis parva* is
 982 probably a *Palaeotragus rouenii*, and there is no evidence of *Bohlinia* in his material. Most of
 983 the bovid identifications are based upon teeth, except for a partial skull that he called "?
 984 *Tragocerus* sp." while acknowledging that its horn-cores are not *Tragoportax*-like. We have
 985 seen no other remain that could be referred to this species. Except the Proboscideans, the
 986 fauna described below is from the collection of R. GAREVSKI.

987 Proboscidea. A mandible figured by SCHLOSSER (1921, p. 13, as *Mastodon longirostris-*
 988 *arvernensis*) belongs to *Anancus*, as seen from the molar structure and apparent brevirostry.
 989 Observable characters are insufficient to discriminate between *A. arvernensis* and the
 990 Turolian *Anancus* sp. (MARKOV 2004, 2008). Considering the Turolian age of the fauna
 991 described by SCHLOSSER (1921), the mandible can be referred to *Anancus* sp.

992 Artiodactyla. Bovidae. *Palaeoreas* cf. *lindermayeri*. Two horn-cores at least (MMNH-
 993 Sk Prev 2652 and MMNH-Sk Prev 2654) can be assigned to this species. The pedicle is
 994 longer anteriorly than laterally, there is a strong posterolateral keel and almost no spiralling.
 995 They are of medium size, intermediate between Kalimantsi-Pikermi and Hadjidimovo
 996 (GERAADS et al. 2003).

997 *Palaeoreas* ? sp. Two partial frontlets, MMNH-Sk Prev 1000 and MMNH-Sk Prev
 998 1595, are probably of a species of *Palaeoreas* because of their strongly angled frontal bone
 999 and, at least on MMNH-Sk Prev 1000, fused frontal suture and large sunken pits close to the
 1000 midline (Table 9). Horn-core divergence is weak basally but increases upwards, so that the
 1001 lateral border is concave in front view; they are not spiralled but twisted, and MMNH-Sk Prev
 1002 1595 shows that the posterolateral rounded keel becomes anterior about 10 cm above the base,
 1003 so that, more proximally, the anterior side of the horn-core looks slightly concave in lateral
 1004 view. We believe that this is the species that ĆIRIĆ (1957) described as *Palaeoreas*
 1005 *lindermayeri* but assignment to this species is not satisfactory. It could be closer to *P. zouavei*
 1006 from RZO (BOUVRAIN 1980), or perhaps to some variety of "*P.*" *elegans* (a Turkish species
 1007 included in his new genus *Majoreas* by KOSTOPOULOS 2004), although there is no more than
 1008 a hint of an anterior keel at Prevalets.

1009 Perissodactyla. Chalicotheriidae. Chalicotheriinae indet. Two associated upper teeth,
 1010 DP4 (c. 32.6 x 33.3) and M1 (c. 44.3 x 40.2), belong to a chalicotheriin, but are too cracked
 1011 and distorted for identification.

1012 Carnivora. Hyaenidae. *Adcrocuta eximia*. An unnumbered right mandible with c–p3 and
 1013 an unnumbered left mandible with c–p4, are probably from two different individuals (Table
 1014 2). In spite of the moderate size of the premolars and of the mandibles depth, the piriform
 1015 shape of p2 and the mesially enlarged p3 best match the middle Turolian samples.

1016 Felidae. *Machairodus (Amphimachairodus) giganteus*. A skull of *Machairodus* is on
 1017 exhibit in the MMNH-Sk (Plate 9, Fig. 5). The occipital part and teeth are strongly damaged.
 1018 The maximal length of the skull is close to 370 mm (restored); the skull width over the
 1019 zygomatic processes is 135 mm; the mesiodistal diameter of the canine, whose tip is broken is
 1020 36 mm; the length of P3 is 22.6 mm. The skull is somewhat distorted and the neurocranium is
 1021 crushed, most of the occipital is missing, as well as most of the teeth. The frontal is depressed
 1022 between the well-expressed temporal crests, as in old male lions. The I3 are positioned behind
 1023 I1–I2 that are all in line. It is one of the largest known skulls of *Machairodus*. Comparable
 1024 ones are (Table 20): a skull of *M. palanderi* ZDANSKY from the Baodean (Middle Turolian) of
 1025 China (SOTNIKOVA 1991), another one from Baode, very broad over the zygomatic processes
 1026 (QIU & SHI 2008), the largest skull of the Batallones-1 sample (MN10) of *M. aphanistus*
 1027 (ANTÓN et al. 2004), the skulls from Grebeniki (MN11), Ukraine and Halmyropotamos,
 1028 Greece (MN12) (PAVLOW 1914; MELENTIS 1967). From the humerus and M1 sizes, *M. kabir*
 1029 from Toros-Menalla and Sahabi (whose age corresponds to the European middle to late
 1030 Turolian) was also very large (PEIGNÉ et al. 2005; SARDELLA & WERDELIN 2007), but its skull
 1031 is unknown.

1032 The canine is rather long. It seems (current research by N.S.) that there is a general
 1033 trend of upper canine size increase from the Vallesian to the middle/Late Turolian (Table 21),
 1034 especially if we take in consideration the easternmost late populations of the so called
 1035 *M. horribilis* (= *M. palanderi*). This form is regarded by some authors (QIU ET AL., 2008) as a
 1036 separate species, but could just be a geographic subspecies of *M. giganteus*. The upper canine

1037 increases mostly in height, but also in mesiodistal length, while possibly becoming thinner
1038 (KOUFOS 2000), but these trends may be obscured by sexual dimorphism, which was strong in
1039 the Machairodontinae (ANTÓN et al. 2004; PEIGNÉ et al. 2005).

1040 The P3 of the Prevalets specimen is reduced. The reduction of this tooth is an evolved
1041 trend in general (current research by N.S.), but it can hardly be used for age estimates because
1042 of individual (and probably geographical) variation. The P3 of the Prevalets skull is shorter
1043 than in the Vallesian *M. aphanistus* population from Batallones-1 (ANTÓN et al. 2004). The
1044 tooth length is 22.8 mm at Prsten (see below); 25 at Grebeniki; 26.3 (pers. data) at
1045 Hadjidimovo; 23 at Pikermi; 23.7 at Halmyropotamos; 23–25 at Taraklia; 22.5–26 in “*M.*
1046 *palanderi*”; 21 mm in *M. kurteni* (PAVLOW 1914; ZDANSKY 1924; RYABININ 1929; MELENTIS
1047 1967; SOTNIKOVA 1991). Thus, on the whole, the few visible features of the skull indicate a
1048 relatively evolved stage, of the *M. (Amphimachairodus) giganteus* group.

1049 In spite of the accumulation of recent *Machairodus* s.l. finds, recent opinions on its
1050 systematics remain controversial (GERAADS et al. 2004; MORLO & SEMENOV 2004;
1051 SOTNIKOVA & NOSKOVA 2004; ANTÓN et al. 2004; PEIGNÉ et al. 2005; SARDELLA &
1052 WERDELIN 2007; QIU ET AL., 2008; CHRISTIANSEN 2013). Geologically younger forms of
1053 *Machairodus* may be united in *Amphimachairodus* (ANTÓN et al. 2004; SARDELLA &
1054 WERDELIN 2007; CHRISTIANSEN 2013), but three successive subgenera were erected for
1055 *Machairodus* by SOTNIKOVA & NOSKOVA (2004). Two species are usually accepted for the
1056 Vallesian to the middle Turolian of Eurasia (BEAUMONT 1975; ANTÓN et al. 2004; PEIGNÉ et
1057 al. 2005), but MORLO & SEMENOV (2004) favour a monospecific taxonomy. Alternatively,
1058 SOTNIKOVA & NOSKOVA (2004) and QIU ET AL. (2008) accept several successive and
1059 geographic Eurasian late Miocene species. In any case, most features improving the shearing
1060 complex appear gradually in mosaic: lengthening of the carnassials, reduction of the P4
1061 protocone and of the m1 talonid-metaconid complex, reduction of p3/P3, enlargement of the

1062 P4 preparastyle and metastyle, development of the canines and crenulations, lengthening of
 1063 the mandibular diastema, development of the mental apophysis (BEAUMONT 1975;
 1064 SOTNIKOVA 1991; SPASSOV & KOUFOS 2002; MORLO & SEMENOV 2004; GERAADS et al.
 1065 2004; PEIGNÉ et al. 2005). BEAUMONT (1975) considers *M. aphanistus* as smaller than
 1066 *M. giganteus*, but the available data shows no obvious trend in this regard (Table 21). The
 1067 skull/body size slightly decreased at the end of the late Turolian, judging after *M. kurteni*
 1068 (SOTNIKOVA 1991) and “*M. ex gr. giganteus*” from Baccinello (ROOK et al. 1991).

1069 Biochronology: The presence of *Anancus* suggests a post-Pikermian age (MARKOV
 1070 2008; SPASSOV et al. 2012) within the Turolian, and nothing in the rest of the fauna really
 1071 contradicts this age.

1072

1073 **II.4. 7. Rashtanski Pat**

1074 Proboscidea: *Deinotherium gigantissimum* is represented by an isolated M2, described
 1075 by GAREVSKI (1976a) as *D. giganteum*.

1076

1077 **II.4.8. Umin Dol (Umen Dol)** (41°45'33" N, 21°47'51" E, elev. 285 m)

1078 Proboscidea. As with Karaslari, two elephantoids occur at Umin Dol: *Ch. pentelici* (a
 1079 mandibular fragment with dp3; tooth measurements: c.47 x 28.0), and ? *Tetralophodon atticus*
 1080 (skull fragment with DP2-DP4 at the exhibition: and a fragment of DP4). The second
 1081 elephantoid is not *Anancus*, judging from the morphology of the teeth but it could also be
 1082 “*Mastodon*” *grandincisivus*: chronological and geographical distribution of *T. atticus* and
 1083 “*M.*” *grandincisivus* overlap, and material such as that from Umin Dol is insufficient for a
 1084 certain identification (see discussion by MARKOV 2008). [Note: Recently, KONIDARIS et al.
 1085 (2014) suggested that *T. atticus* and “*M.*” *grandincisivus* are synonymous, representing a
 1086 single amebelodontid species, *Konobelodon atticus*. This view is not followed here and

1087 *T. atticus* is regarded as a derived *Tetralophodon* species, co-occurring with the
 1088 amebelodontid “*Mastodon*” *grandincisivus*].

1089 Rodentia. A *Hystrix primigenia* maxilla with teeth is noted in a handwritten check-list
 1090 by R. GAREVSKI, but the material was not found after his death.

1091 Artiodactyla. Suidae. *Microstonyx erymanthius*. There are some incomplete upper tooth-
 1092 rows and a mandible (measurements: Tables 6, 7). No specimen shows whether a P1 was
 1093 present. This species is discussed under "Karaslari".

1094 Bovidae. *Palaeoreas lindermayeri*. A poorly preserved incomplete cranium with horn-
 1095 core bases (MMNH-Sk UD 23) can be referred to this species on the basis of size, and of the
 1096 large P4 with strong styles (Table 9). A frontlet (MMNH-Sk UD 2614/2615) is probably of
 1097 the same species. Both specimens are in the size-range of the Kalimantsi and Pikermi
 1098 specimens, but smaller than the Hadjidimovo ones (GERAADS et al. 2003).

1099 *Sporadotragus* sp. MMNH-Sk UD 1590 is a poorly preserved fragment of skull (Plate
 1100 4, Fig. 1); its horn cores (46.5 x 30.5) show the tendency towards a flat anterior surface and
 1101 anteromedial keel typical of this genus, as well as its small molars compared to overall size
 1102 (GERAADS et al. 2006a). Other measurements: width over pedicles = 96.5; width across
 1103 middle of supra-orbital foramina = 44.5; length M1-M3 = 46.9.

1104 *Gazella* sp. Some horn-cores might belong to *Gazella capricornis*.

1105 Perissodactyla. Equidae. From this locality FORSTEN & GAREVSKI (1989) described
 1106 “*Hipparion prostylum* GERVAIS / *schlosseri - dietrichi* ANTONIUS -WEHRLI” and *Hipparion*
 1107 *matthewi* ABEL. We were able to find and examine four of their skulls in the MMNH-Sk: two
 1108 adult skulls (MMNH-Sk UD 1517/66, MMNH-Sk UD 802/66, MMNH-Sk UD no number)
 1109 and one juvenile (MMNH-Sk UD 206/60) we identified as *Hippotherium brachypus* Hensel,
 1110 and another one (MMNH-Sk UD 99/60) as *Hipparion* sp.

1111 *Hippotherium brachypus*. MMNH-Sk UD 802/66 is poorly preserved, but what remains
1112 of the preorbital fossa is deep. The other two adult specimens (MMNH-Sk UD 1517/66,
1113 NMNH-Sk UD no number (Plate 1, Fig. 5) from this species have deep, well delineated,
1114 subtriangular and anteroposteriorly oriented preorbital fossa. The preorbital bar is long (40.3
1115 mm for MMNH-Sk UD 1517/66). The posterior pocketing is reduced, moderately deep to
1116 shallow. The muzzle is long (134 mm on another, unnumbered skull). The tooth row is 131
1117 mm to 145 mm long. The enamel plication is moderate (in a senile specimen) to rich; the pli
1118 caballin is single or double, the protocone is lingually flattened - labially rounded to oval.
1119 FORSTEN & GAREVSKI (1989) described MMNH-Sk UD 1517/66 as *Hipparion dietrichi*
1120 WEHRLI, but its morphology coincides with the diagnosis of *Hippotherium brachypus*. The
1121 same is true of the other adult specimen. Both are distinct from *H. dietrichi*, which is
1122 characterized by shallow to moderately deep preorbital fossa, less plicated teeth and shorter
1123 muzzle with straight incisor line. The measurements are given in Table 1. Comparisons of the
1124 UD material with samples of *Hippotherium brachypus* from other localities reveal its smaller
1125 size. The distance from orbit to anterior point of P2 is also smaller than for the other samples
1126 – 152 mm, but the SIMPSON diagram (Text-fig. 2) shows that the preorbital fossa dimensions
1127 and location are close to the other samples.

1128 *Hipparion* sp. (small): The adult skull MMNH-Sk UD 99/60 is somewhat
1129 dorsoventrally crushed (Plate 5, Fig. 4; Table 11; Text-fig. 7). The orbits are not preserved.
1130 The moderately deep and moderately delineated preorbital fossa is obviously far from the
1131 orbit: its posterior end is above the anterior part of M1 and the anterior one above the
1132 mesostyle of P2. It is anteroventrally oriented and without posterior pocketing. The nasal slit
1133 ends before P2 (most likely at mid-distance P2 – C). The buccinator fossa is deep. The
1134 premolar length is 64 mm. The enamel plication is low to moderate (9–13 plis). The pli
1135 caballin is single, short. The protocone is rounded; on P2 it is connected with the protoloph.

1136 The muzzle is ventrally bent, and is short ($m1 = 94$ mm), and relatively narrow ($m15 = 53$
1137 mm), with more or less straight incisor arch. This badly preserved specimen was described by
1138 FORSTEN & GAREVSKI (1989) as *C. matthewi* ABEL. After its diagnosis, this species is small,
1139 the row P2–M3 is 100–130 mm long, the enamel plication is simple, the protocone is slightly
1140 oval, nearly round, the fossa preorbitalis slightly developed (SONDAAR 1971). According to
1141 BERNOR et al. (1996) the species has a short and narrow muzzle, a short nasal notch with a
1142 posterior end located above P2, a short preorbital bar, a single oval, deep preorbital fossa,
1143 simple enamel plication, and a small, simple pli caballin. A number of features of MMNH-Sk
1144 UD 99/60 are close to the noted diagnostic features of *C. matthewi*, but it clearly differs from
1145 this species in the wider preorbital bar, the elliptical preorbital fossa and ventrally bent muzzle
1146 (perhaps because of distortion). It shares some similarities with *Hipparion dietrichi*, but is
1147 smaller. The specimen is senile, which probably explains the short premolars. Another
1148 specimen also smaller than the known normal for *H. dietrichi* is PER -193 from Perivolaki
1149 (Greece), which is very similar to our specimen (VLACHOU & KOUFOS 2006). The most
1150 important differences are the bent muzzle and location of the posterior end of the preorbital
1151 fossa (posterior end above the anterior part of M1 in MMNH-Sk UD 99/60 versus the anterior
1152 part of M2 at Perivolaki, therefore the preorbital bar in the Umin Dol skull is much wider).

1153 Rhinocerotidae. *Ceratotherium neumayri* is represented by a skull on exhibit at the
1154 MMNH-Sk; it has the typical features of this species (GERAADS 1988; GERAADS & KOUFOS
1155 1990; GERAADS & SPASSOV 2009): the nasals are very wide, deep and rounded; the rugosities
1156 for the nasal and the frontal horns occupy large areas; the ventral orbital surface is inclined
1157 downwards; the temporal crests diverge caudally, reaching the occipital crest and forming a
1158 large V-shaped figure; the occipital crest is wide and overhangs the occipital condyles; the
1159 mandible ventral border is convex.

1160 Carnivora. Hyaenidae. *Adcrocuta eximia*. An unnumbered mandible with p2–p4 (L
1161 =54.2) belongs to this species

1162 Biochronology. The most likely age after the hipparions and *Palaeoreas* is middle
1163 Turolian (MN12), and this is not contradicted by the rest of the fauna.

1164

1165 **II.5. NEGOTINO – KAVADARTSI FOSSILIFEROUS AREA**

1166 **II.5.1. Dolni Disan** (41°25'08" N, 22°07'36" E; elev. 287 m)

1167 Proboscidea. *Deinotherium gigantissimum*. MMNH-Sk DD 2738/1 and MMNH-Sk DD
1168 2738/2, a pair of tusks. Identification is based on the structure of the dentine (no SCHREGER
1169 lines). Lengths: 560/520 (2738/1); 570/520 (2738/2). Diametres: 90 x 70e (1); 97 x 70 (2).

1170 *Choerolophodon pentelici*. MMNH-Sk DD 2742, right m3 (Plate 10, Fig. 4). L: ca. 185;
1171 W: 70/78/83/80/60; H:>>62 ET: 3–5.

1172 *Tetralophodon atticus*. An adult skull (Plate 10, Fig. 6). described by GAREVSKI (1976b)
1173 as *Tetralophodon longirostris* belongs rather to the Turolian species of the genus, *T. atticus*
1174 (being the only known adult *T. atticus* skull in the world). With no associated mandible, an
1175 alternative determination as "*Mastodon*" *grandincisivus* must be considered. Morphology of
1176 the M2 (e.g. posttrite ornamentation present) seems to support this at first glance but a similar
1177 morphology can occur among Eppelsheim *T. longirostris* (G.M., pers. obs. NHMUK 2006).
1178 Besides, morphology of the erupting M3 (mesiodistal compression, reduced accessory
1179 conules) is similar to material referred by MARKOV (2004) to *T. atticus*, and the Dolni Disan
1180 skull most probably belongs in that species too.

1181 *Anancus* sp. MMNH-Sk DD 2741, posterior fragment (4 lophs and cingulum) of a left
1182 M3 (Plate 10, Fig. 5). Lfr: 170; W: 100/100/100e/91.5; H: 64 (on penultimate pretrite).

1183 Artiodactyla. Giraffidae. *Bohlinia* cf. *attica*. A long and slender radius must belong to
1184 this close relative of the giraffe, but is perhaps slightly smaller.

1185 Bovidae. *Tragoportax* cf. *amalthea*. An unnumbered crushed and incompletely prepared
 1186 cranium has very massive horn-cores inserted close together (L M1–M3 = 61.9) (Table 9).

1187 Biochronology. The combination of *Tragoportax* cf. *amalthea* with the archaic *Anancus*
 1188 sp. suggest a post-Pikermian Turolian age.

1189

1190 **II.5.2. Kalnitsa (Kalnica)**

1191 Artiodactyla. Suidae. "*Propotamochoerus*" sp. ? A mandible was described by
 1192 GERAADS et al. (2008). They concluded that the Balkan Turolian sample is clearly distinct
 1193 from both the Vallesian *P. palaeochoerus* and the Pliocene *P. provincialis*, but cannot be
 1194 satisfactorily referred to the Asian species *P. hysudricus* or *P. hyotherioides*, and that this
 1195 form belongs to a separate species, probably distinct from the *P. palaeochoerus* -
 1196 *P. provincialis* lineage. PICKFORD (2015) assigned the Kalnitsa material to *Dasychoerus* sp.
 1197 There is no evidence of *Microstonyx* at Kalnitsa.

1198 Bovidae: We have seen only horn-core fragments from this site; they can be tentatively
 1199 identified as *Gazella* sp., *Tragoportax* sp., and *Palaeoreas* sp.

1200 Biochronology: If PICKFORD's identification of the suid as *Dasychoerus* is correct, the
 1201 age of Kalnitsa could be MN13, but nothing in the fauna really precludes a younger age.

1202

1203 **II.5.3. Tremnik**

1204 Proboscidea. Isolated tusks with the typical curved shape demonstrate the presence of
 1205 *Choerolophodon* (probably *Ch. pentelici*) at this site.

1206

1207 **II.5.4 Veshie (Vesje) (41°22'31" N, 22°07'54" E; elev. 621 m)**

1208 Proboscidea. *Choerolophodon pentelici*. The material includes tusks, a poorly preserved
 1209 mandible with m2-m3, and isolated molars:

1210 - MMNH-Sk-130, posterior fragment (3 lophids and cingulum) of a left m3. Length of
 1211 fragment = 169; W = 89e/92/83; ET = 4.

1212 - MMNH-Sk-129, right m3 Probably same individual as 130. L = 208; W =
 1213 79/82/87/81.5; ET = 3.5-5.5. Both from “Vesje – Pat”.

1214 - MMNH-Sk-82, left M2. L = 110; W = 71e/76/77; ET = 4.

1215 - MMNH-Sk-80, right M3. L = 194; W = 87/95.5/94/82; ET = 4.5-5. Together with a
 1216 right M2, these are from “Vesje – Dol” and most probably belong to the same individual.

1217 Primates. *Mesopithecus pentelicus*. The material includes an incomplete, probably male
 1218 mandible MMNH-Sk- 2671 in bad condition, with detached teeth on the left half-mandible
 1219 and a right half-mandible with all cheek-teeth (p3–m3). The dimensions of the m3 fit better
 1220 the first half of the middle Turolian (Plate 2, Fig. 3), but the material is insufficient for
 1221 reliable taxonomic or biostratigraphic conclusions.

1222 Rodentia. A partial skull of *Hystrix primigenia* is mentioned in an unpublished MS of
 1223 R. GAREVSKI (L M1–M3 = 26.7).

1224 Artiodactyla. Giraffidae. *Palaeotragus rouenii*. A talus with a distal width of 44.2 and
 1225 max. length of 69.5 mm must belong to this species, as no other giraffid is that small.

1226 We have seen no bovid remain from this site.

1227 Perissodactyla. Equidae. We assign the skull MMNH-Sk VSH 2735 to *Hipparion*
 1228 *dietrichi* WEHRLI. Its preorbital bar is long (49.5 mm). The preorbital fossa is shallow,
 1229 subtriangular, anteroventrally oriented and weakly delineated. Posteriorly the fossa is not
 1230 pocketed but has a posterior rim. The nasal notch ends probably above the anterior border of
 1231 P2. The tooth row length is 149 mm. The enamel plication is moderate, the plis varying from
 1232 11 to 17, the pli caballin is single. The protocone is rounded to lingually flattened - labially
 1233 rounded. The muzzle is short (approximately 96 mm). Measurements are given in Table 12.

1234 Chalicotheriinae gen. et sp. indet. A complete upper tooth series (MMNH-Sk VSH
1235 2702; Plate 6, Fig. 1; Table 22) is one of the nicest known specimens of a late Miocene
1236 chalicotheriine, and is worth being described in some detail, paying special attention to the
1237 characters used by ANQUETIN et al. (2007) in their cladistic analysis. The P2 is much shorter
1238 than long, and almost rectangular, in contrast to those of *Anisodon macedonicus* from Dytiko,
1239 *Anisodon grande*, and *Chalicotherium goldfussi* (ZAPFE 1979, Figs. 6-7). P3 and P4 differ in
1240 size, but not in their length/width proportions, unlike the premolars of *Kalimantsia* (GERAADS
1241 et al. 2001), and they are morphologically almost identical. They have no protoloph, as in
1242 most other species, but there is an incipient protoloph in the right P4 of *Kalimantsia*.
1243 ANQUETIN et al. (2007) stated that the protoloph reaches the protocone in *C. goldfussi*, but this
1244 is incorrect, as it is clearly short both on the maxilla HLMD-Din-3168 (figured by ZAPFE
1245 1979, fig. 7) and on an isolated P3, HLMD-Din-3138, both from the *Deinotherium* sands of
1246 Eppelsheim; it seems that the only Turolian form with a well-developed protoloph on P3 and
1247 P4 is the skull from Akkaşdağı referred to *Ancylotherium* by SARAÇ & SEN (2005), but that
1248 obviously belongs to a chalicotheriine. *Kalimantsia* is the only form almost lacking a metaloph
1249 on P3.

1250 On M2, the protocone occupies a central position, but it is more anterior on the other
1251 molars; therefore, state of character (41) of ANQUETIN et al. (2007) (which is hard to
1252 appreciate) is ambiguous. The metacone is distinctly more labial than the paracone, unlike
1253 that of *Anisodon*. The M3 is longer than broad, but the difference is less clear than in
1254 *Kalimantsia*; the second lobe is not much reduced, and the labial wall is not very oblique, as
1255 in this latter genus, and as on the molar from Kiro Kuchuk. This is character 45 of ANQUETIN
1256 et al. (2007), but their coding is incorrect, as this labial wall is much more transverse in the
1257 Dytiko specimen than in *Kalimantsia*, not the opposite. There is no lingual cingulum. The

1258 postfossette is distinctly narrower than on the molar from Kiro Kuchuk, and unlike the
1259 condition of *Anisodon*.

1260 This short comparison highlights the difficulty in assigning Late Miocene European
1261 chalicotheriins to well-defined taxa. It looks as if none of the new specimens (here, the M3
1262 from Kiro Kuchuk and the maxilla from Veshie) can fit into a previously defined taxon. The
1263 problem can be evaded by using parsimony analysis, which always yields a result but heavily
1264 rests upon a number of subjective estimates and a priori assertions. The key problem with
1265 chalicotheriins is that we are unable to evaluate intra-specific variation; once again, what we
1266 need is more fossils.

1267 Carnivora. 'Ictitheres'. *Ictitherium* cf. *viverrinum*. MMNH-Sk VSH 2747 is the cranium
1268 of an adult individual with all incisors and canines, left P1–M2 and right P3–M2 (Plate 12,
1269 Fig. 3). The left zygomatic arch is rounded, the right one is missing. The bones of the cranial
1270 vault are heavily fragmented. The postorbital part is crushed transversally and the shape of the
1271 zygomatic processes of the frontals is unclear. Only the right tympanic bulla is present.
1272 Measurements: L P4–M2 = 40.4 mm; P2 = 11.5 x 5.7; P3 = 13 x 7.2; P4 = 20.2 x 10.6; M1
1273 7.5 x 14.7+; M2 = 6 x 8.9; total skull length = 165+. The nasal bones extend caudally far
1274 beyond the frontal edges of the orbits. The tympanic bulla is rather convex (but see below);
1275 there is a marked concavity (in lateral and ventral view) between the jugular process and the
1276 caudal end of the zygomatic arch. The temporal crests look short. The size of the incisors
1277 increases from I1 to I3. P1 is large, with one root and separated by distinct diastema from C
1278 and P2. P4 is short, its protocone reaches farther mesially than the paracone; P3 is large, broad
1279 distally and with a lingual cingulum; M1 is relatively long; M2 is large relative to M1.

1280 The morphology of the temporal crests, the length and morphology of P4, the size and
1281 proportion of the molars differ from the hyaenotheres sensu SEMENOV (1989, 2008). Among
1282 the ictitheres (sensu SEMENOV 1989) the skull size excludes the genera *Protictitherium* and

1283 *Plioviverrops*. The prejugular concavity of the skull contour, the large and mesially extended
 1284 P4 protocone, the relatively small angle between the labial surfaces of P4 and M1, the
 1285 relatively flat caudal surface of the tympanic bulla as well the relatively large M2 exclude
 1286 *Thalassictis*, but match *Ictitherium*. The palatal notch almost reaches the distal surface of M2;
 1287 M1 is located at the distolingual edge of P4 and the P4 protocone is salient mesially. These
 1288 features are close to those of *I. viverrinum* (= *I. robustum*), *I. gaudryi* (the latter is probably a
 1289 synonym of the former: WERDELIN & SOLOUNIAS 1991; ANDERSON & WERDELIN 2005) and
 1290 *I. pannonicum*, but the latter species is larger (SEMENOV 1989). *Ictitherium viverrinum* ranges
 1291 from Western Europe to China and is well known from Pikermi (ANDERSON & WERDELIN
 1292 2005).

1293 Biochronology: The more probable age of the locality after the hipparions is early to
 1294 early middle Turolian. The size of a single *Mesopithecus* specimen fits better the first half of
 1295 the middle Turolian.

1296

1297 **II.5.5. Vozartsi (Vozarci)** (41°25'24" N, 21°55'01" E, elev. 232 m)

1298 Suidae. *Propotamochoerus* sp. Several specimens of this rare form have been described
 1299 recently (GERAADS et al. 2008). Together with the Kalnitsa material, they were assigned to
 1300 *Dasychoerus* sp. by PICKFORD (2013) but here the age of the locality is definitely Turolian, so
 1301 that this would imply that the genus appears in the Miocene. The revision, in 2008, of the
 1302 MMNH-Sk collections convinced us that, in contrast to what was stated earlier, there is no
 1303 evidence of *Microstonyx* at Vozartsi. It seems, therefore, that in the Vardar Valley at least, the
 1304 two genera are mutually exclusive.

1305 Cervidae indet. A few antler fragments are unidentifiable to genus.

1306 Giraffidae: *Helladotherium* sp. A piece of maxilla MMNH-Sk Voz-1870-79
 1307 (measurements: Table 8), two large and robust metapodials, a first anterior phalanx MMNH-

1308 Sk Voz-915-9 and a talus MMNH-Sk Voz-1325/69 belong to a sivatheriine that is usually
 1309 called *Helladotherium* in the Eastern Mediterranean, but that could be identical with the south
 1310 Asiatic *Bramatherium* (GERAADS & GÜLEÇ 2000; GERAADS et al. 2005; GERAADS 2009).

1311 Measurements of metapodials:

1312		length	prox. W	W of shaft	dist. W
1313	Mc Voz-912-69	408	102	62.5	100
1314	Mt Voz-1681	470	86	52.5	91

1315 Medial height x distal width of talus: 99 x 72.

1316 Bovidae. *Gazella cf. capricornis*. Two frontlets (MMNH-Sk Voz-558 (Plate 4, Fig. 8)
 1317 and MMNH-Sk Voz-1619) and several horn-cores belong to a gazelle with horn-cores that are
 1318 short, little divergent, and only slightly curved and compressed but, despite recent careful
 1319 analyses (KOSTOPOULOS 2005, 2016), these late Miocene gazelles remain imperfectly
 1320 characterized, and we prefer not to attempt a formal identification.

1321 *Palaeoreas cf. lindermayeri*. Two frontlets with incomplete horn-cores (MMNH-Sk
 1322 Voz-559 (Table 9) and MMNH-Sk Voz-1588 show no trace of mid-frontal suture, supra-
 1323 orbital pits close to the midline, and horn-cores that are rather far from the orbit, moderately
 1324 divergent, strongly twisted but not spiralled, and (at least on MMNH-Sk Voz-559 which is
 1325 better preserved) a strong sharp posterolateral keel, and a weaker rounded anterior one. They
 1326 are certainly of *Palaeoreas*, but species identification is tentative.

1327 *Prostrepsiceros cf. axiosi*. We tentatively refer to this species, defined in the early
 1328 Turolian of Ravin des Zouaves-5 (KOSTOPOULOS 2004), a single horn-core (MMNH-Sk Voz-
 1329 29/1 (Table 9) similar to those of *P. zitteli* but smaller and more openly spiralled.
 1330 Unfortunately it is not connected to the frontal, so that precise orientation is impossible. It is
 1331 much like those illustrated by ČIRIĆ (1957, pl. 25-26), identified as *P. zitteli* by GERAADS &
 1332 GÜLEÇ (1999), but referred to the present species by KOSTOPOULOS (2004).

1333 *Prostrepsiceros rotundicornis*. (Table. 9) A frontlet of rather small size (MMNH-Sk
 1334 Voz-694; Plate 4, Fig. 3) has salient orbital rims, supra-orbital pits close to horn-cores that
 1335 have their bases close to each other, their cross-section almost circular, and are probably
 1336 tightly twisted. A frontlet MMNH-Sk Voz-693 and some isolated horn-cores are probably of
 1337 the same species; MMNH-Sk Voz-724 and MMNH-Sk Voz-97 display an anteromedial
 1338 groove at the base, much like in the specimen illustrated by KOSTOPOULOS (2005, fig.9).

1339 *Prostrepsiceros cf. houtumschindleri*. A relatively complete skull with parts of the horn-
 1340 cores (MMNH-Sk Voz-1594, (Table. 9), but with most of the frontal reconstructed in plaster,
 1341 has its horn-cores inserted behind the orbits, more spiralled than in *Palaeoreas*, and with a
 1342 strong posterolateral keel.

1343 It may look hard to accept the occurrence of three different species of *Prostrepsiceros* at
 1344 Vozartsi, but we do not see how to reduce this number; it may be that these three species are
 1345 in fact not of the same genus.

1346 *Oioceros* sp. (Table. 9) A left horn-core base (MMNH-Sk Voz-14) with anticlockwise
 1347 torsion must belong to this genus or to a closely related one.

1348 "*Samodorcas*" cf. *kuhlmanni* ? (Table. 9) A horn-core base (MMNH-Sk Voz-29)
 1349 resembles the single known specimen of this Samos taxon (ANDREE 1926; BOUVRAIN &
 1350 BONIS 1985), but the Vozartsi specimen is smaller.

1351 Cf. *Pachytragus* sp. (Table. 9) Members of the *Palaeoryx-Protoryx-Pachytragus* group
 1352 are remarkably rare in the Republic of Macedonia; unfortunately, the provenance of a couple
 1353 of horn-cores is not definitely recorded. MMNH-Sk Voz-721 is the incomplete base of
 1354 another one; the frontal is extensively pneumatized, and the horn-core is but slightly
 1355 compressed, without keel or torsion. Its rather small size (50.5 x 47.5) is unlike *Protoryx*, but
 1356 not enough of the braincase is preserved to choose between the other two genera.

1357 A frontlet on display (MMNH-Sk Voz-1709/69) belongs to *Pikermiceros gaudryi*.

1358 *Tragoportax* sp. nov. A poorly preserved cranium (MMNH-Sk Voz-1592/68) and an
 1359 unnumbered frontlet (only the horn-core bases are preserved with part of the frontal bone and
 1360 the frontoparietal area) can be assigned to *Tragoportax* (see: SPASSOV & GERAADS 2004)
 1361 (Plate 13, Figs. 1-3), but their frontal morphology differs from that of other representatives of
 1362 the genus. A third skull specimen (MMNH-Sk Voz-1596/68) could belong to the same form,
 1363 but the fronto- parietal area and the horn-cores are strongly damaged (Table 9). In front of the
 1364 horn-cores, two long, prominent swellings, strongly convex in lateral view, but lacking keels,
 1365 delimit the anterior part of the V-shaped intercornual area. Anterior swellings at the horn-core
 1366 bases are not rare in other *Tragoportax*, but they are never so strong nor so clearly distinct
 1367 from the horn-cores themselves. On the frontlet, the horn cores are subtriangular in section
 1368 but were probably rather short and slender. The horn-cores are inserted closer to each other
 1369 than in *T. rugosifrons*. Additional measurements: MMNH-Sk Voz-1592/68: occipital height =
 1370 50. Unnumbered frontlet - postcornual constriction = c. 82 mm, biorbital diameter = c. 128
 1371 mm. MMNH-Sk Voz-1596/68: L P3–M3 = 81.7.

1372 Perissodactyla. Equidae. *Cremohipparion proboscideum*. FORSTEN & GAREVSKI (1989)
 1373 described from Vozartsi *Hipparion schlosseri* ANTONIUS - *dietrichi* WEHRLI, *Hipparion*
 1374 *proboscideum* STUDER and *Hipparion matthewi* ABEL. We found only two of the described
 1375 skulls (MMNH-Sk Voz 74/66, MMNH-Sk Voz 84/69) (Plate 5, Fig. 3) in MMNH-Sk; they
 1376 belong to *Cremohipparion proboscideum* STUDER, but the great number of postcranials stored
 1377 in the MMNH-Sk provide additional taxonomic information. The skulls have a very deep,
 1378 subtriangular, and anteroventrally oriented preorbital fossa. The preorbital bar is short (16–18
 1379 mm). The lacrimal invades the posterior border of the preorbital fossa. The posterior
 1380 pocketing is reduced and moderate in depth. Both skulls have well developed, deep and well
 1381 delineated subnasal fossa. In MMNH-Sk Voz 74/66 it is separated from the buccinator fossa
 1382 by a bar. The subnasal fossa depth in its posterior end is about 10 mm (MMNH-Sk Voz

1383 74/66) and 13 mm (MMNH-Sk Voz 84/69). In the latter specimen, the posterior wall of the
1384 anterior fossa forms a very shallow pocket. The bar between the preorbital fossa and the
1385 subnasal one is wide (11 to 18 mm). The tooth row in MMNH-Sk Voz 74/66 is 146 mm. The
1386 enamel plication is complex with 16–22 plis, but the specimen 74/66 is an adult individual
1387 (the protocone is connected with the protoloph on P² and M¹) and probably the plis were
1388 much more numerous. MMNH-Sk Voz 84/69 is a senile specimen and the teeth are much
1389 erased. The pli caballin is single to double. The protocone is rounded to lingually flattened
1390 and labially rounded. Measurements: Table 11.

1391 Other species with subnasal fossa are *C. mediterraneum* and *C. forstenae*. The
1392 differences with *C. forstenae* are clear: in the latter species the preorbital bar is wider, the
1393 preorbital and subnasal fossae are shallow and poorly delineated. The species
1394 *C. proboscideum* and *C. mediterraneum* share similar features, but are easy to distinguish.
1395 *C. mediterraneum* has a shallower, less clearly delimited subnasal fossa; some specimens lack
1396 it. The enamel is less plicated.

1397 Some metapodials and other postcranials have been assigned by FORSTEN & GAREVSKI
1398 (1989) to *Cremohipparion proboscideum*, *Hipparion dietrichi*, *Hipparion verae* and to
1399 *Cremohipparion matthewi*, but only the first species is represented by skulls. The metapodials
1400 can be sorted into four groups (Text-fig. 9, 10; Tables 23, 24). Most postcranials belongs to a
1401 species with relatively long, robust metapodials (large mid-shaft width), phalanxes and large
1402 astragali; FORSTEN & GAREVSKI (1989) assigned them to *C. proboscideum*, but their diagrams
1403 are similar to those of some specimens of *Hippotherium brachypus* from Pikermi and
1404 Hadjidimovo, therefore they could belong to a large *Hippotherium*. We assign to a second
1405 species metapodials that are as long as those of the first group but more slender, and
1406 phalanxes and medium sized astragali. They show similarities with slender *Hippotherium*,
1407 such as *Hippotherium primigenium* as well as with some samples of *Cremohipparion* with

1408 more robust metapodials (*C. proboscideum* or *C. mediterraneum* from Hadjidimovo). The
 1409 third group includes slender and long metapodials whose Simpson diagrams show similarities
 1410 with *Hipparion dietrichi* from Nikiti-2, RZO, Perivolaki and Vathylakkos 2 (KOUFOS 1987 c,
 1411 1988a; VLACHOU & KOUFOS 2002, 2006; KOUFOS & VLACHOU, 2016). One metacarpal, one
 1412 first phalanx and one astragalus can be referred to a fourth, small species. Their dimensions
 1413 and proportions are close to *C. macedonicum* from Nikiti-2 and Perivolaki (VLACHOU &
 1414 KOUFOS 2002, 2006; KOUFOS & VLACHOU, 2016).

1415 In short, *C. proboscideum* is documented at Vozartsi by two skulls, but on the basis of
 1416 metapodial data tree other hipparions were also present, but remain unidentified.

1417 Carnivora. Hyaenidae. *Adcrocuta eximia*: two hemimandibles (No. 66 & 69, Plate 7,
 1418 Fig. 2; Table 2). The only evolved features are the mesially enlarged third premolars and the
 1419 big depth of the mandible MMNH-Sk Voz-69. Other features are primitive: both p2 are
 1420 ellipsoid in occlusal view and possess well marked anterior additional cuspid; the carnassial
 1421 teeth are small. These features place the small sample from Vozartsi closer to the early
 1422 Turolian than to the middle Turolian (N.S., in progress).

1423 Biochronology: BOUVRAIN & BONIS (2007) suggested that the locality could be of
 1424 MN13 age but, given the presence of *Cremohipparion proboscideum*, *Tragoportax*
 1425 *rugosifrons*, *Prostrepsiceros* cf. *axiosi*, *Propotamochoerus* and of an *Adcrocuta eximia* with
 1426 some primitive features, the age of the locality could be MN11 or early MN12; in any case
 1427 this conclusion is tentative.

1428

1429 **II.5.5. Zmiovets 1 (Zmijovec 1)** (a site situated close to Dolni Disan)

1430 Proboscidea. *Anancus ?arvernensis*. A mandible of *Anancus arvernensis* MMNH-Sk
 1431 ZM 2734 was described by GAREVSKI & MLADENOVSKI (2006), which implies a Pliocene age
 1432 for the locality. Since Zmiovets is situated higher than the deposits at Dolni Disan yielding

1433 Turolian fauna, and since Turolian *Anancus* sp. and Pliocene *Anancus arvernensis* are
 1434 indistinguishable by lower dentition, this remains a plausible assumption.

1435

1436 **II.5.6. Zmiovets 2**

1437 A new rich locality is discovered at the beginning of the century, between Dolni Disan
 1438 and Zmiovets 1, at a lower stratigraphic position than the latter. Field identification of
 1439 metapodials and teeth (N.S. and D.G.) indicates the presence of a slender *Hipparion* and of a
 1440 bovid (*Tragoportax?*) as well as a probable Turolian age of the locality.

1441

1442 **II.6. Morievo area (Mariovo)**

1443 Proboscidea. A mammutid molar fragment from Gradeshnitsa (Gradesnica) described
 1444 by PETRONIJEVIC (1952) as *Mastodon borsoni* could indeed belong to the Pliocene “*Mammut*”
 1445 *borsoni* but also to the Turolian species, “*Mammut*” *obliquephus*. The two taxa cannot be
 1446 distinguished by dental morphology (MARKOV 2004, 2008), and there is no associated fauna,
 1447 so the age of the locality is not clear.

1448 The recently published *Zygodon turicensis* from the coal mines near Bitola
 1449 (GAREVSKI et al. 2012) is the only taxon occurring at the locality, and its age could be from
 1450 early to late Miocene (MN3 to MN10).

1451 Perissodactyla. Rhinocerotidae. *Chilotherium* sp. Several rhino tooth fragments in the
 1452 NMNHS are labelled “Morievo region, Macedonia” (an area between Prilep and Bitola); their
 1453 colouration indicates coal-bearing deposits. Some of them represent the westernmost point of
 1454 distribution of *Chilotherium* s. str. in Europe and indicate a Turolian age (GERAADS &
 1455 SPASSOV 2009). The proto-loph has pinched lingual extremity isolating the protocone that is
 1456 flattened and trapezoid. The antecrochet is long and curves lingually towards the valley
 1457 entrance.

1458 Tapiridae. The scarce *Tapirus* sp. finds from Zivojno, near Bitola, could be late
 1459 Turolian (VAN DER MADE & STEFANOVIĆ 2006) but the coal deposits near Bitola could have
 1460 various ages (see above – *Zygodolophodon turicensis*).

1461 Biochronology: We could conclude that the coal bearing deposits in the Morievo area
 1462 could include different levels, some of which are of late Miocene age.

1463

1464

1465 **II.7. VALANDOVO FOSSILIFEROUS AREA**

1466 **II.7.1. Bashibos (Basibos)** (41°18'41"N, 22°40'30" E; elev. 284 m)

1467 Proboscidea. *Choerolophodon* sp. is represented by poorly preserved dental remains and
 1468 tusks.

1469 Artiodactyla. Suidae: *Microstonyx erymanthius*. There are two specimens with complete
 1470 upper tooth-rows: a maxillary MMNH-Sk BB 1540 and a skull MMNH-Sk BB 1541 (Plate 3,
 1471 Fig. 1), the latter associated with a piece of mandible. Both specimens have a relatively large
 1472 P1 (measurements: Table 6, 7), a character that might indicate an early age, although the
 1473 evidence is admittedly weak.

1474 Bovidae: *Protragelaphus* sp. A skull with complete right horn-core (MMNH-Sk BB
 1475 1645), plus frontlets (MMNH-Sk BB 1582, MMNH-Sk BB 1584, MMNH-Sk BB 1587,
 1476 MMNH-Sk BB 6175) and isolated horn-cores (MMNH-Sk BB 2621 and unnumbered), are of
 1477 rather large size (Plate 4, Figs 2, 4; Table 9). The horn-cores have little spiralisation but strong
 1478 torsion, with a single very strong posterolateral keel. Their measurements compare fairly well
 1479 with those of the Samos specimen SMNL 13279 of *Protragelaphus skouzesi* (ANDREE 1926,
 1480 pl.15, fig.4-5) but the torsion is less strong, as the keel coils for only about a complete whorl.
 1481 The horn-cores are more like those of the antelope from Grebeniki that PAVLOW (1913)
 1482 ascribed to *P. skouzesi*, but that BOUVRAIN (1978) identified as a probable *Prostrepsiceros*.

1483 However, in the species from Bashibos, the supra-orbital pits are farther from the horn-cores,
1484 and the orbital rims less prominent. It also differs from *Helladodorcas* BOUVRAIN, 1997, from
1485 the late Vallesian of Pentalophos, in its larger size, less flange-like posterolateral keel, and
1486 narrower nasals; it is perhaps intermediate between this genus and *Protragelaphus*.

1487 Cf. *Prostrepsiceros* sp. MMNH-Sk BB 2611 is a frontlet with incomplete horn-cores
1488 (Plate 4, Fig. 5). The frontal plane is little angled on the parietal one. The horn-cores are
1489 compressed (46.4 along the main axis x 35.7 perpendicularly), without keels, with their long
1490 axis inclined at 45° on the sagittal plane. They are not very inclined but curved backwards,
1491 and the divergence is moderate basally but increases upwards, so that the spiral is
1492 anticlockwise on the right horn-core. They resemble *P. fraasi* or *P. rotundicornis*, but the
1493 large size and strong compression are unlike these species (see, e.g., KOSTOPOULOS 2006, fig.
1494 7); they fit within this genus, but it seems that they cannot be assigned to any known species.

1495 *Samotragus* sp. The basal part of a left horn-core MMNH-Sk BB 2623 (Plate 4, Fig. 7;
1496 Table 9). has an anticlockwise torsion and an almost circular cross-section with only a lateral
1497 groove underlined by a small ridge posterior to it. This horn-core is slightly larger than those
1498 of *Oioceros*, and about the same size and morphology as those of *S. praecursor* from Ravin
1499 de la Pluie, but the systematics of this group of antelopes is still debated, and even the generic
1500 assignment is tentative.

1501 *Mesembriacerus* sp. The posterior part of a small skull MMNH-Sk BB 2607 (Plate 4,
1502 Fig. 9; Table 9). differs from all bovids of the Balkano-Iranian Turolian. It is not crushed,
1503 except for the area of insertion of the horn-cores. The latter, of which only the base is
1504 preserved, appear still more inclined that they were in life, and were small, even compared
1505 with the size of the skull, and could indicate a female individual. They are oval in cross-
1506 section, with no keel or torsion, and little or no divergence. Details of the posterior part of the
1507 skull are obscured by sediment, but the auditory region was short and deep, with small bulla

1508 and auditory foramen, quite narrow mastoid exposure dorsally, and broad occipital condyles.
1509 The basioccipital is short, with posterior tuberosities much lower (more ventral) than the
1510 basion, indicating stiffening of the atlanto-cranial articulation, as in several "ovibovines"
1511 practising frontal clashing ("Rammkampf"). The interparietal, which has a rough surface, has
1512 a very particular orientation: instead of being almost in the same plane as the parietals in
1513 lateral view, it is here, between the temporal lines, almost in the same plane as the occipital.
1514 The angle between occipital and parietal planes, which usually corresponds to the nuchal
1515 crest, corresponds here approximately (sutures are not visible) to the rostral border of the
1516 interparietal. Among late Miocene bovids of the Balkano-Iranian province, only
1517 *Mesembriacerus* from the Vallesian of Ravin de la Pluie in Greece (BOUVRAIN 1975;
1518 BOUVRAIN & BONIS 1984), of which D. KOSTOPOULOS kindly provided us with photos of the
1519 holotype, displays such morphology, and we are confident in assigning MMNH-Sk BB-2607
1520 to this genus. Not enough of it is preserved for detailed comparisons, but it looks as if the
1521 interparietal of the Bashibos form was still more vertical than in Greece, so that we prefer not
1522 to attempt species identification, as this might reflect an age difference. Still, the presence of
1523 *Mesembriacerus* is indicative of an early age for the locality.

1524 Some measurements of MMNH-Sk BB 2607 (besides those given in Table 9) are: width
1525 over posterior tuberosities of occipital = 26.1; width over mastoids = 71.7; width over
1526 condyles 53.7; minimum width between temporal lines = 34.8.

1527 *Gazella* sp. is represented by two horn-cores, MMNH-Sk BB 2628 and MMNH-Sk BB
1528 69/75.

1529 Perissodactyla. Equidae. FORSTEN & GAREVSKI (1989) described from this locality
1530 *Hipparion schlosseri* ANTONIUS - *dietrichi* WEHRLI and *H. verae* GABUNIA. Unfortunately,
1531 we could not find all of the skulls described by FORSTEN & GAREVSKI in the NMNH-Sk
1532 collections. Our revision of the available material indicates the presence of two species in the

1533 locality, but we identify them as *Hippotherium brachypus* HENSEL and *Hipparion dietrichi*
 1534 WEHRLI.

1535 *Hippotherium brachypus*. The preorbital fossa of all three specimens of this species
 1536 (MMNH-Sk BB 223/77, MMNH-Sk BB 232/77 and MMNH-Sk BB 1551/70) is well
 1537 delineated, subtriangular, deep to moderately deep and anteroposteriorly oriented. The
 1538 preorbital bar is long (40.5 – 48.6 mm). The posterior pocketing is reduced, moderately to
 1539 slightly deep. The nasal notch ends above the P1. The tooth row length is 139 mm for
 1540 MMNH-Sk BB 1551/70 and 158 mm for MMNH-Sk BB 232/77. The enamel plication is
 1541 moderate (in one very old specimen) to rich, with 15 to 29 plis on the premolars and 12 – 27
 1542 plis on the molars. The pli caballin is single to double/complex. The protocone is oval to
 1543 lingually flattened - labially rounded (measurements: Table 1).

1544 The specimens MMNH-Sk BB 232/77 and MMNH-Sk BB 1551/70 were described by
 1545 FORSTEN & GAREVSKI (1989) as *H. verae*. In some of their features, they are close to the
 1546 characteristics of *H. verae* (see above under Karaslari), but they present a number of
 1547 differences: the preorbital bar is wider, the preorbital fossa is deeper, well outlined all around
 1548 and the enamel plication is more complex, so they are considered here as *Hippotherium*
 1549 *brachypus*. The specimen MMNH-Sk BB 223/77 was identified as *H. dietrichi* by FORSTEN &
 1550 GAREVSKI (1989), but its fossa is deeper, with anterior rim and posterior pocket about 5 mm
 1551 deep.

1552 The specimens of *Hippotherium brachypus* from Bashibos are clearly distinct from the
 1553 Vallesian species *Hippotherium primigenium*: the preorbital fossa is shallower with less sharp
 1554 anterior and dorsal borders and shallower posterior pocket, and deeper nasal notch. There is
 1555 also a very short, robust metatarsal that could be assigned to this species.

1556 *Hipparion dietrichi*. We ascribe to this species the skull of a very old individual
 1557 (MMNH-Sk BB 256/75), not mentioned by FORSTEN & GAREVSKI. Its preorbital bar is long

1558 (41 mm). The preorbital fossa is shallow, subtriangular, anteroventrally oriented and weakly
 1559 delineated; it is not pocketed posteriorly but has a posterior rim. The nasal notch ends above
 1560 the anterior rim of P2. The tooth row length is 137 mm, the enamel plication is simple, the pli-
 1561 caballin is vestigial, the protocone is rounded to lingually flattened - labially rounded, almost
 1562 connected with the protoloph on P2, P3 and M3. The muzzle was probably short (distance P2-
 1563 C is 50 mm). All these features allow identifying this skull as *H. dietrichi*. Measurements:
 1564 Table 12).

1565 Rhinocerotidae. *Dihoplus pikermiensis*. A complete skull with attached mandible on
 1566 display shows the typical features listed by GERAADS (1988) and GERAADS & SPASSOV
 1567 (2009), except that the nasal bones are short, with the hooked profile of those of
 1568 *Ceratotherium neumayri*, but this is probably an effect of deformation (Plate 11, Fig. 4; Table
 1569 13). There are well preserved cylindrical i2s, small but not minute, with a wear facet almost
 1570 perpendicular to the long axis of the tooth, which is almost vertically inserted. There is no
 1571 evidence of any upper incisor, but this absence is less secure than at Karaslari, because the
 1572 premaxillae of the Bashibos specimen are less well preserved.

1573 Carnivora. Hyaenidae. *Adcrocuta eximia*. The material includes mandibles No 1781 &
 1574 785 (old 67); and two maxillary fragment with P3–P4 and P2–P3, respectively (Plate 7, Fig. 1
 1575 and Plate 12, Fig. 4; Tables 2, 14). The upper premolars have a strong lingual cingulum and
 1576 P3 has a very strong anterior additional cusp. These features could be considered as primitive.
 1577 The mandibles have also primitive features, including very small carnassials and elongated
 1578 p3s, like early Turolian samples.

1579 Felidae. *Yoshi* aff. *garevskii* (Plate 9, Fig. 1; Table 15). A fragment of right mandible
 1580 has all its teeth broken except p4. The symphysis is not preserved but was probably shallow,
 1581 in contrast with the Machairodontinae. The diastema is short with moderately steep mandible
 1582 upper edge between c and p3 in lateral view. The middle part of the ventral border of corpus

1583 is convex. Two mental foramina are visible under the mesial and distal ends of p3. The teeth
1584 are not serrated. The canine has a robust root and strong distal and lingual ridges. Between
1585 them, the lingual surface is flat; the mesiolabial surface is rounded but the distolabial one is
1586 relatively flat with a sharp change of curvature between them. There is no trace of p2. The
1587 third premolar lacks an anterior additional cuspid; p4 is rather symmetrical with sub-equal
1588 mesial and distal accessory cuspids. The lingual border of the carnassial tooth is very slightly
1589 concave.

1590 In its size the mandible is comparable with the small Machairodontinae of the
1591 *Promegantereon-Paramachaerodus* group, as well as with the representatives of the genus
1592 *Yoshi* SPASSOV & GERAADS, 2015 whose type-species is *Y. garevskii*, based upon a skull from
1593 Karaslari, but which also includes the small forms previously included in *Metailurus*
1594 ZDANSKY. The Bashibos mandible differs from *Paramachaerodus* in the lack of tooth
1595 crenulations, in the clearly shorter c – p3, the steeper upper edge of the diastema, and the
1596 deeper symphysis (canine inserted at a higher level), as well as in the smaller size.
1597 *Promegantereon* (perhaps an early grade of *Paramachaerodus*) also lacks tooth crenulations,
1598 but in other features it also differs from the Bashibos mandible, especially in the size and
1599 shape of the diastema, related to the deep machairodontin symphysis. In addition
1600 *Promegantereon* (i.e. its only species *P. ogygia*) usually retains a vestigial p2 (SALESA et al.
1601 2010). The Bashibos mandible corresponds to the morphology of the mandibles described as
1602 “*Metailurus parvulus*” from Greece (ROUSSIAKIS et al. 2006 and references therein), which in
1603 fact belong to *Yoshi* (*Y. garevskii* SPASSOV & GERAADS, 2015 and *Y. minor* [ZDANSKY,
1604 1924]). The Bashibos specimen is slightly larger than *Y. minor* and closer to *Y. garevskii*, but
1605 data are scarce. The Bashibos mandible is the earliest known member of the genus.

1606 *Paramachaerodus* sp. MMNH-Sk BB 93/69 is an upper canine whose tip is missing.
1607 The two cutting edges are sharp and located at the mesial and distal edges of the crown, so

1608 that the crown cross-section is a very elongated ellipse, with weakly rounded labial surface
 1609 and almost flat lingual surface (mesiodistal x labiolingual diameters: 16.0 x 10.5; restored
 1610 length about 40 mm?). The crenulations on the distal edge are weaker than usual in this genus.

1611 Biochronology. None of the bovids from Bashibos looks identical with those of the
 1612 well-known Turolian of the Balkano-Iranian province, including those of the Axios Valley
 1613 that is geographically very close, and a Turolian age is very unlikely. However, the hipparions
 1614 fit better the first half of the Turolian. The evolutionary stage of *Adcrocuta* indicates an age
 1615 probably older than the middle Turolian and the *Paramachaerodus* morphology fits with the
 1616 early Turolian stage. Pending more detailed study of this material or further collecting at the
 1617 locality, we consider that Bashibos is the earliest site of the R. of Macedonia upper Miocene,
 1618 and is probably of Vallesian or lowermost Turolian age.

1619

1620 **II.7.2. Prsten** (41°18'50"N, 22°39'43" E; elev. 246 m)

1621 Proboscidea: *Choerolophodon* sp. A juvenile skull with mandible, as yet unprepared.

1622 Artiodactyla. Suidae. *Microstonyx erymanthius*. This suid is relatively abundant at this
 1623 site, with two maxillae, two palates, and a mandible (measurements: Tables 6, 7). Specimen C
 1624 has a P1 coming into contact with P2 whereas specimen B definitely lacks this tooth. This
 1625 species is discussed in more detail under "Karaslari". As noted above, the evolution of
 1626 *Microstonyx* remains imperfectly understood, but the presence of a P1 would support an early
 1627 age for Prsten.

1628 Perissodactyla. Rhinocerotidae: *Dihoplus* cf. *pikermiensis*: The anterior part of a skull
 1629 28.8.1997 can unambiguously be assigned to *Dihoplus* rather than to *Ceratotherium neumayri*
 1630 because of its long nasals, infra-orbital foramen situated anteriorly (above the posterior root of
 1631 P3), non sloping ventral orbital border, and by the tooth characters: well-marked paracone
 1632 fold and lingually pinched protocone and hypocone. Measurements are given in Table 13. The

1633 robustness of the zygomatic arch is reminiscent of *D. schleiermacheri*, a Vallesian species
 1634 probably ancestral to the Turolian *D. pikermiensis*, but the nasal notch is slightly deeper than
 1635 in the former species. Unfortunately the premaxillae are missing.

1636 Carnivora. Hyaenidae. *Adcrocuta eximia*. Skull MMNH-Sk Prst 1397/78 is well-
 1637 preserved but lacks teeth except the right P2 and P3 (Table 14). The premolars are taller than
 1638 in the Vallesian material but the P3 is less broad mesially than in the middle Turolian forms.
 1639 In a left mandible fragment Pr2 (Plate 7, Fig. 4; Table 2), the p2 and p3 are narrow, as in the
 1640 teeth from Kavakdere (early Turolian of Turkey – pers. measurements in MNHNP): the p2 is
 1641 piriform in occlusal view, but with vestigial anterior additional cuspid and elongated talonid;
 1642 p3 is broad posteriorly, with marked anterior additional cuspid and elongated talonid. Most of
 1643 these features demonstrate a rather primitive condition (N.S., in progress).

1644 *Adcrocuta* sp. The right half-mandible Pr1 with p2-m1 (ramus partially preserved,
 1645 corpus destroyed and reconstructed in plaster) has an unusual size and morphology (Plate 7,
 1646 Fig. 5). The area of p1 is missing. Due to the reconstruction the p2-p3 are artificially uplifted
 1647 and exceedingly inclined backward. Measurements (L x W): c = 14.3 x 12.4; p2 = 12.8 x 9.8;
 1648 p3 = 16.2 x 11.7; p4 = 19.4 x 12.0; m1 = 25.0 x 11.9; p2-m1 = 72.2

1649 All teeth are very small (see below). The canine is thick labio-lingually. Its
 1650 mesiolingual ridge is located more distally than usual in *Adcrocuta eximia*. The p2 is short
 1651 and broad, broadest distally, and with much reduced posterior cuspid. There is no an anterior
 1652 additional cuspid, but a thick cingulum circles the mesial border of the tooth. The p3 is
 1653 stubby, and broadest mesially. The p4 is also enlarged mesially, with an unusually well
 1654 marked and strong cingulum along the lingual side. The m1 is broad, with a short talonid,
 1655 almost unicuspid: the entoconid is a minute cuspid on the lingual side, while the hypoconid is
 1656 centrally located. The broad and short premolars, the p4 without entoconid and the m1
 1657 without metaconid strongly differ from *Lycyaena*, as well as from “*Chasmaporthetes bonisi*”

1658 (KOUFOS 1987d), which is synonymized with *Adcrocuta eximia* by WERDELIN & SOLOUNIAS
 1659 (1991), while the absence of m2 and the much smaller m1 talonid differ strongly from
 1660 *Hyaenictis graeca*. The tooth-row as well as individual teeth are smaller than in Turolian
 1661 *Adcrocuta* (Text-fig 12, 16), but also than in *A. eximia leptoryncha* from the Vallesian of
 1662 Ravin de la Pluie (Greece) (BONIS & KOUFOS 1981), or than in a specimen of *Lycyaena*
 1663 *chaeretis* from Kalimantsi, Bulgaria. This difference in size with other *Adcrocuta* is stronger
 1664 on the premolars than on m1, which is also a distinctive feature of the Pr1 mandible. On the
 1665 other hand the premolars are similar in morphology to those of the middle Turolian *A. eximia*,
 1666 but p4 and m1 have strong lingual cingula. This combination of features probably warrant
 1667 distinction at a taxonomic level higher than the subspecies, because typical *Adcrocuta eximia*
 1668 is present in the locality (Text-fig. 16; Table 2), but we refrain from naming a new species
 1669 because of the fragmentary character of this single mandible.

1670 Felidae. *Machairodus* sp. A brief description of a *Machairodus* material (neurocranium
 1671 and several teeth) from Prsten was published (but poorly illustrated) by GAREVSKI (1992) as
 1672 *M. aphanistus*. The upper canine is moderately long mesiodistally (c. 30.5; Table 21) and
 1673 thick (13.3). Its compression index (43.6) fits better *M. aphanistus* than *M. giganteus* but their
 1674 ranges widely overlap (KOUFOS 2000; ROUSSIAKIS & THEODOROU 2003). The P3 (22.8 x
 1675 10.5) is smaller than at Batallones-1 (MN10) but close to the mean value of all upper Miocene
 1676 *Machairodus*. Its low posterior additional cusp and weakly expressed cingular mesial and
 1677 distal cusps are plesiomorphic characters.

1678 The dimensions of the P4 Prst-128 (GAREVSKI 1992, fig. 2B) are 40 x 18.1, those of the
 1679 P4 Prst-125 (GAREVSKI 1992, fig. 2A) are 43 x 18.7 (Plate 9, Fig. 6); thus these teeth are
 1680 larger than in Vallesian forms. The parastyle-preparastyle complex is moderately developed.
 1681 The protocone of Prst-128 is strong, slightly weaker than the protocone of the Batallones-1
 1682 *M. aphanistus* (ANTÓN et al. 2004, fig.7L). The postcanine teeth lack crenulations, as in pre-

1683 Turolian forms (SOTNIKOVA 1991), but some Turolian specimens may also lack crenulations.
 1684 The lack of post-canine crenulations and a moderately developed parastyle-preparastyle
 1685 complex correspond to the *Neomachairodus* of SOTNIKOVA & NOSKOVA (2004), which is
 1686 replaced in the Middle Turolian by *Amphimachairodus*, thus suggesting an early age, perhaps
 1687 very end of the Vallesian or MN11, but the large size rules out an earlier age.

1688 Biochronology: The age of the locality could be close to that of Bashibos; it is probably
 1689 not later than the early Turolian, but could even be late Vallesian.

1690

1691 **Discussion and conclusions**

1692 This study shows that the fauna investigated might cover the time span from the early
 1693 Miocene to the late Turolian/early Ruscinian, but most of the fossils represent middle
 1694 Turolian mammals (Text-fig. 17). There are at least 57 identified species, discovered in 25
 1695 different paleontological sites (Table 25), most of them being from the Vardar and Strumitsa
 1696 river basins, but also from the Morievo, Valandovo and Delchevo regions. The richest
 1697 localities are the middle Turolian localities of Karaslari (with 22 species) and Kiro Kuchuk
 1698 (17 sp.). The presence of *Zygodon turicensis* indicates that the Nerezi locality and the
 1699 lower levels of Morievo coal-bearing area are the oldest of the studied localities. The presence
 1700 of *Anancus* sp. (whose earliest occurrence in Europe is probably at Azmaka in Bulgaria:
 1701 SPASSOV et al. 2012) in Dolni Disan, Prevalets, and Zvegor places these localities (together
 1702 with Stamer, where *Sivatherium* was discovered) among the youngest ones, with an age close
 1703 to the Miocene/Pliocene boundary.

1704 The rich fossil material stored in the Macedonian Museum of Natural History, Skopje,
 1705 provides new, important data on the Turolian Hipparion fauna of the Pikermian biome (sensu
 1706 SOLOUNIAS et al. 1999) of the Balkans, previously mostly documented in Greece and
 1707 Bulgaria. The faunas of the Republic of Macedonia display the typical features of the Balkan

1708 Turolian mammal fauna. The main results by taxonomic groups can be summarized as
1709 follows.

1710 Among the Primates, it seems that, contrary to previous statements (RADOVIĆ et al.
1711 2013), *Mesopithecus* is only represented by its typical, more derived stage, *M. pentelicus*.

1712 Among the Carnivora, besides the widespread *Adcrocuta eximia*, another species of
1713 the genus is probably present at Prsten, one of the earliest locality investigated, with a likely
1714 age close to the Vallesian/Turolian transition; *Machairodus* s.l. is represented by two different
1715 evolutionary stages – “*Neomachairodus*” and “*Amphimachairodus*”(see above on PRE and
1716 PRS fauna); *Paramachaerodus* sp. from Kiro Kuchuk demonstrates transitional features
1717 between *Promegantereon* and the younger form *Paramachaerodus*, showing that generic
1718 distinction between these taxa is perhaps not necessary.

1719 The rhinoceros *Dihoplus* is much more common than *Ceratotherium*, and the Morievo
1720 region represents the western-most distribution of *Chilotherium* on the continent. Kiro
1721 Kuchuk and Karaslari demonstrate the rare co-occurrence of the Schizotheriinae and
1722 Chalicotheriinae, previously definitely documented only at Hadjidimovo and Azmaka in
1723 Bulgaria (GERAADS et al. 2001; SPASSOV et al. 2012); it thus seems to be a typical feature of
1724 the Balkan Turolian faunas. Our revision of the Equidae does not confirm the presence of
1725 *Hipparion verae* mentioned by FORSTEN & GAREVSKI (1989) at Karaslari; *Cremohipparion*
1726 *mediterraneum* is surprisingly rare in the Turolian localities in comparison with *H. brachypus*
1727 and *H. dietrichi*; the earliest *H. brachypus* (the samples from BB and KK) demonstrate the
1728 richest enamel plications and presence of a complex pli caballin on the upper cheek teeth.

1729 The diversity of the Bovidae is comparable to that found in Bulgarian and Greek
1730 localities, and greater than that of central Europe. Their most clear feature is the abundance of
1731 spiral-horned forms (especially *Palaeoreas*, *Prostrepsiceros*, and *Protragelaphus*), as in
1732 Greece and Bulgaria but, as in Bulgaria but in contrast to Greece (and Turkey), the large

1733 forms of the *Pachytragus*–*Protoryx* group are extremely rare. A probably new species of
 1734 *Tragoportax* is present at Vozartsi, in addition to more common forms of this genus. Some
 1735 rare bovids, like "*Samodorcas*" cf. *kuhlmanni* ? and Cf. *Pachytragus* sp. were found in the
 1736 same locality, which might be of early Turolian age. The identification of *Samotragus* and
 1737 *Mesembriacerus* suggest that the localities of Bashibos and Prsten could be still earlier, and
 1738 perhaps even Vallesian

1739 Our analyses of the faunas of the R. of Macedonia contribute to the anatomy,
 1740 taxonomy and evolution of several taxa such as *Simocyon*, several hipparion species,
 1741 *Propotamochoerus*, *Bohlinia*, *Metailurus*, and allowed the description of some new ones. The
 1742 new species *Sivatherium garevskii* was described (GERAADS 2009) from the locality of
 1743 Zvegor, whose age could be close to the Miocene/Pliocene boundary, thus representing an
 1744 early member of the genus. The genus *Yoshi* was created (SPASSOV & GERAADS 2005) on the
 1745 basis of a complete skull and mandible discovered among the very rich fauna from Karaslari.
 1746 Its probable first occurrence is at Bashibos.

1747 The rich faunas of Karaslari and Kiro Kuchuk help reconstructing the middle Turolian
 1748 environment in the Vardar region. The most widespread landscapes could be, after the
 1749 supposed ecological requirements of the mammals, the bushlands and open woodlands
 1750 inhabited by schizotheriine and chalicotheriine chalicotheres, giraffids (mainly *Bohlinia*), the
 1751 monkey *Mesopithecus*, the rhino *Dihoplus pikermiensis*, the bovids *Tragoportax* and
 1752 *Pikermicerus*, and the grazer *Choerolophodon* (KONIDARIS et al. 2016), while *Microstonyx*
 1753 could have dwelled closer to the paleo-Vardar river.

1754 The ever-increasing accumulation of data in recent years help improving the picture of
 1755 the semi-open landscapes (scrublands and woodlands) of the Turolian of Eurasia (FORTELIUS
 1756 et al. 2006). They were probably widespread in South-Eastern Europe, the eastern part (at
 1757 least) of Central Europe, the Northern peri-Pontic area, the Middle East, and large territories

1758 of Central Asia. However, their faunal composition was not uniform. Faunal similarities
 1759 (especially regarding spiral-horned bovids and giraffids) support the existence of a Balkan-
 1760 Iranian (Greco-Irano-Afghan) zoogeographic province (BONIS et al. 1992), whose
 1761 westernmost part is now better known, thanks to the field work conducted in the late Miocene
 1762 of the Republic of Macedonia and our analyses of the resulting collections. The Northern peri-
 1763 Pontic region shares a number of similarities with this Balkan-Iranian province, especially
 1764 regarding the hipparions, giraffids, bovids (spiral-horned antelopes, boselaphins, gazelles)
 1765 (KOROTKEVICH 1988; KRAKHMALNAYA 1996), and it may be that it was part of this mega-
 1766 province as well; further research may refine the characteristics of the various sub-provinces.
 1767 Our investigations confirm the typical features of the Balkan part of this province,
 1768 characterized by *Choerolophodon pentelici*, *Mesopithecus pentelici*, *Bohlinia attica*,
 1769 *Palaeoreas lindermayeri*, *Tragoportax*, *Pikermicerus* *Dihoplus pikermiensis*, *Hippotherium*
 1770 *brachypus* (together with the lack of *Hipparion verae* and *C. moldavicum*), as well as the
 1771 typical association of schizotheriines and chalicotheriines.

1772

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1786

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2314 **Text-figures captions**

2315

2316 **Text-fig. 1.**

2317 Map of the Neogene localities of vertebrate fauna investigated in the present work.

2318

2319 **Text-fig. 2**

2320 Logarithmic ratio diagram comparing the skulls of *Hippotherium brachypus* HENSEL, 1862
 2321 from Macedonian localities and other localities from the Balkan peninsula, and *Hippotherium*
 2322 *giganteum* GROMOVA, 1952: Akkaşdağı (**AKK**); Bashibos (**BB**); Belushka (**BEL**);
 2323 Hadjidimovo (**HD**); Grebeniki (**GR**); Karaslari (**KAR**); Kiro Kuchuk (**KK**); Kocherinovo
 2324 (**KCH 2**); Perivolaki (**PER**); Pikermi (**PIK**); Umin Dol (**UD**).

2325 Standard *Hippotherium primigenium* von MEYER, 1829, Höwenegg (BERNOR et al. 1997).

2326 Measurements after EISENMANN et al. 1988:

2327 **1.** muzzle length, prostion-middle of the line connecting the anterior borders of P2; **2.** palatal
 2328 length, middle of the line connecting the anterior borders of P2 to anterior border of choane;
 2329 **3.** vomerine length; **4.** post-vomerine length; **6.** basilar length: basion-prostion; **7.** premolar
 2330 length; **8.** molar length; **9.** upper cheek teeth length; **14.** minimal muzzle breadth; **15.** muzzle
 2331 breadth at I1-I1; **30.** length of the naso-incisival notch; **31.** cheek length, posterior end of the
 2332 narial opening-anterior border of the orbit; **32.** distance orbit-preorbital fossa (POF); **33.**
 2333 length of PF; **35.** height of POF (perpendicular to 33); **36.** distance ventral border of POF-
 2334 crista facialis; **37.** distance infraorbital foramen-alveoles of the tooth series; **38.** distance
 2335 posterior end of PF-alveoli of the cheek teeth.

2336

2337 **Text-fig. 3.**

2338 Size variability of the lingual cusp in P3-P4 in the main S.-E. European Turolian
 2339 *Mesopithecus* samples with time (from the end of the early Turolian – Hadjidimovo till the
 2340 second half of the middle Turolian – Pikermi). All the teeth included are unworn or very
 2341 slightly worn. Legend: the lingual cusp size (large, medium or small) is estimated after its
 2342 height and its surface area (above all its labio-lingual diameter) in relation to the labial one
 2343 (after original observations in MNHNP, NMNHS & PMA)

2344

2345 **Text-fig. 4.**

2346 Logarithmic ratio diagram comparing the skulls of *Hippotherium brachypus* (HENSEL, 1862)
 2347 from Macedonian localities: Bashibos (**BB**); Karaslari (**KAR**); Kiro Kuchuk (**KK**); Umin Dol
 2348 (**UD**).

2349 Standard *Hippotherium primigenium* VON MEYER, 1829, Höwenegg (BERNOR et al. 1997).

2350 See Text-fig. 2. for measurement numbers.

2351

2352 **Text-fig. 5.**

2353 Logarithmic ratio diagram comparing the skulls of *Cremhipparion mediterraneum* ROTH &
 2354 WAGNER, 1855, and *C. proboscideum* STUDER, 1911, from Macedonian localities: Karaslari
 2355 (**KAR**): solid lines; Vozartsi (**VOZ**): dashed lines.

2356 Standard *Hippotherium primigenium* VON MEYER, 1829, Höwenegg (BERNOR et al. 1997).

2357 See Text-fig. 2. for measurement numbers.

2358

2359 **Text-fig. 6.**

2360 Logarithmic ratio diagram comparing the skulls of *Hipparion dietrichi* WEHRLI, 1941 from
 2361 different Macedonian and other localities from the Balkan peninsula, and the type sample of

2362 *H. verae*: Akkaşdağı (**AKK**); Bashibos (**BB**); Grebeniki (**GR**); Karaslari (**KAR**); Perivolaki
 2363 (**PER**); Ravin des Zouaves-5 (**RZO**); Strumyani-2 (**STR-2**); Veshie (**VES**).

2364 Standard *Hippotherium primigenium* VON MEYER, 1829, Höwenegg (BERNOR et al. 1997).

2365 See Text-fig. 2. for measurement numbers.

2366

2367 **Text-fig. 7.**

2368 Logarithmic ratio diagram comparing the skulls of *Hipparion* sp. from Umin Dol (**UD**) and

2369 *Hipparion dietrichi* WEHRLI 1941, from different Macedonian localities: Barovo (**BAR**);

2370 Belushka (**BEL**); Bashibos (**BB**); Karaslari (**KAR**); Veshie (**VES**).

2371 Standard *Hippotherium primigenium* VON MEYER, 1829, Höwenegg (BERNOR et al. 1997).

2372 See Text-fig. 2. for measurement numbers.

2373

2374 **Text-fig. 8.**

2375 Logarithmic ratio diagram comparing the skulls of *Cremohipparion* from Macedonian

2376 localities, localities from the Balkan Peninsula and the type of *C. proboscideum* from Samos:

2377 Hadjidimovo (**HD**); Kalimantsi (**KAL**); Karaslari (**KAR**); Perivolaki (**PER**); Pikermi (**PIK**);

2378 Ravin des Zouaves-5 (**RZO**); Strumyani 2 (**STR2**); Vozartsi (**VOZ**).

2379 Standard *Hippotherium primigenium* VON MEYER, 1829, Höwenegg (BERNOR et al. 1997).

2380 See Text-fig. 2. for measurement numbers.

2381

2382 **Text-fig. 9.**

2383 Logarithmic ratio diagram comparing equid metacarpals from Vozarsti. Standard:

2384 *Hippotherium primigenium* VON MEYER, 1829, Höwenegg (BERNOR et al. 1997).

2385 Measurements after EISENMANN et al. 1988: 1. maximal length; 3. minimum width of shaft; 4.

2386 depth of shaft; 5. proximal articular breadth; 6. proximal articular depth; 10. distal maximum

2387 supra-articular breadth; 11. distal maximum articular breadth; 12. distal maximum depth of
 2388 the keel; 13. distal minimum depth of the lateral condyle; 14. distal maximum depth of the
 2389 medial condyle.

2390

2391 **Text-fig.10.**

2392 Logarithmic ratio diagram comparing equid metatarsals from Bashibos (**BB**) and Vozarsti
 2393 (**VOZ**). Measurements and standard as for Text-fig. 9.

2394

2395 **Text-fig. 11.** Proportions of the upper carnassial tooth in *Adcrocuta eximia* from early to
 2396 middle Turolian localities (original measurements in MNHNP, NMNHS, PMA and MMNH-
 2397 Sk). Early Turolian localities: RZO: Ravin des Zouaves; HD: Hadjidimovo; MAR: Maragha;
 2398 middle Turolian localities: SLQ: Salonique (= Vathylakkos- 3, after G. Koufos, pers. comm.);
 2399 K: Kalimantsi; PIK: Pikermi; KAR: Karaslari.

2400

2401 **Text-fig.12.** Proportions of the lower carnassial tooth in *Adcrocuta eximia* from late Vallesian
 2402 to middle Turolian localities. PRST: Prsten - *Adcrocuta* sp.; RPL: Ravin de la Pluie,
 2403 Vallesian; KD: Kavak Dere, early Turolian; KAL: Kalimantsi, middle Turolian;, the other
 2404 explanations as for Text-fig. 11.

2405

2406 **Text-fig. 13.** Lengths of *Adcrocuta eximia* m1s from early Turolian localities of the Balkan-
 2407 Iranian paleo-zoogeographic province (MAR: Maragha [Maragheh], Bashibos, Kavak Dere,
 2408 RZO: Ravin des Zouaves, HD: Hadjidimovo; VOZ: Vozartsi) and middle Turolian localities
 2409 (SLQ: Salonique [= Vathylakkos- 3, see Text-Fig. 11]; AK: Akkaşdağı; KAL: Kalimantsi;
 2410 PIK: Pikermi). The difference in the mean values of the early Turolian (27.5 mm) and middle
 2411 Turolian (29.3 mm) samples is highly significant ($t = 4.1836$, $df = 10.2$, $p = 0.001798$).

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Text-fig. 14. Lengths of *Adcrocuta eximia* P4s from early Turolian localities of the Balkan-Iranian province (Bashibos, HD; MAR, for the abbreviations see Text-fig= 13) and middle Turolian localities (AZM: Azmaka; SLQ; KAL; PIK [for the other abbreviations see Text-fig. 13]. The difference in the mean values of the early Turolian (37.4 mm) and middle Turolian (39.0 mm) samples is significant ($t = 2.541$, $df = 26.38$, $p = 0.01726$).

Text-fig. 15. Plot of P2-M1 length vs. p2 length in different *Adcrocuta eximia*, *Adcrocuta* sp. from Prsten (PRST) and *Lycyaena chaeretis* from Kalimantsi (unpubl.). (Abbreviations as in Text-fig. 13-14).

Text-fig. 16. Logarithmic ratio diagram comparing size of lower cheek-teeth of different *Adcrocuta* from the late Miocene Balkan-Iranian zoogeographic paleo-province. (PRS2: *Adcrocuta eximia* from Prsten; PRST: *Adcrocuta* sp. from Prsten; the other explanations as for Text-fig. 13-15).

Text-fig. 17. Tentative chronostratigraphic position of some main fossiliferous late Miocene localities from R. of Macedonia and neighbouring Balkan territories (the chronostratigraphic position of the Greek, Bulgarian and Turkish localities is in concordance with data from: (SPASSOV 2002; GERAADS et al. 2005, 2011; KOSTOPOULOS 2009; SPASSOV et al. 2012; HRISTOVA et al. 2013; KOUFOS, & VASILEIADOU 2015; KOUFOS et al. 2016) (for abbreviations see the relevant paragraph in the main text).

2435 **Table captions**

2436

2437 **Table 1.** Measurements of *Hippotherium brachypus* skulls, in mm (after EISENMANN et al.
2438 1988).

2439 **1.**, muzzle length, prostion-middle of the line connecting the anterior borders of P2; **2.** palatal
2440 length, middle of the line connecting the anterior borders of P2 to anterior border of choane;
2441 **3.** vomerine length; **4.** post-vomerine length; **5.** Post-palatal length: basion – anterior border of
2442 choanae; **6.** basilar length: basion-prostion; **7.** premolar length; **8.** molar length; **9.** upper
2443 cheek teeth length; **14.** minimal muzzle breadth; **15.** muzzle breadth at I1-I1; **24.** Posterior
2444 ocular line: last point – middle of the supra occipital crest; **25.** Facial height: height of the
2445 skull in front of P2; **30.** length of the naso-incisival notch; **31.** cheek length, posterior end of
2446 the narial opening-anterior border of the orbit; **32,** distance orbit-preorbital fossa (POF); **33.**
2447 length of PF; **35.** height of POF (perpendicular to 33); **36.** distance ventral border of POF-
2448 crista facialis; **37.** distance infraorbital foramen-alveoles of the tooth series; **38.** distance
2449 posterior end of PF-alveoli of the cheek teeth; **O-P2.** distance from the anteriormost point of
2450 the orbit to the anterior end of P2.

2451

2452 **Table 2.** Mandibular and lower teeth measurements of *Adcrocuta eximia*, in mm.

2453

2454 **Table 3.** Comparative measurements of upper teeth of late Miocene *Mesopithecus*, in mm.

2455 Localities arranged (with the exception of the ones from R. of Macedonia) by decreasing age.

2456 Azmaka 6: SPASSOV et al. (2012); Hadjidimovo-1: KOUFOS et al. (2003) and personal data;

2457 Vathylakkos: KOUFOS et al (2004); Kalimantsi: KOUFOS et al. (2003); Pikerimi: ZAPFE (1991);

2458 Dytiko: BONIS et al (1990).

2459

2460 **Table 4.** Comparative mandible measurements of the Karaslari *Mesopithecus* with other
2461 samples, arranged by decreasing age from top to bottom, in mm. Personal measurements in
2462 MNHNP, NMNHS & PMA, except Ravin des Zouaves 5 (BONIS et al. 1990) and Perivolaki
2463 (KOUFOS 2006).

2464

2465 **Table 5.** Comparative lower teeth measurements of late Miocene male *Mesopithecus*.
2466 Localities outside the Rep. of Macedonia are listed by decreasing age from top to bottom.
2467 Ravin des Zouaves 5: BONIS et al. (1990); Hadjidimovo: unpubl. data; Kalimantsi: KOUFOS et
2468 al. (2003) and unpubl. data; Kromidovo: KOUFOS et al. (2003); Perivolaki: KOUFOS (2006);
2469 Vathylakkos: Coll. ARAMBOURG, MNHNP, pers. data; Pikermi: BONIS et al. (1990), and
2470 ZAPFE, (1991); Dytiko 1 & 3: BONIS et al. (1990). H = labial depth below m2.

2471

2472 **Table 6.** Measurements of *Microstonyx major* teeth, in mm.

2473

2474 **Table 7.** Measurements of *Microstonyx major* teeth, in mm.

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2476 **Table 8.** Measurements of *Helladotherium* upper teeth, in mm.

2477

2478 **Table 9.** Measurements of bovid frontlets and horn-cores, in mm.

2479

2480 **Table 10.** Measurements of *Tragoportax* skulls, in mm.

2481

2482 **Table 11.** Measurements of *Cremohipparion mediterraneum* *C. proboscideum* and *Hipparion*
2483 sp. skulls, in mm (after EISENMANN et al. 1988).

2484

2485 **Table 12.** Measurements of *Hipparion dietrichi* skulls, in mm(after EISENMANN et al. 1988).

2486

2487 **Table 13.** Cranial features and measurements of Rhinocerotidae skulls and tooth-rows (at

2488 occlusal level), in mm. **1** to **7**: *Dihoplus pikermiensis*; **8**: *Ceratotherium neumayri*; **9**:

2489 *Acerorhinus* sp. **1**: Karaslari, on exhibit; **2**: Bashibos, on exhibit; **3**: Kiro Kuchuk 16.9.1997;

2490 **4**: Kiro Kuchuk 221; **5**: Kiro Kuchuk 222; **6**: Kiro Kuchuk 223; **7**: Prsten 28.8.1997; **8**: Umin

2491 Dol, on exhibit **9**: Karaslari 30/73.

2492

2493 **Table. 14.** Cranial and upper teeth measurements of *Adcrocuta eximia*, in mm.

2494

2495 **Table 15.** Comparative mandibular dimensions of *Yoshi* species with *Promegantereon ogygia*

2496 (SALESA et al. 2010; * personal measurements (N.S.) in Museo Nacional de Ciencias

2497 Naturales, Madrid; *Yoshi garevskii*, and *Y. cf. minor* after SPASSOV & GERAADS 2014;

2498 *Y. minor* after ANDERSON 1998; *Paramachaerodus orientalis* : original measurements of the

2499 cast of the type specimen of *Machairodus schlosseri* WEITHOFER from Pikermi.

2500

2501 **Table 16.** Cranial measurements (after TASSY, 1996) of “*Mammuth obliquelophus*” from Kiro

2502 Kuchuk, MMNH 2773.

2503

2504 **Table 17.** Dental measurements of “*Mammuth obliquelophus*” from Kiro Kuchuk, MMNH 2773,

2505 in mm.

2506

2507 **Table 18:** Measurements of *Ancylotherium pentelicum* upper teeth, in mm.

2508

2509 **Table 19.** Comparative mandibular dimensions of *Plioviverrops*, in mm. KK: Kiro Kuchuk

2510 (mandible No.2803); KAL: Kalimantsi, Burdovski pat (PMA, personal data); PER: Perivolaki

2511 (KOUFOS 2006); PIK: Pikermi (MNHNP; first measurement: PIK-3022, type: after BONIS &
 2512 KOUFOS 1991; second measurement: PIK-3016, personal data); Axios: Vathylakkos and
 2513 Ravin des Zouaves (KOUFOS 2000); LM: Los Mansuetos (CRUSAFONT PAIRÓ and PETTER
 2514 1969); BRIS: Brisighella (TORRE 1989).

2515

2516 **Table 20.** Comparative dimensions of the *Paramachaerodus* from Kiro Kuchuk with
 2517 *P. orientalis* from Maragha (MAR), Pikermi (PIK), Concud & Puente Minero (CON & PM)
 2518 and *P. maximiliani* from China. Data from PILGRIM (1931), KITTL (1887), SALESA et al.
 2519 (2010), and ZDANSKY (1924), respectively.

2520

2521 **Table 21.** Skull and upper canine measurements of *Machairodus* s. l. from various localities
 2522 (in mm). ML: maximal length of skull; BL: basal length of skull. Skull width is measured
 2523 over zygomatic processes.

2524 **Table 22.** Measurements of Chalicotheriinae gen. et sp. indet. MMNH-Sk VSH 2702, in mm
 2525 (measurements taken as in Geraads et al., 2001).

2526

2527 **Table 23.** Measurements of the Equid metacarpals from Vozarci, in mm (after EISENMANN et
 2528 al. 1988).

2529 1. maximal length; 3. minimum width of shaft; 4. depth of shaft; 5. proximal articular breadth;
 2530 6. proximal articular depth; 7. Maximal diameter of the articular facet for third carpal
 2531 (magnum); 8. diameter of the anterior facet for the fourth carpal (unciforme); 10. distal
 2532 maximum supra-articular breadth; 11. distal maximum articular breadth; 12. distal maximum
 2533 depth of the keel; 13. distal minimum depth of the lateral condyle; 14. distal maximum depth
 2534 of the medial condyle.

2535 **Table 24.** Measurements of the Equid metatarsals from Vozarci and Bashibos, in mm(after
 2536 EISENMANN et al. 1988). 1. maximal length; 3. minimum width of shaft; 4. depth of shaft; 5.
 2537 proximal articular breadth; 6. proximal articular depth; 7. Maximal diameter of the articular
 2538 facet for the third tarsal (cuneiforme 3); 8. diameter of the anterior facet for the fourth tarsal
 2539 (cuboid); 10. distal maximum supra-articular breadth; 11. distal maximum articular breadth;
 2540 12. distal maximum depth of the keel; 13. distal minimum depth of the lateral condyle; 14.
 2541 distal maximum depth of the medial condyle.

2542

2543 **Table 25.** Distribution of the Neogene mammal taxa of Republic of Macedonia studied by
 2544 localities.

2545

2546 **FIGURE CAPTIONS**

2547 **Plate 1.**

2548 1. *Hippotherium brachypus*, Kiro Kuchuk, Republic of Macedonia. Skull, KK 2003; a. lateral
 2549 view, b. left upper cheek teeth.

2550 2. *Hippotherium brachypus*, Karaslari, Republic of Macedonia. Skull, KAR 20/75; a. lateral
 2551 view, b. left upper cheek teeth.

2552 3. *Hippotherium brachypus*, Karaslari, Republic of Macedonia. Skull, KAR 26/73; a. lateral
 2553 view, b. left upper cheek teeth.

2554 4. *Hippotherium brachypus*, Belushka, Republic of Macedonia. Skull, B 2708; a. lateral view,
 2555 b. left upper cheek teeth.

2556 5. *Hippotherium brachypus*, Umin Dol, Republic of Macedonia. Skull, no number; a. lateral
 2557 view, b. left upper cheek teeth.

2558 Scale bar: for the skulls = 50 mm; for the cheek teeth = 30 mm.

2559

2560 **Plate 2.**

2561 Fig. 1. *Mesopithecus pentelicus*, Karaslari, Republic of Macedonia. Unnumbered skull; a. right
 2562 lateral view, b. frontal view, c. dorsal view; d. left toothrow: P4-M3 of the same skull.

2563 Fig. 2. *Mesopithecus*, Karaslari (or Prevalets?), Republic of Macedonia. Skull MMNH 68; a.
 2564 left lateral view, b. frontal view, c. dorsal view; d. Upper tooth row (P3-M1); e. P3 of the
 2565 same skull in mesial view.

2566 Fig. 3. *Mesopithecus*, Veshie, Republic of Macedonia. Mandible MMNH 2671 in occlusal
 2567 view.

2568 scale bar = 5 cm for the skulls, 3 cm for the tooth rows, Fig. 2e – out of scale.

2569

2570 **Plate 3.**

2571 1. *Microstonyx erymanthius*, Bashibos, Republic of Macedonia. Skull BB-1541; ventral view.

2572 2. *Microstonyx erymanthius*, Karaslari, Republic of Macedonia. Skull Kar-3473; a. lateral
 2573 view; b. occlusal view of P4–M3.

2574 3. *Microstonyx erymanthius*, Prsten, Republic of Macedonia. P1–M1 Prsten-C; occlusal view.

2575 4. *Microstonyx erymanthius*, Prsten, Republic of Macedonia. P2–M2 Prsten-115, occlusal
 2576 view.

2577 5. *Microstonyx erymanthius*, Karaslari, Republic of Macedonia. Skull Kar-1542; a. ventral
 2578 view of snout; b. detail of front teeth, ventral view.

2579 6. *Microstonyx erymanthius*, Bashios, Republic of Macedonia. Mandible BB-1541 (same
 2580 individual as fig.1), p4–m3, occlusal view.

2581 Scale bar = 5 cm for figs. 2b, 3, 4, 6; 7.5 cm for fig. 5b; 15 cm for figs. 1, 5a; 30 cm for fig.

2582 2a.

2583

2584 **Plate 4.**

- 2585 1. *Sporadotragus* sp., Umin Dol, Republic of Macedonia. skull UD-1590; a. lateral view; b.
2586 front view.
- 2587 2. *Protragelaphus* sp., Bashibos, Republic of Macedonia. Skull BB-1645; front view.
- 2588 3. *Prostrepsiceros rotundicornis*, Vozartsi, Republic of Macedonia. Frontlet Voz-694; front
2589 view.
- 2590 4. *Protragelaphus* sp., Bashibos, Republic of Macedonia. Frontlet BB-1645; a. right lateral
2591 view; b. front view.
- 2592 5. Cf. *Prostrepsiceros* sp., Bashibos, Republic of Macedonia. BB-2611; a. right lateral view;
2593 b. front view.
- 2594 6. *Palaeoreas lindermayeri*, Karaslari, Republic of Macedonia. Frontlet Kar-2610; a. right
2595 lateral view; b. front view.
- 2596 7. *Samotragus* sp., Bashibos, Republic of Macedonia. Left horn-core BB-2623; a, left lateral
2597 view; b, front view.
- 2598 8. *Gazella cf. capricornis*, Vozartsi, Republic of Macedonia. Frontlet Voz-558; a. front view;
2599 b. left lateral view.
- 2600 9. *Mesembriacerus* sp., Bashibos, Republic of Macedonia. Braincase with bases of horn-cores
2601 BB-2607; a. ventral view; b. dorsal view; c. postero-lateral view; d. posterior view.
- 2602 Scale bar = 20 cm for figs. 1–6, 10 cm for figs. 7–9.

2603

2604 **Plate 5.**

- 2605 1. *Cremohipparion mediterraneum*, Karaslari, Republic of Macedonia. Skull, KAR 23/73; a.
2606 lateral view, b. left upper cheek teeth.
- 2607 2. *Cremohipparion mediterraneum*, Karaslari, Republic of Macedonia. Skull, KAR 28/73; a.
2608 lateral view, b. left upper cheek teeth.

- 2609 3. *Cremohipparion proboscideum*, Vozartsi, Republic of Macedonia. Skull, VOZ 74/66; a.
2610 lateral view, b. right upper cheek teeth.
2611 4. *Hipparion* sp., Umin Dol, Republic of Macedonia. Skull, UD 90/66; a. lateral view, b. right
2612 upper cheek teeth.
2613 5. *Hipparion dietrichi*, Karaslari, Republic of Macedonia. Skull, KAR 92/73; a. lateral view,
2614 b. left upper cheek teeth.
2615 6. *Hipparion dietrichi*, Karaslari, Republic of Macedonia. Skull, KAR 203/73; a. lateral view,
2616 b. upper cheek teeth.
2617 Scale bar: for the skulls = 50 mm; for the cheek teeth = 30 mm.

2618

2619 **Plate 6.**

- 2620 1. Chalicotheriinae gen. et sp. indet., Veshie, Republic of Macedonia. P2–M3 Veshie 2702;
2621 occlusal view.
2622 2. *Anisodon* sp., Karaslari, Republic of Macedonia. Mandible; a, detail of symphyseal area; b,
2623 p3–m2, occlusal view.
2624 3. *Ancylotherium pentelicum*, Karaslari, Republic of Macedonia. Tooth-row p2–m3; occlusal
2625 view.
2626 4. *Ancylotherium pentelicum*, Karaslari, Republic of Macedonia. Skull; a, lateral view; b,
2627 dorsal view.
2628 5. *Ancylotherium pentelicum*, Republic of Macedonia. Partial hind-limb, front view.
2629 6. *Ancylotherium pentelicum*, Kiro Kuchuk, Republic of Macedonia. Upper left P3, DP4, M1
2630 KK2805, occlusal view.
2631 Scale bar = 5 cm for figs. 1, 2b, 6; 10 cm for fig. 3; 20 cm for fig. 4; 40 cm for fig. 5.

2632

2633 **Plate 7.**

2634 Fig. 1. *Adcrocuta eximia*, Bashibos, Republic of Macedonia. Left mandible MMNH-Sk 785
 2635 (old No. 67); a. labial view, b. occlusal view.

2636 Fig. 2. *Adcrocuta eximia*, Vozartsi, Republic of Macedonia. Right mandible MMNH-Sk Voz
 2637 66; a. from in lingual view, b. occlusal view.

2638 Fig. 3. *Adcrocuta eximia*, Karaslari, Republic of Macedonia. Right half of the mandible
 2639 MMNH-Sk 68; occlusal view.

2640 Fig. 4 . *Adcrocuta eximia*, Prsten, Republic of Macedonia. Left half the mandible MMNH-Sk
 2641 Pr2; occlusal view.

2642 Fig. 5 *Adcrocuta* sp., Prsten, Republic of Macedonia. Right half-mandible Pr1; a labial view,
 2643 b. occlusal view.

2644 Fig. 6. *Eomellivora* cf. *wimani*, Karaslari, Republic of Macedonia. Cranium; a. dorso-lateral
 2645 view, b. dorsal view; c: ventral view of the maxilla, showing the outline of M1.

2646 Scale bar = 30 mm for Fig.6C, = 50 mm for all others.

2647

2648 **Plate 8.**

2649 Fig.1. *Adcrocuta eximia*, Kiro Kuchuk, Republic of Macedonia. Cranium MMNH-Sk KK
 2650 2771; a. right lateral view; b. P2-P4 of the same skull in occlusal view.

2651 Fig. 2. *Adcrocuta eximia*, Kiro Kuchuk, Republic of Macedonia. Cranial fragment MMNH-
 2652 Sk KK2806; right lateral view, b.ventral view.

2653 Fig. 3. *Adcrocuta eximia*, Karaslari, Republic of Macedonia. Cranium MMNH-Sk KAR 2602;
 2654 right lateral view.

2655 Fig. 4. *Adcrocuta eximia*, Kiro Kuchuk, Republic of Macedonia. Teeth (p4-m1) of the
 2656 mandible MMNH-Sk KK 2775 (from 15.9.2000); a. lingual view, b. occlusal view.

2657 Fig. 5. *Adcrocuta eximia*, Kiro Kuchuk, Republic of Macedonia. Mandible MMNH-Sk KK
 2658 2799 (from 19.04.2000); a. right lateral view, b. occlusal view.

2659 Scale bar= 50 mm: the two complete skulls; 30 mm: the rest.

2660

2661 **Plate 9.**

2662 Fig. 1. *Yoshi* aff. *garevskii*, Bachibos, Republic of Macedonia. Unnumbered mandible
2663 fragment; a. lingual view, b. occlusal view. Scale = 20 mm

2664 Fig. 2. *Machairodus* sp., Karaslari, Republic of Macedonia. Unnumbered, right semi-
2665 mandible; a. lingual view, b. occlusal view. Scale = 50 mm

2666 Fig. 3. *Paramachaerodus* sp., Kiro Kuchuk, Republic of Macedonia. Female (?) cranium of
2667 MMNH-Sk KK-2807; a. ventral view, b. right P3-P4 from the same cranium, c. left upper
2668 canine from the same skull. Scale = 50 mm, - the cranium; 30 mm - the teeth

2669 Fig. 4. *Paramachaerodus* sp., Kiro Kuchuk, Republic of Macedonia. Cranial rostrum with the
2670 left canine of MMNH-Sk KK 2813, male (?); restored with plaster, out of scale (for size see
2671 table 20).

2672 Fig. 5. *Machairodus (Amphimachairodus) giganteus*, Prevalets Republic of Macedonia.
2673 Cranium. Scale bar = 80 mm.

2674 Fig. 6. *Machairodus* sp., Prsten, Republic of Macedonia. A cast of the upper carnassial tooth
2675 (Prst-125); a. occlusal view, b. labial view. Scale bar = 30 mm

2676

2677 **Plate 10.**

2678 Fig. 1. “*Mammut*” *obliquelophus*, Kiro Kucuk, Republic of Macedonia. Partially preserved
2679 juvenile skull MMNH 2773; a. dorsal view, b. lateral view, c. ventral view. Scale bar: 10 cm;

2680 Fig. 2. “*Mammut*” *obliquelophus*, Kiro Kucuk, Republic of Macedonia. MMNH 2743; right
2681 M3. Scale bar: 10 cm;

2682 Fig. 3. *Choerolophodon pentelici*, Kiro Kucuk, Republic of Macedonia. MMNH 2811, right
2683 D3. Scale bar: 5 cm;

2684 Fig. 4. *Choerolophodon pentelici*, Dolni Disan, Republic of Macedonia. MMNH 2742, right
2685 m3. Scale bar: 10 cm;

2686 Fig. 5. *Anancus* sp., Dolni Disan, Republic of Macedonia. MMNH 2741, posterior fragment
2687 of a left M3. Scale bar: 10 cm;

2688 Fig. 6. *Tetralophodon atticus*, Dolni Disan, Republic of Macedonia. Skull; a. lateral view, b.
2689 close view of the erupting right M3 in the skull. Scale bar: 10 cm

2690

2691 **Plate 11.**

2692 1. *Dihoplus pikermiensis*, Kiro Kuchuk, Republic of Macedonia. Skull KK-222; a. lateral
2693 view, b. occlusal view of right P2–M3.

2694 2. *Dihoplus pikermiensis*, Kiro Kuchuk, Republic of Macedonia. Skull KK-221; lateral view.

2695 3. *Dihoplus pikermiensis*, Kiro Kuchuk, Republic of Macedonia. Skull KK-16-9-1997; ventral
2696 view.

2697 4. *Dihoplus pikermiensis*, Republic of Macedonia. Unnumbered skull and mandible on
2698 exhibit; lateral view.

2699 5. *Acerorhinus* sp., Karaslari, Republic of Macedonia. Skull and mandible on exhibit MMNH-
2700 Sk KAR 30/73; a. lateral view, b. dorsal view.

2701 Scale bar = 30 cm.

2702

2703 **Plate 12.**

2704 Fig. 1 *Hyaenotheriini* indet., Kiro Kuchuk, Republic of Macedonia, associated right mandible
2705 and maxilla fragments. Mandible MMNH-Sk KK 2768 a. labial view, b. occlusal view; c.
2706 Maxilla MMNH-Sk KK 2769 in occlusal view. Scale bar = 30 mm.

2707 Fig. 2. *Plioviverrops* cf. *orbigny*, Kiro Kuchuk, Republic of Macedonia. Left half-mandible
2708 (NMNH-Sk KK280); a. lingual view, b. labial view. Scale bar = 30 mm.

2709 Fig. 3. *Ictitherium* cf. *viverrinum*, Veshie, Republic of Macedonia. Cranium (MMNH-Sk
2710 VSH 2747); a. ventral view, b. dorsal view, c. right cheek-teeth (P3-M2) of the same
2711 specimen. Scale bar = 50 mm- the skull; 30 mm- the teeth.

2712 Fig. 4. *Adcrocuta eximia*, Republic of Macedonia. Upper premolars in lingual view: P3 (b)
2713 from an unnumbered maxillary fragment and P3-P4 (c) from another one (Bashibos) in
2714 comparison with the same teeth (a) from Kiro Kuchuk (cranium MMNH-Sk KK2806), not at
2715 scale.

2716

2717 **Plate 13.**

2718 Fig. 1. *Tragoportax* sp. nov., Vozartsi, Republic of Macedonia. Unnumbered frontlet in
2719 different (a & b) dorso-lateral views;

2720 Fig. 2. *Tragoportax* sp. nov., Vozartsi, Republic of Macedonia. Cranium MMNH-Sk Voz-
2721 1592/68; a. in dorsal view, b. lateral view. Out of scale.

2722 Fig. 3. *Tragoportax* sp. nov.? Vozartsi, Republic of Macedonia. Cranium MMNH-Sk Voz-
2723 1596/68. Scale 130 mm.

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