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The Late Miocene Mammal Faunas of the Mytilinii Basin, Samos Island, Greece: New Collection

10. Chalicotheriidae

by

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Abstract

In the present study, we describe several postcranial elements of *Ancylotherium pentelicum* (Chalicotheriidae, Schizotheriinae) from the island of Samos (Greece), some of which are recorded for the first time from this site. The material is compared to the known hypodigm of the species, as well as with other chalicotheres. The known Miocene record of the two chalicothere subfamilies, Chalicotheriinae and Schizotheriinae, in the Eastern Mediterranean and adjacent regions is briefly reviewed and evaluated. The potential paleoecological preferences of both subfamilies are briefly discussed. The presence of the schizotheriine *A. pentelicum* and the absence of any chalicotheriine species in the Turolian faunal assemblages of Samos and Anatolia indicate the expansion of more open habitats in these localities compared to continental Greece, FYR of Macedonia and Bulgaria.

Keywords: Turolian, Samos, Greece, Mammalia, Perissodactyla, Chalicotheriidae, Systematics.

Zusammenfassung

In der vorliegenden Untersuchung beschreiben wir neues postcraniales Material von *Ancylotherium pentelicum* (Chalicotheriidae, Schizotheriinae) von der Insel Samos (Griechenland). Einige der postcranialen Elemente werden zum ersten Mal aus dieser Fundstelle beschrieben. Die neuen Funde werden mit dem bisher bekannten Material dieser Art, sowie mit dem anderer Chalicotherien-Arten verglichen. Die miozänen Fundstellen mit Chalicotheriinae- und Schizotheriinae-Funden aus dem östlichen Mittelmeerraum und benachbarter Regionen werden zusammengefasst und ausgewertet. Potenzielle paläoökologische Präferenzen beider Unterfamilien werden kurz besprochen. Die Anwesenheit des Schizotheriinen *A. pentelicum* und das Fehlen von Chalicotheriinae in den turolischen Wirbeltierfaunen von Samos und Anatolien deuten auf die Verbreitung von mehr offenen Lebensräumen in der Umgebung dieser Fundstellen hin, anders als im Vergleich zum kontinentalen Griechenland, FYR of Macedonia und Bulgarien.

Schlüsselworte: Turolium, Samos, Griechenland, Mammalia, Perissodactyla, Chalicotheriidae, Systematik.

1. Introduction

Ancylotherium pentelicum is a characteristic but rare element of the Late Miocene faunas in the Eastern Mediterranean and adjacent regions. The first specimens from the island of Samos were mentioned in a short report by Major (1888). A few years later, Major (1894) recorded several specimens of *A. pentelicum* in the collections of MCGL, Lausanne, and drew attention to an almost complete forelimb belonging to one individual. Schlosser (1921) mentioned the presence of *A. pentelicum* specimens among the Samos collection of the BSPG in Munich. Dietrich (1928:Abb. 1) illustrated a left juvenile mandibular fragment from the collections of the MNHB in Berlin. Schaub (1943) documented in detail the forelimb material of the MCGL reported by Major (1894) together with some additional specimens from BSPG, MNHN and BMNH. Schaub's (1943) analysis on the osteology and functional anatomy of the forelimb of *A. pentelicum* has been used ever since as a standard reference for numerous subsequent studies on

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chalicotheres. Recently, Geraads et al. (2006) recorded several upper deciduous tooth series from Samos housed at the collections of MCGL and illustrated two of them (Geraads et al., 2006:Pl. 1, figs. 2, 3). In the present study, we describe new material of postcranial elements of *A. pentelicum* from the island of Samos. In particular, elements of the hind limb are recorded for the first time from this site. The studied material was unearthed from two localities, Mytilinii-3 (MYT) and Mytilinii-1 (MTL). The locality MYT is situated in Potamies ravine and is dated to early middle Turolian (early MN 12) at ~7.3 Ma. The locality MTL is located in Adrianos ravine and consists of several fossiliferous sites; the chalicotheres have been traced in the sites MTLA and MTLB, dated to the uppermost middle Turolian at ~7.1 Ma. Detailed information about the geological and stratigraphical setting of the different fossiliferous sites of Samos is provided by Kostopoulos et al. (this volume) and Koufos et al. (this volume). Historical data about the excavations in Samos is given by Koufos (this volume).

2. Material and Methods

The specimens of *Ancylotherium pentelicum* described in the present article are stored in the collections of the Natural History Museum of the Aegean, Mytilinii, Samos (NHMA). Methodology of postcranial measurements follows Roussiakis & Theodorou (2001), including a few additional measurements. Measurements ranging 0-150 mm were taken with a digital caliper precise to 0.01 mm and rounded to the nearest 0.1 mm. For larger measurements, a vernier caliper with a precision of 0.1 mm was applied. All measurements are given in millimeters (mm). For specimens from Pikermi and Halmyropotamos, the values of Roussiakis & Theodorou (2001) were in most cases preserved, as no significant interobserver difference was found.

In the present study, *Ancylotherium* and *Metaschizotherium* are treated as two separate genera (Koenigswald, 1932; Butler, 1965; Roussiakis & Theodorou, 2001; Geraads et al., 2007). A subgeneric treatment between *Ancylotherium* and *Metaschizotherium*, as suggested by Zapfe (1967) and Coombs (1974, 1989), may be equally reasonable. However, since the available record of *Metaschizotherium* limited at present, and no cranial and sufficient postcranial evidence has been reported, we prefer to keep them separate at generic level. A discussion on the inapplicability of other generic names (*Macrotherium*, *Colodus*, *Nestoritherium*), previously used for *Ancylotherium pentelicum*, is provided by Roussiakis & Theodorou (2001). Systematic recommendations for Asian and North American Schizotheriinae follow Coombs (1989, 2004). Chalicotheriinae nomenclature and taxonomy follow the recent analysis by Anquentin et al. (2007), but for different perspectives compare also Bonis et al. (1995) and Geraads et al. (2001, 2006).

Comparisons with Eurasian and African chalicotheres have been carried out in the collections of the following institutions: Athens Museum of Paleontology and Geology, University of Athens (AMPG); Laboratory of Geology and Palaeontology, University of Thessaloniki (LGPUT); Bayerische Staatssammlung für Paläontologie und Geologie, München (BSPG); Staatliches Museum für Naturkunde, Stuttgart (SMNS); Hessisches Landesmuseum, Darmstadt (HLMD); Museum für Naturkunde der Humboldt Universität zu Berlin (MNHB); Musée Cantonal de Géologie, Lausanne (MCGL); Naturhistorisches Museum, Wien (NHMW); Muséum National d'Histoire Naturelle, Paris (MNHN); British Museum of Natural History (= Natural History Museum), London (BMNH). Comparisons with North American schizotheriines are based primarily on Coombs (1978, 1979, 2004), as well as Holland & Peterson (1914).

Abbreviations:

L: length; DT: transversal diameter; DAP: anteroposterior (dorsoplantar) diameter; Prox: proximal; Dist: distal; Dia: diaphysis; Art: articular surface; max.: maximum.

The genera *Ancylotherium*, *Moropus*, and *Tylocephalonyx* are abbreviated, while the genera *Anisodon*, *Metaschizotherium*, and *Kalimantsia* are not abbreviated.

3. Systematic Palaeontology

Order Perissodactyla Owen, 1848
Family Chalicotheriidae Gill, 1872
Subfamily Schizotheriinae Holland & Peterson, 1914

Genus *Ancylotherium* Gaudry, 1863

***Ancylotherium pentelicum* (Gaudry & Lartet, 1856)**
(Plates 1, 2)

Localities: Mytilinii-1A, 1B, (MTLA, MTLB), Adrianos ravine, Mytilinii Basin, Samos, Greece; Mytilinii-3 (MYT), Potamies ravine, Mytilinii Basin, Samos, Greece.

Age: Middle Turolian, MN 12 (late Miocene).
Mytilinii-1A (MTLA, B): ~7.1Ma.
Mytilinii-3 (MYT): ~7.3 Ma.
Material:
MTLA: Right Mt-III, MTLA-277; ungual phalanx, MTLA-485.
MTLB: Left radius and ulna, MTLB-173; right radius and ulna, MTLB-328; left femur, MTLB-338.
MYT: Proximal phalanx, MYT-15; right Mt-III, MYT-64.

Measurements: The measurements are given in Tables 1-3.

Description:

Radius and ulna. Radii and ulnae of *A. pentelicum* are presently known from Pikermi and Samos. Gaudry (1863) described a pair from Pikermi, which is housed in the col-

	Samos			Pikermi		
	NHMA MTLB-173	NHMA MTLB-328	MCGL Schaub,1943	AMPG 1972/22	AMPG PG 95/522	MNHN PIK 3549a
R-L	—	ca. 565.0	557.0	519.3	521.0	556.0
U-L	—	—	703.0	661.0	—	ca. 660.0
R-DT prox. max	154.0	156.0	157.0	141.0	159.0	148.0
R-DT prox. art	139.2	140.0	137.0	125.0	140.8	132.0
U-DT prox. art	135.2	134.5	127.0	126.4	131.0	(128.0)
U-H scav	82.5	80.5	76.0	72.0	81.9	—
U-L olecranon	—	—	—	173.0	—	—
U-L olecr. + inc.	—	—	194.0	199.0	—	—
R-DT dia. min	62.8	—	59.0	(54.0)	—	59.3
R-DAP dia. min	54.1	—	—	(57.0)	—	56.4
DT dist. max	—	193.0	199.0	193.2	199.2	194.0
DT dist. art	—	166.0	162.0	164.0	165.2	167.0
R-DT dist. art	—	124.8	123.0	118.0	128.0	124.3
U-DT dist. art	—	(50.0)	52.0	(52.0)	48.0	48.4
DAP dist. max	—	98.2	—	—	97.8	104.8

Table 1: Comparative measurements (in mm) of radii and ulnae of *Ancylotherium pentelicum* (Gaudry & Lartet, 1856) from the Eastern Mediterranean.

lections of MNHN in Paris. Roussiakis & Theodorou (2001) documented seven additional specimens from Pikermi in the collections of AMPG in Athens. Schaub (1943) documented a complete radius and ulna from Samos stored in the collections of MCGL, Lausanne. During the recent excavations on Samos, two new pairs have been recovered from the locality MTLB. MTLB-173 is a left adult specimen, missing the distal epiphyses and part of the distal shaft of both bones, and the olecranon of the ulna (Pl. 1, Fig. 3). MTLB-328 is a right adult specimen. It retains the distal epiphysis, but is preserved in two portions (Pl. 1, Figs. 1, 2). A segment of missing bone in the middle of the diaphysis does not allow a secure contact between the proximal and distal portions, but the total length of the radius could be approximately estimated; the olecranon of the ulna is not preserved. The state of preservation and the texture of MTLB-173 and MTLB-328 are somewhat different, but the metrical and morphological similarities, as well as their taphonomic proximity, may indicate that both specimens could belong to the same individual.

In proximal view, the articular fovea of the radius that articulates with the humeral trochlea is divided into two asymmetrical concavities, which are separated by an incipient, concave ridge at the level of the radial coronoid process. The lateral suboval concavity is larger and deeper than the subcircular medial one. On the cranial side of the proximal epiphysis of the radius, there is no prominent radial tuberosity, but a coarse surface for the attachment of the biceps tendon. In lateral aspect, the tuberosity for the collateral ligament is particularly strong and prominent. In caudal aspect, the arrangement between the articular facets for the ulna cannot be observed, because both specimens are preserved in natural contact. Isolated radii from Pikermi (AMPG: PG 95/522, PG 95/27, PG 95/549) show a transversally widened articular surface for the ulna, which is roughly divided into three confluent portions. The medial portion extends along the caudal border of the medial concavity of the articular fovea. It faces caudally and is rather flattened transversally. At the level where the medial and lateral concavities of the articular fovea join, it bends proximally and blends with the median portion. The median portion has a moderately depressed surface and faces proximally, like the two concavities of the articular fovea. Approximately at the midpoint of the caudal border of the lateral concavity, the median portion of the articular surface for the ulna blends with the lateral one. The lateral portion of the articular surface for the ulna faces caudolaterally and is slightly concave transversally. None of the ulnae preserves the olecranon. The anconeal process of the ulna is strong and prominent. Below the anconeal process, the trochlear notch for the articulation with the humeral trochlea is arched. The medial and lateral coronoid processes are asymmetrical.

The shaft of the radius is long and appears quite slender with respect to the broadened proximal and distal epiphyses. At mid-shaft, the transverse and anteroposterior (craniocaudal) diameters become nearly subequal. The ulna is characterized by a more slender shaft with a subtriangular cross-section. The interosseous space between radius and ulna is small and was probably filled by a dense interosseous membrane during lifetime, as indicated by the presence of bilateral coarse surfaces.

The distal epiphyses of the radius and ulna are co-ossified, prohibiting any relative movements between the two bones. The distal articular facets for the scaphoid, lunatum and pyramidal form a continuous arched cavity (Pl. 1, Fig. 2). Contrary to extant perissodactyls, all articular surfaces for the carpals are quite smooth; none is markedly projecting or depressed. This adaptation enables enhanced flexion capabilities in the joint, as suggested by

Schaub (1943). On the lateral half of the cranial surface of the distal epiphysis of the radius, a pronounced massive tuberosity is developed, most likely for the accommodation of strong ligamentous attachments to support the flexion and extension of the hand. The medial (radial) and the lateral (ulnar) styloid processes are formed as rounded eminences; the medial one is stronger and extends more distally than the lateral one.

Femur. Very few femora of *A. pentelicum* are known. Gaudry (1863) briefly described a juvenile femur from Pikermi. Schlosser (1921) referred to another specimen from Veles. Recently, Roussiakis & Theodorou (2001) documented a complete femur from Pikermi, as well as two fragmentary distal portions. MTLB-338 is the first specimen reported from Samos and is a moderately well-preserved left femur (Pl. 1, Figs. 4-6).

The proximal epiphysis, which bears the femoral head and the greater trochanter, is completely missing. Due to its condition, the only measurable dimensions of the specimen are the minimum transversal and anteroposterior diameters of the shaft (DTdia. = 95.4; DAPdia. = 62.0), which are similar to the specimens from Pikermi (Roussiakis & Theodorou, 2001:Tab. 11). The shaft of the femur is rather flattened and broad; its transverse diameter is always greater than the anteroposterior one throughout its length. The shaft is broader in its proximal half, due to the presence of the lesser and third trochanters. Distal to the third trochanter, the shaft narrows, though less abruptly than in the North American *Moropus elatus* and *Tylocephalonyx skinneri* (Coombs, 1978, 1979), and then widens again towards the distal epiphysis. The cranial surface of the shaft is more rounded transversally, while the caudal surface is nearly flat. In caudal view, the bifurcated linea aspera is not markedly expressed and the popliteal surface is flat. A supracondylar fossa, which is present in some peryssodactyls on the distolateral corner of the caudal aspect of the shaft, is not developed. A marked and deep furrow on the craniolateral side of the distal part of the shaft is the result of a postmortem abrasion.

The lesser trochanter is well-preserved and fairly prominent. It is developed as a coarse but slender projecting prominence on the mediocaudal margin of the proximal half of the shaft. It is slightly more prominent than in one specimen from Pikermi (AMPG: PA 2070/91; Roussiakis & Theodorou, 2001:Fig. 26). In marked contrast to the lesser trochanter, the third trochanter of the femur is not projecting at all. It is developed as an extensive rough area, which occupies almost the entire lateral side of the proximal half of the shaft. This arrangement of the lesser and the third trochanter in *A. pentelicum*, as evinced by two additional specimens from Pikermi (Gaudry, 1863; Roussiakis & Theodorou, 2001), differs considerably from other chalicotheres with known femoral morphology, as well as from extant perissodactyls. In the chalicotheriine *Anisodon grande*, both the lesser and the third trochanter are developed as non-projecting coarse areas (Zapfe, 1979). In the North American schizotheriines *M. elatus* and *T. skinneri*, both the lesser and the third trochanter are developed as projecting flattened processes; in particular, the third trochanter is projecting more prominently than the lesser one, a condition quite similar to the extant perissodactyls (Coombs, 1978:Fig. 13b; 1979: Fig. 17b).

The distal epiphysis of the femur is partly broken off and missing its lateral half. In caudal view, the well-preserved medial condyle is large and ovoid (Pl. 1, Fig. 5). The intercondyloid fossa is moderately depressed and has a coarse surface. It served as the attachment point for the anterior cruciate ligament that prevents inward rotation and forward displacement of the tibia towards the femur. A distinct depression in the inner surface of the medial femoral condyle probably served as the attachment point for the posterior cruciate ligament that prevents backward displacement of the tibia away from the femur. In medial view, the medial epicondyle forms a large, rough, convex eminence, to which the tibial collateral ligament of the knee-joint must have been attached. In cranial view, the articular surface for the patella retains only a small portion of the medial condyle, which is rather short. Complete specimens from Pikermi (Roussiakis & Theodorou, 2001:Fig. 26) have a shallow and rather symmetrical patellar facet that distinguishes the distal epiphysis of ancylothere femurs from sympatric rhinocerotids and giraffids (isolated distal fragments of femurs are frequent in collections). In the rhinoceroses and giraffes, the patellar surface is deeper and markedly asymmetrical, because its medial condyle is markedly larger than the lateral one.

Third Metatarsal. Third metatarsals of *A. pentelicum* have been described from Pikermi (Gaudry, 1883; Zapfe, 1979; Roussiakis & Theodorou, 2001), Veles (Schlosser, 1921), and Salihpaşalar (Saraç et al., 2002). MTLA-277 and MYT-64 are the first specimens documented from Samos (Pl. 2, Figs. 1-6; Tab. 3). Both specimens are missing the distal epiphysis, while the morphology of the proximal end is partly obscured by postmortem abrasion and surface loss. Due to the absence of the distal end, the skeletal maturity of the specimens can not been granted, but they must have been at least of adolescent age, based on the bone size and cortical thickness.

In proximal view, the articular facet for the ectocuneiform is large and roughly subtrapezoidal (Pl. 2, Figs. 3, 6). Its surface is nearly flat and is distally slanted towards its medial side. In specimen MYT-64, the ectocuneiform facet appears to be shallowly depressed, but this is due to postmortem surface loss. In both specimens, a distinct facet for the cuboid is not apparent. Adult specimen AMPG: PG 95/515 from Pikermi also lacks the cuboid facet, whereas juvenile specimen AMPG: PG 95/551 features a well-defined articular stripe for the cuboid in between the ectocuneiform and Mt-IV facets; in adult specimen AMPG: PG 95/513 the condition is not clear. In medial view, a small and slightly concave facet for the Mt-II seems to be present. Due to surface loss in both specimens, it is not clear if it does extend to the medioplantar corner of the proximal epiphysis, or if a second smaller plantar facet was also present. Juvenile specimen AMPG: PG 95/551 is the only one in which this part is preserved; it shows a single, band-like articular facet for the Mt-II. Saraç et al. (2002) also reported a single, low and

	Samos		Pikermi			Veles	Salihpasalar
	NHMA MTLA-227	NHMA MYT-64	AMPG PG 95/513	AMPG PG 95/515	MNHN PIK 3540d	Schlosser, 1921	Saraç et al., 2002
L max	—	—	169.0	175.0	171.0	170.0	140.0
DT prox	57.6	60.7	58.5	62.9	59.3	60.0	46.0
DAP prox	52.5	53.0	60.3	54.1	56.7	—	43.0
DT dia	46.2	48.8	47.9	47.2	46.5	—	39.0
DAP dia	28.8	27.5	28.8	28.7	28.0	—	29.0
DT dist.max	—	—	59.3	(60.5)	57.2	59.0	—
DAP dist.art	—	—	64.8	64.5	60.8	—	54.0

Table 2: Comparative measurements (in mm) of Mt-III of *Ancylotherium pentelicum* (Gaudry & Lartet, 1856) from the Eastern Mediterranean.

narrow Mt-II facet on the medial side of the Mt-III from Salihpaşalar. Coombs (1978:Figs. 17a, 19a, 27e; 1979: Fig. 23a) documented the presence of a bipartite Mt-II facet for *M. elatus*, *M. hollandi*, and *T. skinneri*, consisting of a dorsal and a plantar portion that may be either separated by a shallow groove or variably connected by a narrow strip of articular surface. An Mt-III from northern Eagle County, Colorado, questionably referred to *Tylocephalonyx* by Coombs (1979), exhibits a single, narrow, band-like Mt-II articular facet (Coombs, 1979:Fig. 29f). A similar variation in the arrangement of the articular surface for the Mt-II is documented among chalicotheriine taxa by Butler (1965) and Zapfe (1979). In lateral view, the articular surface for the Mt-IV consist of a large, deeply concave, dorsal portion that occupies most of the lateral side of the proximal end, and a smaller, flattened, plantar portion that is limited to the lateroplantar corner and is to some extent obscured by postmortem abrasion (Pl. 2, Fig. 2, 5). Better preserved specimens from Pikermi that we have examined (AMPG: PG 95/513, PG 95/515, PG 95/551), indicate that these two portions are either in wide contact, or perhaps slightly separated by a very narrow incipient groove. The large, deeply concave, facet is evident in the Mt-III from Salihpaşalar figured by Saraç et al. (2002:Fig. 3.3b), but the status of the plantar flattened portion is not clear in the illustration. Most likely, based on this specimen, Geraads et al. (2007:464) argued that only a single dorsal facet between Mt-III and Mt-IV occurs in *A. pentelicum*, a statement that must be amended based on the present evidence. Guérin & Pickford (2005) reported "un bord lateral déprimé en dessous de la facette articulaire répondant au Mt IV" for the Mt-III of the African *Ancylotherium cheboitense* from the terminal Late Miocene locality of Cheboit, Baringo District, Kenya, but they did not discuss or depict the arrangement of the Mt-IV facets. In the North American *M. elatus*, the dorsal Mt-IV facet is flat to faintly concave. The smaller plantar facet is better delimited than in *A. pentelicum*. Both Mt-IV facets are slightly slanted towards the center of the lateral surface and remain clearly distinct from one another; either separated by a marked groove, or by being directly adjacent. This morphology of the Mt-IV facets in *M. elatus* is apparently more primitive and quite similar to the arrangement observed in tapirs and rhinocerotids. *M. merriami* differs from *M. elatus* by the fact that the dorsal and plantar Mt-IV facets are broadly confluent (Coombs 2004:Fig. 15.6b), a condition also observed in several terminal taxa of different rhinocerotid lineages (*Brachypotherium*, *Coelodonta antiquitatis*). In specimens of *T. skinneri* from the Sheep Creek Formation in Nebraska, including the holotype skeleton, the dorsal Mt-IV facet is concave (Coombs, 1979: 23b, 24d), but not as deeply as in *A. pentelicum*. It usually remains separated from the smaller plantar facet by a shallow groove, as in *M. elatus*. The proximal Mt-III fragment of a partial skeleton from the Split Rock vertebrate fauna in Wyoming, which can be referred to *T. skinneri*, differs from the Sheep Creek specimens in having the concave dorsal and the flattened plantar portions of the Mt-IV articular surface confluent (Coombs, 1979:Fig. 28f). In the latter specimen, a notable articular facet for the cuboid is also present. Other postcranial elements from the Split Rock partial skeleton also exhibit some morphological variation with respect to the typical population of *T. skinneri* from Sheep Creek, indicating that it may represent a different subspecies (Coombs, 1979). The development of a large and deeply concave dorsal Mt-IV facet on the Mt-III of *A. pentelicum* must be a derived feature that enhances the interlocking between the third and fourth metatarsals, thus more stabilizing the tarsometatarsal joint and reducing the abductive and adductive movements in-between these metapodials.

The shaft of the bone is straight and dorsoplantarly compressed with respect to the proximal epiphysis (Pl. 2, Figs. 2, 5). In dorsal view, the most striking feature is a marked longitudinal depression on the medial side of the dorsal surface of the shaft (Pl. 2, Figs. 1, 4). A similar depression is also developed on the lateral side of the dorsal surface of the shaft, but it is less markedly expressed. These depressions are well-developed in the adult specimens from Pikermi, AMPG: PG 95/513, PG 95/515 and MNHN: PIK 3540d (compare also Gaudry, 1883:Pl. 20, Fig. 3; Roussiakis & Theodorou, 2001:Fig. 29.3). In the juvenile specimen AMPG: PG 95/551, both depressions are faintly expressed. In plantar view, the surface of the shaft is flattened to slightly depressed. The medial and lateral aspects of the shaft show longitudinal rugose surfaces for the attachment of the interosseus ligaments connecting the Mt-III with the adjacent metatarsals.

	Samos		Pikermi		Halmyropotamos		Pinaryaka
	NHMA MYT-15	Schaub 1943	AMPG PG 95/523	AMPG PG 95/524	AMPG 1969/128	AMPG 1969/151	Saraç et al., 2002
L max	127.0	114.0	116.5	125.4	121.0	115.5	125.0
DT prox. max	75.6	79.0	74.7	76.3	69.4	69.7	75.0
DAP prox. max	59.2	—	57.6	64,0	(65.2)	59.9	62.0
DT prox. art	65.2	—	(61.8)	(63.6)	(61.9)	61.6	—
DAP prox. art	49.6	—	(43.6)	(44.7)	(47.8)	(46.0)	—
DT dist. max	57.5	56.0	54.3	58.0	—	52.6	—
DT dist. art	47.7	—	49.2	51.8	—	45.2	—

Table 3: Comparative measurements (in mm) of large-sized proximal phalanges of *Ancylotherium pentelicum* (Gaudry & Lartet, 1856) from the Eastern Mediterranean that may be potentially attributed to the third digit of the manus. For dimension of smaller-sized proximal phalanges also compare Roussiakis & Theodorou (2001:Tab. 21).

Phalanges. Due to their peculiar and easily recognizable morphology, phalanges of *A. pentelicum* are among the most common findings of this species and have been reported from almost all of its known localities. Particularly remarkable is the duplex bone (fused proximal and middle phalanges) of the enlarged second digit of the manus, which is followed by a massive ungual phalanx. The presence of smaller duplexes, which belong to the second digit of the pes, has been documented in *Metaschizotherium*, *Moropus* and *Tylocephalonyx*, but remains currently undocumented and prospective in *A. pentelicum* (Coombs & Rothschild, 1999). The precise position of isolated phalanges from other digits is difficult to be ascertained. Generally, the larger specimens are tentatively assigned to the manus, and the smaller ones to the pes, primarily based on the substantial proportional differences observed between metacarpals and metatarsals. The topographical definition of intermediate specimens cannot be granted, also taking into account the potential presence of considerable sexual dimorphism in chalicothere taxa (Coombs, 1975, 1978). Functional interpretations for the phalangeal adaptations of chalicotheres have been thoroughly debated by Koenigswald (1932), Schaub (1943), Borissiak (1945), Butler (1965), Zapfe, (1979), and Coombs (1983, 1989).

MYT-15 is a well-preserved proximal phalanx of an adult individual (Pl. 2, Fig. 9). The size of the bone, in particular its length, indicates that it most probably represents a proximal phalanx of the digit III of the manus (Tab. 3). Morphologically, MYT-15 does not differ from the known specimens of the species (Schaub, 1943; Melentis, 1969a, 1969b; Roussiakis & Theodorou, 2001; Saraç et al., 2002). The articular facet for the corresponding metapod is ovally heart-shaped, bearing a small but marked incision in the middle of its proximoplantar border. Its articular surface is gently concave and proximodorsally oriented, occupying almost one third of the bone in dorsal view. Above the proximoplantar border of the metapodial facet, the two small bilateral tubercles are slightly asymmetrical and separated by a notch. Distally to the metapodial facet, the shaft of the phalanx narrows. In dorsal view, the shaft is transversally convex and longitudinally slightly concave. In palmar view, the medial and lateral marginal ridges form two coarse surfaces separated by a shallow but broad longitudinal depression. The distal articulation for the middle phalanx is displaced almost entirely to the palmar aspect of the bone. Its bilateral keels and median trochlear depression are in line with the marginal ridges and the longitudinal depression of the shaft. The bilateral keels appear somewhat asymmetrical, but their detailed morphology is obscured by surface abrasion.

MTLA-485 is a well-preserved ungual phalanx (Pl. 2, Figs. 7, 8). The specimen may be tentatively assigned to the pes, due to its smaller size with respect to the specimens assigned to the manus by Schaub (1943). Its maximum length is circa 88.0 mm; the length of the plantar surface is 67.7 mm; the maximum transversal diameter is 42.5 mm; the transversal diameter of the articular surface is 28.2 mm, and the anteroposterior one 48.8 mm. The tip of the dorsal process is broken off. The non-articular surfaces of the bone are very coarse, bearing multiple small furrows. The articular surface for the medial phalanx is curved in an arch and consists of two gently concave facets separated by a median ridge. The claws are sharp, slightly asymmetrical, and deeply cloven dorsally, but not plantarly (Pl. 2, Figs. 7, 8). The subungual process is evident as a coarse tubercle on the plantar side and is not particularly strong, such as in the ungual of the enlarged digit II of the manus (Roussiakis & Theodorou, 2001:Fig. 30.6; Saraç et al., 2002:Fig. 4.4). Coombs (1978) noted that pes unguals of *M. elatus* have a very reduced subungual process with respect to the manus. The rest of the plantar surface is extremely coarse.

4. Discussion

Within the family Chalicotheriidae, two well-documented subfamilies can be distinguished by a unique combination of several features (Coombs, 1989). Chalicotheriinae retain a conservative low-crowned dentition, but attain highly modified postcranials with remarkably shortened hindlimbs. Schizotheriinae retain more conservative postcranial proportions and morphology, but they develop a more derived dentition with more elongated and higher-crowned molars. Based on the available evidence, the place

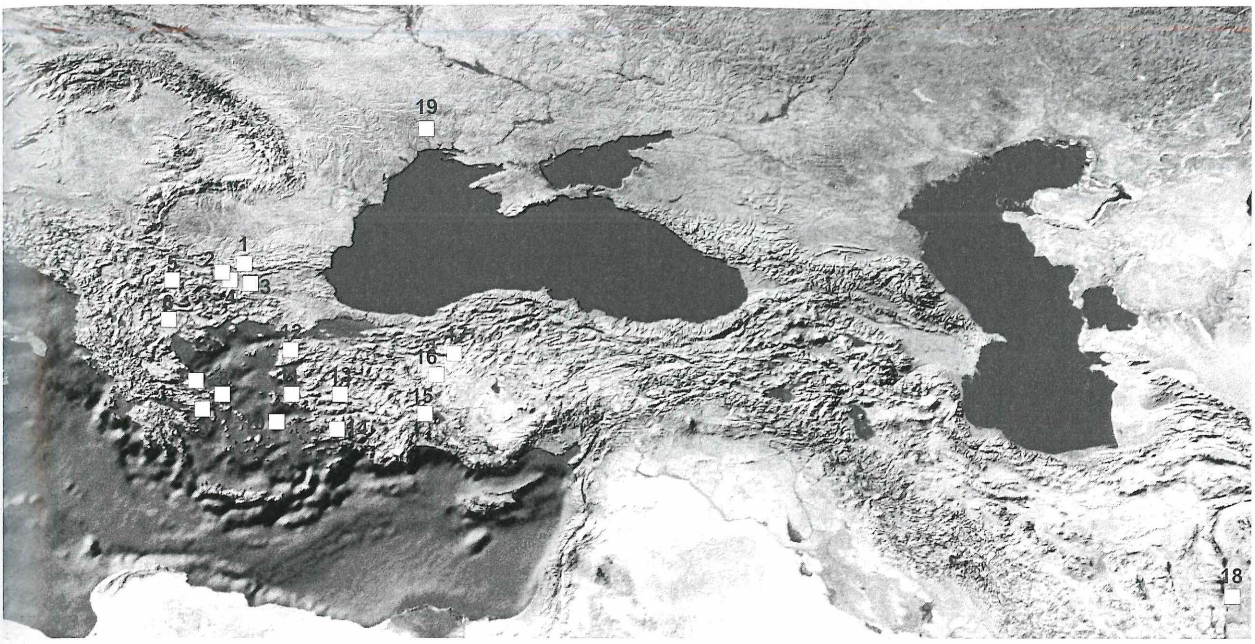

Figure 1: Late Miocene localities with *Ancylotherium pentelicum* (Gaudry & Lartet, 1856) in the Eastern Mediterranean and adjacent regions. 1. Strumyani; 2. Gorna Sushitsa; 3. Hadjidimovo; 4. Kalimantsi ; 5. Veles; 6. Pentalophos; 7. Kerassia; 8. Halmyropotamos; 9. Pikermi; 10. Samos; 11. Karaburun; 12. Gülpınar; 13. Kemiklitepe; 14. Salihpaşalar; 15. Konya-Kızılören; 16. Pinaryaka; 17. Akkaşdaği; 18. Maragheh; 19. Novoukrainka.

and time of divergence of the Chalicotheriinae from the Schizotheriinae cannot be precisely determined (Coombs, 1989). In the present discussion, we will focus on the Eastern Mediterranean schizotheriine record and lay particular emphasis on its well-documented late Miocene representative *Ancylotherium pentelicum*. We will also briefly discuss the Eastern Mediterranean chalicotheriine record, as its synchronic and sometimes sympatric occurrence may offer significant palaeoecological and biogeographical implications (Thenius, 1953; Zapfe, 1979; Coombs, 1989; Geraads et al., 2001; Schulz et al., 2007).

4.1. Middle Miocene Record

The oldest remains of a schizotheriine chalicothere in the Eastern Mediterranean were reported from the late Orleanian/early Astaracian mammalian fauna of Kultak (Milas-Muğla), in southwestern Turkey. A single left proximal phalanx referable to digit IV of the manus was recovered (Kaya et al., 2001:Fig. 3.2a, b) and attributed to *Metaschizotherium fraasi* (Koenigswald, 1932). According to Kaya et al. (2001), the Kultak phalanx closely resembles the size and morphology of the schizotheriine *M. fraasi* from the type locality of Steinheim, Germany (Koenigswald, 1932) and differs, particularly by the shape and dimensions of the proximal articular facet, from the synchronous chalicotheriine *Anisodon grande*. The specimen also resembles the late Miocene *A. pentelicum*, but differs from it by its smaller size. The size difference is considered to be among the key diagnostic features between the genera *Metaschizotherium* and *Ancylotherium*. Kaya (1993:Figs. 4-6) attributes a schizotheriine Mt-IV from the Seyitömer coal basin (Kütahya) to *Moropus elatus*, primarily due to the presence of an articular facet for the ectocuneiform. However, based solely on this evidence, the major extension of the geographic range of the North American species seems ambiguous, given that Mt-IVs of *Metaschizotherium* are not well known (Rinnert, 1956). The last and most recent reference to a middle Miocene schizotheriine in the Eastern Mediterranean is comprised of a quite fragmentary set of dental and postcranial remains from the coal-mine Bursa-Orhaneli (Burmu) in Western Anatolia (Onar & Yildiz, 2005). The most prominent specimens, a well-preserved duplex and the proximal half of a second metacarpal, demonstrate characteristic schizotheriine features (Onar & Yildiz, 2005:Fig. 3). These authors considered the duplex as belonging to the second digit of the manus. The reported dimensions of the Bursa-Orhaneli duplex (Onar & Yildiz, 2005:Tab. 1) are significantly smaller than the manus duplexes of *A. pentelicum*. In particular, its total length is reported to be less than half the length documented for *A. pentelicum* specimens (Schaub, 1943; Roussiakis & Theodorou, 2001; Saraç et al., 2002). It is also about 30% shorter than two manus duplexes from the Austrian localities of Krems and Kaisersteinbruch referable to *Metaschizotherium* (Zapfe 1967; 1974). The peculiar specimen from Bursa-Orhaneli may instead represent a duplex of the second digit of the pes. Such a feature is not unusual in terminal schizotheriines and is documented in *Metaschizotherium*, *Moropus* and *Tylocephalonyx*, though it remains yet undocumented but possible in *Ancylotherium* (Coombs, 1974, 1978; Coombs & Rothschild, 1999). Two duplexes of *Metaschizotherium fraasi* from Steinheim and Häder, Germany, originally referred to the digit II of the manus by Koenigswald (1932:Fig. 21, 22), but correctly attributed to the pes by Coombs (1974), have a very similar size and morphology to the specimen from Bursa-Orhaneli. A schizotheriine duplex from the Aragonian site of Buñol (Valencia, Spain) assigned to the digit II of the pes, also has similar proportions to the Anatolian specimen (Belinchon & Montoya, 1990:Lam. 1, Figs. 7a, b). The size difference observed between well-documented manus and pes duplexes of *Moropus* (Coombs, 1978:Figs. 19c, d) and *Tylocephalonyx* (Coombs, 1979:Fig. 25) also justify the smaller size of the Bursa-Orhaneli duplex.

All three middle Miocene Anatolian schizotheriine references seem to be related with *Metaschizotherium*, but additional material is necessary to allow a reliable determination. *Metaschizotherium* is a rare element in middle Miocene faunas of Western and Central Europe, where it probably includes more than one species (Koenigswald, 1932; Zapfe, 1967, 1974, 1979; Coombs, 1974, 1989). In particular, the ongoing study of the significant *Metaschizotherium* material from Sandelzhausen, Germany, (M. Coombs, in prep.) will further clarify its systematic affinities with respect to its potential late Miocene successor *Ancylotherium pentelicum*. We must note that a schizotheriine DP3 from the early Turolian Bulgarian locality of Kalimantsi-1, initially described as an M2 of *Metaschizotherium fraasi* by Nikolov (1972:Fig. 1), is properly referred to *A. pentelicum* by Coombs (1974) and Geraads et al. (2001, 2006).

The available Middle Miocene record of chalicotheriines in the Eastern Mediterranean is presently as scanty as the one of schizotheriines. The few recovered specimens from Anatolia were referred to as comparable with *Anisodon grande*, a well-documented taxon from several synchronous Western and Central European localities (Zapfe, 1979; Anquentin et al., 2007). Fortelius (1990) documented several isolated teeth from Paşalar, Geraads & Saraç (2003) described a third metacarpal and some phalanges from Çandir, and Becker-Platen et al. (1975) reported its presence in Sofca and Catakbagyaka. Few dental specimens from the locality of Plevlja in Montenegro were also referred to as comparable with *Anisodon grande* (Petronijevic, 1957; Bonis et al., 1995).

Summarizing, the Middle Miocene record of chalicotheres remains still scanty and very incomplete in the Eastern Mediterranean. It appears to include representatives of both schizotheriines and chalicotheriines, but a reliable specific or even generic attribution is hazardous at present, as additional material is required to establish unambiguous systematic affinities with respect to the Western and Central European Middle Miocene chalicothere taxa.

4.2. Late Miocene Record

The available Late Miocene schizotheriine and chalicotheriine record in the Eastern Mediterranean and adjacent regions is primarily restricted to the Turolian, and Vallesian evidence remains extremely rare at present.

Ancylotherium pentelicum is the typical Turolian schizotheriine, demonstrating significantly larger size and higher crowned molars with respect to its potential Middle Miocene forerunner *Metaschizotherium fraasi*. The inadequate Vallesian record does not yet clarify yet the exact evolutionary relationship between these two species (Coombs, 1989). The oldest evidence of *A. pentelicum* is known from the Vallesian locality of Pentalophos in Greece, but the material is scanty (Bonis et al., 1999). During the Turolian, the geographic range of *A. pentelicum* covers the entire Subparatethyan (Bernor, 1983, 1984) or Greco-Iranian (Bonis et al., 1992a, 1992b) zoogeographic province (Fig. 1). It has been firmly documented in the localities of Pikermi (Wagner, 1857; Hensel, 1862; Gaudry, 1863; Thenius, 1953; Roussiakis & Theodorou, 2001), Samos (Major, 1894; Schaub, 1943), Halmyropotamos (Melentis, 1969a, 1969b), Kerassia (Theodorou et al., 2004), and Thermopigi (Geraads et al., 2007) in Greece; Veles in FYR of Macedonia (Schlosser, 1921; Garevski, 1974; Garevski & Zapfe, 1983); Gorna Sushitsa, Kalimantsi, Hadjidimovo, and Strumyani-1 in Bulgaria (Bakalov, 1955; Bakalov & Nikolov, 1962; Geraads et al., 2001, 2006); Gülpinar (Kaya, 1986), Kemiklitepe (Kaya, 1988; Sen, 1994), Salihpaşalar and Pinaryaka (Saraç et al., 2002), Karaburun (Kaya et al., 2005), Konya-Kızılören and Akkaşdaği (Saraç & Sen, 2005) in Turkey; and Maragheh in Iran (Mecquenem, 1924; Geraads et al., 2006). The northern range of *A. pentelicum* may be slightly extended by some specimens documented at Novoukrainka in Ukraine (Pidoplichko, 1959; Korotkevich, 1988), and the eastern range by some unpublished specimens reported from Molayan, Afghanistan (Brunet et al., 1984; Coombs, 1989). The Chinese schizotheriine taxa *Huanghotherium anlungense* Tung, Huang & Qiu, 1975, from Shanxi Province and *Gansuodon pingliangense* Wu & Chen, 1976, from Gansu Province, both based on a few high-crowned and elongated molars, as well as an astragalus from Yushe (Bohlin, 1936), may be related with *Ancylotherium*, but the available material is too scanty to determine precise affinities (Coombs, 1989). The same is true for some schizotheriine specimens reported as *Ancylotherium* aff. *A. pentelicum* from Spanish localities such as Nombrevilla, Los Valles de Fuentidueña, and Concud (Alberdi et al., 1981; Heissig, 1999).

Contrary to the schizotheriines, the Turolian chalicotheriine record is restricted only to the western margin of the Greco-Iranian/Subparatethyan zoogeographic province. Bonis et al. (1995) attributed a complete skull from the locality of Dytiko 3, Greece, to a new species, *Anisodon macedonicum*. Chalicotheriine specimens from Pikermi (Butler, 1965; Symeonidis, 1973) and Vathylakos (Arambourg & Piveteau, 1929) in Greece, and Veles in FYR of Macedonia (Garevski & Zapfe, 1983) may be temporarily referred to as *Anisodon* sp., until more material becomes available for accurate specific affinities (Bonis et al., 1995; Anquetin et al., 2007). Geraads et al. (2001) described a well preserved cranium as a new genus and species, *Kalimantsia bulgarica*, from the locality of Kalimantsi, Bulgaria, and suggested that other Balkan chalicotheriines may be included in this genus. Anquetin et al. (2007) argued that the skull of *Kalimantsia* shows several plesiomorphic features that suggest it should be excluded from the clade *Anisodon* and noted that further comparative studies are required to establish precise generic affinities. Chalicotheriine specimens from the Bulgarian localities of Hadjidimovo, Gorna Sushitsa, Kromidovo and Batishnitsa (Bakalov & Nikolov, 1962; Nikolov, 1975; Geraads et al., 2001, 2006) are temporarily best referred to as Chalicotheriinae indet. Given the scant but evident presence of Chalicotheriinae in Anatolia during the Middle Miocene (Fortelius, 1990; Geraads & Saraç, 2003), their striking absence from the well-sampled Turolian localities of Samos (Greece), Turkey, and Maragheh (Iran) is apparently related to provincial paleoenvironmental changes and constraints.

5. Paleoecological and Biogeographical Remarks

Dietary and paleoecological inferences of chalicotheres have been based on the morphological and physical properties of their dentition, as well as on their peculiar postcranial adaptations (Abel, 1920; Dietrich, 1928; Koenigswald, 1932; Schaub, 1943; Borissiak, 1945; Butler, 1965; Zapfe, 1976, 1979; Coombs, 1983, 1989; Schultz et al., 2007).

Fossils of Chalicotheriinae are commonly associated with denser woodland fauna assemblages. Chalicotheriines had remarkably short hindlimbs that were capable of bearing their body weight in an erect posture, resulting in a clinograde stance comparable to extant gorillas. Due to their low-crowned dentition, a primarily leaf browsing diet has been frequently suggested, assisted by the employment of their elongated forelimbs with a protractable humerus and hooked clawed digits (Koenigswald, 1932; Zapfe, 1976, 1979; Coombs, 1982, 1983, 1989; Heissig, 1999). A recent dental microwear study by Schulz et al. (2007) supported the presence of a strong browsing component in the diet of the chalicotheriines, which is different from that observed in extant browsing ruminants. But a dental mesowear analysis employed by the same authors yielded a substantial abrasive component in the diet that was similar in abrasiveness to that consumed by modern grazing antelopes. Schulz et al. (2007) extensively discussed the apparent inconsistency between the microwear and meso-wear signals, combining the results of both methods. They concluded that the abrasive component, indicated by the mesowear signature, is not related to a grass component, due to the fact that the low numbers of scratches documented by the microwear analysis exclude a substantial amount of graminoids. Owing to the very low scratch density of the microwear signature, frugivory, including hard seeded fruits was also excluded as the abrasive component. A comparison with the mesowear signature of some extant ungulate species classified as "minute abraded brachydonts (mabra)" by Fortelius & Solounias (2000) provided a close resemblance. Similar to chalicotheriines, the mesowear signature of "mabra" species shares a high frequency of high occlusal reliefs with browsers, but also a high frequency of rounded cusps with intermediate feeders, and even with some grazers. The abrasive mesowear signature of the chalicotheriines was convincingly resolved as a result of the consumption of twigs, barks, and branches in addition to the leaf browsing, forming a dietary combination similar to the extant "mabra" western tree hyrax, *Dendrohyrax dorsalis*. This interpretation is further supported by the extensive surfaces for the masticatory muscles on the mandible of the chalicotheriines, and is in accordance with their shortened hindlimbs and protractible, clawed forelimbs (Schulz et al., 2007).

Fossils of Schizotheriinae, in particular *Ancylotherium*, are commonly associated with more open woodlands. Schizotheriines have higher-crowned and more elongated molar teeth compared to chalicotheriines. Among herbivores, this is typically viewed as a selective response to a coarser diet (Koenigswald, 1932; Thenius, 1953; Butler, 1965; Zapfe, 1976, 1979; Coombs, 1983, 1989; Heissig, 1999). However, a mesowear analysis employed on *Metaschizotherium* by Schulz et al. (2007) suggested a less abrasive diet with respect to the lower-crowned chalicotheriines. The obtained mesowear signature classified *Metaschizotherium* within the spectrum of extant intermediate feeders. Nevertheless, as demonstrated by the example of the chalicotheriines that were plotted close to extant grazing antelopes, the mesowear signature alone may be not sufficient to resolve the dietary preferences of the schizotheriines. The abrasive component in the diet of chalicotheriines was attributed to twigs and barks, and a similar abrasive component might have contributed to the diet of schizotheriines, perhaps at a different ratio. A grass component in the diet of schizotheriines can be excluded. Schizotheriines developed more high-crowned teeth in comparison to the chalicotheriines, but their dentition still remained functionally low-crowned brachydont (sensu Fortelius, 1985). The premolars are never noticeably molariform, the occlusal surface of the molars is concave, no cement is developed, the vertical styli on the ectoloph are strong, their intermediate relief is high and the cusp apexes are subjectively sharp or rounded, but never blunt. These morphological properties of the dentition indicate two distinct chewing phases during the occlusal stroke, shearing and crushing, a combination associated with the cominuition of a primarily browsing diet (Fortelius, 1985; Fortelius & Solounias, 2000). We suggest that the higher-crowned and more elongated molars of the functionally brachydont dentition of the schizotheriines reflect an increase in the quantity and abrasiveness of the browse components of their diet, as a response to the expansion of more open and/or seasonal habitats and their nutritionally inferior forage. The less specialized postcranial anatomy of the schizotheriines would also tolerate more evolutionary flexibility towards a modification of their dietary requirements, in order to cope more efficiently with the environmental changes than the chalicotheriines. New postcranial adaptations, such as longer necks and limbs, were evolved to assist these dietary adjustments. Schizotheriines were able to stand erect on the hindlimbs while feeding, in order to increase the browsing height and to allow the forelimbs to hook branches within reach (Coombs, 1983:Fig. 9). Schaub (1943) suggested that the development of a massive forelimb in *A. pentelicum* might have been used in pulling down tree branches and other vegetation in a manner similar to the trunk and tusks of extant elephants. In *A. pentelicum*, the toes of the manus were held back against the dorsal sides of the metacarpals; the elevation and retraction of the claws was interpreted as an adaptation to avoid blunting during walking on hard ground, as is the case in more open and arid habitats (Schaub, 1943; Butler, 1965)

The relative occurrence of schizotheriines and chalicotheriines in the Turolian localities of the Eastern Mediterranean and adjacent regions seems thus to reflect environmentally-controlled provincial differences (Thenius, 1953; Zapfe, 1979; Coombs, 1989). Localities in the western margin of the Greco-Iranian/Subparatethyan zoogeographic province still provided niches with denser tree coverage and more temperate conditions favored by the chalicotheriines. Their absence from the central and eastern parts of the Greco-Iranian/Subparatethyan zoogeographic province (Samos, Turkish localities, Maragheh) is associated with the more rapid expansion of open and dry habitats in these areas (Koufos et al., this volume). On the other hand, the dental and postcranial adaptations of *A. pentelicum* allowed a greater environmental tolerance and thus the ability to successfully dwell in more open and perhaps seasonal habitats. Analogous evidence is provided by the relative distribution of other herbivores in the region, including rhinocerotids, equids, bovids, and giraffids (Koufos et al., this volume). In the cases of sympatry, the dietary and habitual differences between *Ancylotherium* and the chalicotheriines could suggest limited intraspecific competition, as they may have occupied different niches. Based on the available evidence, the major biotic turnover at the Miocene/Pliocene boundary led both subfamilies to disappear from the Eastern Mediterranean and adjacent regions.

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PLATE 1

Ancylotherium pentelicum **(Gaudry & Lartet, 1856), Mytilinii-1B (MTLB), Samos, Greece,**

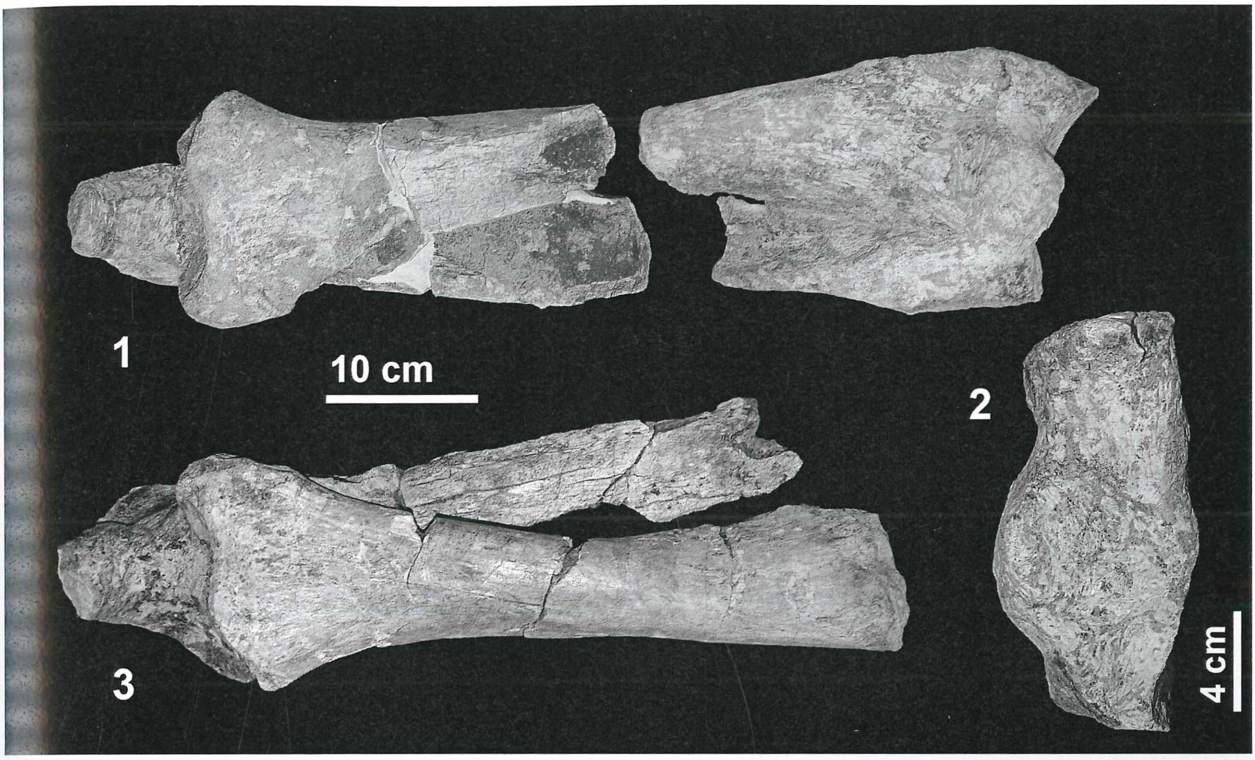
middle Turolian (MN 12).

Fig. 1-2. Right radius and ulna, MTLB-328; 1. cranial and 2. distal view

Fig. 3. Left radius and ulna, MTLB-173; cranial view.

Fig. 4-5. Left femur, MTLB-338; 4. cranial, 5. caudal and 6. medial view.

PLATE 1



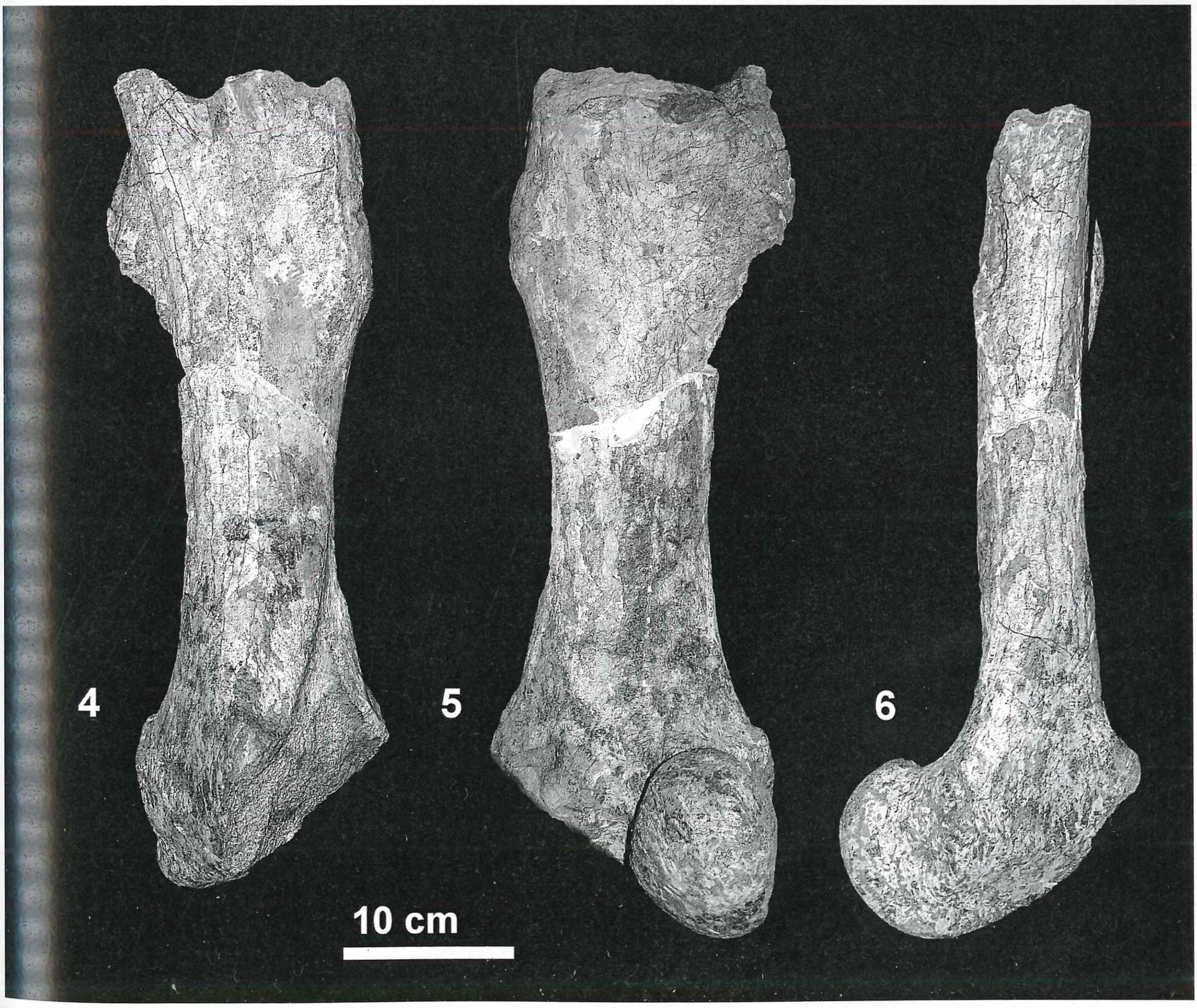


PLATE 2

Ancylotherium pentelicum **(Gaudry & Lartet, 1856), Mytilinii-1A, 3 (MTLA, MYT), Samos, Greece, middle Turolian (MN 12).**

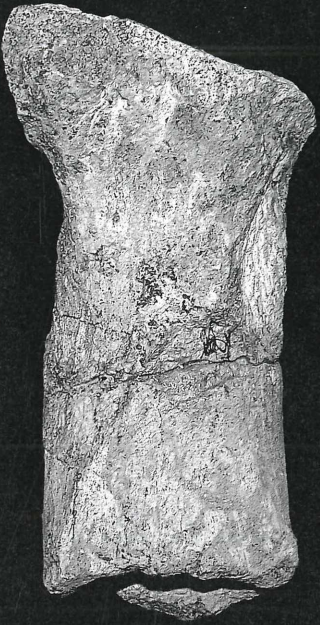
Fig. 1-3. Right Mt-III, MYT-64; 1. dorsal, 2. lateral and 3. proximal view.

Fig. 4-6. Right Mt-III, MTLA-277; 4. dorsal, 5. lateral and 6. proximal view.

Fig. 7-8. Ungual phalanx, MTLA-485; 7. dorsal and 8. plantar view.

Fig. 9. Proximal phalanx, MYT-15; dorsal view.

PLATE 2



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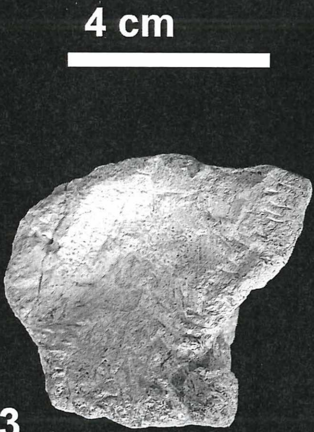

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