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Rhinocerotidae (Perissodactyla)

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For the Rhinocerotidae, the Miocene was a time of maximum species richness and ecological diversity. It was also a time of evolutionary change, driven partly by changes in the physical and biotic environment and partly by palaeogeographic changes (Bernor et al. 1996c; Fortelius et al. 1996b). The first hypsodont rhinoceroses appeared in the late early Miocene, and the late Miocene saw the radiation of forms adapted to increasingly open habitats, as evidenced, for example, by increasing body size and hypsodonty. This trend was particularly marked in Asia, and the Anatolian rhinoceros communities of the late Miocene represent some of the westernmost occurrences of typical Asian taxa, especially of the Aceratheriini of the *Chilotherium* clade.

The Neogene land mammal faunas of Eurasia are mostly from single localities, often without stratigraphic context. Only rarely is there anything like a sequence with successive localities in demonstrable stratigraphic superposition. The chronological framework for analyzing these faunas is vague and of low resolution. The best hope of improving this situation lies in the study of stratigraphically resolved sequences such as those of Sinap, so that they can be used as calibration standards for regional biozonations.

For the rhinoceroses, the problem is complicated because the material from the few other sequences that exist (especially Maragheh, Iran) has not been revised for decades. Furthermore, there are no comprehensive treatments of the Eurasian rhinoceroses except as part of rare family-level overviews, such as Osborn (1900) and Heissig (1973, 1989), and unresolved possible synonymies are common. For the Anatolian Neogene rhinoceroses, the highly condensed synopsis of Heissig (1975) has been the standard reference for a long time, but detailed descriptions and illustrations are needed to develop a stable interpretation and practice.

Because a review of the Neogene rhinoceroses of Eurasia is far beyond the scope of this chapter, we have little choice but follow what, to the best of our understanding, is common usage. We reluctantly agree with Cerdeño (1996) that more work is required before a stable taxonomy is feasible. With one exception, we have tried to retain "current usage" of names and we have refrained entirely from creating new taxa. Our suprageneric taxonomy follows Heissig (1989). The elasmothere taxonomy follows the recent revision of Antoine (2000).

The Sinap Formation (Ozansoy 1957, 1965; Öngür 1976; Sen 1991; Lunkka et al., chapter 1, this volume) has in the past yielded a fine collection of fossil rhinoceroses, curiously ignored by Ozansoy but partly documented in unpublished manuscripts by Sen (1970) and Saraç (1994). It is therefore somewhat surprising that the fossil collection brought together by the Sinap project (see Sen, Introduction, this volume) is relatively poor in rhinoceros material, particularly for the localities of the middle Sinap member. The situation is further complicated by the sudden termination of the Sinap project, as described by Sen (this volume, Introduction). The present treatment must therefore be regarded as preliminary and subject to uncertainties and inadequacies not usually acceptable in a description of this kind.

In an attempt to compensate for these difficulties, some rhinoceros material previously collected from the Sinap Formation has been included here, based on the manuscripts by Sen (1970) and Saraç (1994) and additional material supplied by these authors. Such additional material has been included and revised only to the extent that it adds taxon occurrence information at some Sinap locality. For further details, the reader is referred to the manuscripts themselves, available from the authors. We hope that this important material will be studied more thoroughly in the near future.

Materials and Methods

All dental measurements given here (see appendix tables 12.1–12.3) were taken by MF according to Fortelius (1990) and Fortelius et al. (1993). Measurements of postcrania

were taken by MF and GS according to Guérin (1980). The photographs were taken under field conditions, except for figures 12.2, 12.3, 12.5, 12.13, and 12.16, which were reproduced from old photographic prints.

Information about faunal lists and age of fossil land mammal localities was obtained from the March 2000 version of the NOW (Neogene Old World) database (Bernor et al. 1996a,c; Fortelius et al. 1996b). The database is being continuously revised by the members of the NOW Advisory Board, and the latest public core dataset may be downloaded from the website http://www.helsinki.fi/science/now/. Other datasets may be requested from MF or from the NOW office (mikael.fortelius@helsinki.fi).

Fossil rhinoceros material from the institutions listed below was studied selectively, especially Anatolian material and material from the major Turolian localities of Samos and Pikermi (Greece) and Maragheh (Iran), as well as the Baodean localities of China.

Sinap Material

The fossil collection of the Sinap project was created during seven field seasons in the years 1989–1995. Most of it represents surface collection, but a substantial portion was also obtained by trenching. The rich collection from Loc. 49 was mostly obtained through excavation, and details are available on request from the senior author. Specimens were numbered sequentially in the order of cataloging, starting each year with number 1. Specimens are identified by the prefix AS (for Ankara Sinap), the year, and the catalog number, separated by periods (e.g., AS.95.123). Until 1993, the prefix used was plain S. The collection is stored in the Museum of Anatolian Civilizations in Ankara. For information on the geology and dating of localities, see Kappelman et al. (1996), Kappelman et al. (chapter 2, this volume), Lunkka et al. (1999). Measurements of Sinap specimens are given in appendix tables 12.1–12.3. The collection of the Maden Tetkik ve Arama Enstitüsü (MTA) in Ankara stems mostly from major trenching operations undertaken in the 1950s and the two following decades.

Abbreviations

General: C.V. = coefficient of variation, dex = right, DP = upper deciduous (pre)molar, dp = lower deciduous (pre)-molar, Loc. = Locality, M = upper molar, m = lower molar, mc = metacarpal, mt = metatarsal, P = upper premolar, p = lower premolar, sin = left.

Measurements: AP = anteroposterior diameter, APD = distal anteroposterior diameter, APP = proximal anteroposterior diameter, APS = minimum anteroposterior diameter of shaft, JAPD = anteroposterior diameter of distal joint surface, JAPP = anteroposterior diameter of proximal joint surface, JWD = width of distal joint surface, JWP = anteroposterior diameter of distal joint surface, L = length, LB = buccal length, LL = lingual length, W = width, WD = distal width, WP = proximal (mesial) width, WS = minimum width of shaft.

Institutions: BMNH = Natural History Museum, London; BSPHGM = Bayerische Staatssammlung für Paläontologie und historische Geologie, München; MNHN = Muséum National d'Histoire Naturelle, Paris; MTA = Maden Tetkik ve Arama Enstitüsü, Ankara; NRM = Swedish Museum of Natural History, Stockholm; PDTFAU = Paleoantropoloji, Dil ve Tarih-Cografya Facültesi, Ankara Üniversitesi; PIU = Paleontological Institute, University of Uppsala; SMNS = Staatliches Museum für Naturkunde, Stuttgart.

Catalog of Fossil Material

Lower Sinap Member

Brachypotherium brachypus (Lartet in Laurillard 1848)

Taxonomy:

Aceratheriinae
Teleoceratini
Brachypotherium brachypus (Lartet in Laurillard 1848)

Restricted synonymy:

1981 *Brachypotherium brachypus* Gürbüz fig. 2
1994 *Brachypotherium brachypus* Saraç pl. 4, figs. 1–3

Sinap Material. Loc. 125: astragalus dex AS.95.454, cuboideum dex AS.95.453, mt II dex AS.94.143; MTA collection (İnönü I): mt III dex 06-INÖ-77/1607.

Age. Loc. 125 is stratigraphically older than Locs. 24 and 24A, but beyond this, the age is not known. Locs. 24 and 24A are found in redeposited ash from a volcanic event, possibly related to a basalt flow dated at 15–16 Ma (Kappelman et al., chapter 2, this volume). The localities are unfortunately situated in an isolated block in the middle of a fault zone, and the block's stratigraphic relationship to the surrounding strata remains elusive (Lunkka et al., this volume).

Remarks. The metatarsal from İnönü I (Locs. 24 and 24A of the Sinap project) is unmistakable; it is very similar to a specimen from Sofça figured by Heissig (1976, fig. 39). Only field identifications and a few measurements are available for the fossils from Loc. 125. Judging from the measurements (appendix table 12.3), the metatarsal at least seems more slender than is typical for the species, and the material may represent a more primitive brachypothere species than *Brachypotherium brachypus*.

Discussion. *Brachypotherium* is a conservative and long-lived genus with a wide geographic range in western Eurasia (Heissig 1996). It is one of several rhinoceros lineages to develop short legs and relatively high crowned teeth, but its paleoecology remains enigmatic. A hippopotamus-like life-

style is possible, but this suggestion lacks direct support. Judging by dental wear, the animal seems to have been a mixed feeder (Fortelius 1990; Fortelius and Solounias 2000).

Hoploaceratherium tetradactylum (Lartet, 1837)

Taxonomy:

Aceratheriini
Hoploaceratherium tetradactylum (Lartet, 1837)

Restricted synonymy:

1994 *Hoploaceratherium tetradactylum* Saraç pl. 2, fig. 1

Sinap Material. MTA collection (İnönü I): juvenile maxilla dex with DP2-DP4 06-INÖ-77/1667.

Age. Close to but <15.2 ± 0.3 Ma (see above and Kappelman et al. 1996).

Remarks. The single specimen is very similar to the corresponding specimen from Paşalar described by Fortelius (1990) as *Aceratherium* sp. aff. *tetradactylum*. The DP2 is characteristically elongated, especially in its buccal part, and the ectoloph is strongly inflected at the metacone on all the teeth. The protocone of DP3 and DP4 shows moderate constriction both mesially and distally.

Discussion. This species is not represented in the collections of the Sinap project, nor did Gürbüz (1981) list it from the locality. It is, however, present at the Anatolian localities of Paşalar and Çandir which, like İnönü I, also have Begertherium and Brachypotherium (Heissig 1976; Fortelius 1990).

Hoploaceratherium is part of a plesion that has yet to be revised. Cerdeño (1996) synonymized *Hoploaceratherium* with *Acerorhinus,* but we have retained the genus here, partly because we feel that the complete loss of horns in *Acerorhinus* justifies separation at the generic level and partly to avoid premature changes. This species was a plesiomorphic rhinoceros, best regarded as a browser ecologically similar to the living small southeast Asian rhinoceroses.

Hispanotherium grimmi Heissig, 1974

Taxonomy:

Rhinocerotinae
Elasmotherini
Hispanotherium grimmi Heissig, 1974

Restricted synonymy:

1981 *Hispanotherium grimmi* Gürbüz fig. 2
1994 *Begertherium grimmi* Saraç pl. 5, figs. 1–3
1996 *Begertherium* cf. *B. grimmi* Kappelman et al. table 6.2

Sinap Material. Loc. 24A: M sin superior ectoloph part AS.89.111, astragalus sin AS.92.667, mt III sin proximal part AS.92.664, mt IV sin proximal part AS.91.400; MTA collection (İnönü I): maxilla sin with DP1–M3 06-INÖ-0802, mc III dex 06-INÖ-77/1773.

Age. Matrix is probably derived from volcanic activity at ~15–16 Ma (see above and Kappelman et al. 1996); the fauna indicates a late MN 5 or early MN 6 age, with cooccurrence of *Listriodon splendens* and *Bunolistriodon latidens* (Gürbüz 1981; Fortelius et al. 1996b).

Remarks. The material is similar to that described by Heissig (1974, 1976) and does not add anything critical to previous knowledge of the taxon. The complete upper toothrow shows hypsodont molars and strongly molarized premolars with thick cement coating (Saraç 1994, pl. 5, fig. 1).

Discussion. The tangled taxonomy and nomenclature of the taxon (Heissig 1976; Fortelius and Heissig 1989; Cerdeño 1995) has recently been clarified by Antoine (2000), whom we follow here.

These elasmotherines were the earliest hypsodont rhinoceroses in the Old World, and show grazerlike dental wear (Fortelius 1990). They were also relatively cursorial, as befits animals that first evolved in the open habitats that were beginning to appear in central Asia at this time (Bernor et al. 1996c).

Rhinocerotidae indet.

Sinap Material. Loc. 79: M dex inferior fragment (protoconid) AS.92.103, astragalus dex AS.92.97, calcaneum AS.92.96, proximal mt II sin AS.92.101; Loc. 80: proximal radius dex AS.92.109.

Age. Locs. 79 and 80 are situated north of the major fault in the Sinap-Delikayinçak area and are far outside any stragraphically measured section. Based on general lithostratigraphic relationships, they are thought to represent a stratigraphic position close to or lower than the lower Sinap member (J. Kappelman, pers. comm.).

Remarks. Judging from field notes by MF, at least some of the material from Locs. 79 and 80 may well represent *Alicornops simorrensis,* but without access to the specimens, it has not been possible to verify this. *Alicornops simorrensis* was present in Anatolia from MN 6 to MN 7 + 8 (Heissig 1996), so its presence in the lower Sinap member is to be expected. This record must be regarded as extremely tentative, however.

Middle Sinap Member

Acerorhinus zernowi (Borissiak 1905)

Taxonomy:

Aceratheriinae
Aceratheriini
Acerorhinus zernowi (Borissiak 1905)

Restricted synonymy:

1990 *Chilotherium* sp. Sen p. 250
1994 *Chilotherium* (*Acerorhinus) zernowi* Saraç pl. 8, fig. 3
1994 *Chilotherium (Chilotherium) samium* Saraç pl. 10, fig. 1a,b
1996 *Acerorhinus* cf. *A. zernowi* Kappelman et al. table 6.2

Sinap Material. Loc. 49: skull AS.95.747 + AS.95.24, partial skull with sin tooth row AS.93.823, sin maxilla and upper toothrow AS.94.554, maxillary fragment dex with M1–M3 AS.93.1074, sin M1 or M2 AS.94.500, male mandible AS.90.96 + AS.92.150, partial mandible AS.94.315-316 lacking anterior portion, i2 sin AS.95.72 (male), p2 dex AS.94.1466, p2 sin AS.94.1414, dp2 dex AS.91.188, tibia sin distal part AS.92.138, astragalus sin AS.91.731; MTA collection (Ozansoy's Loc. IB = Loc. 1): male skull (thought to have been subsequently lost) maxilla dex with DP1–M3 06-SIN-0136; MTA collection (Ozansoy's Loc. II = Loc. 12): maxilla sin with P2–M3 06-KAY-5, maxilla sin with P3–M3 06-KAY-11, mandibular ramus dex 06-KAY-12.

Age. The interpolated magnetochronologic ages of these localities are: Loc 12, 9.6 Ma; Loc. 1, 9.3 Ma; Loc. 49, 9.1 Ma (Kappelman et al., chapter 2, this volume).

Remarks. Unfortunately, no photographic documentation is available of the skull AS.95.747 from Loc. 49, discovered late in the 1995 season. Approximate measurements and a brief description are offered here based on preliminary field notes taken by MF. The skull is well preserved but lacks most of the face anterior to P4. The nasal bones were recovered from the surface at the beginning of the same season in which specimen AS.95.24 was recovered. The distance from the tip of the nasals to the nuchal crest is ~485 mm, the distance from the posterior rim of the orbit to the nuchal crest is ~320 mm, the total height of the skull at M1 ~135 mm, and the height of the occiput ~240 mm. The facial crista is confluent with the bulbous anterior rim of the orbit, which is placed above M2 and is not elevated, as it is in *Chilotherium*. The postglenoid process is stout and has a separate vertical semicylindrical joint surface for the mandible, in contrast with *Chilotherium,* where the process is weaker and the joint surface oblique and partly confluent with the glenoid joint surface. The zygomatic arch is quite deep and has a weakly sigmoid outline in lateral view (fig. 12.1A). The nasals are quite long and separated by a strongly developed median groove. They display a characteristic blunt beak separated from the posterior portion of the bone by a distinct shoulder. The upper cheek teeth of the skull are highly similar to those of specimen AS.93.823 (Fig. 1B), with moderately developed buccal folding and a

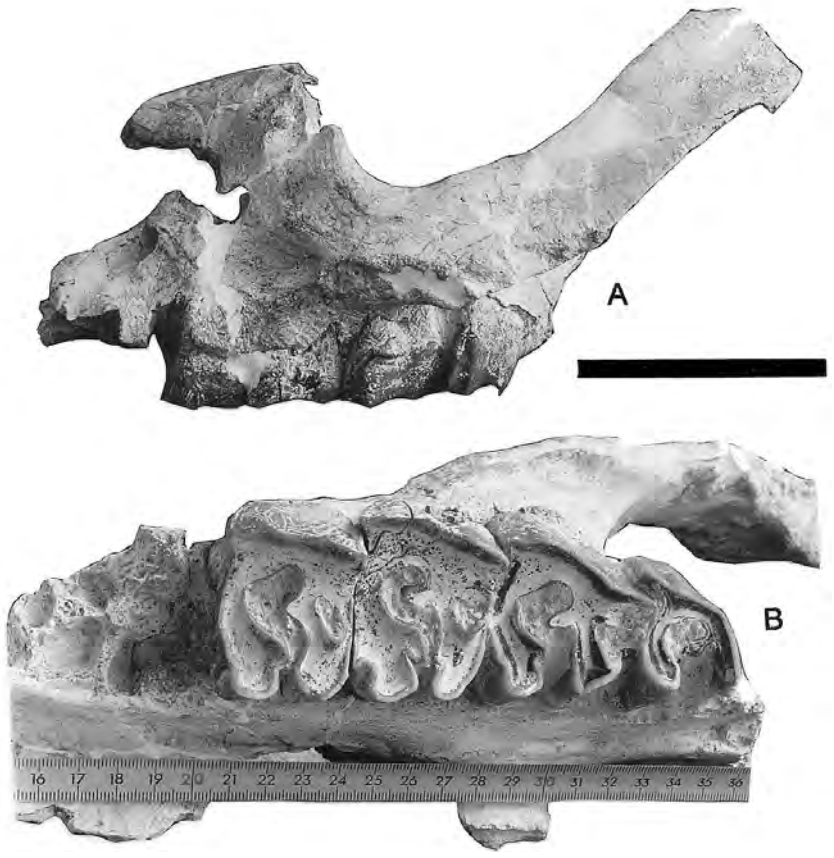

Figure 12.1. (**A**) Lateral view of partial skull AS.93.823 of *Acerorhinus zernowi* from Loc. 49. Scale bar = 10 cm. (**B**) Same specimen, occlusal view of left maxillary tooth row. Ruler in image.

Figure 12.2. Male skull of *Acerorhinus zernowi* from Ozansoy's Loc. IB (=Loc. 1), MTA collection. Based on the only known photograph. The specimen is thought to have been lost. Scale bar ~20 cm.

moderately constricted molar protocone that is not flattened lingually. The M3 is relatively short.

Unfortunately, the unnumbered skull from Loc. 1 appears to have been lost and thus can only be described from the single photograph known to exist (fig. 12.2). At least in general characteristics, it appears to be very similar to the specimen described above. When last examined, the specimen was well preserved and complete, with an associated mandible in place. The occiput is elevated and the nasals curve gently to a blunt tip. There is a weak but distinct elevation of the frontals above the orbit, which, again, is not itself elevated. The narial incision is deep, reaching the anterior margin of M1. The preorbital bar is consequently narrow, with the orbit situated above M2. There is a small anteorbital apophysis and a larger supraorbital one.

The facial crista is present but appears to be quite weak. The zygomatic arch is gently curved and relatively slender. The upper cheek teeth have well-developed buccal folds, including a strong paracone rib and a distinct inflexion at the metacone. The ascending ramus of the mandible makes a slightly open angle with the body. M3 is relatively short and p2 relatively long. The tusk curves quite steeply upward and appears to be oriented almost directly forward, in contrast to the less curved, more horizontal, laterally flaring tusks typically seen in *Chilotherium*. The apparently rounded lateral face is also characteristic of *Acerorhinus* and unlike the angled lateral face of a *Chilotherium* tusk. Unfortunately, no measurements of this specimen are known.

The maxillary dentitions 06-SIN-0136 and 06-KAY-5 are very similar to each other. The teeth are mesodont and have well-developed buccal folds and a moderate cement covering (fig. 12.3). The protocones of M1 and M2 are moderately constricted by mesial and distal folds, and their lingual side is very slightly flattened, with rounded corners to the cusp. The M3 is relatively short (the lingual side is compressed). The maxillary dentition 06-KAY-11 is more worn but shows the rounded lingual cusps that distinguish it from *Chilotherium*.

The mandible (AS.90.96 + AS.92.150) has a long, relatively narrow symphysis and a large, upturned tusk with a rounded cross-section of the lateral side (fig. 12.4 A–B). The mandibular ramus is of even depth and begins to taper toward the symphysis only above p2. The angle of the mandible is somewhat expanded but not turned out toward lateral. The cheek teeth are low crowned and have a rounded metalophid without a distinct ectoflexid (except

Figure 12.3. Right maxillary toothrow 06-SIN-0136 of *Acerorhinus zernowi* from Ozansoy's Loc. IB (=Loc. 1). MTA collection. Occlusal view. Scale bar ~10 cm.

Figure 12.4. Left male hemimandible AS.92.150 of *Acerorhinus zernowi* from Loc. 49. (**A**) Lingual view; (**B**) occlusal view. Scale bar = 20 cm.

on the large p2), and with trigonid and talonid basins that have a V-shaped cross-section. Other mandibles all essentially correspond to this description. The glenoid joint is preserved on AS.94.315 and shows the typical rhinocerotid double arrangement, with a clearly separate, posteromedial cylindrical joint surface that embraces the stout postglenoid process of the skull. In *Chilotherium* from the same locality (e.g., specimen AS.94.316), this arrangement is modified, so that a semicontinuous curved joint surface articulates both with the temporal and the postglenoid process, which is shorter and more tapered.

Of the postcranial remains from Loc. 49, only a distal tibia (AS.92.138) and an astragalus (AS.91.731) can be confidently referred to this species, based on their narrow joint surfaces and pronounced trochlear relief, quite unlike the shallow and broad ankle joint of *Chilotherium*.

Discussion. Heissig (1975) assigned all Anatolian *Acerorhinus* remains to *A. zernowi* (Borissiak 1914), described from the MN 9 locality Sebastopol in the Crimea. This remains the best match for the Sinap material, which spans MN 10 (Locs. 12, 1) to MN 11 (Loc. 49). However, *A. tsaidamense* from Qaidam (Bohlin 1937) is also in several respects similar to the Loc. 1 skull: the occiput leans backward rather than forward, the facial crista is weak, the zygomatic arch is slender, and the angle of the mandible is slightly open (Bohlin 1937, fig. 164). The flattened lingual cusps of the upper molars of *A. tsaidamense* do, however, appear derived in comparison with the more plesiomorphic, rounded cusps of *A. zernowi* (cf. Borissiak 1915, pl. II; Bohlin 1937, pl. VIII, fig. 1). The skulls and mandibles from Tung-gur assigned to *A. zernowi* by Cerdeño (1996, figs. 2, 3) are similar to the Loc. 1 skull in occipital morphology but differ in having a more massive zygomatic arch, a shallower narial incision, longer nasals, and a more vertically oriented ascending ramus on the mandible, all characters in common with the type material of *A. zernowi*. Both *A. zernowi* from Tung-gur and *A. tsaidamensis* were long-limbed forms compared with short-limbed *Chilotherium,* although both were more robust than middle Miocene members of this plesion, such as *Hoploaceratherium tetradactylum* and *"Aceratherium incisivum"* from the Jilancik Beds in the Turgai (Cerdeño 1996). The postcranial *Acerorhinus* material from the Sinap Formation is too incomplete for meaningful comparison of limb proportions, however.

Acerorhinus zernowi was a plesiomorphic rhinoceros, not far removed in terms of ecology from *Hoploaceratherium tetradactylum*. Judging from its dental mesowear pattern (Fortelius and Solounias 2000) it was a browser or a browser with a limited mixed-feeding capability.

Acerorhinus sp. nov.

Restricted synonymy:

1996 *Acerorhinus* cf. *A. zernowi* Kappelman et al. table 6.2 (in part)

Sinap Material. Loc. 26: mc III dex proximal part AS.91.229, mc IV dex AS.90.241 (same individual?); Loc. 33: p2 dex AS.89.279; Loc. 58: p2 dex AS.90.184; MTA collection (level of Loc. 26): Unnumbered adult and juvenile skulls, maxilla dex with upper dentition P4–M3 06-AKK-011.

Age. All these localities are in the upper fossiliferous level of Upper Kavakdere, with a magnetostratigraphic age of 8.1 Ma (Kappelman et al., chapter 2, this volume).

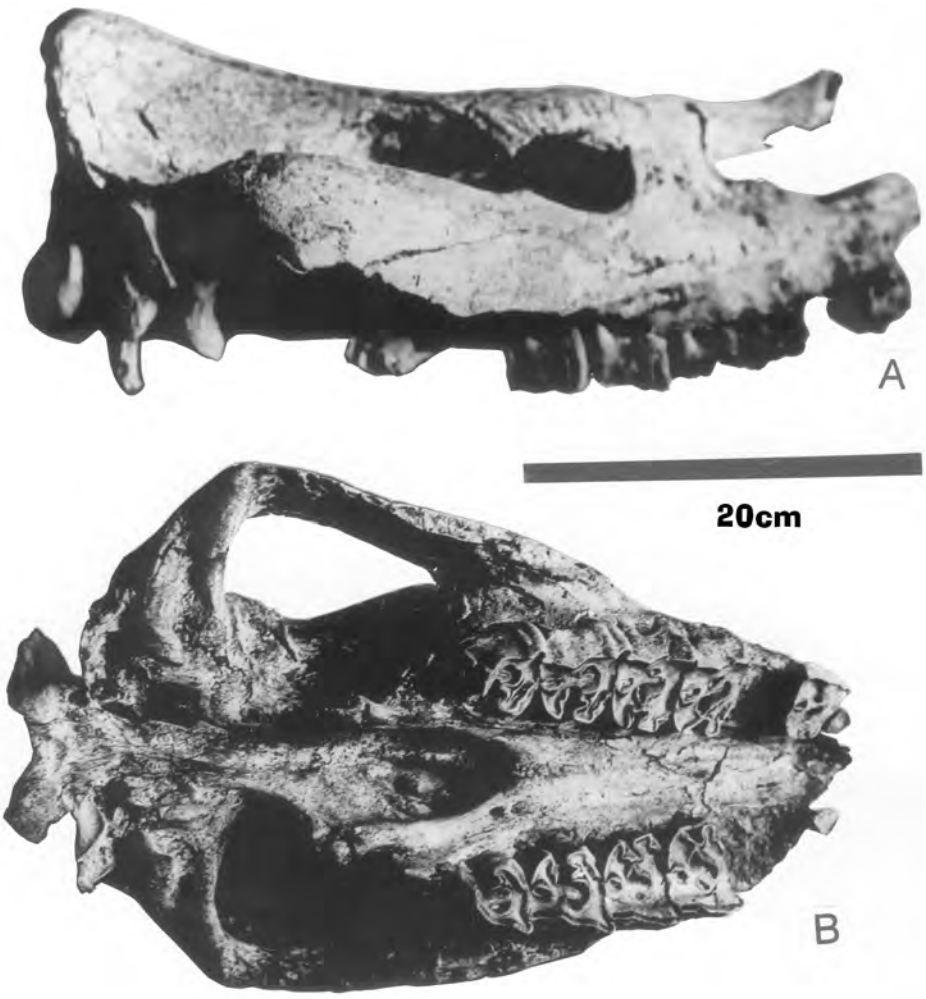

Figure 12.5. Unnumbered skull of *Acerorhinus* sp. nov. from Upper Kavakdere, MTA collection. **(A)** Lateral view; **(B)** ventral view. Scale bar ~20 cm.

Remarks. The adult MTA skull (fig. 12.5A–B) has a highly derived and suggestive combination of characters. It is long and has a concave profile in lateral view, with parietals and nasals both distinctly elevated above the plane of the frontals. The face is short and the orbit high, with a strong postorbital process above M3. The facial crest is strong and the skull tapers abruptly from frontals to nasals, in contrast with the gradual tapering invariably seen in *Chilotherium*. The zygomatic arch is nearly horizontal and very deep, about one-half of the height of the skull itself. The upper molars are hypsodont, with advanced folding of the enamel, and the premolars are relatively very broad and generally large (fig. 12.5B). Features typical of *Acerorhinus* include the strong ribs of the upper molars, the inflexion of the ectoloph at the metacone, the lingually pointed hypocones, and especially, the large and broad premolars. The juvenile skull shows essentially the same set of characters at an earlier ontogenetic stage.

The two isolated p2 specimens are unmistakable owing to their large size and characteristic wear profile descending from an acute tip at the paraconid; they unambiguously record the presence of the genus there. The metacarpals are shortened (fig. 12.6), and might be expected to belong to *Chilotherium kowalevskii,* a species with strongly shortened podials. They are, however, a much better match for *Acerorhinus palaeosinensis* in the Lagrelius collection than for any *Chilotherium* with which we have been able to compare them, and we prefer to associate them with *Acerorhinus.* Compared with mc III UMP M3831a, AS.91.229 has a proximal articular surface only somewhat more extended toward the posterior and has the same strongly developed lip below the articular surface on the plantar side. The mc IV UMP M3831c is also very similar to AS. 90.241, which again has a more anteroposteriorly extended proximal articular surface. The facets between mc III and mc IV are also relatively larger in the Kavakdere form. The small figures of Pavlow (1915, pl. V) permit only the most approximate comparison, but as far as can be judged, the *Acerorhinus* from Tchobrouchi also has metacarpals of about the same proportions as the Kavakdere form.

The main differences relative to derived *Chilotherium* (*C. anderssoni* and *C. persiae*) include larger and less vertical articular surfaces between mc III and the accessory metacarpals, more strongly curved mc IV with relatively broader

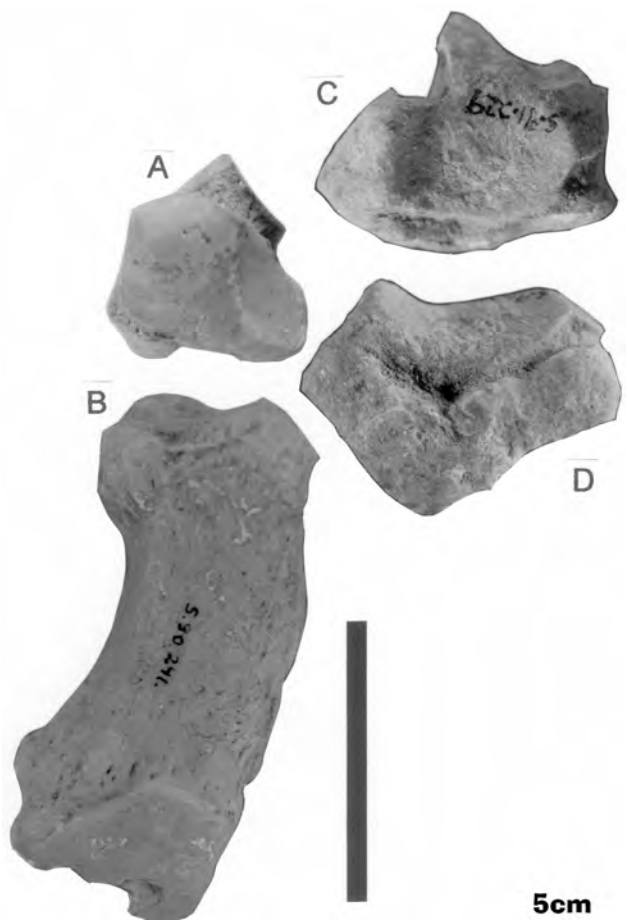

Figure 12.6. Right metacarpals IV and III (same individual?) of *Acerorhinus* sp. nov. from Loc. 26. (**A**) Proximal view of mc IV AS.90.241. (**B**) Plantar view of same specimen. (**C**) Proximal view of mc III (proximal part) AS.91.229. (**D**) Plantar view of same specimen. Scale bar = 5 cm.

articular surfaces both proximally and distally, a less developed ridge on the distal trochlea, and presence of an articular facet for mc V.

Discussion. It seems that two successive species of *Acerorhinus* are recorded in the Sinap Formation, the later one close to the roughly contemporaneous species described from Tchobroutchi by Pavlow (1915) as "*Aceratherium incisivum*" and from Udabno by Tsiskarishvili (1987) as "*Aceratherium* sp." These are derived forms, similar in several aspects to the Chinese *Acerorhinus palaeosinensis,* with a flat skull roof; a high orbit; and shortened, strongly splayed metapodials. The skull is much more elongated in the Kavakdere form than *Acerorhinus palaeosinensis* or in the material from Tchobroutchi, however, and the nasals have a different shape, with a peculiar dorsad twist at the tip. A long-skulled form virtually identical to the Kavakdere species, with the same peculiar nasal morphology, is, however, known from the late Miocene (?Turolian) locality Marmar in Tajikistan (S. Sharapov, pers. comm.). It seems likely that these Turolian forms represent at least one and perhaps two hitherto unrecognized species of *Acerorhinus,* perhaps representing a west Asian clade, but without detailed study of the material this cannot now be determined (cf. Cerdeño 1996, p.17).

The evolutionary history of the group is treated briefly under General Discussion later in this chapter. We note here in passing that Cerdeño's (1996) suggestion to transfer the derived members of the *Acerorhinus* to *Chilotherium* implies either multiple detailed homoplasy (at the least, the shape of mandibular symphysis, tusk position, morphology and proportions of premolars and molars, and construction of temporomandibular joint), or a very late origin of *Chilotherium* from *Acerorhinus.* The former alternative appears inherently unlikely, whereas the latter is contradicted by extensive stratigraphic evidence.

The trends seen in the evolution of *Acerorhinus* seem to indicate a parallel evolution with *Chilotherium,* but the precise nature of the adaptation of these highly successful open-habitat rhinoceroses remains somewhat enigmatic.

Chilotherium kiliasi (Geraads and Koufos 1990)

Restricted synonymy:

1996 *Chilotherium* cf. *C. samium* Kappelman et al. table 6.2 (in part)

Sinap Material. Loc. 49: upper toothrow sin AS.93.963, P4 dex AS.90.98, M2 dex AS.91.695, mandible AS.93.810 (female), mandible AS.93.809 (male), mandible AS.93.815 (female), partial mandibular ramus sin AS.91.701, mandibular ramus sin AS.94.566, partial mandibular ramus dex AS.94.537, m3 dex AS.91.690, m3 sin AS.90.100, m3 dex AS.90.97, juvenile mandible sin AS.93.1193.

Age. The magnetostratigraphic age estimate for Loc. 49 is 9.1 Ma (Kappelman et al., chapter 2, this volume).

Remarks. This is a mesodont form with moderately reduced premolars and a moderately short M3 compared with most more derived species of *Chilotherium.* The upper teeth have weak paracone styles and relatively flat buccal walls with a weak inflexion at the metacone (fig. 12.7). The protocone is constricted from mesial and distal and distinctly flattened lingually—a good distinguishing character from *Acerorhinus* from the same locality, in which M3 is also clearly shorter. The buccal walls of the lower teeth are rounded rather than angled (as in cf. *Chilotherium* from the middle Sinap) and the hypolophids of the premolars have strikingly strong transverse portions that are somewhat recurved. The mandibular ramus of the female mandible AS.93.810 tapers gradually toward the anterior (fig. 12.8), whereas in male specimens (e.g., AS.93.809), it remains equally deep almost to the symphysis, presumably because a deep root for the large tusk is present. The morphology of the lower molars differs from that of *Acerorhinus* cf. *A. zernowi* from the same locality in the following characters: the tooth is somewhat higher crowned, has a less expanded base, more vertical walls, and stronger ectoflexids.

Figure 12.7. Left upper toothrow AS.93.963 of *Chilotherium kiliasi* from Loc. 49. Occlusal view. Scale bar = 10 cm.

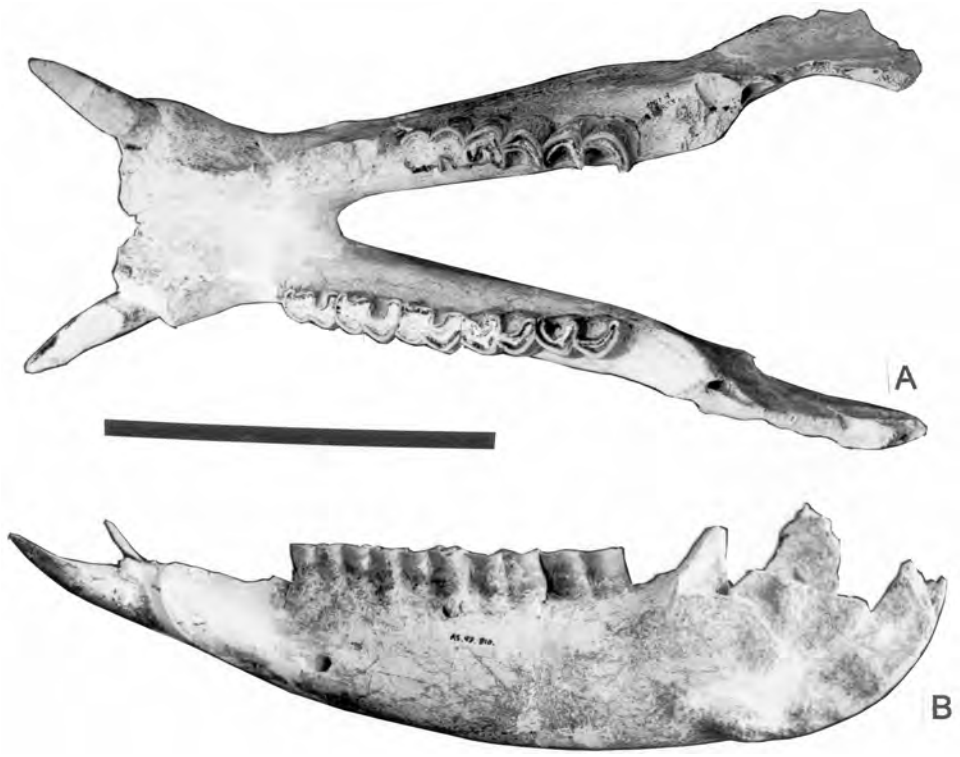

Figure 12.8. Female mandible AS.93.810 of *Chilotherium kiliasi* from Loc. 49. **(A)** Mandible in dorsal view. **(B)** Mandible in lateral view. Scale bar = 20 cm.

The trigonid and talonid basins are more open, with U- to V-shaped cross sections progressively opening up along the tooth row from mesial toward distal. The relative proportions of the cheek toothrow differs dramatically from *C. kiliasi* and *A. zernowi* from the same locality (fig. 12.9). The distinction from the more hypsodont *Chilotherium* from the same locality is described below.

Discussion. The taxonomy of plesiomorphic *Chilotherium* is highly problematic, not least owing to the nature of the type material of *C. samium* (Weber 1905) (an old individual with very worn teeth from an unknown horizon at Samos). *Chilotherium wimani* Ringström, 1924 is a taxon of approximately the same grade of evolution as *C. samium,* but no direct comparison has been undertaken. No skulls of *C. wimani* have been figured, and unfortunately for us, both the lower dentitions figured by Ringström (1924, pl. VIII, figs. 1,2) have worn teeth, making comparison with the Sinap material difficult.

Ironically, the recently described *"Aceratherium"* (=*Chilotherium*) *kiliasi* from Pentalophos I (Geraads and Koufos 1990) is also based on an old individual with worn teeth. Furthermore, the hypodigm of *"Aceratherium" kiliasi* includes a female mandible that clearly belongs to *Acerorhinus*

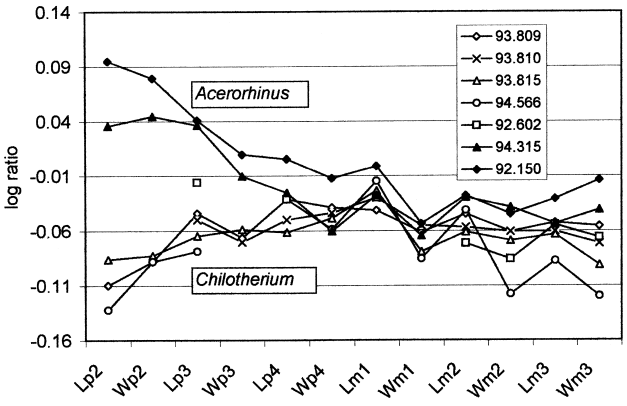

Figure 12.9. Log-ratio diagram of proportions of the lower cheek tooth row of *Acerorhinus zernowi* versus *Chilotherium kiliasi,* both from Loc. 49 only. Standard = *Chilotherium* sample from Maragheh. *Acerorhinus* has relatively much larger premolars, although the difference in molar size and proportions is minimal. As usual, m1 is the tooth showing the least difference. The legend gives Sinap specimen numbers without the prefix "AS."

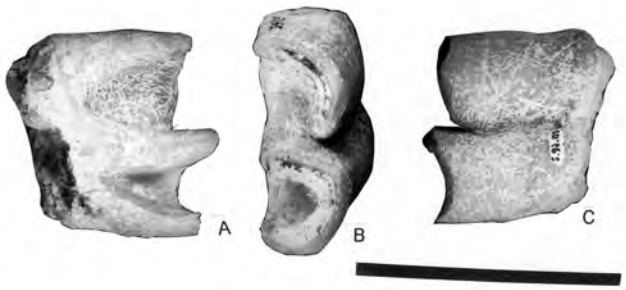

Figure 12.10. Left m3 AS.92.155 of *Chilotherium* cf. *C. habereri* from Loc. 49. **(A)** Lingual view; **(B)** occlusal view; **(C)** buccal view. Scale bar = 5 cm.

(Geraads and Koufos 1990, pl. 3, figs. 2,3,5), as testified by its narrow symphysis, large premolars, obliquely worn p2, and weak ectoflexids on all the characteristically broad cheek teeth, whereas the *Chilotherium* mandible figured (Geraads and Koufos 1990, pl. 2, figs. 3,4) is damaged and lacks the posterior molars.

The lower tooth morphology described above matches that of *Chilotherium kiliasi* well, especially in the strongly developed and recurved hypolophids of the premolars (Geraads and Koufos 1990, pl. 2, fig. 4), a trait apparently missing in *C. wimani* (Ringström 1924, pl. VIII, figs. 1,2), which is furthermore distinctly larger overall. The relatively large upper premolars (fig. 12.7) are also similar to those of the type skull of *C. kiliasi* (Geraads and Koufos 1990, pl. 3, fig. 4). Given the uncertain taxonomy of primitive *Chilotherium,* we tentatively assign the Sinap material to the nomen to which a specific morphological tie can be demonstrated, without implying any statement regarding synonymy. For the purpose of this chapter, we provisionally restrict the name *C. samium* to the type material.

This is a very primitive *Chilotherium,* probably not far removed from the basic, medium-sized aceratherine, with a browser-to-mixed-feeder lifestyle.

Chilotherium cf. *C. habereri*

Restricted synonymy:

1996 *Chilotherium* cf. *C. samium* Kappelman et al. table 6.2 (in part)

Sinap Material. Loc 49: m3 sin AS.92.155, juvenile mandible AS.90.313.

Age. The magnetostratigraphic age estimate for Loc. 49 is 9.1 Ma (Kappelman et al., chapter 2, this volume).

Remarks. The m3 differs from that of *Chilotherium kiliasi* in being distinctly more hypsodont, having more open trigonid and talonid basins, conspicuously thinner enamel lining of the basins, and a less recurved hypolophid outline in occlusal view (fig. 12.10). The lower milk molars (fig. 12.11) show a relatively small and slender dp2, a clear difference from the unidentified Kavakdere *Chilotherium* (see below). Originally a small peglike dp1 was present on the right side, but this was lost during later preparation. The milk teeth have the characteristic hypoplastic band near the base of the crown commonly observed in forms that have recently evolved or are in the process of evolving higher tooth crowns (e.g., very common in *C. persiae* from Maragheh). The m3 differs from the Kavakdere *Chilotherium* in having lingual cusps with short lingual cusps with rounded lingual walls.

Discussion. The high-crowned material from Loc. 49 is too hypsodont to belong to any of the plesiomorphic *Chilotherium* species discussed so far; it is close to the intermediate grade of evolution (especially crown height) represented by the Chinese species *C. habereri.* This specimen probably represents the Anatolian form that Heissig (1975, 1996) referred to *C. habereri.* Comparison with Ringström's (1924) plates and original specimens in the Uppsala collection shows that this tooth differs from the more derived *C. anderssoni* in being somewhat smaller, having a relatively longer metalophid with a slightly flattened buccal wall, and the hypolophid showing a slight flexion toward distal at the distal end, which gives the lophid a slightly sigmoid outline in occlusal view instead of the selenoid recurved profile seen in the Chinese species. To a lesser degree, all these differences also separate the Loc. 49 material from the Chinese *C. habereri,* and instead unite it with the large *Chilotherium* from Maragheh (e.g., MNHN MAR 1905.10).

There is a difficulty in that at least two species of *Chilotherium* are found at Maragheh, and pending revision of the material, one must apply the nomenclature with caution. The larger and more derived Maragheh species, which is similar to but larger than the hypsodont *Chilotherium* from Loc. 49, is the more common in the BMNH and MNHN collections and appears to correspond to the type material of *C. persiae* (de Mequenem 1924). Specimen

Figure 12.11. Juvenile mandible AS.90.313 of *Chilotherium* cf. *C. habereri* from Loc. 49. Scale bar = 10 cm.

AS.92.155 is about 15% smaller in linear dimensions than this form, but morphologically indistinguishable from it. A connection with *C. kowalevskii* appears unlikely, as that species has unreduced or perhaps secondarily enlarged premolars and anterior milk molars. The *Chilotherium* cf. *C. habereri* of Anatolia might represent an early stage of the evolution of the *C. persiae* lineage, but this cannot now be more than a speculation.

Chilotherium indet.

Sinap Material. Loc. 49: DP1 sin AS.94.509, DP1 sin AS.94.1382, i2 sin AS.94.572 (male), i2 sin AS.94.1451 (male), i2 sin AS.91.699 (female), p2 dex AS.94.312, p2 dex AS.94.1412, radioulna sin part AS.94.582; Loc. 50: DP1 sin AS.90.23, Loc. 34: Male mandible with ramus and symphysis sin AS.92.602; Loc. 26: astragalus sin AS.89.286; Loc. 33: radius sin proximal part AS.89.171, distal tibia dex AS.90.52, astragalus dex AS.89.215; Loc. 42: mt II sin proximal part AS.90.78, mt IV sin proximal part AS.89.422; MTA collection (level of Loc. 26): subadult mandible 06-AKK-013.

Age. The magnetostratigraphic age estimate for Loc. 49 is 9.1 Ma (Kappelman et al., chapter 2, this volume). The corresponding age for Loc. 34 is 8.4 Ma and 8.1 Ma for Locs. 26 and 33. Locs. 50 and 42 lack geochronologic age estimates. Loc. 42 (=Çobanpinar) is now placed in MN 13 (Kappelman et al., chapter 2, this volume; Van der Made, chapter 13, this volume).

Remarks. The indeterminate *Chilotherium* material from Loc. 49 consists mostly of worn teeth that are difficult to identify with confidence. There is no indication that an additional taxon is present at the locality. The indeterminate *Chilotherium* material from the Upper Kavakdere Locs. 34 and 26 and from Loc. 42 (Çobanpinar) all appears to represent one or more hypsodont species, smaller than *C. persiae,* a species that has previously been reported from these levels (Saraç 1994). The male mandible AS.92.602 shows lower molars with elongated and strongly flattened lingual walls on the lingual cusps, enclosing rather narrow trigonid and talonid basins (fig. 12.12). The tendency for the elongated entoconid to form an occlusal high point, almost as in brachydont hippomorph perissodactyls, is also a similarity with *C. persiae.* The subadult mandible 06-AKK-013 shows the lingually flattened molar morphology and a row of deciduous teeth, of which dp2 and dp3 are strikingly large (about the size of dp4). A smaller form similar to *C. persiae* but with relatively larger anterior cheek teeth might represent *C. kowalevskii* (cf. Pavlow 1913, pl. IV,

Figure 12.12. Left male hemimandible AS.92.602 of *Chilotherium* indet. from Loc. 34. **(A)** Detail of molars in occlusal view. Scale bar = 10 cm. **(B)** Buccal view of mandible. Ruler in image.

Figure 12.13. Male mandible 06-SIN-0135 of cf. *Chilotherium* sp. (primitive) from Ozansoy's Loc. IB (=Loc. 1). MTA collection. Scale bar = 20 cm.

fig. 8; de Mequenem 1924, p. 145; and Saraç 1994, pl. 12, fig. 3a), but the evidence is hardly conclusive. The tibia 06-AKK-017 is short and similar to a specimen figured by Pavlow (1913, pl. IV, fig. 23). The small astragali have broad trochleas with low relief and thus probably belong to *Chilotherium* rather than *Acerorhinus*.

Discussion. A characteristic that *C. kowalevskii* shares with *C. persiae* (but not with the more derived of the east Asian species of the genus) is the tendency for the lingual walls of the lower teeth to become elongated and strongly flattened, frequently to the extent of closing off the sinuses partly or completely. This presumably corresponds to the high degree of flattening of the lingual cusps of the upper teeth also seen in these west Asian forms, and may indicate that the west and east Asian species belong to separate clades.

As are other derived species of *Chilotherium,* these animals were most probably mixed feeders, judging from dental wear showing moderate rounding of the cusp tips. Grazing, even on fresh grass, leaves a considerably more rounded wear signal, at least in living ungulates (Fortelius and Solounias 2000).

cf. *Chilotherium* sp. (primitive)

Restricted synonymy:

1970 *Chilotherium* Sen Plate IX:2
1996 *Chilotherium* cf. *C. samium* Kappelman et al. table 6.2 (in part)

Sinap Material. Loc. 72: radius sin distal fragment AS.92.217, mt III dex AS.91.312; Loc. 12: associated forelimb dex AS.93.1210 (humerus distal fragment, radius proximal part, complete tetradactyl manus), calcaneum dex fragment AS.95.423; Loc. 51: mandibular rami dex and sin AS.90.132, male i2 dex part AS 90.131, humerus dex and sin AS.90.134, partial ulna AS.90.160, astragalus dex AS.91.387; MTA collection (Ozansoy's Loc. IB = Loc. 1): male mandible 06-SIN-0135; PDTFAU collection: mt II dex unnumbered; Şenyürek's Loc. F2 ("Aşağı yoncalık") in the middle Sinap member.

Age. The magnetostratigraphic age estimates are 10.1 Ma for Loc. 72, 9.6 Ma for Loc. 12, and 9.3 Ma for Loc. 1. Loc. 51 is probably close to Loc. 1 in age, based on general lithostratigraphic relationships and biochronology (Lunkka et al. 1999; Kappelman et al., chapter 2, this volume).

Remarks. The adult male mandible 06-SIN-0135 (fig. 12.13) has a long, broad symphysis, broader than in *Acerorhinus* (fig. 12.4) and *Subchilotherium* (Heissig 1972, pl. 8, fig. 2; Tsiskarishvili 1987, p. 53), and large tusks directed almost directly forward. The symphysis is hollowed-out on the ventral side, as in *Chilotherium* or *Acerorhinus* and unlike *Aceratherium*. The cheek teeth are plesiomorphic, mesodont, with v-shaped sinuses, long paralophids, and a distinct protoconid angle (ectoflexid) to the metalophid profile, which is characteristically "square" in occlusal view, especially on the premolars. The premolars are relatively large for *Chilotherium* and the planar buccal walls with distinct ectoflexids are unlike any other *Chilotherium*. The less complete specimen from Loc. 51 (AS.90.131-132) is similar in all particulars, including the relatively large premolars and the angled lophids.

The humeri AS.90.134 from Loc. 51 are relatively broad, short bones (fig. 12.14), with strong deltoid crests extending relatively further distally than in longer-limbed forms, such as the *Acerorhinus* from Tung-gur (Cerdeño 1996, fig. 6A). The distal end is relatively narrow, and the fossa olecrani narrow and high. The bone as a whole is somewhat shorter and broader than in *Aceratherium incisivum* (Hünermann 1989, fig. 10, table 5), but not nearly as shortened as the humeri of typical *Chilotherium* (e.g., Ringström 1924, pl. VIII, figs. 3, 4).

The right forelimb AS.93.1210 was collected during an undocumented excavation after the 1993 field season and was unfortunately not properly studied. The humerus is very similar to the bones described above. The metacarpals

Figure 12.14. Humerus AS.90.134 of cf. *Chilotherium* sp. (primitive) from Loc. 51. (**A**) Left humerus; (**B**) right humerus. Scale bar = 10 cm.

(fig. 12.15) are, generally speaking, small and slender, not far from the proportions seen in *Aceratherium incisivum* (Hünermann 1989, figs. 31, 32), a species that also has a well-formed mc V. Compared with the measurements given by Hünermann (1989, table 15) all the metapodials are somewhat shorter and less flattened than in *A. incisivum,* however. The metacarpals are much smaller and perhaps relatively shorter than those of *A. tsaidamensis* (Bohlin 1937) and much smaller and stouter than the specimens from Tung-gur assigned to *A. zernowi* by Cerdeño (1996). They are still distinctly less shortened than in typical *Chilotherium.*

The astragalus is shorter and has a broad trochlea with low articular relief compared with *Acerorhinus* (Cerdeño 1996, pl. 7B,D), more like that of *Chilotherium* (Ringström 1924, pl. IX, fig. 3).

The mt III from Loc. 72 and the mt II from Şenyürek's Loc. F2 are both small and slender, similar to *Aceratherium incisivum* but again, somewhat shorter and less flattened (Hünermann 1989, fig. 62, table 15). The mt III is much shorter than a specimen from Tung-gur referred to *Acerorhinus zernowi* by Cerdeño (1996, fig. 9C). Like the metacarpals, the metatarsals are less shortened than in typical *Chilotherium.*

Discussion. The ventrally hollowed-out mandibular symphysis and the flattened tusks shows that this plesiomorphic aceratherine taxon belongs in the *Chilotherium-Acerorhinus* group. The shape of the lower cheek teeth, especially the long paralophids, excludes *Acerorhinus* but might fit an early *Chilotherium,* less derived than *C. kiliasi,* in which the metalophids are already rounded as in later *Chilotherium.*

The postcranial bones could fit an early *Chilotherium* well, being close to the primitive state (as represented by

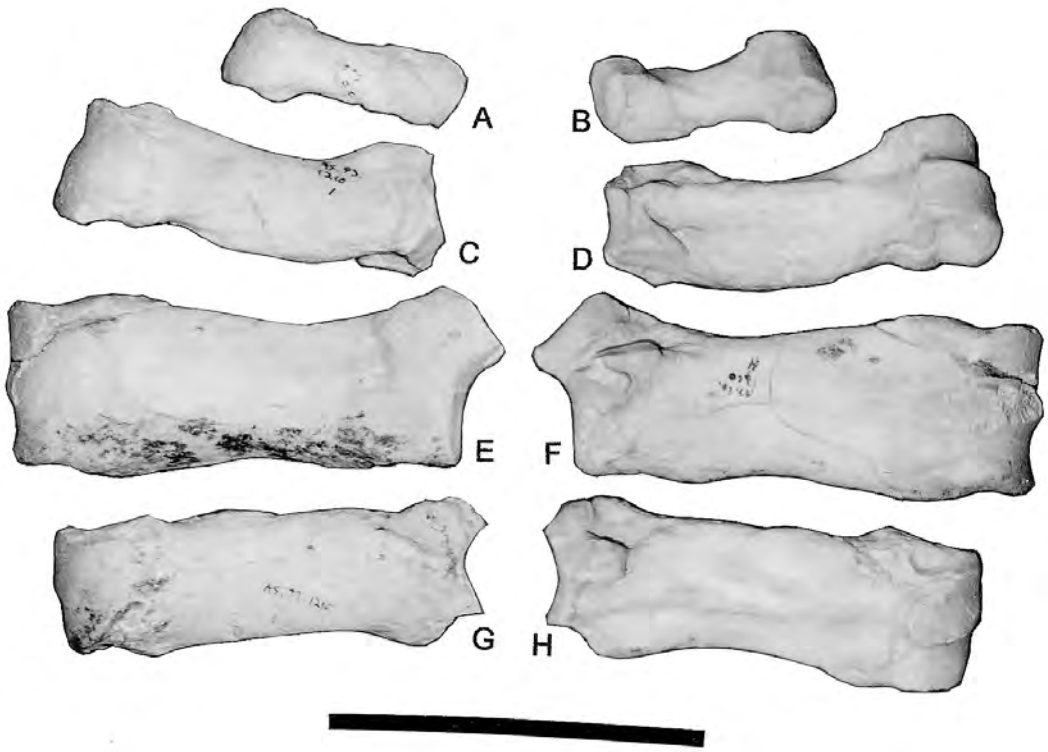

Figure 12.15. Metacarpals of right forelimb AS.93.1210 of *Chilotherium* sp. (primitive) from Loc. 12. Left row: plantar view. (**B**). Right row: palmar view. (**A,B**) mc V; (**C,D**) mc IV; (**E,F**) mc III; (**G,H**) mc II. Scale bar = 10 cm.

Aceratherium) but somewhat shortened, as would be expected. There is no direct association between the mandibles and the postcranial elements, but the shared "primitive *Chilotherium*" characteristics strongly suggest that they belong together. The material may, of course, represent more than one species.

It seems that this taxon is more primitive than any of the *Chilotherium* species so far described (see discussion under *C. kiliasi* above), but we have refrained from creating a new name, at least until the status and relationship of the existing nomina *C. samium, C. kiliasi,* and *C. wimani* are resolved. It differs from all known *Chilotherium* and from *Subchilotherium* in its angular lower cheek tooth morphology and its relatively large premolars. The earliest records of undisputable *Chilotherium* from the eastern Mediterranean reported by Heissig (1996) are from MN 10, a result in accordance with their first occurrence near the MN 10-11 boundary at Loc. 49 in the Sinap Formation. It is conceivable that cf. *Chilotherium* from the Vallesian Sinap localities could be close to the origin of *Chilotherium* s. str.

Stephanorhinus pikermiensis (Toula 1906)

Taxonomy:

Rhinocerotinae
Rhinocerotini
Stephanorhinus pikermiensis (Toula 1906)

Restricted synonymy:

1996 *Stephanorhinus* sp. (*pikermiensis*-group) Kappelman et al. table 6.2

Sinap Material. Loc. 33: isolated i1 AS.89.353, partial astragalus sin AS.90.50; MTA collection (Kavakdere): juvenile maxilla and toothrow dex with DP1–M1 06-AKK-0084, astragalus dex 06-AKK-038.

Age. Loc. 33 and probably all MTA localities are in the upper fossiliferous level of Upper Kavakdere, with a magnetostratigraphic age of 8.1 Ma (Kappelman et al. chapter 2, this volume).

Remarks. The incisor is large and stout for an i1, capped by a bean-shaped enamel crown very similar to the *Dicerorhinus orientalis* specimen figured by Ringström (1924, pl. 1, fig. 4). The DP1 is small relative to the other teeth and DP2 is elongated as is typical of the genus but is too worn to show much morphology (fig. 12.16). The DP3 and DP4 show a distinct paracone style and fold close to the buccomesial corner of the tooth, as figured by Weber (1904, pl. 16, fig. 1) and Ringström (1924, pl. 1, figs. 1, 2). The M1 shows the same feature, and, like DP4, a strong inflection of the ectoloph over the metacone (cf. Ringström 1924, pl. 1, fig. 1). The astragalus has an asymmetrical trochlea with relatively deep relief and a relatively short neck. The distal articular surface is relatively broader than in *Ceratotherium*.

Figure 12.16. Left upper toothrow with DP1–M1 06-AKK-0084 of a subadult *Stephanorhinus pikermiensis* from Upper Kavakdere. MTA collection. Scale bar = 10 cm.

Discussion. The incisor AS.89.353 is unequivocal evidence for *Stephanorhinus,* as *Ceratotherium* lacks incisors entirely and the i1 of the aceratherines, if present at all, is much smaller. With this confirmation, the identification of the other specimens described above may also be regarded as secure. *Stephanorhinus* was evidently present as a rare taxon alongside the somewhat larger and more graviportal *Ceratotherium*.

The large two-horned Rhinocerotini of the later Neogene have long been placed in the wastebasket taxon *Dicerorhinus,* but gradually, over the past several decades, they have been split between *Stephanorhinus* Kretzoi 1942 (extended down from the early Pleistocene type species *S. etruscus*) and *Lartetotherium* Ginsburg 1974 (extended up from the middle Miocene type species *L. sansaniense*). This process has happened by diffusion rather than taxonomic revision, and the result is confused. We have provisionally used *Stephanorhinus* here to emphasize the similarity of the *S. pikerminensis* with the Pliocene *S. megarhinus* and the Pleistocene *S. kirchbergensis,* all part of a well-defined and close-knit clade or lineage (Fortelius et al. 1993), but acknowledge that use of Toula's (1906) name *Dihoplus* is also possible for the late Miocene species. The status of the east Asian *S. orientalis* relative to the roughly coeval *S. pikermiensis* (which has priority) remains unresolved, but the former appears to be of distinctly larger body size throughout its stratigraphic range (unpublished research by M. Fortelius).

We must mention here that Cerdeño's (1995) cladistic analysis proposes a major reinterpretation of rhinoceros taxonomy involving *Stephanorhinus.* Briefly, her preferred cladogram unites *Stephanorhinus,* restricted to dolichocephalic forms, with the dolichocephalic elasmotherines *Ninxiatherium* and *Elasmotherium,* based only on two of the most homoplastic characters imaginable for the Rhinocerotidae: skull length and loss of upper incisors (Osborn 1903; Heissig 1981). It does not help that Cerdeño splits skull lengthening into "normal zygomatic width," "dolichocephaly," "long nasal length," and "backward inclination of ascending ramus [of the mandible]," because all these categories record the same basic (secondary) lengthening of the skull. Neither does it help that the character state

for loss of I2 is missing for *Lartetotherium* in her matrix. For this particular aspect, Cerdeño's analysis effectively substitutes superficial and homoplastic similarity for the detailed evidence from cranial and dental morphology that supports the conventional interpretation (Fortelius and Heissig 1989; Fortelius et al. 1993). We find the proposed reclassification difficult to accept, but a full refutation is beyond the scope of this chapter. For the elasmotheres, Cerdeño's classification was decisively rejected by Antoine (2000).

Ceratotherium neumayri (Osborn 1900)

Taxonomy:

Dicerotini
Ceratotherium neumayri (Osborn 1900)

Restricted synonymy:

1975 *Diceros neumayri* Heissig table 8
1991 *Diceros neumayri* Sen p. 260
1996 *Ceratotherium* cf. *C. neumayri* Kappelman et al. table 6.2
1996 Rhinocerotidae indet. (large) Kappelman et al. table 6.2

Sinap Material. Loc. 12: humerus dex distal part AS.95.319, radioulna dex proximal part AS.95.348, magnum dex AS.95.333, tibia dex AS.95.339, astragalus dex AS.95.422; Loc. 49: p4 or p3 dex AS.91.187, associated astragalus and calcaneum AS.94.1362; Loc. 42: mt III sin AS.94.1286; MTA collection (Sinap): juvenile palate with milk molars 06-SIN-0138, juvenile maxilladex 06-SIN-0149, juvenile maxilla sin 06-SIN-0272, juvenile maxilla dex 06-KAY-21, juvenile mandibular ramus sin with dp1–m1 06-SIN-0134, juvenile mandibular ramus sin with dp1–m1 06-SIN-0273, mc III sin 06-KAY-10; MTA collection (Kavakdere): DP2–DP3 dex 06-AKK-031, humerus sin 06-AKK-032, mc II sin 06-AKK-034, mc III sin 06-AKK-035, mt III sin 06-AKK-036, mt IV sin 06-AKK-037; MTA collection (Çobanpinar): juvenile right maxilla with DP1–DP3, figured by Sen (1970, pl. II, fig. 1), since apparently lost; PDTFAU collection: unnumbered tibia from Şenyürek's Loc. F2 ("Aşağı yoncalık"); MNHN collection (Yassiören): dp3 sin TRQ 1048.

Age. The magnetostratigraphic age estimates are 9.6 Ma for Loc. 12 and 9.1 Ma for Loc. 49. Loc. 42 (Çobanpinar) is here placed in MN 13 (Van der Made, chapter 13, this volume). The other Sinap localities are almost certainly from the middle Sinap member, with an age span of 10.7–9.3 Ma (Kappelman et al., chapter 2, this volume). The taxon, or more properly lineage, thus has a range in the Sinap Formation of ~11–6 m. y.

Remarks. The milk upper dentitions from the middle Sinap localities feature a large DP1; a distally displaced paracone rib not only on DP2 but on the posterior milk molars as well; and a mesiolingually projecting, unconstricted protocone base, all characteristics of the Dicerotini. The specimen from Çobanpinar also has a large DP1 but differs from the earlier form in having strongly developed metacone styli on DP2 and DP3 (cf. Heissig 1975, p. 148). The mandibles show equally distinct characters: deep rami that taper strongly toward anterior, large dp1, shallow buccal folding, and relatively large hypolophid of the lower cheek teeth.

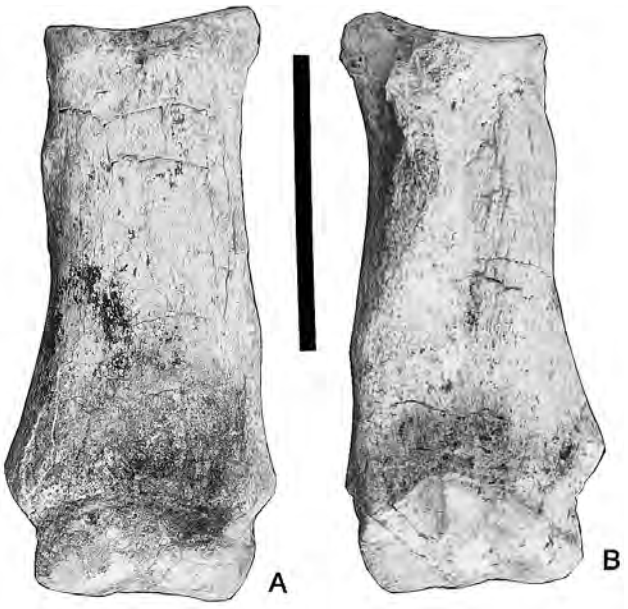

Figure 12.17. Left metatarsal III AS.94.1286 of *Ceratotherium neumayri* from Loc. 42 (Çobanpinar). (**A**) Plantar view; (**B**) palmar view. Scale bar = 10 cm.

The humerus 06-AKK-032 is very short and stocky, easily distinguished from the more slender humerus of *Stephanorhinus*. The astragalus AS.95.348 from Loc. 12 has a trochlea with quasi-equal lateral and medial ridges, unlike the markedly asymmetrical trochlea of *Stephanorhinus* and corresponding to the distal articulation of tibia AS.95.339 from the same locality. The postcrania from Loc. 12 are assigned to *Ceratotherium* primarily by size, as only one large species is known to occur there. The astragalus AS.94.1362 from Loc. 49 is similar to the one from Loc. 12 but is larger. The metapodials are short and plantopalmarly flattened, as is typical of the genus, including the living *C. simum*. They differ from *Stephanorhinus* especially in that the distal trochlea has low relief and a broad, shallow keel (fig. 12.17).

Discussion. It appears that several related taxa of Dicerotini are found in the eastern Mediterranean late Miocene (cf. Heissig 1975), but pending a review of the group, we have conservatively placed them all in the conventional taxon, following Kaya (1994). The material from Loc. 12 and Loc. 1 (Sinap project as well as the MTA collection) seems to be consistently of a smaller size than the material from Loc. 49 and later. It is not possible here to judge whether a single evolving lineage underwent size increase at the beginning of the Turolian, or whether a second, replacing taxon immigrated at this time. Kaya (1994) inter-

preted the Anatolian material to represent a single lineage that increased in size from MN 9 to MN 12. Tshiskarishvili (1987) described the Vallesian form from Eldari-2 in the Caucasus as a separate species, *Diceros gabuniai*.

General Discussion

Chronology and Correlation

A range chart of the Sinap rhinoceroses is given in table 12.1. The rhinoceros assemblage from İnönü I, with *Brachypotherium brachypus, Hoploaceratherium tetradactylum,* and *Hispanotherium grimmi,* is similar to that of Paşalar (Fortelius 1990) and identical to that of Çandir (Heissig 1976). It thus seems to be representative for the early-middle Miocene transition of Anatolia as a whole, and perhaps western Asia generally. The European immigrant *Alicornops simorrensis* appears in the latest middle Miocene, apparently replacing *Hoploaceratherium* (Heissig 1996), but is at most ambiguously recorded at Sinap.

These Anatolian localities have usually been placed in MN 6 (Mein 1989; Steininger et al. 1996). If Locs. 24 and 24A (İnönü I) are indeed closely related to the volcanic events of ~15–16 Ma (Kappelman et al. 1996), these localities would be close to the MN 5/6 boundary in the correlations of Steininger et al. (1996). If the calibration of Krijgsman et al. (1996) is used, İnönü I is placed deep within MN 5. This raises the question of provincial diachrony in the appearance and disappearance of taxa, as one of the most characteristic MN 6 species, *Listriodon splendens,* is present at the locality. *Listriodon splendens* is known to disappear from the eastern Europe and the eastern Mediterranean one MN unit before it becomes extinct in western and central Europe, and it seems quite likely that it also arrived there earlier, given the probable south Asian origin of the group (Fortelius et al. 1996a). For the rhinoceroses, the situation is ambiguous in that *Hispanotherium* disappears from western Europe before MN 6, *Brachypotherium brachypus* has a long range spanning MN 5–6 in a large area, whereas *Hoploaceratherium tetradactylum* is only recorded in western Europe from Sansan, France, the type locality of MN 6 (Heissig 1996; NOW database March 2000). The question of diachrony and the MN system is too complicated to be discussed further here, but it should be mentioned that Alroy et al. (1998) found no evidence of directional diachrony in the MN system as a whole, as represented in the NOW database. A conservative interpretation of the evidence for İnönü I seems to be that it should be placed close to the MN 5/6 transition, always keeping in mind that the MN units strictly speaking do not have boundaries that can be expressed in units of time (de Bruijn et al. 1992).

The range of *Acerorhinus zernowi* at Sinap extends the MN 9–10 given by Heissig (1996) trivially if at all. The derived *Acerorhinus* from the Upper Kavakdere localities (MN 11/12 boundary or MN 11) extends the range of the genus in Anatolia and points to a continuity between the west and east Asian populations.

The primitive cf. *Chilotherium* represents both a stage of evolution and an age interval preceding the appearance of true *Chilotherium* in the eastern Mediterranean in MN 10 (cf. Heissig 1996). True *Chilotherium* first appears at Sinap at Loc. 49, and appears to have entered during the hiatus between Loc. 1 at 9.3 Ma and Loc. 49 at 9.1 Ma, probably within the temporal equivalent of later MN 10.

The name *Chilotherium kiliasi* (Geraads and Koufos 1990) is used here for the first time for material other than the hypodigm from Pentalophos I. As discussed above, the name may be a synonym of *C. samium* (Weber 1905), based on problematical specimens from an unknown horizon of Samos. Heissig (1996) recognized *C. samium* from the eastern Mediterranean from MN 10/11 to MN 11, a short interval that matches the occurrence of *C. kiliasi* at Pentalophos I

Table 12.1. Range Chart of Sinap Rhinoceros Taxa Identified at the Species Level

Sinap Locality	24	72	12	51	1	49	34	26	42
Age (Ma)	15–16?	10.1	9.6	?	9.3	9.1	8.4	8.1	~6
Brachypotherium brachypus	X								
Hoploaceratherium tetradactylum	O								
Begertherium grimmi	X								
Acerorhinus zernowi			O		O	X			
Acerorhinus sp. nov.								X	
cf. *Chilotherium* sp. (primitive)		X	XXXX	X	X				
Chilotherium kiliasi						X			
Ch. cf. *C. habereri*						X			
Chilotherium indet. (derived)							X	X	?
Stephanorhinus pikermiensis								X	
Ceratotherium neumayri			X		O	X		X	X

Notes: X, occurrences documented during the Sinap project; O, occurrences known only from previous collections; ?, questionable occurrences. Loc. 51 was interpolated to minimize range extensions of the occurring taxa.

Source: Lunkka et al. (1999).

and Loc. 49 perfectly. The mammal fauna of Pentalophos I, the type locality of *C. kiliasi,* is quite similar to that of Loc. 49: of 15 large mammal genera at Pentalophos, seven or eight are also found at Loc. 49, at least four of them represented by the same species (NOW database, March 2000). The faunal dating of Pentalophos I is problematic, but an age somewhat earlier than that of the MN 10 localities of the Axios valley has been proposed (de Bonis and Koufos 1999). The presence of *Dinocrocuta gigantea* at Pentalophos I (de Bonis and Koufos 1999), cited in favor of an earlier Vallesian age, does not necessarily constitute a difference from Loc. 49, which has an indeterminate percrocutid (Viranta and Werdelin, chapter 8, this volume). The magnetostratigraphic age of Loc. 49 at 9.1 Ma is just after the temporal equivalent of the MN 10/11 transition, according to the correlation of Steininger et al. (1996) or within late MN 10, according to Krijgsman et al. (1996). The presence at Loc. 49 of a second, rare, and more derived species of *Chilotherium* and the apparently greater degree of reduction of p2 in the Loc. 49 specimens of *Chilotherium kiliasi* are consistent with (but certainly do not prove) the interpretation that Loc. 49 is somewhat younger than Pentalophos I. The presences at both localities of *Chilotherium kiliasi* together with *Acerorhinus zernowi* and *Ceratotherium neumayri* might be taken as an indication that the difference in age cannot be a major one, however.

Chilotherium kowalevskii is one of the more distinct species of *Chilotherium* and a likely identification for at least some of the Upper Kavakdere *Chilotherium* material. The type locality is Grebeniki, with an MN 11–12 correlation (NOW database March 2000), and Heissig (1996) gives the range in the eastern Mediterranean as MN 10–11 to MN 11–12. The magnetostratigraphic correlation of the Upper Kavakdere localities is 8.4–8.1 Ma, spanning the MN 11/MN 12 boundary, according to Steininger et al. (1996) or within MN 11, according to Krijgsman et al. (1996).

The hypsodont *Chilotherium* of Loc. 49 is based on only two specimens, but as already discussed, it is clearly distinct from the Kavakdere form and represents the form referred to *C. habereri* by Heissig (1975, 1996). The range given by Heissig (1996) for *C. habereri* in the eastern Mediterranean is MN 10–11, which comfortably includes the magnetostratigraphic age estimate of Loc. 49 (9.1 Ma, which is within MN 10) (Steininger et al. 1996; Krijgsman et al. 1996). We use the name *Chilotherium* cf. *C. habereri* for this form, in acknowledgment of differences from the Chinese *C. habereri,* and suggest that it may be related to *C. persiae.*

Heissig (1996) lists *Stephanorhinus pikermiensis* only from Samos and Pikermi. The taxon is listed as '"*Dicerorhinus*" *schleiermacheri*' by Bernor et al. (1996b) from Pikermi (8.3–8.2 Ma, correlated with MN 11/12) and from Samos Main Bone Beds (≥7.1 Ma, correlated with MN 12). The occurrence of the species in the upper (8.1 Ma) level of Upper Kavakdere matches this range well.

Ceratotherium neumayri has a very long range in the eastern Mediterranean, MN 9 to MN 12–13, according to Heissig (1996). More or less the same range (Loc. 12 to Loc. 42) is represented in the Sinap Formation, but the material is unfortunately too incomplete to allow study of the evolution of this clade. All that can be said is that the early material seems smaller than the late material, as already noted by Heissig (1975) and recently confirmed by Kaya (1994), and that the material from Loc. 42 shows dental change in the direction of the Pliocene and Recent plagiolophodont representatives of the genus. The changes seen are of a magnitude that by common large mammal standards would justify recognition of separate morphospecies and possibly genera, and it seems that closer study of this group might be rewarding.

Paleoecology

The rhinoceroses of the Sinap Formation record part of the substantial faunal changes that took place from the beginning of the middle Miocene to the end of the late Miocene. The general trend is the same as for other large herbivores: a shift toward larger and more hypsodont species, evidently better adapted to cope with increasingly seasonal environments and their tougher and more abrasive forage.

It is unfortunate that there is a major gap in the record between the early middle Miocene Loc. 24 and 24A (İnönü I) and the MN 9 localities of the middle Sinap member, because a complete turnover of the rhinoceros fauna occurred during this missing interval. Before the gap, there is an ecologically diverse assemblage of species at Sinap, including the fairly generalized and brachydont *Hoploaceratherium,* the large and short-legged mesodont *Brachypotherium,* and the cursorial and hypsodont *Hispanotherium.*

When we first pick up the rhinoceros record after the gap, we see an entirely different assemblage at Sinap, dominated by aceratherine species, which are probably descendants, in a broad sense, of *Hoploaceratherium* and augmented by a recent immigrant from Africa, the large and hypsodont *Ceratotherium.*

The stratigraphic and zoogeographic evidence summarized in the taxonomic discussion (above) suggests that an *Acerorhinus zernowi*-like form evolved in the late middle Miocene of Central Asia (Cerdeño 1996), being essentially a somewhat more robust version of earlier forms such as *Hoploaceratherium tetradactylum* and Borissiak's (1927) middle Miocene Turgai aceratherine (both of which Cerdeño refers to *Acerorhinus*). This form gave rise to a lineage of forms increasingly convergent on *Chilotherium,* from *A. tsaidamensis* and *A. hezhengensis* to *A. palaeosinensis* and, perhaps, specialized forms like *A. cornutus* and *Sinorhinus brancoi* (Ringström 1924; Qiu et al. 1988; Heissig 1989, 1996). The main trends include increased folding of the dental enamel, shortening of the nasals, a shifting of the eye to a more elevated location, and, probably as part of the same complex, a flattening of the skull roof. The postcranial skeleton was eventually reduced to *Chilotherium*-like proportions at the stage of *A. palaeosinensis* (Ringström

1924), but the manus seems to have remained pentadactyl and the metapodials seem to have been both more flattened and more splayed than in *Chilotherium,* as discussed above. *Acerorhinus fuguensis,* described from the late Miocene of Fugu by Deng (2000), appears to be a large form of *A. palaeosinense,* with allometric development of a sagittal crest.

It appears that the earlier form of *Acerorhinus* represented at Sinap is somewhat derived relative to *A. zernowi,* whereas the later form shows a mixture of unique characters and similarities with *A. palaeosinense* and the probably conspecific *"Aceratherium incisivum"* from Tchobrouchi (Pavlow 1915). This suggests a continuously evolving population over much of Asia in the earlier part of the late Miocene. The reason for the greater diversification of this clade in east Asia may be related to the absence of the African Dicerotini there.

The most primitive forms of *Chilotherium* appear to have been little if at all removed from the primitive aceratherine lifestyle, at least as far as diet goes. The weak postcranial skeleton and the flat-topped skull with a high orbit found in the later forms could be interpreted to indicate a hippopotamus-like lifestyle, but, as in the case of *Brachypotherium,* no direct evidence seems to exist. A problem with this reasoning is that it makes it difficult to exclude the more derived *Acerorhinus* from the "hippo guild," particularly in view of its flattened and strongly splayed metapodials. Sympatry of several hippo-like species is difficult to envision, even if the dental evidence points to dietary differences between the species. The lack of any modification of the choanae in these forms may also argue against an aquatic life style.

The material of *Ceratotherium* is too fragmentary to allow assessment of evolutionary change at Sinap, but Heissig (1975) and Kaya (1994) reported size increase in this lineage within Anatolia as a whole. The youngest material from the Sinap Formation comes from Loc. 42 (Çobanpinar) and shows dental changes in the direction of living *Ceratotherium simum,* a true grazer.

A large species of the Eurasian genus *Stephanorhinus,* more cursorial and less hypsodont than *Ceratotherium* but only slightly smaller, is rare but present in the MN 12 assemblage from Kavakdere.

The number of sympatric rhinoceros species is three at most levels, reaching four in the MN 10/11 and MN 12 assemblages. The middle Miocene assemblage is composed of a smallish, plesiomorphic browsing form, a large, short-legged mixed feeder, and a cursorial form, apparently a grazer or a mixed feeder leaning heavily toward the grazing end of the spectrum (Fortelius 1990). In the Vallesian assemblage from the middle Sinap member, only forms in the browser or browser-mixed feeder range are documented. There is still a spread of sizes, but most species are small to medium-sized, and only *Ceratotherium* is large. Loc. 49 at ~9.1 Ma ago has the same structure, with three smallish to medium-sized aceratherines and *Ceratotherium*. Two of the three aceratherines represent *Chilotherium,* which is already at this time beginning to evolve hypsodont cheek teeth. The main change from this level to Kavakdere at ~8.4–8.1 Ma is that only one *Chilotherium* is now present, and instead a second large form appears: *Stephanorhinus pikermiensis.* Compared with *Ceratotherium, Stephanorhinus* appears to be somewhat smaller, more cursorial, and less adapted to feeding on abrasive foods, but the material from Sinap is not sufficiently complete to address this question locally.

Perhaps the most interesting overall feature of the rhinoceros assemblages from the Sinap Formation is the absence in the middle Sinap member of forms clearly adapted to feeding on tough or abrasive vegetation. This is remarkable, as such forms were present both before and after that interval, and might be taken as evidence that unusually mesic (forested?) conditions prevailed during the early part of the late Miocene. This is also the interval during which the mammal taxonomic richness peaks and hominoid primates are recorded from the region.

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Appendix

Appendix Table 12.1. Measurements of Sinap Dental Specimens

Taxon/ Specimen	Tooth	Measurement (mm) LB	LL	WD	WP
cf. *Chilotherium* indet. (primitive)					
AS.90.132	p4	38.8	37.9	26.6	24.2
	m1	39.4	40.3	26.8	25.4
	m2	42.1	42.9	26.1	25.1
Chilotherium kiliasi					
AS.93.963	P3	—[1]	31.5	44.8	46.6
	P4	—	31.0	47.0	48.6
	M1	—	35.0	48.3	49.6
	M2	45.5	37.4	46.9	53.3
	M3	50.9	41	—	46.9
AS.93.1074	M1	—	34.0	—	—
	M2	46.3	38.7	51.0	57.6
	M3	50.8	37.0	—	47.7
AS.93.809	p2	21.5	21.6	15.1	13.9
	p3	30.0	28.0	22.4	17.4
	p4	36.0	34.5	26.7	23.8
	m1	38.0	—	27.7	24.7
	m2	43.4	41.6	26.5	26.7
	m3	44.0	45.1	25.4	25.5
AS.94.566	p2	20.5	20.0	15.1	13.0
	p3	27.7	—	—	
	p4	36.0	34.0	25.5	21.6
	m1	40.4	40.1	26.2	25.2
	m2	43.7	42.2	23.3	23.4
AS.93.810	p3	29.6	27.2	22.2	19.1
	p4	34.5	34.0	26.4	23.0
	m1	39.0	36.0	28.1	24.4
	m2	42.2	41.2	26.7	24.9
	m3	42.6	44.3	24.6	24.4
AS.93.815	p2	22.8	21.7	15.3	14.0
	p3	28.6	28.0	22.8	20.1
	p4	33.6	33.6	26.1	22.5
	m1	39.6	36.9	26.6	25.8
	m2	41.8	40.2	24.7	26.2
	m3	41.0	44.0	23.4	23.5
AS.91.701	m2	42.6	41.2	25.6	26.3
	m3	44.5	46.1	23.1	24.6
AS.94.537	m2	43.1	44.3	23.8	23.7
	m3	41.6	41.1	22.0	22.0
AS.94.316	m3	45.0	42.9	26.4	25.5
	m4	—	38.6	19.0	22.7
AS.93.1193	dp2	31.2	30.6	15.2	14.3
	dp3	39.5	37.9	18.5	18.6
	dp4	42.7	38.7	22.0	22.2
Chilotherium cf. *C. habereri*					
AS.90.313	dp2	26.9	27.2	14.0	12.8
	dp3	35.8	37.6	18.0	17.2
	dp4	40.1	41.8	21.5	19.2
	m1	41.0	—	24.0	—
AS.92.155	m3	—	48.5	23.2	24.2
Chilotherium indet. Upper Kavakdere					
AS.92.602	p3	32.0	—	—	19.6
	p4	36.0	—	—	22.1
	m1	39.0	—	—	—
	m2	40.2	—	24.4	25.2
	m3	44.5	44.1	23.0	24.9
Acerorhinus zernowi					
AS.93.823	P4	36.0	33.2	51.6	51.7
	M1	43.0	31.4	48.8	54.2
	M2	49.0	35.9	44.9	52.5
	M3	48.0	—	—	48.1
AS.95.747	P4	39.8	35.6	47.1	49.0
	M1	42.9	34.4	47.8	49.6
	M2	46.1	38.8	43.2	48.7
	M3	47.1	41.1	—	46.1
AS.94.554	M1	41.0	32.6	45.5	50.4
	M2	45.0	35.6	43.7	51.9
	M3	52.0	34.4	—	47.0
AS.92.150	p2	34.6	34.3	22.2	19.6
	p3	35.7	36.5	26.7	24.0
	p4	39.2	37.9	28.4	26.2
	m1	41.7	39.6	27.8	28.2
	m2	43.9	45.1	27.7	27.6
	m3	45.3	47.4	25.9	28.1
AS.94.315	p3	36.1	34.2	25.5	24.4
	p4	36.5	34.7	25.4	24.4
	m1	38.7	39.2	25.8	27.5
	m2	44.9	41.2	27.5	28.1
	m3	45.0	44.1	25.2	25.9
Acerorhinus sp. nov.					
AS.89.279	p2	—	32.9	22.3	18.2
AS.90.184	p2	36.7	34.4	23.1	19.7
Ceratotherium neymayri					
AS.91.187	p4/3	44.0	—	33.2	29.1

[1]—, Cannot be measured.

Appendix Table 12.2A. Statistics of Dental Measurements of *Chilotherium kiliasi* and *Acerorhinus zernowi* from Sinap, Upper Teeth

Variable/	P4				M1				M2				M3		
Taxon	BL	LL	WP	WD	BL	LL	WP	WD	BL	LL	WP	WD	BL	LL	WP
hilotherium kiliasi															
N of cases	1	2	2	2	0	2	1	1	2	2	3	3	2	2	2
Minimum	37	31	48.6	47	—[1]	34	49.6	48.3	45.5	37.4	53.3	46.9	50.8	37	46.9
Maximum	37	32.7	53.3	51.1	—	35	49.6	48.3	46.3	38.7	57.6	51	50.9	41	47.7
Median	37	31.9	51	49.1	—	34.5	49.6	48.3	45.9	38.1	56.6	50.3	50.9	39	47.3
Mean	37	31.9	51	49.1	—	34.5	49.6	48.3	45.9	38.1	55.8	49.4	50.9	39	47.3
C.V.	1	0.04	0.07	0.06	—	0.02	1	1	0.01	0.02	0.04	0.04	0	0.07	0.01
Acerorhinus zernowi															
N of cases	2	2	2	2	3	3	3	3	3	3	3	3	4	3	4
Minimum	36	33.2	49	47.1	41	31.4	49.6	45.5	45	35.6	48.7	43.2	47.1	34.4	46.1
Maximum	39.8	35.6	51.7	51.6	43	34.4	54.2	48.8	49	38.8	52.5	44.9	52	42.6	48.1
Median	37.9	34.4	50.4	49.4	42.9	32.6	50.4	47.8	46.1	35.9	51.9	43.7	49.5	41.1	47.2
Mean	37.9	34.4	50.4	49.4	42.3	32.8	51.4	47.4	46.7	36.8	51	43.9	49.5	39.4	47.1
C.V.	0.07	0.05	0.04	0.06	0.03	0.05	0.05	0.04	0.04	0.05	0.04	0.02	0.05	0.11	0.02

Appendix Table 12.2B. Statistics of Dental Measurements of *Chilotherium kiliasi* and *Acerorhinus zernowi* from

Variable/ Taxon	p2				p3				p4			
	BL	LL	WP	WD	BL	LL	WP	WD	BL	LL	WP	WD
Chilotherium kiliasi												
N of cases	3	3	3	3	4	3	3	3	4	4	4	4
Minimum	20.5	20	13	15.1	27.7	27.2	17.4	22.2	33.6	33.6	21.6	25.5
Maximum	22.8	21.7	14	15.3	30	28	20.1	22.8	36	34.5	23.8	26.7
Median	21.5	21.6	13.9	15.1	29.1	28	19.1	22.4	35.3	34	22.8	26.3
Mean	21.6	21.1	13.6	15.2	29	27.7	18.9	22.5	35	34	22.7	26.2
C.V.	0.05	0.05	0.04	0.01	0.04	0.02	0.07	0.01	0.03	0.01	0.04	0.02
Acerorhinus zernowi												
N of cases	4	4	4	4	2	2	2	2	3	3	3	3
Minimum	29.6	28.4	18.6	20.5	35.7	34.2	24	25.5	36.5	34.7	24.3	25.4
Maximum	34.6	34.3	21	22.2	36.1	36.5	24.4	26.7	39.2	37.9	26.2	28.4
Median	32.1	30.1	19.6	21.3	35.9	35.4	24.2	26.1	38.5	36.4	24.4	27.1
Mean	32.1	30.7	19.7	21.3	35.9	35.4	24.2	26.1	38.1	36.3	25	27
C.V.	0.08	0.08	0.05	0.04	0.01	0.05	0.01	0.03	0.04	0.04	0.04	0.06

Sinap, Lower Teeth

m1				m2				m3			
BL	LL	WP	WD	BL	LL	WP	WD	BL	LL	WP	WD
4	3	4	4	6	6	6	6	9	9	9	9
38	36	24.4	26.2	41.8	40.2	23.4	23.3	41	41.1	22	22
40.4	40.1	25.8	28.1	43.7	44.3	26.7	26.7	45	46.1	25.5	26.4
39.3	36.9	25	27.2	42.9	41.4	25.6	25.2	43.4	44.3	24.4	23.4
39.3	37.7	25	27.2	42.8	41.8	25.2	25.1	43	43.9	24.1	23.9
0.03	0.06	0.02	0.03	0.02	0.03	0.06	0.06	0.03	0.04	0.05	0.06
3	2	2	2	3	2	2	2	2	2	3	2
38.7	39.2	27.5	25.8	42	41.2	27.6	27.5	45	44.1	25.9	25.2
42	39.6	28.2	27.8	44.9	45.1	28.1	27.7	45.3	47.4	28.1	25.9
41.7	39.4	27.9	26.8	43.9	43.2	27.9	27.6	45.2	45.8	27.8	25.6
40.8	39.4	27.9	26.8	43.6	43.2	27.9	27.6	45.2	45.8	27.3	25.6
0.04	0.01	0.02	0.05	0.03	0.06	0.01	0.01	0	0.05	0.04	0.02

Appendix Table 12.3. Measurements of Postcranial Material from Sinap

Bone/ Taxon	Locality	Number	Side	Measurement (mm)								
				L	WP	APP	WS	APS	WD	APD	JWD	JAPD
Humerus												
cf. *Chilotherium* sp. primitive	12	AS.93.1210	rt.	—	—	—	—	—	—	—	—	—
	51	AS.90.134	rt.	350.0	145.0	118.0	53.0	58.0	128.0	89.0	92.0	—
Ceratotherium neumayri	12	AS.95.319	rt.	—	—	—	66	65	152	—	99	—
Radius												
cf. *Chilotherium* sp. primitive	12	AS.93.1210	rt.	—	77.0	40.0	—	—	—	—	—	—
Acerorhinus zernowi	12	06-KAY-14	rt.	290.4	83.1	55.9	42.7	30.8	88.0	55.2	—	—
Ceratotherium neumayri	12	06-KAY-22	rt.	—	107.4	67.4	—	—	—	—	—	—
	12	06-KAY-8	rt.	363.0	110.0	71.0	58.4	44.3	118.7	73.0	—	—
	12	AS.95.348	rt.	387.0	102.0	84.0	56.0	41.0	100.0	76.0	89.0	48.0
Tibia												
Chilotherium indet. Upper Kavakdere	Kavakdere	06-AKK-017	lt.	276.0	123.7	103.3	42.8	43.4	83.2	58.6	—	—
	33	AS.90.52	rt.	—	—	—	—	—	85.0	57.0	66.0	—
Acerorhinus zernowi	49	AS.92.138	lt.	—	—	—	—	—	93.3	62.1	67.6	—
Ceratotherium neumayri	Oz F2	None	.	400.0	105.0	—	59.0	53.0	103.0	80.0	—	—
	12	AS.95.339	lt.	382.0	—	—	61.0	50.0	105.0	80.0	77.0	63.0
mc II												
cf. *Chilotherium* sp. primitive	12	AS.93.1210	rt.	105.0	39.0	34.0	30.0	15.0	34.0	33.0	31.0	33.0
Ceratotherium neumayri	Kavakdere	06-AKK-034	lt.	108.2	32.0	47.2	40.4	21.2	48.7	41.4	41.6	—
mc III												
cf. *Chilotherium* sp. primitive	12	AS.93.1210	rt.	122.0	44.0	41.0	34.0	15.0	44.0	36.0	40.0	36.0
Chilotherium indet. Upper Kavakdere	Kavakdere	06-AKK-015	rt.	—	—	38.9	36.5	16.6	45.9	33.6	40.2	—
	Kavakdere	06-AKK-029	rt.	135.0	56.6	48.7	41.4	18.5	51.5	40.4	45.3	—
Acerorhinus sp. nov.	26	AS.91.229	rt.	—	55.0	46.0	—	—	—	—	—	—
Ceratotherium neumayri	12	06-KAY-10	lt.	—	60.3	49.2	—	22.3	—	—	—	—
	Kavakdere	06-AKK-035	lt.	—	65.0	51.7	45.7	25.4	—	—	—	—
Begertherium grimmi	Inönü I	06-inö-77/1773	rt.	169.9	54.4	41.0	42.7	19.4	53.7	38.4	47.0	—
	24A	AS.92.664	lt.	—	57.0	—	40.0	21.0	—	—	—	—
mc IV												
cf. *Chilotherium* sp. primitive	12	AS.93.1210	rt.	97.0	31.0	33.0	25.0	14.0	31.0	33.0	29.0	33.0
Chilotherium indet. Upper Kavakdere	Kavakdere	06-AKK-016	rt.	92.5	32.9	35.7	25.1	13.7	31.1	28.8	28.6	—
	Kavakdere	06-AKK-030	rt.	89.4	32.8	39.7	27.5	21.0	31.8	36.4	29.7	—
Acerorhinus sp. nov.	26	AS.90.241	rt.	95.5	36.3	37.1	29.0	14.0	36.0	26.6	32.7	26.6

mc V												
cf. *Chilotherium* sp. primitive	12	AS.93.1210	rt.	61.0	14.5	19.5	13.5	9.8	23.0	19.1	17.9	19.1
mt II												
cf. *Chilotherium* sp. primitive	12	nonr	rt.	100.7	21.4	31.1	18.9	16.9	28.4	31.9	27.5	31.9
Chilotherium indet. Upper Kavakdere	Kavakdere	06-AKK-020	rt.	85.2	26.0	33.2	25.4	19.0	32.8	30.6	28.8	—
mt III												
cf. *Chilotherium* sp. primitive	72	AS.91.312	rt.	106.0	35.2	—	30.1	12.6	40.7	29.4	33.8	—
Chilotherium indet. Upper Kavakdere	Kavakdere	06-AKK-021	rt.	101.5	40.6	—	34.5	18.1	46.1	33.7	37.8	—
Ceratotherium neumayri	Kavakdere	06-AKK-036	lt.	175.3	57.9	52.2	49.7	26.5	68.8	47.3	56.1	—
	42	AS.94.1286	lt.	170.0	63.0	47.0	57.0	24.0	80.0	42.0	58.0	42.0
Brachypotherium brachypus	Inönü I	06-INÖ-77/1607	rt.	116.1	53.3	49.4	44.2	19.8	63.1	41.4	51.7	—
Brachypotherium sp.?	125	AS.94.143	.	86.0	—	38.0	39.0	23.0	49.0	38.0	44.0	38.0
mt IV												
Chilotherium indet. Upper Kavakdere	Kavakdere	06-AKK-022	rt.	83.4	36.3	33.5	26.9	15.8	33.3	33.5	28.1	—
Ceratotherium neumayri	Kavakdere	06-AKK-037	lt.	160.0	45.5	49.8	34.4	29.1	48.0	48.8	41.3	—
Begertherium grimmi	24A	AS.91.400	lt.	—	41.6	43.7	—	—	—	—	—	—
Astragalus				**L**	**W**	**AP**	**WP**	**APP**	**JWP**	**JAPP**		
Chilotherium indet. Upper Kavakdere	Kavakdere	06-AKK-018	lt.	67.1	77.0	43.9	—	—	—	—		
	33	AS.89.215	rt.	67.0	79.0	—	65.0	55.0	69.0	37.0		
	26	AS.89.286	lt.	64.0	76.0	—	61.0	51.0	66.0	33.0		
Acerorhinus zernowi	49	AS.91.731	lt.	61.5	78.5	51.2	65.9	50.0	69.3	39.5		
Ceratotherium neumayri	12	AS.95.423	rt.	77	93	—	82	68	74	52		
	49	AS.94.1362a	—	95.0	100.0	—	93.0	—	84.0	58.0		
Brachypotherium sp.?	125	AS.95.454	rt.	—	—	—	—	—	—	—		
Begertherium grimmi	24A	AS.92.667	lt.	82.0	88.0	55.0	78.0	—	77.0	44.0		

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