Chalicotheriidae (Mammalia, Perissodactyla) from the late Miocene of Akkaşdağı, Turkey

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ABSTRACT
Among over 5000 large mammalian remains collected at Akkaşdağı, only three specimens belong to a Chalicotheriidae, *Ancylotherium pentelicum* (Gaudry & Lartet, 1856). The juvenile skull resembles the one from Hadjidimovo-1 in Bulgaria. A duplex bone and a calcaneum were also found. All these specimens, although similar in morphology, are about 10% smaller than the adult individuals from Pikermi (Greece) which is the type locality of *A. pentelicum*. The occurrence of this species at Akkaşdağı confirms once more the presence of an open woodland bioprovince from Greece to Afghanistan during the Turolian.

KEY WORDS
Chalicotheriidae,
Ancylotherium,
late Miocene,
Akkaşdağı,
Central Anatolia,
Turkey.

RÉSUMÉ
Chalicotheriidae (Mammalia, Perissodactyla) du Miocène supérieur d'Akkaşdağı, Turquie.
Sur plus de 5000 restes de grands mammifères récoltés à Akkaşdağı, seuls trois spécimens appartiennent à un Chalicotheriidae, *Ancylotherium pentelicum* (Gaudry & Lartet, 1856). Le crâne juvénile ressemble par tous ses caractères à celui de Hadjidimovo-1 en Bulgarie. Un os duplex et un calcanéum ont aussi été trouvés. Les dimensions de ces deux spécimens sont environ 10 % plus petites que celles des individus adultes de Pikermi (Grèce) qui est la localité type de *A. pentelicum*, mais leur morphologie ne montre pas de différence notable. La présence de cette espèce à Akkaşdağı et son aire de dispersion des Balkans à l'Afghanistan confirme une fois encore la réalité de la bioprovince gréco-irano-afghane, en particulier durant le Turolien, avec des milieux relativement ouverts et plutôt secs par rapport à d'autres régions en Europe.

MOTS CLÉS
Chalicotheriidae,
Ancylotherium,
Miocène supérieur,
Akkaşdağı,
Anatolie Centrale,
Turquie.

INTRODUCTION

Remains of Chalicotheriidae Gill, 1872 are generally scarce in Eurasian late Miocene mammal localities, even in those which are richly documented. The only exception is probably the classical Pikermi locality in Greece which yielded the richest record with over 100 specimens of dental and postcranial remains (Roussiakis & Theodorou 2001). At Akkaşdağı (in the southern Çankırı basin between the towns of Keskin and Kaman), over 5000 specimens of mammals have been unearthed during the field campaigns of 1997, 2000 and 2001 but only three specimens of Chalicotheriidae. This confirms once more that this group is quite marginal in late Miocene mammalian faunas.

Among the order Perissodactyla, the members of the family Chalicotheriidae have a peculiar status having laterally compressed and deeply cleaved strong claws on hands and feet. In addition, members of the subfamily Schizotheriinae Holland & Peterson, 1913 show an unusual fusion of the proximal and middle phalanges to form a single bone named the duplex. Their dentition is also peculiar in having a W-pattern of lophs in the cheek teeth, allowing a chisel-like action on food, indicating a browser diet.

Ancylotherium pentelicum (Gaudry & Lartet, 1856) is the typical representative of the subfamily Schizotheriinae, and is only known in localities correlated to the zones MN11-12 in eastern Europe and SW Asia. This species is known from an area extending from Macedonia and Bulgaria up to Afghanistan (see Geraads *et al*. 2001; Roussiakis & Theodorou 2001). It is worth mentioning that *A*. aff. *pentelicum* was reported from Concud (MN11), Nombrevilla (MN10) and Los Valles de Fuentidueña (MN10), all in Spain (Alberdi *et al*. 1981; Heissig 1999). The nature of the material from Concud and Nombrevilla is not mentioned (Crusafont & Casanovas 1973). The material from Los Valles de Fuentidueña consists of a left astragalus similar in morphology to that of *A. pentelicum* but 1/4 smaller. To confirm the occurrence of this species in Spain, more material and a more detailed study of the available specimens are needed.

In the past, the species *pentelicum* was often referred to other genera including *Macrotherium* Lartet in Blainville, 1837, *Nestoritherium* Kaup, 1859 and *Colodus* Wagner, 1861 before Schaub (1943) revised its systematic status after an extensive study of all postcranial material available at that time (see history in Roussiakis & Theodorou 2001).

In Turkey the occurrence of *A. pentelicum* was noted in several localities, but it is rare: Gülpınar (Kaya 1986), Kemiklitepe B (Kaya 1988; Sen 1994), Salihpaşalar and Pınaryaka (Saraç *et al*. 2002), Konya-Kızılören (Saraç 1994). All these localities are correlated to MN11-12.

The terminology used in this paper follows Butler (1965) and Coombs (1978). The material is preserved in the Natural History Museum of the MTA in Ankara. The measurements are given in millimetres. AK2 and AK5 are the numbers of bone pockets with *Ancylotherium*.

ABBREVIATIONS

L	length;
W	width;
DT	transverse diameter;
max	maximum;
MTA	General Directorate of Mineral Research and Exploration, Ankara.

SYSTEMATICS

Order PERISSODACTYLA Owen, 1848
Family CHALICOTHERIIDAE Gill, 1872
Subfamily SCHIZOTHERIINAE
Holland & Peterson, 1913

Genus *Ancylotherium* Gaudry, 1863

Ancylotherium pentelicum
(Gaudry & Lartet, 1856)

MATERIAL. — A juvenile skull having the dorsal part crushed and damaged and the ventral part and incomplete dentition including left P2, P3, M1, M2 and erupting M3, right M1, M2 and erupting M3 (AK2-293); a left duplex (AK5-4) and a left calcaneum (AK2-438). This material was unearthed from two different bone pockets about 3 m apart.

DESCRIPTION

Skull (Fig. 1A)

The skull belongs to a young individual, ontogenically similar to that of Hadjidimovo-1 in Bulgaria (Geraads *et al.* 2001), but younger than the one from Titov Veles in Macedonia (Garevski 1974). In the Akkaşdağı specimens, almost nothing is preserved from the top part of the skull, while the ventral part is nearly complete. The skull anatomy of this species is still poorly known; apart from the material from Hadjidimovo-1 and Titov Veles, only some upper jaw fragments were described from Pikermi (Gaudry 1862-1867; Thenius 1953). However, an almost complete skull from Gülpınar (Department of Çanakkale, northwestern Turkey) is preserved at the Ankara Natural History Museum, and it belongs to an adult individual. This skull has not been the subject of any publication. We compared the Akkaşdağı skull with this one in order to appreciate the proportions of missing and damaged parts.

On the skull AK2-293, the dorsal part is completely crushed preventing detailed observation of the nasal, frontal and parietal bones. Also, the posterior part of the skull is missing. Some parts of the temporal bones are preserved, as well as the zygomatic arches, maxillae, palate, glenoid fossae, post-glenoid processes, and some cheek teeth (see Fig. 1A for details). The M3s are just erupting.

In ventral view, the palate narrows slightly forward (narrowest width of the palate between M2s is 67 mm, and between M1s 52 mm). The choanae are large and elliptical in outline. Their anterior border is behind the M1s. The median keel of the basisphenoid forms a bony septum which narrows anteriorly and divides the choanae into two parts. The zygomatic arch is rounded, and it narrows anteriorly. It reaches the maxilla immediately behind the M1. The maximum width of the skull at the level of zygomatic arches is 212 mm. The mandibular fossa is rather flat and, just behind it, the retro-articular process is massive and rounded. In lateral view, the infra-orbital foramen is situated 20 mm above the posterior edge of P3.

Dentition (Fig. 1B; Appendix: Table 1)

On the Akkaşdağı specimen the premolars are still erupting and are unworn, and thus they preserve all details of the occlusal pattern. We emphasize that such fresh premolars of *Ancylotherium* have not previously been described. The premolars are not molarized, so their occlusal pattern is different from that of the molars. The P3 is much smaller than the P4. Both have strong cingula on their anterior, lingual and posterior faces. The lingual cingulum is stronger in P4. Both premolars have a slightly oblique protolophule which is shorter than the metalophule. The protocone is without any crest. It is relatively conical in P3, but rather pinched mesio-distally and lined up with the protolophule in P4. Both premolars have the metalophule thinner than the protolophule and oriented rather transversely. The buccal surface of the premolars is flat, thus distinguishing it from that of *Chalicotherium* Kaup, 1833 which has P3 and P4 with folded or depressed buccal surface (Zapfe 1979). The width/length ratio is 125.3 for P3 and 127.3 for P4.

The M1 is much larger than the P4 but notably smaller than the other molars. Its outline is almost square with a W/L ratio of 98.9. However, the anterior part of the M1 is narrower than the posterior part. The ectoloph is W-shaped. Wear has affected only the anterior faces of the paracone and metacone crests. The protocone is an isolated cusp situated close to the antero-lingual corner of the tooth; it is without any crest or furrow. The protolophule is short. The metacone is slightly higher than the paracone, and their lingual tips protrude lingually beyond the median line. The paracone rib is weak and there is no metacone rib. The parastyle protrudes antero-buccally, the hypocone lingually. The median valley is directed toward the mesostyle. The anterior and posterior cingula are relatively strong; there is no cingulum along the lingual and buccal borders. The crochet is absent as on the specimen HD-633 from Hajidimovo-1, while the other specimen (HD-631) from this locality has a crochet (Geraads *et al.* 2001). The four roots of the M1 are situated under the main cusps.

FIG. 1. — *Ancylotherium pentelicum* (Gaudry & Lartet, 1856), juvenile skull (AK2-293), Akkaşdağı; **A**, ventral view; **B**, occlusal view of the left toothrow with P4-M2 and erupting M3. Scale bars: 50 mm.

The M2 is about 30% larger than the M1. Its occlusal outline is rather rectangular with a W/L ratio 87.5. Wear has slightly affected limited areas on the W-shaped ectoloph. The first lobe is larger and is twice as long as the second lobe. The median valley which separates these lobes is a little narrower than on the M1. In contrast to M1, the paracone is notably higher than the metacone. The conical protocone is a large isolated cusp which occupies a wider area than in the M1. The anterior cingulum is complete between the parastyle and the base of the protocone. The posterior cingulum is weaker and forms a tiny but continuous ridge from the mesostyle to the hypocone. On the lingual face, there is a short thickening which closes the median valley. There is a short crochet on the metaloph as HD-631 from Hadjidimovo-1. The presence of this structure is apparently related to the degree of wear; it disappears in worn teeth. The other characters are similar to that of the M1.

The M3 is still erupting. Only the antero-labial side of the tooth is visible. The paracone rib is weak, and there is no metacone rib. The parastyle and mesostyle are sharp.

FIG. 2. — *Ancylotherium pentelicum* (Gaudry & Lartet, 1856), left duplex (AK5-4), Akkaşdağı; **A**, dorsal view; **B**, medial view. Scale bar: 50 mm.

Duplex (Fig. 2)

This bone is typical for Schizotherinae, and it is formed by the coalescence of the first and second phalanges of the second digit, in both hand and foot, as observed in the genera *Ancylotherium* Gaudry, 1863, *Tylocephalonyx* Coombs, 1979, *Moropus* Marsh, 1877 and *Phylotillon* Pilgrim, 1910 (Coombs & Rothschild 1999). The duplex from Akkaşdağı belongs to the second digit of the left forelimb. Its articular facet with McII is heart-shaped, concave and faced proximo-dorsally. It occupies almost half the surface of the dorsal side of the first phalanx. The proximal edge of the bone is bilobed because of the presence of an almost central notch. The proximo-lateral volar process is stronger but less protruding anteriorly than the medial one. On the dorsal face, the medial side is higher than the lateral one. The volar tuberosity is clear. The distal trochlea is deep (deeper on the medial side).

The duplex is larger in *Ancylotherium pentelicum* than in any species of *Metaschizotherium* von Koenigswald, 1932. The duplex of *A. pentelicum* shows similarities with those of *Moropus elatus* Marsh, 1877 and *Tylocephalonyx skinneri* Coombs, 1979 in having a heart-shaped proximal articular facet. However, in *T. skinneri* the angle between the first and second phalanges is stronger, and the proximo-volar process is more robust (Coombs 1979). The Akkaşdağı duplex is smaller than those of the adult specimens from Pikermi and Pınaryaka (Roussiakis & Theodorou 2001; Saraç *et al.* 2002). It has much weaker muscular connections than in other specimens (Appendix: Table 2). These differences are interpreted as being due to the younger ontogenetic age of the Akkaşdağı individual and/or to sexual dimorphism.

Calcaneum (Fig. 3; Appendix: Table 3)

AK2-438 is a complete calcaneum. Until now, only one complete calcaneum (collections of

FIG. 3. — *Ancylotherium pentelicum* (Gaudry & Lartet, 1856), left calcaneum (AK2-438), Akkaşdağı; **A**, dorsal view; **B**, ventral view. Scale bar: 50 mm.

Vienna Museum, Zapfe 1979) was referred to *Ancylotherium pentelicum*, while the three others specimens from Pikermi (one in Paris and two in Athens; Gaudry 1862-1867; Roussiakis & Theodorou 2001) are all incomplete. Other localities where this species is recognized did not yield any calcanea. The Akkaşdağı specimen preserves all articular facets well delimited and other morphological structures such as processes and grooves, whereas on the Pikermi specimens such structures are partly damaged, eroded or simply not yet well formed (juvenile).

In dorsal view, AK2-438 has a *sustentaculum tali* forming a strong lateral process; it bears on its dorso-anterior face an articular facet for the astragalus. This facet is separated from the main facet for the astragalus by a 5 mm wide notch. The main facet for the astragalus has two parts: the upper one (W = 53 mm) is ellipsoid in outline and covers all the dorsal face of the coracoid process; the lower part (L = 32, W = 29 mm) is round and covers two thirds of the anterior articular process. Both parts form a continuous large facet for the astragalus. On the anterior face, the facet for the cuboid is moon-shaped and extends from the medial edge up to the median notch.

On the medial face of the bone, a deep oblique scar divides the medial tuberosity for the upper portion of the tibial cranial muscle into two unequal parts, the lower one being much larger than the upper one.

An important character of AK2-438 is that the shaft of the *tuber calcanei* is rectilinear, with an almost regular medio-lateral width from the articular part up to the posterior edge of the bone. The left calcaneum from Pikermi (PG 95/20) on which this part is well preserved has the medial and lateral faces concave and, consequently, the shaft is notably narrower in the middle part than in other parts of the bone. Moreover, due to the lateral concavity, the angle between the *sustentaculum tali* and *tuber calcanei* is smooth in all three specimens from Pikermi (Gaudry 1862-1867; Roussiakis & Theodorou 2001), while it is sharper in the Akkaşdağı specimen. This unique difference may be interpreted as an individual or regional variation.

Two calcanei from Omo and Laetoli in East Africa have been assigned to *Ancylotherium hennigi* Butler, 1965, a species that lived in East Africa from latest Miocene up to the latest Pliocene (Butler 1965; Guérin 1985, 1987). The size and morphology of these specimens seem to be almost identical to those from Pikermi (Appendix: Table 3) according to descriptions and illustrations given by Guérin (1985, 1987: fig. 9.1).

Lastly, Guérin & Pickford (2005) described a new species, *Ancylotherium cheboitense*, from the latest Miocene Cheboit locality at Tugen Hills in Kenya. The material consists of a lower molar and some foot bones but nothing comparable to the specimens recorded at Akkaşdağı.

CONCLUSIONS

The skull from Akkaşdağı belongs to a juvenile individual while the duplex and calcaneum belong to young adult individuals. This may partly explain why these specimens are a little smaller than those from Pikermi, which is the type locality of *Ancylotherium pentelicum*. As noted by Roussiakis & Theodorou (2001: 571),

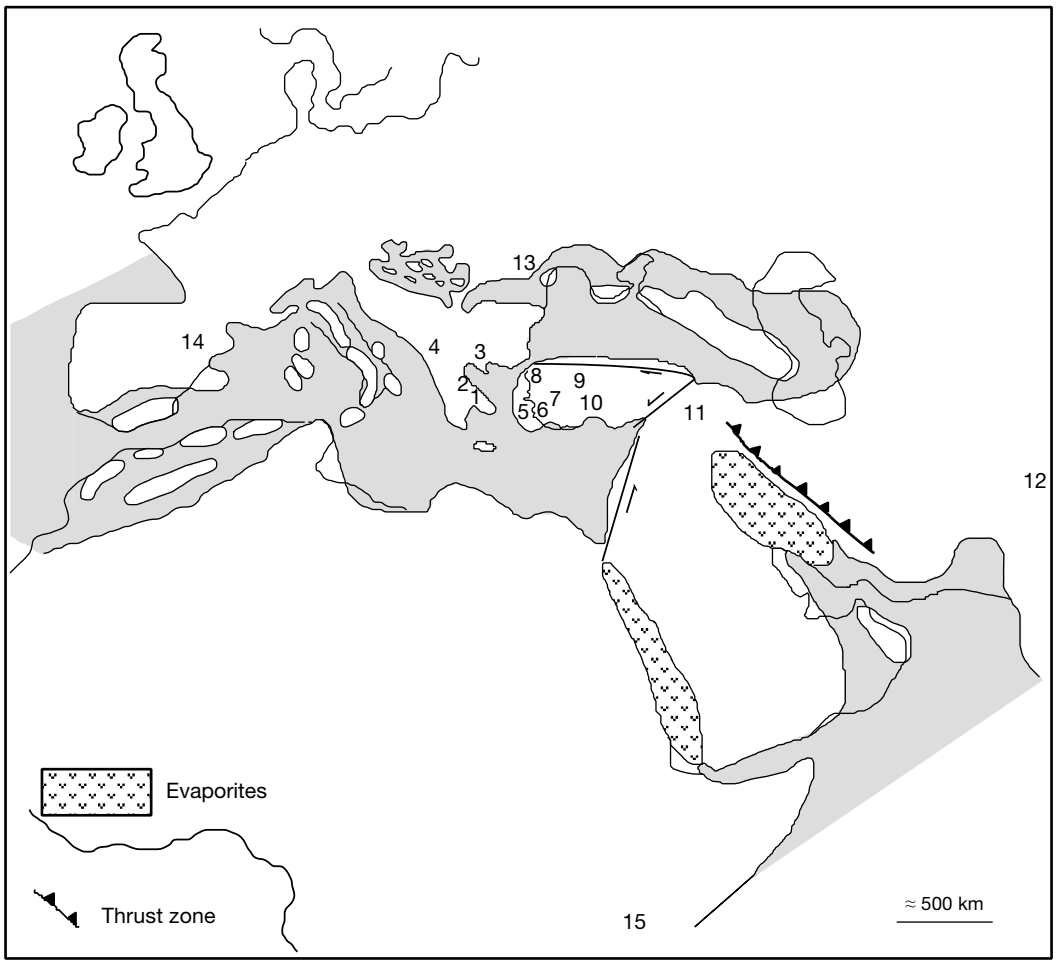

FIG. 4. — Paleogeographic map of middle Tortonian-Meotian showing distribution of localities which yielded *Ancylotherium* remains (after Rögl 1999, modified). **1**, Pikermi; **2**, Evia Island localities (Halmyropotamus and Kerassia); **3**, Bulgarian localities (Hadjidimovo-1, Kalimantci and Gorna Sushitsa); **4**, Titov Veles; **5**, Samos; **6**, Salihpaşalar; **7**, Kemiklitepe A; **8**, Gülpınar; **9**, Pınaryaka; **10**, Konya-Kızılören; **11**, Maragha; **12**, Molayan; **13**, Novo Ukrainka; **14**, Spanish localities (Concud, Nombrevilla and Los Valles de Fuentidueña); **15**, East African localities (Laitoli and Oldwai Bed I in Tanzania, Cheboit and Lukeino in Kenya, Omo localities in Ethiopia, Nkondo and Kaiso Village in Uganda).

there is a clear size difference between juvenile and adult individuals; e.g., they mentioned an adult calcaneum having DTmax 58.3% larger than that of a juvenile one. Such a strong size difference between juvenile and adult individuals seems to be quite specific to *Ancylotherium pentelicum* as opposed to other species of Chalicotheriidae, even though a large ontogenetic and sexual variation is generally observed in all Chalicotheriidae (see Coombs 1975, 1982). Despite this size difference, the Akkaşdağı skull is similar in morphology to those from Hadjidimovo-1 and Titos Veles (Geraads *et al.* 2001; Garevski 1974).

The duplex from Akkaşdağı is about 10% smaller than the specimens from Pikermi, Halmyropotamus and Samos in Greece and Pınaryaka in Turkey. The same is also true for the calcaneum which in some dimensions is 10 to 15% smaller than the Pikermi specimens (PG 95/20 and PIK 3539a), but larger than the juvenile individual (PG 95/23) from the same locality. The main

morphological difference between the calcanea from Akkaşdağı and Pikermi is the bone shaft which is almost regular in width at Akkaşdağı, but variable at Pikermi.

As noted by Geraads *et al.* (2001), all remains of *Ancylotherium pentelicum* in the Balkans, Turkey and Afghanistan are found in localities correlated to early-middle Turolian (MN11-MN12) (Fig. 4). Their co-occurrence with *Chalicotherium* is only mentioned from Pikermi and Titos Veles (Roussiakis & Theodorou 2001) with however some doubt since the material from these localities is from old excavations, and therefore some mixing of material from various horizons is possible.

In the European and western Asian record, the occurrence of *Chalicotherium* is generally related to forest associations whereas *Ancylotherium* seems to have occupied wooded areas in more open country (open woodlands). It is noteworthy that all Turolian localities in Turkey, Afghanistan and southern Greece only yielded *Ancylotherium*, while the contemporaneous *Chalicotherium* occurs in localities further north in Greece and other parts of Europe. This confirms once more the reality of a Greco-Irano-Afghan bioprovince which is particularly well characterized by Turolian mammal faunas.

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APPENDIX

TABLE 1. — Comparative measurements (in mm) of upper cheek teeth for some *Ancylotherium* and *Macrotherium* species from several localities. Abbreviations: **L**, length; **W**, width.

Species	Locality	Reference		P3	P4	M1	M2	M3
A. pentelicum	Akkaşdağı	This paper	L	18.6	22.0	35.4	50.3	56.6
			W	23.3	28.0	35.0	44.0	–
A. pentelicum	Pikermi	Thenius 1953	L	31.0	33.3	48.0	67.2	62.5
			W	32.0	37.5	41.2	50.5	53.0
A. pentelicum	Kemiklitepe A-B	Kaya 1988	L	–	–	48.0	–	–
			W	–	–	42.2	–	–
A. pentelicum	Hadjidimovo-1	Geraads *et al.* 2001	L	–	–	–	49.4-53.2	60.7
			W	–	–	–	42.8-43.0	51.3
M. fraasi	Steinheim	Koenigswald 1932	L	17.0-18.0	32.0	32.0	43.5-46.0	41.0
			W	21.0	26.0	26.0	33.0-36.0	35.0
M. hennigi	Serengeti	Dietrich 1942	L	–	–	–	55.0	–
			W	–	–	–	44.0	–

TABLE 2. — Measurements (in mm) of the duplex bone (phalanges I+II) in *Ancylotherium pentelicum* (Gaudry & Lartet, 1856) from several localities in Turkey and Greece. Abbreviations: **art**, articular; **DAP**, antero-posterior diameter; **dia**, diameter; **diap**, diaphysis; **dist**, distal; **DT**, transverse diameter; **L**, length; **max**, maximum; **Phl**, phalanx I; **prox**, proximal.

Locality	Spec. No.	Reference	L max	DT prox	DAP prox	DT dia max	Dia art dist max	DAP diap Phl	DT dist
Akkaşdağı	AK5-4	This paper	159.0	64.0	62.0	61.1	81.0	48.2	50.5
Pınaryaka	AAP-51	Saraç *et al.* 2002	178.0	74.0	68.0	–	88.0	–	51.0
Pınaryaka	AAP-52	Saraç *et al.* 2002	182.0	72.0	66.0	75.0	86.0	57.3	61.0
Pikermi	–	Roussiakis & Theodorou 2001	181.3	70.0	81.0	66.4	85.0	49.0	50.6
Pikermi	–	Gaudry 1862	178.0	70.4	72.9	66.8	85.0	50.8	51.5
Pikermi	–	Schaub 1943	159.0	–	–	46.0	73.0	42.0	–
Pikermi	–	Schaub 1943	–	–	–	48.0	–	30.0	–
Samos	–	Schaub 1943	182.0	–	–	67.0	85.0	53.0 0	–
Halmyropotamus	–	Roussiakis & Theodorou 2001	179.1	68.3	71.1	64.2	85.7	(51.8)	–

TABLE 3. — Measurements (in mm) of the calcaneum in some species of *Ancylotherium* and *Chalicotherium*. Abbreviations: **DT**, transverse diameter; **max**, maximum.

Locality	Species	Spec. No.	Reference	Total length	DT max	DT max/ length
Akkaşdağı	*A. pentelicum*	AK2-438	This paper	151.5	102.5	62.0
Pikermi	*A. pentelicum*	PG 95/23 (juvenile)	Roussiakis & Theodorou 2001	–	79.6	68.0
Pikermi	*A. pentelicum*	PG 95/20 (adult)	Roussiakis & Theodorou 2001	162.6	110.0	67.7
Pikermi	*A. pentelicum*	–	Zapfe 1979	166.0	115.0	69.0
Pikermi	*A. pentelicum*	PIK 3539a	Gaudry 1862-1867	–	108.9	–
Laetoli	*A. hennigi*	LAET 3514	Guérin 1987	135.0	94.0	69.6
Omo	*A. hennigi*	–	Guérin 1987	140.0	88.0	62.8
Charmoille	*C. goldfussi*	–	Schaefer & Zapfe 1971	134.0	83.0	61.9
Neudorf	*C. grande*	–	Zapfe 1979	134.0-162.0	84.0-110.0	62.0-69.0