

Rhinocerotidae

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Among the Perissodactyla, Rhinocerotidae have traditionally been allied with tapirs because they lack a mesostyle, even though other primitive perissodactyls may also lack it (Hooker and Dashzeveg, 2004). The upper cheek teeth are π -shaped (figure 34.1) except M3, which is triangular. The incisors are separated from the cheek teeth by a diastema, as there is no canine; they consist of a chisel-shaped I1, borne by a slender premaxilla, a tusk-shaped i2, plus much smaller I2 and i1. However, I1, or both I1 and i2, become reduced or disappear in several lineages. Nasal and sometimes frontal horns, consisting of agglomerated hair (thus rarely fossilized), grow on more or less recognizable skull bosses in many genera; they are usually inserted behind one another but may rarely sit side by side. Although extensively pneumatized, the skull is robust, with thick bone and sutures fused in adulthood, and this certainly accounts for the good fossil record of the family. The temporal fossa is long, but the cranial base is shortened. The mandible has a transversely elongated condyle, plus an extra articular facet for the postglenoid process. The latter may be united with the posttympanic process beneath the auditory foramen. Horned forms (roughly the Rhinocerotini of Prothero et al. [1986], Rhinocerotinae of Cerdeño [1995], or Rhinocerotina of Antoine [2002]) lack a mastoid exposure, but it may have been present (as in the tapirs), in some hornless forms. They have three digits in the posterior limb, and three or four (the fifth digit being reduced but functional) in the anterior one. Dental terminology is shown in figure 34.1. The various stages of premolar molarisation are shown in figure 34.1C.

During the past two decades, various attempts have been made to resolve the phyletic relationships within the family. Almost every author agrees that this is a difficult task, mainly owing to the dearth of clearly identifiable synapomorphies, and the broad divergences in the published cladograms confirm this. The most parsimonious recent cladistic analyses, using no less than 282 characters (Antoine, 2002; Antoine et al., 2003), unite under the Rhinocerotini (which includes the bulk of the Rhinocerotinae) as an unresolved trichotomy, the Teleoceratina (Old and New World brachypotheres), the Aceratheriina (Old World aceratheres and related forms), and the Rhinocerotina (nonelasmotheres Old World horned rhinos); the Elasmotheriini are the sister

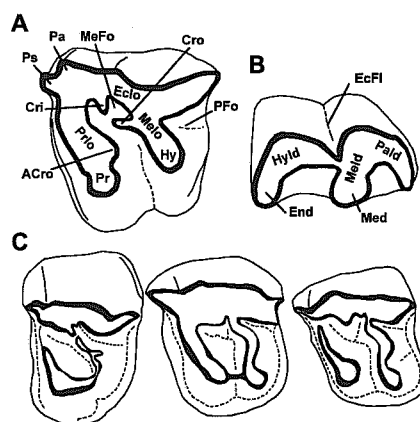


FIGURE 34.1 A) Terminology of upper tooth elements: ACro: antecrochet; Cri: crista; Cro: crochet; Eclo: ectoloph; Hy: hypocone; MeFo: medifossette; Melo: metaloph; Pa: paracone fold; PFo: post-fossette; Pr: protocone; Ps: parastyle. B) Terminology of lower tooth elements: EcFl: ectoflexid; End: entoconid; Hyld: hypolophid; Med: metaconid; Meld: metalophid; Pald: paralophid. C) Morphology of upper premolars; from left to right: submolariform, semimolariform, molariform (from Heissig, 1969).

group of the Rhinocerotinae. Even though many criticisms can be made of parsimony analysis (choice of characters, of coding, of number of states, of equal weighing, subjectivity of state control, etc.), which leads to significantly different results even when performed by renowned specialists, the phylogenies proposed by Antoine et al. (2002, 2003) can be used as working hypotheses.

There are five living species, all of them seriously threatened or even close to extinction. The small two-horned *Dicerorhinus sumatrensis*, found in Sumatra and the Malaysian peninsula, numbers at most a few hundred surviving individuals. Of the two single-horned species of *Rhinoceros*, *R. sondaicus* and *R. unicornis*, also from southeastern Asia, the former is the most seriously threatened, with perhaps 60 animals remaining in the wild. The African forms, *Ceratotherium*

simum and *Diceros bicornis*, are closely related (infra-tribe Dicerotini). Some morphological cladistic analysis (Groves, 1983; Prothero et al., 1986; Cerdeño, 1995; but not Geraads, 1988 and Antoine et al., 2003) and mitochondrial gene sequencing (Tougaard et al., 2001) suggest that, among living forms, African rhinos are the sister group of *Dicerorhinus* + *Rhinoceros*, but more molecular analyses would be welcome.

During the Miocene, African rhinos underwent a diversification comparable to those of the northern continents, but they have received much less attention than the Eurasian forms, especially from systematic and phylogenetic aspects. A number of specific studies, especially by Guérin and Hooijer, have appeared in the last decades, but the last broad review is 30 years old (Hooijer, 1978). As a result, the commonly used taxonomy in Africa is one which was in use a long time ago in Europe, where the meanings of the generic names *Brachypotherium*, *Aceratherium* and *Dicerorhinus* are now much more restricted than they used to be (Heissig, 1999). As in Eurasia, where many species have been wandering through several genera, the phylogeny and systematics of African rhinos are still confused. Much new material, a large part of it still unpublished, has come to light in recent decades, and there is little doubt that serious revisions of the African rhinos are needed. The present account takes a rather conservative view; I have tried to update the systematics, and raise a few phyletic issues, but this account should not be considered as more than preliminary.

ABBREVIATIONS

BMNH, Natural History Museum, London; FSL, Faculté des Sciences, Lyon; KNM, Kenya National Museums, Nairobi; MNHN, Muséum National d'Histoire Naturelle, Paris; NME, National Museum of Ethiopia, Addis Ababa.

Systematic Paleontology

Family RHINOCEROTIDAE Gray, 1821
 Subfamily RHINOCEROTINAE Gray, 1821
 Tribe RHINOCEROTINI Gray, 1821
 Subtribe TELEOCERATINA Hay, 1902
 Genus *BRACHYPOTHERIUM* Roger, 1904

Type Species *Brachypotherium goldfussi* (Kaup, 1834), from the early late Miocene (Vallesian) of Eppelsheim, Germany.

Diagnosis Large rhinos with broad and low skull, short hornless nasals, orbit far forward, powerful anterior dentition and especially large I1s with a short root, brachyodont cheek teeth and short but broad premolars. Upper and lower molars tend to have flattened labial walls and the latter have shallow ectoflexids. Short massive terminal limb segments, with a characteristically low talus.

BRACHYPOTHERIUM nov. sp.?

Figure 34.2

Some fossils from Buluk (= West Stephanie) in northern Kenya, collected and kindly made available to me by E. Miller, apparently belong to a new species. The best specimen is a relatively complete skull, KNM-WS-46072 (figure 34.2), which is low and broad, especially in the occipital area, with an almost flat cranial profile, a deep zygoma, and short hornless nasals. The short and broad premolars match those of the brachypotheres, and there are several typical brachypother

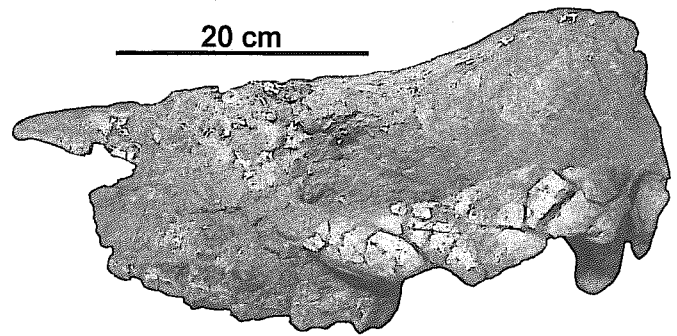


FIGURE 34.2 *Brachypotherium* nov.sp. ?, skull KNM-WS 46072 from the lower Miocene of Buluk, Kenya. © Publications Scientifiques du Muséum national d'Histoire naturelle, Paris (Cerdeño, 1993).

upper incisors and tali in the Buluk collection. The size is that of the small European brachypother *Prosantorhinus*, but this genus has a saddle-shaped skull, with a sagittal crest and a small nasal horn (Heissig, 1972). The Buluk skull is more like *Brachypotherium brachypus* from Europe (e.g., Cerdeño, 1993: plate 4, figure 11), and, pending detailed study, I tentatively include it in this genus, although the Kenyan material is certainly younger.

BRACHYPOTHERIUM SNOWI Fourtau, 1918

Figure 34.3

Synonymy *Aceratherium campbelli* Hamilton, 1973.

Type Maxilla figured by Fourtau (1920, fig. 26); housed in the Cairo Geological Museum.

Type Locality Wadi Moghara, Egypt, ca. 17–18 Ma. (Miller, 1999).

Diagnosis A *Brachypotherium* of large size (length of cheek tooth row about 270 mm); skull low and wide, nasals rather long, probably carrying a small (pair of) horn(s), very broad zygomatic arches, temporal lines almost fused into a sagittal crest, dorsal profile strongly concave, occipital rounded, nasal notch above front of P3, anterior border of orbit above M2.

Remarks *Brachypotherium snowi* was established by Fourtau on the basis of a maxilla with worn teeth and the socket of the upper incisor, plus a fragment of mandible and some teeth. He pointed out the large size of the animal, the shortness and great width of the upper premolars, their lack of a labial cingulum and the reduction of the lingual one (a difference from European brachypotheres), and the moderate development of the antecrochet on all teeth. On the lower teeth he noticed the lack of cingula and of labial flattening, the large size of i2, and the presence of i1. A referred third metatarsal is stout, but not extremely so.

Several specimens from Jebel Zelten, Libya, a set of localities probably mostly dating to about 16 Ma., were referred to this species by Hamilton (1973). The i2s are large and separated by minute i1s; the cingulum is reduced on the upper teeth; P2 is much narrower than P3, which is broad. A third metacarpal is smaller than the Mt III from Moghara. Most of the specimens described by Hamilton as *Aceratherium campbelli* also belong here, as first recognized by Gentry (1987: 430). The holotype skull of the latter species, as well as another, uncollected skull (Hamilton, 1973: plate 3) are clearly from brachypotheres, as shown by their large size, skull regularly broadening from front to rear, with very

robust zygomatic arches and posteriorly very broad, low rounded occipital surface, short, broad upper teeth with flat labial walls, and large upper incisor. Several of the diagnostic features of the species are based upon these specimens. The nasals, if correctly identified by Hamilton, decrease in width toward the anterior end, but are rather thick and broad. Paired dorsal swellings suggest that some kind of horn may have been present.

In East and South Africa, this species has been called *B. heinzellini*, but this name should be restricted to the type specimen (discussed later). It is represented by sparse remains from Rusinga, (Hooijer, 1966), and has been reported from a few other sites. The most complete specimen is an unpublished mandible from Mwitani (Kajong), Kenya, dated to ca. 16–17 Ma (figure 34.3). It has a straight ventral edge and a widely expanded angular area, as in the European *B. brachypus* (Cerdeño, 1993: plate 5, figure 12); the large i2s are followed by a long diastema; the cheek teeth are brachyodont and have a shallow ectoflexid; the premolars are short, and the missing p2 was certainly small.

As in other brachypotheres, the talus may be very characteristic in its broad and low proportions at Jebel Zelten (Hamilton, 1973: plate 6, figure 7), but, as in Eurasia, the distinction from other rhinos may not always be so clear-cut. The talus from Gumba (Hooijer, 1966: plate 14, figure 3) is high and might not belong to this genus.

Brachypotherium snowi shows some resemblances to the contemporaneous European *Prosantorhinus* (Heissig, 1972; Cerdeño, 1996), but the latter has well-marked terminal horn bosses on the nasals, probably a lower and broader skull, and metapodials that are still shorter.

BRACHYPOTHERIUM LEWISI Hooijer and Patterson, 1972

Synonymy ?*Brachypotherium heinzellini* Hooijer, 1963

Type Skull KNM-LT 88.

Type Locality Lower member of the Nawata Formation at Lothagam, Kenya (Hooijer and Patterson, 1972).

Diagnosis Mostly from Hooijer and Patterson (1972). Size very large: condylobasal length of type skull over 70 cm, anterotransverse diameters of M1–2 some 90 mm as opposed to 70 mm in *B. snowi*. Nasals hornless, slender, not very long, deepest point of nasomaxillary notch above P4, anterior border of orbit above anterior end of M2, frontals flat and hornless, inferior squamosal processes united below sub-

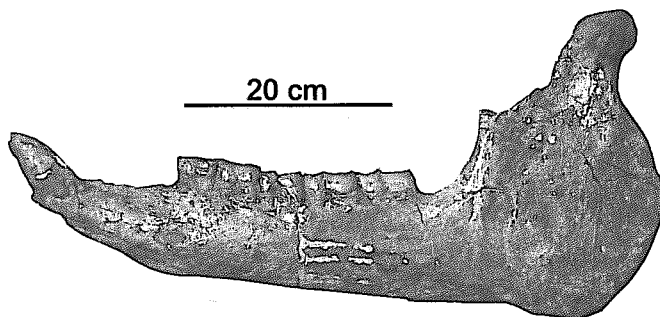


Figure 34.3 *Brachypotherium* cf. *snowi*, mandible KNM-MI 3 from the lower Miocene of Mwitani, Kenya.

aural channel. Upper incisors very large, upper cheek teeth brachyodont, ectoloph flattened behind paracone style, antecrochet moderate, protocone constriction slight, external cingula often present. Lower i2s of small to moderate size, brachyodont cheek teeth, external cingula often developed. Trochanter tertius of femur strongly developed.

Differs from *B. snowi* in its larger size, straight dorsal cranial profile, dorsal orbital border at least as high as the skull roof, V-shaped choanae, nasal notch deeper, shorter diastemas, lack of i1, smaller i2s.

Remarks The material from Lothagam (Hooijer and Patterson, 1972) includes a rather complete but crushed skull, and a second, less deformed skull lacking most of the teeth; a few more specimens were added more recently (Harris and Leakey, 2003). The material is basically similar to that of *B. snowi* but differs in the characters mentioned in the diagnosis.

Metacarpals from Lothagam are larger than those of *B. snowi* from Jebel Zelten or Rusinga, but not significantly different in their proportions; a molar from Sahabi, Libya (d'Erasmus, 1954), probably of similar age, is truly gigantic. The talus (Hooijer 1963: plate 5, figure 10) is larger and more trapezoidal than that of *B. snowi*.

Brachypotherium heinzellini was established on a P4 from Sinda-Ongoliba (Zaire), as well as on some tooth fragments and a talus, all supposed by Hooijer (1963) to be of early Miocene age. The P4 was mainly characterized by the presence of a labial cingulum, flattened ectoloph, and weak antecrochet, the first of these features being the main distinction from *B. snowi*. It has been shown since (Pickford et al., 1993) that Sinda is probably of latest Miocene age; thus, *B. heinzellini* should rather be compared with *B. lewisi*, and Pickford et al. (1993: 109) suggested that these names may be synonymous. However, the labial cingulum is "virtually absent" on the type of *B. lewisi* (Hooijer and Patterson, 1972: 5), while another difference between them is size, *B. lewisi* being larger, though if the type of *B. heinzellini* is a P3, not a P4, this difference would vanish. If the two names are synonymous, *B. heinzellini* has priority, and some confusion would arise, as this name as hitherto been widely given to early and middle Miocene forms. To avoid confusion, this name should be restricted to the type specimen, while other specimens hitherto called *B. heinzellini* can be referred to *B. snowi*.

Brachypotherium lewisi is best known from the late Miocene, and the transition from *B. snowi* is poorly documented (table 34.1). The latest definite record of the genus is from the Upper Member of the Nawata Formation of Lothagam, dated to ca. 6 Ma, but a possible later record is from the Apak Member, dated to ca. 4.2 Ma (Harris and Leakey, 2003); the extinction of *Brachypotherium* therefore took place about 2 to 4 Ma later than in Europe.

Subtribe ACERATHERIINA Dollo, 1885

Genus PLESIACERATHERIUM Young, 1937

Type Species *Plesiaceratherium gracile* Young, 1937.

Diagnosis Modified from Yan and Heissig (1986). Medium-sized to large Aceratheriini with primitive type of skull and dentition. Upper incisors reduced but still shearing against the lower ones in some species. Lower i2 flattened, horizontal and weakly curved. Skull hornless, with deep nasal notch and narrow braincase. Upper cheek teeth with

TABLE 34.1
List of the main African fossil localities with Rhinocerotidae
Many ages are estimates, not necessarily supported by absolute dating.

Site	Country	Age (Ma)	Key References	Published Identifications	Present Identifications
Haua Fteah	Libya	0.1	Klein and Scott, 1986	<i>C. simum</i> ; <i>D. mercki</i>	<i>C. simum</i> ; <i>S. mercki</i>
Bouknadel	Morocco	0.1	Michel, 1992	<i>C. simum</i> ; <i>D. hemitoechus</i>	<i>Ceratotherium</i> sp.; <i>D. hemitoechus</i>
Aïn Bahya, Doukkala	Morocco	0.2	Michel, 1992	<i>C. simum</i> ; <i>D. hemitoechus</i>	<i>C. mauritanicum</i> ?
Isenya	Kenya	0.5	Brugal and Denys, 1989	Rhinocerotidae	Rhinocerotidae indet.
Grotte des Rhinocéros	Morocco	0.5	Raynal et al., 1993	<i>C. mauritanicum</i>	<i>C. mauritanicum</i>
Duinefontein	South Africa	0.5	Klein et al., 1999	<i>D. bicornis</i> ; <i>C. simum</i>	<i>D. bicornis</i> ; <i>C. simum</i>
Asbole	Ethiopia	0.6	Geraads et al., 2004	<i>Diceros</i> sp.	<i>Diceros</i> sp.; <i>C. simum</i>
Elandsfontein (Hopefield)	South Africa	0.6	Hooijer and Singer, 1960	<i>D. bicornis</i> ; <i>C. simum</i>	<i>D. bicornis</i> ; <i>C. simum</i>
M. Awash-Bodo	Ethiopia	0.7	Kalb et al., 1980	Rhinocerotidae	Rhinocerotidae
Tighenif	Algeria	0.7	Geraads et al., 1986	<i>C. simum</i>	<i>C. mauritanicum</i>
Olorgesailie	Kenya	0.9	Hooijer, 1969	<i>C. simum</i>	<i>C. simum</i>
Buia	Eritrea	1	Martinez-Navarro et al., 2004	<i>C. simum</i>	<i>C. simum</i>
Bouri Daka	Ethiopia	1	Asfaw et al., 2002	<i>Ceratotherium</i> sp.	<i>Ceratotherium</i> sp.
Kanjera Fm. (N)	Kenya	1	Pickford, 1986; Ditchfield et al., 1999	<i>D. bicornis</i> ; <i>C. simum</i>	<i>D. bicornis</i> ; <i>C. simum</i>
Olduvai upper Bed II, III, IV	Tanzania	1	Hooijer, 1969	<i>D. bicornis</i> ; <i>C. simum</i>	<i>D. bicornis</i> ; <i>C. simum</i>
Aïn Hanech	Algeria	1.4	Arambourg, 1970	<i>C. simum germanoaffricanum</i>	<i>C. mauritanicum</i>
Chemoigut	Kenya	1.5	Bishop et al., 1975	<i>Ceratotherium</i> sp.	<i>Ceratotherium</i> sp.
Anabo Koma	Djibouti	1.6	Bonis et al., 1988	<i>Ceratotherium</i> sp.	<i>C. mauritanicum</i>
Peninj	Tanzania	1.7	Geraads, 1987	<i>C. simum</i>	<i>C. simum</i>
Konso Fm.	Ethiopia	1.8	Suwa et al., 2003	<i>D. bicornis</i> ; <i>C. simum</i>	<i>D. bicornis</i> ; <i>C. simum</i>
Olduvai Bed I, lower Bed II	Tanzania	1.8	Hooijer, 1969	<i>C. simum</i>	<i>C. simum</i>
Nyabusosi	Uganda	1.8	Guérin, 1994b	<i>D. bicornis</i>	Dicerotini
Aïn Boucherit	Algeria	2.0	Arambourg, 1970	<i>C. simum mauritanicum</i>	<i>C. mauritanicum</i>
Baard's Quarry lower levels	South Africa	2.0	Hendey, 1978	<i>D. bicornis</i> ; <i>Ceratotherium</i> sp.	<i>D. bicornis</i> ; <i>Ceratotherium</i> sp.
Semliki—Lusso	Congo	2.1	Boaz et al., 1992	cf. <i>Ceratotherium</i> sp.	<i>B. lewisi</i> ?; Rhinocerotidae indet.
Koobi Fora	Kenya	2.5	Harris, 1983	<i>D. bicornis</i> ; <i>C. praecox</i> ; <i>C. simum</i>	<i>D. praecox</i> ; <i>D. bicornis</i> ; <i>C. mauritanicum</i>
Ahl al Oughlam	Morocco	2.5	Geraads, 2006	<i>C. mauritanicum</i>	<i>C. mauritanicum</i>
Lactoli—Upper Ndolanya	Tanzania	2.6	Kovarovic et al., 2002	<i>C. simum</i>	<i>C. mauritanicum</i>
Hohwa	Uganda	2.6	Guérin, 1994b	<i>C. praecox</i>	<i>C. mauritanicum</i> ?
Rawi Fm.	Kenya	2.8	Ditchfield et al. 1999	<i>C. simum</i>	<i>C. mauritanicum</i> ?
Omo	Ethiopia	3.0	Hooijer, 1973; Guérin, 1985; Hooijer and Churcher, 1985	<i>D. bicornis</i> ; <i>C. simum</i>	<i>Diceros</i> sp.; <i>C. mauritanicum</i>
Hadar—Kada Hadar	Ethiopia	3.0	Geraads, 2005	<i>D. praecox</i> ; <i>C. mauritanicum</i>	<i>D. praecox</i> ; <i>C. mauritanicum</i>
West Turkana	Kenya	3.0	Harris et al., 1988	<i>D. bicornis</i> ; <i>Ceratotherium</i> sp.; <i>C. simum</i>	<i>Diceros</i> sp.; <i>C. mauritanicum</i>
Lothagam-Kaiyumung	Kenya	3.0	Harris and Leakey, 2003	<i>C. praecox</i>	<i>D. praecox</i>
Makapansgat	South Africa	3.0	Hooijer, 1958	<i>D. bicornis</i> ; <i>C. simum</i>	<i>Diceros</i> sp.; <i>Ceratotherium</i> sp.
Aïn Brimba	Tunisia	3.0	Arambourg, 1970	<i>C. simum germanoaffricanum</i>	<i>C. mauritanicum</i>
Koro Toro 13	Chad	3.2	Likius, 2002	<i>D. cf. bicornis</i> ; <i>C. praecox</i> ; <i>Stephanorhinus</i> sp.	<i>C. mauritanicum</i> ; <i>Stephanorhinus</i> sp.
Hadar—Denen Dora	Ethiopia	3.2	Geraads, 2005	<i>D. praecox</i> ; <i>C. mauritanicum</i>	<i>D. praecox</i> ; <i>C. mauritanicum</i>
Turkwell South	Kenya	3.2	Ward et al., 1999	Rhinocerotidae	Rhinocerotidae indet.
Hadar—Sidi Hakoma	Ethiopia	3.3	Geraads, 2005	<i>D. praecox</i> ; <i>C. mauritanicum</i>	<i>D. praecox</i> ; <i>C. mauritanicum</i>

Site	Country	Age (Ma)	Key References	Published Identifications	Present Identifications
Ekora	Kenya	3.5	Hooijer and Patterson, 1972	<i>C. praecox</i>	<i>D. praecox</i>
Laetoli	Tanzania	3.6	Guérin, 1987	<i>D. bicornis</i> ; <i>C. praecox</i>	<i>D. cf. praecox</i> ; <i>C. mauritanicum</i>
Kanapoi	Kenya	4.0	Hooijer and Patterson, 1972	<i>C. praecox</i>	<i>D. praecox</i>
Ichkeul	Tunisia	4.0	Arambourg, 1970	<i>C. simum</i> ; <i>D. africanus</i>	<i>C. mauritanicum</i> ; <i>Stephanorhinus</i> sp.
Kanam East and West	Kenya	4.3	Hooijer, 1969; Pickford, 1987	<i>D. bicornis</i> ; <i>C. simum germanoaffricanum</i>	<i>Diceros</i> sp.? <i>C. mauritanicum</i> ?
Lothagam-Apak	Kenya	4.3	Harris and Leakey, 2003	<i>D. bicornis</i> ; <i>C. praecox</i> ; <i>B. lewisi</i>	<i>D. praecox</i> ; <i>Ceratotherium</i> sp.; <i>B. lewisi</i>
Manonga-Kiloleli	Tanzania	4.3	Harrison and Baker, 1997	<i>C. praecox</i>	<i>Ceratotherium</i> sp.
M. Awash-Aramis	Ethiopia	4.4	WoldeGabriel et al., 1994	<i>C. cf. praecox</i>	Rhinocerotidae indet.
Chemeron	Kenya	4.5	Hooijer, 1973; Guérin, 2000	<i>C. simum</i> , <i>C. praecox</i> ; <i>B. heinzellini</i> ; <i>D. leakeyi</i> ; <i>A. acutirostratum</i>	<i>C. mauritanicum</i>
Kollé	Chad	4.5	Likius, 2002	<i>D. cf. bicornis</i> ; <i>C. praecox</i>	<i>C. mauritanicum</i> ; Rhinocerotidae indet.
Warwire	Uganda	4.5	Guérin, 1994b	<i>D. bicornis</i> ; <i>C. praecox</i>	Dicerotini
Kossom Bougoudi	Chad	5.0	Likius, 2002	<i>D. cf. bicornis</i>	Rhinocerotidae indet.
Hamada Damous	Tunisia	5.0	Coppens, 1971	<i>C. simum</i>	Rhinocerotidae indet.
Nkondo	Uganda	5.0	Guérin, 1994b	<i>D. bicornis</i> ; <i>C. praecox</i>	Dicerotini
Langebaanweg PPM	South Africa	5.1	Hooijer, 1972; Hende, 1981	<i>C. praecox</i>	<i>Ceratotherium</i> sp.
Langebaanweg QSM	South Africa	5.2	Hooijer, 1972; Hende, 1981	<i>C. praecox</i>	<i>Ceratotherium</i> sp.
M. Awash-late Miocene	Ethiopia	5.5	Giaourtsakis et al., 2009	<i>Diceros</i> sp.; <i>D. douariensis</i>	<i>Diceros</i> ? sp.
Lukeino A-B	Kenya	6.0	Pickford and Senut, 2001	<i>Diceros</i> ?; <i>C. praecox</i>	<i>Brachypotherium</i> sp.?
Lissasfa	Morocco	6.0	Raynal et al., 1999	Rhinocerotidae	<i>Ceratotherium</i> sp.
Hondeklip	Namibia	6.0	Pickford and Senut, 1997	<i>C. praecox</i>	<i>Ceratotherium</i> sp.?
Lothagam-upper Nawata	Kenya	6.5	Harris and Leakey, 2003	<i>D. bicornis</i> ; <i>C. praecox</i> ; <i>B. lewisi</i>	<i>Ceratotherium</i> sp.; <i>B. lewisi</i>
Mpesida	Kenya	6.5	Hooijer, 1973; Kingston et al., 2002	<i>C. praecox</i> ; <i>B. lewisi</i>	<i>Ceratotherium</i> sp.; <i>B. lewisi</i>
Menacer (Marceau)	Algeria	7.0	Thomas and Petter, 1986	Rhinocerotidae	Rhinocerotidae indet.
Sinda	Congo	7.0	Hooijer, 1966; Guérin, 2000	<i>B. heinzellini</i> ; <i>A. acutirostratum</i>	Rhinocerotidae indet.
Lothagam-lower Nawata	Kenya	7.0	Hooijer and Patterson, 1972; Harris and Leakey, 2003	<i>C. praecox</i> ; <i>B. lewisi</i>	<i>Ceratotherium</i> sp.; <i>B. lewisi</i>
Sahabi	Libya	7.0	d'Erasmus, 1954; Bernor et al., 1987	<i>D. neumayri</i> ; <i>Brachypotherium</i> sp.	<i>Brachypotherium</i> sp.; <i>C. douariense</i> ?
Douaria	Tunisia	7.0	Guérin, 1966	<i>D. douariensis</i>	<i>C. douariense</i> ; Rhinocerotidae indet.
Karugamania	Congo	8.0	Guérin, 2000	<i>B. heinzellini</i> ; <i>A. acutirostratum</i>	<i>B. snowi</i> ?; Rhinocerotidae indet.
Oued-Mya-1	Algeria	9.0	Sudre and Hartenberger, 1992	<i>Aceratherium</i> sp.	Dicerotini?
Ngeringerowa	Kenya	9.0	Pickford, 1983	Rhinocerotidae	Rhinocerotidae indet.
Namurungule	Kenya	9.5	Nakaya et al., 1987; Nakaya, 1993	<i>Paradiceros</i> sp.; <i>Kenyatherium bishopi</i> ; <i>Chilotheridium</i> sp.	<i>Ceratotherium</i> sp.? <i>Kenyatherium bishopi</i> ?
Nakali	Kenya	9.5	Aguirre and Guérin, 1974; Antoine, 2002	<i>Kenyatherium bishopi</i>	<i>Kenyatherium bishopi</i>
Bou Hanifia	Algeria	10.0	Arambourg, 1959	<i>D. primaevus</i>	<i>C. cf. primaevum</i>
Ngorora E	Kenya	10.0	Hooijer, 1971; Guérin, 2000	<i>B. lewisi</i> ; <i>Aceratherium</i> or <i>Dicerorhinus</i> ; <i>C. pattersoni</i>	<i>Brachypotherium</i> sp.; Elasmotheriinae?
Bled Douarah (upper Beglia Fm.)	Tunisia	10.0	Robinson and Black, 1974	Rhinocerotidae	Rhinocerotidae indet.
Djebel Krechem	Tunisia	10.0	Geraads, 1989	<i>D. cf. douariensis</i> ; <i>B. cf. lewisi</i>	<i>C. douariense</i> ?; Rhinocerotidae indet.

TABLE 34.I
(CONTINUED)

Site	Country	Age (Ma)	Key References	Published Identifications	Present Identifications
Chorora	Ethiopia	10.5	Geraads et al., 2002	Dicerotini	<i>Ceratotherium</i> sp.?
Ngorora A-D	Kenya	12.0	Nakaya, 1993; Guérin, 2000	<i>B. lewisi</i> ; <i>C. pattersoni</i>	Rhinocerotidae indet.
Kabasero	Kenya	12.5	Hill et al., 2002	Rhinocerotidae	Rhinocerotidae indet.
Beni Mellal	Morocco	12.5	Guérin, 1976	cf. <i>Paradiceros mukirii</i>	cf. <i>P. mukirii</i>
Alengerr	Kenya	13.0	Hooijer, 1973; Guérin, 2000	<i>D. leakeyi</i> ; <i>A. acutirostratum</i>	Rhinocerotidae indet.
Fort Ternan	Kenya	13.0	Hooijer, 1968	<i>Paradiceros mukirii</i>	<i>P. mukirii</i>
Kisegi	Uganda	13.5	Guérin, 1994b; Guérin, 2000	<i>Paradiceros mukirii</i>	Rhinocerotidae indet.
Muruyur-Kipsaramon	Kenya	13.7	Pickford, 1988	<i>A. acutirostratum</i>	Rhinocerotidae indet.
Kirimun	Kenya	15.0	Hooijer, 1971; Guérin, 2000	<i>Dicerorhinus</i> or <i>Aceratherium</i> ; <i>Chilotheridium pattersoni</i>	<i>B. snowi</i> ?; Rhinocerotidae indet.
Nyakach	Kenya	15.0	Pickford, 1986	<i>Brachypotherium</i> sp.	<i>Brachypotherium</i> sp.; <i>Plesiaceratherium</i> sp.?
Maboko-Ombo	Kenya	15.5	Hooijer, 1973; Pickford, 1986	<i>B. heinzellini</i> ; <i>D. leakeyi</i> ; <i>A. acutirostratum</i> ; <i>C. pattersoni</i>	Elasmotheriinae?; <i>Chilotheridium</i> sp.?
Nachola	Kenya	15.5	Pickford et al., 1987	Rhinocerotidae	Elasmotheriinae?
Moroto I and II	Uganda	16.0	Pickford et al., 1986	Rhinocerotidae	Rhinocerotidae indet.
Mwiti (Kajong)	Kenya	16.5	Savage and Williamson, 1978	Rhinocerotidae	<i>Brachypotherium</i> cf. <i>snowi</i>
Buluk (W. Stephanie)	Kenya	16.5	Leakey and Walker, 1985	<i>D. leakeyi</i> ; <i>A. acutirostratum</i> ; <i>Chilotheridium pattersoni</i>	<i>Brachypotherium</i> nov. sp.? Rhinocerotidae indet.
Jebel Zelten	Libya	16.5	Hamilton, 1973	<i>B. snowi</i> ; <i>A. campbelli</i>	<i>B. snowi</i>
Loperot	Kenya	17.0	Hooijer, 1971; Guérin, 2000	<i>Chilotheridium pattersoni</i>	<i>Chilotheridium pattersoni</i>
Langental	Namibia	17.0	Heissig, 1971; Hooijer, 1973; Guérin, 2000	<i>B. heinzellini</i>	<i>Brachypotherium</i> sp.
Ryskop	Namibia	17.0	Pickford and Senut, 1997	Rhinocerotidae	Rhinocerotidae indet.
Moruorot	Kenya	17.2	Deraniyagala, 1951; Hooijer, 1968	<i>A. acutirostratum</i>	<i>T. acutirostratum</i> ; Rhinocerotidae indet.
Moghara	Egypt	17.5	Fourtau 1920, Miller, 1999	<i>B. snowi</i> ; <i>Aceratherium</i> sp.	<i>B. snowi</i> ; Rhinocerotidae indet.
Karungu	Kenya	17.5	Hooijer, 1966; Pickford, 1986	<i>B. heinzellini</i> ; <i>D. leakeyi</i> ; <i>A. acutirostratum</i> ;	<i>Brachypotherium</i> sp.; <i>R. leakeyi</i> ?
Bukwa	Uganda	17.5	Walker, 1968; Hooijer, 1971	<i>B. heinzellini</i> ; <i>C. pattersoni</i>	Elasmotheriinae?;
Kulu Fm. (Rusinga)	Kenya	17.7	Hooijer, 1966; Pickford, 1986	<i>D. leakeyi</i> ; <i>A. acutirostratum</i> ; <i>Chilotheridium pattersoni</i>	<i>R. leakeyi</i> ; <i>T. acutirostratum</i>
Uyoma peninsula	Kenya	17.7	Pickford, 1986; Guérin, 2000	<i>B. heinzellini</i> ; <i>Dicerorhinus</i> or <i>Aceratherium</i>	<i>B. snowi</i> ?
Hiwegi Fm. (Rusinga)	Kenya	17.8	Hooijer, 1966, 1968	<i>B. heinzellini</i> ; <i>D. leakeyi</i> ; <i>A. acutirostratum</i>	<i>B. snowi</i> ; <i>R. leakeyi</i>
Mfwangano	Kenya	17.8	Pickford, 1986	<i>B. heinzellini</i> ; <i>D. leakeyi</i>	<i>B. snowi</i> ; <i>R. leakeyi</i>
Wayando Fm. (Rusinga)	Kenya	18.0	Pickford, 1986; Hooijer, 1966	<i>B. heinzellini</i> ; <i>D. leakeyi</i> ; <i>A. acutirostratum</i> ; <i>C. pattersoni</i> ?	<i>B. snowi</i> ; <i>R. leakeyi</i>
Arrisdrift	Namibia	18.0	Guérin, 2000; Guérin, 2003	<i>D. australis</i> ; cf. <i>C. pattersoni</i>	" <i>D.</i> " <i>australis</i> ; <i>Chilotheridium</i> sp.?
Auchas	Namibia	19.5	Pickford and Senut 2003; Guérin, 2000	Rhinocerotidae	Rhinocerotidae indet.
Napak-Napak	Uganda	19.5	Pickford et al., 1986; Guérin and Pickford, 2003	<i>D. leakeyi</i> ; <i>A. acutirostratum</i> ; <i>Ougandatherium napakense</i>	<i>Ougandatherium napakense</i> ; Rhinocerotidae indet.
Koru-Songhor	Kenya	20.0	Pickford, 1986; Hooijer, 1966	<i>D. leakeyi</i>	Rhinocerotidae indet.
Napak-Iriri	Uganda	20.0	Pickford et al., 1986; Hooijer, 1966, 1973	<i>B. heinzellini</i> ; <i>D. leakeyi</i>	<i>Brachypotherium</i> sp.; Rhinocerotidae indet.

faint constriction of the inner cusps. Premolars with high lingual cingulum. Lower premolars long and narrow, with shallow labial groove and protoconid flattened labially. Vertical rugosities on the labial wall are common. Limbs long and slender, mainly their distal segments. Manus tetradactyl.

PLESIACERATHERIUM sp.

I provisionally refer to this genus two incomplete skulls from Nyakach, Kenya, found by M. Pickford, numbered KNM-NC 10486 and KNM-NC 10510, and dated to about 15 Ma. The nasals are remarkably long, straight, and hornless. The nasal notch is deep, and its bottom is U shaped, almost rectangular. The dorsal skull profile is concave, and the orbit is elevated, with an inflated and rounded supraorbital tuberosity. The premaxillae are slender, but probably carried incisors (an isolated upper incisor of medium size could be of the same species). The cheek teeth have a simple morphology (quite distinct from that of the next genus), with slightly pinched protocones on the molars, weak or absent crochet, but the premolars are reduced in size and their lingual cingulum is weak.

These skulls resemble those of early-middle Miocene Eurasian forms included in *Plesiaceratherium*, but these have larger premolars with a strong, continuous lingual cingulum (Heissig, 1972; Antunes and Ginsburg, 1983). The related genus "*Hoploaceratherium*," best known from "*H.*" *tetradactylum* from Sansan, France, has teeth more like the Nyakach ones, but there are small terminal horns (a minor difference), and it is said to have lost its upper incisors (Heissig, 1999).

The Nyakach rhino is probably a member of this *Plesiaceratherium*-*Hoploaceratherium* group, but more detailed evidence, especially relating to its upper incisors and postcrania, are still needed to ascertain its phyletic position. It may well be that some specimens from various sites previously referred to *Aceratherium* or *Dicerorhinus* belong here.

Genus *TURKANATHERIUM* Deraniyagala, 1951

Type Species Turkanatherium acutirostratum Deraniyagala, 1951.

Diagnosis Skull dolichocephalic, occiput vertical, frontoparietal profile concave, temporal lines meet to form a sagittal crest, nasals elongate, nasal notch U shaped and shallow (bottom above front of P3), anterior orbital margin above front of M2. Premolars with long transverse loph, vestigial bridge between protocone and hypocone, molars without crista, antecrochet strong, at least on M1.

TURKANATHERIUM ACUTIROSTRATUM Deraniyagala, 1951
Figure 34.4

Type Skull (housed in the Colombo Museum, Sri Lanka).

Type Locality Moruorot, Kenya, about 17 to 17.5 Ma.

Diagnosis As for genus.

Remarks The type skull is preserved in the Sri Lanka National Museum but seemingly has never been examined by western researchers, who have had to rely mostly on the descriptions and figures of Deraniyagala (1951). The skull (figure 34.4) is high and narrow, the dorsal profile is concave, the condyles much higher than the tooth row, the temporal lines meet to form a long sagittal crest, the nasal notch has the shape of a wide U, and its bottom is above the middle of P3, and thus rather far from the anterior orbital border, which is above the front of M2. The nasals carry no horn,

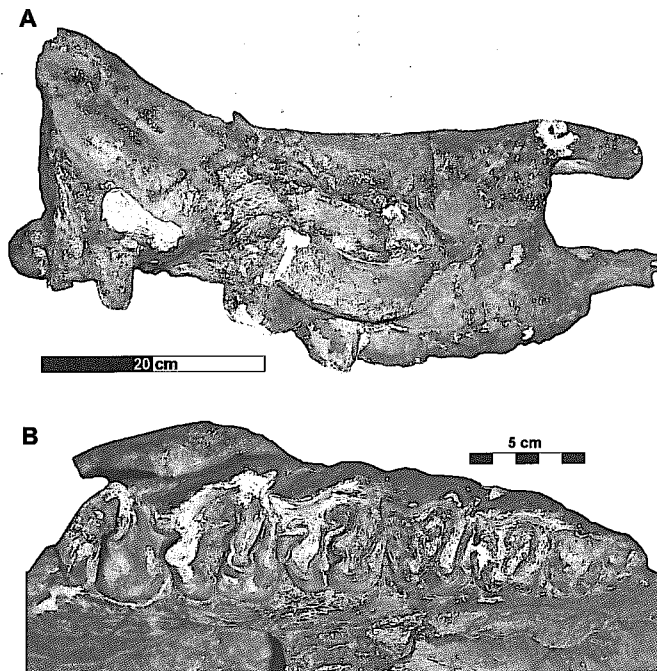


FIGURE 34.4 *Turkanatherium acutirostratum*, holotype skull from Moruorot; lateral view (A) and occlusal view (B) of teeth. Courtesy of Ceylon Journal of Science.

but they are long and slender, extending forward well beyond the level of P2. The long premaxillae were said by Deraniyagala (1951) to be edentulous; this is very unlikely, as noted by Hooijer (1966), but the size of I1 is unknown. The protoloph is constricted on the molars, especially M1, which has a strong antecrochet, but the crochet is weak. The premolars are small, broad, with loph, converging lingually, a lingual connection between them, an incomplete internal cingulum and the postfossette is transversely elongated.

An incomplete mandible from the same locality (MT-66 in Hooijer 1968, now KNM-MO 43) shows, from the shape of their alveoli, that the lateral incisors had long roots and some outward curvature. Arambourg (1933) described from Losodok in the same area two slender metatarsals, but they might not belong to the same taxon.

Arambourg (1959) and Hooijer (1963, 1966) referred *T. acutirostratum* to *Aceratherium*, without much discussion, and this generic attribution has been accepted ever since, but this was done at a time when the latter genus had a very broad meaning, including most middle and many of the late Miocene nonbrachypothere hornless rhinos from Eurasia. The type species of *Aceratherium* is *A. incisivum* from the early late Miocene of Germany, and recent revisions (Heissig, 1999) favor restriction of the generic name to this species. Even though this can be disputed, *T. acutirostratum* clearly differs from *A. incisivum*, which has a shorter skull, an almost flat cranial profile, a very robust zygomatic arch, a deeper nasal notch extending closer to the orbit, and larger and more molariform premolars with a lingual connection occurring only in late wear. *Turkanatherium* can thus be retained as a valid generic name, because its type species differs considerably from that of *Aceratherium*.

The cheek teeth of a lower jaw KNM-RU 3012 (850-47 in Hooijer, 1966) do not differ from those of the sympatric "*Dicerorhinus*"; the associated nasals were relatively long and broad, but not bowed anteroposteriorly, and certainly carried no large horn, but identification of all these remains is uncertain.

Hooijer (1966) found it difficult, if not impossible, to tell apart the limb bones of "*Dicerorhinus*" and "*Aceratherium*," in spite of the occurrence at Rusinga of two skeletons that he referred to each of these genera; both had primitive limb proportions. *Turkanatherium* (and *Plesiaceratherium*) might be expected to differ in the retention of the fifth digit of the manus, but it has not yet been found.

"*Aceratherium*" has been reported from a number of African sites, often on the basis of fragmentary remains, but identification of isolated or even incomplete teeth of rhinos is seldom reliable. For instance, identification of teeth from Karugamania, Democratic Republic of Congo as *A. acutirostratum* by Hooijer (1963) was made on the assumption of an early/middle Miocene age of the deposits. Their reassignment to the late Miocene (Pickford et al., 1993) rules out their belonging to this species (especially as the P4 lacks the remarkable transverse broadening of the type specimen). It is likely that *T. acutirostratum* was a common species in the early and middle Miocene of Africa but, besides the type, it is hard to refer any specimen to this species with certainty.

Genus *CHILOTHERIDIUM* Hooijer, 1971

Type Species *Chilotheridium pattersoni* Hooijer, 1971.

Diagnosis Slightly modified from Hooijer (1971). Small single nasal horn in both sexes; frontals and parietals pneumatized; orbit not placed as near upper contour of skull as in *Chilotherium*; cranium and occiput rather narrow; parietal crests not widely separated; inferior squamosal processes not united below; symphyseal portion of mandible narrow, slightly expanding anteriorly. Cheek teeth fully hypsodont as in *Chilotherium* and with the same pattern: uppers with paracone style fading away basally and posterior portion of ectoloph flattened; protocone well set off by folds and flattened internally; anterior fold in metaloph, marking off hypocone; antecrochet prominent basally, curving inward to medisinus entrance; crochet usually well developed, and crista weak or absent; metacone bulge at base in M3; anterior cingulum strong, internal cingulum weak and usually forming cusp at medisinus entrance. i2 subtriangular in cross section, depressed dorsoventrally, internal edge sharpened by wear, outer lower edge rounded, and outer upper edge ridged. Scapula low and wide; limb and foot bones not much shortened; radius and ulna, and tibia and fibula not ankylosed; radius with pyramidal facet; metacarpal V present, three-fifths the length of metacarpal IV; lateral metapodials somewhat divergent posteriorly; femur with small third trochanter; calcaneum without tibia facet; talus with trochlea markedly shifted laterally; navicular nearly rectangular; cuboid wider than high; metatarsal III with small cuboid facet.

CHILOTHERIDIUM PATTERSONI Hooijer, 1971

Type Skull figured by Hooijer (1971: plate 1); numbered 70-64K, B12 in KNM.

Type Locality Loperot, Kenya, ca. 17 Ma.

Diagnosis As for genus.

Remarks The species was erected on a large collection of fossils, but they are much fragmented and distorted. The skulls are made up of a mosaic of fragments that make their actual shape hard to figure out, although tooth features and limb bone proportions are certainly correct.

Upper incisors were said to be lacking, but the premaxillaries are broken off on both skulls from Loperot, and the absence of isolated upper incisors in the Loperot collection is

not a strong argument against their actual presence (there are only two isolated i2s).

The main feature of the postcranial skeleton is the retention of a functional fifth metacarpal, but since even a vestigial Mc V articulates with a similar facet on the Mc IV, occurrence of this fifth digit is hard to demonstrate at other localities. Although not noted by Hooijer, the tali are characteristic, with a low medial lip of the trochlea, and a very salient distomedial tuberosity with a slanting proximal border. This morphology is absent from sites other than Loperot, showing that *Chilotheridium* is certainly a rare form.

However, Hooijer (1971) identified *Chilotheridium* from a few other sites, mostly on the basis of isolated teeth. An i2 of large size from Kirimun would perhaps better match *Brachypotherium*. A few upper cheek teeth from Bukwa (Walker, 1968) also referred to *Chilotheridium* by Hooijer, are much worn but are remarkable in the depth of the grooves that tend to isolate pillars: the antecrochet is strong, the protocone is double, and the hypocone is sharply set off from the metaloph. All these features perhaps better fit an elasmothere. Two tooth fragments from Rusinga were assigned to *Chilotheridium* mostly because of their hypsodonty. An upper tooth series from Ngorora (Hooijer, 1971: plate 11, figure 1; now KNM-BN 133) is too worn to be reliably identified. Some isolated teeth from the Samburu Hills (Nakaya et al., 1987) are also hardly identifiable.

Chilotheridium was assumed by Hooijer to be close to the mainly Asiatic late Miocene genus *Chilotherium*, but resemblances concern mostly cheek tooth morphology, estimated depth of the nasal notch, some shortening of the metapodials, and the presence of an articulation between radius and pyramidal. The latter feature is primitive, and the others are prone to parallelism. On the other hand, *Chilotherium* differs considerably from the Kenyan genus in its broad skull, flat frontals, high orbits, short hornless nasals, broadened mandibular symphysis with large i2s, and much shortened metapodials, and the two genera are probably not closely related.

Subtribe RHINOCEROTINA Gray, 1821

Genus *RUSINGACEROS* nov. gen.

Type Species *Dicerorhinus leakeyi* Hooijer, 1966.

Diagnosis Simplified from Hooijer (1966) for *Dicerorhinus leakeyi*. A rhino of medium size, with a long and low skull. Frontal and nasal horns present; nasal notch very shallow; long, slanting premaxilla bearing moderate-sized incisors; small i1s present, i2s parallel, medium sized; occiput as highly elevated as in *Lartetotherium*. Upper premolars with protoloph and metaloph united lingually up to at least 15 mm from crown base, cingulum weak. Upper molars with internal cingulum very weak or absent, protocone not or hardly constricted off, antecrochet absent, ectoloph depressed between the roots, crochet and crista weak or absent, M3 bulging out at junction of ectoloph and metaloph.

RUSINGACEROS LEAKEYI (Hooijer, 1966)

Type Skull and associated mandible, KNM-RU 2821 (Hooijer, 1966: plates 1 and 2, figures 1 and 2).

Type Locality Rusinga, precise locality unknown.

Diagnosis As for genus.

Remarks This species was described by Hooijer (1966) on the basis of the type, plus another associated maxilla and mandible (now KNM-RU 2822). It was originally referred to the genus *Dicerorhinus* Gloger, 1841, of which the modern

D. sumatrensis is the type species. There are some similarities in the cranial profile, shape and orientation of the nasals and premaxillae, size of the main incisors, but the Rusinga type skull is longer and lower with a longer facial portion, the orbit is more posterior, the zygomatic arch is extremely robust, and the cheek teeth are much more primitive, with submolariform premolars, weaker cristae on the molars, and no metacone fold (the very strong metacone fold of the premolars of the Sumatran rhino is certainly a derived feature), and the posterior limb is relatively longer. There is no evidence of a close relationship between the Rusinga material and the modern species, and including the Rusinga form in *Dicerorhinus* would expand the content of this genus to virtually every two-horned rhino with front teeth.

Several authors (Groves, 1983; Geraads, 1988; Cerdeño, 1995) have included the Rusinga species in *Lartetotherium*, a genus based on *L. sansaniense* from the late middle Miocene site of Sansan in France, thus much later in age than Rusinga. The resemblances include a high occiput, the size of the front teeth, and probably (the Rusinga teeth are highly worn) the molarisation stage of the upper premolars, but the skull of *L. sansaniense* is much higher and shorter, the zygomatic arch is weaker, the antorbital part shorter (the anterior orbital margin is above the anterior end of M2), the nasal notch is deeper (bottom above P2–P3), the symphysis is broader and shorter. An earlier form of *L. sansaniense*, from Sandelzhausen in Germany, has a nasal notch situated farther rostrally (Heissig, 1972), and the skull looks relatively longer than that from Sansan (but both are crushed). It partly bridges the chronological and morphological gaps between the Rusinga and Sansan rhinos, but the lack of a frontal horn is a difference from both.

Hooijer (1966) reported *R. leakeyi* from various sites at Rusinga, and from Songhor and Napak, and some other occurrences were added more recently (see table 34.1) but, besides Rusinga, most of the identifications are based on isolated teeth. Regardless, *R. leakeyi* is the earliest rhino of modern type, i.e., with a strong nasal and smaller frontal horn. In Eurasia, the earliest "*Dicerorhinus*" is documented by a few isolated teeth (of doubtful generic attribution) from Baigneaux in France (Ginsburg and Bulot, 1984), a locality dated to late MN4, i.e., somewhat later than Rusinga.

Genus *STEPHANORHINUS* Kretzoi, 1942

Type Species *Stephanorhinus etruscus* (Falconer in Murchison, 1868) from the Plio-Pleistocene of Italy.

This is a mostly European genus, the limits of which are controversial. It includes several Pliocene and Pleistocene species previously referred to *Dicerorhinus* and perhaps dates back to the late Miocene; the whole genus is in need of revision.

STEPHANORHINUS ? *AFRICANUS* (Arambourg, 1970)

Type M3, MNHN-1948-2-21 (Arambourg, 1970: plate 15, figure 1).

Type Locality Lake Ichkeul, Tunisia, early to middle Pliocene.

Diagnosis Translated from Arambourg (1970). Intermediate in size between *S. etruscus* and *D. sumatrensis*, with molars more brachyodont but morphologically similar to those of the living species.

Remarks The type locality yielded only the type, a mandible fragment, and an atlas. Given its age, it is unlikely to be of African origin, since only Dicerotini and brachypotheres survive in the rich East African sites after the middle Miocene.

The large mammals from Ichkeul are mostly of African affinity, but some genera are known on both sides of the Mediterranean at that time, and *S. ? africanus* is probably of northern origin. This is confirmed by the occurrence of the genus at Koro Toro 13 in Chad, a locality dated at about 3–3.5 Ma. (Likius, 2002), but not in East Africa.

STEPHANORHINUS HEMITOECHUS (Falconer in Murchison, 1868)

Synonymy *Rhinoceros subinermis* Pomel, 1895: 21.

Type Skull figured by Falconer in Murchison (1868: plate 15); BMNH M27836.

Type Locality Clacton, Essex, Great Britain; middle Pleistocene.

Remarks The species has been revised by Guérin (1980) and Fortelius et al. (1993). No rhino related to European forms is known in the late Pliocene or early and middle Pleistocene of North Africa, and the *Stephanorhinus* found in the late Pleistocene of Morocco and Algeria must be an immigrant from the North, together with *Sus* and cervids. Long referred to *S. mercki*, it is now believed to belong to *S. hemitoechus*, the last species of the genus, with a large nasal horn supported by wide nasals buttressed by a robust nasal septum.

Genus *PARADICEROS* Hooijer, 1968

Type Species *Paradiceros mukirii* Hooijer, 1968.

Diagnosis Mostly from Hooijer (1968). Two horns, placed on nasals and frontals, respectively. Inferior squamosal processes separate. Lower orbital border rounded. Bottom of nasal notch above front of P3. Mandibular symphysis abbreviated but not widened; edentulous in the adult. Cheek teeth brachyodont, protocone constricted, antecrochet prominent in milk and first molars rather than in last and premolars. Last upper molar subtriangular. Upper molars with wide and low medisinus entrance, upper premolars with high internal pass. Limbs and some of the foot bones more shortened than in *Aceratherium* or *Dicerorhinus* though not to the extent seen in *Brachypotherium* or *Chilotherium*.

PARADICEROS MUKIRII Hooijer, 1968 Figure 34.5

Type Juvenile skull, figured by Hooijer (1968, pl. 1); KNM-FT 2866.

Type Locality Fort Ternan, ca. 13–14 Ma.

Diagnosis As for genus.

Remarks The species has also been reported from Kisegi in Uganda (Guérin, 1994b) and Beni Mellal in Morocco (Guérin,

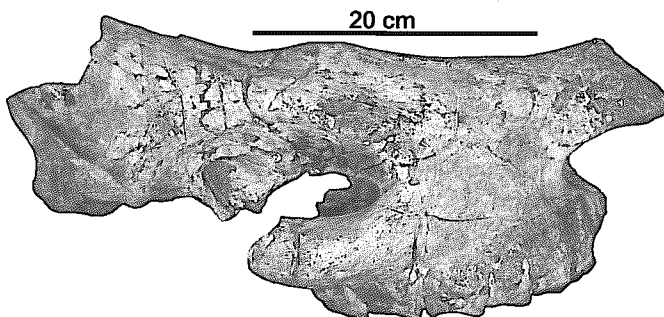


FIGURE 34.5 *Paradiceros mukirii*, skull KNM-FT 3328 from the middle Miocene of Fort Ternan, Kenya.

1976) on the basis of very poor remains; these identifications are likely but may have been influenced by the age of these sites.

An unpublished, almost complete skull, KNM-FT 3328 (figure 34.5), shows further features. The occiput is inclined backward. There is no true postorbital process. The frontal horn forms a conspicuous median boss, which is much more posterior than that of the African living forms, of *Rusingaceros*, and even of *Dicerorhinus sumatrensis*, casting some doubt on their homology. Behind the orbits, the temporal lines remain far apart before turning medially, suggesting that this frontal horn had a very broad base. The few metapodials, which exhibit marked size variation, are similar in robustness to those of the Dicerotini.

Many features of *Paradiceros* would fit a primitive Dicerotini, but none definitively supports a close relationship, and the peculiar features of the posterior horn seem to speak against it.

Genus *CERATOTHERIUM* Gray, 1868

Synonymy *Serengeticeros* Dietrich, 1942.

Type Species *Ceratotherium simum* (Burchell, 1817), living African "white" or square-lipped rhino.

Diagnosis Nasal and frontal horns; nasal bones rounded and short, not contacting lacrimal; lower border of orbit sloping downward; weak postorbital process; broad nuchal crest; premaxilla much reduced; upper and lower incisors vestigial or absent; paracone fold weak; antecrochet absent (Geraads, 2005).

Remarks *Ceratotherium* obviously shares a common ancestry with *Diceros*, but there is some disagreement about what should be included in either genus. It had long been assumed that modern *Diceros* is closer to the ancestral morphology, but I have argued (Geraads, 2005) that its cranial morphology is in fact derived and that Miocene forms should rather be placed in *Ceratotherium*. I follow this classification here, although the affinities of the incompletely known African Miocene forms are certainly debatable.

CERATOTHERIUM ? PRIMAEVUM (Arambourg, 1959)

Type Incomplete juvenile skull, MNHN 1951-9-222 (Arambourg, 1959: plate 6).

Type Locality Oued el Hammam (= Bou Hanifia), Algeria, early late Miocene.

Diagnosis A two-horned rhino, the anterior horn on a strongly convex nasal boss, no postorbital process on the frontal, lower orbital floor inclined. Incisors reduced or lost, strong parastyle but no cristae on the molars, protocone slightly pinched. Metapodials rather slender.

Remarks This species has been described only from the type locality. The sample is large, but cranial and dental specimens are mainly from juvenile individuals. Arambourg (1959) viewed it as a relative of the Sumatran rhino, but I showed (Geraads, 1986) that its skull displays some apomorphic features of the Dicerotini (see diagnosis). Many important elements of the adult skull, front dentition, and premolars, are absent from the type locality, so that the precise phyletic position of this species is unclear, but it is certainly valid, and I provisionally include it in the paraphyletic genus *Ceratotherium*.

A P2 from the late Miocene of Chorora, Ethiopia (Geraads et al., 2002) has its lingual lobes almost free from the ectoloph, as in the earlier *Paradiceros mukirii*, but it probably also belongs to an early *Ceratotherium*. A maxilla from the late Miocene Namurungule Fm. (Nakaya et al., 1987: plate 6, figure 1), assigned to *Paradiceros mukirii*, is more likely to belong here.

CERATOTHERIUM DOUARIENSE (Guérin, 1966)

Type Associated partial skull and mandible, FSL-16750 and 16751, figured by Guérin, 1966: figures 1, 3, 4 (top), 5, 7-10.

Type Locality Douaria, Tunisia. Age not known with precision, but almost certainly late Miocene.

Diagnosis Translated and simplified from Guérin (1966). Large two-horned skull; nasal notch at the level of P2-P3, anterior orbital border above M1-M2; strong lacrimal processes directed posteroventrally; strong postglenoid process; posterior border of symphysis at the level of p3. Upper premolars with strong lingual cingulum, strong crochet, weak antecrochet. Upper molars with strong crochet.

Remarks The occipital region is unknown, but the rest of the skull does not display the derived features of *Diceros*, and it seems better to leave this species in the paraphyletic genus *Ceratotherium*, pending discovery of a more complete specimen. It is doubtfully distinct from *C. neumayri* from the late Miocene of the Balkano-Iranian province, but more North African specimens would be welcome. It has also been reported from Jebel Krechem, mostly on the basis on geographic proximity (Geraads, 1989), but not outside Tunisia. A tooth from the latest Miocene of Sahabi, Libya, identified as *Diceros neumayri* by Bernor et al. (1987), can be included here, too.

CERATOTHERIUM sp.

The rhino from the early Pliocene of Langebaanweg, South Africa, was described by Hooijer (1972) as *Ceratotherium praecox*. This species should be included in *Diceros* (discussed later), but the Langebaanweg rhino displays derived features of the Pliocene *Ceratotherium* clade, such as a flattened ectoloph, more plagiolophodont teeth, and tendency to close the medi- and postfossettes (Geraads, 2005).

Some other specimens are difficult to fit into the evolution of *Ceratotherium*. A maxilla from the Mio-Pliocene of Lissasfa, Morocco, is unusual in its high premolars but lingually fused protocone and metacone, reminiscent of the primitive Vallenian *Ceratotherium* from Pentalophos, Greece (Geraads and Koufos, 1990), but also of modern *C. simum*.

CERATOTHERIUM MAURITANICUM (Pomel, 1888)

Figure 34.6

Synonymy *Serengeticeros efficax* Dietrich, 1942.

Type M2, MNHN no. TER-2261, figured by Pomel (1895: plate 1, figures 1 and 2).

Type Locality Tighenif (= Ternifine, = Palikao), Algeria, lower/middle Pleistocene.

Diagnosis Size larger than in *C. neumayri*; nuchal crest stretched more caudally; nasal notch shallower; premolar row shortened; transverse lophes of upper teeth long and narrow; metaloph extending distolingually into distal cingulum, closing postfossette (Geraads, 2005).

Remarks North African *Ceratotherium mauritanicum* (figure 34.6) is clearly distinct from *C. simum*, and Guérin (1994a) and Guérin and Faure (2007) recognized its specific distinctness; in this region it survives until the late middle Pleistocene. I observed (Geraads, 2005) that its main features can also be found in East Africa in most of the specimens usually referred to *C. simum germanoaffricanum* (discussed later), and many of those called *Ceratotherium praecox* (Geraads, 2005: table 4), and accordingly referred these East African

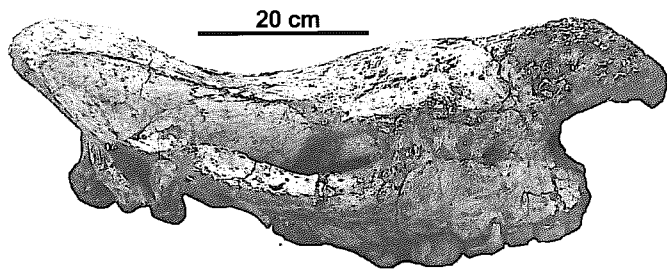


FIGURE 34.6 *Ceratotherium mauritanicum*, skull from the middle Pleistocene of "Grotte des Rhinocéros," Casablanca, Morocco.

specimens to *C. mauritanicum*. Again, precise delimitation of the species may be difficult, as there is little doubt that, in East Africa, it is directly ancestral to the living *C. simum*.

CERATOTHERIUM SIMUM (Burchell, 1817)

Diagnosis Geraads (2005). Strong postorbital constriction; nuchal crest narrow; postglenoid process weak; craniomandibular articulation horizontal; upper cheek teeth hypsodont, with very long narrow lophs and enlarged fossettes; labial walls sinuous in the upper part of crown; occlusal surface flat; premolar row shortened, DP1 shed before adulthood, P2 small; on molars, curved protoloph, oblique narrow metaloph, closed medifossette, post and prefossettes closed in advanced wear; lower cheek teeth rectangular, with closed fossettids on worn teeth; metapodials short and stout.

Remarks In historical times, the "white" rhino had a more restricted range than its "black" cousin, but in the Pleistocene it extended as far as the Mediterranean. Of the two living subspecies, *C. simum cottoni*, which was the more common 100 years ago, is now restricted to a few individuals in northeastern Congo. The southern *C. simum simum*, whose numbers had plummeted to 20 in 1895, now includes about 12,000 individuals, almost all of them in South Africa (International Rhino Foundation data). Late Holocene records of white rhinos in Kenya suggest that their distributions in the recent past were less widely separated.

The fossil form *Rhinoceros simus germanoaffricanus* Hilzheimer, 1925, whose subspecific name is often used as a species name for the Pleistocene form, is based on a lost skull from Olduvai, probably from its upper levels, where definite *C. simum* are known. Since it also shows an oblique metaloph, like the modern form, there is no reason to separate them. In any case, using a species name based on a type that survives only through a sketch of two teeth could easily lead to confusion.

Ceratotherium simum is clearly descended from *C. mauritanicum*. The transition, which took place near the Plio-Pleistocene boundary in East Africa, is mainly marked by features associated with an increasingly grazing diet, with some convergences with other grazing species, such as *Coelodonta* and *Elasmotherium*, in tooth morphology. Except for a somewhat larger size, early Pleistocene forms are already identical with the modern one.

Genus DICEROS Gray, 1821

Type Species *Diceros bicornis* Linnaeus, 1758, living African "black" rhino.

Diagnosis Geraads (2005). Premaxilla absent or vestigial. Cranium short and relatively broad. Neurocranium tilted anterodorsally relative to the splanchnocranium, resulting in

more vertically oriented occipital plane or even one inclined anterodorsally, nuchal crest less expanded posteriorly, more deeply concave cranial profile, basioccipital angled relative to basisphenoid, shortened face with orbits more anteriorly positioned and closer to nasal notch, and often nasolacrimal contact.

"DICEROS" AUSTRALIS Guérin, 2000

Type Left third metacarpal, AD 52'97, figured by Guérin (2000: figures 5.3–5.4), housed in the Geological Survey of Namibia, Windhoek.

Type Locality Arrisdrift, Namibia, ca. 17 Ma.

Diagnosis Guérin (2000). A very large cursorial rhinoceros of the Dicerotine type. Upper cheek teeth brachyodont, with a more or less continuous crenulated inner cingulum, and a crochet as the only or main internal fold. Ectoloph of upper premolars with a strong parastyle, paracone fold thick but not very prominent, and no mesostyle or metacone fold. Upper molars have a large paracone fold on their ectoloph, with a weak vertical bulge in the middle of it, and a protocone weakly constricted on its anterior face. Tall and slim but sturdy limb bones. Lateral and medial metapodials very long with respect to the central one.

Remarks This species is known only from isolated teeth and limb bones. The upper incisors are unknown; the lower ones are smaller than in *R. leakeyi*, although not vestigial. The P4 has no constricted protocone, a rather flat ectoloph behind the paracone fold, and no lingual connection between the lophs. These features, plus the large size for this age, led Guérin to include the Arrisdrift species in the Dicerotini, hence in *Diceros*, as he considers this genus as the earliest and most primitive member of this tribe. Indeed, Tougaard et al. (2001) rooted the tribe into the late Oligocene, but the characters of *D. australis* are not exclusive of it. This is certainly a valid species, but only cranial material would shed more light on its affinities.

DICEROS PRAECOX (Hooijer and Patterson, 1972)

Type Poorly preserved incomplete skull, KNM-KP 36 (Hooijer and Patterson, 1972: figure 9A).

Type Locality Kanapoi, Kenya, about 4 Ma.

Diagnosis Geraads (2005). The original diagnosis consists entirely of plesiomorphic characters. This species has only a few apomorphic features with respect to its likely ancestor *C. neumayri*: orbit more anterior with respect to tooth row; skull profile more concave; occipital plane more vertical; nuchal crest less extended posteriorly.

Remarks This species had long been included in *Ceratotherium*, but I showed (Geraads, 2005) that the type and a referred skull from Ekora, which formed the basis of the original description, are both closer to *Diceros* in their tooth morphology, concave cranial profile, and occiput more vertical than in *Ceratotherium*. The distinction from *D. bicornis* may not be easy. I referred (Geraads, 2005) a fragmentary skull from the base of the Sidi Hakoma member of the Hadar Fm to *D. praecox*, and an as yet uncollected skull from higher up in the sequence at Dikika appears transitional but is less derived than *D. bicornis* in its larger size, less shortened skull, less anteriorly shifted orbit, and wide nuchal crest. I also referred (Geraads, 2005) to this species several specimens previously called either *C. praecox* or *D. bicornis*, but most of the material previously reported under the name "*Ceratotherium praecox*" belongs to what is called here *C. mauritanicum*.

Diagnosis Geraads (2005). Size smaller than *D. praecox*; face more angled on neurocranium; nuchal crest not expanded; cheek teeth narrower, loph more transverse; premolar row shortened.

Remarks The living "black" rhino was once widespread outside dense forest in sub-Saharan Africa, but it has never been reported north of the present-day Sahara. Numbers sharply declined with the introduction of firearms, and several subspecies have recently become extinct. A minimum was reached in 1995, with only 2400 remaining wild individuals, but a slight rise since then has brought the number to about 3700 (IRF data), scattered from Kenya to South Africa and Namibia, with three remaining subspecies.

This species has been recorded from as early as the late Miocene (e.g., Lothagam), but I preferred (Geraads, 2005) to regard these pre-Pleistocene forms as *D. praecox*. The best early representative of the living species is skull KNM-ER 636, from the KBS member of Koobi Fora (Harris, 1983).

Subfamily ELASMOTHERIINAE Bonaparte, 1845
Genus *KENYATHERIUM* Aguirre and Guérin, 1974

Type Species *Kenyatherium bishopi* Aguirre and Guérin, 1974.

Diagnosis Translated from Aguirre and Guérin (1974). A medium-sized Elasmotheriinae; upper premolar hypsodont with regularly convex ectoloph and a very weak paracone fold. Opening of the median valley fully blocked by a wall uniting protocone to hypocone. Medifossette lacking true folds but with localized microfolds. Protocone constricted by a groove on the mesial side of the protoloph.

KENYATHERIUM BISHOPI Aguirre and Guérin, 1974

Type Upper premolar, probably P4, KNM-NA 198.

Type Locality Nakali, Kenya, early late Miocene.

Diagnosis As for genus.

Remarks The holotype and an incomplete molar are indeed remarkable in the features mentioned in the diagnosis, plus the presence of cement, large postfossette, distally closed by a high cingulum, and small protocone and hypocone well set off from the loph. The authors viewed *Kenyatherium* as close to the Eurasian Miocene genera *Iranotherium*, *Hispanotherium*, and *Caementodon*. In the cladistic analysis of Antoine (2002), it occupies a basal position among the elasmotheres because of its transverse metaloph on P4, long metaloph on M1 or M2, lack of cristae, presence of lingual cingulum on upper teeth, and hypocone fully merged into the metaloph on the molar, though the latter two characters are disputable. In any case, the material from Nakali is too poor to precisely determine its systematic position.

The species has also been reported from the roughly contemporaneous lower member of the Namurungule Formation (Nakaya et al., 1987); this is the more likely identification, as the antecrochet is stronger than in *Chilotheridium*, and the grooves isolating the protocone and hypocone on the molars are deeper.

Genus *OUGANDATHERIUM* Guérin and Pickford, 2003

Type Species *Ougandatherium napakense* Guérin and Pickford, 2003.

Diagnosis Translated from Guérin and Pickford (2003). Small Elasmotheriinae with short, hornless nasals. Hypsodont upper cheek teeth, mesial width greater than distal width; medifossette filled with cement, and with crochet as single fold. Upper premolars small, with a lingual wall connecting protocone to hypocone; ectoloph with well-marked folds; slanting lingual cingulum; constricted protocone. Upper molars with much folded labial wall; protocone strongly constricted; no lingual or labial cingulum, but a strong anterior cingulum encloses a prefossette in the protocone groove. Cursorial limbs, with lengthened second and third segments. Long slender metapodials, the central ones with broadened distal diaphysis, the lateral ones relatively long.

OUGANDATHERIUM NAPAKENSE Guérin and Pickford, 2003

Type Guérin and Pickford (2003) listed as holotype two third metacarpals and two third metatarsals, but the whole material from Napak belongs to only two individuals (Guérin and Pickford, 2003: 8), and these authors did not state why they assumed that these four bones, and only they, belong to one of these individuals. Stored in the Uganda Museum, Kampala.

Type Locality Napak I, Uganda, ca. 19 Ma.

Diagnosis As for genus.

Remarks This species is known only from the lower level of Napak from remains of two incomplete skeletons and skull fragments. The nasals are not fused, triangular, and quite short; the premaxillae look long, but whether they carried an incisor is not known. The upper premolars resemble the P4 of *Kenyatherium*, with a transversely elongated postfossette, but the hypocone is more reduced, especially on P3, and more closely appressed to the protocone, so that the teeth are more premolariform (i.e., more primitive).

Evolution

Like that of several other mammalian groups, the Miocene record of African Rhinocerotidae is relatively good between 18 and 15 Ma, and after 7 Ma, but more patchy between these periods, and before 18 Ma. The late early to early middle Miocene is the period of greatest diversity, with at least four contemporaneous genera in Kenya. Of these, only the brachypotheres are clearly linked to later forms, although it is likely that *Rusingaceros* is related to later *Paradiceros* and Dicerotini, despite the significant time gap.

Chilotheridium remains a mysterious genus, partly owing to the poor preservation of the Loperot material. Unfortunately, the holotype of *Turkanatherium acutirostratum* is not available, but it may play a central role in the evolution of African rhinos, as one may suspect that it is in fact an elasmothere. The systematic status of this group is not fully settled; a recent revision (Cerdeño, 1995) considered it diphyletic, but the latest ones (Antoine, 2002; Antoine et al., 2003) viewed it as a valid clade. The main features suggesting that *Turkanatherium* belongs here are the transversely elongated postfossette on P3-4, and the lingual connection, through a high narrow bridge, of the loph on these teeth. This is the "semimolariform" morphology of Heissig (1969). *Turkanatherium* would then document part of the ghost lineage of African elasmotheres leading to *Kenyatherium*, as postulated by Antoine (2002).

In fact, at the time of its description, *Kenyatherium* was clearly separated from the other known African middle

Miocene forms, which had mainly been described and illustrated by Hooijer. Now that more of them have been described or discovered, the distinction dwindles, and several African rhinos have premolars reminiscent of the elasmotheres. A complete skull and parts of a skeleton found at Nachola (Baragoi), a site dated to 15–16 Ma., by a Japanese team led by H. Ishida, are now under study by H. Tsujikawa, who kindly allowed me to mention them. The premolars are similar to those from Moruorot, while the molars with strongly pinched hypocone and protocone, and the high zygomatic arches and very long nasals (but without lateral flange) recall those of the elasmothere *Procoelodonta*. Well-preserved skulls from Máboko, kindly made available by B. Benefit, also have strongly pinched protocones and hypocones on the (much worn) molars, antecrochet almost connecting the hypocone and transversely elongated postfossette on a premolar, plus a protruding orbital border and a strong nasal horn.

The question is whether features of the cheek teeth suffice to identify a rhino as an elasmothere. One of the strongest synapomorphies of this group according to Antoine (2002; also Antoine et al., 2003) is the purportedly “submolariform” morphology of P3–P4 but, while this is probably true of *Ougandatherium*, the type of *Kenyatherium* fully matches the description of the “semimolariform” morphology, distinct from the former one by “protocone and hypocone wider apart, bridge between them longer and shifted labially, so that the protocone becomes lingually separated from it by the protocone grooves” (Heissig, 1969: 16, my translation, and figure 4c therein). If both *Ougandatherium* and *Kenyatherium* are elasmotheres, molarisation does increase in this group, and it is hard to keep premolar morphology as a major distinctive feature of it, especially as its members have diverse cranial morphologies. Furthermore, non-molariform premolars are common in Oligocene and early Miocene rhinos, and it may be difficult to distinguish the elasmothere morphology from the primitive condition. Full study of the recently collected material may clarify these issues.

Biogeography

Rhinos are absent from the Oligocene sites, and the African fauna of that time is so clearly endemic that it is unlikely that an Oligocene African rhino will ever be discovered. By contrast, their absence from the earliest Miocene of Meswa Bridge might be due to incomplete sampling, as the fauna is poor but contains a Eurasian immigrant (*Dorcatherium*); the earliest African rhinos, obviously of northern origin, may thus prove to be older than those presently recorded at Songhor and Napak, at about 20 Ma.

For the rest of the Miocene, uncertainties about real affinities hinder the reconstruction of past ranges and migration routes. *Rusingaceros* predates all Eurasian two-horned rhinos, which may have immigrated from Africa together with the Proboscideans; if the Nyakach rhino really belongs to *Plesiaceratherium*, this genus must also be part of the pre-Langhian exchange, together with the brachypotheres. The period between 15 and 10 Ma. is very poorly sampled; if *Paradiceiros*, unknown in Eurasia, is not ancestral to the Dicerotini, the next exchange concerns *Ceratotherium* or its immediate ancestors, at the beginning of the late Miocene. Later immigrations from the North are those of the two *Stephanorhinus* species.

Conclusions

The diversity of African Miocene Rhinocerotidae is clearly greater than was assumed by Hooijer (1978). An undesirable consequence is that it becomes impossible to identify them by their teeth only, as different genera may share similar dental morphology (e.g., the cheek teeth of *Paradiceiros mukirii* are almost identical to those of the ? *Plesiaceratherium* from Nyakach, although the skulls are quite distinct). It follows that many previous identifications, based upon fragmentary remains, must be treated with the utmost caution. Table 34.1 lists the main rhino-bearing Cenozoic African localities, with both published and revised identifications. The latter are usually more conservative, and often tentative, because the material is incomplete, or not described and not seen by me. The great number of “Rhinocerotidae indet.” gives an idea of what remains to be done.

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