The late Miocene mammal faunas of the Republic of Macedonia (FYROM)

Nikolaï Spassov, Denis Geraads, Latinka Hristova, Georgi N Markov, Biljana Garevska, Risto Garevski

SPASSOV, N., GERAADS, D., HRISTOVA, L., MARKOV, G., GAREVSKA, B, & GAREVSKI, R. 2018.
The late Miocene mammal faunas of the Republic of Macedonia (FYROM).
Palaeontographica A, 311: 1-85.

Authors' addresses
N. SPASSOV
National Museum of Natural History at the Bulgarian Academy of Sciences
1, Blvd. Tzar Osvoboditel, 1000 Sofia, Bulgaria
e-mail: nspassov@nmnhs.com

D. GERAADS
Sorbonne Universités, CR2P-MNHN, CNRS, UPMC-Paris6, CP 38, 8 rue Buffon, 75231 Paris Cedex 05, France
and
Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103 Leipzig, Germany
e-mail: geraads@mnhn.fr

L. HRISTOVA
National Museum of Natural History at the Bulgarian Academy of Sciences
1, Blvd. Tzar Osvoboditel, 1000 Sofia, Bulgaria
latihristova@abv.bg

G. MARKOV
National Museum of Natural History at the Bulgarian Academy of Sciences

1, Blvd. Tzar Osvoboditel, 1000 Sofia, Bulgaria
markov@nmnhs.com

B. GAREVSKA
Macedonian Museum of Natural History, Blvd. Ilinden 86, 1000 Skopje, R. of Macedonia
bgarevska@yahoo.com

R. GAREVSKI †
Macedonian Museum of Natural History, Blvd. Ilinden 86, 1000 Skopje, R. of Macedonia

ABSTRACT This study represents the first extensive systematic investigation of the Miocene mammalian faunas of the Republic of Macedonia (FYROM), stored in the Macedonian Museum of Natural History, Skopje. They range in age from perhaps the early Miocene to the early Ruscinian, but the bulk of the fossils represent middle Turolian mammals. At least 57 taxa have been identified, from 25 different paleontological sites, mostly from the Vardar and Strumitsa river basins, but also from the Morievo and Delchevo regions. The richest localities are the middle Turolian localities of Karaslari (with 22 species) and Kiro Kuchuk (17 species). The rich fossil material greatly improves our knowledge of the Turolian Hipparion faunas of the Balkan-Iranian zoogeographic paleo-province, whose westernmost part was mostly documented in Greece and Bulgaria. The fauna displays the typical faunal features of the Balkan Pikermian biome, with dominance of hipparions (especially *H. brachypus*, but our revision does not confirm the presence of *Hipparion verae* in the Turolian faunas) and bovids such as *Gazella, Tragoportax,* and spiral-horned antelopes. Other forms usually found in the area, such as *Microstonyx erymanthius, Dihoplus pikermiensis,* chalicotheres, *Choerolophodon pentelici, Mesopithecus pentelicus,* or *Adcrocuta eximia* are also common. Several new forms have been identified among the carnivores, the giraffids and the bovids. The Macedonian material contributes to reconstructing the history of several taxa such as *Simocyon, Metailurus,* several hipparion species, *Propotamochoerus, Bohlinia, Sivatherium*. The most noticeable features of these Turolian faunas are: the abundance of spiral-horned antelopes, and rarity of antelopes of the *Protoryx-Pachytragus* group, as in Bulgaria; the co-existence of chalicotheriins and schizotheriins; the frequency of *Dihoplus* compared to *Ceratotherium*; the presence of *Chilotherium*, which reaches its westernmost longitude; and the presence of *Anancus* sp. in some localities, considered here as post-Pikermian.

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

I. INTRODUCTION

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

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

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

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

Abbreviations

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

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

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

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

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

II. THE LATE MIOCENE LOCALITIES AND THEIR FAUNAS

II.1 KUMANOVO AREA

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

II.2. SKOPJE REGION

II.2.1. Nerezi

Proboscidea. This locality has yielded two elephantoid taxa. A right M3, misidentified as m3 and referred by LASKAREV (1936, pl. 3, Fig. 4) to “*Mastodon angustidens* f. *subtapiroidea*” actually belongs to *Zygolophodon turicensis* (as well as probably the unfigured “m3 sin” from the same locality and possibly from the same individual described by LASKAREV, 1936, p. 112: see GAREVSKI et al. 2012). A mandible referred by LASKAREV (1936, pl. 1 and 2) to “*Mastodon angustidens* f. *typica* var. *skopljensis*” cannot be unequivocally determined on morphological grounds. It could indeed belong to *G. angustidens* but also to the amebelodontid *Archaeobelodon filholi* – while these two taxa are readily set apart by a number of cranio-mandibular characters, their dental morphology (especially the m3s which are preserved with the Nerezi specimen) can be very similar (TASSY 1985). The symphysis of the mandible is unfortunately not preserved, and LASKAREV’s description does not mention the shape of the alveoli. Measurements of the third molars provided by LASKAREV (1936) fit with the size observed in male *G. angustidens* (see TASSY 1996, figs. 11.12 and 11.14) – the same size, however, would correspond to female individuals of *A. filholi* (see TASSY 1985). As far as mandibular measurements are concerned, the maximum height of the mandible (dental age XXII of TASSY 1996) plots closer to the *A. filholi* values for XXI (TASSY 1985, fig. 171) but does not surpass the *G. angustidens* values in such a way as to preclude affinities with the latter, and plots very close to the value for *G. angustidens* from Villefranche d'Astarac (see TASSY 1985, fig. 178; TASSY 2013, fig. 40). Results from the other measurements provided by LASKAREV (1936) (and comparable to those in TASSY 1985) are also equivocal. Thus, the identification of the Nerezi mandible remains uncertain, but in any case the two elephantoids at the locality point at a pre-Turolian age – quite rare for Republic of Macedonia, where most fossil vertebrates localities are Turolian or later. Among the exceptions are two other closely situated localities: Dolno Sonje (Donje Solnje in LASKAREV 1936) has yielded a molar fragment, referred by LASKAREV (1936, pl. 4, fig. 1) to "*Mastodon* aff. *angustidens* f. *subtapiroidea*"; while precise identification is impossible, the figured fragment apparently belongs to a pre-Turolian elephantoid, judging from its primitive morphology. Similarly, fragmentary remains from Skopje, Zhelezara neighbourhood (GAREVSKI 1985) cannot be determined with precision but indicate a pre-Turolian age: the figured tusk fragment has a well pronounced lateral enamel band, a character absent in all Turolian elephantoids.

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

II.3. DELCHEVO FOSSILIFEROUS AREA

II.3.1. Stamer

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

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

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

Perissodactyla. Equidae. *Hipparion* indet. (sp. 1): Three molars (M1–M3) discovered 2–3 meters above the *Sivatherium* remains are from a medium to large sized hipparion. They are moderately plicated, the pli caballin is single on M3 and absent on the other molars. The hypoconal sinus is of medium depth, the lingual one is well developed on M3. The protocone is lingually rounded and labially flattened, subtriangular in outline. These teeth are larger than in the small *H. macedonicum*, *H. matthewi*, *H. periafricanum*, but the molar length (65.4 mm) is within the range of variation of all medium to large late Miocene hipparions of the Balkans, *Hippotherium brachypus*, *H. dietrichi*, *Cremohipparion proboscideum* and *C. mediterraneum*. They differ from the Pliocene *H. crassum* in their less plicated enamel and less open hypoconal sinus.

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

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

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

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

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

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

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

II.4. VELES FOSSILIFEROUS AREA

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

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

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

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

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

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

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

Perissodactyla. Equidae. *Hippotherium brachypus*. The description by ĆIRIĆ (1957) of materials from this locality is insufficient for an identification. We found only one cranium, MMNH-Sk B 2708 (Plate 1, Fig. 4; Table 1 [all equid measurements follow EISENMANN et al. 1988]). It is of a sub-adult individual, with M3 erupting. The orbit is above M3. The preorbital bar is long (42 mm) and the lacrimal bone occupies more than half of its width. The preorbital fossa is moderately deep, egg-shaped, anteroposteriorly oriented and well delineated all around, with a weak pocket (about 5 mm). Judging by the premolar length (P2–P4 = 86 mm), the tooth row appears to be long. The enamel plication on M1 is moderate (19 folds). The pli caballin is single. The protocone is oval. The single, relatively deep preorbital fossa located far from the orbit is similar to that of *Hippotherium*. As the preorbital fossa in *Hippotherium primigenium* is deeper and better outlined, and the tooth plication richer, we can exclude it from the comparison. The other species with close features are *Hippotherium giganteum* and *Hippotherium brachypus*. The species *Hippotherium giganteum* was erected by GROMOVA (1952) for the large sized specimens from Grebeniki on the basis of only one adult specimen. GABUNIA (1959) extended the diagnosis of the species with several adult skulls from the same locality. After the more precise description of *Hippotherium brachypus* from Pikermi by KOUFOS (1987b) and the discovery of new samples of this species (HD, KAL, AKK, KHC 2) (HRISTOVA et al. 2003, HRISTOVA & KOVACHEV, 2005, KOUFOS & VLACHOU 2005, HRISTOVA et al. 2013,) it is now obvious that the two species are quite similar and characterized by: large size, elongated skull, long and wide muzzle, simple and oval preorbital fossa, elongate preorbital bar, rich enamel plication in the upper cheek teeth, and elliptical protocone. A possible difference between them could be a slightly shorter nasal notch in the sample from Grebeniki, but the ranges of variation of this feature also overlap. Pending a revision of the Grebeniki hipparions we can accept *Hippotherium giganteum* as a synonym of *Hippotherium brachypus* (HENSEL, 1862), and MMNH-Sk B2708 falls within its range of variation, as also shown by the Simpson diagrams (Text-fig 2).

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

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

II.4.2. Chashka (Čaška or Caska)

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

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

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

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

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

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

Biochronology: Middle Turolian ?

II.4.4. Karaslari (41°41’21” N, 21°49’31” E; elev. 168 m)

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

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

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

RADOVIĆ et al. (2013) published the *Mesopithecus* material collected by ĆIRIĆ and LASKAREV from three localities in the vicinity of Veles and stored in the NHMB. Following KOUFOS (2009a, b) they identified *M. pentelicus*, *M.* cf. *pentelicus*, *M. delsoni*, and *M.* cf. *delsoni*. The M3 size of NHMB-EO-0332656, identified as *M.* cf. *pentelicus*, is similar to that of a female *M. pentelicus* from the middle Turolian of Kalimantsi, thus confirming the presence of this species. By contrast, RADOVIĆ et al. (2013) identified the mandibles NHMB-EO-0332657 and NHMB-EO-0332658 as *Mesopithecus delsoni*. The presence of two different *Mesopithecus* species in the same locality is unlikely, especially if they are chronospecies. In fact, on the basis of the mandible dimensions and symphysis shape (judging from the published photos), we are not convinced of the presence of *M. delsoni* in this locality.

The genus *Mesopithecus* has been recorded from the late Miocene and Pliocene of Eurasia, where three species have been distinguished: *M. delsoni*, *M. pentelicus* (early and Middle Turolian) and the smaller *Mesopithecus monspessulanus* (latest Turolian [?] and Pliocene) (Delson 1973, 1974; Bonis et al. 1990; Delson et al. 2005; Alba et al. 2014, and references therein). Its occurrence in the Vallesian (Wissberg) (Delson 1973, 1974) is questionable (Andrews et al. 1996); it may result from stratigraphic mixture. The taxonomic status of the earliest form, *M. delsoni* Bonis et al., 1990, from Ravin des Zouaves n°5 is debated, as the differences between the late Miocene samples are rather subtle. They may be regarded as two species, *M. delsoni* and *M. pentelicus* (Bonis et al. 1990; Koufos et al. 2003), one species, *M. pentelicus* (Andrews et al. 1996; Delson et al. 2000), one species with two subspecies *M. p. delsoni* and *M. p. pentelicus* (Alba et al. 2014) or two species and intermediate stages with possible specific status (Koufos 2006a, 2009a, b). In any case, several differences usually separate the earlier form *M. delsoni* from *M. pentelicus* (best represented at Pikermi): longer tooth-row, little inclined planum alveolare, deeper mandibular corpus (see also Table 4), and larger m3 hypoconulid (Bonis et al. 1990), a list to which Koufos et al. (2003) added a larger protocone on the upper premolars. One of us (N.S. unpublished results) confirms this last difference in the late early Miocene population of Hadjidimovo (Text-fig. 3), and adds the presence of a crista connecting the protocone to the labial cone in upper premolars. It is clear, however, that transitional forms exist in localities that are intermediate in age between RZO/ Hadjidimovo, and Pikermi. Overall, dental size decreases (with some exceptions) from the early Turolian *M. delsoni* to the late Turolian form from Dytiko, this trend being especially clear in m3, while it may be that the relative premolar length slightly increases in relation to the molar length (Table 5). This change could be related to a change in diet towards consumption of less abrasive/more arboreal food with time (Spassov & Geraads 2007; Merceron et al. 2009). In its overall size, and the probable small size of the premolar protocone, the Karaslari *Mesopithecus* is intermediate between the populations from the early/middle Turolian transition and that of Pikermi.

Artiodactyla. Suidae. *Microstonyx erymanthius* . (Plate 3, Fig. 2, 5). The best specimen is the skull NMNH-Sk KAR-1542/73 (Plate 3, Fig. 5). This species is well represented in the Republic of Macedonia by several specimens, including more or less complete skulls; some of them were illustrated by Garevski (1956). Measurements are given in Tables 6 and 7. Their morphology and dimensions leave no doubt as to their belonging to *Microstonyx*, a genus common in the Turolian of Europe, but whose systematics has been much debated. Some authors (Bonis & Bouvrain 1996) recognize an evolution from the early Turolian (with the species or subspecies *erymanthius* to the middle-late Turolian (*Microstonyx major* s. str.), while others reject this distinction; by contrast, van der Made & Moyà-Solà (1989) and van der Made et al. (1992) distinguished the late Vallesian and early Turolian forms as *M. major major*, whereas van der Made (1997) preferred to regard them as two distinct co-existing lineages. Liu et al. (2004) argued that differences in skull morphology could be related to the environment rather than to geological age. In any case, it is certainly true that there is no simple relationship between size (especially that of the third molars) and age. In the localities that have yielded enough material, the range of variation of M3/m3 length covers a large part of the variation of all other sites combined, and Karaslari is no exception. Like most other authors (van der Made et al. 1992; Kostopoulos 1994; van der Made 1997; Kostopoulos et al. 2001; Geraads 2013), we failed to find any significant difference in the morphology of the cheek-teeth of *M. major/erymanthius* from the various localities. Liu et al. (2004) stated that the Akkaşdağı population has "a somewhat complicated M3/m3 occlusal pattern", but the lack of detailed illustrations makes comparisons difficult; they also stated that "the main lingual cusp of P4 [is] placed as far forward as the labial one"; none of the specimens that we have seen, from the R. of Macedonia or elsewhere, has such a mesially shifted protocone.

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

PICKFORD (2015) reviewed these forms, and considered *Microstonyx* as a synonym of *Hippopotamodon* Lydekker, whose type-species is *H. sivalense*. However, the latter species is large, and has a large upper canine and a short snout (PICKFORD 1988), in contrast to *M. erymanthius*, so that the synonymy is not obvious. In addition, PICKFORD (2015) assumed that "*H." major* (type-locality: Cucuron) and "*H." erymanthius* (type-locality: Pikermi) belong to different lineages, the former (his "group A") having shorter snout, bigger canines, P1 and p1 present, and broader cheek-teeth than in group B (in which P1/p1 are often shed) that includes *"H." erymanthius*. He also noted, as a major distinctive feature, that M3 is as long as m3 in *"H." major* from Cucuron, whereas it is shorter in *"H." erymanthius*. We are not convinced that this distinction is valid, because:

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

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

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

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

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

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

Helladotherium sp. A maxilla MMNH-Sk KAR 2752 (Table 8) was described elsewhere (Geraads 2009). A metacarpal is slightly larger than most of those from Pikermi, and matches better those from Bulgaria or Gülpinar, but some specimens from Maragha and Ravin des Zouaves 5 are still larger.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Hipparion dietrichi: cranials: adult - MMNH-Sk KAR 79/73, MMNH-Sk KAR 92/73, MMNH-Sk KAR 93/73, MMNH-Sk KAR 158, MMNH-Sk KAR 203/73; juvenile - MMNH-Sk KAR 95/73, MMNH-Sk KAR 159 (Plate 5, Figs. 5, 6; Text-fig. 7). The preorbital bar is slightly reduced in length (36–41 mm) but the anterior edge of the lacrimal reaches farther anteriorly than its mid-length. The preorbital fossa is moderately deep to shallow, subtriangular, anteroventrally oriented and moderately to weakly delineated. Posteriorly the fossa is not pocketed but with a posterior rim. The nasal slit ends above anterior part of P2 or just before it. Tooth row length is about 142–150 mm. The enamel plication is moderate to rich with 10–24 plis, the pli caballin is single, the protocone is lingually flattened, and labially rounded. The muzzle is short (110–111 mm) and wide (57–65 mm). Measurements are given in Table 12.

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

Recently, Koufos & Vlachou (2016) erected a new *Hipparion* species, *H. philippus*. They unite under this name all samples described until now as *H. dietrichi* from the Balkan Peninsula, leaving only in *H. dietrichi* s.s. the samples from AKK and Samos. Their arguments about this splitting of *H. dietrichi* are the different size of the hipparions from both area: larger and more robust at AKK and Samos, smaller in continental Greece, Bulgaria and Republic of Macedonia. In their description of the new species they state: "...differs from *H. dietrichi* in having a smaller size, shorter muzzle, shorter POB, shorter snout and symphysis, and relatively more elongated and slenderer metapodials." In fact, the size difference between the skulls of *H. dietrichi* from Samos and AKK on the one side and those from Bulgaria and R. of Macedonia on the other side, is not big, just a few millimetres. The skull length at Samos varies from 385 to 411 mm, and from 380 to 420 mm at STR2. The distance anterior rim of the orbit – anterior end of P2 is also very similar: 136 –146,6 mm at Samos *H. dietrichi*, and 145 – 149 mm for STR 2, 146 – 163 mm for the specimens from the R. of Macedonia. The preorbital bar length of STR2 and R. of Macedonia samples are in the range of variation of the AKK sample. The tooth row length varies from 133 to 155 mm at Samos, 152 – 158 mm at AKK, 137 – 150 mm in the R. of Macedonia, and 136 to 155 mm at STR2. The muzzle length varies from 106 to 117 mm at AKK, from 96 to 111 mm in the R. of Macedonia, and from 112 to 115 mm at STR2. Thus, these skull size differences are minute. Body size (reflected in the metapodial proportions) is highly sensitive to climate and to the quality and quantity of food resources, and differences are not necessarily of genetic origin. Its variations across the populations of *H. dietrichi* could be explained by the differences in paleoecological conditions between the Balkan Peninsula and the Samos/Turkey area during the Late Miocene, as well as by slight differences in age between the localities; they do not imply species distinction, and we prefer to keep the name *H. dietrichi* for the populations from Bulgaria and R. of Macedonia.

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

1999; Fortelius et al. 2003; Geraads & Spassov 2009; Athanassiou et al. 2014), although detailed study of the Sinap material could clarify the issue.

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

Chalicotheriidae. *Anisodon* sp. An unnumbered mandible, described in detail and illustrated by Garevski & Zapfe (1983), has also been discussed by Bonis et al. (1995) and Anquetin et al. (2007) (plate 6, fig. 2). Not much can be added to the already published descriptions, but it must be made clear that a p2 was certainly present, albeit small and single-rooted, as Garevski & Zapfe (1983) had correctly noted in their text, although their figure is imperfect. State (0) of character (48) of Anquetin et al. (2007) is therefore incorrect. These latter authors included this mandible in their *Anisodon* group because of its symphysis extending more posteriorly than in *Chalicotherium*, and because of the ventral tubercle on the symphysis, also present in the Dytiko (*Anisodon macedonicus*) mandible. Although we believe that the number of known specimens is too low to provide a satisfactory support to this conclusion (the occurrence of the ventral tubercle is unknown in *C. goldfussi*, and no mandible of *Kalimantsia* has been found yet), we provisionally follow their conclusions.

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

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

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

We follow here the taxonomic concept of VALENCIANO et al. (2015) who recognizes *E. piveteaui* OZANSOY for the Vallesian of Europe and Turkey, *E. ursogulo* ORLOV for the early Turolian of Eastern Europe (Grebeniki), *E. wimani* ZDANSKY for the middle and late Turolian of Europe, Central Asia and N. America and *E. hungarica* KRETZOI for the late Turolian of Central Europe (Polgárdi). The M1, the only tooth that can be compared, is slightly more slender than the known Eurasian specimens (WOLSAN & SEMENOV 1996, fig. 1; VALENCIANO et al. 2015, fig. 4) but matches the dimensions of *E. piveteaui* and *E. wimani*. The size difference between its paracone and metacone seems larger than in *E. piveteaui* and *E. ursogulo*. The M1 of the Karaslari skull differs from that of the latter form in the mesio-distally shorter lingual part of the tooth. It fits better with *E. wimani*, which is acceptable from a chronostratigraphic point of view. We tentatively assign it to the latter species, of which Karaslari would document the only occurrence in the Balkans, and the last record of the genus there.

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

1. Morphometric trends:

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

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

2. Morphological trends:

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

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

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

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

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

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

Felidae. *Yoshi garevskii*. A complete, undistorted skull and mandible, MMNH-Sk KAR 69 (Table 15) is the type of this species, characterized by a round, short, and deep skull with domed frontals, and short canines that are somewhat transversely compressed but are not serrated. SPASSOV & GERAADS (2015) assigned to the same genus the poorly preserved skulls from the Aegean region described as *Metailurus parvulus* (HENSEL, 1862), the Chinese type of "*Metailurus*" *minor* ZDANSKY, as well as some other skulls from China, and a partial skull from the middle Turolian of Kalimantsi (Bulgaria). The latter name thus becomes *Y. minor* (ZDANSKY, 1924), but *M. parvulus* is a nomen dubium. *Metailurus* ZDANSKY, 1924, is represented by the type-species *M. major* ZDANSKY, 1924, and *M. ultimus* (see LI, 2014) and perhaps also by *M. hengduanshanensis*, *M. mongoliensis* and *M. teilhardi* (see also ANDERSON & WERDELIN 2005). The new genus *Yoshi* was distributed from South Europe to Central Asia. Although plesiomorphic in dental features, *Yoshi* (which is assigned to the Pantherini), especially *Y. garevskii*, reaches a high specialization in its skull shape, parallel to that of the cheetah, suggesting that it represents the first attempt towards the morphofunctional model of this modern felid.

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

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

II.4.5. Kiro Kuchuk (Kiro Kucuk) (41°42’20” N, 21°45’21” E)

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Plioviverrops cf. *orbignyi*. We refer to this species a left half-mandible NMNH-Sk KK2803 with p2–m1 and a large m2 alveolus (Plate 12, Fig. 2; Table 19). The rostral part and the mandibular ramus are broken off. The corpus is slender, the masseteric fossa hardly reaches the distal border of the m2 alveolus. Two mental foramina are present, under p2 and p3. The labial cingulum is present mainly on the mesiolabial and distolabial parts of the premolars. The p2 and p3 are low and long, with distal edges much longer than the mesial ones and bearing small but clear cuspids. The anterior cingula are also cuspid-like, so that the mesial edges of the teeth bear small but clear additional cuspids at their bases. The distal cingula are strong. A small but salient lingual protuberance is visible at mid-length of the crown base of p3, probably above an extra-root. The p4 is molariform, with a strong anterior cuspid and a very large talonid (much broader than the rest of the tooth). In spite of heavy wear, a large posterior additional cuspid is visible on the labial border of the talonid, whose lingual cingulum is well developed and bears a small, worn cusplet on its top. The m1 is much worn, so the relative heights of the conids can only be estimated. The metaconid and paraconid are of similar height. The protoconid was at most as high as the metaconid. The talonid is very large. The hypoconid was much lower than the entoconid. The latter is very tall, its apex is worn but it could have been only a little lower than the metaconid.

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

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

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

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

Hyaenidae. Hyaenotheriini indet. A right mandible fragment (MMNH-Sk KK 2768) with c and p2–m1, and a fragment of a maxilla (MMNH-Sk KK 2769) are probably from the same individual (Plate 12, Fig. 1). The ventral mandibular border under p3 is concave. A small additional cuspid is present on the lingual edge of the distal cingulum as in *Hyaenotherium wongii* whose teeth are of similar size and which is present in the late Miocene of Greece (SOLOUNIAS 1981; WERDELIN & SOLOUNIAS 1991). The P3 is broad distally and its lingual border is concave. The mesial border of the protocone of P4 is at the level of the mesial border of the minute parastyle. Tooth measurements (length x width): c = 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 = 11.7 x 4.0; P3 = 14.5 x 7.7; P4 = 23.6 x 13.5.

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

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

Felidae. *Paramachaerodus* sp. Material: MMNH-Sk KK 2813, male (?) cranial rostrum, restored with plaster with I1–3 and left canine; MMNH-Sk KK-2807, female (?) cranium with most teeth preserved but strongly crushed dorsoventrally (Plate. 9, Figs. 3,4; Table 20). The canine of MMNH-Sk KK 2813 is strongly compressed transversally. Its mesial edge is damaged, but clear crenulations are visible along its distal edge. On MMNH-Sk KK 2807 the sagittal crest is damaged, but was probably weak. It has an elongated rostral part and well developed zygomatic processes of the frontal. The canines are also machairodont: elongated and transversally compressed, with a flattened lingual surface; the tooth edges are damaged and coated with glue, but thin crenulations are present at least on the mesial edges, and probably also on the metacone of P4. The C–P3 diastema is long. I3 is distinctly larger than I1–2, conical, and caniniform. The diastema is damaged, but no trace of P1 or P2 is visible. P3 is elongated, broad distally because of a clear distolingual expansion; there is only a minute mesial accessory cusp but a large distal one. P4 is much longer, with a small protocone located between the levels of the paracone and parastyle, a minute preparastyle and an almost straight buccal border, slightly concave distally. P3 and P4 are almost in line with each other.

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

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

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

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

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

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

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

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

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

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

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

The canine is rather long. It seems (current research by N.S.) that there is a general trend of upper canine size increase from the Vallesian to the middle/Late Turolian (Table 21), especially if we take in consideration the easternmost late populations of the so called *M. horribilis* (= *M. palanderi*). This form is regarded by some authors (QIU ET AL., 2008) as a separate species, but could just be a geographic subspecies of *M. giganteus*. The upper canine increases mostly in height, but also in mesiodistal length, while possibly becoming thinner (Koufos 2000), but these trends may be obscured by sexual dimorphism, which was strong in the Machairodontinae (Antón et al. 2004; Peigné et al. 2005).

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

In spite of the accumulation of recent *Machairodus* s.l. finds, recent opinions on its systematics remain controversial (Geraads et al. 2004; Morlo & Semenov 2004; Sotnikova & Noskova 2004; Antón et al. 2004; Peigné et al. 2005; Sardella & Werdelin 2007; Qiu et al., 2008; Christiansen 2013). Geologically younger forms of *Machairodus* may be united in *Amphimachairodus* (Antón et al. 2004; Sardella & Werdelin 2007; Christiansen 2013), but three successive subgenera were erected for *Machairodus* by Sotnikova & Noskova (2004). Two species are usually accepted for the Vallesian to the middle Turolian of Eurasia (Beaumont 1975; Antón et al. 2004; Peigné et al. 2005), but Morlo & Semenov (2004) favour a monospecific taxonomy. Alternatively, Sotnikova & Noskova (2004) and Qiu et al. (2008) accept several successive and geographic Eurasian late Miocene species. In any case, most features improving the shearing complex appear gradually in mosaic: lengthening of the carnassials, reduction of the P4 protocone and of the m1 talonid-metaconid complex, reduction of p3/P3, enlargement of the

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

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

II.4. 7. Rashtanski Pat

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

II.5. NEGOTINO – KAVADARTSI FOSSILIFEROUS AREA

II.5.1. Dolni Disan (41°25’08” N, 22°07’36” E; elev. 287 m)

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

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

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

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

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

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

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

II.5.2. Kalnitsa (Kalnica)

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

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

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

II.5.3. Tremnik

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

II.5.4 Veshie (Vesje) (41°22’31” N, 22°07’54” E; elev. 621 m)

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

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

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

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

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

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

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

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

We have seen no bovid remain from this site.

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

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

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

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

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

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

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

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

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

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

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

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

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

Measurements of metapodials:

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

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

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

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

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

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

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

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

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

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

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

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

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

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

74/66) and 13 mm (MMNH-Sk Voz 84/69). In the latter specimen, the posterior wall of the anterior fossa forms a very shallow pocket. The bar between the preorbital fossa and the subnasal one is wide (11 to 18 mm). The tooth row in MMNH-Sk Voz 74/66 is 146 mm. The enamel plication is complex with 16–22 plis, but the specimen 74/66 is an adult individual (the protocone is connected with the protoloph on P^2 and M^1) and probably the plis were much more numerous. MMNH-Sk Voz 84/69 is a senile specimen and the teeth are much erased. The pli caballin is single to double. The protocone is rounded to lingually flattened and labially rounded. Measurements: Table 11.

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

Some metapodials and other postcranials have been assigned by FORSTEN & GAREVSKI (1989) to *Cremohipparion proboscideum*, *Hipparion dietrichi*, *Hipparion verae* and to *Cremohipparion matthewi*, but only the first species is represented by skulls. The metapodials can be sorted into four groups (Text-fig. 9, 10; Tables 23, 24). Most postcranials belongs to a species with relatively long, robust metapodials (large mid-shaft width), phalanxes and large astragali; FORSTEN & GAREVSKI (1989) assigned them to *C. proboscideum*, but their diagrams are similar to those of some specimens of *Hippotherium brachypus* from Pikermi and Hadjidimovo, therefore they could belong to a large *Hippotherium*. We assign to a second species metapodials that are as long as those of the first group but more slender, and phalanxes and medium sized astragali. They show similarities with slender *Hippotherium*, such as *Hippotherium primigenium* as well as with some samples of *Cremohipparion* with more robust metapodials (*C. proboscideum* or *C. mediterraneum* from Hadjidimovo). The third group includes slender and long metapodials whose Simpson diagrams show similarities with *Hipparion dietrichi* from Nikiti-2, RZO, Perivolaki and Vathylakkos 2 (Koufos 1987 c, 1988a; Vlachou & Koufos 2002, 2006; Koufos & Vlachou, 2016). One metacarpal, one first phalanx and one astragalus can be referred to a fourth, small species. Their dimensions and proportions are close to *C. macedonicum* from Nikiti-2 and Perivolaki (Vlachou & Koufos 2002, 2006; Koufos & Vlachou, 2016).

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

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

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

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

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

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

II.5.6. Zmiovets 2

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

II.6. Morievo area (Mariovo)

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

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

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

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

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

II.7. VALANDOVO FOSSILIFEROUS AREA

II.7.1. Bashibos (Basibos) (41°18’41”N, 22°40’30” E; elev. 284 m)

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

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

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

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

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

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

Mesembriacerus sp. The posterior part of a small skull MMNH-Sk BB 2607 (Plate 4, Fig. 9; Table 9). differs from all bovids of the Balkano-Iranian Turolian. It is not crushed, except for the area of insertion of the horn-cores. The latter, of which only the base is preserved, appear still more inclined that they were in life, and were small, even compared with the size of the skull, and could indicate a female individual. They are oval in cross-section, with no keel or torsion, and little or no divergence. Details of the posterior part of the skull are obscured by sediment, but the auditory region was short and deep, with small bulla and auditory foramen, quite narrow mastoid exposure dorsally, and broad occipital condyles. The basioccipital is short, with posterior tuberosities much lower (more ventral) than the basion, indicating stiffening of the atlanto-cranial articulation, as in several "ovibovines" practising frontal clashing ("Rammkampf"). The interparietal, which has a rough surface, has a very particular orientation: instead of being almost in the same plane as the parietals in lateral view, it is here, between the temporal lines, almost in the same plane as the occipital. The angle between occipital and parietal planes, which usually corresponds to the nuchal crest, corresponds here approximately (sutures are not visible) to the rostral border of the interparietal. Among late Miocene bovids of the Balkano-Iranian province, only *Mesembriacerus* from the Vallesian of Ravin de la Pluie in Greece (BOUVRAIN 1975; BOUVRAIN & BONIS 1984), of which D. KOSTOPOULOS kindly provided us with photos of the holotype, displays such morphology, and we are confident in assigning MMNH-Sk BB-2607 to this genus. Not enough of it is preserved for detailed comparisons, but it looks as if the interparietal of the Bashibos form was still more vertical than in Greece, so that we prefer not to attempt species identification, as this might reflect an age difference. Still, the presence of *Mesembriacerus* is indicative of an early age for the locality.

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

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

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

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

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

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

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

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

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

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

Felidae. *Yoshi* aff. *garevskii* (Plate 9, Fig. 1; Table 15). A fragment of right mandible has all its teeth broken except p4. The symphysis is not preserved but was probably shallow, in contrast with the Machairodontinae. The diastema is short with moderately steep mandible upper edge between c and p3 in lateral view. The middle part of the ventral border of corpus is convex. Two mental foramina are visible under the mesial and distal ends of p3. The teeth are not serrated. The canine has a robust root and strong distal and lingual ridges. Between them, the lingual surface is flat; the mesiolabial surface is rounded but the distolabial one is relatively flat with a sharp change of curvature between them. There is no trace of p2. The third premolar lacks an anterior additional cuspid; p4 is rather symmetrical with sub-equal mesial and distal accessory cuspids. The lingual border of the carnassial tooth is very slightly concave.

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

Paramachaerodus sp. MMNH-Sk BB 93/69 is an upper canine whose tip is missing. The two cutting edges are sharp and located at the mesial and distal edges of the crown, so that the crown cross-section is a very elongated ellipse, with weakly rounded labial surface and almost flat lingual surface (mesiodistal x labiolingual diameters: 16.0 x 10.5; restored length about 40 mm?). The crenulations on the distal edge are weaker than usual in this genus.

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

II.7.2. Prsten (41°18’50”N, 22°39’43” E; elev. 246 m)

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

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

Perissodactyla. Rhinocerotidae: *Dihoplus* cf. *pikermiensis*: The anterior part of a skull 28.8.1997 can unambiguously be assigned to *Dihoplus* rather than to *Ceratotherium neumayri* because of its long nasals, infra-orbital foramen situated anteriorly (above the posterior root of P3), non sloping ventral orbital border, and by the tooth characters: well-marked paracone fold and lingually pinched protocone and hypocone. Measurements are given in Table 13. The robustness of the zygomatic arch is reminiscent of *D. schleiermacheri*, a Vallesian species probably ancestral to the Turolian *D. pikermiensis*, but the nasal notch is slightly deeper than in the former species. Unfortunately the premaxillae are missing.

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

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

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

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

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

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

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

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

Discussion and conclusions

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

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

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

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

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

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

The diversity of the Bovidae is comparable to that found in Bulgarian and Greek localities, and greater than that of central Europe. Their most clear feature is the abundance of spiral-horned forms (especially *Palaeoreas*, *Prostrepsiceros*, and *Protragelaphus*), as in Greece and Bulgaria but, as in Bulgaria but in contrast to Greece (and Turkey), the large forms of the *Pachytragus−Protoryx* group are extremely rare. A probably new species of *Tragoportax* is present at Vozartsi, in addition to more common forms of this genus. Some rare bovids, like"*Samodorcas*" cf. *kuhlmanni* ? and Cf. *Pachytragus* sp. were found in the same locality, which might be of early Turolian age. The identification of *Samotragus* and *Mesembriacerus* suggest that the localities of Bashibos and Prsten could be still earlier, and perhaps even Vallesian

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

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

The ever-increasing accumulation of data in recent years help improving the picture of the semi-open landscapes (scrublands and woodlands) of the Turolian of Eurasia (FORTELIUS et al. 2006). They were probably widespread in South-Eastern Europe, the eastern part (at least) of Central Europe, the Northern peri-Pontic area, the Middle East, and large territories of Central Asia. However, their faunal composition was not uniform. Faunal similarities (especially regarding spiral-horned bovids and giraffids) support the existence of a Balkan-Iranian (Greco-Irano-Afghan) zoogeographic province (Bonis et al. 1992), whose westernmost part is now better known, thanks to the field work conducted in the late Miocene of the Republic of Macedonia and our analyses of the resulting collections. The Northern peri-Pontic region shares a number of similarities with this Balkan-Iranian province, especially regarding the hipparions, giraffids, bovids (spiral-horned antelopes, boselaphins, gazelles) (Korotkevich 1988; Krakhmalnaya 1996), and it may be that it was part of this mega-province as well; further research may refine the characteristics of the various sub-provinces. Our investigations confirm the typical features of the Balkan part of this province, characterized by *Choerolophodon pentelici*, *Mesopithecus pentelici*, *Bohlinia attica*, *Palaeoreas lindermayeri, Tragoportax, Pikermicerus Dihoplus pikermiensis, Hippotherium brachypus* (together with the lack of *Hipparion verae* and *C. moldavicum*), as well as the typical association of schizotheriines and chalicotheriines.

ACKNOWLEDGEMENTS

N.S., D.G., L.H. and G.M. are especially grateful to S. Petkovski for providing access to collections of the MMNH-Sk and for his much appreciated help there. Travel funds were provided by the Development of the Bulgarian Science Foundation (Bulgarian Academy of Science) and CNRS. G.M. gratefully acknowledges NHMUK and the financial support of the European Union for a visit to London (SYNTHESYS GB-TAF-1641) and P. Tassy (MNHN) for discussion of the Nerezi specimens. L.H. is thankful for the financial support of the European Union for her visits to Vienna (SYNTHESYS AT-TAF-2283) and London (SYNTHESYS GB-TAF-1678). N.S. is grateful to S. Stoyanov (Univ. of Forestry, Sofia) for the help in the statistical processing of numerical data (hyaenid material). Thanks to

P. Brewer, S. Chapman, A. Currant, J. Hooker (NHMUK), G. Daxner-Höck (NHMW) and P. Tassy (MNHN) for access to collections. The comments of the reviewers (Nikos Solounias and Sevket Sen) greatly improved the manuscript.

References

Abel, O. (1904): Über einen Fund von *Sivatherium giganteum* bei Adrianopel. – Sitzungs. math. nat. Kl. kaiser. Akad. Wissensch. **113**: 1–22.

Alba, D., Delson, E., Carnevale, G., Colombero, S., Delfino, M., Giuntelli, P., Pavia, M.& Pavia, G. (2014): First joint record of *Mesopithecus* and cf. *Macaca* in the Miocene of Europe. – J. Hum. Evol. **67** (1): 1–18.

Alcalá, L., 1994. Macromamíferos neógenos de la fosa de Alfambra-Teruel. Ph.D. thesis. Museo Nacional de Ciencias Naturales. Madrid, 554 p.

Andersson, K. (1998): Redescription of the Uppsalamaterial ofMetailurus, with a review of the genus. – Master of Science Thesis, Uppsala University, 30 pp.

Andersson, K. & Werdelin, L. (2005): Carnivora from the late Miocene of Lantian, China. – Vert. PalAsiat. **43**: 256–271.

Andree, J. (1926): Neue Cavicornier aus dem Pliocän von Samos. – Palaeontographica **67**: 135–175.

Andrews, P., Harrison, E., Delson, E., Bernor, R.L. & Martin, L.(1996): Distribution and biochronology of European and southwest Asian Miocene Catarrhines. – In: Bernor R.L., Fahlbusch, V. & Mittmann, H.W. (eds): The evolution of Western Eurasian Neogene mammal Faunas. – 168–207, Columbia University Press.

Anquetin, J., Antoine, P.-O. & Tassy, P. (2007): Middle Miocene Chalicotheriidae (Mammalia, Perissodactyla) from France, with a discussion on chalicotheriine phylogeny. – Zool. J. Linn. Soc. **151**: 577-608.

Antón, M., Salesa, M.J., Morales, J. & Turner, A. (2004): First known complete skulls of the scimitar–toothed cat *Machairodus aphanistus* (Felidae, Carnivora) from the Spanish late Miocene site of Batallones-1. – J. Vert. Paleont. **24** (4): 957–969.

Athanassiou, A., Roussiakis, S.J., Giaourtsakis, I.X., Theodorou , G.E. & Iliopoulos, G. (2014): A new hornless rhinoceros of the genus *Acerorhinus* (Perissodactyla: Rhinocerotidae) from the upper Miocene of Kerassiá (Euboea, Greece), with a revision of related forms. – Palaeontographica A **303** (1–3): 23–59.

Bakalov, P. (1934): Die Hipparionenfauna von Kalimanzi und Kromidovo, bezirk Sweti Wratsch, SW Bulgarien, part I (Fissipedia und Suidae). – Jahrbuch der Universität. Sofia, Phys. mat. Fak. **30** (3): 313–349.

Bakalov, P. & Nikolov, I. (1962): Les fossiles de Bulgarie – X – Mammifères tertiaries. Académie des Sciences de Bulgarie, 170 p.

Beaumont, G. de (1975): Recherches sur les félidés (mammifères, carnivores) du Pliocène inférieur des sables à *Dinotherium* des environs d'Eppelsheim (Rheinhessen). – Arch. Sci. **28** (3): 369–405.

Beaumont, G.D. & Mein, P. (1972): Recherches sur le genre *Plioviverrops* Kretzoi (Carnivora, ?Hyaenidae). – C. R. Séances Soc. Phys. Hist. Nat. Genève **25** (3): 383–394.

Bernor, R.L., Kovar–Eder, J., Suc, J.P. & Tobien, H. (1990): A contribution to the evolutionary history of European late Miocene age hipparionines (Mammalia : Equidae). – Paléobiol. Contin. **17**: 291–309.

Bernor, R., Koufos, G., Woodburne, M. & Fortelius, M. (1996): The evolutionary history and biochronology of European and southwest Asian late Miocene and Pliocene hipparionine horses. – In: Bernor R.L., Fahlbusch, V. & Mittmann, H.W.

(eds): The evolution of Western Eurasian Neogene mammal Faunas. 307–338, Columbia University Press.

Bernor, R.L., (1985): Systematic and evolutionary relationships of the hipparionine horses from Maragheh, Iran (late Miocene, Turolian age). — Palaeovertebrata **4**: 15:173–269.

Bernor, R., Mirzai Ataabadi M, Meshida, K., & Wolf, D. (2016): The Maragheh hipparions, late Miocene of Azarbaijan, Iran. –In Mirzaie Ataabadi M.& Fortelius M. (eds.): The late Miocene Maragheh mammal fauna; results of recent multidisciplinary research. Palaeobiodiversity and Palaeoenvironments, **96**(3) 453–488.

Bernor, R., Tobien, H., Hayek, L.-A., Mittmann, H.-W. (1997): *Hippotherium primigenium* (Equidae, Mammalia) from the late Miocene of Höwenegg (Hegau, Germany). – Andrias **10**: 1–230.

Bonis, L. de & Bouvrain, G. (1996): Suidae du Miocène supérieur de Grèce. – Bulletin du Muséum National d'Histoire Naturelle **18** (1): 107–132.

Bonis, L. de, Koufos , G. (1981): A new hyaenid (Carnivora, Mammalia) in the Vallesian (late Miocene) of northern Greece. – Sci. An., Fac. Phys. Math., Univ. Thessaloniki **21**: 79-94.

Bonis, L. de & Koufos, G.D. (1991): The late Miocene small carnivores of the Lower Axios Valley (Macedonia, Greece). – Geobios **24** (2): 361–379.

Bonis, L. de, Bouvrain, G., Geraads, D. & Koufos, G.D. (1990): New remains of *Mesopithecus* (Primates, Cercopithecidae) from the late Miocene of Macedonia with the description of a new species. – J. Vert. Paleont. **10**: 473–483.

Bonis, L. de, Bouvrain, G., Koufos, G.D. & Tassy, P. (1995): Un crâne de chalicothère (Mammalia, Perissodactyla) du Miocène supérieur de Macédoine (Grèce) : remarques sur la phylogénie des Chalicotheriinae. – Palaeovertebrata **24**: 135–176.

Bonis, L. de, Brunet, M., Heintz, E. & Sen, S. (1992): La province gréco-irano-afghane et la répartition des faunes mammaliennes au Miocène supérieur. – Paleontol. i Evol. **24–25**: 103–112.

Bouvrain, G. (1975): Un nouveau bovidé du Vallésien de Macédoine (Grèce). – C. R. Acad. Sci. **280**: 1357–1359.

Bouvrain, G. (1978): *Protagelaphus theodori* n. sp. (Mammalia, Artiodactyla, Bovidae) du Miocène de Macédoine. – Géol. Médit. **5** (2): 229–236.

Bouvrain, G. (1979): Un genre nouveau de Bovidé de la fin du Miocène. – Bull. Soc. Géol. Fr. **21** (4): 507–511.

Bouvrain, G. (1980): Le genre *Palaeoreas* (Mammalia, Artiodactyla, Bovidae), systématique et extension géographique. – Paläont. Z. **54** (1–2): 55–65.

Bouvrain, G. (1997): Les Bovidés du Miocène supérieur de Pentalophos (Macédoine, Grèce). – Münchner Geowiss. Abh. **34**: 5–22.

Bouvrain, G. & Bonis L. de (1984): Le genre *Mesembriacerus* (Bovidae, Artiodactyla) : un oviboviné primitif du Vallésien de Macédoine (Grèce). – Palaeovertebrata **14**: 201–223.

Bouvrain, G. & Bonis, L. de (1985): Le genre *Samotragus* (Artiodactyla, Bovidae), une antilope du Miocène supérieur de Grèce. – Ann. Paléont. **71**: 257–299.

Bouvrain, G. & Bonis, L. de (2007): Ruminants (Mammalia, Artiodactyla: Tragulidae, Cervidae, Bovidae) des gisements du Miocène supérieur (Turolien) de Dytiko (Grèce). Ann. Paléont. **93**: 121–147.

Brunner, J. (1939): Neue Funde zur Hipparionfauna von Veles in Mazedonien. Anzeiger Akad. Wissensch. Wien, Math.-Naturwiss. Kl. **2**: 11–13.

Christiansen, P. (2013): Phylogeny of the sabertoothed felids (Carnivora: Felidae: Machairodontinae). – Cladistics **29**: 543–559.

Ćirić, A. (1957): Pikermiska fauna iz okoline titovog velesa. – Bull. Mus. Hist. Nat. Pays serbe A **8**: 1–82.

Ćirić, A. (1964): About *Tragoceras velesis* n.sp. from pikermian fauna surroundings of Titov Veles. – Geol. Maced. **1** (1): 35–38.

Coombs, M.C. (1989): Interrelationships and diversity in the Chalicotheriidae. – In: Prothero, D.R. & Schoch, R.M. (eds): The evolution of Perissodactyls. – 438–457, Clarendon press.

Crusafont-Pairo, M., G. Petter, G. (1969). Contribution à l'étude des Hyaenidae. La sous-famille des Ictitheriinae. − Ann. Paléont. **35** (1): 89–127.

Delson, E. (1973): Fossil colobine monkeys of the circum-Mediterranean region and the evolutionary history of the Cercopithecidae (Primates, Mammalia). – Ph.D., Columbia University.

Delson, E. (1974): Preliminary review of cercopithecid distribution in the circum Mediterranean region. – Mém. BRGM **78**: 131–135.

Delson, E., Thomas, H., & Spassov, N. (2005): Fossil old world monkeys (Primates, Cercopithecidae) from the Pliocene of Dorkovo, Bulgaria. – Geodiversitas **27**: 159–166.

Delson,E., Terranova, C., Jungers, W., Sargis, E., Jablonski, N., Dechow, P. (2000): Body Mass in Cercopithecidae (Primates, Mammalia): Estimation and Scaling in Extinct and Extant Taxa. – Anthrop. Papers Amer. Mus. Nat. Hist. **83**: 1–159.

Eisenmann, V., Alberdi, M., de Giuli, C., Staesche, U.(1988): Studying fossil Horses. – In: Woodburne, M. & P. Sondaar (eds.) "New York International Hipparion Conference, 1981", pp 71.

Forstén, A.-M. (1980): Hipparions of the *Hipparion mediterraneum* group from south-western USSR. – Ann. Zool. Fennici, **17**:27-38.

Forstén, A.-M. & Krakhmalnaya, T., (1997): The hipparions (Mammalia, Equidae) from the late Miocene of Cherevinchoe on the northern Black Sea coast, Ukraina. — Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, H**8**: 489–499.

Forsten, A. & Garevski, R. (1989): Hipparions (Mammalia, Perissodactyla) from Macedonia (Yugoslavia). – Geol. Maced. **3** (2): 159–206.

Fortelius, M., Heissig, K., Saraç, G. & Sen, S. (2003): Rhinocerotidae (Perissodactyla). – In: Fortelius, M., Kappelman, J., Sen, S., and Bernor, R. L. (eds): Geology and paleontology of the Miocene Sinap Formation, Turkey. – 282–307, Columbia University Press.

Fortelius M., Eronen J., Liu L., Pushkina D., Tesakov A., Vislobokova I., Zhang Z. (2006). Late Miocene and Pliocene large land mammals and climatic changes in Eurasia. – Palaeogeog., Palaeoclim., Palaeoecol. **238**: 219–227.

Gabunia, L. (1959): Histoire du genre Hipparion. – Izdatelstvo Akademii Nauk SSSR, 570 pp. [in Russian]

Gabunia, L. (1979): New name about *Hipparion gromovae*. – Palaeontologicheskii Zhurnal, **1**: 136. [in Russian]

Garevski, R. (1956): Neue Fundstellen von Pikermifauna in Mazedonien. – Acta Mus. Maced. Sci. Nat. **4** (35): 67–96.

Garevski, R. (1960a): Neuer Fund von Mastodon in den Diatomeenschichten bei Barovo (Kavadarci) Mazedonien. – Fragm. Balcan. Mus. Maced. Sci. Nat. **3** (16): 133–144

Garevski, R. (1960b): Die Mastodonreste beim Bahnhof Caska in Mazedonien. – Acta Mus. Mac. Sci. Nat. **7** (4): 75–87.

Garevski, R. (1974a): Beitrag zur Kenntnis der Pikermifauna Mazedoniens. Fossilreste der Simocyoniden. – Fragm. Balcan. Mus. Maced. Sci. Nat. **9** (19): 189–197.

GAREVSKI, R. (1974b): Beitrag zur Kenntnis der Pikermifauna Mazedoniens. Fossilreste der Chalicotheriiden. – Fragm. Balcan. Mus. Maced. Sci. Nat. **9** (20): 201–206.

GAREVSKI, R. (1976a): Ein weiterer Beitrag zur Kenntnis der Pikermifauna Mazedoniens. Die Dinotherienreste von der Umgebung T. Veles. – Fragm. Balcan. Mus. Maced. Sci. Nat. **10** (3): 21–25.

GAREVSKI, R. (1976b): Weiterer Beitrag zur Kenntnis der Pikermifauna Mazedoniens. Der Mastodonschädel von der Umgebung des Dorfes Dolni Disan (Negotino). – Posebno Izdanie Musei Macedonici Scientiarum Naturalium **7**: 21–26.

GAREVSKI, R. (1985): Die Mastodonreste aus Umgebung der Stadt Skopje in Mazedonien. – Razprave IV, Razreda Sazu, 26, Zbornik Ivana Rakovca / Ivan Rakovec Volume **26**: 61–68. Ljubljana.

GAREVSKI, R. (1989a): Ein *Aceratherium* Schädel von dem Dorf Karaslari in der Umgebung von Titov Veles (Mazedonien). – Geol. Maced. **4** (1): 133–150.

GAREVSKI, R. (1989b): Hipparions (Mammalia, Perissodactyla) from Macedonia (Yugoslavia). – Geol. Maced. **3** (2): 159-206.

GAREVSKI, R. (1991): Beitrag zur Kenntnis der Pikermifauna Mazedoniens. Die Nashornreste (Mammalia). – Geol. Maced. **5** (1): 39–48.

GAREVSKI, R. (1992): Die Machairodusreste von der Fundstelle Prsten in der Umgebung Valandovo (Mazedonien). – Geol. Maced. **6** (1): 61–70.

GAREVSKI, R. (1997): Ein Schädel samt Unterkiefer von *Choerolophodon pentelici* Gaudry & Lartet aus der Pikermifauna von Makedonien. – Geološki zbornik **12**: 247–264.

GAREVSKI, R. & MLADENOVSKI, G. (2006): Weiterer Fund von Mastodon aus Lokalität “Zmijovec” beim Dorfe Dolni Disan, Kreis Negotino.– Mus. Maz. Sci. Nat. Anniversary proceedings (1926–2006); 31–37.

GAREVSKI, R. & MARKOV, G.N. (2011): A *Deinotherium gigantissimum* (Mammalia, Proboscidea) palate with deciduous dentition from the area of Veles, Republic of Macedonia. – Paläont. Z. **85** (1): 33–36.

GAREVSKI, R. & ZAPFE, H. (1983): Weitere Chalicotheriiden-Funde aus der Pikermifauna von Titov Veles (Mazedonien, Jugoslawien). – Acta Mus. Mac. Sci. Nat. **17** (1): 1–19.

GAREVSKI, R., GAREVSKA, B., & MARKOV, G.N. (2012): Remains of *Zygolophodon turicensis* (Proboscidea, Mammutidae) from the coal mines near Bitola, Republic of Macedonia. – Hist. nat. bulgar. **20**: 157–162.

GERAADS, D. (1988): Révision des Rhinocerotidae (Mammalia) du Turolien de Pikermi. Comparaison avec les formes voisines. – Ann. Paléont. **74** (1): 13–41.

GERAADS, D. (2009): Giraffidae (Mammalia) de la fin du Néogène de la république de Macédoine (ARYM). – Geodiversitas **31** (4): 893–908.

GERAADS, D. (2013): Large mammals from the late Miocene of Çorakyerler, Çankırı, Turkey. – Acta zool. bulgar. **65** (3): 381–390.

GERAADS, D. & GÜLEÇ, E. (1999): On some spiral-horned antelopes from the upper Miocene of Turkey, with remarks on their distribution. – Paläont. Z. **73** (3–4): 403–409.

GERAADS, D. & GÜLEÇ, E. (2000): A *Bramatherium* skull (Giraffidae, Mammalia) from the upper Miocene of Kavakdere (central Turkey). Biogeographic and phylogenetic implications. – Bull. Min. Res. Expl. **121**: 51–56.

GERAADS, D., KAYA, T., and MAYDA, S. (2005): Late Miocene large mammals from Yulafli, Thrace region, Turkey, and their biogeographic implications. – Acta Palaeontologica Polonica **50** (3): 523–544.

GERAADS, D. & KOUFOS, G. (1990): Upper Miocene Rhinocerotidae (Mammalia) from Pentalophos-1, Macedonia, Greece. Palaeontographica A **210**: 151−168.

GERAADS, D. & SPASSOV, N. (2009): Rhinocerotidae from the late Miocene of Bulgaria. – Palaeontographica A **287**: 99–122.

GERAADS, D., KAYA, T. & TUNA, V. (2004): A skull of *Machairodus giganteus* (Felidae, Mammalia) from the late Miocene of Turkey. – N. Jhb. Geol. Paläont. Monatsh. **2004** (2): 95–110.

GERAADS, D., SPASSOV, N. & GAREVSKI, R. (2008): New specimens of *Propotamochoerus* (Suidae, Mammalia) from the late Miocene of the Balkans. – N. Jhb. Geol. Paläont. Monatsh. **248** (1): 103–113.

GERAADS, D., SPASSOV, N., HRISTOVA, L., MARKOV, G.N. & TZANKOV, T. (2011): Upper Miocene mammals from Strumyani, south-western Bulgaria. – Geodiversitas **33** (3): 451–484.

GERAADS, D., SPASSOV, N. & KOVACHEV, D. (2001): New Chalicotheriidae (Perissodactyla, Mammalia) from Bulgaria. – J. Vert. Pal**. 21** (3): 596–606.

GERAADS, D., SPASSOV, N. & KOVACHEV, D. (2003): *Palaeoreas lindermayeri* (Wagner, 1848) from the upper Miocene of Bulgaria, and a revision of the species. – Geodiversitas, **25** (2): 405–415.

GERAADS, D., SPASSOV, N. & KOVACHEV, D. (2005): Giraffidae (Artiodactyla, Mammalia) from the late Miocene of Kalimantsi and Hadjidimovo, south-western Bulgaria. – Geol. balcan. **35** (1–2): 11–18.

GERAADS, D., SPASSOV, N. & KOVACHEV, D. (2006a): A new *Sporadotragus* (Bovidae, Mammalia) from the late Miocene of Bulgaria. – Riv. Ital. Paleont. Strat. **112** (3): 473–479.

GERAADS, D., SPASSOV, N. & KOVACHEV, D. (2006b): The Bulgarian Chalicotheriidae (Mammalia): an update. – Rev. Paléobiol. **25** (2): 429–436.

GERAADS, D., TSOUKALA, E. & SPASSOV, N. (2007): A skull of *Ancylotherium* (Chalicotheriidae, Mammalia) from the late Miocene of Thermopigi (Serres, N. Greece), and the relationships of the genus. – J. Vert. Pal**. 27** (2): 461–466.

GIAOURTSAKIS, I. (2009): The late Miocene mammal faunas of the Mytilinii Basin, Samos Island, Greece. 9. Rhinocerotidae. – Beitr. Paläont. **31**: 157–187.

GROMOVA, V. (1952): Hipparions (gen. Hipparion). – Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR, 36: 475 pp. [in Russian]

HEISSIG, K. (1999): Family Rhinocerotidae. – In: RÖSSNER, G. & HEISSIG, K. (eds). the Miocene land mammals of Europe. Pfeil, 175–188.

HRISTOVA, L., GERAADS, D., MARKOV, G. & SPASSOV, N. (2013): Late Miocene mammals from Kocherinovo, southwestern Bulgaria. – Acta Zool. Bulgar. **65** (4): 517–529.

HRISTOVA, L., KOVACHEV, D., SPASSOV, N. (2002): The Hipparions (Equidae, Mammalia) from the Upper Miocene locality Hadzhidimovo, SW Bulgaria. – Rev. Bulg. Geol. Society, **63** (1-3): 89-98. [in Bulgarian, English abstract]

HRISTOVA, L., KOVACHEV, D., SPASSOV, N., (2003): Hipparion brachypus Hensel, 1862 from the Late Miocene of Hadzhidimovo, Southwestern Bulgaria. – Comptes rendus de l'Academie bulgare des Sciences, **56** (2): 77-84.

HRISTOVA, L., KOVACHEV, D. (2005): Notes on taxonomy on the Middle Turolian hipparions from localities near Kalimantsi village. – Mathematics and natural sciences. Proceedings of the International scientific conference 8-11.06.2005. South-West University, Blagoevgrad, V. **2**: 180-184.

KITTL E. (1887): Beiträge zur Kenntnis der fossilen Säugethiere von Maragha in Persien. 1. Carnivoren. – Annalen des k.k. Naturhistorischen Hofmuseums, **2**: 317-338.

KONIDARIS, G.E., ROUSSIAKIS, S.J., THEODOROU, G.E. & KOUFOS G.D. (2014): The Eurasian occurrence of the shovel-tusker *Konobelodon* (Mammalia, Proboscidea) as illuminated by its presence in the late Miocene of Pikermi (Greece). – J. Vert. Paleont. **34** (6): 1437–1453.

Konidaris, G., Koufos, G., Kostopoulos, D. & Merceron, G. (2016): Taxonomy, biostratigraphy and palaeoecology of *Choerolophodon* (Proboscidea, Mammalia) in the Miocene of SE Europe-SW Asia: implications for phylogeny and biogeography. – J. Syst. Palaeont. **14** (1): 11–27.

Korotkevich, E. (1988): History of the formation of the Hipparion-fauna of East Europe. Naukova Dumka. Kiev, 161 pp. (in Russian).

Kostopoulos, D.S. (1994): *Microstonyx major* (Suidae, Artiodactyla) from the late Miocene locality of "Nikiti-1", Macedonia, Greece: some remarks about the species. – Bull. Geol. Soc. Greece **30** (1): 341–355.

Kostopoulos, D.S. (2004): Revision of some late Miocene spiral horned antelopes (Bovidae, Mammalia). – N. Jb. Geol. Paläont. Abh. **231** (2): 167–190.

Kostopoulos, D.S. (2005): The Bovidae (Mammalia, Artiodactyla) from the late Miocene of Akkaşdağı, Turkey. – Geodiversitas **27** (4): 747–791.

Kostopoulos, D.S. (2006): The late Miocene vertebrate locality of Perivolaki, Thessaly, Greece. 9. Cervidae and Bovidae. – Palaeontographica A **276** (1–6): 151–183.

Kostopoulos, D. (2009): The Pikermian Event: Temporal and spatial resolution of the Turolian large mammal fauna in SE Europe. – Palaeogeography, Palaeoclimatology, Palaeoecology **274**: 82–95.

Koufos, G., Kostopoulos, D., Vlachou T., Konidaris G. (2016): Palaeontology of the upper Miocene vertebrate localities of Nikiti (Chalkidiki Peninsula, Macedonia, Greece). Synthesis. – Geobios **49**, 147–154

Kostopoulos, D.S. (2016): Palaeontology of the upper Miocene vertebrate localities of Nikiti (Chalkidiki Peninsula, Macedonia, Greece). Artiodactyla. – Geobios **49**: 119–

134.

KOSTOPOULOS, D.S. & KOUFOS, G.D. (1999): The Bovidae (Mammalia, Artiodactyla) of the "Nikiti-2" (NIK) Faunal Assemblage (Chalkidiki Peninsula, N. Greece). – Ann. Paléont. **85** (3): 193–218.

KOSTOPOULOS, D.S., SPASSOV, N. & KOVACHEV, D. (2001): Contribution to the study of *Microstonyx*: evidence from Bulgaria and the SE European populations. – Geodiversitas **23** (3): 411–437.

KOUFOS, G.D. (1987a): Study of the Turolian Hipparions of the Lower Axios Valley (Macedonia, Greece). 2. Locality "Prochoma–1" (PXM). – Paläont. Z. **61** (3–4): 339–358.

KOUFOS, G.D. (1987b): Study of the Pikermi Hipparions. Part I: generalities and taxonomy. – Bull. Mus. Nat. Hist. Nat. C **9** (2): 197–252.

KOUFOS, G.D. (1987c): Study of the Turolian Hipparions of the Lower Axios Valley (Macedonia, Greece).1. Locality "Ravin Des Zouaves-5" (RZO). – Geobios **20** (3): 293–312.

KOUFOS, G.D. (1987d): *Chasmaporthetes bonisi*, a new hyaenid (Carnivora, Mammalia) from the late Miocene of Macedonia (Greece). – Bull. Soc. géol. Fr., 8, **3** (5): 913–920.

KOUFOS, G.D. (1988a): Study of the Turolian Hipparions of the Lower Axios Valley (Macedonia, Greece). 3. Localities of Vathylakkos. – Paleontologia i Evolució, **22**: 15−39.

KOUFOS, G.D. (1988b): Study of the Turolian *Hipparions* of the Lower Axios Valley (Macedonia, Greece). 4. Localities of Dytiko – Palaeovertebrata. **18** (4): 187−239.

KOUFOS, G.D. (2000): Revision of the late Miocene carnivores from the Lower Axios Valley. – Münch. Geowiss. Abh. A **39**: 51–92.

KOUFOS, G.D. (2006a): The late Miocene Vertebrate locality of Perivolaki, Thessaly, Greece.3. Primates. – Palaeontographica A **276** (1–6): 23–37.

KOUFOS, G.D. (2006b): The Late Miocene Vertebrate locality of Perivolaki, Thessaly, Greece. 4. Carnivora. – Palaeontographica A **276** (1–6): 39–74.

KOUFOS, G.D. (2006c): The Late Miocene Vertebrate locality of Perivolaki, Thessaly, Greece. 5. Proboscidea, Rhinocerotidae. – Palaeontographica A **276** (1–6): 75–80.

KOUFOS, G. (2009a): The Genus *Mesopithecus* (Primates, Cercopithecidae) in the late Miocene of Greece. – Boll. Soc. Paleont. Ital. **48** (2): 157–166.

KOUFOS, G. D. (2009b): The Neogene cercopithecids (Mammalia, Primates) of Greece. – Geodiversitas **31** (4): 817–850.

KOUFOS, G. (2011): The Miocene carnivore assemblage of Greece. – Est. Geol. **67** (2): 291–320.

KOUFOS, G. (2013): Neogene mammal biostratigraphy and chronology of Greece. - In: X. WANG, L. FLYNN, M. FORTELIUS (eds.): Fossil mammals of Asia – Neogene Biostratigraphy and Chronology, 595−621.

KOUFOS, G. D., BONIS, L. DE, KOSTOPOULOS, D., K., VIROT, L & VLACHOU, T. (2004): New material of *Mesopithecus* (Primates, Cercopithecidae) from the Turolian locality of Vathylakkos 2, Macedonia, Greece. – *Paläont. Zeitschrift,* **78** (1): 213-228, Bonn.

KOUFOS, G., SPASSOV, N. & KOVACHEV, D. (2003): Study of *Mesopithecus* (Primates, Cercopithecoidea) from the late Miocene of Bulgaria. – Palaeontographica A **269** (1–3): 39–91.

KOUFOS, G. & VASILEIADOU K. (2015): Miocene/Pliocene mammal faunas of southern Balkans: implications for biostratigraphy and palaeoecology. – Palaeobio Palaeoenv **95**:285–303

Koufos, G.D. & Vlachou, T. (2005): Equidae (Mammalia, Perissodactyla) from the late Miocene of Akkaşdağı, Turkey. – In Sen S. (ed.), Geology, mammals and environments at Akkaşdağı, late Miocene of Central Anatolia. *Geodiversitas* **27** (4): 633–705.

Koufos, G. & Vlachou, T. (2016): Palaeontology of the upper Miocene vertebrate localities of Nikiti (Chalkidiki Peninsula, Macedonia, Greece) Equidae. – Geobios, **49**: 85–115.

Kovachev, D. (2002): First finds of *Machairodus giganteus* Wagner in theUpper Meotian around the village Hadjidimovo, Gotze DelchevDistrict (Southwest Bulgaria). Review of the Bulgarian Geological Society, 63:77–88.

Krakhmalnaya, T. (1996a): The Early Maeotian Hipparion-fauna of the region to the North of Black Sea. Naukova Dumka. Kiev, 225 pp.

Krakhmalnaya T. (1996b): Hipparions of the Northern Black Sea coast area (Ukraine and Moldova): species composition and stratigraphic distribution - Acta zoologica cracoviensia, **39** (1): 261-267.

Laskarev, V. (1921): Sur la découverte de la faune de Pikermi près de Veles (Serbie méridionale). – Glasnik Geografskog Drustva **6**: 156–159.

Laskarev, V. (1936): Sur les restes du *Mastodon angustidens* Cuv. trouvés en Yougoslavie. – Bull. Soc. scient. Skoplje, sect. sci. nat. **17** (5): 105–129. [Serbian, French summary].

Laskarev, V. (1948): Sur les restes fossiles de *Dinotherium* en Serbie. – Bull. Mus. Hist. Nat. Pays serbe A, **1**: 1–20. [Serbian, French summary].

Li, Y. (2014): Restudy of *Metailurus major* from Yushe Basin, Shanxi Province reported by Teilhard de Chardin and Leroy. – Vert. PalAsiat., **52** (4): 467–485.

Liu, L., Kostopoulos, D.S. & Fortelius, M. (2004): Late Miocene *Microstonyx* remains (Suidae, Mammalia) from northern China. – Geobios **37** (1): 49–64.

MARKOV, G.N. (2004): The fossil proboscideans of Bulgaria. – Ph.D. thesis, 225 + 81 pp., University of Sofia [in Bulgarian with English summary].

MARKOV, G.N. (2008): The Turolian proboscideans (Mammalia) of Europe: preliminary observations. – Hist. Natur. Bulgar. **19**: 153–178.

MELENTIS, J. (1967): Die Pikermifauna von Halmyropotamos (S. Euböa/Griechenland). – Praktika Akad. Hellen. **41**: 261–266.

MERCERON, G., SCOTT, J., SCOTT, R.S., GERAADS, D., SPASSOV, N. & UNGAR, P.S. (2009): Folivory or fruit/seed predation for *Mesopithecus*, an earliest colobine from the late Miocene of Eurasia. – J. Hum. Evol. **57**: 732–738.

MORALES, J. (1984): Venta del Moro: su macrofauna de mamíferos y biostratigrafía continental del mioceno terminal mediterráneo. – Editorial universidad complutense, Madrid, 340 pp.

MORLO, M. & SEMENOV, Y.A. (2004): New Carnivora (Mammalia) from the early Vallesian (late Miocene, MN 9) of Ukraine. – J. Vert. Pal**.** **24** (sup. 3): 96a.

PAPP, A. (1939): Zur Kenntnis der Hipparionfauna von Veles in Mazedonien. Sitzung der mathematisch –naturwissenschaftlichen klasse vom 30 november und 14 dezember . – Akad. Wissensch. Wien. **18/19**: 119–121.

PAVLOW, M. (1913): Mammifères tertiaires de la Nouvelle Russie. 1ère partie : Artiodactyla Perissodactyla (*Aceratherium kowalevskii* n.s.). – Nouv. Mém. Soc. Imp. Natur. Moscou **17** (3): 1–67.

PAVLOW, M. (1914): Mammifères tertiaires de la Nouvelle Russie. 2ème partie. *Aceratherium incisivum*, Hipparion, Proboscidea, Carnivora. – Nouv. Mém. Soc. Imp. Natur. Moscou **17** (4): 1–78 .

PEIGNE, S., BONIS, L. DE, LIKIUS, A., MACKAYE, H.T., VIGNAUD, P. & BRUNET, M. (2005): A New Machairodontine (Carnivora, Felidae) from the late Miocene Hominid locality of

TM 266, Toros-Menalla, Chad. – C. R. Palevol **4** (3): 243–253.

PETRONIJEVIC, Z.M. (1952): *Mastodon borsoni* HAYS from the village Gradesnice (Morihovo), Macedonia – Bull. Mus. Hist. Nat. Pays Serbe A, **5**: 243–248. [in Serbian]

PICKFORD, M. (1988): Revision of the Miocene Suidae of the Indian subcontinent. – Münchner Geowiss. Abh. **12**: 1–95.

PICKFORD, M. (2013): Re-assessment of the suids from the sables marins de Montpellier and selections of a lectotype for *Sus provincialis* Blainville, 1847. – Geodiversitas **35** (3): 655–689.

PICKFORD, M. (2015): Late Miocene Suidae from Eurasia: the *Hippopotamodon* and *Microstonyx* problem revisited. – Münchner Geowiss. Abh. **42**: 1–126.

PILGRIM G. 1931. Catalogue of the Pontian Carnivore of Europe in the departament of geology. – British Museum (Natural History), London, 164 pp.

QIU, Z-X., & SHI, Q-Q. (2008): Description of skull material of *Machairodus horribilis* Schlosser,1903. – Vert. PalAsiat. **10**: 265–283.

RADOVIĆ, P., ALABURIC, S., MARKOVIĆ, Z. & VLASTIĆ, S. (2013): New view on the old collection – “Pikermian fauna” from the vicinity of Veles (Republic of Macedonia). Part 1 – Primates. – Bulletin of the Natural History Museum, **6**: 7–29.

ROOK, L., FICCARELLI, G. & TORRE, D. (1991): Messinian carnivores from Italy. – Boll. Soc. Paleont. Ital. **30** (1): 7–22.

ROUSSIAKIS S. & THEODOROU, G. (2001): *Ancylotherium pentelicum* (Gaudry & Lartet, 1856) (Perissodactyla, Mammalia) from the classic locality of Pikermi (Attica, Greece), stored in the Paleontological and Geological Museum of Athens. – Geobios **34**: 563–584.

ROUSSIAKIS S. & THEODOROU, G. (2003): Carnivora from the late Miocene of Kerassiá

(Northern Euboea, Greece). – Deinsea **10**: 269–277.

Roussiakis, S.J., Theodorou, G.E. & Iliopoulos, G. (2006): An almost complete skeleton of *Metailurus parvulus* (Carnivora, Felidae) from the late Miocene of Kerassia (Northern Euboea, Greece). – Geobios **39**: 563–584.

Ryabinin, A. (1929): Carnivora vera, Rodentia, Subungulata. – Travaux du Musee Geologique pres l'academie des Sciences de l'URSS, 5, 75-143. [in Russian, with French summary]

Salesa, M., Anton, M., Turner, A., Alcala, L., Montoya, P. & Morales, J. (2010): Systematic revision of the late Miocene saber-toothed felid *Paramachaerodus* in Spain. – Palaeontology **53** (6): 1369–1391.

Saraç, G. & Sen, S. (2005): Chalicotheriidae (Mammalia, Perissodactyla) from the late Miocene of Akkaşdağı, Turkey. – Geodiversitas **27** (4): 591–600.

Sardella, R. & Werdelin, L. (2007): *Amphimachairodus* (Felidae, Mammalia) from Sahabi (latest Miocene – earliest Pliocene, Libya) with a review of African Miocene Machairodontinae. – Riv. Ital. Paleont. Strat. **113** (1): 67–77.

Schlosser, M. (1921): Die Hipparionenfauna von Veles in Mazedonien. – Abh. bayer. Akad. Wiss., math.-phys. Kl. **29** (4): 1–55.

Semenov, Y. (1989): Ictitheres and morphologically related hyaenas from the Neogene of the USSR. – Naukova Dumka, Kiev

Semenov, Y. (2008): Taxonomical reappraisal of "ictitheres" (mammalia, carnivora) from the late Miocene of Kenya. – C. R. Palevol **7** (8): 529–539.

Solounias, N. (1981): The Turolian fauna from the island of Samos, Greece. With special emphasis on the hyaenids and the bovids. – Contrib. Vert. Evol. **6**: 1–232.

SOLOUNIAS, N., PLAVCAN, J. & WITMER, L. (1999): The paleoecology of the Pikermian Biome and the Savanna myth. – In: AGUSTI, J., ROOK, L. ANDREWS P. (eds.). The evolution of Neogene terrestrial ecosystems in Europe. Cambridge University Press, Cambridge, 436-453.

SONDAAR, P.Y. (1971): The Samos Hipparion. – Proc. Kon. Nederl. Akad. Wetensch., B. **74** (4): 417–441.

SOTNIKOVA, M.V. (1991): A new species of *Machairodus* from the late Miocene Kalmakpai locality in eastern Kazakhstan (USSR). – Ann. Zool. Fenn. **28** (3–4): 361–369.

SOTNIKOVA, M. & NOSKOVA, N. (2004): The History of Machairodus in Eurasia. – In: 18th International Senckenberg Conference in Weimar, L. C. MAUL & KAHLKE, R.-D. (eds) Terra Nostra **2**: 238.

SPASSOV, N. & GERAADS, D. (2004): *Tragoportax* PILGRIM and *Miotragocerus* STROMER (Mammalia, Bovidae) from the Turolian of Hadjidimovo, Bulgaria, and a revision of the late Miocene Mediterranean Boselaphini. – Geodiversitas **26** (2): 339–370.

SPASSOV, N. & GERAADS, D. (2007): *Dolichopithecus balcanicus* sp. nov., a new colobinae (Primates, Cercopithecidae) from the early Pliocene of south-eastern Europe, with a discussion on the taxonomy of the genus. – J. Hum. Evol. **52**: 434–442.

SPASSOV, N. & GERAADS, D. (2011): A skull of *Simocyon primigenius* (ROTH & WAGNER, 1854) from the late Miocene of Karaslari (Republic of Macedonia), with remarks on the systematics and evolution of the genus. – N. Jb. Geol. Paläont. Abh. **262** (2): 151–161.

SPASSOV, N. & GERAADS, D. (2015): A new felid from the late Miocene of the Balkans and the contents of the genus *Metailurus* Zdansky, 1924 (Carnivora, Felidae). – J. Mamm. Evol. **22**: 45–56.

Spassov, N. & Koufos, G. (2002): The first appearance of *Dinocrocuta gigantea* and *Machairodus aphanistus* (Mammalia, Carnivora) in the Miocene of Bulgaria. – Mitt. Bayer. Staats. Paläont. hist. Geol. **42**: 83–101.

Spassov, N., Geraads, D., Hristova, L., Markov, G. N., Merceron, G., Tzankov, T., Stoyanov, K., Böhme, M. & Dimitrova, A. (2012): A hominid tooth from Bulgaria: the last pre-human hominid of continental Europe. – J. Hum. Evol. **62**: 138–145.

Spassov, N., Tzankov, T. & Geraads, D. (2006): Late Neogene stratigraphy, biochronology, faunal diversity and environments of south-west Bulgaria (Struma River Valley). – Geodiversitas, **28** (3): 477–498.

Studer, T. (1911): Eine neue Equidenform aus dem Obermiocän von Samos. – Verhandl. Deutschen Zool. Gesell., **20-21**: 192–200.

Tassy, P. (1984): Le mastodonte à dents étroites, le grade trilophodonte et la radiation initiale des Amebelodontidae. – In: Buffetaut E., Mazin J.-M., Salmon E. (eds): Actes du symposium paléontologique Georges Cuvier. p. 459–473, Montbéliard.

Tassy, P. (1985): La place des mastodontes miocènes de l'ancien monde dans la phylogénie des Proboscidea (Mammalia): hypothèses et conjectures. Thèse doctorat ès Sciences, 862 pp., Université Pierre et Marie Curie.

Tassy, P. (1990): The "proboscidean datum event": how many proboscideans and how many events? – In: Lindsay E.H., Fahlbusch V., Mein P. (eds): European Neogene mammal chronology. p. 237–252, Plenum press.

Tassy, P. (1994a): Gaps, parsimony, and early Miocene elephantoids (Mammalia), with a re-evaluation of *Gomphotherium annectens* (Matsumoto, 1925). – Zool. J. Linn. Soc. **112**: 101–117.

Tassy, P. (1994b): Les gisements de mammifères de Miocène supérieur de Kemiklitepe, Turquie: 7. Proboscidea (Mammalia). – Bull. Mus. Nat. Hist. Nat. C, sér. 4, **16** (1): 143–157.

Tassy, P. (1996): Growth and sexual dimorphism among Miocene elephantoids: the example of *Gomphotherium angustidens*. – In: Shoshani J., Tassy P. (eds): The Proboscidea. Evolution and palaeoecology of elephants and their relatives. p. 92–100, Oxford University Press.

Tassy, P. (2013): L'anatomie cranio-mandibulaire de *Gomphotherium angustidens* (Cuvier, 1817) (Proboscidea, Mammalia): données issues du gisement d'En Péjouan (Miocène moyen du Gers, France). – Geodiversitas **35** (2): 377–445.

Torre, D. (1989): On *Plioviverrops faventinus* n.sp. a new carnivore of Late Messinian age. – Boll. Soc. Paleont. Ital. **28**: 2–3.

Valenciano, A., Abella, J., Sanisidro, O., Hartstone-Rose, A., Álvarez-Sierra, M.A. & Morales, J. (2015): Complete description of the skull and mandible of the giant mustelid *Eomellivora piveteaui* Ozansoy,1965 (Mammalia, Carnivora, Mustelidae), from Batallones (MN10), late Miocene (Madrid, Spain). – J. Vert. Pal., **35**: 4, e934570.

Van der Made, J. (1997): The fossil pig from the late Miocene of Dorn-Dürkheim 1 in Germany. – Cour. Forsch-Inst. Senck. **197**: 205–230.

Van der Made, J. & Moyà-Solà, S. (1989): European Suinae (Artiodactyla) from the late Miocene onwards. – Boll. Soc. Paleont. Ital. **28** (2–3): 329–339.

Van der Made, J. & Stefanovic, I. (2006): A small tapir from the Turolian of Kreka (Bosnia) and a discussion on the biogeography and stratigraphy of the Neogene tapirs. – N. Jb. Geol. Paläont. Abh. **240** (2): 207–240.

Van der Made, J., Montoya, P. & Alcalá, L. (1992): *Microstonyx* (Suidae, Mammalia) from the upper Miocene of Spain. – Geobios **25** (3): 395–413.

VILLALTA, J.F. & CRUSAFONT, M. (1945): Nuevas aportaciones al conocimiento de los carnivoros Pontienses del Valles-Penedes. Dip. Prov. Barcelona. Publ. Inst. Geol. Miscelanea Almera, **7**: 11–121.

VILLATA, J. & CRUSAFONT, M. (1957): Dos nuevas especies de Hipparion del Pikermiense Español. − Curs. Conf. Inst. Lucas Mallada **4**: 65–69.

VISLOBOKOVA, I. (1990): [The fossil cervids of Eurasia]. – Trudy Paleont. Inst. **240**: 1–208 [Russian, English summary].

VLACHOU, D. & KOUFOS, G.D. (2002): The hipparions (Mammalia, Perissodactyla) from the Turolian locality “Nikiti-2” (NIK), Macedonia, N. Greece. – Ann. Paléont. **88**: 215−263.

VLACHOU, D. & KOUFOS, G.D. (2006): The late Miocene vertebrate locality of Perivolaki, Thessaly, Greece. 6. Equidae. Palaeontographica **276**: 81–119.

VLACHOU, D. & KOUFOS, G.D. (2009): The late Miocene mammal faunas of the Mytilinii Basin, Samos Island, Greece: new collection. 11. Equidae. – Beitr. Paläont. **31**: 207–281.

WANG, X. (1997): New cranial material of *Simocyon* from China, and its implications for phylogenetic relationships to the red panda (*Ailurus*). – J. Vert. Paleont. **17**: 184–198.

WATABE, M. & NAKAYA, H. (1991): Cranial Sekeletons of Hipparion (Perissodactyla, Mammalia) from Maragheh (Turolian, late Miocene), Northwest Iran. Memoirs of the Faculty of Science, Kyoto University, Series of Geology & Mineralogy. **56** (1-2): 55-125.

WEHRLI, H. (1941): Beitrag zur Kenntnis der “Hipparionen” von Samos. – Paläont. Z. **22**: 321−386.

WERDELIN, L. & SOLOUNIAS, N. (1991): The Hyaenidae: taxonomy, systematics and evolution. – Fossils and Strata **30**: 1–106.

Wolsan, M. (1989): Dental polymorphism in the genus *Martes* (Carnivora: Mustelidae) and its evolutionary significance. – Acta Theriol. **34** (40): 545–593.

Wolsan, M. & Semenov, Y.A. (1996): A revision of late Miocene mustelid carnivoran *Eomellivora*. – Acta Zool. Cracov. **39** (1): 593–604.

Zapfe, H. (1979): *Chalicotherium grande* (Blainv.) aus dem miozänen Spaltenfüllung von Neudorf an der March (Devinska Nová Ves), Tschechoslowakei. – N. Denkschr. natur. Mus. Wien **2**: 1–282.

Zapfe, H. (1991): *Mesopithecus pentelicus* Wagner aus dem Turolien von Pikermi bei Athen, Odontologie und Osteologie (Eine Dokumentation). – Neue Denkschriften des Naturhistorischen Museums in Wien, pp. 203.

Zdansky, O. (1924): Jungtertiäre Carnivoren Chinas. – Pal. Sinica **2**: 1–149.

Zhegallo, V. (1971): Hipparions from the Neogene deposits of western Mongolia and Tuva. – Sovm. Svet.-Mongol Nauch-Issled. Geol. Eksped. Tr., **3**: 98–119 (in Russian).

Text-figures captions

Text-fig. 1.

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

Text-fig. 2

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

Standard *Hippotherium primigenium* von Meyer, 1829, Höwenegg (Bernor et al. 1997).

Measurements after Eisenmann et al. 1988:

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

Text-fig. 3.

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

Text-fig. 4.

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

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

See Text-fig. 2. for measurement numbers.

Text-fig. 5.

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

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

See Text-fig. 2. for measurement numbers.

Text-fig. 6.

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

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

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

See Text-fig. 2. for measurement numbers.

Text-fig. 7.

Logarithmic ratio diagram comparing the skulls of *Hipparion* sp. from Umin Dol (**UD**) and *Hipparion dietrichi* WEHRLI 1941, from different Macedonian localities: Barovo (**BAR**); Belushka (**BEL**); Bashibos (**BB**); Karaslari (**KAR**); Veshie (**VES**).

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

See Text-fig. 2. for measurement numbers.

Text-fig. 8.

Logarithmic ratio diagram comparing the skulls of *Cremohipparion* from Macedonian localities, localities from the Balkan Peninsula and the type of *C. proboscideum* from Samos: Hadjidimovo (**HD**); Kalimantsi (**KAL**); Karaslari (**KAR**); Perivolaki (**PER**); Pikermi (**PIK**); Ravin des Zouaves-5 (**RZO**); Strumyani 2 (**STR2**); Vozartsi (**VOZ**).

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

See Text-fig. 2. for measurement numbers.

Text-fig. 9.

Logarithmic ratio diagram comparing equid metacarpals from Vozarsti. Standard: *Hippotherium primigenium* VON MEYER, 1829, Höwenegg (BERNOR et al. 1997).

Measurements after EISENMANN et al. 1988: 1. maximal length; 3. minimum width of shaft; 4. depth of shaft; 5. proximal articular breadth; 6. proximal articular depth; 10. distal maximum supra-articular breadth; 11. distal maximum articular breadth; 12. distal maximum depth of the keel; 13. distal minimum depth of the lateral condyle; 14. distal maximum depth of the medial condyle.

Text-fig.10.

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

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

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

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

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 abreviations see Text-fig. 13]. The difference in the mean values of the early Turolian (37.4 mm) and middle Turrolian (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).

Table captions

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

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

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

Table 3. Comparative measurements of upper teeth of late Miocene *Mesopithecus*, in mm. Localities arranged (with the exception of the ones from R. of Macedonia) by decreasing age. Azmaka 6: SPASSOV et al. (2012); Hadjidimovo-1: KOUFOS et al. (2003) and personal data; Vathylakkos: KOUFOS et al (2004); Kalimantsi: KOUFOS et al. (2003); Pikermi: ZAPFE (1991); Dytiko: BONIS et al (1990).

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

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

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

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

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

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

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

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

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

Table 13. Cranial features and measurements of Rhinocerotidae skulls and tooth-rows (at occlusal level), in mm. **1** to **7:** *Dihoplus pikermiensis*; **8:** *Ceratotherium neumayri*; **9:** *Acerorhinus* sp. **1**: Karaslari, on exhibit; **2**: Bashibos, on exhibit; **3**: Kiro Kuchuk 16.9.1997; **4**: Kiro Kuchuk 221; **5**: Kiro Kuchuk 222; **6**: Kiro Kuchuk 223; **7**: Prsten 28.8.1997; **8:** Umin Dol, on exhibit **9**: Karaslari 30/73.

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

Table 15. Comparative mandibular dimensions of *Yoshi* species with *Promegantereon ogygia* (SALESA et al. 2010; * personal measurements (N.S.) in Museo Nacional de Ciencias Naturales, Madrid; *Yoshi garevskii*, and *Y.* cf. *minor* after SPASSOV & GERAADS 2014; *Y. minor* after ANDERSON 1998; *Paramachaerodus orientalis* : original measurements of the cast of the type specimen of *Machairodus schlosseri* WEITHOFER from Pikermi.

Table 16. Cranial measurements (after TASSY, 1996) of "*Mammut obliquelophus*" from Kiro Kuchuk, MMNH 2773.

Table 17. Dental measurements of "*Mammut obliquelophus*" from Kiro Kuchuk, MMNH 2773, in mm.

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

Table 19. Comparative mandibular dimensions of *Plioviverrops*, in mm. KK: Kiro Kuchuk (mandible No.2803); KAL: Kalimantsi, Burdovski pat (PMA, personal data); PER: Perivolaki

(Koufos 2006); PIK: Pikermi (MNHNP; first measurement: PIK-3022, type: after Bonis & Koufos 1991; second measurement: PIK-3016, personal data); Axios: Vathylakkos and Ravin des Zouaves (Koufos 2000); LM: Los Mansuetos (Crusafont Pairó and Petter 1969); BRIS: Brisighella (Torre 1989).

Table 20. Comparative dimensions of the *Paramachaerodus* from Kiro Kuchuk with *P. orientalis* from Maragha (MAR), Pikermi (PIK), Concud & Puente Minero (CON & PM) and *P. maximiliani* from China. Data from Pilgrim (1931), Kittl (1887), Salesa et al. (2010), and Zdansky (1924), respectively.

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

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

Table 23. Measurements of the Equid metacarpals from Vozarci, in mm (after Eisenmann et al. 1988).

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

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

Table 25. Distribution of the Neogene mammal taxaof Republic of Macedonia studied by localities.

FIGURE CAPTIONS

Plate 1.

1. *Hippotherium brachypus*, Kiro Kuchuk, Republic of Macedonia. Skull, KK 2003; a. lateral view, b. left upper cheek teeth.
2. *Hippotherium brachypus*, Karaslari, Republic of Macedonia. Skull, KAR 20/75; a. lateral view, b. left upper cheek teeth.
3. *Hippotherium brachypus*, Karaslari, Republic of Macedonia. Skull, KAR 26/73; a. lateral view, b. left upper cheek teeth.
4. *Hippotherium brachypus*, Belushka, Republic of Macedonia. Skull, B 2708; a. lateral view, b. left upper cheek teeth.
5. *Hippotherium brachypus*, Umin Dol, Republic of Macedonia. Skull, no number; a. lateral view, b. left upper cheek teeth.

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

Plate 2.

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

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

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

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

Plate 3.

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

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

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

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

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

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

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. 2a.

Plate 4.

1. *Sporadotragus* sp., Umin Dol, Republic of Macedonia. skull UD-1590; a. lateral view; b. front view.

2. *Protragelaphus* sp., Bashibos, Republic of Macedonia. Skull BB-1645; front view.

3. *Prostrepsiceros rotundicornis,* Vozartsi, Republic of Macedonia. Frontlet Voz-694; front view.

4. *Protragelaphus* sp., Bashibos, Republic of Macedonia. Frontlet BB-1645; a. right lateral view; b. front view.

5. Cf. *Prostrepsiceros* sp., Bashibos, Republic of Macedonia. BB-2611; a. right lateral view; b. front view.

6. *Palaeoreas lindermayeri,* Karaslari, Republic of Macedonia. Frontlet Kar-2610; a. right lateral view; b. front view.

7. *Samotragus* sp., Bashibos, Republic of Macedonia. Left horn-core BB-2623; a, left lateral view; b, front view.

8. *Gazella* cf. *capricornis*, Vozartsi, Republic of Macedonia. Frontlet Voz-558; a. front view; b. left lateral view.

9. *Mesembriacerus* sp., Bashibos, Republic of Macedonia. Braincase with bases of horn-cores BB-2607; a. ventral view; b. dorsal view; c. postero-lateral view; d. posterior view.

Scale bar = 20 cm for figs. 1–6, 10 cm for figs. 7–9.

Plate 5.

1. *Cremohipparion mediterraneum*, Karaslari, Republic of Macedonia. Skull, KAR 23/73; a. lateral view, b. left upper cheek teeth.

2. *Cremohipparion mediterraneum*, Karaslari, Republic of Macedonia. Skull, KAR 28/73; a. lateral view, b. left upper cheek teeth.

3. *Cremohipparion proboscideum*, Vozartsi, Republic of Macedonia. Skull, VOZ 74/66; a. lateral view, b. right upper cheek teeth.

4. *Hipparion* sp., Umin Dol, Republic of Macedonia. Skull, UD 90/66; a. lateral view, b. right upper cheek teeth.

5. *Hipparion dietrichi*, Karaslari, Republic of Macedonia. Skull, KAR 92/73; a. lateral view, b. left upper cheek teeth.

6. *Hipparion dietrichi*, Karaslari, Republic of Macedonia. Skull, KAR 203/73; a. lateral view, b. upper cheek teeth.

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

Plate 6.

1. Chalicotheriinae gen. et sp. indet., Veshie, Republic of Macedonia. P2–M3 Veshie 2702; occlusal view.

2. *Anisodon* sp., Karaslari, Republic of Macedonia. Mandible; a, detail of symphyseal area; b, p3–m2, occlusal view.

3. *Ancylotherium pentelicum*, Karaslari, Republic of Macedonia. Tooth-row p2–m3; occlusal view.

4. *Ancylotherium pentelicum*, Karaslari, Republic of Macedonia. Skull; a, lateral view; b, dorsal view.

5. *Ancylotherium pentelicum*, Republic of Macedonia. Partial hind-limb, front view.

6. *Ancylotherium pentelicum*, Kiro Kuchuk, Republic of Macedonia. Upper left P3, DP4, M1 KK2805, occlusal view.

Scale bar = 5 cm for figs. 1, 2b, 6; 10 cm for fig. 3; 20 cm for fig. 4; 40 cm for fig. 5.

Plate 7.

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

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

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

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

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

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

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

Plate 8.

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

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

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

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

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

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

Plate 9.

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

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

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

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

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

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

Plate 10.

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

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

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

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

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

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

Plate 11.

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

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

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

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

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

Scale bar = 30 cm.

Plate 12.

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

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

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

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

Plate 13.

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

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

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