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A SKULL OF *ANCYLOTHERIUM* (CHALICOTHERIIDAE, MAMMALIA) FROM THE  
LATE MIOCENE OF THERMOPIGI (SERRES, N.GREECE), AND THE RELATIONSHIPS  
OF THE GENUS

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RH: relationships of *Ancylotherium*

## ABSTRACT

The locality of Thermopigi in northern Greece has yielded a well- preserved skull of *Ancylotherium pentelicum*, among a rich collection of late Miocene mammals. It is the most complete *Ancylotherium* skull ever reported, and lack of crushing makes it especially valuable. Its most remarkable feature is the inflation of the frontal bone, which is strongly reminiscent of the dome of the North American *Tylocephalonyx* Coombs, 1979, although the degree of inflation is weaker than in that genus. An analysis of some characters found in the Miocene Schizotheriinae leads to the conclusion that *Ancylotherium* is more likely to be closely related to other Eurasian and African members of this subfamily than to *Tylocephalonyx*, and that the domes evolved in parallel.

## INTRODUCTION

The Chalicotheriidae are frequent constituents of late Miocene mammalian faunas of the Eastern Mediterranean, although they are never common at any given locality. Among them, the Schizotheriinae are represented by the single species *Ancylotherium pentelicum*. It is known from Pikermi (its type-locality), Halmyropotamos and Samos in Greece (Gaudry, 1862-67; Schaub, 1943; Melentis, 1970; Roussiakis and Theodorou, 2001), Titov Veles in FYROM (formerly in Yugoslavia; Garevski and Zapfe, 1983), Bulgaria (Geraads et al., 2001), Turkey (Sen, 1994; Saraç et al., 2002), probably Novoukrainka in Ukraine and Maragha in Iran, and a closely related or identical form has been reported from Concud and Nombrevilla in Spain, Molayan in Afghanistan, and several Chinese localities (Coombs, 1989; Geraads et al., in press, and references therein). We describe herein material from the new locality of Thermopigi (Sidirokastro, Serres), in the province of Macedonia, Greece. We will compare it with other published material of *A. pentelicum*, with the African species *A. hennigi* and *A. cheboitense* (Dietrich, 1942; Webb, 1965; Pickford, 1979; Guérin, 1985, 1987; Guérin and Pickford, 2005) as well as with the North American forms *Moropus* (Holland and Peterson, 1914; Coombs, 1978a, 1979, 2001, 2004) and *Tylocephalonyx* (Coombs, 1979).

The site of Thermopigi (N 41°17'16", E 23°21'51") is located in northern Greece (Serres Prefecture, Macedonia), 100 km east of Thessaloniki, 4 km from the municipal centre of Sidirokastro and 18 km from the Bulgarian border (Fig. 1). The first reconnaissance of the site took place in 1998; systematic excavations were carried out from 1999 onwards, and are still in progress, under the leadership of one of us (E.T.). The locality (the name of which, "thermal spring" comes from the thermal waters of the area, used as a spa center) yields a rich fauna from consolidated reddish sandstones. The fossils are well-preserved but often fragmented, probably as a

result of neotectonic events. They are stored in the DGUA, and in the renovated school of Thermopigi village, which became the Municipal Museum of Natural History in 2005.

Preliminary faunal list of the large mammals from Thermopigi includes: *Felis attica*, *Paramachairodus* sp., *Machairodus* sp., *Adcrocuta eximia*, *Hipparion* cf. *dietrichi*, *Hipparion* cf. *matthewi*, *Ancylotherium pentelicum*, *Dicerorhinus pikermiensis*, *Microstonyx major*, *Propotamochoerus* cf. *hysudricus*, *Bohlinia* cf. *attica*, cf. *Palaeotragus rouenii*, *Helladotherium duvernoyi*, *Tragoportax* cf. *amalthea*, *Palaeoreas lindermayeri*, *Prostrepsiceros* cf. *axiosi*, *Criotherium* ? sp., and *Gazella* sp. This list unambiguously points to a Turolian age, but precise dating must await detailed study of the collection.

**Institutional abbreviations**—**DGUA**, Department of Geology, University of Athens; **DGUS**, Department of Geology, University of Sofia; **LGPUT**, Laboratory of Geology and Paleontology, University of Thessaloniki; **MCGL**, Musée Cantonal de Géologie, Lausanne; **NME**, National Museum of Ethiopia, Addis Ababa; **NMK**, National Museums of Kenya, Nairobi; **NMNHS**, National Museum of Natural History, Sofia.

**Other abbreviations**—**PIK**, Pikermi; **SAM**, Samos; **SIT**, Thermopigi (for Sidirokastro, Thermopigi). The terminology is based on Butler (1965) and Coombs (1978a).

## SYSTEMATIC PALEONTOLOGY

Order PERISSODACTYLA Owen, 1848

Superfamily CHALICOTHERIOIDEA Gill, 1872

Family CHALICOTHERIIDAE Gill, 1872

Subfamily SCHIZOTHERIINAE Holland and Peterson, 1914

Following common use, we include in this subfamily chalicotheriids with elongated molars, although there is no definite evidence for the inclusion of *Schizotherium* itself.

Genus *ANCYLOTHERIUM* Gaudry, 1863

**Diagnosis**—A schizotheriine of large size. Metaloph of upper molars short, ectoloph relatively flat between very prominent styles, crochet sometimes present. Second lobe of m3 short. Manus as a whole, and each individual metacarpal, concave dorsally; trapezium lost; proximal carpal row shifted in the volar direction in respect to the distal one; scaphoid contacting Mc-II in extreme flexion; lunar and magnum with volar process much reduced or absent. Mc-V lost. Talus low, but rather symmetrical.

*ANCYLOTHERIUM PENTELICUM* (Gaudry and Lartet, 1856)

(Figs. 2–4)

**Diagnosis**—Inflated frontal bone, forming a large hump in the middle of the skull. Muzzle deep. P4 with well-marked protocone. Upper molars with strong mesio-lingual cingulum. Lower incisors much reduced. Ungual phalanx of digit II of the manus very long. Metatarsals not much shortened; Mt-III longer than Mt-IV, the latter broad but not contacting ectocuneiform.

**Material**—Skull SIT-770, stored in LGPUT.

### **Description and Comparisons**

**Skull**—The skull lacks the whole occipital, and the left parietal area, but the right side is almost complete except part of the premaxilla, which is present on the left side. It has suffered no crushing or deformation. Its most conspicuous feature is the inflated cranial roof, which gives this part of the skull a distinctly convex lateral profile (Fig. 2). This inflation starts above the orbits, rises caudally, reaches its highest point well behind the orbit, and then decreases towards the fronto-parietal suture (which is not traceable) where a clear, but low, step marks the caudal

end of the inflated area. Therefore, the pneumatization affects mostly, if not exclusively, the frontal bones. The highest point of the skull is about mid-way between the rostral orbital border and the occipital, but the inflated area has no well-marked summit. There is a well-marked post-orbital process; rostro-medial to it is a circular depression with the supra-orbital foramen opening directly into the orbit, as in *Moropus* (Holland and Peterson, 1914, pl. 50), and other chalicotheres. There are no temporal lines, even immediately behind the post-orbital processes but, although the left side is missing, one can see that there was almost certainly a short sagittal crest.

Part of the frontal and most of the parietal bones are missing on the left side. The braincase and frontal sinus are filled with sediment, so the internal structure is not visible. No thick septa or reinforcing walls appear in section, but it is unlikely that there was really a single sinus, as such a hollow structure, not cortically thickened, would have been exceedingly fragile if not supported by internal septa. More probably, there were at least some walls, but there is no doubt that the internal structure was fully hollowed, not just cancellous.

The rostral border of the orbit is above the caudal border of M3. There is a single lacrymal foramen on the orbital border. The ventral post-orbital process is but a slight bump on the zygomatic arch; it is much more rostral than the dorsal one, so that the orbit has an elongated axis, slanting rostro-ventrally. The muzzle is deep, as the dorsal border of the nasal bones is well above the orbits, and it increases in depth rostrally. Although some sutures are indistinct, the nasal bones were probably broad in their caudal part, and depressed medially in a long groove along the sagittal line. Above the cheek-teeth, the maxillae decrease slightly but regularly in width rostrally, and especially sharply before P2. A large preorbital fossa, more extensive than in *Tylocephalonyx*, occupies most of the facial part of the maxilla. It strongly resembles that found in many hipparions, where it probably housed the caudal origins of the rhinal musculature

(Žhegallo, 1978). The premaxillae had a long (ca. 40mm) contact with the nasals, but the pre-dental part of the skull is much reduced: there were definitely no upper incisors or canines, and the premaxillae consist mostly of two short vertical blades with only a reduced horizontal portion (much as in the rhinos lacking upper incisors), although they had a short contact in the midline. The premaxilla of *Moropus elatus* (Coombs, 1978b) is also edentulous, but is long and slender. The position of the infra-orbital foramen is not quite clear, but it probably opens above the first half of M2, as in *Moropus*, and the choanae reach the caudal third of M3, as in *Tylocephalonyx*, but more rostrally than in *Moropus*. The palate is narrow, and slightly increases in width caudally.

The zygomatic arch is stout but not deep, and its lower border is almost straight. The ventral border is sharp in its rostral half, but caudally it is flattened and gradually passes into the glenoid "fossa" which is in fact remarkably flat. The post-glenoid process is relatively small, with a rounded triangular cross-section, as in the rhinos, in contrast to *Moropus*, where it is transversely elongated and even contacts the large auditory bulla. By contrast, the bulla in the Thermopigi skull is rather small and widely separated from the post-glenoid process.

The optic foramen is much more rostral than the sphenoidal fissure. Ventrally, an incompletely preserved alisphenoid canal remains, as in most chalicotheres. Lateral to its caudal opening, a long groove leads to the foramen ovale (Fig. 3). Medially, a long crest connects the auditory bulla to the pterygoid wing, as in *Moropus*.

Few measurements can be taken on the Thermopigi skull. Measurements in mm include : length from external auditory meatus to M3 = 283; length from auditory foramen to front of orbit = 290; length from external auditory meatus to front of P2 = 570.

The inflated cranium seen in the Thermopigi skull has never been reported in any other Schizotheriinae, except *Tylocephalonyx* Coombs, 1979, from the early and middle Miocene of the United States. In *Tylocephalonyx*, the degree of inflation varies significantly but is probably always greater than in *A. pentelicum*: even the less inflated dome of the skull from the Astoria Formation, Oregon (Munthe and Coombs, 1979, fig. 1) extends farther caudally, into the parietal bone (Coombs, 1979:19). Other differences are that, in *A. pentelicum*, the orbit and perhaps also the infra-orbital foramen are less rostrally placed, that the muzzle depth increases, rather than decreases, towards the rostrum (in this feature, it is more like *Moropus*), and that the temporal fossa is less clearly delimited dorsally (probably a consequence of the less laterally expanded "dome").

The teeth of the Thermopigi skull are much worn, but well preserved (Fig. 4), and very large. Little morphological variation has been described in *A. pentelicum* cheek-teeth (Thenius, 1953; Bakalov and Nikolov, 1962; Garevski, 1974; Geraads et al., 2001; Geraads et al., in press). The P2 is triangular. The ectoloph is straight on P2 and very weakly W-shaped on P3-P4. The protocone of P3-P4 is rounded and large; it is connected by a mesial crest to the ectoloph, whereas the distal transverse crest does not merge into the protocone on P4. Lingually, the premolars are circled by a strong cingulum, but there is no buccal cingulum. Only the Pikermi specimen (DGUA; Thenius, 1953) has accessory spurs in the central valley of the premolars.

M2 and M3 are much longer than broad (Tab. 1), with an abrupt narrowing distal to the protocone. The latter is rounded and connected mesially to the protoloph; there is a strong mesiolingual cingulum. The ectoloph is strongly W-shaped. The distal part of M3 has a short metacone directed distolingually, and is strongly reduced, especially in width, more so than on all other specimens, such as those from Pikermi (Wagner, 1857, and DGUA) and Kalimantsi (DGUS). No crochet is visible, at this wear stage. There are some differences in tooth

proportions among the various specimens of *A. pentelicum*; P4 is here much narrower than M1, as at Pikermi, whereas the difference is smaller at Gorna Sushitsa (DGUS), and especially at Kalimantsi (DGUS). Lengthening of M3 is here more extreme than in any other specimen; this is doubtless a derived character, but relative biochronological dating of these sites is still unclear.

Other Miocene Schizotheriinae are also similar in tooth morphology, although there are a number of small differences (Coombs, 1979, tab. 4). The metaloph is longer, especially on M3, in *Moropus*; *A. pentelicum* has a stronger cingulum than both American genera, which never have a crochet. The premolars may be very slightly longer (Pm / M ratio = 52–53, compared to 45–53 in the American genera).

### **Phylogenetic Relationships**

The frontal inflation of the Thermopigi skull is morphologically similar to the strange dome of the skull of the North American genus *Tylocephalonyx* Coombs, 1979. It had never been reported previously in any Old World schizotheriine but, in the light of the discovery of the Thermopigi skull, it becomes clear that other specimens, such as the one from Veles (Garevski, 1974), and perhaps even the juvenile specimen from Hadjidimovo (Geraads et al., 2001) might well have had also an inflated frontal that was flattened by post-mortem crushing. The dome might also have been sexually dimorphic, the Veles and Hadjidimovo skulls being from female individuals, but both explanations are not mutually exclusive, as sexual dimorphism may have been present even if these are crushed male skulls.

Does this major skull feature shared by *Ancylotherium* and *Tylocephalonyx*, imply that they are sister taxa ? A brief survey of the characters of other schizotheriines may provide some hints. In North America, *Moropus* is a well-known genus with several species (Holland and Peterson, 1914; Coombs, 1978a, 2004), and *Tylocephalonyx* is also well sampled and described (Coombs,

1979). By contrast, Eurasian Miocene Schizotheriinae are mostly known from teeth and a few limb-bones, but no skull (except in *Ancylotherium*). They have been referred to three genera, besides *Ancylotherium*: *Phyllotillon*, *Metaschizotherium*, and *Moropus* (Pilgrim, 1912; Koenigswald, 1932; Beliaeva, 1954; Rinnert, 1956; Antunes, 1966; Coombs, 1974; Zapfe, 1974; Belinchon and Montoya, 1990; Kaya, 1993; Montoya et al., 1996), but evidence for more than one genus is slender, although Coombs (pers.comm.) recognizes three genera. Antunes and Ginsburg (2000) recently recognised three taxa, but this was based only upon details of the upper premolars. From the published data, we can see no reason for including *Chalicotherium wetzleri* Kowalewsky, 1873 in *Metaschizotherium* (Fejfar et al., 1997).

Comparison of *A. pentelicum* with American genera is hampered by the large number of highly autapomorphic features in its skeleton (Schaub, 1943; Coombs, 1978a, 1979, 2004). They are mainly related to the peculiar functional anatomy of the manus: its dorsal side is concave, the carpals are set in transverse rows instead of dorsally convex arches, and the articulation between both carpal rows, especially its central part, is shifted in the volar direction. All this improves hyper-extension of the fingers on the metacarpals, and hyper-flexion of the carpus. The carpal bones of *Tylocephalonyx* are similar to those of *Moropus* in their detailed structure, and so much distinct from those of *A. pentelicum* that it is likely that the few similarities that could be found between either of them and *Ancylotherium* have no real significance. For instance, the articular facets for the trapezoid on the magnum are more similar in *A. pentelicum* and *Tylocephalonyx*; the Mc-III has a long facet for Mc-IV in *A. pentelicum*, more like the double facet of *Moropus* than like the simple dorsal facet of *Tylocephalonyx*. Loss of the trapezium occurs in *A. pentelicum* and in *M. hollandi*, but not in *Tylocephalonyx*. In *Moropus*, the disto-dorsal part of the trapezoid forms an acute angle that fits into a notch of the Mc-II (Coombs, 1978a, fig. 8A); this angle is more obtuse in *Tylocephalonyx* (Coombs, 1979, fig. 15) and *A. pentelicum*. In

several aspects, *Tylocephalonyx* looks morphologically intermediate between *Moropus* and *A. pentelicum*. For instance, the distal humerus articulation is more oblique in *Tylocephalonyx* than in *Moropus*, and still more so in *A. pentelicum*. The epicondylus lateralis is stronger in *Tylocephalonyx* than in *Moropus*, and still more so in *A. pentelicum*. In the foot of *Moropus*, but not in the foot of other genera, Mt-IV is longer than Mt-III, and articulates with the ectocuneiform. It is on the basis of this latter feature that the genus has been identified in Europe (e.g., Coombs, 1974; Kaya, 1993) but, on isolated Mt-IVs, it may be hard to tell an ectocuneiform facet from the dorso-proximal part of the Mt-III facet.

Teeth are extremely similar in all three genera, except that the cingulum is decidedly stronger, on all upper teeth, in *Ancylotherium*, and that *Ancylotherium* and *Tylocephalonyx* share a shorter metaloph, especially on M3, and much reduced lower incisors. The premaxilla assigned by Coombs (1978b) to *Moropus* suggests that this genus shared with *Ancylotherium* the loss of upper incisors. P4 is relatively broader in *Moropus* than in *Tylocephalonyx* (Coombs, 1978a, 1979), but the difference between them does not exceed that found between various specimens of *A. pentelicum* (range of WP4 / WM1 = 0.81 - 0.92).

Thus, no clear picture emerges from the comparison of these three genera. On the whole, *Tylocephalonyx* looks more similar, but the case for uniting it with *Ancylotherium* is not strong. It may be that some of their shared characters were acquired in parallel. Like *Ancylotherium*, *Tylocephalonyx* is geologically younger than most *Moropus*, but the most recent species of *Moropus*, *M. merriami*, also displays derived features, such as a low and broad talus, and united facets between Mt-III and Mt-IV, plus several others (Coombs, 2004).

*Ancylotherium pentelicum* can also be compared with its poorly known forerunner, often held as its ancestor, *Metaschizotherium fraasi*, from the middle Miocene of Europe (Koenigswald, 1932; Rinnert, 1956). They share a few features, unknown in America: (1)

sometimes a crochet on the molars; (2) a volar process reduced on the lunar (the only known carpal bone); and perhaps (3) a single dorsal facet between Mt-III and Mt-IV (if the Mt-IV described by Rinnert [1956] does belong to *Metaschizotherium*). The first of these features, at least, is shared by *Phyllotillon* Pilgrim, 1912, from Pakistan. This list is short, but (2) is significant, because it shows that *Metaschizotherium* had already developed the peculiar carpal articulation of *Ancylotherium*. On the basis of published information, it is likely that they belong to the same Old World clade, but current revision of *Metaschizotherium* by M. Coombs will shed further light on their relationships.

The Schizotheriinae have a shorter record in Africa, from the early late Miocene of Chorora (Geraads et al., 2002) until the lower Pleistocene of Konso-Gardula (Suwa et al., 2003), both in Ethiopia, and their remains are scarce. Plio-Pleistocene *Ancylotherium hennigi* is the most frequently cited species. Butler (1965) and Guérin (1985, 1987) have shown that several bones, including the carpals, are similar to those of *A. pentelicum*: the dorsal face of the Mc-III is concave; according to Coombs (1989), the scaphoid contacted the Mc II during extreme flexion, but the latter bone is more derived than that of *A. pentelicum* because of its flat trapezoid facet, whereas it is deeply concave in the European form. The talus is low and wide; on the Mt-IV (Omo 210-73-1927), there is a single facet for Mt-III, as in *A. pentelicum*, but it extends farther in the plantar direction than in this species. Earlier African forms are mostly known by elements of the pes, especially Mt-IVs, but none of them has an articulation between Mt-IV and the ectocuneiform. The Mt-IV of *Chemositia tugenensis* from Mpesida (KNM-MP-229), roughly contemporaneous with *A. pentelicum*, is not transversely broadened; Pickford (1979) reported two facets for Mt-III, but they could perhaps be better described as a single long facet, still larger than at Omo. From the slightly later site of Lukeino, *A. cheboitense* Guérin and Pickford, 2005, has instead very massive metatarsals, and further differs, according to its authors, by the fusion

of navicular and ectocuneiform, and the lack of a sustentacular facet on the talus, which is otherwise similar to that of *A. pentelicum* in its low and wide proportions. These features would be unique among schizotheriines. Furthermore, the talus is rather symmetrical, with a rounded lateral lip, whereas those of *A. pentelicum* and *M. fraasi* are more asymmetrical, with a more angular lateral lip. It is hard to fit *A. cheboitense* within *Ancylotherium* but, as its features are autapomorphic, it might indeed be a highly derived member of this genus.

Phylogenies are hard to draw from such fragmentary material, but *A. hennigi*, although later in age, looks closer to *A. pentelicum* than its late Miocene African predecessors, which might be closer to some other Eurasian Chalicotheres. It might thus have a northern, rather than endemic, origin.

## **Ethology**

Munthe and Coombs (1979) made a detailed review of the possible functional roles of the dome in *Tylocephalonyx*, giving sound arguments for discarding explanations linked to aquatic specializations, muscular support, and olfactory or acoustic function, and we will not repeat their rationale here. Eventually, they assumed that the dome probably acted either in visual display and / or in low-impact butting, in a way similar to that of the giraffe. We agree that such an ethological interpretation is more likely than any physiological one, but the ritual fight of the giraffe, although it does not cause serious wounds, is not so 'soft', and is facilitated by the great length of the neck and dense heavy ossicones, which transform the head into a club able to deliver heavy blows. By contrast, the neck of *Ancylotherium* was certainly shorter, the cranial roof is not thickened, and there were certainly much fewer reinforcing septa, if any. This also precludes 'Rammkampf', as performed by caprine bovids. It should be noted here that the identification of the specimen described by Hunt (2005) as a *Tylocephalonyx* dome is doubtful,

as it shows many more septa than other domes (Munthe and Coombs, 1979, fig.6), so that its internal aspect is cancellous rather than fully hollowed. Extensive pneumatisation of the cranial roof is found in a variety of mammals, especially large members of each Order, for some kind of skull restructuring (Moore, 1981), probably mostly to compensate for the allometrically smaller brain, but it seldom produces inflated bosses. It is rare in perissodactyls. Median humps in rhinos support the horn(s), but the lack of rugosities in *Ancylotherium* and *Tylocephalonyx* rule out such a function. Perhaps the closest analogues are to be found in some elephants, whose parietal bosses probably contribute to increase apparent head size (as external ears do ?). In support of the visual display hypothesis in *Ancylotherium*, it can be noted that its head is relatively small compared to body size, and that some strategy may have been needed to make it more impressive. We may guess that the dome was produced by hyper-inflation of frontal sinuses that were already large (as in, e.g., the cave-bear) to increase efficiency of the head profile display. It would therefore be analogous to a variety of mammalian head outgrowths, horns, mane, dewlap and warts. Whether it played a role in courtship display or male to male confrontation is hard to tell, as we do not know the sex of the fossil skulls, including those of *Tylocephalonyx* (Munthe and Coombs, 1979). It may even be that the skull from Thermopigi is from a female, and that the dome of the male was larger.

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## LITERATURE CITED

- Antunes, M. T. 1966. Un schizotheriiné du genre *Phyllotillon* (Chalicotherioidea, Perissodactyla) dans l'Helvétien V-b de Charneca do Lumiar. Remarques écologiques sur la faune de Mammifères. Boletim da Sociedade Geológica de Portugal 16:159–178.
- Antunes, M. T., and L. Ginsburg. 2000. Les Périssodactyles (Mammalia) du Miocène de Lisbonne. Ciências da Terra (UNL) 14:349–354.
- Bakalov, P., and I. Nikolov. 1962. Les Fossiles de Bulgarie. X. Mammifères Tertiaires. Académie des Sciences de Bulgarie, Sofia, Bulgaria, 162 pp.
- Beliaeva, E. I. 1954. [Chalicotheriids from the Soviet Union and Mongolia]. Akademia Nauk SSSR, Trudy Paleontologiceskogo Instituta 55:44–84 [Russian].
- Belinchon, M., and P. Montoya. 1990. Presencia de *Phyllotillon naricus* Pilgrim, 1910 (Chalicotheriidae, Perissodactyla, Mammalia) en el Aragoniense de Buñol (Valencia). Breve síntesis de los calicotéridos en el registro español. Paleontologia i Evolució 23:171–180.
- Butler, P. M. 1965. East African Miocene and Pleistocene Chalicotheres. Fossil mammals of Africa, 18. Bulletin of the British Museum (Natural History) Geology 10:163–237.
- Coombs, M. C. 1974. Ein Vertreter von *Moropus* aus dem europäischen Aquitanien und eine Zusammenfassung der europäischen postoligozänen Schizotheriinae (Mammalia, Perissodactyla, Chalicotheriidae). Sitzungsberichten der Österreichische Akademie der Wissenschaften, Mathematisch-naturwissenschaftliche Klasse I, 182:273–288.
- Coombs, M. C. 1978a. Reevaluation of early Miocene North American *Moropus* (Perissodactyla, Chalicotheriidae, Schizotheriinae). Bulletin of Carnegie Museum of Natural History 4:1–62.

- Coombs, M. C. 1978b. A premaxilla of *Moropus elatus* Marsh, and evolution of Chalicotherioid anterior dentition. *Journal of Paleontology* 52:118-121.
- Coombs, M. C. 1979. *Tylocephalonyx*, a new genus of North American dome-skulled Chalicotheres (Mammalia, Perissodactyla). *Bulletin of the American Museum of Natural History* 164:1-64.
- Coombs, M. C. 1989. Interrelationships and diversity in the Chalicotheriidae; pp. 438-457 in D. R. Prothero and R. M. Schoch (eds.), *The evolution of Perissodactyls*. Oxford University Press, New York.
- Coombs, M. C. 2001. Stratigraphy, chronology, biogeography, and taxonomy of early Miocene small chalicotheres in North America. *Journal of Vertebrate Paleontology* 21:607-620.
- Coombs, M. C. 2004. *Moropus merriami* in the Early Barstovian Lower Snake Creek Fauna of Nebraska, with comments on biogeography of North American Chalicotheres. *Bulletin of the American Museum of Natural History* 285:191-208.
- Dietrich, W. O. 1942. Altstquartäre Säugetiere aus der Südlichen Serengeti, Deutsch-Ostafrika. *Palaeontographica A*, 94:43-133.
- Fejfar, O., E. P. J. Heizmann, and P. Major. 1997. *Metaschizotherium* cf. *wetzleri* (Kowalewsky) from the early Miocene of Czech republic and South Germany. *Mémoires et Travaux de l'EPHE, Institut de Montpellier* 21: 707-709.
- Garevski, R. 1974. Beitrag zur Kenntnis der Pikermifauna Mazedoniens. Fossilreste der Chalicotheriiden. *Fragmenta Balcanica Musei Macedonici Scientiarum Naturalium* 9:201-209.
- Garevski, R., and H. Zapfe. 1983. Weitere Chalicotheriiden-Funde aus der Pikermi-Fauna von Titov Veles (Mazedonien, Jugoslawien). *Acta Musei Macedonici Scientiarum Naturalium* 17:1-20.

- Gaudry, A. 1862–67. Animaux fossiles et géologie de l'Attique. Savy, Paris, 474 p. [the chapter on *Ancylotherium* was published in 1863].
- Gaudry, A., and E. Lartet. 1856. Résultats des recherches paléontologiques entreprises dans l'Attique sous les auspices de l'Académie. Comptes-rendus des séances de l'Académie des Sciences 43:271–274.
- Geraads, D., Z. Alemseged, and H. Bellon. 2002. The late Miocene mammalian fauna of Chorora, Awash basin, Ethiopia: systematics, biochronology and  $^{40}\text{K}$ - $^{40}\text{Ar}$  age of the associated volcanics. Tertiary Research, 21:113–122.
- Geraads, D., N. Spassov, and D. Kovachev. 2001. New Chalicotheriidae (Mammalia) from Bulgaria. Journal of Vertebrate Palaeontology 21:596–606.
- Geraads, D., N. Spassov, and D. Kovachev. In press. The Bulgarian Chalicotheriidae (Mammalia): an update. Revue de Paléobiologie.
- Gill, T., 1872. Arrangement of the families of mammals with analytical tables. Smithsonian Miscellaneous Collections 11: 1-98.
- Guérin, C. 1985. Les rhinocéros et les chalicothères (Mammalia, Perissodactyla) des gisements de la vallée de l'Omo en Ethiopie (collections françaises); pp. 67–89 in Y. Coppens and F. Clark Howell, Les faunes plio-pléistocènes de la basse vallée de l'Omo. Tome 1. Editions du CNRS, Paris, France.
- Guérin, C. 1987. Chalicotheriidae (Mammalia, Perissodactyla) remains from Laetoli; pp. 315–320 in M. D. Leakey and J. M. Harris (eds.), Laetoli: a Pliocene site in Northern Tanzania. Clarendon Press, Oxford.
- Guérin, C. and M. Pickford. 2005. *Ancylotherium cheboitense* nov. sp., nouveau Chalicotheriidae (Mammalia, Perissodactyla) du Miocène supérieur des Tugen Hills (Kenya). C. R. Palevol. 4:225–234.

- Holland, W. J., and O. A. Peterson. 1914. The osteology of the Chalicotherioidea with special reference to a mounted skeleton of *Moropus elatus* Marsh, now installed in the Carnegie Museum. *Memoirs of the Carnegie Museum* 3:189–406.
- Hunt, R. M. 2005. An early Miocene dome-skulled chalicothere from the "Arikaree" conglomerates of Darton: calibrating the ages of high plains paleovalleys against Rocky Mountain tectonism. *American Museum Novitates* 3486:1–45.
- Kaya, T. 1993. First record of *Moropus elatus* (Chalicotheriidae-Perissodactyla) in Turkey (Seyitömer-Kütahya). *Turkish Journal of Earth Sciences* 2:189–194.
- Koenigswald, G.H.R. von. 1932. *Metaschizotherium fraasi* n.g.n.sp., ein neuer Chalicotheriide aus dem Obermiozän von Steinheim a. Albuch. (Die tertiären Wirbeltiere des Steinheimer Beckens VIII). *Palaeontographica, Supplement Bd. 8*, 8:11–24.
- Kowalewsky, W. 1873. Monographie der Gattung *Anthracotherium* Cuv. und Versuch einer natürlichen Classification der fossilen Hufthiere.etc. *Palaeontographica* 22:131–210.
- Melentis, J. K. 1970. Studien über fossile Vertebraten Griechenlands. 28. Die Pikermifauna von Halmyropotamos (Euboa-Griechenlands), *Annales Géologiques des Pays Helléniques* 5:217–229.
- Montoya, P., E. Peñalver, F. J. Ruiz-Sánchez, C. de Santisteban, L. Alcalá, M. Belinchón, and J. I. Lacomba. 1996. Los yacimientos paleontológicos de Rubielos de Mora (Aragón). *Revista española de paleontología, N° extraordinario*: 215–224.
- Moore, W. 1981. *The Mammalian Skull*. Cambridge Univ. Press, Cambridge, 369 p.
- Munthe, J., and M. C. Coombs. 1979. Miocene dome-skulled chalicotheres (Mammalia, Perissodactyla) from the Western United States: a preliminary discussion of a bizarre structure. *Journal of Paleontology* 53:77–91.
- Owen, R. 1848. *Contributions to the history of British fossil mammals*. Taylor, London, 71 pp.

- Pickford, M. 1979. New evidence pertaining to the Miocene Chalicotheriidae (Mammalia, Perissodactyla) of Kenya. *Tertiary Research* 2:83–91.
- Pilgrim, G. E. 1912. The vertebrate fauna of the Gaj series in the Bugti hills and the Punjab. *Paleontologia Indica* NS, 6:1–83.
- Rinnert, P. 1956. Die Huftiere aus dem Braunkohlenmiozän der Oberpfalz. *Palaeontographica A* 107:1–65.
- Roussiakis, S.J., and G. E. Theodorou. 2001. *Ancylotherium pentelicum* (GAUDRY & LARTET, 1856) (Perissodactyla, Mammalia) from the classic locality of Pikermi (Attica, Greece), stored in the palaeontological and geological museum of Athens. *Géobios* 34:563–584.
- Saraç, G., T. Kaya, and D. Geraads. 2002. *Ancylotherium pentelicum* (Perissodactyla, Mammalia) from the upper Miocene of central and western Turkey. *Géobios* 35:241–251.
- Schaub, S. 1943. Die Vorderextremität von *Ancylotherium pentelicum* GAUDRY and LARTET. *Schweizerische Paläontologische Abhandlungen* 64:1–36.
- Sen, S. 1994. Les gisements de mammifères du Miocène supérieur de Kemiklitepe, Turquie: 5. Rongeurs, Tubulidentés et Chalicothères. *Bulletin du Muséum National d'Histoire Naturelle*, 4ème sér., C, 16:97-110
- Suwa, G., H. Nakaya, B. Asfaw, H. Saegusa, A. Amzaye, R. T. Kono, Y. Beyene, and S. Katoh, S. 2003. Plio-Pleistocene terrestrial mammal assemblage from Konso, Southern Ethiopia. *Journal of Vertebrate Paleontology* 23:901–916.
- Thenius, E. 1953. Studien über fossile Vertebraten Griechenlands. III. Das Maxillargebiss von *Ancylotherium pentelicum* GAUDRY und LARTET. *Annales Géologiques des Pays Helléniques* 5:97–106.

- Wagner, A. 1857. Neue Beiträge zur Kenntnis der fossilen Säugthier-Ueberreste von Pikermi. Abhandlungen der königlich bayerischen Akademie der Wissenschaften Mathematisch-Physikalische Klasse 8:109–158.
- Webb, G. L. 1965. Notes on some halicothere remains from Makapansgat. *Palaeontologia Africana* 9:49-73.
- Zapfe, H. 1974. Ein schizotheriiner Chalicotheriidae aus pannonischen Schottern der Umgebung von Krems, Niederösterreich. *Sitzungsberichten der Österreichische Akademie der Wissenschaften, Mathematisch-naturwissenschaftliche Klasse I*, 182:289–299.
- Žhegallo V. 1978. The Hipparions of Central Asia. *The Joint Soviet-Mongolian Paleontological Expedition, Transactions* 7: 1-155.

## Figure Captions

FIGURE 1. Map of Greece and surrounding areas with the location of *Ancylotherium* sites. 1:

Thermopigi; 2: Bulgarian sites of the Struma valley; 3: Veles-Karaslari; 4: Pentalophos;  
5: Halmyropotamos; 6: Pikermi; 7: Gülpinar; 8: Karaburun; 9: Samos.

FIGURE 2. *Ancylotherium pentelicum*, skull SIT-770 from Thermopigi, LPGUT. **A**, lateral view; and **B**, dorsal view. Scale bar equals 20 cm.

FIGURE 3. Same specimen as Figure 2. Ventro-lateral view of the right side of the cranial base.

FIGURE 4. Same specimen as Figures 2 and 3. Occlusal view of cheek-teeth. Scale bar equals 5 cm.