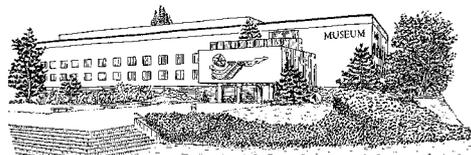


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The Bulgarian Chalicotheriidae (Mammalia): an update

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Abstract

All available chalicotheriid material from the late Miocene Bulgarian localities is revised. It belongs to three taxa: *Ancylotherium pentelicum*, *Chalicotherium* cf. *goldfussi* and *Kalimantsia bulgarica*, the former being the most common. The new material of *A. pentelicum* increases its known variability, but there is still no evidence of evolutionary changes in this species, as the smaller size of the fossils from Hadjidimovo might be explained by sexual dimorphism. On the basis of its forearm and manus morphology, we challenge the view that *Ancylotherium* was a leaf-eater.

Key-words

Chalicotheriidae, Mammalia, Bulgaria, late Miocene.

Résumé

Tout le matériel de Chalicotheriidae du Miocène supérieur de Bulgarie est révisé. Il appartient à trois taxons: *Ancylotherium pentelicum*, *Chalicotherium* cf. *goldfussi* et *Kalimantsia bulgarica*, le premier étant le plus commun. Les nouveaux matériaux de *A. pentelicum* accroissent sa variabilité connue, mais rien ne démontre l'existence de changements évolutifs dans cette espèce, car la faible taille des fossiles de Hadjidimovo pourrait s'expliquer par le dimorphisme sexuel. En nous basant sur la morphologie de son avant-bras et de sa main, nous ne pensons pas que *Ancylotherium* ait été un brouteur de feuilles.

Mots-clés

Chalicotheriidae, Mammalia, Bulgarie, Miocène supérieur.

INTRODUCTION

More than 40 late Miocene mammalian localities are known in southwestern Bulgaria, along the Mesta and Struma rivers, which flow south through Greece to the Aegean sea. They have been referred recently to several lithostratigraphic complexes (see faunal lists, revised stratigraphy of the Struma localities and map in SPASSOV *et al.*, in press a). The richest areas are Hadjidimovo and Kalimantsi. Hadjidimovo, in the Mesta valley, consists of a main fossiliferous locality (Hadjidimovo-1), which is one of the richest sites of the whole Eastern Mediterranean, and 2 other minor spots, all of them of Turolian age (SPASSOV, 2000). At Kalimantsi, more than 10 sites that are certainly not exactly contemporaneous have been recognized, but all of them are also of Turolian age (SPASSOV *et al.*, in press) and there is no evidence of Vallesian assemblages, in contrast to previous opinions (KOJUMDZIEVA *et al.*, 1982). The Kalimantsi and Hadjidimovo faunas are becoming increasingly better known, after the classic monograph of BAKALOV & NIKOLOV (1962), and following the recent systematic studies on the carnivores (KOVACHEV, 1988), Suidae (KOSTOPOULOS *et al.*, 2001), Bovidae (GERAADS *et al.*, 2003; SPASSOV & GERAADS, 2004; SPASSOV *et*

al., 2004), hipparions (HRISTOVA *et al.*, 2002a, b), and Cercopithecidae (KOUFOS *et al.*, 2003).

A new Chalicotheriidae, *Kalimantsia bulgarica*, was recognized at Kalimantsi (GERAADS *et al.*, 2001) and described together with some other chalicotheriid remains. The present paper is a systematic survey of all available Bulgarian chalicotheriid material, sorted by localities. All of them are of Turolian age, since the lowest fossiliferous level at Kalimantsi, which yielded the tooth referred to *Metaschizotherium fraasi* by NIKOLOV (1972), has an early Turolian, and not Vallesian, fauna.

Upper teeth are in uppercase, lower teeth in lowercase. Measurements are in mm. Unless otherwise indicated, all material is kept in the Museum of Paleontology (branch of the NMNH, Sofia), Assenovgrad.

SYSTEMATIC STUDY

Order Perissodactyla OWEN, 1848

Family Chalicotheriidae GILL, 1872

**Sub-family Schizotheriinae HOLLAND & PETERSON,
1913**

Genus *Ancylotherium* GAUDRY, 1863

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Ancylotherium pentelicum* (GAUDRY & LARTET, 1856)*Strumyani-1**

The medial half of a right talus (FM-2027, NMNH Sofia) is the only chalicothere remain from the new locality of Strumyani-1 (= Ilindentsi). The tibial facet is very rounded, the navicular facet is strongly convex transversely, and narrows sharply laterally. This preserved part of the talus does not significantly differ from other Bulgarian tali (see below, and GERAADS *et al.*, 2001), and we refer it to *Ancylotherium*. Their measurements are given in Table I.

Hadjidimovo-Tumbichkite (HD-2)

From this locality, which is distinct from the main Hadjidimovo locality (HD-1), we have a duplex of very large size, HD-2-713 (Table II), probably gnawed by a hyena, and both rami (lacking the symphyseal part) of a lower jaw, HD-2-712 (Pl. I, fig. 5).

The depth of the mandibular ramus decreases regularly from rear to front, and the lower border is almost straight, as in a specimen from Pikermi, whereas that from Veles is convex below the premolars (GAREVSKI & ZAPFE, 1983, resp. figs 5B and 4B). The anterior edge of the ascending ramus is extremely oblique, as in the Pikermi specimen, and therefore quite distinct from the American genera *Moropus* and *Tylocephalonyx* (COOMBS, 1978, 1979). The level of the rear part of the symphysis is intermediate between both other specimens. The mandible is broken anteriorly at the level of a hole, 37 mm before p2 (Pl. I, fig. 5b). This hole is clearly homologous with the similarly located "Sediment erfülltes Loch" mentioned by GAREVSKI & ZAPFE (1983), on the Veles specimen, and attributed by them to a canine alveolus. This interpretation is, in our opinion, hardly tenable, as already surmised by COOMBS (1989), because no mental foramen is visible behind it, and this hole must be the mental foramen itself. On the specimen from Pikermi (GAREVSKI & ZAPFE, 1983,

Table I: Comparative measurements of talus

	Maximum width	Medial height	Lateral height	Medial depth (A-P)	Depth distal facet (A-P)
Strumyani, FM-2027	-	71	-	78	
Kalimantsi, K-708	110	68	70	77	58
Kalimantsi, K-608	102.5	62.5	61	67	45
Pinaryaka (Turkey) *	101	70	61	57	48
Salihpaşalar (Turkey) *	108	65	63	-	46
Pikermi, Vienna, Athens**	105-122	70-79	62-78	-	-
Pikermi, BM M11431	112	76.5	75	76	-
Pikermi, BM M11432	104.5	69.5	64	65	-

* From SARAÇ *et al.*, 2002; ** N = 3, from ROUSSIAKIS & THEODOROU, 2001

Table II: Comparative measurements of duplex

	Max. length	Length phal.I	Prox. width	Distal width phal. I
HD-2-713	-	-	73	71
HD-662	-	112.5	57	52.5
K-711	-	-	ca. 70	63
Pinaryaka *	178-182	122-124	72-74	-
Pikermi, Halmyropotamos, Samos **	159-182	-	68-70.5	-

* N = 2, from SARAÇ *et al.*, 2002

** N = 5, from ROUSSIAKIS & THEODOROU, 2001

pl. 5B), the mental foramen is closer to p2, partly because this tooth is larger, but the overall difference between the Pikermi and Veles specimens is slight (contra GAREVSKI & ZAPPE, 1983). The mental foramen is slightly more anterior in *Moropus* (COOMBS, 1978, fig. 3; 2004, fig. 15.2A).

The lower teeth from HD-2 (Pl. I, fig. 5c) are less worn than those of the other specimens, but their dimensions are similar. There is a continuous cingulum on the buccal side. Otherwise, they do not much differ from those of *Moropus*, except that the second lobe of m3 is not significantly longer than the first, and is more symmetrical. The p2 is smaller than at Veles.

Measurements:

Depth of mandible behind m3 = 102; before m1 = 86; before p2 = 47.

Occlusal length p2-p4 = 70; m1-m3 = ca. 156; p2-m3 = ca. 225

p2 = 15.5 x 10.3; p3 = 27.6 x 16; p4 = 31.2 x 23.1

m1 = 42.5 x 24.5; m2 = 52.7 x 28.6; m3 = 59.4 x 31.1.

Hadjidimovo-1

From the main Hadjidimovo locality, GERAADS *et al.* (2001) have already described a good deal of cranial material, and mentioned a duplex HD-662 (measurements: Table II), perhaps associated with a 3rd phalanx HD-661. HD-664 is a 1st phalanx (L max = 93; prox. width = 55.5). There is also a mandibular fragment, HD-669 (m1 = 42.7 x 22.2).

Since our 2001 paper, we have been able to examine several unpublished deciduous tooth series from Samos in the Musée Cantonal de Géologie, Lausanne (MCGL). All of them are remarkably alike; the only variable feature is the lingual closure of the median valley of DP2: it is open on S59, S60, S65, but blocked by a wall connecting the protocone and hypocone on S61 and S64. HD-634 from Hadjidimovo is intermediate (Pl. I, figs 1-3). Even size is remarkably homogeneous: all 7 measurable DP3s (4 from Samos, 2 from Hadjidimovo, 1 from Pikermi) have lengths in the 30-33 mm range. A DP3 from Samos Quarry A in the American Museum of Natural History is slightly shorter (27.9 mm), probably because it is strongly worn (M. COOMBS, pers. comm.).

The best new specimens from Hadjidimovo are an associated set of three left metacarpals, McII-McIV, with the trapezoid still attached, and perhaps even fused with McII (Pl. I, fig. 4). An unnumbered magnum is perhaps of the same individual.

The trapezoid is more triangular in proximal view than the one from Pinaryaka (SARAÇ *et al.*, 2002) and the volar articulation is less spherical (measurements: Table III). The dorsal, non-articular, part of the magnum is less reduced than at Pinaryaka; this seems to agree with the less broadened dorsal part of the trapezoid, but it is also reduced on a specimen from Pikermi (ROUSSIAKIS & THEODOROU, 2001, fig. 24.3) in which the

trapezoid is not so broad (measurements: Table IV). The trapezoid of *Ancylotherium* is quite distinct from that of *Tylocephalonyx* (COOMBS, 1979, fig. 13) by its almost spherical scaphoid articulation, allowing extreme carpal flexion.

The massiveness of the McII varies strongly (compare SCHAUB, 1943, fig. 17a, from Samos, and ROUSSIAKIS & THEODOROU, 2001, fig. 25.5, from Pikermi), but the HD specimen is still more slender than the latter. It is also, like the other metacarpals, smaller than all other published specimens from Pinaryaka, Samos, and Pikermi (Table V).

As at Pinaryaka and Pikermi (in both sites associated metacarpals are known), the McIII is longer than the McIV, whereas they are of the same length in the Samos specimen described by SCHAUB (1943). It is also more slender than in the other sites, the proximal end being narrower, and especially more so than at Pinaryaka. There is a single, long facet for the unciform; parallel and distal to it is also a single, long facet for the McIV; both are similar to the specimen from Pinaryaka (SARAÇ *et al.*, 2002). The McIV is also slender, but has a stronger proximo-lateral process than in the other sites. The proximal surface is less oblique than at Samos.

On the whole, this hand from Hadjidimovo is noticeable by its rather small size and slenderness. Since the sample from other localities is not exceedingly small, the difference is likely to be significant, but might well be due to sexual dimorphism, especially because the teeth are

Table III: Comparative measurements of trapezoid

	Max. AP	Max. transverse
HD-518	76.5	45
Pinaryaka *	90	61
Pikermi, Samos**	68-95	44-72

* From SARAÇ *et al.*, 2002

** N = 7, from ROUSSIAKIS & THEODOROU, 2001

Table IV: Comparative measurements of magnum

	Max. A-P	Max. H
HD, no N°	100	55
Pinaryaka *	107.5	65
Pikermi, Samos**	108-121	64-76

* From SARAÇ *et al.*, 2002

** N = 3, from ROUSSIAKIS & THEODOROU, 2001

Table V: Comparative measurements of McII

	Length	Proximal width	Proximal depth	Min. width shaft
HD-518	ca. 215	72	75.5	43
Pikermi, Samos. *	233-251	87-100	87-99	50-64
Maragha, MNHN	-	82	92	6

* N = 3, from ROUSIAKIS & THEODOROU, 2001

Table VI: Comparative measurements of McIII

	length	proximal depth	min. width of shaft	distal artic. width	distal artic. depth
HD-528	245	67	48.5	63	66.5
Pinaryaka *	288	78	61	75	84
Samos (SCHAUB, 1943)	276	72	59	65	83
Pikermi N = 3-4 **	279-296	74-84	64-69	75-80	77-96
Maragha, MNHN	-	79	60	-	-

* From SARAÇ *et al.*, 2002. These McIII/IV are from the right side, not left as indicated by mistake; ** from ROUSIAKIS & THEODOROU, 2001

Table VII: Comparative measurements of McIV

	length	proximal depth	min. width of shaft	distal artic. width	distal artic. depth
HD-527	226	ca. 60	42	60	64
Pinaryaka *	270	74	56	63	77
Samos (SCHAUB, 1943)	274	68	54	62	79
Pikermi, Samos. **	244-279	66-73	43-60	50-78	67-84

* From SARAÇ *et al.*, 2002; ** N = 5, from ROUSIAKIS & THEODOROU, 2001

not smaller than in other sites, and because both duplexes from Hadjidimovo are also strongly dimorphic.

Kalimantsi

Besides the talus already mentioned in our 2001 paper, the only new specimens are a new talus K-708 (Pl. I, fig. 6; measurements: Table I), a duplex K-711 (measurements: Table II), and a first phalanx. All these fossils come from the main levels of Kalimantsi, with a middle Turolian fauna.

A complete upper tooth series from Kalimantsi (most probably from the middle Turolian level) had been illustrated by BAKALOV (1955) and by BAKALOV &

NIKOLOV (1962, pl. 15, fig. 1). A DP3 from the basal level of this locality (KAL-1, early Turolian) was figured by NIKOLOV (1972, fig. 1) as an M2 of *Metaschizotherium fraasi*. Its length was given by NIKOLOV (we could not find this tooth in the Sofia University) as 34.8 mm, which would make it a trifle larger than the other DP3s, but we refer it to *A. pentelicum*.

Gorna Sushitsa

This is known in the literature as a single locality, but recent survey there by N.S. and D.G. revealed at least 4 different fossiliferous spots, over a vertical distance of at least 40 meters (SPASSOV *et al.*, in press a). Thus, the

exact provenance of the maxilla figured by BAKALOV and by BAKALOV & NIKOLOV (1962, pl. 15, fig. 2) is unknown, but all localities are probably of Turolian age.

DISCUSSION

The upper dentition of *A. pentelicum* is known by a few specimens only. Both the Kalimantsi and Gorna Sushitsa tooth rows are less worn than the specimen from Pikermi figured as *Rhinoceros pachygnathus* by WAGNER (1857), but more so than the one in Athens described by THENIUS (1953) from the same locality. GAREVSKY (1974) briefly described a skull from Veles-Karaslari with most of the upper dentition. There are some differences between these various specimens, mainly in the development of accessory spurs and cingulum, and in the relative size of the premolars. The Athens premolars have a crochet

and a crista, which enclose a medifossette on P4. These spurs are absent on the Bulgarian specimens. The P4 from Kalimantsi is almost as broad as M1, whereas the others are narrower. On the molars, the lingual closure of the median valley is less complete in the Bulgarian specimens, except HD-633, than in the one in Athens. The latter also has a stronger mesio-lingual ridge from the top of the protocone to the cingulum (note that THENIUS' fig. 1 is incorrect in that there is no wear facet in this area). These differences might denote an advanced evolutionary stage of the Pikermi form over the Bulgarian ones, but they might fit into individual variation as well.

Ancylotherium pentelicum has a restricted geographic range, from Veles in Macedonia to Maragha in Iran (Fig. 1). It is therefore a typical element of the Balkano-Iranian province. There are a few mentions outside this range; some of them are also of earlier age, but definite specific

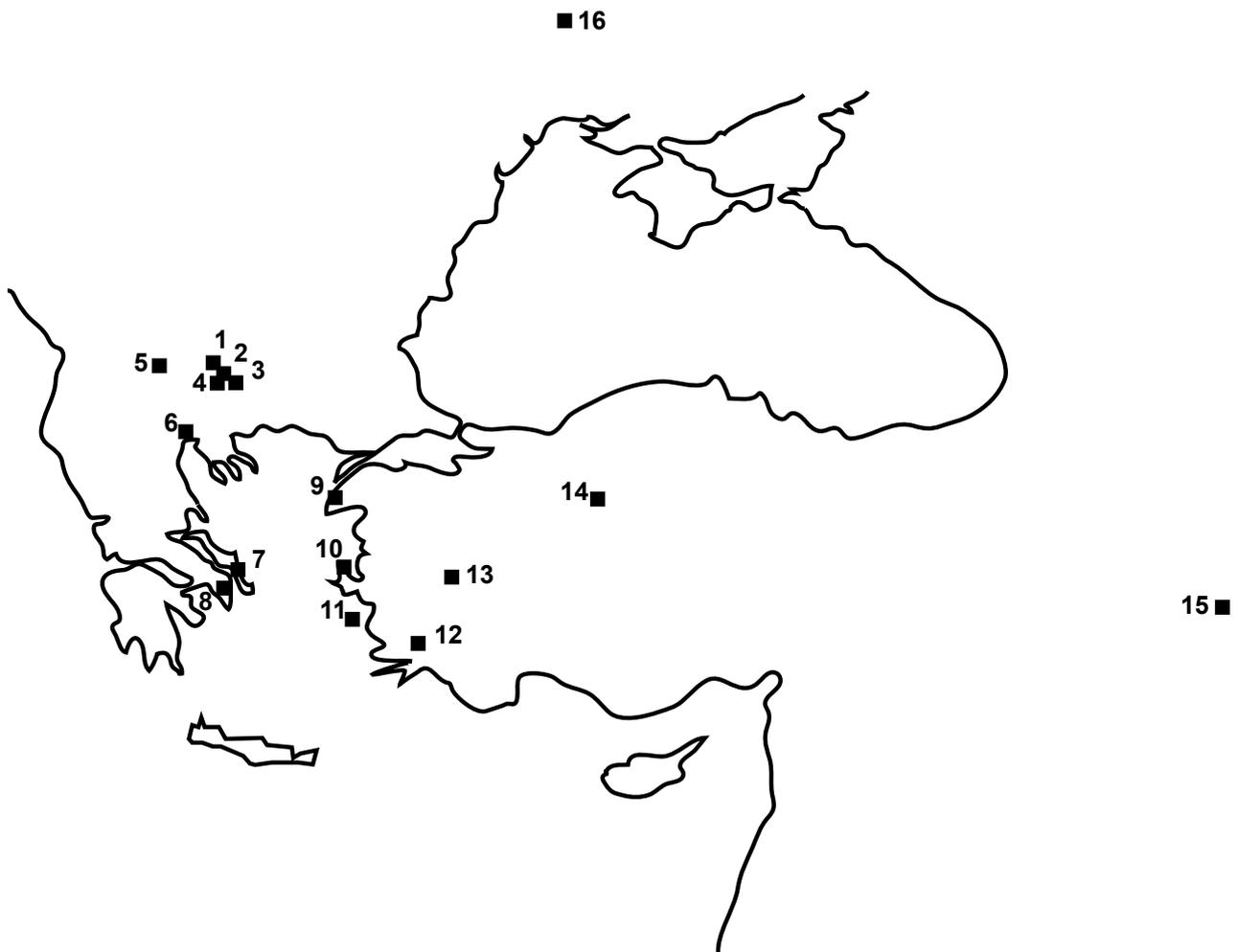


Fig. 1: Late Miocene Eastern Mediterranean localities with *Ancylotherium*.

1: Strumyani; 2: Gorna Sushitsa; 3: Hadjidimovo; 4: Kalimantsi; 5: Veles; 6: Pentalophos; 7: Halmyropotamos; 8: Pikermi; 9: Gülpınar; 10: Karaburun; 11: Samos; 12: Salihpaşalar; 13: Kemiklitepe; 14: Pinaryaka; 15: Maragha; 16: Novoukrainka.

identification is difficult. It has been reported from Molayan in Afghanistan (BRUNET *et al.*, 1984) but details have yet to be published. The names *Huanghootherium anlungense* TUNG, HUANG & QIU, 1975, and *Gansuodon pingliangense* WU & CHEN, 1976 might be synonymous, and synonymous with *A. pentelicum* as well, but each of these Chinese Turolian forms is known by two upper molars only. A manus from Novoukrainka (MN11 ?; KOROTKEVICH & SULIMSKI, 1990) was figured and perhaps correctly referred to *A. pentelicum* by KOROTKEVICH (1988, pl. 12, fig. a). According to M. COOMBS (pers. comm.), a digit II of the manus figured by PIDOPLICHKO (1959), actually the first mention of *Ancylotherium* from this site, does belong to *A. pentelicum*. A talus from the early Vallesian of Los Valles de Fuentidueña (ALBERDI *et al.*, 1981) does not differ from those of *Ancylotherium*, but a specific identification is risky. Thus, the earliest definite occurrence of the species might be at Pentelophos (BONIS *et al.*, 1999). Only the study of these early forms would tell us if the lineage has undergone any significant changes in the upper Miocene, before its extinction in this area before the end of the Turolian, but evidence for this is still wanting.

In Africa, sparse and incomplete remains dating from the late Miocene to the earliest Pleistocene have been referred to *Ancylotherium*. The talus from Laetoli (GUÉRIN, 1987, fig. 9.1.B) looks lower than that of the Eastern Mediterranean form, and is not thicker medially than laterally, with a very narrow navicular facet. Relying on GUÉRIN's figure, a specific difference is warranted. The Tanzanian form postdates the northern one by several million years, but according to BUTLER (1965), its metacarpal is less derived.

Much has been written on the ecology and mode of life of the chalicotheres. *Ancylotherium* is assumed to differ from the Chalicotheriinae by its very peculiar metacarpodigitigrady, the weight of the forequarters resting on a cushion pad under the distal end of the metacarpals, the proximal phalanges and the sesamoids. According to ZAPFE (1979), *Chalicotherium* rested instead either on the lateral side of the hand or, more probably, on the dorsal part of the ungual phalanx. This latter position is, in our opinion, quite unlikely, first because the metacarpop-

phalangeal articulation would have been permanently prone to dislocation, and because the Hadjidimovo material has shown (GERAADS *et al.*, 2001) that the sesamoids are much larger than ZAPFE (1979) thought, and are therefore more similar to those of *Ancylotherium*. We believe that both genera might have had a similar hand bearing on the ground but, in any case, since the hand was clearly not designed for walking, this is less important than its main function.

Ancylotherium is usually assumed to have been a browser feeding upon leaves, using its long arms and claws to bring branches to the mouth. We believe that this interpretation fails to account for the very peculiar set of adaptations of the fore-limb, which include radio-ulnar fusion, preventing hand rotation, but ability to extreme carpal flexion and extreme phalangeal extension, fused first and second phalanges of digit II, at least, and cloven third phalanges, presumably fitted with very powerful claws. Even if some of these adaptations were designed to keep the claws out of contact from the ground during walking, the whole set is ill-suited for branch grasping. Because of its lack of rotation ability, the forearm was certainly inefficient in bringing food to the mouth; it is so unlike that of, e.g., Primates, that a similar use of their arm and hand must be ruled out. On the other hand, it lacked fossorial adaptations (COOMBS, 1983). Still, it is hard to imagine that the claws had no specific function. Being half bipedal, *Ancylotherium* must have stood more or less upright, using its long arms to collect food from the trees, but if standing against a tree or any tall plant, the hands could not have rested on the trunk in the way shown by Borissiak (1945, fig. 8). Instead, the hands had to lie on either side of the trunk with the claws directed inwards (medially). In this position, the most likely use of the strong, clawed fingers was ripping or peeling off the bark or the whole plant. Thus, we hypothesize that the food of *Ancylotherium* consisted basically of the bark of some tree, or of a plant stem itself. This kind of food would be tough but not very abrasive. This is in good agreement with their dentition, which includes a powerful sub-hypsodont shearing component and a crushing component that is large but low-crowned.

Plate I

Ancylotherium pentelicum

Fig. 1: DP2-DP4 from Hadjidimovo, HD-634 (photo of cast).

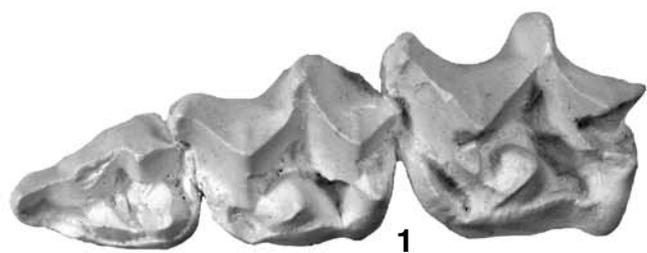
Fig. 2-3: DP2-DP4 from Samos in MCGL for comparison. 2 : S-60 (reversed), 3 : S-64.

Fig. 4: Associated left McII-McIV and trapezoid from Hadjidimovo (HD-518, 527, 528). Anterior view.

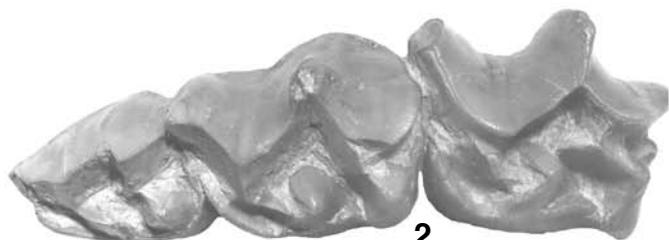
Fig. 5: Left mandibular ramus from Hadjidimovo-Tumbichkite, HD-2-713. a : lateral view, b : detail of the anterior portion, c : occlusal view.

Fig. 6: Talus from Kalimantsi, K-708. a : anterior view, b : plantar view, c : distal view.

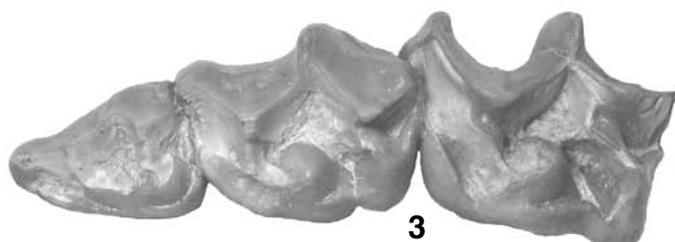
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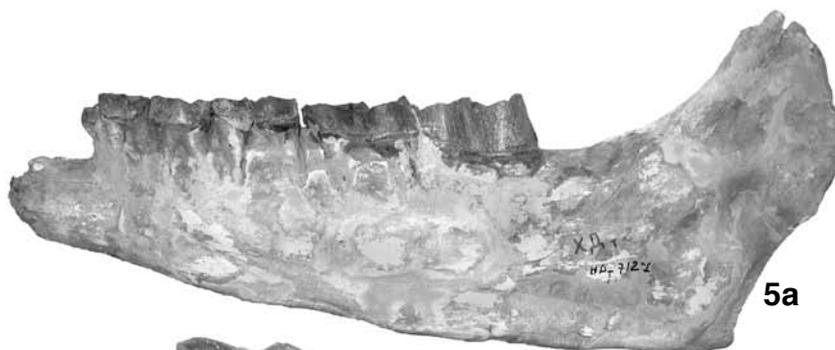
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4



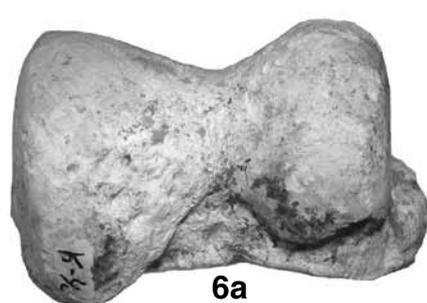
5a



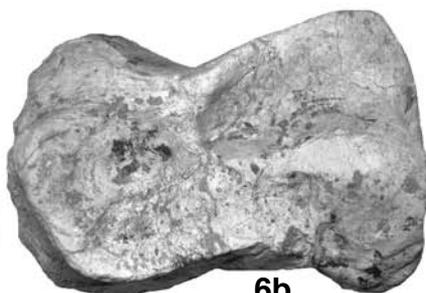
5b



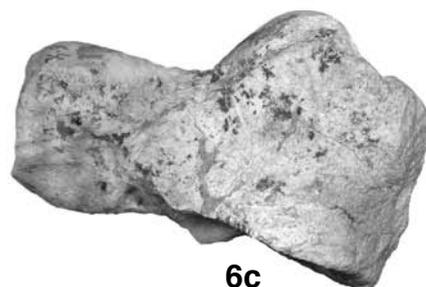
5c



6a



6b



6c

Sub-family Chalicotheriinae GILL, 1872

No new material of this sub-family has come to light. *Kalimantsia bulgarica* is known from Kalimantsi-Pehtsata only. *Kalimantsia* is characterized by a high skull, very long cerebral (post-orbital) part and reduced facial part, upper teeth with a short protoloph as in other late Miocene forms (“*Macrotherium*» *macedonicum* and *Ch. goldfussi*), but unlike the middle Miocene “*Chalicotherium*” *brevirostris* and *Anisodon*. The molars are much longer than broad with long and less oblique distal half of the ectolophs, P3 is broad, with an isolated protocone. The “*Macrotherium*” *macedonicum* skull from Dytiko in Greece could be a species of the genus *Kalimantsia*, but the muzzle is still shorter, and the molars are not long. A cf. *Chalicotherium goldfussi* is known from Hadjidimovo, Gorna Sushitsa and Kromidovo (all these localities are probably of early to middle Turolian age). A lower molar from Batishnitsa in the Ruse region was also figured by NIKOLOV (1975) under this name.

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