

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

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ABSTRACT

More than 120 rhinocerotid remains unearthed in the middle Turolian locality of Akkaşdağı (Central Anatolia) are described. The fauna is diversified, with a pair of large two-horned species, *Ceratotherium neumayri* (Osborn, 1900) and *Stephanorhinus pikermiensis* (Toula, 1906), and two smaller species of short limbed aceratheriines (*Chilotherium* sp. and *Acerorhinus* sp.). *Ceratotherium neumayri* is by far the most common species, with a complete skull, 114 specimens and at least 11 individuals. The cranial, dental and postcranial remains of *C. neumayri* are among the largest ones described so far for this species. The coexistence of *C. neumayri*, *S. pikermiensis*, and chilothers is common in the Turolian of Eastern Mediterranean: comparable rhinocerotid associations are known at Kavakdere (MN 12, Turkey) and Samos (MN 12, Greece). The large size of the *C. neumayri* specimens is consistent with the middle Turolian age for Akkaşdağı (MN 12), as stated on the whole mammalian fauna and radiometric data.

KEY WORDS

Mammalia,
Rhinocerotidae,
Ceratotherium neumayri,
middle Turolian,
Akkaşdağı,
Central Anatolia,
Turkey.

RÉSUMÉ

Rhinocerotidae (Mammalia, Perissodactyla) du Miocène supérieur d'Akkaşdağı, Turquie.

Plus de 120 restes de rhinocérotidés découverts dans le gisement Turolien moyen d'Akkaşdağı (Anatolie centrale) sont décrits. La faune est diversifiée, avec deux espèces de grands rhinocéros bicornes, *Ceratotherium neumayri* (Osborn, 1900) et *Stephanorhinus pikermiensis* (Toula, 1906), et deux espèces

de petits acérathères aux membres trapus (*Chilotherium* sp. et *Acerorhinus* sp.). *Ceratotherium neumayri* est de loin l'espèce la mieux représentée, avec un crâne complet, 114 spécimens et au moins 11 individus. Les restes crâniens, dentaires et postcrâniens comptent parmi les plus grands jamais attribués à cette espèce. La coexistence de *C. neumayri*, *S. pikermiensis* et de chilothères est fréquente dans le Turolien de la Méditerranée orientale : des associations comparables de rhinocérotidés sont connues à Kavakdere (MN 12, Turquie) et Samos (MN 12, Grèce). La grande taille des restes de *C. neumayri* est conforme à l'âge du gisement (MN 12), établi sur l'ensemble de la faune mammalienne et sur la base de données radiométriques.

MOTS CLÉS

Mammalia,
Rhinocerotidae,
Ceratotherium neumayri,
Turolien moyen,
Akkaşdağı,
Anatolie Centrale,
Turquie.

INTRODUCTION

The middle Turolian locality of Akkaşdağı, between Kaman and Keskin (Central Anatolia; Kazancı *et al.* 1999), has yielded a diversified mammalian fauna thanks to the large excavations under the leadership of S. Sen (Kazancı *et al.* 1999). Among the mammals, the Perissodactyla play a leading part, with four species of Equidae (Koufos & Vlachou 2005) and as many species of Rhinocerotidae. More than 100 specimens have been attributed to this family. Two large two-horned and two small hornless rhinocerotids are present: *Ceratotherium neumayri* (Osborn, 1900) (114 specimens), *Stephanorhinus pikermiensis* (Toula, 1906) (nine specimens), *Chilotherium* sp. (one specimen) and *Acerorhinus* sp. (seven specimens), respectively. These taxa occur more or less frequently in the Eastern Mediterranean area during Turolian times (Heissig 1975a, b, 1996, 1999; Geraads 1988; Geraads & Koufos 1990; Bonis *et al.* 1992a, b; Saraç 1994; Antoine *et al.* 2003; Fortelius *et al.* 2003).

ABBREVIATIONS

Akkaşdağı specimens, inventory

AK 2000-2001 excavations;
AKA and AKB 1997 excavation;
AKK surface collects and unknown pockets;
GOK Heintz-Ginsburg excavation (formerly Gökeşme).

Institutions

GDAU Geological Department of the Ankara University;

MNHN Muséum national d'Histoire naturelle, Paris;
MTA General Directorate of Mineral research and exploration, Ankara;
NHM The Natural History Museum, London.

Anatomy

TD transverse diameter;
APD antero-posterior diameter;
H height;
L length;
W width (when different from TD);
ant. anterior;
post. posterior;
w.n. without number.

In the text, the generic names *Ceratotherium*, *Stephanorhinus*, *Chilotherium*, *Acerorhinus*, and *Alicornops* will be abbreviated in *C.*, *S.*, *Ch.*, *A.*, and *Al.* respectively.

MATERIAL AND METHODS

All the specimens from Akkaşdağı described hereunder are stored in the Natural History Museum of the MTA, in Ankara. The specimens GOK-1 to GOK-14 and GOK-16 to GOK-19 are deposited in the Département Histoire de la Terre of the MNHN.

Capital letters are used for upper teeth (D, P, M), and lower-case for lower teeth (d, p, m). For the astragalus/calcaneus facets, the terminology is that of Heissig (1972: pl. 13). The suprageneric systematics follows that proposed by Antoine (2002) and Antoine *et al.* (2003).

SYSTEMATICS

Order PERISSODACTYLA Owen, 1848
 Superfamily RHINOCEROTOIDEA Owen, 1845
 Family RHINOCEROTIDAE Owen, 1845
 Subfamily RHINOCEROTINAE Owen, 1845
 Tribe RHINOCEROTINI Owen, 1845

Genus *Ceratotherium* Gray, 1867

TYPE SPECIES. — *Ceratotherium simum* (Burchell, 1817) by original designation (Gray 1867: 1027).

Ceratotherium neumayri (Osborn, 1900)

Atelodus neumayri Osborn, 1900: 263, text-fig. 16.

Diceros pachygnathus Guérin, 1980: 202-400, text-figs 30, 31, 33, 39-43, 46, 51-56, tabl. 45-49, 51-56, 59-63, 65, 67-72, 75-78.

Ceratotherium neumayri — Geraads 1988: 13-41, text-figs 1-5, pl. 2; 1994: 82-85, text-figs 1, 2, pl. 2, fig. 5. — Geraads & Koufos 1990: 151-154, pl. 1. — Kaya 1994: 13-22, pls 1, 2. — Heissig 1996: 341-342, 347, text-fig. 27.1.

For synonymy anterior to 1980, see Geraads (1988: 36).

MATERIAL. — Complete skull with P2-M3, AK4-212; right M1, much worn, AK2-294; fragment of left M1/2, AK4-243; left p4, AK2-295; left maxilla with D1-3 and D4 erupting, AK5-502; right maxilla with D3 and alveolus of D4, AK6-61; fragment of a left juvenile mandible, with d3 and the alveolus of d2, AK2-296; right D1, AK5-424; fragment of left D2, AK2-435; anterior fragment of left d3, AK5-425 and right d3, AK6-134 (same individual); left ulna lacking distal end, AK6-132; right humerus, right radius and right ulna from the same individual, AK4-w.n.; proximal part of a right humerus, AK6-301; distal part of a right humerus, AK-w.n.; fragment of diaphysis of a left humerus (juvenile), AK4-183; distal epiphyses of a left (GOK-17) and a right radius (GOK-16) from the same young individual; left radius in two parts, GOK-18 and GOK-19; left radius, AK5-627; proximal end of a left radius, AK4-213; left radius lacking distal end, AK4-241; proximal end of a left radius, AK5-67; left ulna, AK6-133; left ulna lacking distal end (juvenile), AK6-131; left ulna lacking distal end, AK7-156; right ulna, AK3-118; right ulna, AK4-184; right ulna (predated olecranon), AK6-302; proximal part of a right ulna, AK2-95; proximal part of a right ulna, AK6-303; left scaphoid, AK2-437; right scaphoid, AK5-630; right pyramidal (fragment), AK5-631; left magnum without posterior tuberosity (GOK-11), left unciform (GOK-10), left metacarpus (McII, GOK-2; McIII,

GOK-4; McIV, GOK-3) and right metacarpus (McII, GOK-6; McIII, GOK-1; McIV, GOK-5) from the same individual; left magnum, AK5-632; right magnum, AK7-38; left unciform, AK5-633; left unciform lacking posterior tuberosity, AK6-58; left unciform lacking posterior tuberosity, AKK-157; right unciform, AK4-74; right unciform, AK7-147; posterior tuberosity of a right unciform, AKK-156; posterior tuberosity of a right unciform, AKK-282; left McII, AK6-55; proximal part of a left McII, AK7-37; proximal part of a left McII (juvenile), AK5-182; left McIII, AK5-68; proximal part of a left McIII, AK3-202; proximal part of a left McIII, AK14-23; distal part of a left McIII, AKB-83; left McIV, AK3-230; right McIV, AK5-436; proximal fragment of a right McIV, AK13-2; left femur, AK4-253; left femur (diaphysis), AK5-367; left femur (diaphysis), AK6-153; distal part of a left femur, AK7-39; femoral head, AK5-323; distal end of a right femur, AK3-63; left patella, AK11-82; fused left tibia and fibula, AK7-40; distal end of a right tibia, AK5-366; distal end of a right tibia, AK7-63; distal end of a right tibia, AKK-154; distal epiphysis of a left fibula, AK13-3; left astragalus (young), AK2-438; left astragalus, AK4-75; left astragalus, AK5-523; left astragalus, AK5-423; lateral part of a left astragalus (young), AK5-319; left astragalus (young), AK6-56; left astragalus, AK7-148; left astragalus, AK11-1; right astragalus, AK5-69; right astragalus, AK5-634; medial fragment of a right astragalus, AK13-4; left calcaneus, AK3-66; right calcaneus, AK7-36; left navicular, AK4-76, and broken left ectocuneiform, AK4-77, from the same individual; right navicular, AK5-439; right cuboid, AK5-636; left entocuneiform, AK13-5; right mesocuneiform, AK5-637; left ectocuneiform, GOK-13; right ectocuneiform, AK5-635; left metatarsus (MtII, GOK-9; MtIII, GOK-7; MtIV, GOK-8); proximal end of a right MtII, AK5-440; left MtIII, AK2-163; right MtIII lacking distal epiphysis (young), AKA-44; distal end of a right MtIII, AK4-238; proximal end of a right MtIV, AK5-437; distal fragment of a metapodial, AK4-214. Additional material: cervical vertebra, AK3-61; cervical vertebra, AK3-67; cervical vertebra, AK4-182; cervical vertebra, without caudal epiphysis, AK5-435; thoracic vertebra, AK7-186; thoracic vertebra, AK6-300; thoracic vertebra, AK3-133; thoracic vertebra, AK5-324; thoracic vertebra, AK14-22. These specimens are tentatively referred to *C. neumayri*, based on their large size and the domination of that very species with respect to other associated rhinos in Akkaşdağı. However, their assignment to *S. pikermiensis* cannot be ruled out.

DESCRIPTION

Skull (Fig. 1; Appendix: Table 1)

The adult skull AK4-212, complete and not deformed, is large and dolichocephalic (width/length

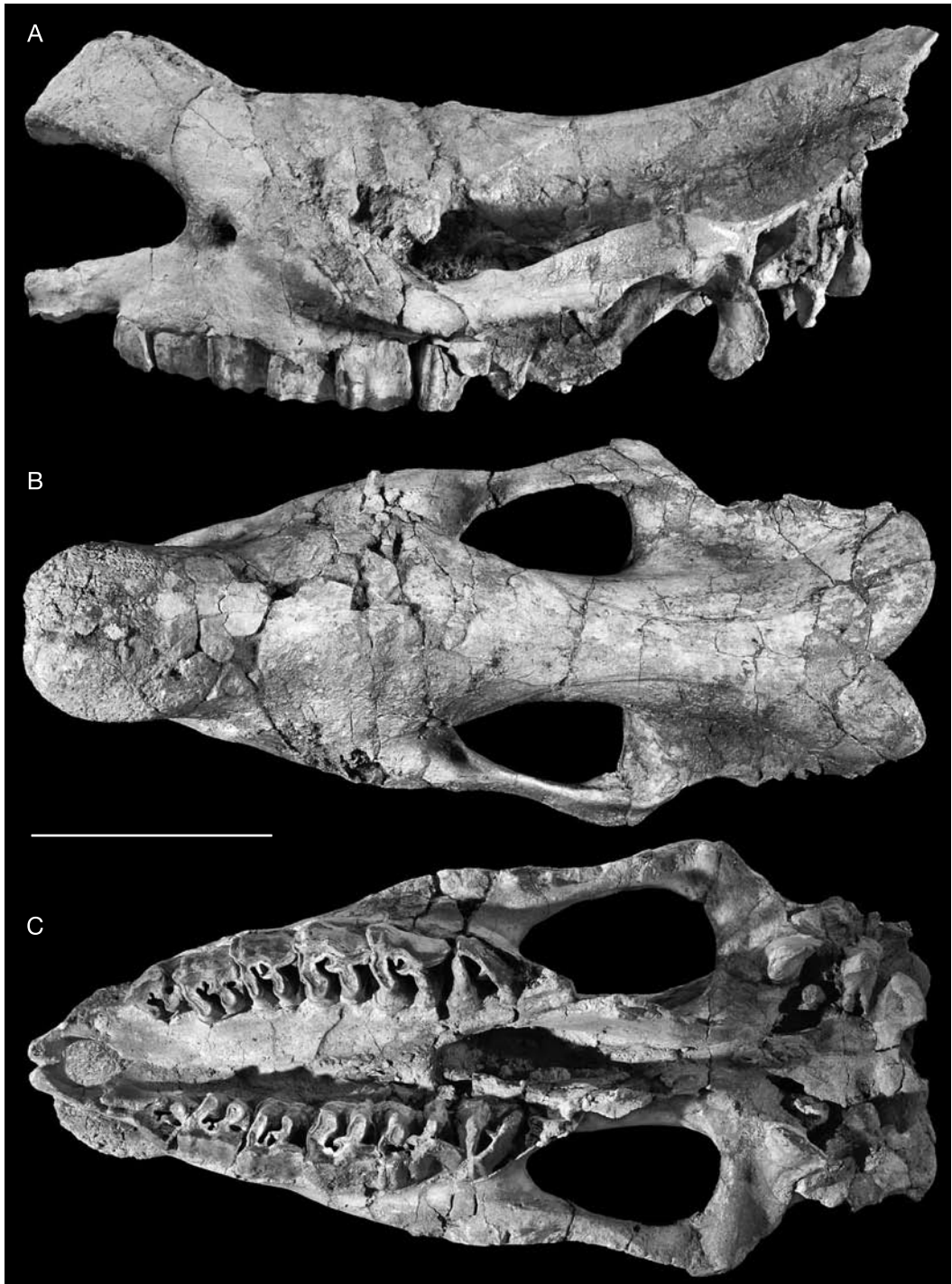


FIG. 1. — *Ceratotherium neumayri* (Osborn, 1900), Akkaşdağı (Anatolia, Turkey), middle Turolian, skull (AK4-212); **A**, left lateral view; **B**, dorsal view; **C**, palatine view. Scale bar: 20 cm.

ratio = 0.46). The premaxillae are rather long (length = 75 mm) and edentulous. The nasal bones do not bear any lateral apophysis. The *foramen infraorbitale* is open above the P3/P4 limit. The nasal notch reaches the middle of P3 while the anterior border of the orbit is above the middle of M2. There is no nasal septum ossification. The only preserved suture is the jugal/squamosal one, which is straight and smooth. The *processus lacrymalis* is absent, but a strong lateral projection of the orbit widens the skull (zygomatic width/frontal width ratio = 1.47). The *processus postorbitalis* is absent on the frontal. The base of the *processus zygomaticus maxillari* is high: it begins several centimetres above the neck of M2/3. The zygomatic arch is low and poorly developed. It forms a thin stripe, without any *processus postorbitalis*. The dorsal profile of the skull is mainly flat, only rising in its posterior third. The *foramen sphenorbitale* and the *foramen rotundum* are fused. The temporal crest is short, so that the area between the latter and the nuchal crest is flat. The external auditory pseudomeatus is partially closed. The occipital side is inclined backward: the occipital condyle is anterior to the occipital crest. The nuchal tubercle is poorly developed. Yet, there is a deep axial fossa reaching the occipital crest. The toothrow is restricted to the anterior half of the skull. The thin and straight *hamulus pterygoideus* is very close to the M3. The posterior margin of the pterygoid is nearly horizontal. The rostral end of the nasal bones is very broad and rounded. The nasal dome and the rough vascular prints testify the presence of a well developed median nasal horn. The nasal bones are totally fused, but there is a shallow median groove from the tip of the nasals until the top of the horn dome. They are long (about the third of the total skull length). A wide and low dome on the frontals further indicates the presence of a smaller frontal horn. The fronto-parietal crests are smooth and widely separate (minimum distance = 50 mm). The occipital crest is strongly concave, nearly forked. The temporal fossa is hugely developed, forming a platform at each side of the braincase.

In distal view, the anterior start of the *processus zygomaticus maxillari* is progressive, following the curvature of the teeth row. The palate is narrow (Appendix: Table 1). The palatine fossa reaches the posterior part of the M2. The vomer is thick and rounded. The articular tubercle for the mandible, transversally concave, forms a high and salient semi-cylindre in lateral view. The *foramen postglenoideum* is not visible. The *processus postglenoidalis* is long, strong and narrow transversally. The articular surface of the latter defines a right dihedron in cross section. The *foramen nervi hypoglossi* is open in the middle of the condylar fossa. A sagittal crest runs all along the basilar process of the basioccipital. The posterior part of the *processus zygomaticus* of the squamosal is concave, due to a transverse groove. The *processus posttympanicus* is curved forward and very short, while the *processus paraoccipitalis* is long and well developed. Their bases are fused. The *foramen magnum* is circular. A median transverse ridge runs all over the occipital condyle, but there is no axial truncation on the condyle (at least at adult stage).

Two juvenile maxillae (with D4 erupting) are also preserved (AK5-502; AK6-61). They show a few morphological features: the *foramen infraorbitale* is located above the posterior third of D2 and the nasal notch reaches the middle of D2 on both specimens. The *processus zygomaticus maxillari* begins at the level of D4. The alveolus for M1 is preserved on AK5-502. The palate is narrow.

The only mandible referable to *C. neumayri* is a fragmentary mandible with an unworn d3 (i.e. new born individual; Hillman-Smith *et al.* 1986). The inferior border is convex. The *foramen mentale* is located under the d2/d3 limit. The *sulcus mylohyoideus* is very deep.

Dentition

Except for the complete series of the skull AK4-212 (Fig. 2A) and the milk series of the juvenile maxillae (AK5-502; AK6-61; Fig. 2B-D), dental remains are very rare in Akkaşdağı, with respect to postcranial specimens.

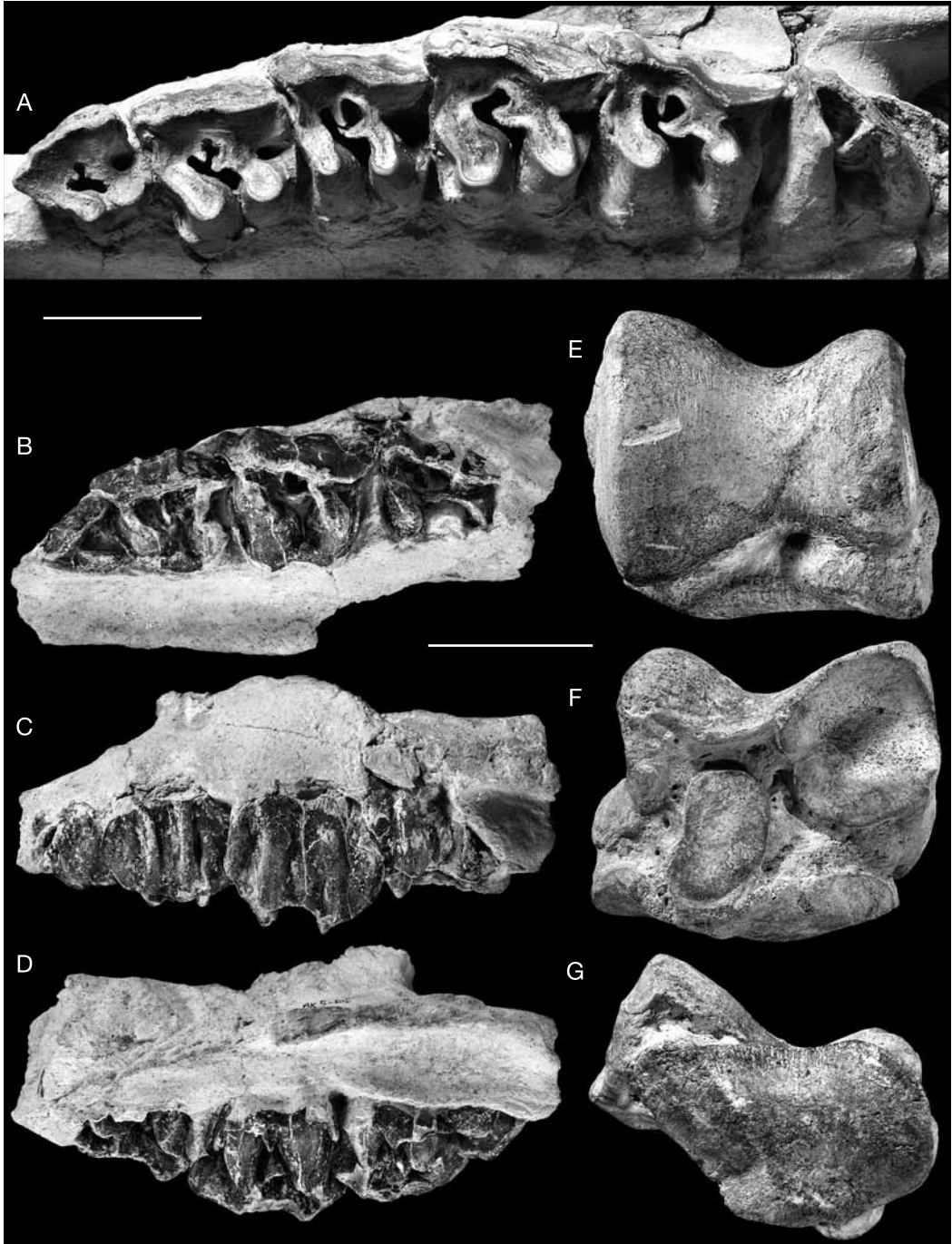


FIG. 2. — *Ceratotherium neumayri* (Osborn, 1900), Akkaşdağı (Anatolia, Turkey), middle Turolian; **A**, upper left series (P2-M3) from the skull AK4-212, occlusal view; **B-D**, left juvenile maxilla with D1-D3 and erupting D4 (AK5-502); **B**, occlusal view; **C**, labial view; **D**, lingual view; **E-G**, right astragalus (AK5-69); **E**, anterior view; **F**, posterior view; **G**, distal view. Scale bars: 5 cm.

The upper dental formula is 3P-3M (there is neither alveolus nor any trace of D1/P1 on P2). The premolar series is long when compared to the molar series (L_{P3-4}/L_{M1-3} ratio = 0.62). There are no enamel foldings on the crowns. A thin layer of cement is present on the ectolophs. Elsewhere, the cement is scarcely preserved. The enamel is thin, wrinkled at the neck and corrugated on the top of the crowns (permanent and milk teeth). The crowns are high but neither hypsodont nor subhypsodont (*sensu* Antoine 2002). No isolated permanent tooth has been unearthed, thus the morphology of the roots is unknown. The dental structures are very simple. There is neither antecrochet nor anterior constriction on the protoloph on upper molars and premolars. The protoloph is curved backwards on the whole upper series. The crochet and the crista are always present. Both are simple, acute and sharp. The former is sagittal, while the crista is transverse. There is no medifossette, despite the constant strong development of the crochet and the crista. They nearly join, especially on P4. The paracone fold is present but weak. The parastyle is sagittal. The metacone fold is absent from the whole series, except on P4, where it is restricted to the basal half of the teeth.

Upper premolars. The premolars are molariform, with separate lingual cusps. There is no labial cingulum, but a reduced lingual cingulum is always present. The metaloph is not constricted. The postfossette is deep and narrow. On P2, the protocone is less developed than the hypocone. The protoloph is thin but continuous and connected with the ectoloph. The hypocone is posterior to the metacone on P2-4. There is no pseudometaloph on P3.

Upper molars. The molars are lacking labial and lingual cingula, except on M3, where a wide and low tubercle is laying at the entrance of the median valley. The metastyle is long. The metaloph is short and the posterior part of the ectoloph is concave on M1-2. There is no cristella. The posterior cingulum is low and reduced. There is no antero-lingual groove on the hypocone of M1-2: the metaloph is continuous. The central valley is open lingually (no junction

between antecrochet and hypocone). There is no lingual groove on the protocone of M2. The mesostyle is thick on M1 and M2. M3 has a triangular outline, with fused ectoloph and metaloph. The protoloph is transverse, even if curved backwards. There is no posterior groove on the ectometaloph.

Lower series. The only permanent lower tooth unearthed in Akkaşdağı and referred to *C. neumayri* is a left p4. The ectolophid groove is developed until the neck. The paraconid and the protoconid are angulous. Thus, the trigonid is angulous and it forms a right angle. There is no constriction on the metaconid and the entoconid. The posterior valley is V-shaped in lingual view. There is neither lingual nor labial cingulum.

Upper milk teeth. Two juvenile maxillae are preserved. The first one bears D1-3 and erupting D4 (AK5-502) whilst AK6-61 bears D3. Isolated D1 (AK5-424) and D2 (AK2-435) have also been unearthed. The teeth have large dimensions (Appendix: Table 2). The crowns are high, but not so.

The upper milk molars bear a mesostyle and a long sagittal parastyle. The mesostyle is sharper and stronger in D2. The paracone fold is thick and salient while the metacone fold is lacking. The protoloph is curved backwards, without anterior constriction or antecrochet. The crista is long and transverse, reaching the lingual half of the tooth (AK5-502). The crochet is strong and straight, sagittal (D1-4), getting longer from D1 to D4. The metaloph is lacking any antero-lingual groove. There is no labial cingulum. The lingual cingulum is variably developed: present and continuous on both D2, it is weak on the D3 AK5-502 (one spur at the entrance of the median valley). There is no trace of lingual cingulum on the D3 AK6-61. The postfossette is narrow and deeper than the median valley. The posterior cingulum is low while the anterior one is thick and high.

D1 is triangular, with a lingual wall. Its postfossette is open backwards. D2 has no lingual wall nor mesoloph, but secondary folds and small structures (medifossette-like). D3-4 may present

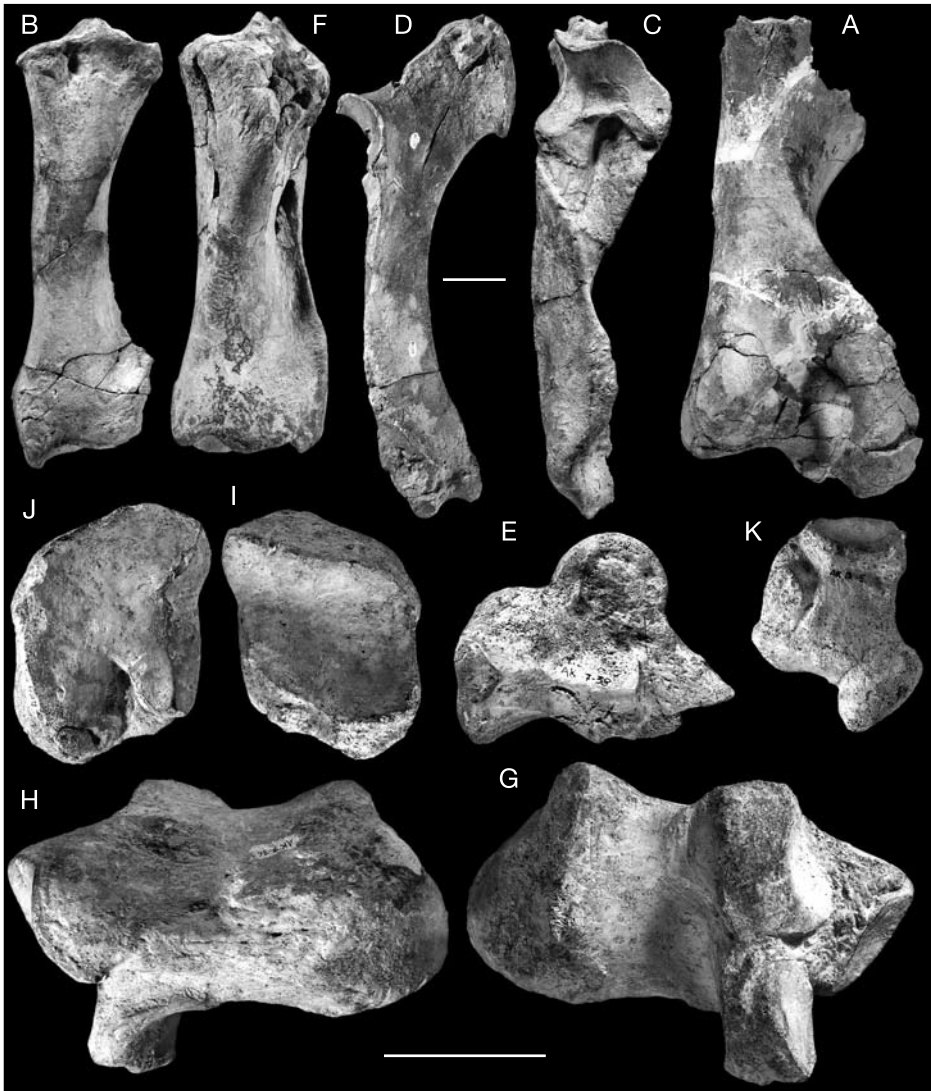


FIG. 3. — *Ceratotherium neumayri* (Osborn, 1900), Akkaşdağı (Anatolia, Turkey), middle Turolian; **A**, right humerus, distal end (AK4-w.n.), posterior view; **B**, left radius, anterior view (AK5-627); **C**, **D**, right ulna (AK3-118); **C**, anterior view; **D**, medial view; **E**, right magnum, lacking the posterior tuberosity (AK7-38), medial view; **F**, left fused tibia and fibula (AK7-40), anterior view; **G**, **H**, left calcaneus (AK7-36); **G**, anteromedial view; **H**, posterolateral view; **I**, **J**, left navicular (AK4-76); **I**, proximal view; **J**, distal view; **K**, left ento-cuneiform (AK13-5), anterior view. Scale bars: 5 cm.

a small vertical ridge posteriorly to the crochet, on the posterior side of the metaloph (AK5-502). **Lower milk teeth.** Three germs of d3 are preserved, among which two belong to the same individual (AK5-425 and AK6-134). The enamel is corrugated. The metaconid and entoconid are constricted. The protoconid fold is lacking or

weak (AK2-296). There are no vertical roughnesses, nor anterior groove nor median fold on the ectolophid. The external groove is developed but smooth. The paralophid is double. It determines a small and wide closed pit in front of the tooth. Only the reduced cingula exist on the anterior and posterior faces. The posterior valley

is widely open, as is the trigonid valley. There is no lingual groove on the entoconid. The crown is moderately high.

Postcranial skeleton

The bones from Akkaşdağı are large and robust, with thick long bones and broad and low manus and pes. The dimensions and proportions correspond essentially to those of the large/largest individuals of *Ceratotherium simum* as listed by Guérin (1980, 2000); they even sometimes reach the average of *Rhinoceros unicornis* (Guérin 1980). On the other hand, they are 5 to 30% smaller than corresponding remains referred to the Miocene African rhinocerotine *Diceros australis* Guérin, 2000.

Atlas. AK5-w.n. is badly preserved, lacking the *processi transversi*. The bone is thick and the articular width fits the skull AK4-212, which leads us to assign it tentatively to the same individual. The *foramen vertebrale* has a wide piriform outline. The *foramen transversarium* is large, only connected with the *foramen vertebrale*. The condylar facets are kidney-shaped, while the axis-facets are slightly concave transversally.

Cervical and thoracic vertebrae. They bear no significant character.

Humerus (Appendix: Table 3; Fig. 3A). This bone is robust. The length is approximately 440 mm, owing to the proximal end AK6-30 and the distal end AK4-w.n. The proximal end is thick and deep (APD), with a high and strong *tuberculum majus*. The *caput humeri* is wide, weakly rounded. The *tuberculum minus* is low. Both are separate by a shallow depression. The deltoid tuberosity is wide and high, thickly developed, with a strong and extended insertion for the *m. deltoideus*. The diaphysis is narrowing below the deltoid tuberosity. The lateral epicondyle is again wide, but rather low, forming a right angle at its proximal end in anterior view. The trochlea is huge, especially the medial lip. The latter is much more developed (APD) than the lateral one. The median narrowing is strong. The *fossa olecrani* is wide and low. There is no synovial fossette on the antero-proximal part of the trochlea. A shallow distal gutter separates the

lateral epicondyle from the trochlea. The lateral epicondyle is the lowest tip of the humerus.

Radius (Fig. 3B). The bone is strong, with thick ends. The proximal cochlea is higher in its posterior border. The proximal end is wide and deep (APD), much deeper medially. The anterior border is straight in proximal view. The posterior facets, for the ulna, are separate. The medial one is low (10 mm) while the lateral one is very high and hugely developed (triangular). The insertion for the *m. biceps brachii* is wide and marked by roughnesses, but there is no deep depression. The diaphysis is straight medially and strongly concave laterally. The contact between the radius and the ulna extends all along the diaphysis, except for a short *spatium interosseum*, located at the proximal third of the bone. These observations indicate a twisted diaphysis for the ulna. In lateral view, the diaphysis is curved, with a convex anterior border. The distal widening is strong (Appendix: Table 4). No radius-ulna fusion has been observed in Akkaşdağı. The gutter for the *m. extensor carpi* is deep and wide, deepened by the latero-distal tubercle (*tuberculum dorsale*) laying close to it. The lateral ulna-facet is unique, crescentiform and low. It is vertical and sagittally orientated. The distal articulation is only for the scaphoid and semilunate. The distal end is getting lower medially than laterally. The scaphoid-facet is visible in anterior view on a considerable height. This facet has a sigmoid sagittal cross section. Its posterior expansion forms a high rounded triangle. The semilunate-facet is wide, concave antero-posteriorly and flat transversally. There is no pyramidal-facet.

Ulna (Fig. 3C, D). There is an unexpected number of preserved ulnae (10 more or less complete specimens). They are as long as the femora, with a variable length (Appendix: Tables 5; 12). The olecranon is thick, and developed with variable shapes. It is always long, forming a closed angle with the diaphysis. The posterior tip of the olecranon (insertion of the *m. triceps brachii*) is salient with respect to the distal border of the process. The humeral cochlea is wide, as high medially as laterally. The median constriction is particularly marked. Distally to this articular

surface, there is a broad oval area which is not articulated with the humerus. It forms a shallow depression on the whole sample. The radius-facets are separate: the medial facet is vertical and transversally elongated, determining a low stripe, while the lateral facet is higher than wide. The medial facet is transversally convex, with a transverse lateral end and a sagittal medial end. The fossa between both facets is deep. The roughness corresponding to the contact with the radius runs all along the diaphysis, except for a short *spatium interosseum*, at the proximal third of the diaphysis. The diaphysis is curved and twisted. Its cross section is triangular, with sharp ridges. The distal end widens strongly. The distal radius-facet is low and crescentiform. The distal articulation, for the carpus, shows three facets. The smallest and medial one is for the semilunate (almond-shaped); the rest of the surface corresponds to the pyramidal-facet (quarter circle) and the pisiform-facet. The latter is large but restricted to the postero-lateral side of the articulation. It is triangular and nearly vertical. Both are separated by a smooth ridge. There is no distal tubercle (*tuberculum dorsale*) on the antero-lateral side of the ulna. All these features are also shared by the juvenile ulnae (e.g., AK6-131).

Scaphoid. Two specimens are complete. They are cubic (Appendix: Table 6). The anterior and posterior heights are equal. The proximal facet is deep (ADP) and concave in medial view. There are only two facets for the semilunate. The proximal one is flat and wide. There is a large and rounded tubercle in the vicinity of the latter. On the distal side, the magnum-facet forms an equilateral triangle. Its surface is concave antero-posteriorly and slightly convex transversally. The trapezoid-facet is wide (TD) and saddle-shaped. The trapezium-facet is triangular, narrow (APD) and very high (Appendix: Table 6).

No semilunate, trapezium, trapezoid nor pisiform have been discovered in Akkaşdağı.

Pyramidal. The specimen AK5-631 is badly preserved and broken. It is low and wide. The proportions and structures correspond to those of *Ceratotherium neumayri* from other Turolian localities of Turkey (Saraç 1994). The proximal

facet, for ulna, is small. So is the pisiform-facet. There is a strong tubercle on the lateral side. The medial facets for the semilunate are not preserved. On the distal side, the unciform-facet is flat transversally and concave antero-posteriorly.

Magnum (Fig. 3E). The posterior tuberosity is lacking in the three specimens (GOK-11, AK5-632, AK7-38). The anterior side is broad and low (Appendix: Table 7), with a salient central tubercle (*m. interossei dorsales*). Its lateral border is oblique and straight. In proximal view, the scaphoid-facet is wide and transversally concave. The semilunate-facet has a question mark outline in lateral view. The proximal process is high, with a small diameter, and rounded. This facet reaches the anterior side of the bone. It is difficult to distinguish it from the unciform-facet, which is drop-shaped. On the medial side, there is a shallow anterior indentation between the scaphoid and the McII-facets. The latter forms a flat sagittal stripe, horizontal and nearly rectangular. Distally, the McIII-facet is wide and saddle-shaped, tapering backwards.

Unciform. The unciform is well represented (eight specimens). It is a large bone, with a broad anterior side and a long posterior tuberosity (low and wide). The anterior side is smooth, nearly flat, except on the medial corner where a sharp horizontal tubercle is salient (insertion of the *m. interosseus dorsalis*). The proximal facets are separate by an acute ridge. The semilunate-facet determines a quarter-circle. It may be transversally flat (AK7-147, AK4-74) or concave (GOK-10, AK6-58, AKK-157). The pyramidal-facet is larger, flat transversally and regularly convex sagittally. There is a wide and short postero-lateral expansion to this facet, which generally connects it to the McV-facet (except on AK7-147). The distal facets (magnum, McIII, McIV) are not distinct, except the most lateral one, for the McV. In anterior view, the latero-distal border of the bone is straight (McV-facet) while the rest of the distal border is rounded. This McV-facet forms an angle about 60° with the horizontal line. This orientation points out a tridactyl manus. AK5-633 and GOK-10 are about 25% larger than other specimens (Appendix: Table 8).

McII (Fig. 4A, B). The McII is wide on all its length (Appendix: Table 9). The proximal facet, for the trapezoid, is pentagonal and saddle-shaped, transversally concave and sagittally convex. There is no trapezium-facet. The proximo-lateral facet (magnum) forms a sagittal stripe which widens backwards, at 45° from the horizontal line. There is only one McIII-facet, the anterior one, which is triangular, vertical and sagittally elongated. This facet is slightly concave. A large tubercle widens the proximal end on the medial side. The diaphysis is wide and deep, slightly flattened sagittally. It is nearly straight, only a little bit curved inwards. The insertion for the *m. interossei* is short. There is no distal widening. The distal trochlea is roughly square in distal view. Its anterior border is straight, as the lateral border (at right angle). The intermediate relief is low but sharp and restricted to the posterior side. The medial lip is wider than the lateral one. The latter is transversally flat, while the former is deeply concave. The medial part is deeper (APD) than the lateral lip.

McIII (Fig. 4A, B). The McIII is a wide bone, slightly widened distally. The proximal end is wide, due to the strong lateral development of the unciform-facet. The magnum-facet is visible in anterior view. It is regularly concave transversally and separate from the unciform-facet by a sharp ridge (80° angle). The latter is wide (TD), slightly convex sagittally and triangular. The McII-facet has large dimensions. It is semi-circular and nearly vertical. The surface for the *m. interossei* is restricted to the proximal quarter of the diaphysis on the medial side, and it extends down to the distal third on the lateral side. The McIV-facets are large, well developed and fused on AK5-68 (close in AK3-202). The anterior one is drop-shaped and the posterior one is circular and vertical. It is distally displaced with respect to the proximal end of the bone. The diaphysis is straight and flattened. On the anterior side, the insertion for the *m. extensor carpalis* is broad but without relief. There is no distal tubercle on the posterior side of the diaphysis. The distal trochlea has an antero-proximal border regularly rounded. In distal view, this surface is wider than deep

(Appendix: Table 10). It is deeper medially. The anterior border is slightly convex while the medial and lateral ones are straight. The intermediate relief is sharp and high, visible in anterior view. It separates the trochlea into two equal halves.

McIV (Fig. 4A, B). The McIV is shorter than the McII and McIII (Appendix: Table 11). The bone is wide, without median narrowing. The proximal side, exclusively devoted to the unciform, forms a rectangle triangle. On the medial side, the McIII-facets are separate by a few millimetres. The anterior one is drop-shaped, while the posterior one is circular (45° angle between them). The diaphysis is curved laterally, at the half of the bone. The *m. interosseus* area reaches the half of the diaphysis. It is very salient, determining a large pad. The diaphysis is a little flattened. The distal trochlea is nearly square in distal view. The intermediate relief is low but sharp and restricted to the posterior side of the trochlea. This relief is displaced medially, so that the lateral lip is wider than the medial one. The latter is transversally flat whilst the former is concave.

Femur. AK4-253 is the only femur almost complete. The only part lacking is the *trochanter major*. Other specimens are distal ends, except for AK5-323, which is a *caput femoris* from a juvenile individual. The femur is rather slender. The head is wide and hemispheric. The surface of epiphysis is marked by a sharp transversal ridge (nor flat, nor crescentiform). The third trochanter is developed but not so much. It is high (Appendix: Table 12) and only forming a wide stripe. The *trochanter minor* determines a thin and narrow ridge, almond-shaped in anterior view. The proximal border of the wide patellar condyle is curved, in anterior view. The distal end is thickly developed, with well separate condyles for the tibia.

Patella. The only specimen is as high as wide (Appendix: Table 13). It is thick, with rounded structures. The APD is high. On the articular side, the medial lip is large and broad. The lateral one is narrower and transversally concave, as is the former. The proximal process (for the tendon *m. quadriceps*) is strongly developed but not very

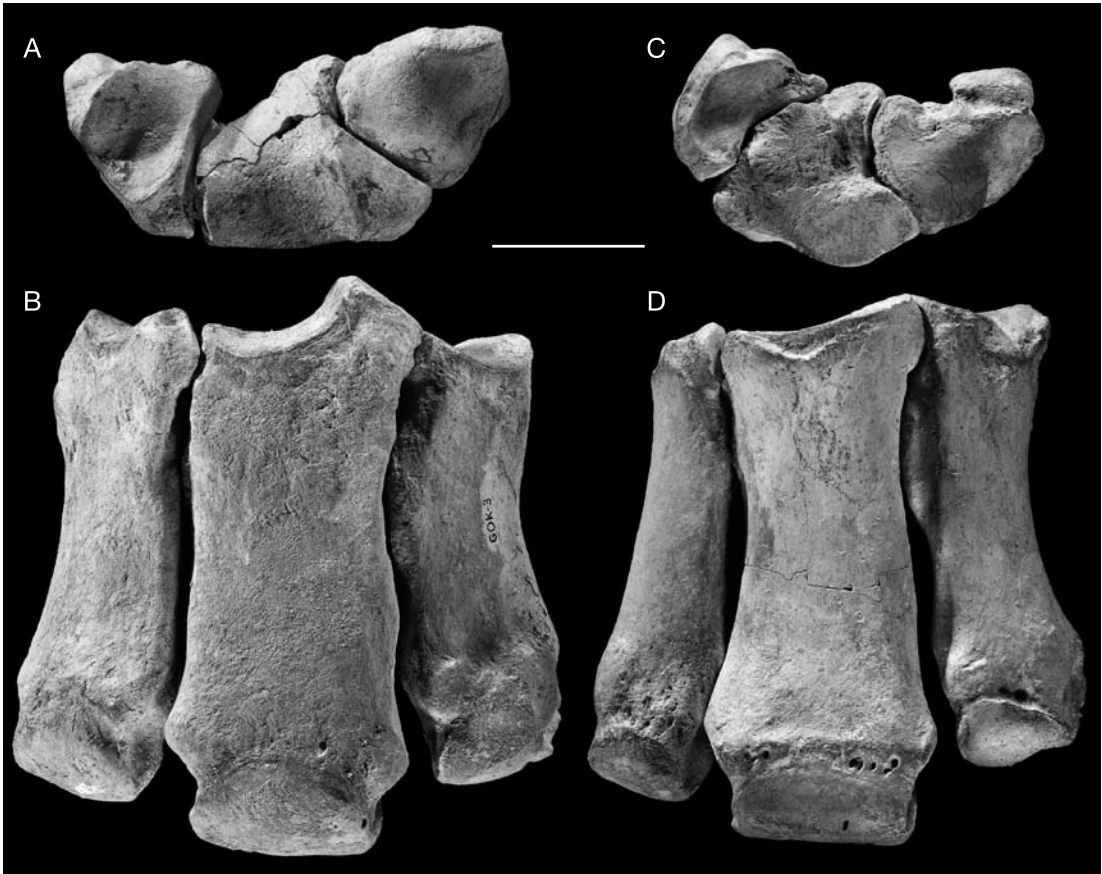


FIG. 4. — *Ceratotherium neumayri* (Osborn, 1900), Akkaşdağı (Anatolia, Turkey), middle Turolian; **A, B**, left metacarpus (GOK-2 to GOK-4); **A**, proximal view; **B**, anterior view; **C, D**, left metatarsus (GOK-7 to GOK-9); **C**, proximal view; **D**, anterior view. Scale bar: 5 cm.

salient. The latero-proximal border of the articular surface is straight.

Tibia. The tibia is robust, with broad ends (Appendix: Table 14). AK7-40 corresponds to fused tibia and fibula. The contact probably occurs at early growth stages, because all the specimens bear traces of the contact between both bones. The fusion may occur later, at adult stage (Fig. 3F). The proximal condyles are well separated by a deep intercondylar fossa. The medial condyle is sagittally flat and transversally concave – horizontal in its medial part and nearly vertical in its lateral tip. The lateral condyle for the femur is convex antero-posteriorly and slightly concave transversally. The latter is smaller (TD, APD),

but equally high. It is oblique (45° with respect to the horizontal line). The *tuberositas tibiae* is very developed, with a broad and rough surface. In posterior view, the fibula is totally fused proximally with the tibia. Its proximal end is high but it does not bear any articular facet for the femur. The diaphysis is narrowing in its median part, with a triangular cross section. The *spatium interosseum* is the only area where the tibia and the fibula are not fused. It is restricted to the second proximal quarter of the bone. The tibia thickens strongly in its distal part (TD, APD). The antero-distal groove is wide and rather deep, running obliquely to the medial lip of the astragalus cochlea. The *sulcus malleolaris* is much deeper

and narrower. It occurs at the posterior third of the bone, in medial view. The posterior apophysis is rounded and low, very broad. The medial lip of the astragalus cochlea is deeper (APD), more concave (transversally and sagittally) and narrower (transversally) than the lateral one. The latter is almost flat transversally.

Fibula (Fig. 3F). The only specimens are the fused tibia/fibula (AK7-40) and a distal epiphysis from a young individual (AK13-3). The proximal end is merely crushed. The thin diaphysis, with sharp ridges, thickens distally. The TD is twice lesser than the APD (Appendix: Table 15), so it keeps a slender shape in front view. Latero-distally, the *sulcus malleolaris* is deep, with sharp ridges, especially on the adult fibula. It is located in the posterior third of the bone. The astragalus-facet is flat, low, and nearly vertical.

Astragalus (Fig. 2E-G). The astragalus is well represented (11 specimens). It is a large, wide and deep bone (TD/H ratio = 1.16; APD/H ratio = 0.70; Appendix: Table 16). On the lateral side, the fibula-facet is flat and nearly vertical. It forms a narrow stripe, tapering in its proximal quarter. The trochlea is high, with acute borders. The medial lip is shorter and more convex transversally than the lateral one. On the medial side, the articular surface corresponding to the *malleolus medialis* is narrow and it tapers regularly proximally. The caudal border of the trochlea is nearly straight in proximal view. The *collum tali* is high on adult specimens and even higher on juvenile specimens (AK2-438, AK6-56, AK5-319). The medial tubercle is very high, nearly reaching the mid-height of the bone, both in juveniles and adults. It is slightly salient from the trochlea, with a vertical medial border in anterior view. The posterior side shows three facets for the calcaneus, as usual. The facet 1 is strongly concave, with a distal horizontal ridge determining a wide latero-distal expansion. The latter forms a right angle with respect to the rest of the facet, both in juveniles and adults. The facet 2 is high, narrow, and oval-shaped. Its surface is strongly convex transversally. The facet 3 is always separate from the facet 2. The former is wide and low, almond-shaped. In distal view, the trochlea is very oblique

with respect to the axis of the distal articulation. This articulation (navicular and cuboid) is well developed. The navicular-facet is lozengic, while the cuboid-facet is wide and short (oval), with a smooth posterior break.

Calcaneus (Fig. 3G, H). The specimens are robust, with a massive *tuber calcanei*. The fibula-facet is lacking, while the tibia-facet is hugely developed and drop-shaped. The astragalus-facet 1 is question mark-shaped in lateral view. The facet 2 is oval, higher than wide and transversally concave. It is separate from the facet 3, which is smaller and almond-shaped. The *sustentaculum tali* is thick, but not wide (TD) when compared to the general dimensions of the bone (Appendix: Table 17). The proximal tip of the *tuber calcanei* is deeper (APD) than the *processus* in lateral view, but it is still massive. The cuboid-facet, on the distal side, is saddle-shaped and very wide. The insertion for the *m. fibularis longus* forms a smooth tubercle, without any sharp ridge.

Navicular (Fig. 3I, J). Two specimens are preserved (Appendix: Table 18). They have a lozengic but subrectangular proximal outline; so is the outline of the proximal facet. The lateral facets are roughly separated. The proximal one runs all along the proximal border, while the distal one (hemicircular) is restricted to the posterior half of the bone. The distal side bears three facets for the cuneiforms. The ectocuneiform-facet is L-shaped and separated from the drop-shaped mesocuneiform-facet by a shallow groove. The entocuneiform-facet is smaller, semi-circular and oblique, whilst the ectocuneiform- and mesocuneiform-facets are horizontal.

Cuboid. The only specimen (AK5-636; Appendix: Table 19) lacks the distal part of the anterior side. The proximal articulation is oval and bears two facets. The medial one (astragalus) is oblique and flat transversally while the lateral one (calcaneus) is saddle-shaped: concave sagittally and convex transversally. They are separated by an acute sagittal ridge. On the medial side, the posterior facets are not equally developed: the proximal one is larger and much higher. The preserved part of the MtIV-facet, on the distal side, is flat and not elongated posteriorly. The

posterior tuberosity is very high, vertical and not broad (TD) nor deep (APD).

Entocuneiform (Fig. 3K). The only specimen (AK13-5) is large (Appendix: Table 20), with a laterally projected distal tuberosity. The proximal facet, for the navicular, is almond-shaped and biconcave. The ectocuneiform-facet is low and crescentiform, while the MtII-facet is nearly circular and flat. The distal border is horizontal, except for the developed latero-distal tuberosity, which is particularly salient. The posterior side is smooth, lacking any relief.

Mesocuneiform. It is semi-circular in proximal view. The proximal facet is flat transversally and concave sagittally. The anteromedial side is smooth. The entocuneiform-facet is semi-circular. The ectocuneiform-facet is long (APD) and low (Appendix: Table 21). The distal facet is flat sagittally and convex transversally, with a semi-circular outline.

Ectocuneiform. The bone is low and wide (Appendix: Table 22). The navicular-facet occupies the whole proximal side. A broad tubercle for the *m. interossei dorsales* runs all along the anterior side. In anterior view, this side has a concave proximal border and a convex distal one. On the medial side, three facets are preserved: the antero-proximal one (for the mesocuneiform) is drop-shaped, with a higher posterior tip; the antero-distal facet (for the MtII) forms a distally truncated circle; the postero-distal facet is badly preserved. On the distal side, the MtIII-facet is convex transversally and flat sagittally.

MtII (Fig. 4C, D). The proximal end is triangular, in proximal view. The antero-medial side is lacking any proximal tubercle. The proximal facet, for the mesocuneiform, is kidney-shaped. On the posterior side, the entocuneiform-facet is high and it forms a proximally truncated oval (AK5-440), in contact with the proximal facet. On the lateral side, there are two facets. Both are high, separate from the proximal facet in AK5-440. The anterior facet is oval and vertical. The posterior facet is rectangular and split into two equal halves. It is higher than the former and the sub-facets are rather distinct, owing to a horizontal ridge. The distal sub-facet corresponds to the MtIII.

The insertion for the *m. interossei dorsalis* reaches the distal half of the diaphysis. The diaphysis is nearly straight, with a circular cross section. The distal widening is slight but present. The distal trochlea is deeper than wide (Appendix: Table 23), with parallel medial and lateral borders. In distal view, the anterior border is rounded, while the posterior one is sigmoid: the intermediate relief is low and smooth, displaced into the lateral half of the trochlea. The medial lip is concave, with a lateral deepening, whilst the lateral one is flat transversally, tapering laterally.

MtIII (Fig. 4C, D). Two complete adult specimens have been unearthed (GOK-7, AK2-163; Appendix: Table 24). Another one, lacking the distal epiphysis, belongs to a juvenile individual (AKA-44). They have comparable structures and proportions: they are rather slender, with straight diaphyses. The distal widening is very slight, except for AKA-44, where it is stronger. In proximal view, the proximal end is trapezium-shaped, with a straight medial border, a nearly straight lateral border, and a convex anterior border forming an open dihedron. There is no cuboid-facet. In anterior view, the proximal border is concave, higher laterally. The MtII-facets are high, semi-circular, the anterior one being lower. On the lateral side, the MtIV-facets are close to each other, only separate by a few millimetres. The anterior one is vertical, while the posterior one is visible in proximal view. Both are circular and equally developed. The insertion for the *m. interossei* is shorter for the MtII (proximal third) than for the MtIV (half of the diaphysis). There is no posterior tubercle on the posterior side of the diaphysis. The distal trochlea is deep (APD) and rather narrow (TD). It is much deeper medially. The intermediate relief is low and smooth, but it is visible in anterior view. This relief determines two equally developed halves.

MtIV (Fig. 4C, D). There is a complete specimen (GOK-8, from the left metatarsus) and a proximal end (AK5-437). It is more robust than that of the MtII (Appendix: Table 25). The proximal outline is triangular, much wider than deep. The proximal facet, for the cuboid, is trapezoid, slightly concave transversally and sigmoid

sagittally. The postero-lateral tuberosity is hugely developed and continuous, pad-shaped. It is partly destroyed on GOK-8. On the anterior side, the insertion for the *m. fibularis* is thick and salient. Between the cuboid-facet and the medial facets, runs a narrow oblique sagittal stripe, for the ectocuneiform. A few millimetres separate the MtIII-facets, which are circular and equally developed. The diaphysis is strongly curved and distally widened. It has a semi-circular cross section and a thick antero-distal tubercle. The distal articulation is trapezoid in distal view, and it has a smooth and low intermediate relief; the medial lip is flat, while the lateral lip is concave transversely. The insertion for the *m. interossei* forms a salient pad, which thickness almost reaches 1 cm.

No phalanx has been attributed to *C. neumayri*.

DISCUSSION

Ceratotherium neumayri is very widespread in the late Miocene of Greece, Turkey, and Iran (Geraads 1988; Geraads & Koufos 1990; Saraç 1994; Heissig 1996). The most abundant rhinocerotid taxon in Akkaşdağı bears cranial, dental, and postcranial features that are characteristic for *C. neumayri*: dolichocephalic two-horned skull, with a very broad and rounded nasal tip, a nearly flat dorsal profile, a forked occipital crest, a strongly inclined occipital side, long and edentulous premaxillae, forwards bent *processus postglenoidalis*, laterally projected orbits, short temporal crests, teeth rows restricted to the anterior half of the skull; no anterior constriction on the protocone nor antecrochet on the upper teeth, backwards bent protoloph, molariform upper premolars, D1 lacking a metaloph, upper milk teeth with a crista; frequent absence of a trapezium-facet on the McII, early fusion of tibia and fibula, high and narrow medial tubercle on the astragalus, low and transversally convex calcaneus-facet 2 on the astragalus, low ectocuneiform, large articular facets between second and third metapodials, low and acute intermediate relieves on central metapodials; as a preliminary result of a cladistic analysis in process (Antoine unpubl. data), these features are provisionally

assumed as diagnostic (autapomorphies) for *C. neumayri*.

According to age estimation of recent white rhinos (*C. simum*) by Hillman-Smith *et al.* (1986), the juvenile maxillae belong to individuals aged less than 1.5 year, meanwhile the adult skull corresponds to a 10-15 years old individual.

The dimensions of the remains found at Akkaşdağı and identified as *C. neumayri* are very large (Appendix: Tables 1-25). The cranial and dental remains are equal in size and proportion to the average of *C. simum*, while the postcranials fit with the large individuals of the latter taxon (Guérin 1980). Some bones are even larger (scaphoid, McII, patella, astragalus, cuneiforms, MtII), reaching the average size observed in *Rhinoceros unicornis* (Guérin 1980). In addition, several specimens of *C. neumayri* from Akkaşdağı exceed in size the conspecific remains from other late Miocene Eastern Mediterranean localities, such as Samos, Maragha, Pikermi, Pentalophos-1, or Kemiklitepe (Guérin 1980, 2000; Geraads 1988, 1994; Geraads & Koufos 1990; direct observation by P.-O. A.), being up to 10% larger than the largest specimens ever described for this species (radius, McII, astragalus, MtII; Guérin 2000). According to Heissig (1975b) and Kaya (1994), the size of *C. neumayri* increases from the late Vallesian to the late Turolian in Turkey and Greece. The same tendency might exist between Kemiklitepe D (MN 11) and Kemiklitepe A+B (MN 12), but the material is scant (Bonis *et al.* 1994; Geraads 1994). Even though latest Miocene (MN 12-13) localities bearing *C. neumayri* are too scarce to make a consistent comparison, there seems to be no contradiction between the large size of *C. neumayri* and the late middle Turolian age of Akkaşdağı (MN 12), as argued owing to the associated fauna and radiometric ages (Karadenizli *et al.* 2005).

Genus *Stephanorhinus* Kretzoi, 1942

TYPE SPECIES. — *Stephanorhinus etruscus* (Falconer, 1859) by original designation.

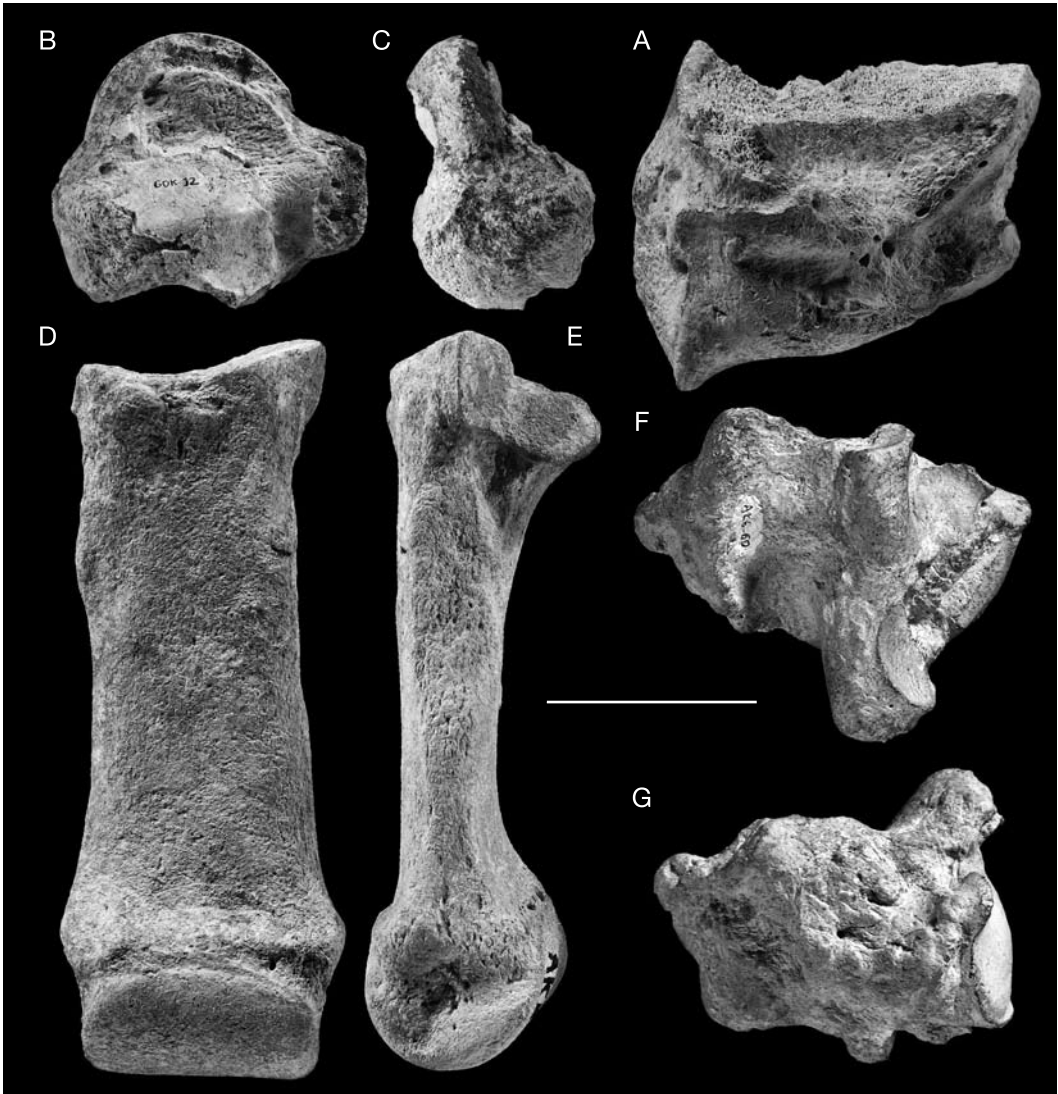


FIG. 5. — **A-E**, *Stephanorhinus pikermiensis* (Toula, 1906), Akkaşdağı (Anatolia, Turkey), middle Turolian; **A**, distal end of a right radius (GOK-14), posterior view, displaying the diagnostic horizontal ridge; **B**, **C**, right magnum, lacking the posterior tuberosity (GOK-12); **B**, medial view; **C**, anterior view; **D**, **E**, left MtIII (AKA-45); **D**, anterior view; **E**, lateral view. Notice the fusion of the MtIV-facets, visible in **E**; **F**, **G**, *Chilotherium* sp., Akkaşdağı (Anatolia, Turkey), middle Turolian, left calcaneus (AK6-60); **F**, antero-medial view; **G**, posterior view. The Y-shaped vascular print is noticeable in **G**. Scale bar: 5 cm.

Stephanorhinus pikermiensis (Toula, 1906)

Rhinoceros schleiermacheri pikermiensis Toula, 1906: 34, pl. 2, fig. 2.

Rhinoceros schleiermacheri samius Toula, 1906: pl. 2, fig. 3.

Rhinoceros (Ceratorhinus) schleiermacheri var. *orientalis* Schlosser, 1921: pl. 1, fig. 8.

Stephanorhinus pikermiensis – Heissig 1996: 341-343, 347, text-fig. 27.2.

MATERIAL. — Left worn M1, AK5-w.n.; distal end of a right radius, GOK-14; right broken and eroded magnum, GOK-12; medial part of a left astragalus, AK6-57; left mesocuneiform, AK5-197; left MtII and MtIII from the same individual, AKA-45; (?) distal end of a left MtII (distal APD = 37), AK5-2; left MtIII, AK3-65.

DESCRIPTION AND COMPARISON

The remains belong to at least two individuals (e.g., two left MtIII are preserved).

Dentition

The M1 AK5-w.n. is much worn, so most of the morphological features have disappeared. The enamel is thin and wrinkled at the neck. The roots are joined, but not as thickly as it could be expected from an old individual. There is neither labial nor lingual cingulum. The crochet is simple. The lingual cusps are separate. There is neither anterior constriction isolating the protocone, nor antecrochet. No crista is preserved at this stage of wear. The hypocone is devoid of any groove. This tooth (L = 49; ant. W = 74; post. W = 65; H = 13) is very wide with respect to the M1 of the skull AK4-212 attributed to *C. neumayri* (see above; Appendix: Table 2). Indeed, these dimensions and structures are similar to the M1 from the skull NHM M 10144 (*S. piker-miensis*, Pikermi; Geraads 1988: pl. 2, fig. C).

Radius

Only a distal end is preserved (GOK-14; Appendix: Table 26; Fig. 5A). It is large, with an oblique distal border in anterior view (getting lower medially than laterally). The *tuberculum dorsale* is very reduced and smooth. Thus, the anterior side is flat transversely. The single lateral ulna-facet is crescent-like, vertical and oblique sagittally. The posterior side is keeled and deepened by a wide fossa beginning 3 cm above the distal articulation. The scaphoid-facet is visible in anterior view on a considerable height. This facet has a sigmoid sagittal cross section. Its posterior expansion forms a high rounded triangle. The semilunate-facet is wide, concave antero-posteriorly and slightly convex transversally. There is no pyramidal-facet.

Magnum

The posterior tuberosity is lacking in the only specimen (GOK-12; Appendix: Table 27; Fig. 5B, C), which is badly damaged. The anterior side is roughly square, without a salient central tubercle (contrary to GOK-11, referred to

C. neumayri). In proximal view, the scaphoid-facet is narrow. The semilunate-facet has a semi-circular outline in lateral view: there is no anterior inflection as in *C. neumayri*. The proximal process is very large, with a huge diameter, and rounded. This facet reaches the anterior side of the bone. It is separate from the unciform-facet by a shallow groove. On the medial side, there is a shallow anterior indentation between the scaphoid- and the McII-facets. The former forms a flat and oblique sagittal stripe, nearly rectangular. Distally, the McIII-facet is wide and saddle-shaped, without posterior tapering.

Astragalus

The only specimen is a broken astragalus, lacking the lateral part (AK6-57). The proportions are similar to those from *C. neumayri* (see above; Appendix: Tables 17; 28). The size is comparable (H, APD, TD) but some features differ anyway. The medial lip of the trochlea is identical to that of *C. neumayri*, except in the facet for the *malleolus medialis*: this articular stripe for the tibia is much wider in AK6-57. It forms a broad stripe, with a brutal thinning in its proximal third. The lip is also smoother (sharp ridge in *C. neumayri*). The *collum tali* is lower than in *C. neumayri*, especially medially, where the trochlea nearly reaches the proximal tip of the navicular-facet. The medial tubercle is very different in the two taxa: it is more laterally projected, forming a sharp and salient tubercle in AK6-57 (thin, with a vertical medial border in *C. neumayri*); the most striking difference concerns the height of this tubercle. It does not reach the distal third of the bone in AK6-57, while it reaches the half of it in *C. neumayri*. On the posterior side, some differences appear. The calcaneus-facet 2 is large and circular, nearly flat, whilst it is high, oval and transversally strongly convex in *C. neumayri*. Furthermore, this facet joins the facet 3, contrary to *C. neumayri*, where both are separate – the astragalus-facets 2 and 3 are also separate on the calcanei attributed to *C. neumayri* (see above). On the distal side, the navicular-facet has the same outline, but its posterior tip is marked by a high and brutal break (AK6-57), visible in

anterior view. This facet is concave transversally whereas it is nearly flat in *C. neumayri*. The cuboid-facet is broad, short, and it tapers posteriorly in AK6-57. The distal articulation is narrower (TD) in AK6-57 than in *C. neumayri*. Further comparison with 30 astragali attributed to *C. neumayri*, three specimens identified as *D. orientalis* (Schlosser, 1921) by Saraç (1994) from several Turolian localities of Turkey (MTA collections), and the material from Pikermi (Gaudry Collection, MNHN), confirms the consistency of these differences. Furthermore, the astragalus of "*D. orientalis*" from the Turolian of Shanxi (Ringström 1924: 15, text-fig. 10) is identical to AK6-57, at least in anterior view (dimensions, proportions, structures).

Mesocuneiform

AK5-197 has the same size as AK5-637, attributed to *C. neumayri* (Appendix: Tables 21; 29). The main differences consist of the triangular proximal outline (semi-circular in AK5-637), the presence of a tubercle on the antero-medial side (smooth in AK5-637), the low and drop-like entocuneiform-facet (semi-circular in AK5-637), and the high and short ectocuneiform-facet (low and long in AK5-637).

MtII

Although bearing similar dimensions with the MtII referred to *C. neumayri* (Appendix: Tables 23; 30), the specimens (AKA-45, AK5-2) somehow differ from the latter: the entocuneiform-facet is lower and circular; the postero-lateral facet joins the proximal facet; both anterior and posterior lateral facets are split into two equal parts by a median horizontal groove; the posterior facet is higher and the sub-facets are more distinct. Both distal halves (anterior and posterior) correspond to the MtIII, thus pointing out the presence of high MtII-facets on the MtIII.

MtIII (Fig. 5D, E)

AK3-65 and AKA-45 display similar proportions with the MtIII referred to *C. neumayri* (Appendix: Tables 24; 31). Some morphological differences can anyway be observed: in proximal

view, the anterior border of the proximal articulation is depressed while the lateral border is strongly concave; the proximal end is as deep (APD) as wide (TD); the MtII-facets are high and nearly joined; the MtIV-facets are fused; the distal trochlea is strongly thickening medially; the intermediate relief is high and acute; there is no distal widening of the diaphysis.

DISCUSSION

Toula (1906) established *Rhinoceros schleiermacheri pikermiensis* on the basis of some specimens from Pikermi. Later, *Rhinoceros (Ceratorhinus) schleiermacheri* var. *orientalis* was described on similar remains discovered in Veles, Pikermi and Samos (Schlosser 1921). We agree with Geraads (1988), assuming that these fossils are conspecific, especially those from Pikermi, the type locality of *Rhinoceros schleiermacheri pikermiensis*. Thus, and following the current *International Code of Zoological Nomenclature* (ICZN 1999), the principle of priority states that the valid name is *R. pikermiensis* Toula, 1906.

On the other hand, we do follow the opinion of Heissig (1996) and Fortelius *et al.* (2003) concerning its assignment to the genus *Stephanorhinus* Kretzoi, 1942, under the name *Stephanorhinus pikermiensis* (Toula, 1906), rather than to the genus *Dicerorhinus* Gloger, 1841. The type species of *Dicerorhinus* and *Stephanorhinus* Kretzoi, 1942 are *D. sumatrensis* (Fischer, 1814) and *S. etruscus* (Falconer, 1859), respectively. As a preliminary result of an unpublished cladistic analysis including most one-horned and two-horned fossil and recent rhinocerotine species (*sensu* Antoine *et al.* 2003), at least six synapomorphies differentiate the clade [*S. etruscus*, *S. pikermiensis*] from *Dicerorhinus sumatrensis*: a small *processus paraoccipitalis*, a thick protocone on P2, a constricted metaloph on P2-4, a spur-like paralophid and a reduced paraconid on p2, and the presence of vertical roughnesses on the ectolophid of d2-3 support robustly the *Stephanorhinus* clade and prevent any generic assignment of *R. pikermiensis* Toula, 1906 to *Dicerorhinus*. However, the phylogenetic relationships of *Stephanorhinus pikermiensis* and

Ceratotherium neumayri would probably be resolved by a thorough study of the whole rhino material from Pikerimi (e.g., the Gaudry collections, MNHN).

Tribe ACERATHERIINI Dollo, 1885

Genus *Chilotherium* Ringström, 1924

TYPE SPECIES. — *Chilotherium anderssoni* Ringström, 1924.

Chilotherium sp.

MATERIAL. — Left calcaneus, AK6-60.

DESCRIPTION

Calcaneus

AK6-60 shares most of the characters with the two calcanei attributed to *Acerorhinus* sp. (AK6-130, AK7-98; see below), but it is thicker, shorter and smaller (Appendix: Tables 32; 35). AK6-60 bears a large and concave fibula-facet; the cuboid-facet is circular and saddle-shaped, with a postero-lateral salient tip. The presence of deep vascular prints on the postero-distal side of the *processus calcanei* further distinguishes this specimen from the other ones unearthed at Akkaşdağı (Fig. 5F, G).

DISCUSSION

All these features (size, proportions, thickness, fibula-facet and vascular prints) are common with the calcaneus 06-AKK-019 from Kavakdere (MN 12; Turkey), referred to *Ch. habereri* Ringström, 1924 by Saraç (1994: pl. 14, fig. 1). Both specimens belong probably to the same taxon. *Ch. habereri* is a small and robust *Chilotherium* species, with strongly shortened limbs and hypsodont teeth, originally described in the early Turolian of China (Ringström 1924; Heissig 1975a). Some Turkish remains, ranging from the late Vallesian up to the middle Turolian, were attributed to this species in the last decades (Kayadibi and Garkın faunal sets: Heissig 1975a, 1996; Kınık faunal set: Saraç

1994). Fortelius *et al.* (2003: 291) describe a single tooth and a juvenile mandible from Loc. 49 (Igbek, North Central Anatolia; c. 9.1 Ma), referring them to "*Chilotherium* cf. *C. habereri*" and assuming that this isolated tooth "probably represents the Anatolian form that Heissig (1975a, b, 1996) referred to *C. habereri*". On the other hand, Fortelius *et al.* (2003: 292) consider that younger remains "from the Upper Kavakdere Locs. 34 and 26" [c. 8.4-8.1 Ma, i.e. slightly earlier than Akkaşdağı] belong to an "indeterminate *Chilotherium*", rather than to *Ch. habereri* as previously assumed by Saraç (1994).

Specific features within *Chilotherium* are essentially based on cranial, mandibular, and dental comparison (e.g., Fortelius *et al.* 2003). As the available material from Akkaşdağı is restricted to a single calcaneus (AK6-60) and pending a revision of the whole genus, we provisionally identify it as *Chilotherium* sp., following the proposition of Fortelius *et al.* (2003).

Genus *Acerorhinus* Kretzoi, 1942

TYPE SPECIES. — *Acerorhinus zernowi* (Borissiak, 1914).

Acerorhinus sp.

MATERIAL. — Distal part of a left humerus, AKB-47; distal part of a left humerus, AK5-1; distal part of a right humerus, AK6-88; right radius, AK5-629; left calcaneus, AK7-98; right calcaneus, AK6-130; right MtII, AK5-678.

DESCRIPTION

Humerus

Three distal parts have been unearthed. The bones seem to be rather slender and long (Appendix: Table 33). The diaphysis is triangular in cross section, below the lacking deltoid tuberosity. The lateral epicondyle is high and wide, with sharp ridges. In anterior view, its lateral border forms a sharp dihedron (130°), with a proximal tubercle oriented upward. The trochlea is narrow, with a broad (TD) lateral lip. The medial one is regularly conical, except for its last

centimetre, where it further tapers. The median strangulation is not very marked. The trochlea is eggcup-like. The lateral lip is first conical, widening laterally, and then it tapers until its lateral tip. The frontier between these two parts is smooth. There is no synovial fossa on the trochlea. The *fossa olecrani* is wide and low. A distal gutter isolates the lateral epicondyle. In anterior view, the distal end is lower on the lateral side.

Radius

AK5-629 is complete. It is high and slender, thickening downward (Appendix: Table 34). In proximal view, the proximal articulation has a straight anterior border. This articulation is separate into two equally wide cochleae, the medial one being deeper (APD). The frontier between both cochleae is a smooth ridge, slightly higher posteriorly. The insertion for the *m. biceps brachii* is developed, but shallow, and medially displaced. The ulna-facets are vertical and widely separate. The medial one is low, crescent-like. The lateral one is higher, but still small. The diaphysis is twisted, with a convex medial border and a concave lateral border. The posterior side of the diaphysis shows a long trace corresponding to the contact with the ulna. It is essentially concentrated in the distal half of the bone, down from the *spatium interosseum*. This surface forms a rough triangle. The diaphysis widens distally, but it does not get deeper (APD). There is only one distal ulna-facet, almond-shaped. The gutter for the *m. extensor carpi* is shallow. There is no *tuberculum dorsale* laying on the anterior side. The distal end is lower on the medial side. The scaphoid-facet is just a little visible in anterior view. The distal articulation bears three facets. The scaphoid-facet is not deep (APD), but strongly furrowed. The median one, for the semilunate, is transversally flat and sagittally concave. The pyramidal-facet forms a long and straight oblique stripe.

Calcaneus

The bone is very thick and robust, with a very short *tuber* and *processus calcanei*. The dimensions are variable but the proportions are similar

(Appendix: Table 35). The *tuber calcanei* is triangular and massive. The insertion for the *m. fibularis longus* is salient. The *sustentaculum tali* is broad (TD > APD) and thick. The astragalus-facet 1 is flattened in its proximal part. A distal circular expansion is always present, separate from the main facet 1 by a shallow groove. There is no fibula-facet, but a large tibia-facet on both specimens (AK6-130; AK7-98). The astragalus-facets 2 and 3 are widely separate. The facet 2 is oval and concave. The facet 3 forms a narrow stripe. The distal facet (for the cuboid) is saddle-shaped, but the postero-lateral tip is broken on both specimens.

MtIII

AK5-w.n. is rather slender, with a slightly curved diaphysis and distal widening. The proximal end is hemicircular in proximal view. The mesocuneiform-facet occupies most of the surface. It is also hemicircular and nearly flat. The entocuneiform-facet is high and narrow, in contact with the mesocuneiform-facet. On the lateral side, the anterior facet is broken; the posterior one is circular and split into two equivalent sub-facets. The proximal subfacet corresponds to the ectocuneiform and the distal one to the MtIII. The insertion for the *m. interosseus* is very long. It nearly reaches the bottom of the diaphysis. An oblique groove runs on the antero-lateral side of the diaphysis. The distal trochlea is deeper than wide (APD > TD; Appendix: Table 36), wider posteriorly. The depth is equal medially and laterally. The intermediate relief is nearly absent but it determines a large medial lip and a narrow lateral lip. The former is slightly concave.

DISCUSSION

These postcranial specimens display characteristic traits of several late Miocene aceratheriine genera from Eurasia, i.e. *Alicornops* Ginsburg & Guérin, 1979, *Acerorhinus* Kretzoi, 1942, and *Chilotherium* (Antoine *et al.* 2003). Their representatives are convergent with Neogene teleoceratines in that they have acquired independently more or less shortened limbs ("hippo-like"; e.g., Heissig 1999; Antoine *et al.* 2003).

The relatively slender proportions of these seven postcranials – which are likely to document a single taxon – prevent any assignment to *Chilotherium*, the most “hippo-like” aceratheriine genus. In return, these proportions and dimensions (Appendix: Tables 33-36) recall those observed in *Acerorhinus* (Ringström 1924; Cerdeño 1996; Fortelius *et al.* 2003), and at a lesser degree *Alicornops* (Guérin 1980, 1988; Cerdeño 1997; Cerdeño & Sanchez 2000; Antoine *et al.* 2003). For instance, the humeri and the radius from Akkaşdağı are strongly similar to the specimens referred to *Acerorhinus zernowi* (Cerdeño 1996) but much larger than the largest ones identified as *Al. simorreense* and *Al. complanatum* (Appendix: Tables 33; 34; e.g., APDs). The calcanei are wider and more massive than any calcaneus assigned so far to *Alicornops* or to *Acerorhinus*, which is especially visible on the *tuber calcanei* (Appendix: Table 35). However, the closest affinities exist with *A. zernowi* (Cerdeño 1996) and “*Alicornops*” *alfambrense* Cerdeño & Alcalá, 1989, the generic assignment of which has already been challenged by Antoine *et al.* (2003), who tentatively referred it to *Acerorhinus*. In that respect, the characteristics of the MtII AK5-w.n. (morphology, proportions, and dimensions) are quite puzzling, in that they match perfectly those of *Alicornops simorreense* (Appendix: Table 36). The MtII is at the same time more robust than those of *A. zernowi* (middle Miocene; Cerdeño 1996) and much more slender than the McIV assigned to *Acerorhinus* sp. by Fortelius *et al.* (2003: 289, fig. 12.6; c. 8.1 Ma). The trend toward shorter metapodials is generalised – though probably independently acquired – within *Chilotherium* and *Acerorhinus* (Fortelius *et al.* 2003). Thus, and in the case of a linear trend, such morphology for the MtII would rather point to an intermediate age for Akkaşdağı.

However and pending new discoveries – notably associated cranial, mandibular and/or dental material in Akkaşdağı –, we propose to assign these postcranials to *Acerorhinus* sp. It should be added that Akkaşdağı counts among the latest occurrences of *Acerorhinus* (MN 7-MN 12;

Qiu & Qiu 1995; Cerdeño 1996; Deng 2000; Fortelius *et al.* 2003).

CONCLUSION

Among the four rhinocerotid species recognised in Akkaşdağı, *C. neumayri* is by far the most abundant (114 specimens, at least 11 individuals). Besides, these specimens are among the largest ones attributed so far to *C. neumayri*. The comparison with other Turolian rhinocerotid faunas from Eastern Mediterranean reveals a strong similarity between Akkaşdağı and Kavakdere (Anatolia, MN 12; Saraç 1994; Fortelius *et al.* 2003), with three out of four taxa in common (*C. neumayri*, *S. pikermiensis*, *Chilotherium* sp.). Furthermore, the large size of *C. neumayri* is consistent with the Ar/Ar dating for the Akkaşdağı tuff (7.1 ± 0.1 Ma; Karadenizli *et al.* 2005).

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APPENDIX

Abbreviations: **AK**, 2000-2001 excavations; **AKA** and **AKB**, 1997 excavation; **AKK**, surface collects; **ant.**, anterior; **APD**, antero-posterior diameter; **astrag.**, astragalus; **art.**, articulation; **Calc.**, calcaneus; **Cub.**, cuboid; **D**, distance (between two elements); **dia.**, diaphysis; **diag.**, diagonal length; **delt.**, deltoide; **dist.**, distal; **Ectocun.**, ectocuneiform; **Entocun.**, entocuneiform; **epiph.**, epiphysis; **ext.**, extremity; **fac.**, facet; **GOK**, Heintz-Ginsburg excavation (formerly Gökeşme); **H**, height; **j**, juvenile; **l**, left; **L**, length; **lat.**, lateral; **mag.**, magnum; **max.**, maximum; **med.**, medial; **mesocf.**, mesocuneiform; **mid.**, middle; **min.**, minimum; **Navic.**, navicular; **post.**, posterior; **prox.**, proximal; **Pyram.**, pyramidal; **r**, right; **Rad.**, radius; **sust.**, sustentaculum; **S.-L.**, semilunate; **TD**, transverse diameter; **Trap.**, trapezium; **Trapzd.**, trapezoid; **trochl.**, trochlea; **tuber.**, tuberosity; **Uncif.**, unciform; **W**, width (when different from TD); **w.n.**, without number. Values between brackets are doubtful.

TABLE 1. — *Ceratotherium neumayri* (Osborn, 1900), Akkaşdağı, middle Turolian of Central Anatolia, dimensions of the adult skull AK4-212 (in mm).

Length occipital crest/tip of nasals	755
Length occipital crest/tip of premaxilla	770
Length occipital crest/caudal end of M3	380
Length occipital condyle/front of orbit	390
Length occipital condyle/tip of premaxilla	690
Length of nasal notch	140
Maximum zygomatic width	345
Maximum frontal width	235
Occipital crest width	234
Occipital condyle width	130
Foramen magnum width	46
Palate width (at P2 level)	56
Palate width (at P4-M1 level)	80
Palate width (at M3 level)	67
Occipital face height	220
Length of P2-M3 (left/right)	294/292
Length of P2-P4 (left/right)	136/137
Length of P3-P4 (left/right)	105/104
Length of M1-M3 (left/right)	170/166

TABLE 2. — *Ceratotherium neumayri* (Osborn, 1900), Akkaşdağı, middle Turolian of Central Anatolia, dental measurements (in mm).

Specimen	L	ant. W	post. W	H
I P2	42	39	38	35
I P3	48	54	51	40
I P4	51	59	52.5	49
I M1	58	62.5	57.5	42
I M2	64	66	54	65
I M3	54	60	61.5 (l max.)	> 60
r P2 AK4-212	40	39	39	34
r P3	49	53.5	50	42
r P4	51	60	53.5	50
r M1	58	63	59	43
r M2	65	67	55	> 55
r M3	53	61	62.5 (l max.)	> 60
r M1 AK2-294	48	63	57.5	8
l p4 AK2-295	43	26	31	38
r D1 AK5-424	24.5	18	24.5	21
I D1	24	20	25	25
I D2 AK5-502	43.5	37	38.5	33
I D3	50	45	44	42
r D3 AK6-61	50	47.5	45	34
l d3 AK2-296	42	–	–	–
r d3 AK6-134	44.5	18.5	21.5	31

TABLE 3. — *Ceratotherium neumayri* (Osborn, 1900), Akkaşdağı, middle Turolian of Central Anatolia, dimensions of the humeri (in mm).

Number	prox. ext.		tuber. delt.	diaphysis		dist. ext.		APD trochl.	
	TD	APD	TD	TD min.	APD	TD	APD	med.	mid.
AK4-w.n.	–	–	(> 150)	79	77	(160)	139	120	(58)
AK6-301	197	158	160	73	72	–	–	–	–
AK-w.n.	–	–	(> 138)	77	–	168	–	105	53
AK4-183	–	–	–	57	56	–	–	–	–

TABLE 4. — *Ceratotherium neumayri* (Osborn, 1900), Akkaşdağı, middle Turolian of Central Anatolia, dimensions of the radii (in mm).

Number	L	prox. ext.		prox. art.			diaphysis		dist. ext.		dist. art.		
		TD	APD	TD	APD med.	APD mid.	APD lat.	TD	APD	TD	APD	TD	APD
GOK-18/19	> 405	133	88	125	73	50	(48)	75	50	127	84	112	53
GOK-16 (j)	—	—	—	—	—	—	—	—	—	108	75	89	49
GOK-17 (j)	—	—	—	—	—	—	—	—	—	107	(73)	91	49
AK4-w.n.	412	125	86	121	81	(54)	(48)	70	40	126	83	116	53
AK4-213	—	> 123	—	(> 119)	—	—	—	—	—	—	—	—	—
AK4-241	—	119	(74)	116	—	—	—	68	45	—	—	—	—
AK5-67	—	123	(71)	118	64	48	48	—	37	—	—	—	—
AK5-w.n.	380	120	79	116	76	50	45	65	39	114	70	99	52

TABLE 5. — *Ceratotherium neumayri* (Osborn, 1900), Akkaşdağı, middle Turolian of Central Anatolia, dimensions of the ulnae (in mm). Abbreviation: L*, L without olecranon.

Number	L	L*	olecranon		humerus cochlea				diaphysis		dist. ext.		Pyram. fac.	
			TD	H	TD max.	H med.	H mid.	H lat.	TD	APD	TD	APD	TD	APD
AK4-w.n.	—	—	—	—	113	75	44	82	53	59	—	—	—	—
AK6-132	—	—	80	117	112	77	44	82	52	59	—	—	—	—
AK6-133	470	408	91	112	107	63	43	78	51	59	62	60	45	58
AK6-131	—	—	—	—	(> 87)	62	43	—	39	43	—	—	—	—
AK7-156	—	—	—	(120)	(> 112)	70	42	81	52	58	—	—	—	—
AK3-118	497	430	95	126	121	75	40	83	52	62	67	65	44	57
AK4-184	—	423	—	—	105	75	—	81	43	56	54	69	41	57
AK6-302	—	385	—	—	107	75	37	77	46	57	57	62	42	53
AK2-95	—	—	—	—	(110)	77	40	82	—	—	—	—	—	—
AK6-303	—	—	—	120	104	73	41	81	—	—	—	—	—	—

TABLE 6. — *Ceratotherium neumayri* (Osborn, 1900), Akkaşdağı, middle Turolian of Central Anatolia, dimensions of the scaphoids (in mm).

Number	TD	APD	H		Rad. fac.	Trap.	fac. Trapzd.	fac. mag. fac.	D S.-L. fac.				
			ant.	mid.						post.	APD	H	APD
AK2-436	—	88	65	49	65	56	28	14	38.5	33.5	31	33	(13)
AK5-630	65	86	67	47	62	53	29	14	39	34	30	35	10

TABLE 7. — *Ceratotherium neumayri* (Osborn, 1900), Akkaşdağı, middle Turolian of Central Anatolia, dimensions of the magnums (in mm).

Number	TD	H ant.	H	S.-L. fac.	McllI fac.	
					APD	TD
GOK-11	58	45	72	60	53	52
AK7-38	51.5	42	68	62	(38)	(57)
AK5-632	54	42	67	—	49	—

TABLE 8. — *Ceratotherium neumayri* (Osborn, 1900), Akkaşdağı, middle Turolian of Central Anatolia, dimensions of the unciforms (in mm).

Number	TD	H	APD max.	APD	post. tuber.		S.-L. fac.		Pyram. fac.		McV fac.	
					TD	H	TD	APD	TD	APD	TD	APD
GOK-10	83	72	–	–	–	–	43	39	50	50	23	31
AK5-633	(76)	73	109	100	45	29	–	44	48.5	42	–	40
AK6-158	76	69	–	–	–	–	37	38	47	(40)	–	–
AKK-157	74	62	–	–	–	–	36	37	44	44	–	–
AK4-74	75	65	95	76	37	25	34	38	42	45	25	37
AK7-147	75	67	97	79	38	25	33	38	38	41	22	36
AKK-156	–	–	–	–	36	26	–	–	–	–	–	–
AKK-280	–	–	–	–	(37)	(24)	–	–	–	–	–	–

TABLE 9. — *Ceratotherium neumayri* (Osborn, 1900), Akkaşdağı, middle Turolian of Central Anatolia, dimensions of the McII (in mm).

Number	L	prox. ext.		Trapzd. fac.		H lat. fac.			diaphysis		dist. art.	
		TD	APD	TD	APD	ant.	mid.	post.	TD	APD	TD	APD
GOK-2	167	52	57.5	33	51	27	20	20	46	27	50	48
GOK-6	168	52	57	35	51	28	18	18	48	28	50	47
AK6-55	179	53	57	35	52	–	17	19	51	28	50	48
AK7-37	–	50	56	35	54	22	15	20	51	24	–	–
AK5-182	–	44	52	32	48	14	12	12	38	21	–	–

TABLE 10. — *Ceratotherium neumayri* (Osborn, 1900), Akkaşdağı, middle Turolian of Central Anatolia, dimensions of the McIII (in mm).

Number	L	prox. art.		D fac. McIV	Uncif. fac.		mag. fac.		diaphysis		dist. ext.	dist. art.	
		TD	APD		TD	APD	TD	APD	TD	APD			
GOK-1	194	75	59	6	52	60	28	33	63	30	76	60	51
GOK-4	193	75	60	8	52	58	28	34	65	31	78	60	53
AKB-83	–	–	–	–	–	–	–	–	–	–	82	59	55
AK5-68	190	74	55	2	48	53	29	37	58.5	28	76.5	60	51
AK3-202	–	–	58	7	–	–	–	–	62	27	–	–	–
AK14-w.n.	–	–	–	–	–	–	–	–	59	28	–	–	–

TABLE 11. — *Ceratotherium neumayri* (Osborn, 1900), Akkaşdağı, middle Turolian of Central Anatolia, dimensions of the McIV (in mm).

Number	L	prox. art.		Uncif. fac.		McV fac.		diaphysis		dist. art.	
		TD	APD	TD	APD	H	APD	TD	APD	TD	APD
GOK-3	158	57	56	49	47	10	20	46	30	45	43
GOK-5	159	58	55	49	47	11	–	46	30	46	44
AK3-230	142	49	48	40	46	7	24	45	23	46	43
AK5-436	144	48	50	40	48	7	25	43	23	44	44
AK13-2	–	51	54	43	52	9	24	41	22	–	–

TABLE 12. — *Ceratotherium neumayri* (Osborn, 1900), Akkaşdağı, middle Turolian of Central Anatolia, dimensions of the femora (in mm).

Number	L	trochl. major H	3rd trochl.		diaphysis		dist. ext.		condyles	
			TDdia.	H	TD	APD	TD	APD	max. TD	D
AK4-253	490	–	(> 150)	110	97	63	159	(160)	131	27
AK5-w.n.	–	–	143	93	84	63	–	–	–	–
AK6-153	–	–	138	115	78	59	155	(155)	125	19
AK7-39	–	101	(> 125)	106	94	61	–	–	–	–
AK3-63	–	–	–	–	–	–	–	183	–	–

TABLE 13. — *Ceratotherium neumayri* (Osborn, 1900), Akkaşdağı, middle Turolian of Central Anatolia, dimensions of the patella (in mm).

Number	TD	APD		H	art.	TD med. art.		lat. art.	
		max.	min.			TD	H	TD	H
AK11-82	117.5	72	53	116	113	100	73	40	81

TABLE 14. — *Ceratotherium neumayri* (Osborn, 1900), Akkaşdağı, middle Turolian of Central Anatolia, dimensions of the tibiae (in mm).

Number	L	prox. ext.		diaphysis		dist. ext.		astrag. cochlea			
		TD	APD	TD	APD	TD	APD	TD	med.	APD mid.	lat.
AK7-40	370	126	142	61	56	102	86	85	63	46	59
AK5-366	–	–	–	74	66	–	88	–	69	50	–
AK7-63	–	–	–	69	59	115	90	92	62	50	68
AKK-154	–	–	–	–	–	111	93	87	–	–	(60)

TABLE 15. — *Ceratotherium neumayri* (Osborn, 1900), Akkaşdağı, middle Turolian of Central Anatolia, dimensions of the fibulae (in mm).

Number	L	prox. ext.		diaphysis		dist. ext.		Tibia fac.		astrag. fac.	
		TD	APD	TD	APD	TD	APD	APD	H	APD	H
AK7-40	310	28	46	26	30	30	58	54	21	–	–
AK13-3 (j)	–	–	–	–	–	26	52	–	–	44	19

TABLE 16. — *Ceratotherium neumayri* (Osborn, 1900), Akkaşdağı, middle Turolian of Central Anatolia, dimensions of the astragali (in mm).

Number	TD max.	TD trochl.	APD max.	H			Calc. fac. 1		Calc. fac. 2		dist. art.	
				med.	mid.	lat.	TD	H	TD	H	TD max.	APD
AK5-w.n.	108	100	(> 63)	92	77	97	53	52	32	45	97	65
AK4-75	106	96.5	65	85	–	–	51	52	27	38	–	–

TABLE 16. — *Ceratotherium neumayri* (Osborn, 1900), Akkaşdağı, middle Turolian of Central Anatolia, dimensions of the astragali (in mm) (continuation).

Number	TD max.	TD trochl.	APD max.	H			Calc. fac. 1		Calc. fac. 2		dist. art.	
				med.	mid.	lat.	TD	H	TD	H	TD max.	APD
AK5-423	119	104	69	93	79	100	53	60	31	45	–	58
AK11-1	106	98	65	88	76	93	48	52	32	46	92	60
AK7-148	–	–	–	–	–	–	–	–	(32)	48	–	–
AK6-56 (j)	–	86.5	54	73	68	78	46	42	27	42	(> 77)	54
AK5-319 (j)	–	–	–	–	–	82	48	52	–	–	–	–
AK5-69	113	94	64	84	74	94	46	53	28	44	92	55
AK5-634	101	93	(63)	80	71	86	47	53	31	49	89	56
AK13-4	–	–	–	83	–	–	–	–	–	–	–	–

TABLE 17. — *Ceratotherium neumayri* (Osborn, 1900), Akkaşdağı, middle Turolian of Central Anatolia, dimensions of the calcanei (in mm).

Number	H	H art.	tuber.		beak	sust.	min. TD post.	min. APD post.	astrag. fac. 3		Cub. fac.	
			TD	APD					APD	TD	TD	H
AK7-36	137	74	60	77	74	84	42	62	40	11	44	32
AK3-66	136.5	67	63	74	–	–	49	67	–	–	–	–

TABLE 18. — *Ceratotherium neumayri* (Osborn, 1900), Akkaşdağı, middle Turolian of Central Anatolia, dimensions of the naviculars (in mm).

Number	TD	APD	H			prox. art.
			ant.	mid.	post.	
AK4-76	56	82	31	25	37	68
AK5-439	55	78	36	27	36	63

TABLE 20. — *Ceratotherium neumayri* (Osborn, 1900), Akkaşdağı, middle Turolian of Central Anatolia, dimensions of the ento-cuneiform (in mm).

Number	TD	APD	H	Navic. fac.		D fac.
				TD	APD	
AK13-5	56	23	66	29	19	11

TABLE 19. — *Ceratotherium neumayri* (Osborn, 1900), Akkaşdağı, middle Turolian of Central Anatolia, dimensions of the cuboid (in mm).

Number	TD	H	prox. art.		TD	APD	D ant.	H post.
			ant.	post.				
AK5-636	45	54	–	70	49	51	–	38

TABLE 21. — *Ceratotherium neumayri* (Osborn, 1900), Akkaşdağı, middle Turolian of Central Anatolia, dimensions of the meso-cuneiform (in mm).

Number	TD	APD	H	Ectocun. fac.	
				APD	H
AK5-637	24	45.5	22	24	6

TABLE 22. — *Ceratotherium neumayri* (Osborn, 1900), Akkaşdağı, middle Turolian of Central Anatolia, dimensions of the ecto-cuneiforms (in mm).

Number	TD	APD	H	Navic. fac.	
				TD	APD
GOK-13	58	53	29	53	(52)
AK4-77	–	–	28	–	–
AK5-635	65	(> 60)	29	56	52

TABLE 23. — *Ceratotherium neumayri* (Osborn, 1900), Akkaşdağı, middle Turolian of Central Anatolia, dimensions of the MtIII (in mm).

Number	L	prox. art.		mesocf. fac.		lat. fac.			diaphysis		dist. art.	
		TD	APD	TD	APD	H ant.	H post.	D	TD	APD	TD	APD
GOK-9	163	35	53	25	43	22	22	13	32	26	37	45
AK5-40	–	35	48	21	41	18	–	10	–	–	–	–

TABLE 24. — *Ceratotherium neumayri* (Osborn, 1900), Akkaşdağı, middle Turolian of Central Anatolia, dimensions of the MtIII (in mm).

Number	L	L without dist. epiph.	prox. art.		TD dia.		diaphysis		TD max. dia.		dist. art.	
			TD	APD	TD	APD	TD	APD	TD	APD		
GOK-7	183	–	66	61	38	55	28	75	59	51		
AKA-44 (j)	–	146.5	63	60	37	49	28	(69)	–	–		
AK2-163	175	–	64	59	44	53.5	29	69	56	48		
AK4-238	–	–	–	–	–	–	–	–	61	53		

TABLE 25. — *Ceratotherium neumayri* (Osborn, 1900), Akkaşdağı, middle Turolian of Central Anatolia, dimensions of the MtIV (in mm).

Number	L	prox. ext.		prox. art.			med. fac.			diaphysis		TD max. dia.	dist. art.	
		TD	APD	TD	APD ant.	APD ant.	H post.	APD post.	H	TD	APD		TD	APD
GOK-8	163	58	48	51	41	26	25	21	20	37	29	46	34	46
AK5-437	–	50	50	47	37	21.5	21	–	20	–	–	–	–	–

TABLE 26. — *Stephanorhinus pikermiensis* (Toula, 1906), Akkaşdağı, middle Turolian of Central Anatolia, dimensions of the radius (in mm).

Number	dist. ext.		dist. art.	
	TD	APD	TD	APD
GOK-14	100	68	86	45

TABLE 27. — *Stephanorhinus pikermiensis* (Toula, 1906), Akkaşdağı, middle Turolian of Central Anatolia, dimensions of the magnum (in mm).

Number	TD	H ant.	H S.-L. fac.		MclIII fac.	
			APD	TD	APD	APD
GOK-12	(43)	33	63	60	(42)	(53)

TABLE 28. — *Stephanorhinus pikermiensis* (Toula, 1906), Akkaşdağı, middle Turolian of Central Anatolia, dimensions of the astragalus (in mm).

Number	APD max.		H		dist. art.	
	med.	mid.	lat.	TD	max.	APD
AK6-57	65	88	71	–	87	53

TABLE 29. — *Stephanorhinus pikermiensis* (Toula, 1906), Akkaşdağı, middle Turolian of Central Anatolia, dimensions of the mesocuneiform (in mm).

Number	TD	APD	H	Ectocun. fac.		Entocun. fac.	
				APD	H	TD	H
AK5-197	26	45	23	25	8	20	6

TABLE 30. — *Stephanorhinus pikermiensis* (Toula, 1906), Akkaşdağı, middle Turolian of Central Anatolia, dimensions of the MtlI (in mm).

Number	L	prox. art.		mesocf. fac.		lat. fac.		diaphysis		dist. art.		
		TD	APD	TD	APD	H ant.	H post.	D	TD	APD	TD	APD
AKA-45	164	37	51	22	42	22	24	7	34.5	24.5	41.5	50

TABLE 31. — *Stephanorhinus pikermiensis* (Toula, 1906), Akkaşdağı, middle Turolian of Central Anatolia, dimensions of the MtlII (in mm).

Number	L	prox. art.		TD diag.		diaphysis		TD max. dia.		dist. art.	
		TD	APD	TD	APD	TD	APD	TD	APD	TD	APD
AKA-45	181	62	55	40	51	24	67	56	49		
AK3-65	161	59	53	38	49	25	67	52	44		

TABLE 32. — *Chilotherium* sp. (Schlosser, 1903), Akkaşdağı, middle Turolian of Central Anatolia, dimensions of the calcaneus (in mm).

Number	H	H art.	tuber.		sust. TD	min. TD post.	astrag. fac. 3		Cub. fac.	
			TD	APD			TD	H	TD	H
AK6-60	94	56	47	63	74	38	25	6	23	42

TABLE 33. — *Acerorhinus* sp., Akkaşdağı, middle Turolian of Central Anatolia, dimensions of the humerus (in mm). Comparison with other late Miocene aceratheriines from Eurasia (data from Cerdeño [1996], Cerdeño & Sanchez [2000] and Fortelius *et al.* [2003]), for which values correspond to size range and numbers between brackets indicate the size of the sample.

Taxon	Number	diaphysis		dist. ext.		trochl.	APD trochl.		
		TD min.	APD	TD	APD		TD	med.	mid.
<i>Acerorhinus</i> sp.	AKB-47	52	52	124	–	88	73	39	53
<i>Acerorhinus</i> sp.	AK5-1	56	62	126	95	91	71	43.5	59
<i>Acerorhinus</i> sp.	AK6-88	–	–	–	–	(90)	80	45	–
<i>Acerorhinus zernowi</i>	–	49.2-58.2 (3)	53.4 -67.1 (3)	111-126.4 (3)	93.3 -110.8 (3)	84-88.2 (3)	71.1-78.2 (3)	–	–
<i>Alicornops simorrese</i>	–	40-50 (4)	39-57 (4)	72-97.6 (5)	63.5-76.7 (4)	–	–	–	–
cf. <i>Chilotherium</i> sp. (primitive)	AS.90.134	53	58	128	89	92	–	–	–

TABLE 34. — *Acerorhinus* sp., Akkaşdağı, middle Turolian of Central Anatolia, dimensions of the radius (in mm). Comparison with other late Miocene aceratheriines from Eurasia (data from Ringström [1924], Heissig [1972], Guérin [1980, 1988], Cerdeño [1996], Cerdeño & Sanchez [2000], and Fortelius *et al.* [2003]), for which values correspond to size range and numbers between brackets indicate the size of the sample.

Taxon	Number	L	prox. ext.		diaphysis		dist. ext.		dist. art.	
			TD	APD	TD	APD	TD	APD	TD	APD
<i>Acerorhinus</i> sp.	AK5-629	330	89	56	47	33	99	57	83	(42)
<i>Acerorhinus palaeosinense</i>	–	285	–	–	39	–	–	–	–	–
<i>Acerorhinus zernowi</i>	–	290.4	82.8	50.6	42	30.8	88	55.2	–	–
		-320.6 (4)	-87.3 (4)	-55.9 (5)	-49.5 (5)	-38.7 (5)	-90.2 (3)	-62.2 (3)		
<i>Alicornops simorreense</i>	–	242	60	32.5	33.6	18	58.5	33.6	–	–
		-300 (4)	-85 (16)	-50.5 (16)	-48 (7)	-30 (7)	-91.5 (12)	-52.5 (12)		
<i>Alicornops complanatum</i>	–	–	66	38	–	–	64 (2)	39-41(2)	–	–
cf. <i>Chilotherium</i> sp. (primitive)	AS.93.1210	–	77	40	–	–	–	–	–	–

TABLE 35. — *Acerorhinus* sp., Akkaşdağı, middle Turolian of Central Anatolia, dimensions of the calcanei (in mm). Comparison with other late Miocene aceratheriines from Eurasia (data from Heissig [1972], Guérin [1980, 1988], Cerdeño & Alcalá [1989], Cerdeño [1996, 1997], and Cerdeño & Sanchez [2000]), for which values correspond to size range and numbers between brackets indicate the size of the sample.

Taxon	Number	H	H art.	tuber.		beak	sust.	min. TD	min. APD	Cub. fac. H
				TD	APD					
<i>Acerorhinus</i> sp.	AK7-98	101	62	47	–	58	78	42	(55)	(42)
<i>Acerorhinus</i> sp.	AK6-130	109	61	56	74	64	80	49	60	(45)
<i>Acerorhinus zernowi</i>	–	97.9	–	39.3	54.1	50.9	56.4	31	–	–
		-111.7 (9)		-57.8 (9)	-65.4 (9)	-58 (9)	-68.2 (7)	-38.4 (9)		
<i>Alicornops simorreense</i>	–	76.7	–	31	41.5	40	41.2	23	–	–
		-107 (27)		-42 (31)	-59.5 (32)	-63 (29)	-63 (22)	-33.6 (23)		
<i>Alicornops complanatum</i>	–	78-98 (2)	–	33-41	44-54	37-41	62 (j)	24-35	–	–
			(2)	(2)	(2)		(2)			
“ <i>Alicornops</i> ” <i>alfambrense</i>	–	93-105.5	–	36.8	57.3	54.5	67	30	–	–
		(5)		-45 (7)	-67.7 (8)	-65.7 (4)	-68.6 (2)	-36.4 (8)		

TABLE 36. — *Acerorhinus* sp., Akkaşdağı, middle Turolian of Central Anatolia, dimensions of the MtII (in mm). Comparison with other late Miocene aceratheriines from Eurasia (data from Heissig [1972], Guérin [1980], Cerdeño [1996], Cerdeño & Sanchez [2000], and Fortelius *et al.* [2003]), for which values correspond to size range and numbers between brackets indicate the size of the sample.

Taxon	Number	L	prox. art.		mesocf. fac.		lat. fac. H post.	diaphysis		dist. art.	
			TD	APD	TD	APD		TD	APD	TD	APD
<i>Acerorhinus</i> sp.	AK5-w.n.	111	24	34.5	14.5	29	16	(25)	(21)	29	34
<i>Acerorhinus zernowi</i>	AMNH 129903	122.1	25.1-28.8	36.4	–	–	–	21.5	19.6	33.4-	35.8
		-126.8 (3)	(3)	-41.3 (3)				-28.4 (3)	-20.8 (3)	33.7 (2)	-37.8 (3)

TABLE 36. — *Acerorhinus* sp., Akkaşdağı, middle Turolian of Central Anatolia, dimensions of the Mtil (in mm). Comparison with other late Miocene aceratheriines from Eurasia (data from Heissig [1972], Guérin [1980], Cerdeño [1996], Cerdeño & Sanchez [2000], and Fortelius et al. [2003]), for which values correspond to size range and numbers between brackets indicate the size of the sample (continuation).

Taxon	Number	L	prox. art.		mesocf. fac.		lat. fac. H post.	diaphysis		dist. art.	
			TD	APD	TD	APD		TD	APD	TD	APD
<i>Alicornops simorreense</i>	-	87.3 -111.5 (12)	19-27.5 (20)	28 -37.5 (18)	-	-	-	18 -26.5 (14)	14-21 (15)	24.2 -31 (11)	22.2-36 (12)
<i>Alicornops complanatum</i>	-	-	28	22	-	-	-	-	-	-	-
<i>Chilotherium</i> indet.	06-AKK-020	85.2	26	33.2	-	-	-	25.4	19	32.8	30.6
cf. <i>Chilotherium</i> sp. (primitive)	-	100.7	21.4	31.1	-	-	-	18.9	16.9	28.4	31.9