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Original article

New material of Chalicotheriidae (Perissodactyla, Mammalia) from the Late Miocene of Axios Valley, Macedonia (Greece) with the description of a new species

Nouveau matériel de Chalicotheriidae (Perissodactyla, Mammalia) du Miocène supérieur de la vallée de l'Axios, Macédoine (Grèce) et description d'une nouvelle espèce

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Abstract

Chalicotheriids are rare in the late Miocene mammal localities of Axios Valley, Macedonia (Greece). The new campaign of excavations, since 1972, has provided some specimens, which are studied in this article. They are coming from two different localities. The late early Vallesian locality of Pentalophos 1 (PNT) has provided a skull and a mandible of an *Ancylotherium*. The morphological characters of the PNT material as the small size, the long snout, the shallow mandibular corpus, the strong cingulum in the teeth, the short tooth rows and the short M3/m3 indicate that it differs from the known Turolian species *A. pentelicum* and allow the erection of a new species, named *Ancylotherium hellenicum* n. sp., which can be used as a biostratigraphic marker of the Vallesian. The middle Turolian locality Prochoma 1 (PXM) has provided only one M3, which is determined to the chalicotheriine *Anisodon macedonicus*. This species was earlier described from the middle Turolian locality Vathylakkos 3 (VAT) and the late Turolian one of Dytiko 3 (DKO) of Axios Valley. The biogeography and biostratigraphy of the late Miocene chalicotheres of the Greco-Iranian Palaeoprovince (GRIP), as well as their palaeoecology are also discussed. The common chalicothere of GRIP is *A. pentelicum*, expanded from the Balkans to Afganistan and ranging stratigraphically from the early to the late Turolian.

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Chalicotherium goldfussi is certainly present in GRIP and it also ranges from the early to the late Turolian; its possible Vallesian occurrence needs confirmation. The other two late Miocene chalicotheres of GRIP *A. macedonicus* and *Kalimantsia bulgarica* are restricted to the Turolian of the Balkan Peninsula.

Keywords: Chalicotheriidae; Vallesian; Greece; New species; Biostratigraphy; Biogeography

Résumé

Les Chalicotheriidae sont rares dans les localités du Miocène supérieur de la vallée de l'Axios (Macédoine, Grèce). Les nouvelles campagnes de fouilles depuis 1972 ont fourni quelques spécimens étudiés dans cet article. Ces spécimens proviennent de deux gisements. Un crâne et une mandibule de *Ancylotherium* ont été mis au jour à Pentalophos 1 (PNT), un site calibré au Vallésien inférieur. Les caractères morphologiques du matériel de PNT tel que la taille réduite, le long museau, le haut corps mandibulaire, le fort cingulum des dents, la courte série dentaire et notamment les courtes M3/m3 diffèrent de l'espèce turolienne *A. pentelicum* et permet la détermination d'une nouvelle espèce, nommée *Ancylotherium hellenicum* n.sp., qui peut être utilisée comme un marqueur biostratigraphique du Vallésien. La localité Prochoma 1 (PXM) du Turolien moyen a fourni une seule M3, qui a été attribuée au chalicotheriine *Anisodon macedonicus*. Cette espèce avait été précédemment décrite à Vathylakkos 3 (VAT) et Dytiko 3 (DKO) respectivement du Turolien moyen et supérieur de la vallée de l'Axios. La biogéographie et la biostratigraphie des chalicothères du Miocène supérieur de la province gréco-iranienne (GRIP) de même que leur paléoécologie sont discutées. Le chalicothère commun de la GRIP est *A. pentelicum*, réparti depuis les Balkans jusqu'en Afghanistan et distribué du Turolien inférieur au Turolien supérieur. *Chalicotherium goldfussi* est présent dans la GRIP et distribué du Turolien inférieur au Turolien supérieur. Sa possible présence au Vallésien nécessite confirmation. Les deux autres chalicothères du Miocène supérieur de la GRIP, *A. macedonicus* et *Kalimantsia bulgarica*, sont restreints au Turolien de la péninsule balkanique.

Mots clés : Chalicotheriidae ; Vallésien ; Grèce ; Nouvelle espèce ; Biostratigraphie ; Biogéographie

1. Introduction

Chalicotheres represent a peculiar group of perissodactyls, characterized by the absence of hooves, which were replaced by large bifid claws (Heissig, 1999). The chalicotheres are present in several late Miocene faunas, but their remains are scarce. They are divided in two subfamilies: Chalicotheriinae Gill, 1872 and Schizotheriinae Holland and Peterson, 1914, both recorded in Greece (Fig. 1). Ten certain taxa of Chalicotherioidea are referred worldwide; additional valid taxa are known by cranio-dental or postcranial material but they lack significant parts of their skeleton (Coombs, 2009). The most common Greek chalicothere is *Ancylotherium pentelicum* known from several localities, mainly by postcranials; except its type locality Pikermi it is referred from Halmyropotamos, Kerassia, Samos, Thermopigi (Melentis, 1969; Roussiakis and Theodorou, 2001; Theodorou et al., 2003; Geraads et al., 2007; Giaourtsakis and Koufos, 2009). Some chalicothere remains are also known from the locality Chomateres (CHO), near Pikermi, described as *Chalicotherium goldfussi* (Symeonidis, 1973).

The first chalicotheres from Axios Valley were described as *Chalicotherium* cf. *goldfussi* (Arambourg and Piveteau, 1929), transferred later to *Macrotherium macedonicum* (Bonis et al., 1995). The new excavations in the late Miocene localities of Axios Valley, since 1972, brought to light a great amount of fossils, but the chalicotheres are scanty. A skull and the associated mandible

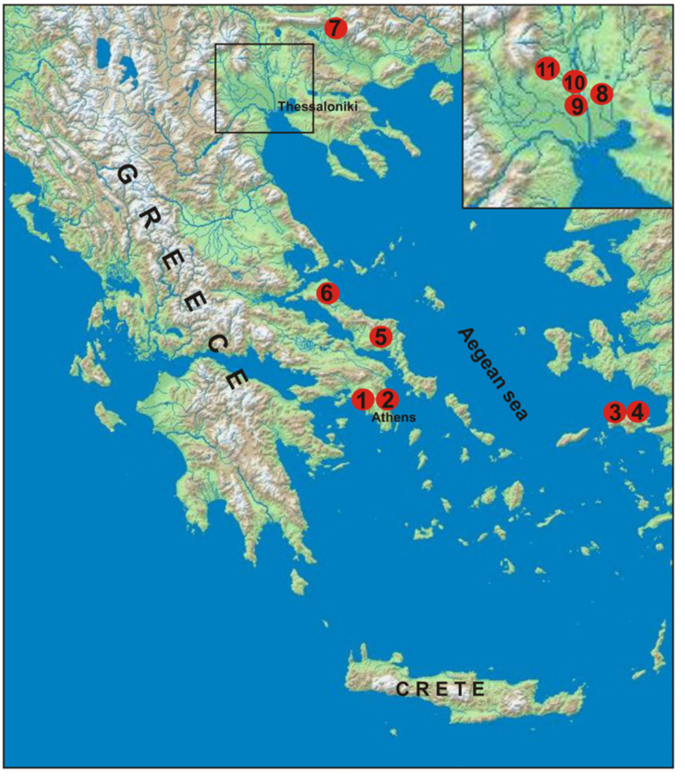

Fig. 1. Geographic map of Greece, indicating the chalicothere-bearing mammal localities.
*Localisation des sites fossilifères de Grèce avec des chalicothères. **1**. Pikermi (PIK) ; **2**. Chomaters (CHO) ; **3**. Mytilinii-3 (MYT), Mytilinii-1 (MTL) ; **4**. Halmyropotamos (HAL) ; **5**. Kerassia (KER) ; **6**. Thermopigi, (TMP) ; **7**. Pentalophos 1 (PNT) ; **8**. Vathylakkos 3 (VAT) ; **9**. Prochoma 1 (PXM) ; **10**. Dytiko 3 (DKO).*

of a chalicothere from the locality Dytiko 3 (DKO) have been described as *M. macedonicum* (Bonis et al., 1995), which recently transferred to *Anisodon macedonicus* (Anquetin et al., 2007). Except those, some more chalicothere remains were found in the different fossiliferous sites of Axios Valley during the recent field trips. This new material is studied and compared in the present article, providing additional information for the chalicotheres of Greece. It is also given a revision of the biostratigraphy and biogeography of the Miocene chalicotheres in southeastern Europe and southwestern Asia.

2. Material and localities

The studied material originates from two distinct localities of Axios Valley, belonging to different stratigraphic levels. The locality Pentalophos 1 (PNT) (Fig. 1) is situated into Nea Messimvria Fm, dated to Vallesian (Koufos, 2006a, Koufos, in press). The other chalicothere-bearing mammal locality is Prochoma 1 (PXM) (Fig. 1), situated into Vathylakkos Fm and dated to the middle Turolian, MN 12; the magnetostratigraphic record indicates an estimated age of ∼7.4 Ma (Koufos, in press and refs cited). The new material of chalicotheres described earlier (Bonis et al., 1995) has been found in the locality Dytiko 3 (DKO) (Fig. 1), located in Dytiko Fm and dated to the late

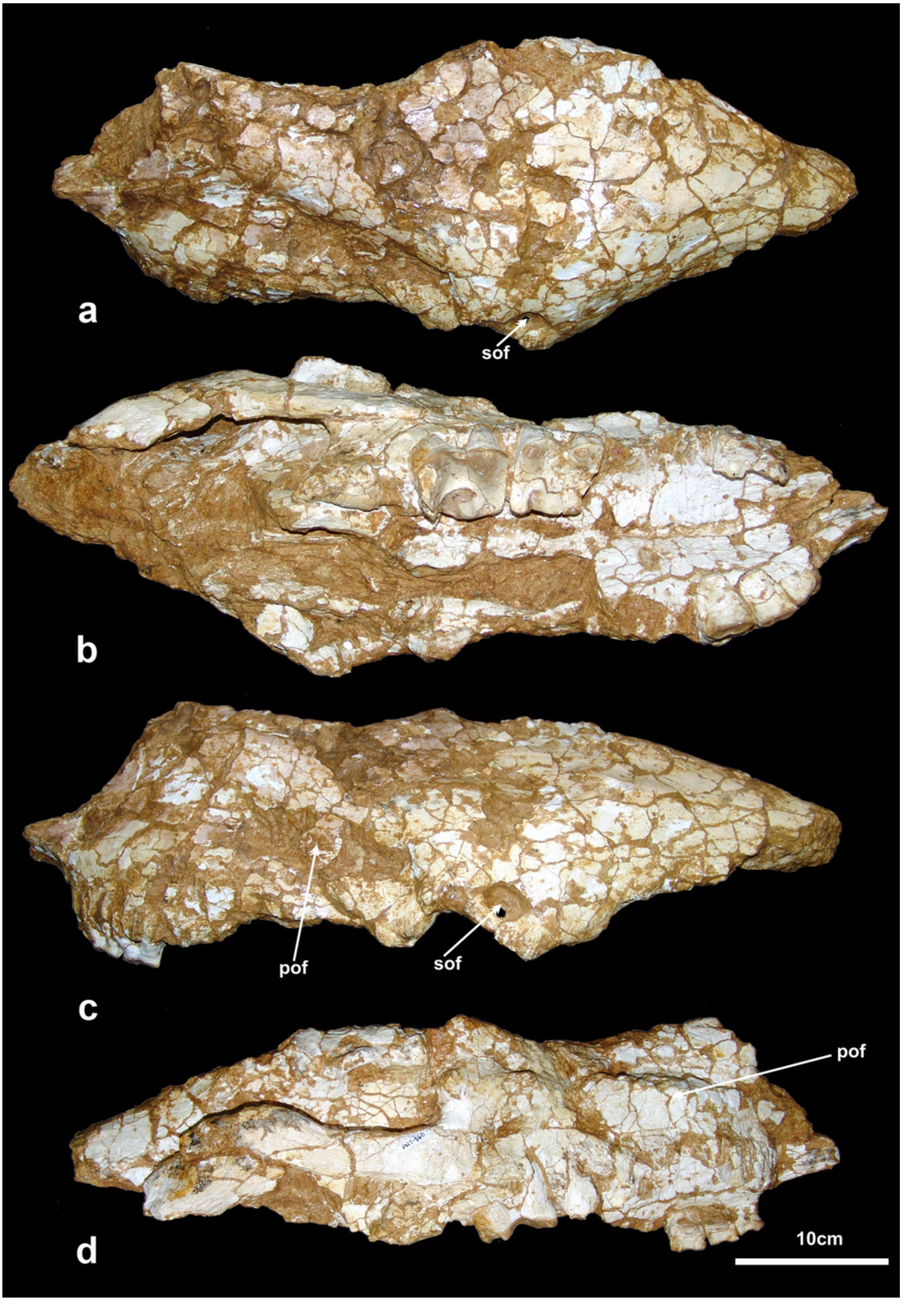

Fig. 2. *Ancylotherium hellenicum* n. sp., Pentalophos 1, PNT, Axios Valley, Macedonia, Greece, early Vallesian, MN 9. Partial skull with P2-P3, M2-M3 dex and P2-P4 sin, PNT-160: **a**: dorsal; **b**: ventral; **c**: right lateral; and **d**: left lateral view.
Ancylotherium hellenicum *n.sp., Pentalophos 1, PNT, vallée de l'Axios, Macédoine, Grèce, Vallésien inférieur, MN 9.*

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Turolian, MN 13 (Koufos, in press). The old chalicothere material from Axios Valley, housed in MNHN and described by Arambourg and Piveteau (1929), originates from the locality Ravin du Vatilük (R.G.), which corresponds to the new one Vathylakkos 3 (VAT) (Fig. 1), and is dated to the middle Turolian with a magnetostratigraphically estimated age of ~7.3 Ma (Koufos, in press and refs cited). All the new material from Axios Valley is housed in the Laboratory of Geology and Palaeontology, University of Thessaloniki (LGPUT). The measurements are taken with a digital caliper and they are given in millimeters. The dental nomenclature is according to Coombs (1978).

Abbreviations
AMPG: Athens Museum of Palaeontology and Geology
BSPM: Bayerische Staatssammlung für Paläontologie und Historische Geologie, München
DKO: Dytiko 3, Axios Valley
GRIP: Greco-Iranian Palaeoprovince
HD-1: Hadjidimovo 1, Bulgaria
HD-2: Hadjidimovo-Tubischikite, Bulgaria
LGPUT: Laboratory of Geology and Palaeontology, University of Thessaloniki
MNHN: Muséum nationalé d'Histoire naturelle, Paris, France
PNT: Pentalophos 1, Axios Valley
PXM: Prochoma 1, Axios Valley
R.G: Ravin du Vatilük, Axios Valley
VAT: Vathylakkos 3, Axios Valley
XIR: Xirochori-1, Axios Valley

3. Palaeontology

Order: PERISSODACTYLA Owen, 1848
Family: CHALICOTHERIIDAE Gill, 1872
Subfamily: SCHIZOTHERIINAE Holland and Petterson, 1914
Genus ***Ancylotherium*** Gaudry, 1863
***Ancylotherium hellenicum* n. sp.**

Type locality. Pentalophos 1 (PNT), Axios Valley, Macedonia (Greece).
Age. Late early Vallesian, (late MN 9); late Miocene.
Holotype. Skull PNT-160.
Paratype. Mandible, PNT-33; it is probably associated to the skull PNT-160.
Origin of the name. Hellas, the name of the country found.
Diagnosis. Small size; elongated skull; well-developed post-orbital process with open supra-orbital foramen; mesial margin of the orbit above the distal margin of the M3; stout and shallow zygomatic arc; elongated, oval-shaped and parallel to the nasals preorbital fossa; narrow and deep palate; elliptical and wide choanae with their mesial border well behind the M3; elongated, low and narrow snout; shallow mandibular corpus with increased depth distally and straight ventral

Fragment de crâne avec P2-P3, M2-M3 droites et P2-P4 gauches, PNT-160 : **a** : vue dorsale ; **b** : vue ventrale ; **c** : vue latérale droite ; et **d** : vue latérale gauche.

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border; no ventral expansion in the mandibular angle; strong cingulum in the teeth; short tooth rows; decreased M3/m3.

Description.

Skull (Fig. 2). The skull PNT-160 lacks the braincase, and the basal part behind the choanae. It is strongly compressed dorso-ventrally and laterally crushed and deformed. The strong deformation of the skull does not allow accurate measurements; those which can be measured are given in the text. The skull is elongated with possibly an elongated and narrow muzzle; the distance from the mesial margin of the orbit to the mesial one of the P2 is ±225.0 mm. The hump described in the skull of *A. pentelicum* from Thermopigi (Geraads et al., 2007: fig. 2a) is not observed in the studied skull, may be because of the crushing. The post-orbital process is well marked and bears a circular depression with the supra-orbital foramen opening directly to the orbit (Fig. 2a, c), as it is in the skull of *A. pentelicum* from Thermopigi and in *Moropus* (Holland and Peterson, 1914; Geraads et al., 2007). The whole nasal area is crushed and deformed and it is difficult to see its morphology. It seems that the nasals were high, elongated and possibly there was a groove across them. Despite the skull deformation, the preorbital fossa can be traced in both sides of the skull. In the better-preserved left side, there is a depression, which preserves a small part of the bone in its base, which can be correlated to the preorbital fossa (Fig. 2c). In the right part, the presence of the fossa is more evident. The nasal bone is compressed laterally from left to right and the base of the preorbital fossa blows up along the mesio-distal axis of the skull (Fig. 2d). The preorbital fossa seems to be oval-shaped, elongated mesio-distally and parallel to the nasals. The right orbit is preserved but it is compressed dorso-ventrally and we cannot realize its shape. The mesial border of the orbit is situated above the distal margin of the M3. The zygomatic arch is stout but not very deep with a sharp ventral margin; its zygomatic process is straight with constant height till the middle of the orbit; then it curves dorsally and its height gradually decreases distally, across the temporal process. The palate is crushed across its mesio-distal distance but it seems to be deep with constant breadth; its breadth starts to decrease mesially from the P3/P2 contact and the muzzle is abruptly narrowing in front of the P2 (Fig. 2b). The choanae are wide and elliptical in outline; their mesial border is well behind the M3. The median keel of the basisphenoid is extended mesially and forms a bony septum, separating the choanae into two parts.

Mandible (Fig. 3). The mandible PNT-33 lacks both ascending rami and the most mesial part of the snout. It is possibly associated with the skull PNT-160 as it fits with it, the teeth are in the same wearing stage and they were found close one to each other. The snout is elongated, low and narrow. The external symphysis inclines roughly from the incisors to the point below the mesial border of the mental foramen (Fig. 3b–d) and then it continues horizontally (parallel to the ventral border of the mandibular corpus), quite behind the distal border of the mental foramina (length of the ventral part of the external symphysis ∼ 41.0 mm). The external breadth of the symphysis is 46.8 mm at the distal border of the mental foramina, while its minimum breadth (26.0 mm) is observed in the middle of its inclined part. The internal symphysis is horizontal till the line connecting the mesial border of the mental foramina and then it is roughly inclined distally (Fig. 3a). The two mandibular branches are parallel in the snout till the beginning of symphysis and then the snout is slightly widened mesially. The distance from the mesial border of the p3 alveole to the distal margin of the mental foramen is ∼57.3 mm in the right and ∼60.0 mm in the left side. The mental foramina are single and large (Fig. 3b, c). The mandibular corpus has a straight ventral border and its depth increases distally (Table 3). There is no ventral expansion in the mandibular angle (Fig. 3b, c). The tooth rows seem to be straight in buccal view and almost parallel with a large retromolar space (Fig. 3a, c). The left hemimandible preserves a small part

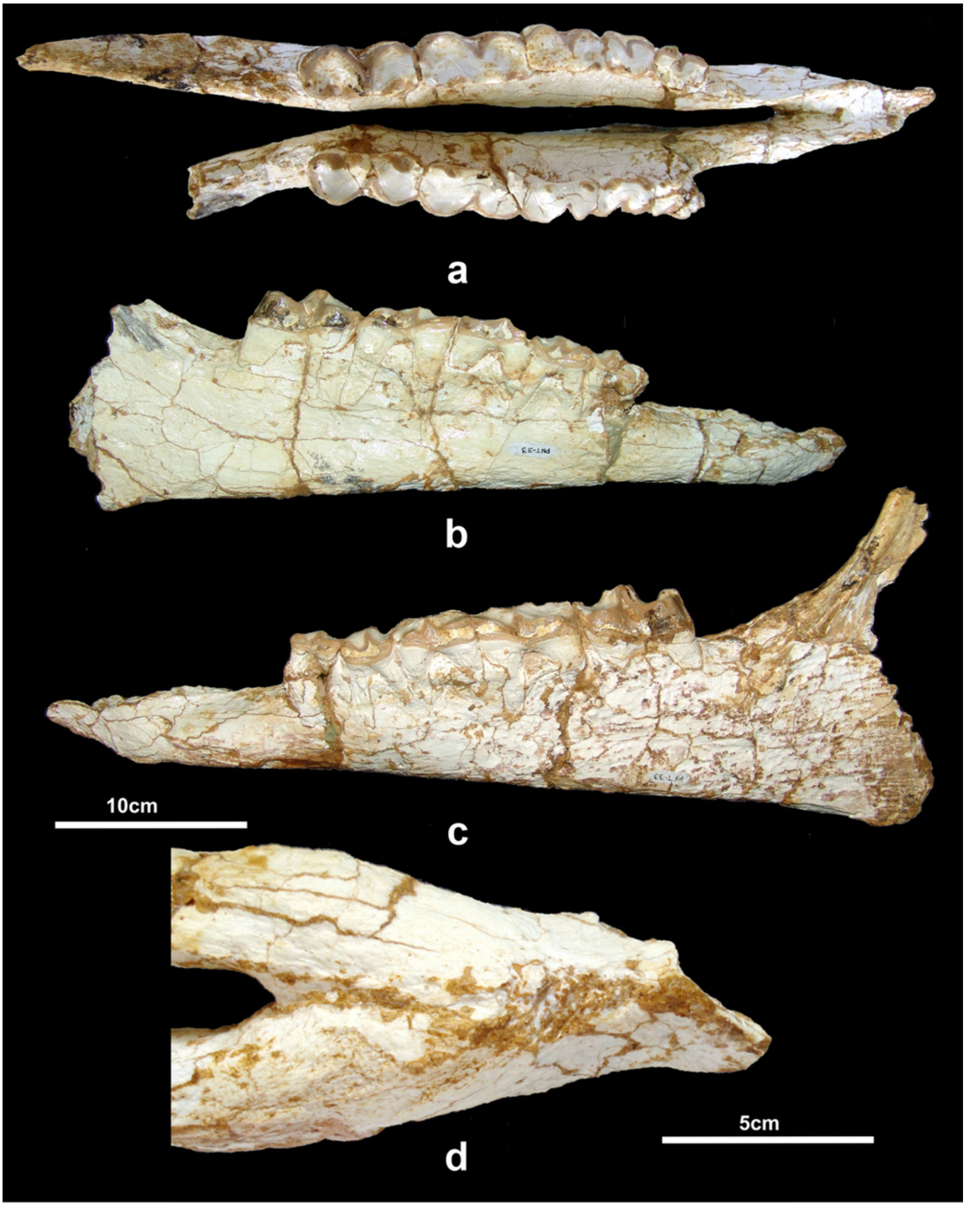

Fig. 3. *Ancylotherium hellenicum* n. sp., Pentalophos 1, PNT, Axios Valley, Macedonia, Greece, early Vallesian, MN 9. Mandible with P2-M3 dex and sin, PNT-33: **a**: occlusal; **b**: right lateral; **c**: left lateral view; and **d**: external symphysis.
Ancylotherium hellenicum *n.sp., Pentalophos 1, PNT, vallée de l'Axios, Macédoine, Grèce, Vallésien inférieur, MN 9. Mandibule avec P2-M3 droites et gauches, PNT-33 :* ***a*** *: vue occlusale ;* ***b*** *: vue latérale droite ;* ***c*** *: vue latérale gauche ; et* ***d*** *: symphyse extérieure.*

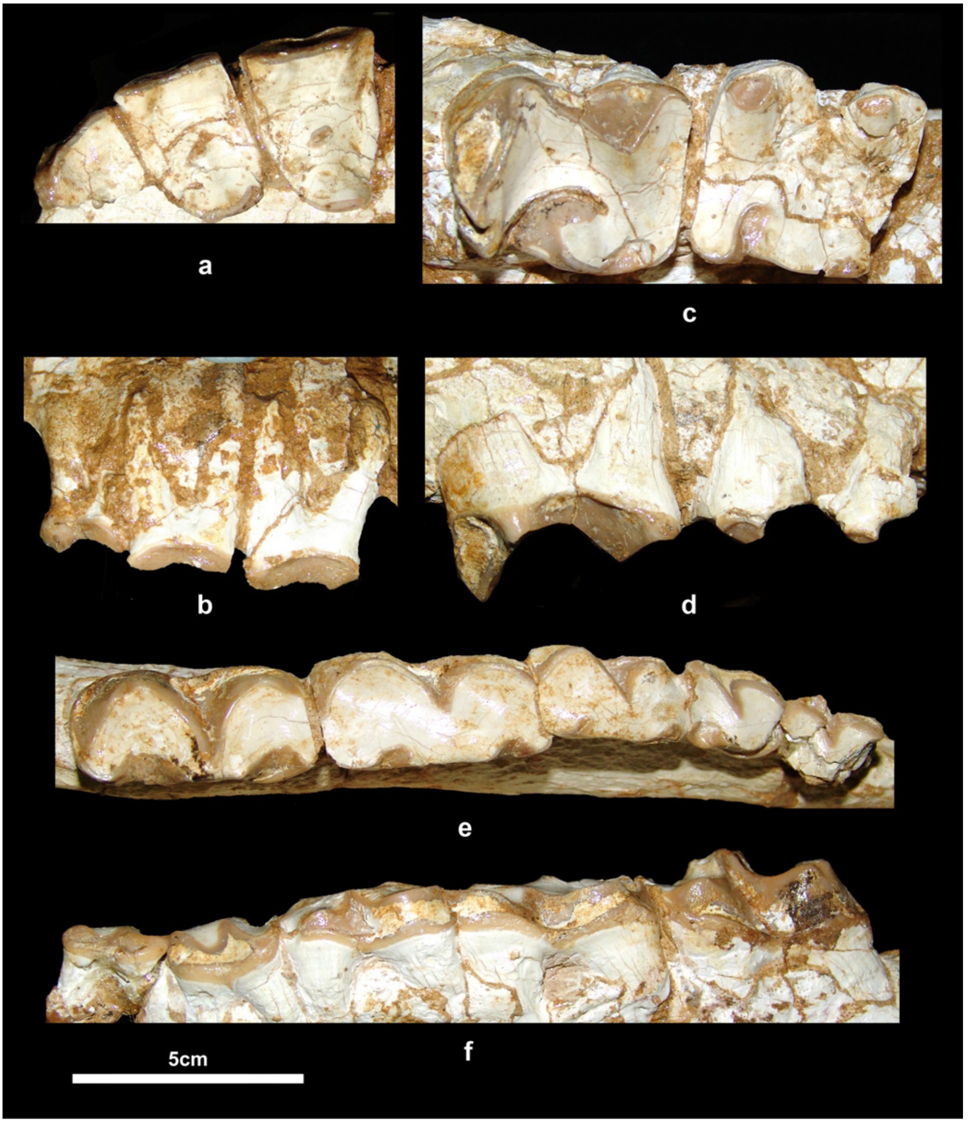

Fig. 4. *Ancylotherium hellenicum* n. sp., Pentalophos 1, PNT, Axios Valley, Macedonia, Greece, early Vallesian, MN 9: **a**, **b**: Left upper premolar row with P2-P4: **a**: occlusal, and **b**: buccal view; **c, d**: right upper molar row with M2-M3; **c**: occlusal, and **d**: buccal view; **e**, **f**: left lower tooth row with p3-m3; **e**: occlusal, and **f**: buccal view.
Ancylotherium hellenicum *n.sp., Pentalophos 1, PNT, vallée de l'Axios, Macédoine, Grèce, Vallésien inférieur, MN 9 :* ***a**,* ***b** : série des prémolaires supérieures gauches :* ***a** : vue occlusale, et* ***b** : vue buccale ;* ***c, d** : série des molaires supérieures droite ;* ***c** : vue occlusale et* ***d** : vue buccale ;* ***e**,* ***f** : série dentaire inférieure avec p3-m3 gauche ;* ***e** : vue occlusale, et* ***f** : vue buccale.*

of the ascending ramus; its mesial margin seems to be nearly perpendicular to the ventral margin of the mandibular corpus (Fig. 3c).

Upper dentition (Fig. 4a–d). The tooth rows of the studied skull are partially preserved; the right tooth row lacks P4-M1 and the left one all the molars; the teeth are extremely worn and they

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have lost the occlusal morphology. The preserved part of the muzzle does not bear any trace of the canines or incisors (Fig. 2b). The P2 has triangular occlusal outline; the preserved part of the ectoloph seems to be slightly concave (Fig. 4a). The P3, 4 are wider than long. All the premolars have a strong lingual cingulum and a weaker buccal one (Fig. 4a, b). The M2 is extremely worn, lacking most of the enamel in its occlusal surface; small enamel pieces are preserved in the tips of the parastyle, mesostyle and in the protocone/hypocone valley (Fig. 4c). The M3 is less worn than all other teeth, preserving some morphological characters (Fig. 4c, d). It is longer than wide with an abrupt narrowing of its distal part, behind the protocone. The ectoloph is strongly W-shaped in occlusal view (Fig. 4c); the distal half of the ectoloph is nearly perpendicular to the mesio-distal axis of the tooth and covered by a thick layer of cement. The metacone is weak and it is directed disto-lingually, separated from the small hypocone by an open V-shaped distal valley. The protocone is large, rounded, connected mesially to the protoloph and situated almost in the middle of the lingual margin. The valley between the protocone and hypocone is open lingually. There are strong buccal and lingual cingula.

Lower dentition (Fig. 4e, f). The teeth are extremely worn, providing limited data for the occlusal dental morphology. The tooth rows lack the p2, while both p3 are broken. The preserved part of the p3 bears a well-developed buccal cingulum (Fig. 4e, f). In the p4 and the molars, the talonid is longer and wider than the trigonid (Fig. 4e). The p4 is molarized with U-shaped trigonid and talonid lingual basin; their bucco-lingual axis is oblique to the mesio-distal axis of the tooth (Fig. 4e). The buccal valley, distinguishing trigonid and talonid basin, has closed-V shape and it is deep; the buccal cingulum is strong. The molars are relatively elongated and narrow (especially the m2, 3) with an open, U-shaped lingual groove and a V-shaped buccal one separating the trigonid and talonid basins; there is a strong buccal cingulum in all molars (Fig. 4e, f). The lingual cingulum cannot be traced in the extremely worn m1, 2 (possibly existed) but it is clearly distinguished mesio-lingually and disto-lingually in the m3 (Fig. 4e). In the less worn m3, the metastylid and metaconid are strong and separated (this separation is much clearer in the left m3), but they are connected in more advanced wearing stages. The trigonid and talonid basins are open lingually. The m3 bears an elevated distal cingulum, running across the distal limit of the entoconid (Fig. 4d).

Comparison. The first evidence for the occurrence of a chalicothere in Greece is that of Duvernoy (1854: p. 256); among some bones from Pikermi he recognized a "*grand tardigrade*" with similarities to *Macrotherium* from Sansan. At the same time, two phalanges from Pikermi were assigned to *Macrotherium* indet. (Roth and Wagner, 1854: p. 416; pl. 10, figs 1–2). Two years later, Gaudry and Lartet (1856) reported without description or figures several postcranials from Pikermi to *Macrotherium pentelicum*. This material was probably the one, which later allowed Gaudry to erect the new genus *Ancylotherium*, the type species of which is *A. pentelicum* (Gaudry, 1862–67; p. 129; pls 19–21; this part was published in 1863). In the mean time, Wagner (1857: p. 137; pl. 7, fig. 15) described a maxillary fragment with P3-M3 from Pikermi as "*Rhinoceros" pachygnathus*, which actually belongs to *A. pentelicum*. *A. pentelicum* has successively been referred to the genera *Nestoritherium, Colodus* and *Chalicotherium* until its current generic assignment by Schaub (1943). Except Pikermi the ancylotheres were later found in other Greek localities, as well as in the neighbouring countries Turkey, FYROM and Bulgaria (Forsyth Major, 1894; Melentis, 1969; Garevski, 1974; Garevski and Zapfe, 1983; Geraads et al., 2001, 2007; Roussiakis and Theodorou, 2001; Saraç et al., 2002; Saraç, 2003; Theodorou et al., 2003; Giaourtsakis and Koufos, 2009).

Comparison with the Pikermi material. There is no skull of *A. pentelicum* from the type locality of Pikermi but there is a mandible, housed in BSPM; it is almost complete, preserving the incisors

Table 1
Mandibular dimensions of *Ancylotherium* from various localities.
*Dimensions mandibulaire d'*Ancylotherium *de diverses localités.*

Mandible	*A. hellenicum*		*Ancylotherium pentelicum*		
	Pentalophos 1		Pikermi	Karaslari (Titov Veles)	Hadjidimovo-2
	PNT-33		BSPM-AS II 147	n.n.	HD-2-712
	dex	sin	Garevski and Zapfe (1983)	Garevski and Zapfe (1983)	Geraads et al. (2006)
Length of symphysis	–	–	±96.0	–	–
Depth in the middle of the diastema p2-mental foramen	34.5	36.0	50.0	50.0	–
Depth in p2	39.0	39.0	62.0	~63.0	–
Depth in m3	70.0	71.0	83.5	79.0	–
Depth before p2	~42	42.5	–	–	47.0
Depth before m1	61.0	60.0	–	–	86.0
Depth behind m3	76.0	75.5	–	–	102.0
Lp2-p4	–	–	78.5	72.0	70.0
Lm1-m3	130.0	130.5	155.0	148.0	~156.0
Lp2-m3	–	–	232.0	220.0	225.0
Lp3-m3	~184	~185	–	–	–

and lacking the ascending rami (Garevski and Zapfe, 1983: taf. 5). The mandibular ramus has a straight ventral margin and its depth increases distally, like in PNT-33, but its mandibular depth is larger than in the studied mandible (Table 1). Based on the photos of Garevski and Zapfe (1983), the PNT-33 mandible has a more elongated snout and its dental dimensions are smaller than those of the Pikermi specimen (Tables 1 and 2). The dental morphology of the PNT mandible seems to be similar to that of Pikermi but the buccal cingulum of the teeth is stronger. Garevski and Zapfe (1983) reported that the big hole observed in front of the p2 is the canine alveole. In PNT-33, it is clear that this hole corresponds to a very large mental foramen, coinciding to that observed in the HD-2 mandible (Geraads et al., 2006). Two maxillary fragments of *A. pentelicum* are known from Pikermi, the one described as "*Rhinoceros" pachygnathus* by Wagner (1857) and another one with P2-M3, housed in AMPG (Thenius, 1953). Although the PNT-160 dentition is extremely worn, the occlusal outline of the studied premolars, as well as the presence of a lingual cingulum is similar to the Pikermi ones (Fig. 4d). On the other hand, the teeth of PNT-160 differ from those of Pikermi in having stronger buccal cingulum and remarkably smaller size (Table 3).

Comparison with the Thermopigi material. A skull of *A. pentelicum* is known from the Greek Turolian locality of Thermopigi (Fig. 1); it is almost complete with both tooth rows (Geraads et al., 2007). Although the PNT skull is strongly deformed, it preserves several characters similar to those of the Thermopigi skull (SIT-770), as the elongated skull, the well-developed post-orbital process with open supra-orbital foramen, the position of the orbit, the presence of a preorbital fossa, the narrow palate and the stout zygomatic arches. The PNT-160 teeth have similar morphology to

Table 2
Dimensions of the lower teeth of *Ancylotherium* from various localities.
*Dimensions des dents inférieures d'*Ancylotherium *de diverses localités.*

Lower teeth	*A. hellenicum*		*A. pentelicum*	*A. pentelicum*	*A. pentelicum*
	Pentalophos 1		Pikermi	Karaslari (Titov Veles)	Hadjidimovo-2
	PNT-33		BSPM-AS II 147	n.n.	HD-2-712
	dex	sin	Garevski and Zapfe (1983)	Garevski and Zapfe (1983)	Geraads et al. (2006)
Lp2	–	–	22.0	16.5	15.5
$Bp2_{trig.}$	–	–	12.5	11.0	10.2[a]
$Bp2_{tal.}$	–	–	12.8	10.5	–
Lp3	–	–	25.0	25.0	27.6
$Bp3_{trig.}$	19.5	–	16.0	17.0	16[a]
$Bp3_{tal.}$	–	–	17.5	17.5	–
Lp4	26.6	24.4	31.0	31.4	31.2
$Bp4_{trig.}$	19.7	19.9	22	22.5	–
$Bp4_{tal.}$	–	19.6	22+	22.0	–
Lm1	34.4	35.3	41.0	37.5	42.5
$Bm1_{trig.}$	19.8	19.5	21.5	20.5±	24.3[a]
$Bm1_{tal.}$	20.1	20.7	23.0	23.3±	–
Lm2	47.0	48.1	55.0	53.0	52.7
$Bm2_{trig.}$	–	22.8	27.7	27.0	28.6[a]
$Bm2_{tal.}$	25.0	25.3	29.5	29.3	–
Lm3	51.2	50.2	61.5	59.5	59.4
$Bm3_{trig.}$	25.2	25	28+	28.0	31.2[a]
$Bm3_{tal.}$	24.5	24.4	29.0	28.0	–

[a] Max breadth.

those of the Thermopigi skull, but they differ from them in having stronger buccal cingulum, shorter M3 and smaller dental dimensions (Table 3). The Thermopigi total tooth row is ~30% longer and the M3 ~43% longer than those of PNT-160.

Comparison with the Hadjidimovo material. Some cranial remains of *A. pentelicum* have been recently described from the middle Turolian Bulgarian locality of Hadjidimovo 1 (Geraads et al., 2001). The HD-1 sample includes mainly deciduous dentitions, which preserve M1, 2. The position of the protocone and the shape of the M2 of PNT-160 fit morphologically those from HD-1, but its dental dimensions are remarkably smaller than in the latter (Table 3). Another Bulgarian locality close to HD-1 is Hadjidimovo-Tumbichkite (HD-2) from which two mandibular rami without symphysis of *A. pentelicum* are known (Geraads et al., 2006: p. 430, pl. 1, figs 5a–c). Based on Geraads et al. (2006) description and figures, the PNT mandible is morphologically similar to them but its dental dimensions are smaller (Tables 1 and 2). According to Geraads et al. (2006), the HD-2 mandible suggests that the mesial margin of the ascending ramus is "extremely oblique". The studied mandible preserves a larger part of the ascending ramus, indicating that its mesial margin is nearly perpendicular to the ventral border of the mandibular corpus (Fig. 3c).

Comparison with the Titov Veles material. A skull of *A. pentelicum* is known from the Turolian locality Karaslari, Titov Veles, FYROM (Garevski, 1974: figs 1–3). This skull belongs to a relatively young individual (the M3 is not fully erupted), having similar morphology but larger dental size than the PNT-160 (Table 3). Garevski and Zapfe (1983) described a mandible of *A. pentelicum* from Titov Veles, lacking the greater part of the symphysis. Judging from their figures, the Tito

Table 3
Dimensions of the upper teeth of *Ancylotherium* from various localities.
*Dimensions des dents supérieures d'*Ancylotherium *de diverses localités.*

Upper teeth	*A. hellenicum*		*Ancylotherium pentelicum*						
	Pentalophos 1		Pikermi	Thermopigi	Hadjidimovo		Kalimanci	Gorna Sushitsa	Karaslari (Titov Veles)
	PNT-160		AMPG-nn	SIT-770	HD-633	HD-635	n.n.	n.n.	n.n.
	dex	sin	Thenius (1953)	Geraads et al. (2007)	Geraads et al. (2001)		Bakalov and Nikolov (1962)		Garevski (1974)
LP2	20.0	20.1	22.2	25.0	–	–	20.5	20.0	20.5
BP2	16.3	16.8	21.2	26.0	–	–	23.0	20.0	20.5
LP3	23.2	21.3	31.0	30.5	–	–	28.5	24.5	27.7
BP3	–	30.7	32.0	34.0	–	–	32.5	30.0	31.5
LP4	–	25.8	33.3	38.0	–	–	32.5	32.0	31.0
BP4	–	34.5	37.5	37.0	–	–	38.5	38.0	35.0
LM1	–	–	48.0	45.0	53.2	49.4	45.0	45.0	46.0
BM1	–	–	41.2	46.0	43.0	42.8	40.5	43.0	39.5
LM2	49.5	–	67.2	62.0	–	60.7	58.5	–	63.5
BM2	45.0	–	50.5	50.0	–	51.3	47.5	46.0	48.5
LM3	49.8	–	62.5	71.5	–	–	54.0	–	–
BM3	44.1	–	53.0	49.5	–	–	50.0	–	–
LP2-P4	–	68.5	90.0	94.0	–	–	–	–	–
LM1-M3	–	–	184.0	178.0	–	–	–	–	–
LP2-M3	206.5	–	272.0	270.0	–	–	–	–	–

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Veles mandible is similar to that from Pikermi and differs from PNT-33 in the smaller size and dental dimensions (Tables 1 and 2).

The study and comparison of the PNT ancylothere indicate that it has the general morphology of *Ancylotherium* but it differs from the type species *A. pentelicum* being quite smaller than it (Tables 1–3). The teeth of the Thermopigi skull (Geraads et al., 2007) are more or less in the same wearing stage as those of the studied skull. Therefore, someone expects similar dental dimensions in the two skulls. However, the Thermopigi dental dimensions are larger with an extreme lengthening of the M3 (Table 3). The same metrical differences are also observed in the lower dentition of the PNT-33, Pikermi and HD-2 mandible (Tables 1 and 2). The lengthening of the M3, observed in Thermopigi skull, is reported as a possible derived character but the limited age data cannot certify it (Geraads et al., 2007). The new material from Axios Valley, which is dated to the Vallesian, has quite smaller M3/m3 than the Turolian material from Pikermi, Hadjidimovo and Thermopigi. This supports the above opinion of Geraads et al. (2007) but the poor fossil record and the limited age data still avoid certifying it. The cingulum is strongly developed in the teeth of the PNT material, giving to them a primitive feature and distinguishing them from *A. pentelicum* of Pikermi, Thermopigi and Hadjidimovo. The snout of the PNT-33 mandible is longer than that of *A. pentelicum* and distinguishes it from the type species. The mandibular depth of the PNT mandible is smaller than that of *A. pentelicum* (Table 1). The shortening of the snout and the increase of the depth in the mandibular corpus from the Vallesian to the Turolian could be also considered as possible derived features but again, the poor material and the limited age data do not allow certifying them. However, all these characters of the PNT ancylothere distinguish it from the Turolian *A. pentelicum* and allow the erection of a new species, named *Ancylotherium hellenicum* n. sp.

Subfamily: CHALICOTHERIINAE Gill, 1872
Genus ***Anisodon*** Lartet, 1851
Anisodon macedonicus (Bonis et al., 1995)

Synonyms. 1995. *Macrotherium macedonicum* nov. sp. – Bonis et al., p. 138, pls 1–6.
2001. "*Macrotherium*" *macedonicum* – Geraads et al., p. 601–602.
2007. *Anisodon macedonicus* – Anquetin et al., p. 581.

Type locality. Dytiko 3 (DKO), Axios Valley, Macedonia, Greece (Fig. 1).

Age of the type locality. Late Turolian, MN 13 (late Miocene).

Holotype. Skull associated with the mandible, DKO-234, described and figured by Bonis et al. (1995); it is stored in the LGPUT.

Locality. Prochoma 1 (PXM), Axios Valley, Macedonia, Greece (Fig. 1).

Age. Middle Turolian, MN 12; late Miocene.

Material. M3 dex, PXM-263.

Measurements. M3: 39.5 × 40.0 mm

Description. The studied tooth is well preserved and little worn (Fig. 5a, b); it is low-crowned and its breadth decreases distally. The paracone is strong and its buccal surface (mesial half of the ectoloph) is flattened and strongly inclines inwards. The protoloph stops by a small, but clear paraconule, separated from the protocone by a wide valley. The protocone is a strong isolated cusp, situated in the middle of the lingual margin. The metaloph is relatively short and the hypocone is reduced with its buccal margin strongly curved. The central valley is deep and open between the hypocone and protocone. The metacone and hypocone are separated distally by a deep valley.

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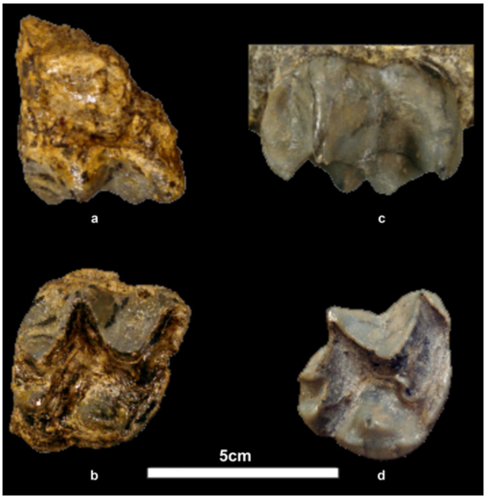

Fig. 5. *Anisodon macedonicus* n. sp., Axios Valley, Macedonia, Greece, middle Turolian, MN 12: **a**, **b**. Right M3, Prochoma 1, PXM-263: **a**: buccal, and **b**: occlusal view; **c**, **d**: right M3, Dytiko 3, DKO-234; **c**: buccal, and **d**: occlusal view.
Anisodon macedonicus *n.sp., vallée de l'Axios, Macédoine, Grèce, Turolien moyen et supérieur, MN 12 : **a**, **b** : M3 droite, Prochoma 1, PXM-263 ; **a** : vue buccale, et **b** : vue occlusale ; **c, d** : M3 droite, Dytiko 3, DKO-234 ; **c** : vue buccale, et **d** : vue occlusale.*

The buccal walls of the metacone and metastyle are sub-parallel to the mesio-distal axis of the tooth. The post-fossette is relatively wide and not pinched. The ectoloph is flattened, while the parastyle and mesostyle are strongly projected buccaly, the first more than the second one. The cingulum is well separated across the mesial border but it is weak in the mesio-lingual base of the hypocone.

Comparison. A skull and the associated mandible (DKO-234) of a chalicothere from the late Turolian locality DKO in Axios Valley have been described as *M. macedonicum* (Bonis et al., 1995). A maxilla with both toothrows from the old locality "Ravin du Vatilük" (it corresponds to the new locality Vathylakkos 3, VAT) described by Arambourg and Piveteau (1929) was also referred to this species. The revision of the middle Miocene chalicotheriids from France and the historical revision of their nomenclature, indicate that the valid generic name for the Sansan material is *Anisodon* instead of *Macrotherium*; given these close phylogenetic relationships, the DKO chalicothere might be transferred to this genus and named *A. macedonicus* (Anquetin et al., 2007).

A direct comparison of the studied tooth from PXM with the DKO-234 indicates that they are morphologically and dimensionally similar (Fig. 5; Table 4). PXM-263 is more worn than DKO-234 but the protocone size and position, the presence of a paraconule, the flat and strongly inclined inwards mesial half ectoloph, the strongly projected parastyle, the small hypocone, the short metaloph, the nearly perpendicular to the mesio-distal axis of the tooth distal half of the ectoloph, the open central valley, the post-fossette not pinched, and the development of the cingulum fit well the features of *A. macedonicus*.

The type species of *Anisodon* is *A. grande* known from the early Astaracian (MN 6) locality of Sansan; it was described under various generic and specific names. The Sansan material of *A. grande* includes the maxilla MNHN-Sa 3339 (lectotype) and the skull MNHN-Sa 15670

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Table 4
Dimensions of the M3 of *Anisodon* from various localities.
*Dimensions de M3 d'*Anisodon *de diverses localités.*

	Anisodon macedonicus			*Anisodon grande*						
	Prochoma 1	Dytiko 3		Neudorf						
	PXM-263	DKO-234		C24	C39	B23	C24X	A42	[15]	[16]
		Bonis et al. (1995)		Zapfe (1979)						
	dex	dex	sin	dex	sin	sin	dex	sin	dex	dex
LM3	39.5	40.1	40.9	36.0	39.0	39.0	41.5	43.0	43.0	45.5
BM3	40.0	40.4	40.0	41.4	42.0	42.2	46.0	44.8	48.0	46.8
LM3/BM3	99	99	102	87	93	92	90	96	90	97

(Anquetin et al., 2007: p. 581–582, figs 1, 3). The comparison of PXM-263 with *A. grande* M3 indicates that it has a slightly larger and more distally situated protocone, slightly weaker metastyle and hypocone, absence of buccal cingulum and weaker lingual one. A great amount of chalicothere material from the early Astaracian (MN 6) locality of Neudorf (now Devinska Nova Ves, Slovakia) has been described and assigned to *Chalicotherium grande* by Zapfe (1979). The conspecific status of the Neudorf and Sansan chalicotheres is argued and it is quite possible that the Neudorf sample includes two chalicotheres, probably *Anisodon grande* and a *Chalicotherium* (Geraads et al., 2001; Anquetin et al., 2007). Therefore a revision of the Neudorf material is necessary for certain comparisons. However, a comparison of PXM-263 with the Neudorf M3s (Zapfe, 1979; Fig. 8) indicates that the protocone of the Neudorf M3 is stouter and projected lingually, giving a more rounded occlusal outline in the tooth. The buccal cingulum in the Neudorf M3 is well developed but it is absent in PXM-263, while the PXM-263 is narrower than the Neudorf M3; this narrowness is clearly expressed by the L/B index which is larger in PXM-263 and DKO-234 (Table 4).

4. Biostratigraphy-biogeography-palaeoecology

Chalicotheres are well known in the Greco-Iranian Palaeoprovince (GRIP), a region extended from the Balkan Peninsula to Afghanistan (Bonis et al., 1992a), found in several Miocene localities (Garevski, 1974; Garevski and Zapfe, 1983; Bernor et al., 1996; Sen, 1998; Koufos, 2006a; Geraads et al., 2006, 2007; Saraç, 2003; Saraç and Sen, 2005). The presence of *A. pentelicum* in the late Miocene locality of Akkaşdağı is questionable. Saraç and Sen (2005) described a young skull as belonging to this taxon. Geraads et al. (2012) dispute the identification of the skull but they believe that *Ancylotherium* is present in Akkaşdağı, represented by a calcaneum (Saraç and Sen, 2005: fig. 3).

The early-middle Miocene chalicotheres are scanty in the GRIP, but the known localities of this age are also scarce in this province. Their presence is only reported from two Turkish localities. *Moropus* sp. is known from the early-middle Miocene locality of Linyit Isletmes, as well as *C. grande* and *Metaschizotherium fraasi* from the middle Miocene localities of Kultak, Nebisuyu, Paşalar and Sofça (Kaya et al., 2001; Saraç, 2003).

The late Miocene localities of GRIP with chalicotheres are relatively abundant (Fig. 6) and include five different taxa: *A. pentelicum*, *A. hellenicum*, *C. goldfussi*, *A. macedonicus* and *Kalimantsia bulgarica*. The main distribution of the chalicotheres is observed in the Balkans and

Fig. 6. Late Miocene mammal localities with chalicotheres in the Greco-Iranian Palaeoprovince (GRIP). The data are taken from NOW (2012) with some additions. Open circles indicate the chalicothere localities with *Ancylotherium pentelicum*.
Sites fossilifères du Miocène supérieur à chalicothères dans la Paléoprovince Gréco-Iranienne. Les données proviennent de la base de données NOW (2012) avec quelques ajouts. Les cercles blancs signalent les localités avec Ancylotherium pentelicum.

Turkey, but this is probably due to the long-time and extended research in these areas. The predominant chalicothere is *A. pentelicum*, covering the whole GRIP from the Balkan Peninsula to Afghanistan (Fig. 6).

So far, *A. pentelicum* was mainly known from the middle Turolian, MN 12; it is rarely or questionably intedified from the early Turolian, MN 11 (Saraç, 2003; Geraads et al., 2011). However, its Vallesian presence is referred from Spain. *A. pentelicum* is reported from Nombrevilla (Sondaar, 1961), as well as *A.* aff. *pentelicum* from Los Valles de Fuentidueña (Alberdi et al., 1981: fig. 2). In the revised Vallesian faunal lists of Spain, *Ancylotherium* is absent from Nombrevilla 1 and 2 but it is mentioned from Los Valles de Fuentidueña (Morales et al., 1999). The material from the last locality is an astragalus morphologically similar to *A. pentelicum* but one quarter smaller (Saraç and Sen, 2005). I did not see this astragalus and there is not any description of it, but based on its small size it is possible to belong to *A. hellenicum*, if it is an ancylothere. However, the absence of comparative material cannot allow certifying it. Therefore, the Vallesian occurrence of *Ancylotherium* in Spain needs more material and a detailed study to be confirmed.

The new material from the Greek locality PNT confirms the occurrence of *Ancylotherium* in the Vallesian of Europe. The locality PNT is situated in the Nea Messimvria Fm (Axios Valley), the upper levels of which are dated to Vallesian. The PNT fauna has a peculiar character, indicating more primitive features than those of the late Vallesian faunas Ravin de la Pluie (RPl) and Xirochori-1 (XIR) of Axios Valley. Taking in mind that an estimated age of ∼9.6 Ma has been proposed for the XIR fauna and the possible MN 9/10 boundary is at ∼9.6 Ma, then an early Vallesian (MN 9) age is possible for the PNT fauna (Koufos, in press and ref. cited). Therefore, the PNT *A. hellenicum* n. sp. is the older known representative of the taxon, characterized by smaller size and dentition, more elongated snout, shallower mandibular corpus, short M3/m3, and stronger cingulum than the Turolian *A. pentelicum*; it can be used as a biostratigraphic marker of the Vallesian.

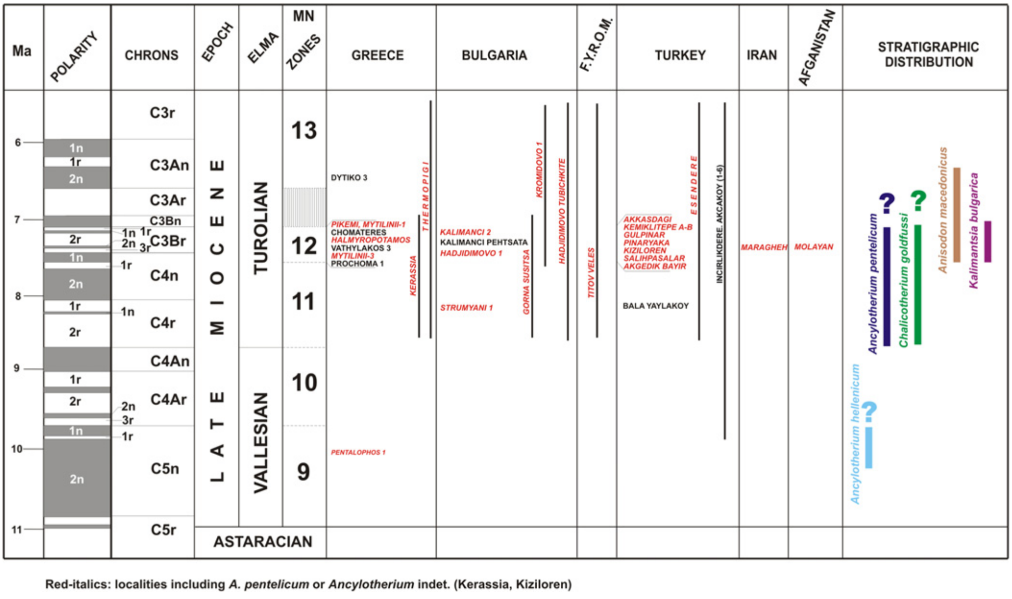

Fig. 7. Biostratigraphic table of the chalicothere-bearing mammal localities of the Greco-Iranian Palaeoprovince.
Tableau biostratigraphique des sites fossilifères avec chalicothères du Paléoprovince Gréco-Iranienhe.

During the early Turolian, *A. pentelicum* is only present in two localities of GRIP due to the weak age data for several localities (Fig. 7) and the rarity of early Turolian (MN 11) localities in Eastern Mediterranean. During the middle Turolian (MN 12), *A. pentelicum* is common, reported from several localities of GRIP (Fig. 7). Its last occurrence in GRIP is also questionable; during late Turolian (MN 13), there is not a certain evidence for the occurrence of *A. pentelicum*. This is due to the weak age data; there are several localities, the age of which is not precisely determined, either because their fauna was not thoroughly studied or because the collection is old without or limited locality indications (the ranges of their age are given by a vertical line in Fig. 7).

The less common *C. goldfussi* is also known from several localities of GRIP and certainly appears in the early and middle Turolian (Fig. 7). However, also occurs in two Turkish localities, Akçakoy (1-6) and Incirlikdere of questionable age; their age is ranging from MN 9 to MN 12 (Saraç, 2003; NOW, 2012). Thus, the occurrence of *C. goldfussi* in the Vallesian of the GRIP is possible. Likely, its last occurrence is questionable for the same reasons referred for *A. pentelicum.* The other two chalicotheres of GRIP are rare, restricted in the Balkans. *A. macedonicus* is known from the Greek localities PXM and VAT (middle Turolian) as well as DKO (late Turolian), while *K. bulgarica* is restricted to the middle Turolian localities Kalimantsi 2 and Kalimantsi-Pehtsata in Bulgaria (Fig. 7).

The biostratigraphic distribution of the late Miocene chalicotheres indicates that they are mainly present in the Turolian, although *Ancylotherium* occurred in the Vallesian; more precisely, they dominate in the middle Turolian with the presence of all known taxa. During middle Miocene the conditions in the Eastern Mediterranean region were tropical/sub-tropical; e.g. a similar habitat is proposed for the two well-known and studied middle Miocene Turkish localities of Paşalar and Çandir (Andrews, 1990; Geraads et al., 2003). The middle Miocene tropical/sub-tropical conditions replaced by more open landscapes during late Miocene. This change starts from Southeastern

Mediterranean at the end of M. Miocene and gradually spreads to the west, where it was appeared during the middle Vallesian (Bonis et al., 1992b; Fortelius et al., 2002; Koufos, 2006b; Mirzaie Ataabadi, 2010). The study of the late Miocene palaeoenvironment of Eastern Mediterranean by different methods suggested that it was an open landscape (similar to different types of the modern savannahs) and the climate was warm and dry (Bonis et al., 1992b, 1994; Suc et al., 1999; Bruch et al., 2006, 2007; Koufos et al., 2006, 2009; Merceron et al., 2004, 2005, 2006, 2007, 2009; Spassov et al., 2006; Strömberg et al., 2007; Eronen et al., 2009; Kostopoulos, 2009; Mirzaie Ataabadi, 2010; Koufos and Konidaris, 2011). It is accepted that the two subfamilies of the Chalicotheriidae have different habitats (Coombs, 1979; Bonis et al., 1999). The schizotheriines prefer mainly open environments, while the chalicotheriines are related with more closed conditions, associated with tragulids and tapirids (Bonis et al., 1999). Based on this, the presence of the schizotheriine *Ancylotherium* in GRIP during late Miocene confirms the open character of the palaeoenvironment.

The dental microwear of the chalicotheriines classifies them as browsers, while mesowear indicates a grazer or intermediate feeder (Schulz et al., 2007). However, the authors consider that the limited dental remains and the lack of studies on the limb bones cannot allow a certain determination of their ecology. The stereo-microwear analysis of the chalicothere teeth determined all of them as browsers (Semprebon et al., 2011). More precisely, the probable food of the chalicotheriines *A. grande* and *C. goldfussi* was leaves/fruits, while that of the schizotheriine *A. pentelicum* was leaves/bark; however, the food preferences of *A. pentelicum* are not clear because of the limited data (Semprebon et al., 2011). The co-existence of the two subfamilies, reported from Bulgaria (Geraads et al., 2001) makes more difficult the correlation with the environment. Geraads et al. (2001) consider that the two subfamilies were exploiting different vegetation. Another interpretation should be that the chalicotheres were living in different microhabitats of the open landscape; the chalicotheriines were living in more closed microhabitats with thicker vegetation (riparian forests, mountain cliffs), where it was possible to find more soft food. On the other hand, the schizotheriine *A. pentelicum* was better adapted to open landscapes, eating harder food. However, the ecology of the various chalicotheres is limited known, and I shall agree with the above mentioned authors that more material and studies are necessary to clarify them.

5. Conclusions

The chalicotheres of Axios Valley, Macedonia (Greece) suggest a continuous presence throughout the late Miocene (Vallesian and Turolian). They are represented by three species *A. pentelicum, A. hellenicum* and *A. macedonicus.* The second taxon represents the first certain occurrence of the genus in the Vallesian of Europe; its reference in Spain needs confirmation. It differs from *A. pentelicum* in having smaller size, longer snout, shallower mandibular corpus, shorter tooth rows, shorter M3/m3 and stronger cingulum. The ancylotheres, although they are known in the whole GRIP, they mainly occurred in the Balkans and Asia Minor; however, they are present in Iran and Afghanistan. The biostratigraphic distribution of the chalicotheriids in GRIP indicates that the most common taxon is *Ancylotherium*, ranging from the Vallesian (MN 9) to the late Turolian, MN 13. *C. goldfussi* is known from the early to the middle Turolian but its presence in the Vallesian is also suspected. The other two chalicotheres of GRIP, *A. macedonicus* and *K. bulgarica* are rare and restricted to the Balkan Peninsula. The chalicothere ecology is limited known, although there are some data indicating that the subfamilies Schizotheriinae and Chalicotheriinae occupied different environments.

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Disclosure of interest

The author declares that he has no conflicts of interest concerning this article.

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