Upper Miocene mammals from Strumyani, South-Western Bulgaria

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ABSTRACT

The localities of Strumyani in the Struma valley (South-Western Bulgaria) yield a rich assemblage of large mammals, including more than 20 species, hipparions and rhinos being especially well represented. Many species are commonly found in the Balkano-Iranian province, but there are also some rarely found taxa, such as *Tapirus* Brünnich, 1771, *Dorcatherium* Kaup, 1833, and a cervid that looks different from other contemporaneous finds. The instantaneous nature of the deposition shows that the association of taxa with likely diverse ecological requirements reflects a truly mosaic environment. The close similarity of the faunal association with that of Pikermi implies a similar middle Turolian age, although some differences suggest that Strumyani is earlier than this Greek locality. The issue of the age of Turolian sites of the Balkans is discussed.

KEY WORDS
Bulgaria,
Upper Miocene,
mammalian fauna,
paleoenvironments.

RÉSUMÉ

Mammifères du Miocène supérieur de Strumyani, Bulgarie du sud-ouest .

Les localités de Strumyani dans la vallée du Struma (sud-ouest de la Bulgarie) livrent un riche assemblage de grands mammifères, comprenant plus de 20 espèces, les hipparions et les rhinocéros étant particulièrement bien représentés. De nombreuses espèces sont fréquemment rencontrées dans la province balkano-iranienne, mais on trouve aussi quelques taxons rares, comme *Tapirus* Brünnich, 1771, *Dorcatherium* Kaup, 1833, et un cervidé qui semble différent des formes contemporaines. La nature instantanée du dépôt montre que l'association de taxons à exigences écologiques probablement différentes reflète vraiment un environnement mosaïque. L'étroite ressemblance de l'association faunique avec celle de Pikermi implique un âge semblable, Turolien moyen, bien que quelques différences suggèrent que Strumyani est plus ancien que ce site grec. La question de l'âge des sites turoliens des Balkans est discutée.

MOTS CLÉS
Bulgarie,
Miocène supérieur,
faune mammalienne,
paléoenvironnement.

INTRODUCTION

More than 40 Upper Miocene vertebrate localities have been recognized in South-Western Bulgaria, and several others in the central part of Southern Bulgaria, as a result of our geological and palaeontological surveys from 1999 to 2009 (Spassov 2002; Spassov *et al.* 2006). Most of them are located in the Middle Struma River basin, the Turolian localities of the Strumyani genetic lithocomplex (Tzankov *et al.* 2005) being the most numerous (Fig. 1). Many local formations were named in the past for the Middle Struma continental Neogene; the reasons for discarding them here, and for using "genetic lithocomplexes" for the alluvial terrigenous continental deposits of the Struma valley instead, are discussed in Tzankov *et al.* (2005: 25-29, 124) and in Spassov *et al.* (2006). This allows better taking into account climatic data, data on the genesis and age of the deposits, using the biochronologic data in the lithocomplex definitions, and tracing contemporaneous deposits over long distances. The locality of Strumyani-1 (Str-1; coordinates 41°37'43"N, 23°13'07"E, altitude 130 m), formerly called Ilindentsi (Spassov 2002), was discovered by one of us (NS) in 2001. A survey by NS, DG and GM in 2002 led to the discovery of a second fossiliferous spot, Strumyani-2 (Str-2; 41°37'43"N, 23°13'02"E, altitude 152 m), on the other side of a ravine, topographically above Str-1.

The first brief notes on the fauna, stratigraphy and preliminary biochronology of the Strumyani localities were given in Spassov *et al.* (2006). The fossiliferous area of Strumyani is one of the richest Upper Miocene fossil sites of Bulgaria, together with Hadjidimovo (Mesta river basin), Azmaka (Maritsa river basin), Kalimantsi, Gorna Sushitsa and Ploski (Struma river Basin) that have already provided a total of about 35 000 fossils.

Both Strumyani localities were excavated by the authors in 2002, 2003 and 2007, but Str-2 is by far the richest spot, and unless otherwise indicated, all fossils described below come from this locality. The material from Strumyani is housed in the National Museum of Natural History, Sofia. Preservation of the fossils is rather good, with only minor crushing or deformation, and a bone surface that is not weathered, although often heavily cracked, making preparation difficult.

ABBREVIATIONS

Dental nomenclature for Proboscidea follows Tassy (1996). Upper teeth are in upper case, lower teeth in lower case. Measurements are in mm.

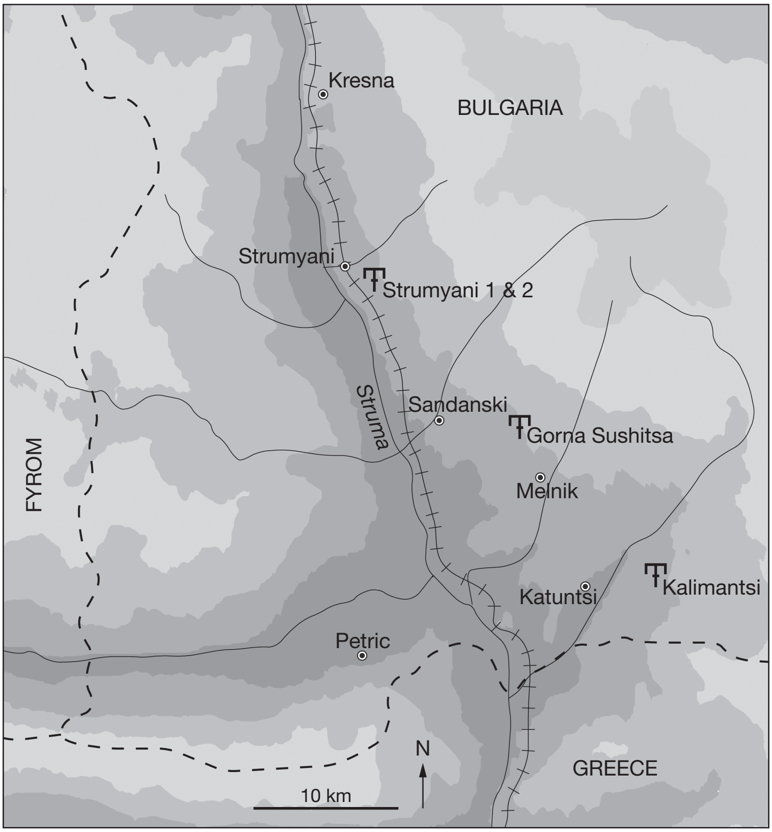

Fig. 1. — Map of South-Western Bulgaria with the location of Strumyani and of some other fossil localities.

Institutions

FM	Fossil Mammal collection, NMNHS;
HGI	Hungarian Geological Institute, Budapest;
HNHM	Hungarian Natural History Museum, Budapest;
MNHN	Muséum national d'Histoire naturelle, Paris;
NHM	Natural History Museum, London;
NHMW	Naturhistorisches Museum Wien, Vienna;
NMNHAs	Palaeontological Museum (Branch of NMNHS), Assenovgrad;
NMNHS	National Museum of Natural History, Sofia;
UW	Universität Wien, Vienna.

Anatomical abbreviations

APD	antero-posterior dimension;
dext.	right;
dist.	distal;
ET	enamel thickness;
H	height;
L	length;
max.	maximum;
MDD	mesio-distal dimension;
prox.	proximal;
sin.	left;
TD	transverse dimension;
VLD	vestibulo-lingual dimension;
W	width.

GEOLOGY AND STRATIGRAPHY

The Strumyani area gave its name to the Upper Miocene Strumyani Genetic Lithocomplex (Tzankov *et al.* 2005; Spassov *et al.* 2006). The lower boundary of the stratigraphic unit is transitional upon the rocks of the Gradishte Bench Mark Group of strata, while the upper boundary presents a rapid transition to the base of the

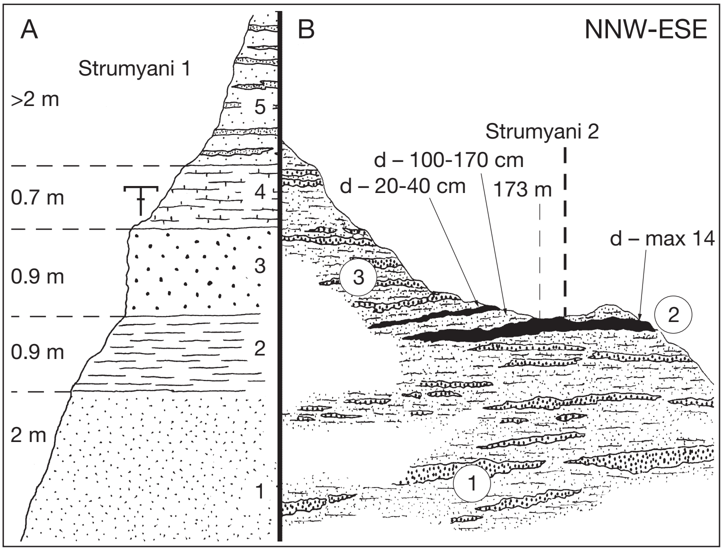

FIG. 2. — **A**, Lithostratigraphic sketch of Strumyani-1: **1**, yellowish sands; **2**, brownish clays; **3**, consolidated sandstones with abundant sandy cement; **4**, fossiliferous sandy clays; **5**, bedded sandstones; **B**, lithostratigraphic sketch of Strumyani-2: **1**, unsorted conglomerates with abundant sandy cement; **2**, compact unclear banded grey-brown carbonate sandy clays (**d**, thickness in centimeters); **3**, irregular succession of incoherent sandstones with conglomerates and clayey beds.

Piperitsa Genetic Lithocomplex. The Strumyani Genetic Lithocomplex includes what are often called the Sandanski and Kalimantsi Formations. It crops out in a wide belt on the left bank of the Struma River from the south of the city of Dupnitsa to Northern Greece. Its type area is between the villages of Strumyani, Ploski and Kresna. The Strumyani lithocomplex, as defined in Tzankov *et al.* (2005) includes a number of fossiliferous localities that yield faunas of Turolian age. As we will see, the detailed analysis of the fauna from the type locality, Strumyani, refines our previous biochronological assessment, by showing that the base of this lithocomplex yields a fauna of middle Turolian age.

Deposits in the investigated area are composed mostly of white-grey, grey, yellow-grey or yellow alluvial-proluvial terrigenous sands or sandy-clays and alleurolite-clays with rich terrigenous-carbonate cement. These layers usually have a very limited horizontal extent, with quick lateral changes of facies, and frequent intercalations of centimetric to decimetric thin irregular beds and lenses, which preclude direct correlation between closely located sections. The lithologic sequence of Str-1 (Fig. 2A) clearly differs from that of Str-2 (Fig. 2B). The uppermost part of the section at Str-1 consists of sandstones of various granulometry and clear bedding. The fossil locality Str-1 was found in sandy clays, immediately on top of a thin bank (about 90 cm) of consolidated sandstones with abundant sandy cement. These sandstones are underlain by a layer of about 70-150 cm thick brownish clays that crops out for several tens of meters on the left bank of the main erosion ravine that follows a normal fault (see below), itself underlain by 2 m of yellowish sands at the base of the Str-1 exposures. These layers are not clearly observable on the other side (right bank) of the ravine, where the fossil locality Str-2 was found in a greyish sandy clay layer (Fig. 2B).

The two sections Str-1 and Str-2 are separated by a North-South oriented high angular normal fault. Its fault plane is complicated by a meridional oriented secondary normal listric fault. The main fault and the other dislocations (high- or low-angle normal faults) of the local fault net determined Upper Neogene and Quaternary vertical block movements in the investigated area. These complex movements and the lack of a layer that could definitely correlate them precludes identification of the uplifted block, and the estimation of the throw, as this type of sediments is characterized by rapid vertical and lateral changes of lithology. The present-day altitude difference between the two localities is about 22 m. A patch of brownish clays, resembling the brownish clay layer under Str-1 is visible on the right bank, near the base of the outcrop, at about the level of the clay layer mentioned above at Str-1; if it correlates with the brownish clay level at Str-1 (see Fig. 2A[2]), the relative position of the sites was not much affected by the fault, implying that Str-1 was slightly lower than Str-2.

SYSTEMATIC PALAEONTOLOGY

Order RODENTIA Bowdich, 1821
Family HYSTRICIDAE Fischer, 1817

Hystrix primigenia (Wagner, 1848)

Scarce remains of this species were collected from Str-2: upper and lower incisors with a mandible fragment, some phalanges and fragments of metapodials, all probably from a single individual. The metapodials and phalanges are more robust than in modern *Hystrix* Linnaeus, 1758. The length and proximal width of first two (anterior ?) phalanges are: 19 × 11 mm and 17 × 10.9 mm. The length of a complete lower incisor, measured along the curve, is 105 mm.

The recent *Hystrix* have a solitary mode of life or lives in pairs and are not abundant in comparison to many other mammals of the same zoocoenosis. Probably because of a similar biology, *H. primigenia*, although frequent in the Upper Miocene of the Balkano-Iranian province, is never abundant. In the Turolian of Bulgaria it is known from the middle Turolian of Kalimantsi (Sen & Kovachev 1987), and from the early/middle Turolian of Hadjidimovo-1 (Spassov 2002), where it is represented by an almost complete skeleton (Kovachev & Atanasova 2008).

TABLE 1. — Dental measurements (in mm) of ?*Tetralophodon atticus* (Wagner, 1857) teeth from Strumyani.

Coll. no.	Position	L	W max	H	ET
FM-2187	DP2 sin.	33.3	28.2	20.0	1.2
FM-2798	DP3 dext.	53.5	35.5	*c.* 25	1.5-2.0
FM-2797	DP3 dext.	>49	38.5	>30	2.5
FM-2799	dp2 dext.	31.0	22.4	23.5	1.5

Order CARNIVORA Bowdich, 1821

Some long bones from a single individual of a small carnivore (among them a humerus with supracondylar foramen indicating a probable Mustelidae) as well as three metacarpals and some phalanges of a carnivore, the size of a fox and the proportions of a small ictithere, are the only carnivore remains in the Strumyani fauna.

Order PROBOSCIDEA Illiger, 1811
Superfamily ELEPHANTOIDEA Gray, 1821

?***Tetralophodon atticus*** (Wagner, 1857)

Four deciduous teeth at various stages of preservation demonstrate the presence of bunodont tetralophodont elephantoids in Str-2. Their measurements are given in Table 1.

FM-2187 is a relatively well-preserved DP2 sin. (Fig. 3A; the second loph is damaged on the posttrite side). The tooth is bilophodont, with strongly developed anterior and posterior cingula. The first loph consists of a large paracone and a very weak protocone fused with the paracone. The second loph is wider than the first, and is separated from it by a narrow interloph that, despite the presence of weak crests on the posterior wall of the paracone and the anterior of the hypocone, remains open. The valley between the second loph and the well-developed posterior cingulum is blocked by a cusp situated behind the median sulcus.

FM-2798 (Fig. 3C) is a DP3 dext. Although parts of the crown are missing, those that are preserved provide a fairly good idea of the tooth size and shape. It is trilophodont, with a strong anterior cingulum, a part of which is preserved on the pretrite side, and a posterior cingulum closely pressed to the third loph.

FM-2797 is a DP3 dext. posterior fragment. Compared to FM-2798, the posterior cingulum is more extended buccally, and more clearly separated from the posterior loph, lacking the multicuspid connection to the pretrite semiloph observable in FM-2798. The pre- and posttrite halves of the posterior loph are of equal height, aligned and separated from the penultimate loph by a broad interloph. A strong cingulum is present on the linguo-distal part of the crown.

FM-2799 (Fig. 3B) is a right dp2 bearing little to no trace of use. The crown is mostly intact, with a fragment on the lingual side (between the first and second posttrite cusps) missing. The tooth is bilophodont, with a posterior cingulum clearly separated from the second lophid. The anterior cingulum is strongly reduced. The first loph, which is nearly twice as high as the second one, consists of a strongly developed protoconid and a low metaconid closely attached to it. On the second lophid, the entoconid and the hypoconid are clearly separated from each other, and the interlophid is free on the pretrite side. As far as can be judged from the preserved part of the second posttrite, the interlophid was blocked on the posttrite side, with a weak cross-contact between the first pretrite and the second posttrite cusps. On both the pretrite and the posttrite sides, the cusps of the second lophid are connected with the posterior cingulum by an additional posterior cuspid on each side.

Morphologically, as well as metrically (Fig. 4), the DP2 from Str-2 is very similar to those in the two DP2-DP3 tooth rows of *Tetralophodon atticus* from Pikermi described by Wagner (1857; type specimen of *T. atticus*) and Gaudry (1862-1867). It differs from the DP2s of the earlier *T. longirostris* (Kaup, 1832) in the strongly reduced protocone and from the later *Anancus arvernensis* (Croizet & Jobert, 1828) in its larger size (see Metz-Muller 1996, 2000). Presence of a well-developed posterior cingulum in FM-2187 sets it apart from DP2s of *A. kenyensis* (MacInnes, 1942) from the Middle Awash described by Saegusa & Haile-Selassie (2009). The Turolian species *T. atticus* is known from various localities in Europe and west Asia, including Bulgaria (Markov 2008) and attribution of FM-2187 to that taxon seems plausible. It must be noted, however, that morphology of DP2 (and several other teeth, including most of the deciduous premolars) is not known for "*Mastodon*" *grandincisivus* Schlesinger, 1917, an amebelodontid (see Tassy 1985, 1999, 2005) that not only developed tetralophodont intermediary teeth in parallel with tetralophodont gomphotheres but also has a stratigraphical and geographical distribution largely overlapping with those of *T. atticus*. Thus, except for the two specimens from Pikermi mentioned above, the status of all available material from Strumyani as well as the comparable finds from the Turolian of Europe and west Asia listed below, is somewhat ambiguous, as they might potentially belong to *T. atticus* or "*M.*" *grandincisivus*.

Comparable material includes deciduous teeth from the locality Taraklia in Moldova referred by Khomenko (1914) to *Tetralophodon longirostris* and identified as *T. atticus* by Tassy (1985), followed by Metz-Muller (1996, 2000). Additional finds from Taraklia described by Riabinin (1929), and teeth from Grebeniki (Ukraine) published by Burchak-Abramovich (1940), seem to belong to *T. atticus* too (Markov 2008). At Hadjidimovo in Bulgaria, *T. atticus* seems to have co-occurred with "*M.*" *grandincisivus* (Markov 2004, 2008). There is also a DP2-DP4 tooth row from Pikermi referred by Marinos & Symeonidis (1974) to *Ch. pentelici* (Gaudry & Lartet, 1856) and identified as a tetralophodont elephantoid (i.e. either *T. atticus* or "*M.*" *grandincisivus*) by Markov (2004); unfortunately, no measurements are provided by the authors.

Metrically, the DP3 from Str-2, FM-2798, clearly surpasses the teeth of *T. longirostris* from Eppelsheim and Laaerberg, falling within the variation range of material from several Turolian localities in Europe and west Asia (Fig. 5). In addition to Pikermi, Taraklia, Grebeniki and Hadjidimovo, these include Akkaşdağı in Turkey (Tassy 2005), Cimişlia in Moldova (material described by Simionescu & Barbu [1939] as *T. longirostris* and referred to *T. atticus* by Markov [2008]), Kalimantsi in Bulgaria (Markov 2004, 2008), and Maragheh (material published by Mecquenem [1924] as *Ch. pentelici* and identified as *T. atticus* by Markov [2008]). Again, except for the Pikermi specimens described by Wagner (1857) and Gaudry (1862-1867), the rest of the material might be heterogeneous and include teeth

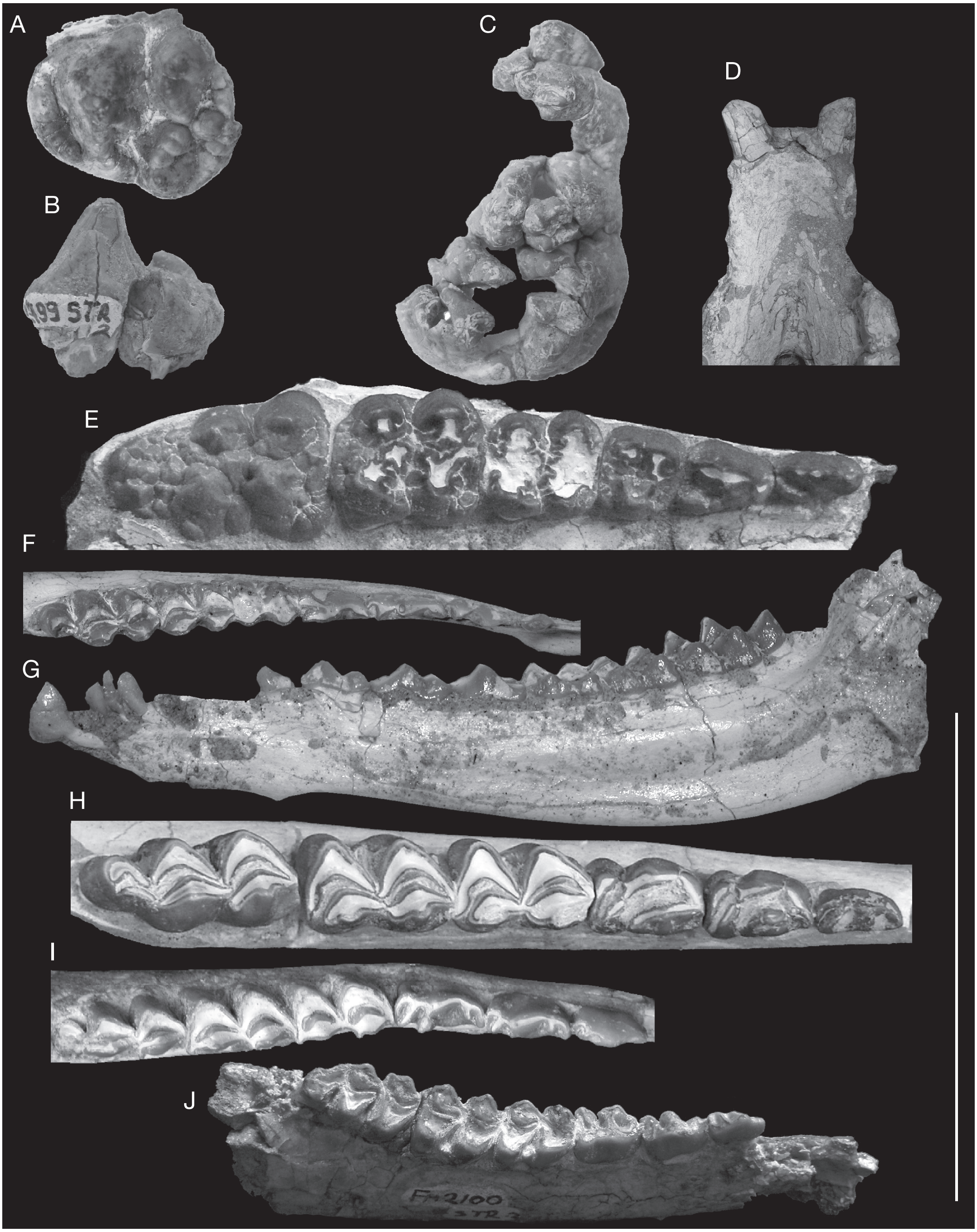

FIG. 3. — Fossil mammals from the Miocene of Strumyani (SW Bulgaria): **A**-**C**, ?*Tetralophodon atticus* (Wagner, 1857); **A**, DP2 FM-2027, occlusal view; **B**, dp2 FM-2799, lingual view, **C**, DP3 FM-2798, occlusal view; **D**, *Dihoplus pikermiensis* (Toula, 1906), dorsal view of symphysis FM-2470; **E**, *Microstonyx major* (Gervais, 1848), maxilla FM-2801; **F**, **G**, *Dorcatherium* cf. *puyhauberti* Arambourg & Piveteau, 1929, mandible FM-2741 in occlusal (**F**) and lateral (**G**) views; **H**, *Palaeotragus rouenii* Gaudry, 1861, mandible FM-2778; **I**, *Miotragocerus* (*Pikermicerus*) *gaudryi* (Kretzoi, 1941), mandible FM-2103; **J**, Cervidae gen. et sp. indet., mandible FM-2100. Scale bar: A-C, F-J, 7.5 cm; D, 30 cm; E, 10 cm.

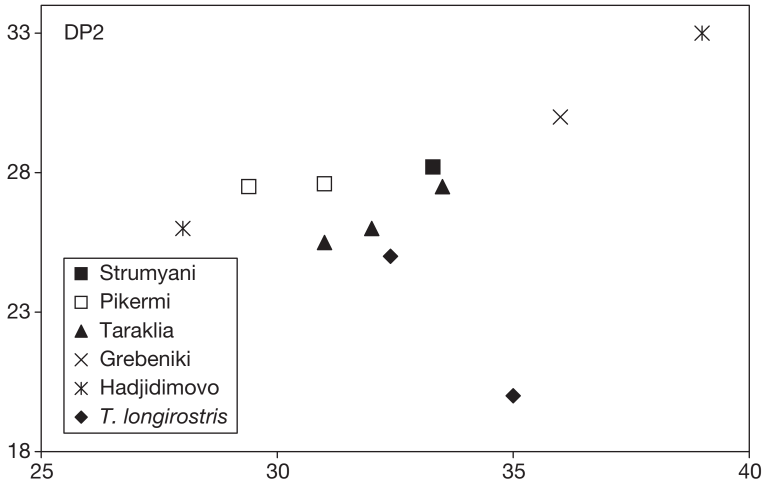

Fig. 4. — Bivariate plots (L × W) of DP2 in tetralophodont elephantoids from Strumyani and other Late Miocene sites. Data: GM (own measurements MNHN, NHM, NHMW, NMNHAs) and sources quoted in the text. Abbreviation: **T.**, *Tetralophodon*.

of "*M.*" *grandincisivus*. The alignment of the halves of the preserved loph in FM-2797 is a derived trait observed in *T. atticus*, yet the state of this character is unknown in "*M.*" *grandincisivus*.

As for the lower dp2, FM-2799, it is readily distinguished from dp2s of *Anancus arvernensis* analyzed by Metz-Muller (1996, 2000), a dp2 from the Upper Pliocene of Ahl al Oughlam (Morocco) referred by Geraads & Metz-Muller (1999) to *Anancus* cf. *osiris* Arambourg, 1946, and *A. kenyensis* dp2s from Middle Awash (Ethiopia) described by Saegusa & Haile-Selassie (2009). Larger than all these anancine teeth, it further differs from *A. kenyensis* and *A. arvernensis* in the development of the posterior cingulum, and from the Ahl al Oughlam specimen in the incomplete fusion of the meta- and protoconid. On the other hand, the only positively identifiable dp2 of "*M.*" *grandincisivus* (in the unpublished mandible from Hadjidimovo, NMNHAs HD-38029) has a meta- and paraconid that are clearly set apart from each other and do not differ in height as drastically as in FM-2799. Interestingly, the dp2 from Taraklia published by Khomenko (1914) and referred to *T. atticus* by Tassy (1985) and Metz-Muller (1996), has a meta- and paraconid less closely attached to each other than in the Strumyani dp2, and is metrically closer to the dp2 of "*M.*" *grandincisivus* from Hadjidimovo than to FM-2799. On the other hand, a dp2 from Csákvár in Hungary (HGI V.11393: see Gasparik 2001: 70) is metrically close to the dp2s from Taraklia and Hadjidimovo (GM pers. obs. HGI, 2005) but quite similar to the Str-2 dp2 in the closely attached meta- and paraconid.

Rather than casting doubt on the attribution of the Taraklia dp2 to *T. atticus*, this example aptly demonstrates the difficulties in identifying isolated deciduous teeth as either *T. atticus* or "*M.*" *grandincisivus*, two poorly known, co-occurring taxa with homoplastic characters.

Str-1 yielded only a few fragmentary post-cranial proboscidean remains.

Order PERISSODACTYLA Owen, 1848
Family Tapiridae Gray, 1821

Tapirus sp.

The tapir is represented at Str-1 by a right distal tibia FM-2247 (dist. TD = 37; dist. APD = 30.2). As in suids, it shows a large and rugose synchondral articulation for the fibula, but differs in: the more anterior position of the medial maleolus; the wide, flattened and oblique lateral articular facet of the

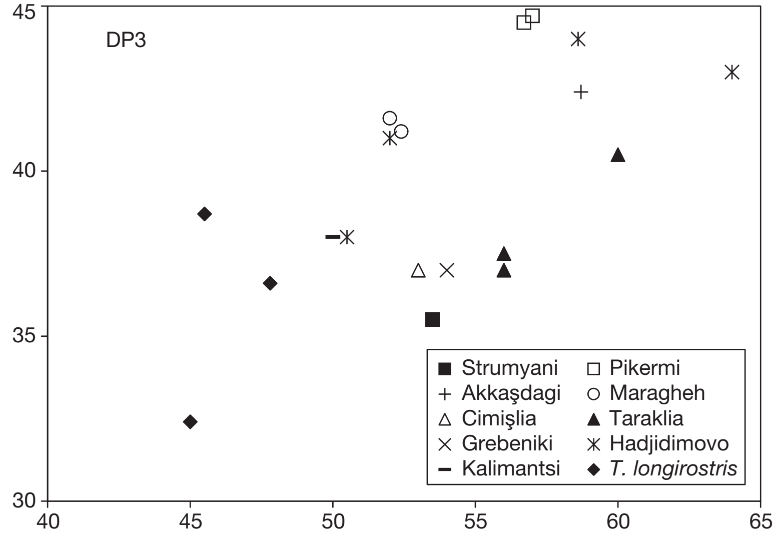

FIG. 5. — Bivariate plots (L × W) of DP3 in tetralophodont elephantoids from Strumyani and other Late Miocene sites. Data: GM (own measurements MNHN, NHM, NHMW, NMNHAs) and sources quoted in the text. Abbreviation: **T.**, *Tetralophodon*.

tibial cochlea; the shallow distal articular surface (in lateral and medial views); the weak development of the distal tuberosity of the caudal surface. All these features are typical of some perissodactyls, especially rhinos and tapirs, and match those of a small tapir. Its maximum weight could be estimated, after a direct comparison with the corresponding bone of wild boars of known weight, at about 150 kg, comparable to that of the modern Andean tapir, *Tapirus pinchaque* (Roulin, 1829).

Turolian tapirs are rare in Europe. With a few exceptions (Dorn-Dürkheim and Sarmasag), all of them are from Southern Europe, and most of them are probably of late Turolian age: Autley and Arc (France); Baccinello V3 and Casino (Italy); Kreka (Bosnia); Djonaj (Kosovo); Beli Breg, Balsha and Hrabarsko (Bulgaria). Early to middle Turolian finds are rare: Camallera II (Spain), Aubignas II (France), Dorn-Dürkheim (Germany), Sarmasag (Romania), Hadjidimovo (Bulgaria) (Made & Stefanovic 2006; Spassov & Ginsburg 1999 and pers. obs.). The Zivoino find, from the Republic of Macedonia (FYROM), near Bitola, could be late Turolian (Made & Stefanovic 2006): the Miocene deposits of this coal bearing area yield a Turolian fauna (pers. obs. NS) but the presence of *Zygolophodon* Vacek, 1877 (Garevski, Markov & Garevska unpublished) in the coal deposits of the region indicate the possibility of an earlier age. The age of Barro (France) is also uncertain (Turolian or Ruscinian) (Spassov & Ginsburg 1999; Made & Stefanovic 2006). Unpublished finds from the Turolian of Bulgaria (Staniantsi, Beli Breg, Kanina quarry and Ploski), together with the find from Strumyani 2, make Bulgaria and the northern Balkan area the region with the largest number of Turolian *Tapirus* remains in Europe.

The systematics of those tapirs is unclear. As a rule they are small, and a small form is already present in the Vallesian of Central Europe, where it coexists with the large *T. priscus* Kaup, 1833. This small form was referred to a distinct genus, *Tapiriscus* Kretzoi, 1951 (Guérin & Eisenmann 1994), but generic separation is doubtful (Spassov & Ginsburg 1999; Made & Stefanovic 2006) as the type material is restricted to a few isolated lower premolars and is rather uninformative. Another species of small Turolian tapir, *Tapirus balkanicus* Spassov & Ginsburg, 1999, was erected on the basis of a mandible from Balsha and a maxilla from Hrabarsko (Bulgaria). Thus, a phylum of small tapirs might have existed in Europe from the Vallesian to the late

Turolian with two successive species, progressively adapting (including in their decreasing body size and improved mobility) to harder vegetation and more arid and open conditions.

Family RHINOCEROTIDAE Gray, 1821

Geraads & Spassov (2009) provide a detailed account of all Bulgarian Upper Miocene Rhinocerotidae, including those from Strumyani. There is no evidence of any hornless rhino (*Acerorhinus* Kretzoi, 1942 or *Chilotherium* Ringström, 1924) at Strumyani, but the two taxa commonly found in the Upper Miocene of the Balkans, *Dihoplus* Brandt, 1878 and *Ceratotherium* Gray, 1868, are present. Str-2 is probably the best example of coexistence of these two forms in the very same layer.

Dihoplus pikermiensis (Toula, 1906)

The best specimen is skull FM-2469, which is complete but with a bone surface that is heavily eroded and fragmented (Geraads & Spassov 2009: fig. 2, pl. 1, G, H). It clearly displays all the features by which the skull of this species can be distinguished from that of *Ceratotherium neumayri* (Osborn, 1900) (Geraads 1988; Geraads & Spassov 2009), such as the sharp ventral orbital border, the shortened cranial basis with the post-tympanic overlapping the post-glenoid process, and a constricted protocone on the molars. The rarely preserved premaxillae are complete, and show no trace of incisors. Such incisors are large in its likely ancestor *D. schleiermacheri* (Kaup, 1832), and may still occasionally be found in *D. pikermiensis*.

The mandible FM-2470, found close to the skull and probably belonging to the same individual, has a straight ventral border, unlike *C. neumayri*, and a pair of large incisors (Fig. 3D), much smaller than in *D. schleiermacheri*, but less reduced than in other specimens of *D. pikermiensis*. Measurements are given in Table 2.

In Bulgaria, *D. pikermiensis* is also present at Kalimantsi and common at Hadjidimovo. It is also quite common in its type-locality, Pikermi, and has also been described from several other Turolian localities of the Aegean region (Geraads 1988, 1994; Giaourtsakis 2003, 2009; Giaourtsakis *et al.* 2006; Geraads & Spassov 2009). At Str-2, the absence of upper incisors, and the presence of relatively large lower ones, suggest an age slightly earlier than Pikermi, if we are correct in assuming a trend towards reduction of the incisors.

Ceratotherium neumayri Osborn, 1900

FM-2468 is a mandible that can easily be distinguished from that of *Dihoplus* by its strongly convex ventral border and complete lack of incisors (Geraads & Spassov 2009). The anterior border of the ascending ramus is more inclined than in *Diceros bicornis* (Linnaeus, 1758), a correlate of the less forwardly inclined occipital than in this species. Another mandible, FM-2800, previously undescribed, lacks most of the rami, but is otherwise similar to the previous one: not very large, but robust, with deep and convex ventral border. The spade-like symphysis is somewhat damaged but clearly lacked incisors. Measurements are given in Table 2.

In Bulgaria, the only other occurrence of this species is at Kalimantsi, but it has a good record in the Late Vallesian and Turolian of the Eastern Mediterranean (Geraads 1988, 1994; Giaourtsakis 2003; Giaourtsakis *et al.* 2006; Geraads & Spassov 2009). Antoine & Saraç (2005) accepted the idea of a size increase during the Turolian, although it rests upon scant evidence. The material from Str-2 is not particularly large, as most post-cranial measurements are within the range of the modern *C. simum* (Guérin 1980); therefore, it gives no clear biochronological indication.

Some rhino limb bones, especially metapodials, could belong to either of the two large horned species present at Strumyani. From Str-1, there is a Mc II FM-2236 (L = 159; proximal APD = 51.6, dist. transverse diameter = 40.4) with a curved magnum facet and a short palmar tuberosity more like *C. neumayri*, and from Str-2 there are some metapodials including a Mc II with a straighter facet and a longer palmar tuberosity. None of these

TABLE 2. — Measurements (in mm) of Rhinocerotidae Gray, 1821 mandibles from the Miocene of Strumyani (SW Bulgaria). *****, length of pre-dental portion; **C.**, *Ceratotherium*; **D.**, *Dihoplus*.

Species	Collection number	Overall length	Depth to sigmoid notch	Length of diastema	Length of symphysis	Width of symphysis	p2-p4	m1-m3
D. pikermiensis	FM-2470	630	235	106	151	76	117	168
C. neumayri	FM-2468	555	180	63*	121	*c.* 90	109	156
C. neumayri	FM-2800	–	–	78*	128	80	103	151

clearly match either of the two types recognized by Geraads (1988) at Pikermi, and we prefer not to attempt identification.

Measurements of some other bones: Uncinate FM-2234 (Str-1): L max. = 93.7; anat. L = 70. Uncinate FM-2771: L max. = 102; anat. L = 86.5. Astragalus FM-2167 is broad, with a shallow trochlea; Max. TD ≈95.7; Max. dist. TD ≈83; max. TD of trochlea = 89; H ≈86. Dist. humerus FM-2290: max. W = 182 mm; dist. articular W = 113. MC III FM-2237: W of shaft ≈65; prox. W = 68.4. MC III FM-2215-A: W of shaft = 67; prox. W = 69.7. MT III FM-2420: prox. W = 62; dist. articular W = 56.

Family CHALICOTHERIIDAE Gill, 1872

Ancylotherium pentelicum (Gaudry & Lartet, 1856)

FM-2027 from Str-1 is the medial half of a right talus (medial height = 71; medial depth = 78). The lip of the trochlea is very rounded; the navicular facet is strongly convex transversely and sharply narrows laterally. What is preserved of this talus does not significantly differ from other tali of *Ancylotherium* Gaudry, 1863, a genus best known from the Balkano-Iranian province and rather common in most of our Upper Miocene localities of SW Bulgaria (including the recently surveyed localities of Gorna Sushitsa and Ploski), but which might in fact range from Spain to China (see e.g., Geraads *et al.* 2006a). Although mostly found in Turolian assemblages, it occurs earlier, and lingers as late as the Pleistocene in Africa; it is therefore of little biochronological use.

Family EQUIDAE Gray, 1821

The vernacular name "hipparion" is used here for equids with an isolated protocone on upper cheek teeth and, as far as known, tridactyl feet. It includes species of the genera *Cormohipparion*, *Neohipparion*, *Nannipus*, *Pseudohipparion*, *Hippotherium*, *Cremohipparion*, *Hipparion*, "*Sivalhippus*", *Eurygnathohippus*, *Proboscidipparion*, "*Plesiohipparion*" (after Bernor *et al.* 1996).

Hipparion dietrichi (Wehrli, 1941)

There are two relatively well preserved skulls of this species. FM-2029 is a subadult individual, with unerupted I3s, C and M3 just erupted (Fig. 6C). FM-2030 belongs to an adult individual, but is not well-preserved, so that some of the characters described are those of FM-2029. The muzzle is short and broad. The nasal slit ends above the anterior end of P2; the crista facialis reaches the middle of P4; the choanae reach the limit M1-M2; the orbit is above the posterior half of M3. The antero-posteriorly oriented preorbital fossa is small and shallow, without posterior pocket and with a weak anterior rim. It extends from above the anterior part of P3 to above the posterior border of M1. The infraorbital foramen is large, located below the anterior border of the fossa. Tooth row length is about 136 mm for FM-2029 and 153 mm for FM-2030. There is no DP1. The anterostyle of P2 is elongated. The enamel is moderately plicated, with rounded folds whose number ranges from 14 on the premolars to 21 on the molars. The *pli caballin* is single. The protocon is oval, and lenticular on the less worn teeth. The hypocone is elongated, angular on P4; the hypoconal sinus is comparatively deep in the subadult skull and medium to absent in the adult one.

The short and broad muzzle, antero-posteriorly oriented oval preorbital fossa without well defined peripheral rims and without posterior pocket, relate this skull to *H. dietrichi*, and the tooth features support this conclusion. *Hipparion dietrichi* is known from many localities in Greece, Turkey and Republic of Macedonia (Koufos 1987c, 1988; Forstén & Garevski 1989; Vlachou & Koufos 2002, 2006, 2009; Koufos & Vlachou 2005). From its muzzle length the skull from Str-2 is close to *H. dietrichi* from Akkasdağı, but in cheek tooth length it is intermediate between the Perivolaki and Vathylakkos samples on the one side and the Akkasdağı form on the other (Koufos 1988; Koufos & Vlachou 2005; Vlachou & Koufos 2006).

***Hippotherium* cf. *brachypus* (Hensel, 1862)**

There is only one skull of a young individual, FM-2326, with deciduous teeth (DP1-DP4), M1 and the tips of M2 (Fig. 6A). The region above the cheek teeth, with the left preorbital fossa, is preserved. The orbit is about 7 mm behind M2. The preorbital fossa is oriented antero-ventrally, sub-triangular, and deep. The peripheral rims are well defined, with a slight posterior pocket. The infraorbital foramen is located at the antero-ventral border of the preorbital fossa, above the limit DP2-DP3. The facial crest ends at the limit P4-M1. The choanae reach the middle of M1. Enamel plication of the deciduous teeth is rich, with multiple *plis caballins* and rounded protocon. M1 is slightly worn, the posterior fossette is still open and the enamel features are not clearly visible. The protocon is elliptical, the *pli caballin* is simple.

As the specimen is not well-preserved and belongs to a young individual, it is difficult to draw reliable conclusions about its taxonomical appartenance. The species with well-developed, sub-triangular preorbital fossa situated far from the orbit are *H. primigenium*, *H. giganteum*, and *H. brachypus*. The preserved portion of the skull resembles all of them. We can exclude *H. primigenium* as the rest of the fauna is unlikely of Vallesian age. *Hippotheriun brachypus* is known from several Turolian localities: Hadjidimovo, Kalimantsi, Akkasdağı, Pikermi and Samos (Hristova *et al.* 2003; Hristova & Kovachev 2005; Koufos 1987a; Koufos & Vlachou 2005; Vlachou & Koufos 2009). Gromova (1952) described a closely related species, *H. giganteum*, from the early Turolian of Grebeniki (GREB), Ukraine, but its differences from *H. brachypus* are not clear. Vlachou & Koufos (2009) think that they are related to the degree of retraction of the nasal slit, but the problem looks more complex. Gromova erected the species *H. giganteum* on the basis of one juvenile and one adult skulls. From her description, one of the distinctive features of the species is a nasal slit positioned slightly anterior to P2. Gabunia (1959) expanded the diagnosis of the species, based upon this feature, on the basis of eight new skulls from the type locality. According to his observations, the level of the bottom of the nasal slit varies from just before P2 to above its anterior half. Thus, it partly overlaps its range in the sample of *H. brachypus* from Pikermi (above P2) and Hadjidimovo (usually above P2; only one specimen has a nasal slit above the anterior end of P3). The slightly shorter, more primitive, nasal slit of some specimens from Grebeniki, could be related to the earlier age of this site. The material from the type locality of *H. giganteum* needs revision but from the recent data, the position of the nasal slit cannot be used to separate *H. giganteum* from *H. brachypus*.

Cremohipparion mediterraneum
(Roth & Wagner, 1855)

We refer to this species: a skull, FM-2028, that belongs to an adult animal with the protocon of P2 almost connected to the protoloph (Fig. 6B), and a partial skull, FM-2325, with unerupted M3. The nasal notch ends above the anterior part of P2, the facial crest ends above the posterior end of P4 (FM-2325) or the first half of M1 (FM-2028). The choanae reach the posterior half of M2. The preorbital bar is short (28 mm) and in both skulls the lachrymal bone does not reach the rim of the

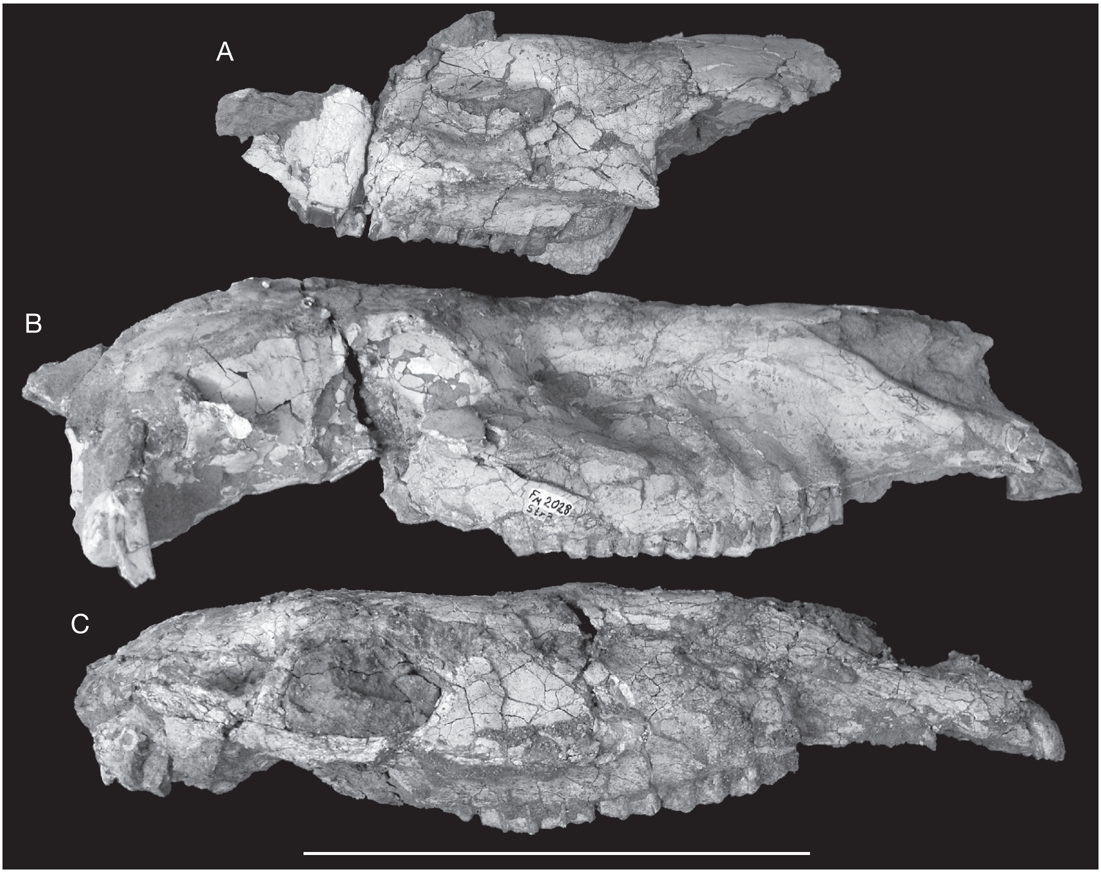

Fig. 6. — Fossil mammals from the Miocene of Strumyani (SW Bulgaria): **A**, *Hippotherium* cf. *brachypus* (Hensel, 1862), lateral view of skull FM-2326; **B**, *Cremohipparion mediterraneum* (Roth & Wagner, 1855), lateral view of skull FM-2028; **C**, *Hipparion dietrichi* (Wehrli, 1941), lateral view of skull FM-2029. Scale bar: 20 cm.

preorbital fossa. The preorbital fossa is large, moderately deep (about 10 mm), with moderate posterior pocket (about 7 mm). There is no trace of a canine fossa. The distance from orbit to facial crest is long: 29-32 mm. The infraorbital foramen is situated at the antero-ventral border of the preorbital fossa. The buccinator fossa is shallow. The muzzle of FM-2028 is short and narrow, with arc-shaped incisor series. The small size of the upper canine of FM-2028 suggests that it is from a female. The upper tooth row is slightly curved. The anterostyle of the P2 is elongate. The enamel plication is moderate, with 12-17 wide and shallow folds. The *pli caballin* is single, rudimentary on M1 and M2. The protocon is oval, with a thick, flattened lingual wall. The hypoglyph is shallow (on M1 and M2) to deep (on M3); only M3 has a labial sinus.

Cremohipparion mediterraneum is characterized by its medium size, a well-developed preorbital fossa located close to the orbit, and a narrow muzzle (Koufos 1987a). After Bernor *et al.* (1996) the diagnosis is: medium size, presence of the three distinct facial fossae (preorbital, canine, and buccinator); short preorbital bar; lacrimal invading preorbital fossa; nasal notch above P2 mesostyle; skull relatively short; snout short and narrow; complex to moderate enamel plication. According to Vlachou & Koufos (2009) in all specimens of *C. mediterraneum* from

Pikermi there exists an anterior, canine fossa, but the sample of the same species from Hadjidimovo-1 (Hristova *et al.* 2002; Hristova 2009) consists of specimens with and without canine fossa. The same is true of the *C. mediterraneum* specimens from Karaslari (Macedonia). Thus, at most, the diagnosis of the species could include the occasional presence of a canine fossa.

The species was described from several localities: Hadjidimovo, Perivolaki, Kemiklitepe A-B, Kalimantsi, Karaslari, Pikermi (Koufos 1987a, b; Koufos & Kostopoulos 1994; Hristova *et al.* 2002; Hristova & Spassov 2005; Vlachou & Koufos 2006). There are some differences between the various samples. Most specimens of early *C. mediterraneum* from Hadjidimovo (Bulgaria) and the one *C.* cf. *mediterraneum* from Perivolaki (Greece) have a well-developed canine fossa and a larger preorbital fossa located closer to the orbit, as well as deeper nasal notch and a longer muzzle (Hristova *et al.* 2002; Vlachou & Koufos 2006; Hristova 2009). The enamel plication of the Hadjidimovo sample is moderate to strong, with simple to double or multiple *pli caballin*. The later *C. mediterraneum* from Pikermi has a preorbital fossa situated slightly farther from the orbit and developed canine fossa (preserved only in PIK-259). The enamel plication is simple to moderate and the *pli caballin* is simple "very small and sometimes absent" (Koufos 1987a).

The differences between skull FM-2028 on the one side and the samples from Perivolaki and Hadjidimovo on the other side lie in the shorter preorbital bar, the larger and much deeper preorbital fossa, the longer tooth row, the presence of a well-developed canine fossa in most of the skulls from Hadjidimovo and in the one from Perivolaki, and deeper nasal notch. FM-2028 closely resembles the hipparions from Pikermi, but differs from them in the longer palate and shorter preorbital fossa. The dimensions of FM-2028 are within the range of the Pikermi sample and they show the greatest similarity with it.

Another species with a preorbital fossa placed close to the orbit and the facial crest is *C. moldavicum*, described from the Northern Black Sea coast, Maragheh and Akkasdağı (Gromova 1952; Forstén 1980; Bernor 1985; Watabe & Nakaya 1991; Krakhmalnaya 1996a, b; Forstén & Krakhmalnaya 1997; Krakhmalnaya & Forstén 1998; Koufos & Vlachou 2005). The differences between the Strumyani sample and samples of *C. moldavicum* from Taraklia (TAR-Moldavia) and Novoelisavetovka (Ukraine, after Gabunia 1959), Maragheh (Iran) and Akkasdağı (Turkey) are in the absolute and relative dimensions and morphology of the preorbital fossa (in *C. moldavicum* it is sub-rhomboidal, larger and deeper), in the deeper buccinator fossa, narrower muzzle, and in different skull proportions. There are differences in the data about the sample from Novoelisavetovka. According to Gabunia (1959), the preorbital bar length ranges from 20 to 31 mm, but for Krakhmalnaya (1996b) it ranges from 22 to 44 mm; the distance from the facial crest to the preorbital fossa ranges from 16 to 27 mm after Gabunia, but from 21.4 to 45.2 after Krakhmalnaya, who might have mixed data from two different species. The sample from Novaya Emetovka-2 (Ukraine) has longer skulls dimensions (400-414 mm), wider preorbital bar length (30-38 mm), larger (74-82 mm) and higher (48-57 mm) preorbital fossa. The specimens from Cherevichnoe are slightly smaller in overall size: tooth row length ranges from 123 to 134 mm and the distance from the anterior point of P2 to the most anterior point of the orbit is about 143-150 mm versus 140 mm and 160.6 mm respectively for FM-2028 from Str-2.

The sample from Str-2 shares some similarities with "*Hipparion*" *verae* Gabunia, 1959. This species has similar skull size, close dimensions of the preorbital fossa, and in one specimen the position of the nasal notch is above the anterior end of P2 as in FM-2028. But some other features, such as less plicated tooth enamel, longer preorbital bar and longer distance between the preorbital fossa and the facial crest distinguish "*H.*" *verae* from the Str-2 specimens. The species was described also from the Republic of Macedonia (Forstén & Garevski 1989), but our personal observations (L/H) do not confirm their species determination, as it seems that under this name these authors lumped *H. brachypus* and *C. mediterraneum* from Karaslari and *H. brachypus* from Basiboz.

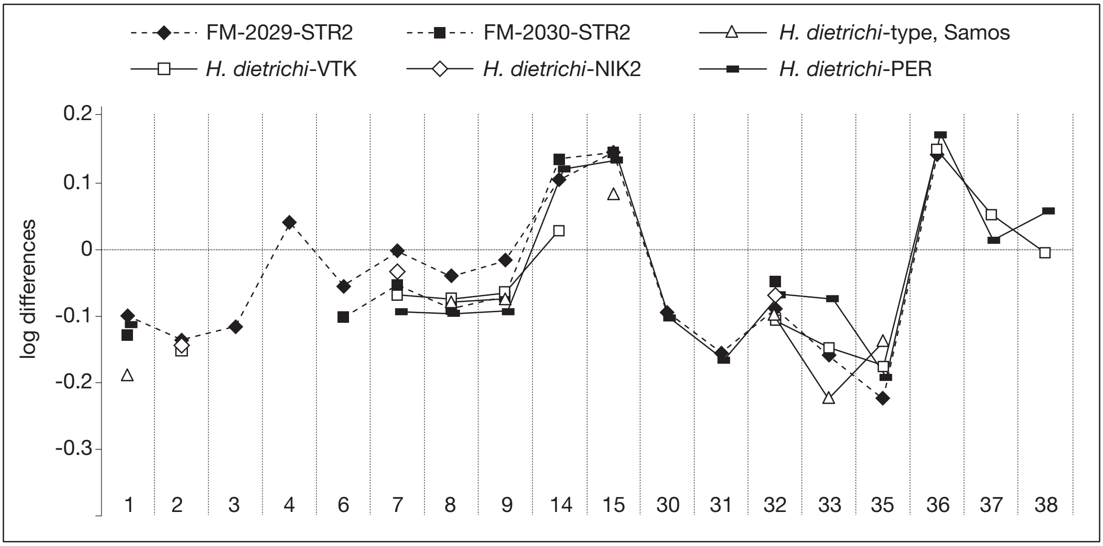

FIG. 7. — Logarithmic ratio diagram comparing the skulls of *Hipparion dietrichi* (Wehrli, 1941) from localities: Strumyani-2 (**STR-2**); Samos (**S**); Nikiti-2 (**NIK-2**); Vathilakkos (**VTK**); Perivolaki (**PER**). Standard *Hippotherium primigenium*, Höwenegg. Measurements: **1**, muzzle length, 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.

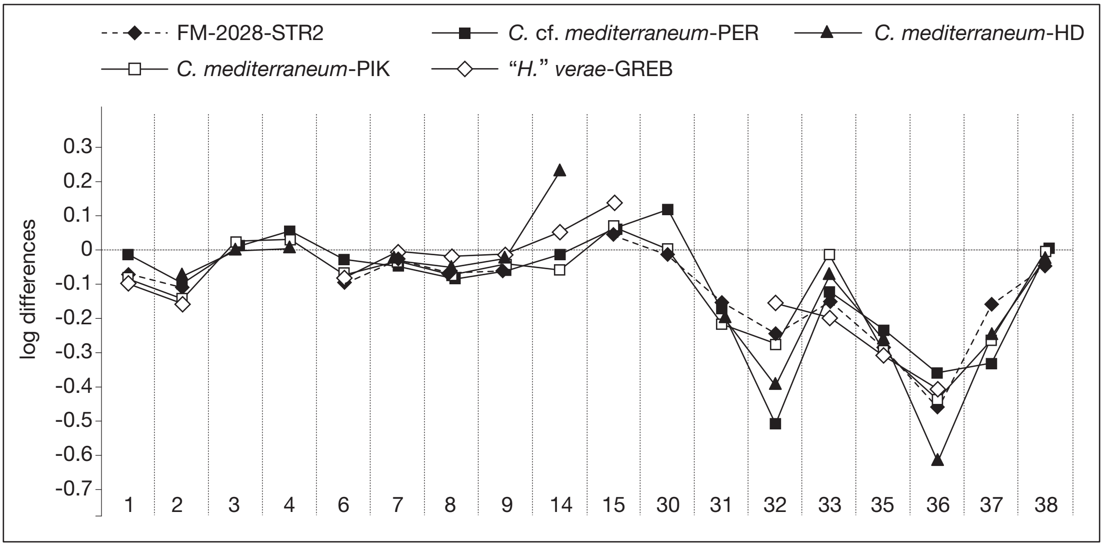

FIG. 8. — Logarithmic ratio diagram comparing the skulls of *Cremohipparion mediterraneum* (Roth & Wagner, 1855) and "*Hipparion*" *verae* Gabunia, 1959 from localities: Strumyani-2 (**STR-2**); Hadjidimovo-1 (**HD**); Pikermi (**PIK**); Perivolaki (**PER**); Grebeniki (**GREB**). Measurements and standard as for Figure 7.

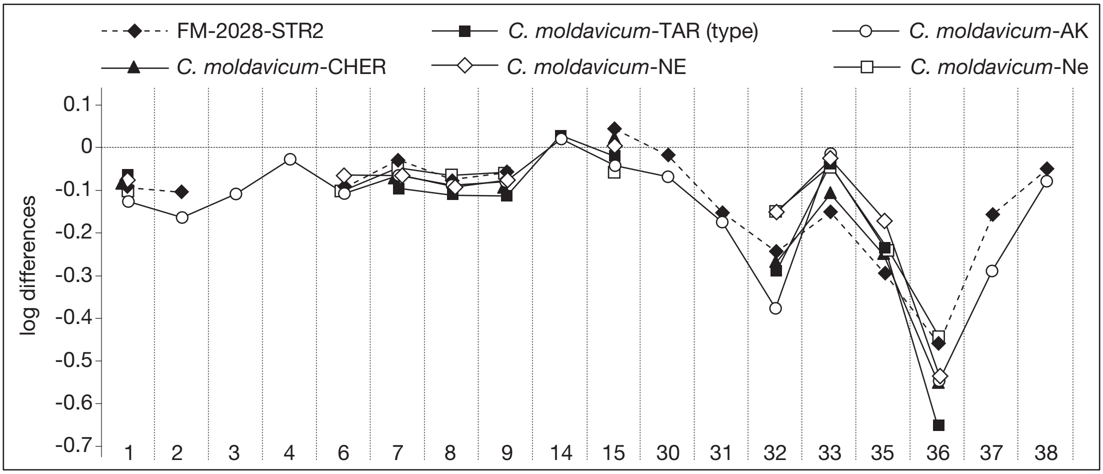

FIG. 9. — Logarithmic ratio diagram comparing the skulls of *Cremohipparion mediterraneum* (Roth & Wagner, 1855) and *Cremohipparion moldavicum* Gromova, 1952 from localities: Strumyani-2 (**STR-2**); Taraklia (**TAR**); Novaya Emetovka-2 (**NE**); Novoelizavetovka (**Ne**); Cherevichnoe (**CHER**); Akkasdağı (**AK**). Measurements and standard as for Figure 7.

"*Hipparion*" sp. (small sized)

A distal metatarsal of small size (FM-2814) from Str-1 differs from all other hipparion remains, having the dimensions of *Cremohipparion macedonicum* and *C. matthewi*. The close size of the metapodials from these two species and the bad preservation of this metatarsal prevent its exact species affiliation.

Hipparion postcranials are abundant at Str-2, but most of them are deformed or badly preserved. Metacarpals can be divided into two groups (Fig. 10). The first one includes robust metacarpals that match *Hippotherium* in size (FM-2035, FM-2296A). The second one consists of slender metacarpals (FM-2295, FM-2705, FM-2776, FM-2704, FM-2709A, FM-2703) close in size and proportions to *H. dietrichi* but, as some metacarpals of *C. mediterraneum* (e.g., from Hadjidimovo and Perivolaki) are of the same length and are as slender, it is hard to provide a definite species identification.

Metatarsals can be sorted into three groups (Fig. 11). The robust ones (FM-2340A, FM-2722A, and FM-2317) fall within the range of *H. brachypus* from Pikermi and Hadjidimovo and probably belong to this species; the second group includes long, slender metapodials (FM-2405, FM-2355, FM-2728A, FM-2315); the third one is represented also by slender but slightly shorter metatarsals (FM-2727, FM-2729A, FM-2077, FM-2085A), but a more or less gradual transition is observed between the three groups. As the skulls of *H. dietrichi* and *C. mediterraneum* from Strumyani-2 have similar lengths (380-420 mm for the first and 388 mm for the second species), and as no complete hipparion skeletons has been found at the locality, it is impossible to reach a final conclusion about the specific identity of each individual metatarsal.

The hipparions constrain the age of the locality between the end of the early Turolian and the first half of the middle Turolian. Most significant are the advanced features of *C. mediterraneum*. The absence of subnasal fossa, the position of its preorbital fossa, slightly shorter nasal notch and the moderately developed enamel plication show affinities with the Pikermi sample and could indicate a close age. However, the presence of *H. dietrichi* indicates a pre-Pikermian age for Str-2, since this species seems to become extinct before the level of Pikermi.

All the material identified above is from Str-2. The species composition of the hipparion material from Str-1 is probably similar to that of Str-2 and includes several postcranials (metapodials, astragali),

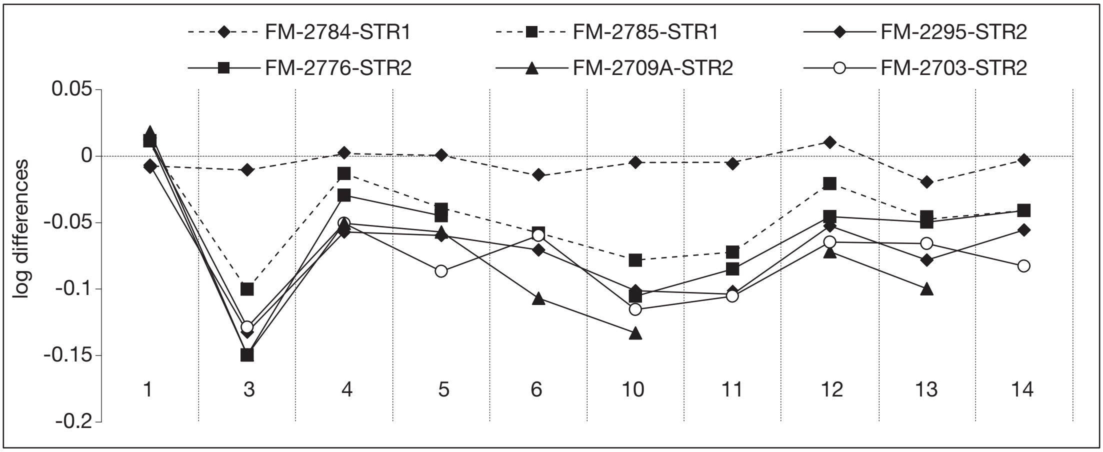

FIG. 10. — Logarithmic ratio diagram comparing equid metacarpals from Str-1 and Str-2. Standard: *Hippotherium primigenium* von Meyer, 1829, Höwenegg. Measurements: **1**, maximal length; **3**, minimum width of shaft; **4**, depth of shaft; **5**, proximal articular breadth; **6**, proximal articular 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.

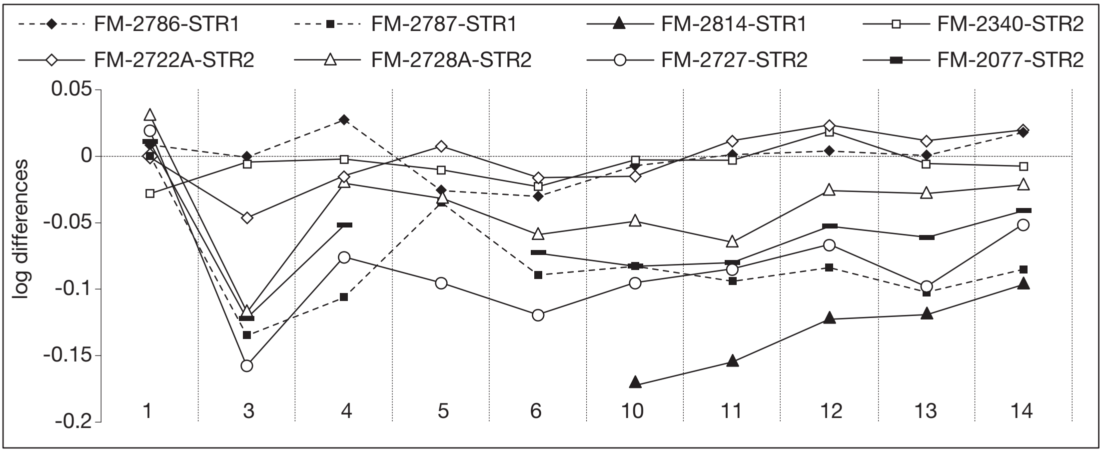

FIG. 11. — Logarithmic ratio diagram comparing equid metatarsals from Str-1 and Str-2. Measurements and standard as for Figure 10.

plus mandibular and maxillary fragments from young individuals, but is too scarce to reach precise taxonomic conclusions. There are two metacarpals. One is slender (FM-2785), resembling *C. mediterraneum*, and its measurements are close to the mean value of the Pikermian sample of this species (Koufos 1987a, b); the second metacarpal (FM-2784) is robust: its line on the Simpson diagram is more or less parallel to the lines of *H. brachypus* from Hadjidimovo and Pikermi (Koufos 1987a, b; Hristova *et al.* 2003), but it has more slender proximal and distal ends. Metatarsals can be sorted in three groups. The most robust metatarsal (FM-2786) resembles those of *H. brachypus* from Pikermi, but with larger antero-posterior diameter of the diaphysis and smaller dimensions of the proximal

TABLE 3. — *Microstonyx major* (Gervais, 1848) from Strumyani. Lengths of tooth rows and L × W of teeth (in mm).

Lower teeth	**FM-2327**	**FM-2802**	**Upper teeth**	**FM-2801**
c1		10 × 7.4		
p2	13.9 × 7.2		P2	18 × 10.4
p3	20.0 × 10.5		P3	19.9 × 15.9
p4	21.2 × 16.1		P4	15.9 × 19.6
m1	22.5 × 16.9	15.8 × 23.6	M1	24.4 × 22.2
m2	29.2 × 21.7	29.7 × 20.9	M2	30.0 × 27.9
			M3	45.4 × 30.8
p2-p4	55.0		P2-P4	53.2
			M1-M3	101
			P2-M3	154.4

and distal epiphyses. The second "group" consists of slender metatarsals (FM-2786, FM-2787, FM-2788), close to the morphotype of *H. dietrichi*. As a third "group" could be separated the single metatarsal of the small hipparion (FM-2814). The single astragalus (FM-2794) is comparatively small (maximal length 45 mm), close in its dimensions to the astragalus of *H. dietrichi* from Nikiti 2 (46.3 mm), but larger than the astragali of *C. macedonicum* (41.5 for "Ravin des Zouaves"-5 and 39.7 mm for Nikiti-2) (Vlachou & Koufos 2002). The hipparion fauna of Str-1 looks slightly different to the better known fauna of Str-2. The presence of a small hipparion might indicate a difference in age and/or paleoecological conditions in comparison with Str-2.

Order ARTIODACTYLA Owen, 1848
Family SUIDAE Gray, 1821

Microstonyx major (Gervais, 1848)

From Str-2, the material includes a maxilla with both complete cheek-tooth rows FM-2801 (Fig. 3I) and two subadult mandibles FM-2327 and FM-2802, with missing rami (measurements are given in Table 3). The only find from Str-1 is a large i1. There was no p1 on either mandible. The cheek-teeth are close in their dimensions to the Kalimantsi ones (Kostopoulos *et al.* 2001). The same is true of the maxillary teeth that reach or slightly exceed the maximum size of the Kalimantsi population. The apex of the P4 protocone (FM-2801) is positioned midway between the tips of the labial cones. The part of the maxilla anterior to P2 is not preserved and the presence/absence of P1 is unclear, but if present, it was not in close contact with P2.

The evolutionary trends, the significance of tooth size and the taxonomy of *Microstonyx* Pilgrim, 1926 are debated. Like former authors (Made *et al.* 1992; Kostopoulos 1994; Made 1997; Kostopoulos *et al.* 2001; Liu *et al.* 2004) we failed to find any significant morphological difference between the various populations, but metric differences have been variously interpreted. Kostopoulos (1994) and Bonis & Bouvrain (1996) hypothesized that the early Turolian *M. erymanthius* (Roth & Wagner, 1854) (or the subspecies *M. major erymanthius*) can be distinguished from the middle/late Turolian *M. major* (or *M. major major*); Sylvestrou & Kostopoulos (2006) included them all in a single species but acknowledged that "the populations of small-medium molar size prevail during MN11-12, while the medium-large sized ones are more common during MN12-13". The M3 from Str-2 is among the largest in this group, being surpassed only by a few teeth from the late Turolian of Lubéron and Dytiko, but some teeth that are certainly earlier are almost as large; these include teeth from Nikiti-1 (Kostopoulos 1994), Çorak Yerler, and a maxilla from Kopran in the NHMW, the M3 of which is 44.4 mm long. Although it is probably true that differences in size and proportions of the third molars do exist between the various populations, sample sizes are small, and most confidence intervals of the mean values overlap (Fig. 12). In particular, the distinction between a "small-medium" and a "medium-large" group (Sylvestrou & Kostopoulos 2006) looks to us artificial, as neither the m3s nor the M3s (Fig. 12; also Sylvestrou & Kostopoulos 2006: respectively figs 6, 7; 2009: respectively figs 4, 3) show any clear distinction between two groups, and there is certainly no simple relationship between size and chronology. The fact that suids have been so useful (with much larger sample sizes!) in East-African Plio-Pleistocene biochronology should not lead us to believe that they are bound to play the same role in the Eurasian Upper Miocene.

Family TRAGULIDAE Milne Edwards, 1864

Dorcatherium cf. ***puyhauberti*** Arambourg & Piveteau, 1929

A well-preserved half-mandible with full complete dentition from i1 to m3 FM-2741 is one of the nicest fossils from Strumyani, and one of the best known mandibles of *Dorcatherium* Kaup, 1833 (Fig. 3F, G). Its measurements are: diastema length = 16; length p1-p4 = 39.4; length p2-p4 = 33; length m1-m3 = 38.2; length of p3 = 12.5; length of p4 = 11.3; length of m3 (at occlusal level) = 17.5.

The ventral border of the mandible has a gentle regular curve, except below the symphysis (that extends to below the middle of p1), where it is straight. The central incisor is by far the largest of the front teeth, being broader than the other three combined. The i2 is slightly broader than i3 and about as broad as the canine. These proportions are identical to those of the Eppelsheim mandible of *Dorcatherium naui* Kaup, 1836, and to those of the living water chevrotain, *Hyemoschus aquaticus* (Ogilby, 1841). The diastema is short. A small p1 is present, separated by a very short diastema from a p2 that is slightly shorter than p4, itself shorter than p3. The mesial lobe of p2 consists of a single long main cuspid (eoconid), but the distal one, separated from the former by deep vertical furrows, certainly consisted of two cristids that are united by wear at this stage. The p3 is more complex, with a short curved cristid (epicristid) enclosing a small enamel island distal to the main cuspid, and a transverse distal cristid (telocristid). The p4 displays the typical tragulid morphology, with two parallel mesio-distally oriented cristids in the distal part of the crown. There is a strong wear gradient on the molars, m3 being only moderately worn; the so-called "*Dorcatherium*-fold" is clear, but the cristids that form the Σ are short.

Another mandibular fragment of a younger individual (FM 2329) with little worn teeth has only p2 and m1-2 preserved (L p2 = 9.2; L m1 = 11.1; L m2 = 11.7).

FM-2742 is a fragment of maxilla with a partially erupted canine (length of the canine along the anterior curve: 62 mm).

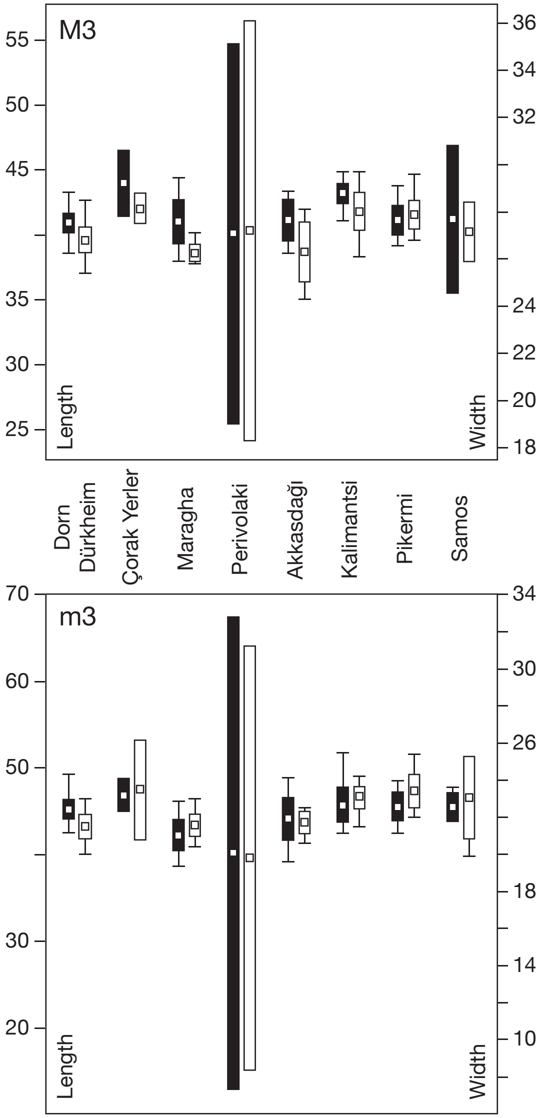

FIG. 12. — Box and whisker plots of third molar measurements (in mm) of *Microstonyx* Pilgrim, 1926 from various sites, roughly arranged by chronological order. Length in black, left scale; width in white, right scale; □, mean; box, 95% confidence interval of the mean; whiskers, range. Measurements from Bonis & Bouvrain (1996), van der Made (1997), Kostopoulos *et al.* (2001), Liu *et al.* (2004), Sylvestrou & Kostopoulos (2006, 2009) and our own data.

By contrast with African *Dorcatherium*, whose largest members were about 10 times heavier than the lightest ones (Geraads 2010), European forms of this genus are remarkably homogeneous in size from the late Middle to the latest Miocene, and size is of little help for systematics. Unfortunately, morphology is also hard to use, because: 1) the often cited persistence of a p1 is unlikely to be of taxonomic significance beyond subspecies level; 2) premolar morphology is variable in a single site; and 3) our perception of morphological features of the molars (especially selenodonty vs. bunodonty) changes with wear. The only named Turolian form is *Dorcatherium puyhauberti* Arambourg & Piveteau, 1929 from Vathylakkos in northern Greece. It is a poorly known species, but the entoconid of m3 is more lingual than the distal labial branch of the metaconid, an unusual feature for *Dorcatherium* (Geraads *et al.* 2005a). The Str-2 mandible shows an approach to this morphology, and we tentatively refer it to this species, while acknowledging that perhaps not more than a single species name is needed for all late Middle to Late Miocene European *Dorcatherium*.

As far as we know, front teeth had not previously been reported in *Dorcatherium*, the only published fossil tragulid incisor being an i2 from the Upper Miocene of Kenya (Pickford *et al.* 2004), whose similarity with that of modern *Hyemoschus* Gray, 1845 led these authors to assign it to this genus. The similarity of the Strumyani incisors to those of the living chevrotain shows that this morphology is in fact common to both genera, and cannot be used to assign a fossil form to either of them (Rössner 2007; Geraads 2010).

Family Cervidae Gray, 1821

Gen. et sp. indet.

A right mandible, FM-2100 (Fig. 3J), and its left counterpart, FM-2101, are the only cervid remains from the Miocene of Strumyani (SW Bulgaria). The teeth are in medium wear, and well preserved. The premolars are long relative to the molars, especially p2 that is almost as long as p3 and p4. The parastylid is distinct from the paraconid on p3 and p4. The p3 has a conical metaconid, but on p4 this cuspid produces distal and mesial flanges, the latter closing the central valley by contacting the paraconid. In contrast to most other Upper Miocene cervids, the labial groove of p4 is shallow. The molars have no *Palaeomeryx*-fold, and the lingual wall of the m3 hypoconulid is oblique in occlusal view. Measurements are: L p2-p4 = 28.3; L m1-m3 = 42.9.

Without antler, identification of a cervid is highly speculative, and we prefer to refrain from naming the Strumyani one, especially as there are a number of different species (and perhaps many more different names) in the late Miocene. Furthermore, this cervid displays some remarkable features (large p2, p4 much more molarized than p3) unmatched in other localities, and its teeth have no special resemblance to any of them. Unidentified cervid remains from the Turolian of South-Western Bulgaria are known also from the localities of Hadjidimovo and Ploski-Bairamitsa.

Family Giraffidae Gray, 1821

?***Helladotherium duvernoyi*** Gaudry & Lartet, 1856

The giraffid material is abundant, and comes from both Str-1 and Str-2. The Str-1 material includes an incomplete metatarsal, FM-2233 (max. prox. diameter = 90, width of shaft = 60); a scaphoid, FM-2235 (APD = 76, max. H = 49.2); a distal humerus (FM-2811) in connection with a proximal radius (FM-2812: TD = 134); a DP2, FM-2240 (28.5 × 20.5); and a DP3, FM-2239 (L = 37) with a bifurcated parastyle and a long first lobe. The latter is the most informative specimen, as it is clearly distinct from the DP3 of *Samotherium* Major, 1888 that has a shorter first lobe (Bohlin 1926; Geraads 1974). The large size of the metatarsal and radius also fits better *Helladotherium* Gaudry, 1860 than *Samotherium* (Geraads 1974). Although definitely present in Northern Greece (Geraads 1974), the latter genus is absent from other Greek and Bulgarian sites (Geraads *et al.* 2005b).

From Str-2, the measurements of a first phalanx, FM-2323 (L = 117, dist. TD = 52; prox. DT = 54.5; dist. APD = 38.1; prox. APD = 55.5; W of shaft = 43) fit much better *Helladotherium* than *Samotherium* (Geraads 1974). By comparison with

TABLE 4. — Measurements (in mm) of bovid frontlets. **1**, PIUW; **2**, NHM; **3**, Kostopoulos 2005; **4**, Kostopoulos 2006.

Species and collection number	**APD**	**TD**	**width over pedicles**	**width across middle of supra-orbital foramina**
Tragoportax sp.				
FM-2094	60+	37+	*c.* 120	*c.* 40
Palaeoreas lindermayeri Wagner, 1848				
FM-2738	36.2	42.7	95	–
FM-2740	32.5	34	81	27
Prostrepsiceros rotundicornis (Weithofer, 1888)				
FM-2739	35	34	84.7	32.5
Pikermi, type (1)	36.4	39.7	82	–
Pikermi, M11437 (2)	29.6+	34.8-	87	36.5
Pikermi, M10844 (2)	31.5	29.7	82.5	36.5
Pikermi, M11436 (2)	28.1	27.6	81	–
Pikermi, M12999 (2)	30.2	30	–	–
Akkasdağı (3)	25.5-34	27-39.7	88.1-94.8	–
P. cf. *fraasi* ?				
Perivolaki, PER-811 (4)	36.8	39.7	94	–
Perivolaki, PER-1326 (4)	42	45	103	–
Gazella Blainville, 1816				
FM-2466	28	24	–	–
FM-2105	–	24	76	–
FM-2424	–	–	72	–

material from various sites in Macedonia (Geraads 1974, 2009; Geraads *et al.* 2005b), we assign to *Helladotherium* separate left incisors from the same specimens FM-2755 and 2756: i3 (MDD = 19.1; VLD = 14.7), i2 (MDD = 17.4; VLD = 14.9); a mandible fragment, FM-2467, with dp3 and the first two lobes of dp4; a proximal metatarsal, FM-2218 (APD = 90; DT = 97); a distal radius, FM-2160 (TD = 134); and a calcaneus fragment, FM-2324.

?***Bohlinia attica*** (Gaudry & Lartet, 1856)

A metacarpal fragment, FM-2289 from Str-1 (min. width of shaft = *c.* 55 mm) can be tentatively assigned to *Bohlinia* Matthew, 1929, as it is more elongated and slender than in any other genus. From Str-2 a first phalanx (FM-2269) and two second ones, FM-2147 and 2147b (all likely from the same individual) probably also belong to this genus, as their measurements fit those of its Greek representatives (Geraads 1974): Ph I: L = 109; prox. TD = 44.6; dist. TD = 35.8; prox. APD = *c.* 44; dist. APD = *c.* 30; min. W of shaft = 35.6; Ph. II (FM-2147): L = 62.8; prox. TD = 35.8; dist. TD = 32. The first phalanx is too long and slender for *Samotherium*: it is long enough, but too slender, for *Helladotherium*, but is close in its dimensions and proportions to a *Bohlinia* from Vathylakkos. The phalanges II are also smaller than those of *Helladotherium* (Geraads 1974).

Palaeotragus rouenii Gaudry, 1861

FM-2778 is a nice complete left lower tooth row (Fig. 3H) that can unambiguously be assigned to *Palaeotragus rouenii* because of its small size and strong molarization of the premolars: p3 is almost identical to p4, with a long metaconid closing the central valley, and the hypoconid is isolated from the rest of the tooth. Its dimensions (premolar length = 47.6; molar length = 75.3) are similar to those of other *P. rouenii* specimens from Pikermi or Dytiko in Greece, or Hadjidimovo and Kalimantsi in Bulgaria (Geraads *et al.* 2005b: table 3), but the species might already be present in the Vallesian of Ravin de la Pluie.

Family Bovidae Gray, 1821

Tragoportax sp.

FM-2094 (Fig. 13H) is the poorly preserved skull of a large *Tragoportax* Pilgrim, 1937 preserving the splanchnocranium (without the rostral part) as well as the basal half of the horn-cores (measurements: Table 4). The shape and divergence of both horn-cores are symmetrical, showing that they do not result from post-mortem deformation. There is a deep, large anteorbital fossa. The intercornual distance is large (about 42 mm): in frontal view the bases of the horn-cores make with the frontal bone a U-shaped figure, as in *T. rugosifrons* (Schlosser, 1904) (not V-shaped as in *T. amalthea* (Roth & Wagner, 1854)). The horn-cores are strongly divergent at the base (about 70 degrees), and this divergence increases upwards. In lateral view the anterior edges of the horn-cores are strongly curved backwards. The posterior surfaces are damaged and the shape is not clear, but it seems that the posterior borders are also arched, not straight, and the medial side is clearly convex. The anterior keels of the horn-cores lack rugosities and steps, but from the damaged frontal bone it seems that the keels extend onto the frontals for about 1/3 of the orbit diameter. The increase of divergence of the horn-cores is stronger than in *T. rugosifrons*; at Hadjidimovo, only a few specimens have a slight normal torsion of the keel (Spassov & Geraads 2004). This morphology could be derived for *Tragoportax*, as it is reminiscent of *T. amalthea*, although it is also less expressed in this species, which has horn-cores closer to each other, and with steps along the anterior keel; FM-2094 is more similar to *T. rugosifrons* in these features, but *T. rugosifrons* (that is well represented at Hadjidimovo) has less divergent and less backwardly curved horn-cores, with much weaker torsion of the keels and the convex horn-core surface is the lateral instead of the medial one.

The frontlet figured as *T. amalthea* by Andree (1926: pl. 10, fig. 5) with its long twisted horn-cores also has some similarities with the skull from Strumyani, but the most similar to the latter are the skull PXM-93 from the early Turolian of Prochoma, Greece referred to *T. rugosifrons* by Bouvrain (1994), with its backwardly curved horn-cores and torsion of the anterior keel, and perhaps also the unpublished material from Molayan.

There are also a right mandible with p4-m3, FM-2758 (L m1-m3 = 67 mm), and another one, FM-2737, with p3-m3 and the roots of p2, probably its counterpart. The teeth are much worn and identification is not straightforward, especially as the metaconid of p4 is more expanded lingually than is usual in *Tragoportax*, but the presence of basal pillars and of convex lingual walls on the molars fits better this genus than similar-sized members of the *Protoryx-Pachytragus* group. The latter have much shorter premolars than *Tragoportax*, but this is mostly due to their small p2, absent here. We also assign to *Tragoportax* several maxillary and mandibular remains with the size and morphology of *Tragoportax* (Spassov & Geraads 2004): a maxilla, FM-2155, with DP3-M3 (M3 unerupted; M1-M3 = 63.5 mm.); mandibles and mandibular fragments, FM-2154, FM-2219 (Lm3 = 29.5), FM-2338 (Lm3 = 28), FM-2294 (Lm3 = *c.* 30); an astragalus, FM-2121 (H = *c.* 51, dist. TD = *c.* 33), and a proximal metacarpus, FM-2425 (TD = 39.3).

Miotragocerus (*Pikermicerus*) cf. *gaudryi*
Kretzoi, 1941

FM-2103 is a complete lower tooth row with very long and very primitive premolars (Fig. 3I). Its dimensions (Table 5) fit within the variation range of *Miotragocerus* (*Pikermicerus*) *gaudryi* (*sensu* Spassov & Geraads 2004: fig. 11), but lack of cranial remains precludes definite species identification. We tentatively refer to this form two other mandibles with relatively long premolar rows, FM-2757 and FM-2803. Str-2 is thus one more site where both boselaphine genera coexist.

Sporadotragus vasili
Geraads, Spassov & Kovachev, 2006

A partial frontlet, FM-2026, from Str-1 has been referred to this recently erected species, the type locality of which is Kalimantsi, not far from Strumyani.

FIG. 13. — Fossil mammals from the Miocene of Strumyani (SW Bulgaria): **A**-**C**, **F**, **G**, *Palaeoreas lindermayeri* Wagner, 1848; **A**, skull FM-2738, front view; **B**, mandible FM-2744; **C**, mandible FM-2783; **F**, frontlet FM-2740; **G**, frontlet FM-2780; **D**, **I**, **J**, *Prostrepsiceros rotundicornis* (Weithofer, 1888); **D**, mandible FM-2331; **I**, frontlet FM-2779; **J**, frontlet FM-2739; **E**, *Palaeoryx* sp., tooth row p2-m2 FM-2251; **H**, *Tragoportax* sp., skull FM-2094. Scale bar: A, G-J, 20 cm; B-E, 5 cm.

TABLE 5. — Measurements (in mm) of bovid lower tooth-rows from the Miocene of Strumyani (SW Bulgaria).

Collection number	Taxon	p2-m3	p2-p4	m1-m3	index pm/m
FM-2732	*Palaeoreas*?	67.7	25.4	43.4	0.59
FM-2744	*Palaeoreas*?	68.2	24.8	43.3	0.57
FM-2733	*Palaeoreas*?	69	24.4	43.8	0.56
FM-2330	*Palaeoreas*	71	27	44.7	0.60
FM-2783	*Palaeoreas*?	65.7	24.6	41.3	0.60
FM-2099	*Palaeoreas*?	–	–	38.7	–
FM-2743	*Palaeoreas*	–	–	43	–
FM-2758	*Tragoportax*	–	–	66.8	–
FM-2154	*Tragoportax*	–	–	66	–
FM-2103	*Pikermicerus*	90.5	41.5	54	0.77
FM-2757	*Pikermicerus*	–	45	–	–
FM-2803	*Pikermicerus*	106	45	61	0.74
FM-2332	*Prostrepsiceros*?	69.4	26.8	41.4	0.65
FM-2331	*Prostrepsiceros*?	74.3	29.4	45.8	0.64
FM-2099	*Prostrepsiceros*?	–	~25.8	38.9	–
FM-2098	*Gazella*	–	21	34.7	0.61
FM-2267	*Gazella*	54.9	21.4	33.8	0.63

The genus itself seems to have a restricted range, been definitely present in Greece at Pikermi and Samos only, although it may extend to Afghanistan and China (Geraads *et al.* 2006b), but is unknown west of Bulgaria and Greece.

Palaeoryx sp.

A mandible fragment with p3-m2, FM-2251, from Str-1 (Fig. 13E), belongs to a very large bovid (L p3-p4 = 35.2, L m1-m2 = 43.2). The premolars have transverse entoconid and hypoconid cristids, rather shallow labial groves, a paraconid quite distinct from the parastylid, and a metaconid that is oblique on p3 but with a long mesial flange closing the central valley on p4. The molars have slightly convex lingual walls, an incipient goat fold on m1, and an angular protoconid. These metric and morphological features agree well with those of *Palaeoryx* Gaudry, 1861, a genus that includes two species according to Kostopoulos (2005). Identification of mandibles that are not associated with skulls is seldom straightforward, but the close similarity of FM-2251 with a complete tooth-row from Samos that is definitely of *Palaeoryx*, no. 110 in Münster (Paläontologische Institut), leaves little doubt about its identification. Another mandible fragment from Str-1 (FM-2242) of a subadult individual with dp4-m2 has an m1-m2 length of 44 mm and can be assigned to the same taxon.

Palaeoreas lindermayeri Wagner, 1848

This antelope is quite common at Strumyani. It is represented by a complete skull, FM-2738, (Fig. 13A), two frontlets, FM-2740 (Fig. 13F) and FM-2780 (Fig. 13G), and several mandibles (Fig. 13B, C; measurements: Tables 4; 5). They display the typical features of this species (Bouvrain 1980; Geraads *et al.* 2003). The horn-cores are moderately inclined posteriorly, with their anterior edge in the same plane as the frontals, and rather far from the orbits. They are massive relative to skull size, divergent by an angle of about 50°, strongly twisted on their axis but with no spiralling, slightly compressed medio-laterally, with a sharp but not very strong postero-lateral keel and a more blunt anterior one. The mid-frontal suture is fused, only a trace of it being visible on the frontlet; the supra-orbital foramina open into large and deep depressions that are not very wide apart. Both sides of the occipital face mostly posteriorly; the basioccipital is quite long for the size of the animal, it has a long central grove, and strong anterior tuberosities. The parietal has

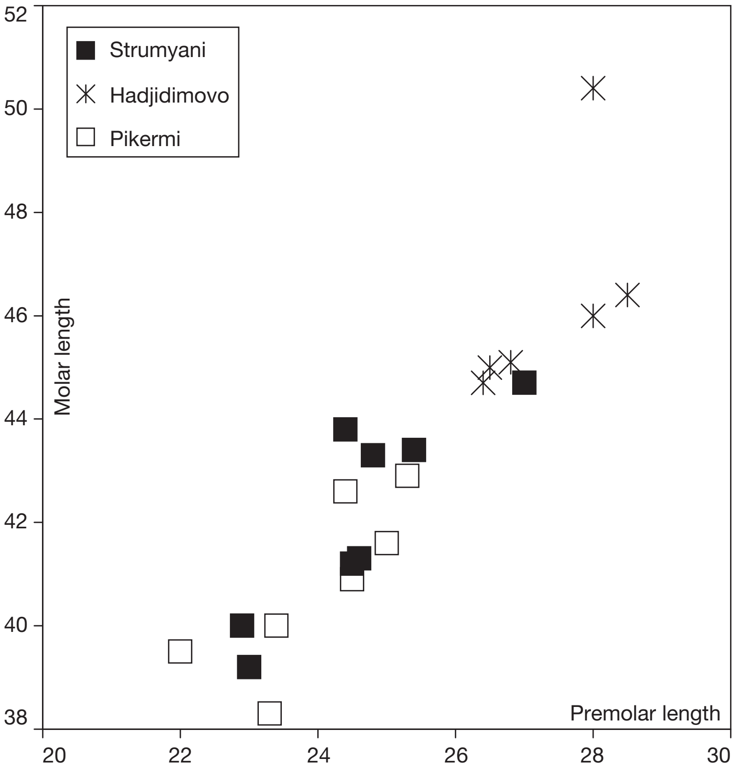

FIG. 14. — Plot of premolar *vs* molar length (in mm) in *Palaeoreas lindermayeri* Wagner, 1848 from Strumyani, Hadjidimovo and Pikermi.

a straight top surface that is much inclined in respect to the facial plane, the frontals being much raised between the horn-cores.

Several mandibles can probably also be referred to this species. On the molars, the labial walls are somewhat convex, there is a small ectostylid, at least on m1, a clear goat fold, and the third lobe of m3 is rather small. The premolars are moderately long (index Pm/M = 55-60), p3 and p4 are similar to each other, with a parastylid well distinct from the paraconid, an oblique metaconid cristid only slightly more transverse and inflated lingually on p4, and a broad labial groove between protoconid and hypoconid. The size range of the tooth rows is about the same as those of *P. lindermayeri* from Pikermi, but average smaller than those from Hadjidimovo. The horn core diameters (Fig. 14) are also smaller than at Hadjidimovo and close to the ones from Pikermi and Kalimantsi (Geraads *et al.* 2003).

Prostrepsiceros rotundicornis (Weithofer, 1888)

The best preserved specimen is a frontlet with most of the right horn-core and the base of the left one, FM-2739 (Fig. 13J; measurements: Table 4). FM-2765 and 2766 are horn-cores in bad condition. This taxon is also represented by a frontlet from Str-1, FM-2779 (Fig. 13I). The neurocranium was certainly little inclined on the face, as the frontal is little bent. The supra-orbital foramina open at the lateral sides of large depressions that nearly meet at a mid-frontal suture; the latter is slightly raised and open, as is also the fronto-parietal one. There is a large post-cornual fossa. The orbital rims are prominent.

The pedicles are extremely short, as the horn-cores rise directly from the frontal bone. They are inserted rather uprightly, diverge from the very base, and the divergence increases upwards before decreasing in the second half. They are strongly spiralled but lack keels, although grooves run along their lateral surface.

These frontlets obviously belong to a group of *Prostrepsiceros* Major, 1891 whose horn-cores virtually lack keels, and which includes *P. rotundicornis* and *P. fraasi* (Andree, 1826). The former species was defined at Pikermi (Weithofer 1888; Gaudry 1862-1867; Pilgrim & Hopwood 1928), the latter at Samos (Andree 1926). The boundary between these species, and their occurrences in other localities have long been debated (Gentry 1971; Bouvrain 1982) but recent discoveries and taxonomic revisions tend to support the distinction (Kostopoulos 2005, 2006). *Prostrepsiceros fraasi* is larger, has a more strongly angled face on the neurocranium, less salient orbital rims, shallower post-cornual fossa, and more divergent horn-cores. It occurs at Samos, Maragha, and perhaps Perivolaki (although Kostopoulos [2009b] now believes that the Perivolaki form is closer to *P. houtumschindleri* (Rodler & Weithofer, 1890)), while *P. rotundicornis* is present at Pikermi, Halmyropotamos, Akkasdağı, Ravin des Zouaves 5 (Gentry 1971; Bouvrain 1982; Kostopoulos 2005, 2006) and at Vozarci in the Republic of Macedonia (FYROM). Further finds are needed before the issue can be settled, because it may look hard to accept the occurrence of two contemporaneous and partly sympatric closely related species. If the distinction between these two species is accepted, the characters of the Str-2 frontlet clearly align it with *P. rotundicornis*. Both species are best known from sites similar in age to Pikermi, although some records may be earlier.

Two mandibles, FM-2332 and 2331 (Fig. 13D), differ from those assigned above to *Palaeoreas* by their longer premolar row (Table 5), but they are otherwise little different, and their assignment to *Prostrepsiceros* is tentative.

Gazella cf. ***capricornis*** (Wagner, 1848)

The gazelles are well represented in both Strumyani localities. The material includes: FM-2424, a neurocranium with the bases of the horn-cores (max. occipital W = 62; min. post-orbital W = 52); a frontlet, FM-2105, with damaged horn cores; a partial skull, FM-2328, with the base of the left horn core; the basal half of a horn core, FM-2466; three mandibles (FM-2098, FM-2099 and FM-2267) and a number of postcranials, including some metapodials (Table 6).

The horn-cores are poorly preserved, but they were moderately long, moderately divergent at the base, curved backwards, little compressed, and they bear strong grooves. These features suggest that they could belong to *G. capricornis*, known at Pikermi, Samos, Akkasdağı, etc., but the systematics of Upper Miocene gazelles is still uncertain despite recent improvements (e.g., Kostopoulos 2005, 2006, 2009a) and, above all, the Strumyani material is too scarce for definite assignment.

BIOCHRONOLOGY

AGE OF THE STRUMYANI FAUNA

The faunal assemblage from Strumyani-2 includes the following species: *Hystrix primigenia*, Carnivora indet., ?*Tetralophodon atticus*, *Ceratotherium neumayri*, *Dihoplus pikermiensis*, *Hipparion dietrichi*, *Hippotherium* cf. *brachypus*, *Cremohipparion mediterraneum*, *Microstonyx major*, *Dorcatherium* cf. *puyhauberti*, Cervidae gen. et sp. indet., ?*Helladotherium duvernoyi*, ?*Bohlinia attica*, *Palaeotragus rouenii*, *Tragoportax* sp., *Miotragocerus* cf. *gaudryi*, *Palaeoryx* sp., *Palaeoreas lindermayeri*, *Prostrepsiceros rotundicornis*, *Gazella* cf. *capricornis*. To these should be added *Cremohipparion macedonicum/matthewi*, *Ancylotherium pentelicum*, *Tapirus* sp., *Palaeoryx* sp., and *Sporadotragus vasili*, known only from Str-1 by single specimens. Sample size is too small to conclude that this implies a real difference in faunal composition between the two Strumyani localities, which are topographically very close, and the difference in age, if any, is probably not great given the likely rapid deposition of this kind of sediments. We will cautiously consider their faunas as a single one, although Str-1 could be slightly older.

To assess its biochronological age, it can be compared to some similar faunas of the Aegean region (Table 7). All of them belong to the Middle Turolian, and the similarity of the faunal lists shows that the Strumyani fauna must also be assigned to this mammalian age. It is especially close to the reference locality for this period in the Balkano-Iranian province, Pikermi. Most of the Strumyani bovid species are also known in this Greek locality, except perhaps the *Tragoportax* that looks different from the *T. amalthea* of Pikermi. By contrast, the slightly earlier locality of Perivolaki, also in Greece, is more different in its bovid fauna, although it has *T. rugosifrons*, as in the Samos sites that are also slightly earlier, and perhaps also as at Strumyani. It should be noted here that the most remarkable feature of Strumyani is the lack of antelopes of the *Pachytragus-Protoryx* group; they are virtually absent from all Bulgarian sites, showing that this difference is not related to chronology. Among the hipparions, the most significant occurrence is that of *H. dietrichi*, present in most of the sites earlier than Pikermi, but absent in this latter site; if this absence is not due to ecology, it indicates an age earlier than Pikermi. Most of the other Strumyani mammals are also found at Pikermi: the three giraffids, the tragulid, the suid, the two rhinos, the ancylothere, the mastodont, and the porcupine. The noticeable occurrence of a tapir at Str-1 certainly has no chronological significance, while the absence of *Choerolophodon* is probably due to incomplete sampling, and those of *Samotherium* and *Chilotherium* to biogeography, as they are quite rare in the Balkans.

The obvious conclusion is that the faunal composition of Strumyani indicates an age close to that of Pikermi, although probably earlier. This is confirmed by the evolutionary stages of some species: the i2s of the *Dihoplus pikermiensis* mandible from Str-2 are less reduced than at Pikermi (even though this morphology has been observed on a single specimen and could reflect an extreme case of sexual dimorphism), and the morphology of the *Tragoportax* is different from that of *T. amalthea*.

The main biochronologically significant taxa of Str-1 is *Sporadotragus*, known at Pikermi and Samos; *S. vasili* from Str-1 is also present in the upper levels of Kalimantsi, whose age is probably slightly earlier than that of Pikermi (Spassov *et al.* 2006; Hristova & Spassov 2005). The presence of *C. macedonicum/matthewi* in Str-1 might also indicate some age, and perhaps also ecological, difference from Str-2.

Table 6. — Measurements (in mm) of *Gazella* Blainville, 1816 metapodials.

	L	prox. TD	W shaft	dist. TD
Mt-FM-2249 (Str-1)	–	20.6	–	11.6
Mc-FM-2009	144	17	10.2	18.4
Mt-FM-2008	148	16	10	–

Duration of the Middle Turolian in the Southern Balkans

Doubts can be expressed about the absolute ages of the Turolian faunal assemblages of the Southern Balkans. In a recent review of the "Pikermian event", Kostopoulos (2009c: fig. 1) provided a chronological chart of the main sites of the Aegean region (Bulgaria, Greece and Turkey). While those of Samos and Turkey appear more or less evenly distributed over the 8.5-6.5 Ma time period, corresponding more or less to the Turolian, those of the Southern Balkans are strongly clustered in the 7-7.5 Ma time-range, corresponding to his MN 12 zone: there are 7 localities in this zone (counting Kalimantsi as a single one), to which should now be added Strumyani, but none in the 8-7.5 Ma time-range. The probability that chance alone is responsible for such a distribution in the 8-7 Ma time-range is about 0.008, and this hypothesis can be discarded. Therefore, either some external factor (e.g., tectonic and/or climatic) must have acted, favouring the accumulation of fossils in the second half of this period, or the dating is wrong. Although it cannot be definitely rejected, no obvious evidence supports the first hypothesis, and we consider it unlikely that it could have acted simultaneously in three different basins of Macedonia, as well as in Thessaly, Euboea and Attiki. It is more likely that what is called MN 12 in the Southern Balkans region had a longer duration, perhaps even longer than assumed by Koufos *et al.* (2006) who allowed it almost 1 Ma. Because of the limited extent of the stratigraphic sections, none of these localities can be *independently* dated by palaeomagnetism, so that conclusions about their absolute ages are not free of circular reasoning.

For instance, the Prohoma section shows only one palaeomagnetic inversion but, on the basis of

TABLE 7. — Distribution of large mammals (excluding Carnivora) in some middle Turolian Eastern Mediterranean sites. From various authors, mostly Spassov *et al*. (2006), Koufos *et al*. (2006, 2009), Sen (2005), with some identifications revised by ourselves.

Taxa	**Strumyani-1 + 2**	**Kalimantsi**	**Pikermi**	**Akkasdağı**	**Samos Q2+MLN**	**Samos A1**	**Samos MTL**	**Perivolaki**	**KTA**
Hystrix primigenia (Wagner, 1848)	×	×	×			×			×
Mesopithecus Wagner, 1839		×	×					×	
Choerolophodon pentelici Gaudry, 1862		×	×	×		×	×		×
Deinotherium gigantissimum Stefanescu, 1892			×			×		sp.	
"*Mammut*" *obliquelophus* Mucha, 1980			×				×		
Tetralophodon atticus (Wagner, 1857)	?	×	×	×					
Ancylotherium pentelicum (Gaudry & Lartet, 1856)	×	×	×			×	×		sp.
Chalicotheriinae Gill, 1872		×		×					
Tapirus Brünnich, 1771	×								
Acerorhinus Kretzoi, 1942		×	×	×					
Ceratotherium neumayri (Osborn, 1900)	×	×	×	×		×	×	sp.	×
Dihoplus pikermiensis (Toula, 1906)	×	×	×	×		×	×		
Chilotherium Ringström, 1924				×		×			×
Brachypotherium Roger, 1904		×							
Cremohipparion matthewi (Abel, 1926)						cf.	cf.		×
Cremohipparion mediterraneum (Roth & Wagner, 1855)	×	×	×					cf.	
Cremohipparion moldavicum (Gromova, 1952)				×					
Cremohipparion proboscideum (Studer, 1911)					aff.	cf.	cf.		×
Hipparion dietrichi (Wehrli, 1941)	×					×	×	×	
Hipparion forstenae (Zhegallo, 1971)				×		cf.	cf.		
Hipparion macedonicum Koufos, 1984	?							×	
Hipparion longipes Gromova, 1952				cf.					
Hippotherium brachypus (Hensel, 1862)	cf.	×	×	×		×	×		
Hipparion prostylum Gervais, 1849					aff.				×
Pliohyrax graecus (Gaudry, 1862)			×			×	×		×
Orycteropus gaudryi Major, 1888				×		×	×		×
Microstonyx major (Gervais, 1848)	×	×	×	×		×	×	×	×
Propotamochoerus Pilgrim, 1925						×			
Dorcatherium Kaup, 1833	×		×						
Cervidae Gray, 1821	×		×			×		×	
Bohlinia attica (Gaudry & Lartet, 1856)	?	×	×						
Helladotherium duvernoyi Gaudry & Lartet, 1856	?	×	×	sp.		×	×	×	
Palaeotragus rouenii Gaudry, 1861	×	×	×	×	×	×	×	cf.	×
Palaeotragus size *coelophrys* (Rodler & Weithofer, 1890)					×	×	×		
Samotherium boissieri Major, 1888					×	×			
Samotherium major Bohlin, 1926				×			×		×
Tragoportax rugosifrons (Schlosser, 1904)	sp.				×	×	×	×	?
Tragoportax amalthea (Roth & Wagner, 1854)		×	×	×					
Miotragocerus gaudryi Kretzoi, 1941	cf.	×	×	×	×		×	sp.	
Tragoreas oryxoides Pilgrim, 1926						×			
Pheraios chryssomallos Kostopoulos, 2006								×	
Urmiatherium rugosifrons (Sickenberg, 1932)							×		
Criotherium Major, 1891		×			×	×			
Palaeoreas lindermayeri Wagner, 1848	×	×	×						
Sporadotragus Kretzoi, 1968	×	×	×		×	×	×		
Pseudotragus capricornis Schlosser, 1904					×	×			
Protoryx carolinae Major, 1888			×						
Protoryx laticeps Andree, 1926						×	×	aff.	×
Pachytragus crassicornis Schlosser, 1904				×					

TABLE 7. — Continuation.

Taxa	**Strumyani-1 + 2**	**Kalimantsi**	**Pikermi**	**Akkasdağı**	**Samos Q2+MLN**	**Samos A1**	**Samos MTL**	**Perivolaki**	**KTA**
Palaeoryx Gaudry, 1861	×		×	×	×	×	×	aff.	×
Prostrepsiceros rotundicornis (Weithofer, 1888)	×		×	×				sp.	
Prostrepsiceros zitteli (Schlosser, 1904)						×			
Nisidorcas planicornis (Pilgrim, 1939)								×	
Protragelaphus skouzesi Dames, 1883			×			sp.			
Helladodorcas Bouvrain, 1997								×	
Gazella capricornis (Wagner, 1848)	cf.	sp.	×	×			sp.	sp.	×
Gazella pilgrimi Bohlin, 1935				×		×	×	×	
Gazella mytilinii Pilgrim, 1926					sp.		×		
Oioceros rothi (Wagner, 1857)			×						
Oioceros wegneri Andree, 1826						×			?

its "late Vallesian or early Turolian" fauna, Kondopoulou *et al.* (1992) nevertheless suggested an age "younger than 8.9 Ma, including it in the Turolian mammalian stage." This assignment to a "mammalian stage" on the basis of an inferred absolute age is questionable, to say the least. Later, Koufos *et al.* (2006) included it in C3Br.3r, presumably on the assumption that, yielding a middle Turolian fauna, the site cannot be earlier, but the hypothesis that it belongs in fact to Chron C4 cannot be rejected on the basis of palaeomagnetic evidence.

Palaeomagnetic dating of other Axios sites allowed Sen *et al.* (2000: 203) "to suggest some tentative correlation hypotheses". Later, the Vathylakkos section was assigned (Koufos *et al.* 2006) to C3Br.3r/C3Br.2n, but we believe that it could in fact be earlier and belong to C4n.1r/C4n.1n.

The Perivolaki section shows two reverse and two normal periods, and was assigned (Koufos *et al.* 2006) to C3Br with the fossil site at the top, in C3Br.2r. This correlation is based on the presence in the section of "long reverse polarity zones", where "long" means in fact "thick deposits", but in this sedimentary context such direct inference needs better substantiation; perhaps the 45 m-thick reverse deposits at the top of the section can have been deposited in less than *c.* 60 ky, the duration of C3Br.3r, so that Perivolaki could as well be assigned to this chron.

In recent years, an increasing role has been allotted to palaeomagnetism in the setting of the chronologic framework of the Eastern Mediterranean Neogene mammalian faunas. We believe that, although this method may contribute, it remains of limited use in many localities, especially those without extensive exposures, and in any case, it should not take precedence over biochronology. For instance, the bizarre idea that MN "zone boundaries" should correspond to paleomagnetic events now implies that no fauna of MN 12 composition can be older than 7.43 Ma (the age of the limit C4n/C3Br), which is nonsense because assignment to this zone should rest upon fauna alone. It is well-known that faunal events may be diachronous even at the scale of Europe (see e.g., Kälin & Kempf [2009] for the Middle Miocene, and Spassov [2003] for the Pliocene and Pleistocene), and "zone boundaries" certainly cannot be expected to be contemporaneous from Spain to Turkey.

TAPHONOMY AND PALAEOECOLOGY

Although less than 80 bones and bone fragments were collected at Strumyani-1, about 800 were collected at Strumyani-2 from a small volume of sediment. A skull and mandible of the same *Dihoplus* individual, two *Ceratotherium* mandibles, a *Microstonyx* mandible, as well as *Hipparion* and *Tragoportax* skulls and two rhino humeri and a number of other skeletal remains were discovered in an excavation of about 5 m^2. Some bones of smaller animals were trapped by large bones of rhinos and giraffes: a subadult *Microstonyx* mandible together with large vertebrae were trapped between the two mandibular rami of a *Ceratotherium* mandible; the horn core of a gazelle skull was discovered within the neural canal of a large bovid atlas. Such taphonomic features indicate bone and carcass accumulation and quick embedding by water flows, resulting from seasonal river flooding; the Str-2 assemblage can certainly be considered as instantaneous at the geological, if not human, scale. The main orientation of the bones is E-W, but some of them are oriented transversally to the main direction.

In numbers of specimens, hipparions are largely predominant at Str-2 (about 60% of the remains), followed by gazelles and *Tragoportax*; spiral-horned antelopes, giraffids, and horned rhinos are also well represented. These relative abundances are similar to those of the other Turolian localities of South-Western Bulgaria, such as Hadjidimovo and Kalimantsi. A difference from Hadjidimovo-1, where hipparions, *Tragoportax* and *Gazella* are also dominant, is the lower number of *Palaeoreas*, the most abundant taxon in Hadjidimovo. *Hipparion dietrichi*, common here, is unknown in all of the Kalimantsi localities; since some of them are probably contemporaneous with Strumyani, this absence is likely related to ecology (more humid conditions and denser vegetation in the Kalimantsi area ?).

The instantaneous nature of the bone accumulation rules out the addition of several successive faunal assemblages as a possible factor for the mixture of elements with various ecological requirements. Thus, their association truly reflects the γ-diversity of a mosaic of contemporaneous environments, and not an artefact of time-averaging. These environments cover a rather wide range of landscape physiognomies, probably with a dominance of open woodlands. Animals preferring the more open part of the range could be *Hystrix*, *Ceratotherium*, *Gazella*, *Hipparion dietrichi*, the small cursorial "*Hipparion* sp." perhaps also *Tragoportax* (for the ecology of the latter genus see Merceron *et al.* 2006); those of the woodlands could be *Dihoplus* (see e.g., Giaourtsakis *et al.* 2006; Giaourtsakis 2009), *Prostrepsiceros*, *Miotragocerus (Pikermicerus)* (Spassov & Geraads 2004), the giraffes, the cervid, *Microstonyx*, the broad-hoofed *Hippotherium brachypus*, the mastodonts and perhaps also *Ancylotherium*, a genus that might have fed on soft stems (Geraads *et al.* 2006a; Schulz *et al.* 2007). The presence of closer and humid biotopes, probably near the river banks, is indicated by *Dorcatherium* and *Tapirus*.

As a whole, such faunal associations are characteristic for the "Pikermian biome" (*sensu* Solounias *et al.* 1999) of the Balkano-Iranian (Greco-Iranian sensu Bonis *et al.* 1979) zoogeographic province, but there are some regional variations. Perhaps the most remarkable feature of the Bulgarian middle Turolian faunas is the virtual absence of antelopes of the *Protoryx-Pachytragus* group that are so common in Greece and Turkey; together with the presence of *Dorcatherium* and *Tapirus*, this might suggest that in this part of Bulgaria begins a transitional zone leading to the more forested province of central Europe.

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