

PLIOCENE RHINOCEROTIDAE (MAMMALIA) FROM HADAR AND DIKIKI (LOWER AWASH, ETHIOPIA), AND A REVISION OF THE ORIGIN OF MODERN AFRICAN RHINOS

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ABSTRACT—Fossil representatives of the two extant African rhinoceros lineages, *Ceratotherium* and *Diceros*, co-occur in the Pliocene deposits of the Hadar Formation, Ethiopia. Both arose, in turn, from *Ceratotherium neumayri* of the late Miocene. The first of these Pliocene species, *Ceratotherium mauritanicum*, can be distinguished from the living *C. simum*, to which it probably gave rise in the earliest Pleistocene, by its less plagiolophodont cheek teeth. The second, *Diceros praecox*, is closely related to *D. bicornis*, although many specimens, including the type, were previously referred to *Ceratotherium*. The teeth of *D. praecox* are little changed relative to those of its Miocene ancestor, but its skull displays the apomorphic rearrangements typical of *D. bicornis*, suggesting increased browsing specialization. The split between the two lineages probably indicates ecological divergence and character displacement between browsing versus grazing specializations.

INTRODUCTION

Beginning with the early geological and paleontological survey of Taieb in the 1970s (Taieb, 1974), extensive field research has been conducted in the Awash valley of Ethiopia over the last 30 years. In the lower part of the basin, the International Afar Research Expedition, led by Y. Coppens, D. Johanson, and M. Taieb, concentrated on the northern bank of the Awash River in the Hadar area, which yielded many hominid fossils, including the famous "Lucy." Paleontological research in the Hadar area continues today by the Hadar Research Project. In addition to the hominid discoveries (Lockwood et al., 2000, and references therein), tens of thousands of vertebrate remains collected at Hadar provide data on the biostratigraphic and paleoenvironmental setting of the area. Most of the fossil-bearing sediments, dated to 2.3–3.5 Ma, are formally assigned to the Hadar Formation, which consists of the following members in ascending stratigraphic order: Basal Member (BM), Sidi Hakoma (SH), Denen Dora (DD), Kada Hadar (KH). These members are divided into numbered sub-members. Studies of the mammalian fauna other than primates remain scarce. Some of the Hadar rhinos were mentioned in passing by Guérin (1979, 1987), but no systematic study was undertaken.

In addition to the Hadar area, fossil rhino material was recovered from an adjacent study area on the opposite bank of the Awash River, called Dikika. This area was briefly surveyed in the 1970s and then beginning in 1999 has been the target of a thorough survey by a new interdisciplinary research project, the Dikika Research Project, led by Zeresenay Alemseged. The almost complete sequence of the Hadar Formation is exposed on the Dikika side, but fieldwork has focused on the SH Member. Some specimens were also collected in the Asbole area, southwest of Hadar, of early middle Pleistocene age (Alemseged and Geraads, 2000; Geraads et al., 2004).

The Hadar and Dikika rhinos described in this paper are housed in the National Museum of Ethiopia, Addis Ababa. Specimens were compared with the two living African species, *Ceratotherium simum* and *Diceros bicornis*, which doubtless form a clade among living rhinos. The former is a pure grazer, while *D. bicornis* is mostly a browser feeding on leaves and twigs. The Hadar and Dikika rhinos have also been compared with fossils from a number of localities, the most important of which are:

Late Miocene: Pikermi, Samos, Pentalophos, Thessaloniki (Greece: Arambourg and Piveteau, 1929; Geraads, 1988; Gera-

ads and Koufos, 1990); Kemiklitepe (Turkey: Geraads, 1994); Douaria (Tunisia; Guérin, 1966); Lissasfa (Morocco; unpublished); Maragheh (Iran; Thenius, 1955; Geraads, 1988).

Pliocene: Koobi Fora, West Turkana, Kanapoi, Lothagam (Kenya: Hooijer and Patterson, 1972; Harris, 1976, 1983; Harris and Leakey, 2003); Omo Valley (Ethiopia: Hooijer, 1973; Hooijer and Churcher, 1985; Guérin, 1985); Ahl al Oughlam (Morocco; unpublished data).

Pleistocene: Oulad Hamida (Morocco; Geraads and Bernoussi, in press); Olduvai, Peninj (Tanzania; Leakey, 1965; Hooijer, 1969; Geraads, 1987).

The material from Laetoli and Langebaanweg, published by Guérin (1987) and Hooijer (1972), respectively, was not directly examined. Measurements are in millimeters, and follow Guérin (1980). Diagnoses list only derived features.

Institutional Abbreviations—BMNH, Natural History Museum, London; FSL, Faculté des Sciences, Lyon; INSAP, Institut National des Sciences de l'Archéologie et du Patrimoine, Rabat; KNM, National Museums of Kenya, Nairobi; MGML, Musée Géologique et Minéralogique, Lausanne; MNHN, Muséum National d'Histoire Naturelle, Paris; MTA, Maden Tetkik ve Arama Museum, Ankara; NHB, Naturhistorisches Museum Basel; NHMW, Naturhistorisches Museum Wien; NME, National Museum of Ethiopia, Addis Ababa; NMT, National Museum of Tanzania, Dar-Es-Salaam; PIUM, Paläontologisches Institut, Münster; SMNS, Staatliches Museum für Naturkunde, Stuttgart.

Other Abbreviations—AL, Afar Locality (Hadar sample); DIK, Dikika; ER, Koobi Fora; WT, West Turkana.

SYSTEMATIC PALEONTOLOGY

Family RHINOCEROTIDAE Gray, 1821
Subfamily RHINOCEROTINAE Gray, 1821
Tribe DICEROTINI Ringström, 1924, emend.
Genus *CERATOTHERIUM* Gray, 1868

Serengeticerus Dietrich, 1942

Type Species—*Ceratotherium simum* (Burchell, 1817), living African 'white' rhinoceros.

Diagnosis—Nasal and frontal horns: nasal bones rounded and short, not contacting lacrimal; lower border of orbit sloping downwards; weak post-orbital process; broad nuchal crest; pre-

maxilla much reduced; upper and lower incisors vestigial or absent; paracone fold weak; anterochet absent.

Range—Late Miocene, Eastern Mediterranean; latest Miocene to Recent, Africa.

Remarks—The genus *Ceratotherium*, as here understood, is paraphyletic, and includes all Dicerotini except *Diceros*, to which it gave rise in the early Pliocene. Its earliest representative is *C. neumayri* from the late Miocene of the Eastern Mediterranean. Another option, not followed here, would be to restrict this generic name to Pliocene and Pleistocene forms, after the *Diceros* split, and to keep *C. neumayri* as a plesion, or to erect a new generic name for it, as none is available (Geraads, 1988:24).

CERATOTHERIUM MAURITANICUM (Pomel, 1888)

Rhinoceros (Atelodus) mauritanicus Pomel, 1885; nomen nudum.
Rhinoceros mauritanicus Pomel, 1888:210.
Serengeticerus efficax Dietrich, 1942.

Lectotype—Pomel (1888) did not designate a type, nor did he list the contents of the type series from the Pleistocene of Palikao (= Ternifine, now Tighenif, Algeria), but there is no reason to believe that the specimens he illustrated in 1895 were not part of it. I hereby select as lectotype the upper M2 (MNHNP no. TER-2261) figured on his Plate 1, Figures 1–2.

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

Range—Late Pliocene to late Pleistocene, North Africa; middle Pliocene to early Pleistocene, East Africa; late Pliocene, South Africa.

Description of the Lower Awash Material—Skull DIK-1-10 (SH1): this skull was found associated with a juvenile hominid skeleton. It is from an old individual, the much-worn M2s and M3s being the only remaining teeth. The medifossettes are closed. The metaloph of M2 is narrow and slightly oblique, but its axis is more posterior than the medifossette. M3 is trapezoidal, with a wide entrance to the medisinus. The labial wall is concave behind a reduced paracone fold. The paroccipital processes are long and slender. The basioccipital is but slightly angled relative to the basisphenoid. The nuchal crest does not extend caudally much beyond the occipital condyles.

Skull AL-129-25 (SH1) is the most complete skull (Fig. 1).

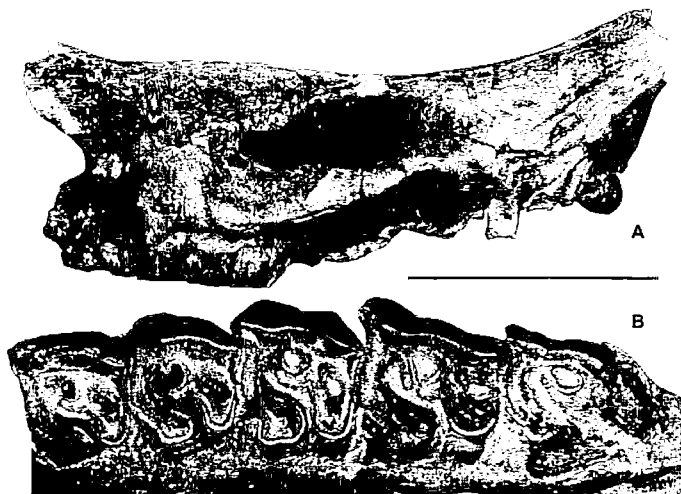


FIGURE 1. *Ceratotherium mauritanicum*, skull AL-129-25. A, lateral view; B, occlusal view of the cheek teeth. Scale equals 30 cm for A, 10 cm for B.

missing only the region anterior to P3 and most of the nasal bones. Its morphology is similar to that of the modern form. Both wings of the nuchal crest stretch caudally beyond the occipital condyles, with a deep sagittal notch. Cheek teeth are in medium wear. The labial wall is sinuous, but there is no paracone fold. A long crochet is present on all teeth, as well as a well-developed crista on the molars, enclosing the medifossette on the left molars. The proto-loph is long and narrow. The posterior cingulum is high, and the postfossette is closed on all teeth except M3, which has a trapezoidal outline.

Skull AL-125-1 (SH1) is also an almost complete skull. The only significant difference from the previous one is that the occipital notch is shallow. The depth of this notch has no specific value, as shown by the variation in the living form (see Loose, 1975:pl. 2). The teeth are more worn, but share all the features of AL-129-25.

Maxilla AL-137-28 (SH1) is from a young specimen, with P4 just erupted. It shows that the medifossette closes early in wear, that there is no paracone fold even in the upper part of the crown, and that the transverse lophs are long relative to their thickness. DPI is not preserved, but was certainly present in life.

Most of the measurements of these skulls (Table 1, Fig. 2) fall within the range of modern *C. simum*. The main exception is the nuchal crest, which is broader in the Hadar specimens (measurement no. 15).

AL-86-8 (member unknown) is a fragment of a maxilla with DP2-DP4. The external walls of DP3-DP4 are gently undulated, but the paracone fold is weak. The crochet, arising from the metaloph close to its junction with the ectoloph, meets the crista to enclose a rounded medifossette of small size. Both the proto-loph and metaloph are curved, and the metaloph continues posteriorly into a high distal cingulum, but the lophs are shorter than in *C. simum*. There is a small postfossette on DP2.

Mandibles and Lower Teeth—All lower teeth from the Hadar Formation lack the derived features that characterize those of Recent *C. simum*, such as increased hypsodonty, rectangular outline, and closed fossettids. Since some of these teeth are certainly of *C. mauritanicum*, they show that these features had not yet evolved in this lineage. However, this also prevents differentiation between the mandibles of the two taxa present in the Hadar Formation. Other features, such as corpus depth or extent of the symphysis, have not proved useful for specific distinction, but the condyle of AL-125-1 is parallel to the occlusal plane as in *C. simum*, whereas it slopes medio-ventrally in *Diceros bicornis*. Although a biomechanical analysis was not undertaken, this orientation, together with the smaller size of the post-glenoid process and flatness of the occlusal surfaces, are clearly linked to transverse chewing movements (Fortelius, 1985).

Postcranials—Taxonomic distinction is also very difficult or impossible for limb bones. The proportions of the cranial material of both taxa suggest that most postcranials are of *Ceratotherium*, but no great size difference should be expected. Only the distal radii show a difference of proportions, the two smaller ones (*Diceros*?) being relatively wider than the larger ones. The best specimen is an associated set of limb bones, AL-382-5 (DD2). The humerus and femur are close in length to the maximum recorded for living *C. simum*, but the radius, ulna, tibia, and metapodials are longer, showing that the distal limb elements were more elongated, and indicating a more cursorial mode of locomotion (Table 2).

Ceratotherium simum (Burchell, 1817)

In addition to the two living subspecies, the fossil form *Rhinoceros simus germanoaffricanus* Hiltzheimer, 1925, is included.

Diagnosis—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 upper part of

TABLE 1. Measurements (in mm) of *Ceratotherium* skulls (those of KNM-ER-328C in part from Harris, 1983)

Measurement	<i>C. simum</i> N = 23-26	Ain Hanech 1953-21-371	AL-125-1	AL-129-25	Dikika 1	KNM- ER-328C	KNM- WT-18675	KNM- KL-6
1-L condylo-Pmx	708	750	730?	720*	—	752	720	—
2-L condylo-Na	742	—	—	—	760	—	—	—
3-L occipito-Na	797	785	—	810*	760	800	760	870
8-L occipito-orbital	486	—	480	500	—	500	470	535
9-L orbit-nasal notch	182	—	—	170	190	195	160	200
13-L condylo-M3	374	—	400	375	395	435	380	380
15-W nuchal crest	224	—	260	270*	280	275	—	—
16-W over paroccipital processes	257	—	250	250	280	283	—	—
21-Bizygomatic W	339	380	365*	—	360	373	—	—
22-Minimum nasal W	164	—	—	175	158	—	—	—
23-Occipital height	169	130+	180	—	—	156	—	—
32-Bicondylar W	155	—	161	140	164	151	—	—

Measurement numbers and mean values of *C. simum* from Guérin (1980). Symbols: *, approximate measurement; ?, estimated measurement.

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.

Range—Lower Pleistocene to Recent, East Africa; middle Pleistocene to Recent, South Africa; late Pleistocene, North Africa.

Referred Specimens—Fossil remains of *Ceratotherium* from the Pleistocene of the Lower Awash valley are too fragmentary to be identified to species, but are probably assignable to *C. simum*. A talus from Asbole, southwest of Hadar, is larger (maximum breadth = 110 mm; lateral height = 98 mm) than the maximum recorded by Guérin (1980) for the living form. It confirms the size reduction of this species since the middle Pleistocene (Hooijer, 1969).

Comparisons

⁷ *Ceratotherium mauritanicum*, the first fossil rhinoceros ever named from Africa, was described on fragmentary remains from

Tighenif by Pomel (1888, 1895). The teeth that he illustrated clearly show a transverse metaloph; this morphology is distinct and more primitive than in the living *C. simum* in which the metaloph is much more oblique, its axis passing through the medifossette. More complete North African material of comparable age, from Ain Hanech (Arambourg, 1970) and Oulad Hamida (Geraads and Bernoussi, in press) can confidently be referred to *C. mauritanicum*. The North African specimens reveal the species' few distinguishing cranial features, a weak post-orbital constriction and wide nuchal crest, and the slenderness of its metapodials. The material from Hadar and Dikika resembles North African *C. mauritanicum* in all these features, and is referred accordingly to the same species.

Serengeticerus efficax Dietrich, 1942, from Laetoli, has a similar molar morphology (Dietrich, 1942:fig. 2; 1945:fig. 36). More material from Laetoli was described by Guérin (1987) as *Ceratotherium praecox*. A crushed skull (Guérin, 1987:pl. 9.4) is similar to those from the Lower Awash, especially in its broad nuchal crest. Guérin's assertion (1987:322) that its cranial vault is "markedly concave" is not consistent with his Figure 9.4A. His

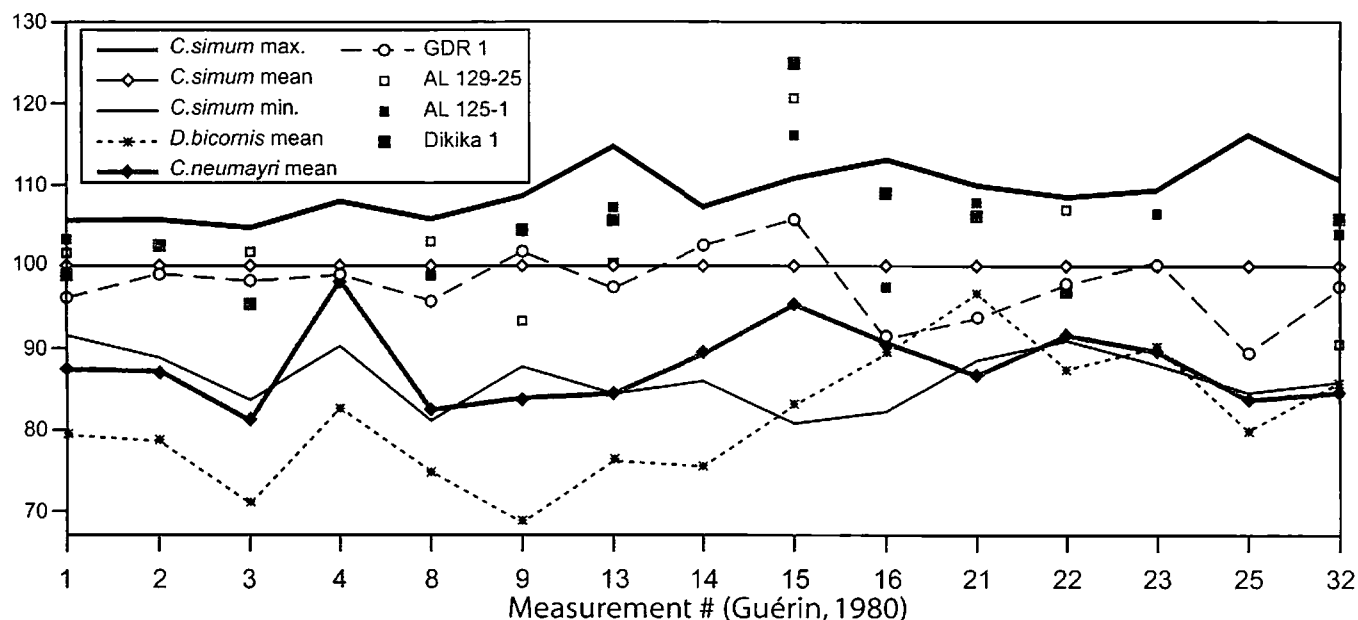


FIGURE 2. Ratio diagram of Dicerotini skulls. Standard = mean of living *C. simum* (N = 21 to 26). *Diceros bicornis* and *C. simum* are extant representatives (Guérin, 1980:table 2). GDR-1 is a well-preserved *C. mauritanicum* from the middle Pleistocene of Morocco (INSAP; Geraads and Bernoussi, in press). Squares are *C. mauritanicum* from the Lower Awash. The values of *C. neumayri* are from 10 skulls from the Eastern Mediterranean (MNHNP, NHB, NHMW, PIUM, SMNS); the actual number of specimens for which each measurement could be taken is given in brackets after the measurement numbers, which follow Guérin (1980:tables 1 and 2; Table 1): 1 (3), 2 (3), 3 (8), 4 (9), 8 (7), 9 (9), 13 (7), 14 (4), 15 (4), 16 (6), 21 (4), 22 (1), 23 (2), 25 (2), 32 (4).

TABLE 2. Limb measurements (in mm) of *Ceratherium mauritanicum* AL-382-5

Element	Maximum length	
Humerus	440 (418, 445)	Distal width = 185 (169, 184)
Radius	425 (386, 406)	Proximal width = 111 (119, 130)
Ulna	530 (486, 509)	Depth of olecranon = 105 (105, 127)
Femur	550 (508, 550)	Distal width = 155+ (145, 161)
Tibia	415* (374, 395)	
Mt III	200 (168, 180)	

Mean and maximum of living *C. simum* in brackets (Guérin, 1980).
*, approximate measurement.

detailed descriptions of the numerous teeth point out their similarities with those from Hadar and Dikika. The same is true of the upper milk teeth illustrated by Dietrich (1945:pl. 17, fig. 32); the DP4 differs from that of *C. simum* by the shorter protoloph and more transverse metaloph, as on the material from Hadar. Therefore, *Serengeticeros efficax* is considered a synonym of *Ceratherium mauritanicum*.

The earliest undoubted representative of the African Pliocene *Ceratherium* clade is the form from Langebaanweg that Hooijer (1972) incorrectly called *C. praecox*. The flattening of the ectoloph, long narrow proto- and metaloph with tendency to close the postfossette, the deep lingual opening of the median valley, as well as the lengthening of the crochet and crista of DP4, which foreshadow the closure of the medifossette in the modern form (Hooijer, 1972:pl. 29), are apomorphies of the Pliocene *Ceratherium* clade, indicating that the Langebaanweg form belongs to this clade. The lack of crista, weakness of crochet, and straight protoloph on the premolars are primitive features that would perhaps warrant a specific name distinct from *C. mauritanicum*.

In other East African sites, *C. mauritanicum* is often called *C. germanoaffricanum*, but this name (Hilzheimer, 1925) is based upon a (lost) skull from Olduvai whose M2 (Arambourg, 1948:fig. 24) has an oblique metaloph, similar to that of the living form. It probably comes from the upper levels of Olduvai (Leakey, 1965:25), where definite *C. simum* fossils are known (Hooijer, 1969). Thus, *C. germanoaffricanum* is probably synonymous with *C. simum*, as indeed Arambourg (1948:300) had suggested first. East African *C. mauritanicum* is known best by the material, including several skulls, from east and west of Lake Turkana, Kenya, mostly of late Pliocene age (Harris, 1976, 1983; and pers. obs.). There is also a skull from the late Pliocene of Rawi, Kenya, in the BMNH. This material does not differ from that of the Hadar Formation, except that, as noted by Guérin (1987), the medifossette of P3 is usually closed, obviously a derived character linked with its younger geologic age. Likies (2002) has noted the same evolutionary pattern in the Pliocene of Chad, from Kollé to Koro Toro. As at Hadar and Dikika, the nuchal crest is broader than in the living form (Fig. 2), but overall size does not exceed that of the latter before the early Pleistocene.

The transition to *C. simum* probably took place shortly after the Plio-Pleistocene boundary in East Africa. Molars from Olduvai Bed II (Hooijer, 1969:pl. 2, fig. 4-5, pl. 3, fig. 8) often have long protoloph, and all teeth from Olduvai, as well as those of the Ileret skull KNM-ER-328C (whose age is probably Pleistocene: Brown and Feibel, 1991:19) have metalophs that are more oblique than in the Pliocene *C. mauritanicum*. Cross sections through the M2 of one of these early representatives of *C. simum* from Peninj (Geraads, 1987) show that this is not a result of tooth wear; although the lophs become straighter with wear, their overall obliqueness is not altered (Fig. 3). The protoloph extends beyond mid-length of the tooth, and the axis of the metaloph passes through the medifossette.

In North Africa, *C. mauritanicum* is present from the late

Pliocene until the late Pleistocene. At Ahl al Oughlam in Morocco, dated to ca. 2.5 Ma (Geraads et al., 1998), the teeth, which are all deciduous, are identical to those of Hadar AL-86-8 or KNM-ER-2320 from the Upper Burgi Member at Koobi Fora. Specimens from Oulad Hamida in Morocco (Geraads and Bernoussi, in press), dated to the second half of the middle Pleistocene (Rhodes et al., 1996) and from the late Pleistocene (Arambourg, 1938:pl. 6, fig. 2, pl. 7), are clearly referable to this species and not to the modern form.

Changes in size and proportions of the metapodials reflect the evolution of locomotor adaptations in the *C. mauritanicum*-*C. simum* lineage (Fig. 4). Those of the earliest forms from Langebaanweg or from the Kenyan sites of Mpesida, Chemeron, and

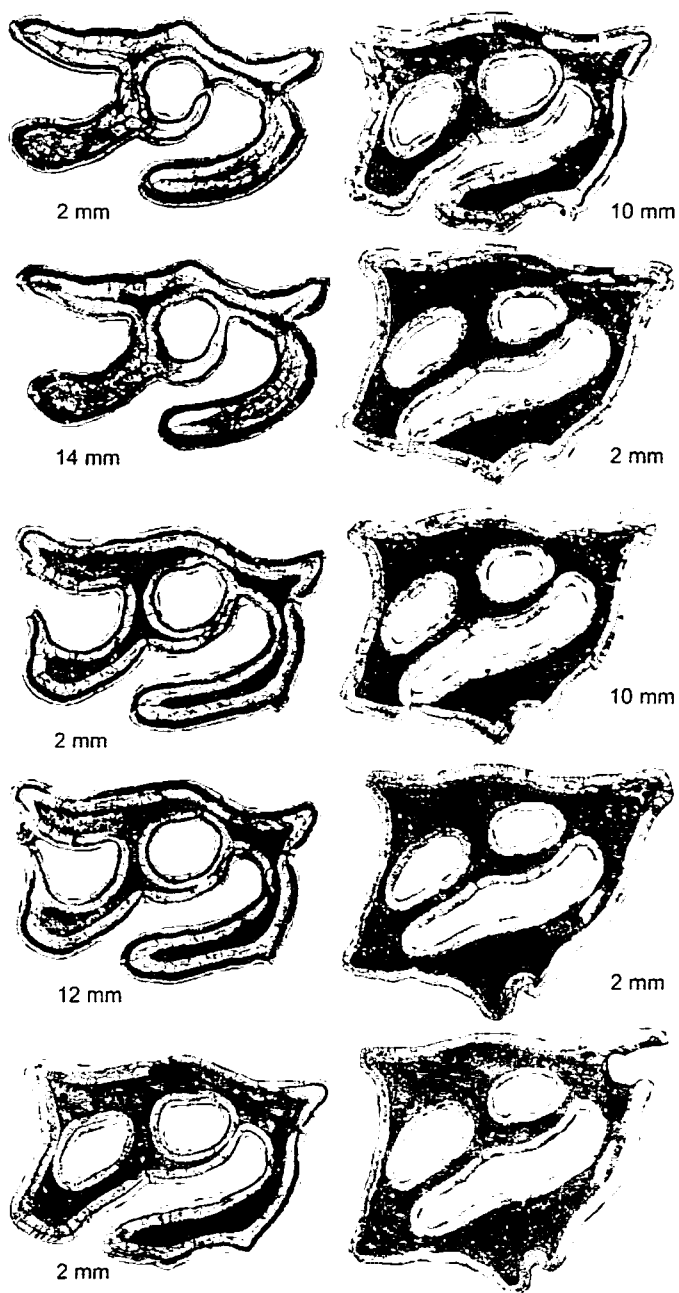


FIGURE 3. Cross-sections through the crown of the M2 of an early *C. simum* from the early Pleistocene of Peninj, Tanzania (NMT; Geraads, 1987). Early 'wear' stages in left column, from top to bottom, later stages in right column. Measurements are the distances between successive sections.

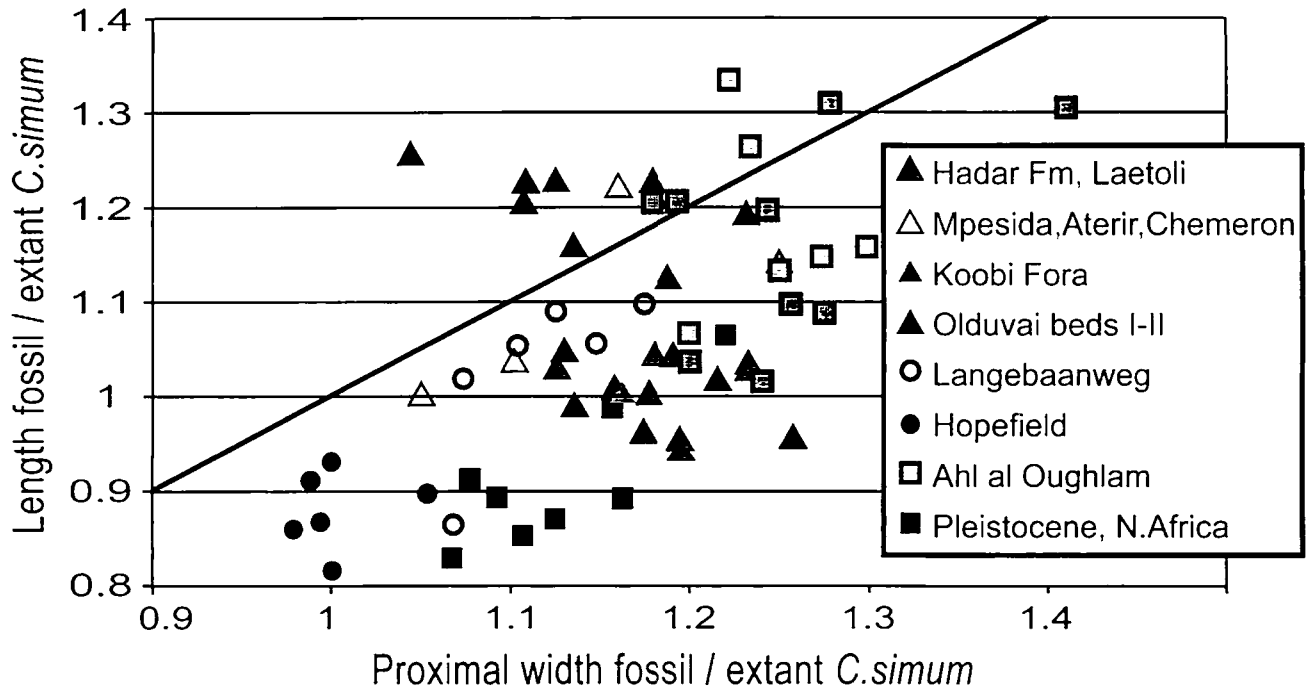


FIGURE 4. Proportions of the metapodials (Mc II-IV, Mt II-IV) of fossil *Ceratotherium*, compared to the means of extant *C. simum* (Guérin, 1980: tables 18-20, 31-33). Most metapodials are below the 1/1 line, except most of those from Olduvai, which are stouter. Triangles, East Africa; circles, South Africa; squares, North Africa.

Aterir, are rather slender and of medium size; later Pliocene forms, from Ahl al Oughlam, Dikika, Hadar, and Laetoli, are larger but of similar proportions. Size distribution is not clearly bimodal in the latter sites, suggesting that either *Diceros* and *Ceratotherium* were of similar proportions, or that *Diceros* is absent in their metapodial sample. There is no doubt, however, that these metapodials mostly represent *C. mauritanicum*. The early Pleistocene metapodials from Olduvai are robust and similar in proportions to those of the modern form. Middle and late Pleistocene specimens from East and North Africa (the South African form might represent *Diceros*) are slightly smaller. Thus, it is likely that the modern form derived from the Olduvai one by size reduction, while the North African populations retained the slender metapodials of *C. mauritanicum*. Therefore, both the dentitions and postcranials suggest that the transition from *C. mauritanicum* to *C. simum* took place in East Africa.

Genus *Diceros* Gray, 1821

Type species—*Diceros bicornis* Linnaeus, 1758, living African 'black' rhinoceros; lower Pleistocene to Recent, Africa.

Diagnosis—Premaxilla absent or vestigial; cranium short and relatively broad; neurocranium tilted anterodorsally relative to 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 praecox (Hooijer and Patterson, 1972)

Ceratotherium praecox Hooijer and Patterson, 1972:19

Type—Poorly preserved incomplete skull from Kanapoi, Kenya, KNM-KP-36 (Hooijer and Patterson, 1972:fig.9A).

Diagnosis—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.

Range—Early to late Pliocene, East Africa.

Description of the Lower Awash Material—Skull AL-126-21 (SH1) is broken into several pieces. A large fragment consists mainly of the occipital and part of the cranial base; it is too damaged to be fully described. The only clear feature is the sharp

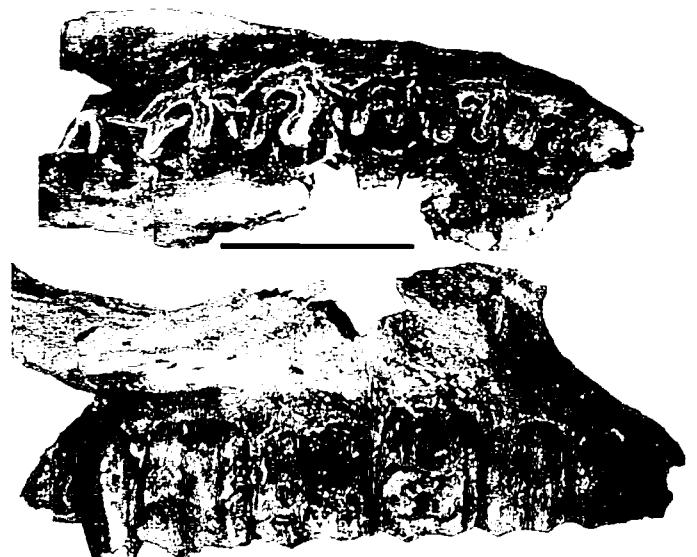


FIGURE 5. *Diceros praecox*, maxilla AL-126-21. Occlusal (top) and labial (bottom) views. Scale equals 10 cm.

sagittal keel, at least 10 cm long, on the basioccipital. This keel is also found in *C. neumayri* and *D. bicornis*, but it is much weaker in *C. mauritanicum* and *C. simum*. The nuchal crest is developed more posterolaterally than in *D. bicornis*, but the occipital is probably less inclined posteriorly than in *C. mauritanicum*. The base of the occipital was not much broader than the top, in contrast to that of *D. bicornis*. In superior view, the sagittal notch between both wings of the nuchal crest is shallow. Below the crest, the medial part of the occipital is deeply hollowed, as in *C. simum*. On the whole, the occipital is similar to that of *C. neumayri* of the late Miocene.

Another piece consists of most of the maxilla (Fig. 5). The back of the nasal notch is above the rear of P2, that of the infraorbital foramen above the rear of P3, and the front of the orbit reaches the level of M1. These positions are more anterior than in all species of *Ceratotherium* and clearly show that this species had a tooth row more posteriorly set, as in *D. bicornis*, attesting that the skull rearrangement of this lineage had already taken place (Fig. 6).

Both tooth rows of AL-126-21 are well preserved and moderately worn, except M3, which is essentially unworn, and DP1, which is so worn that none of its pattern remains visible. The height of M3 is 81 mm, and the teeth are therefore probably

slightly more hypsodont than those of *D. bicornis*. All teeth are similar to those of *C. neumayri*, with a strong crochet, but no crista. The protoleph is nearly transverse, only slightly curved or essentially straight on the premolars, distinctly S-shaped on the molars, but thick relative to its length. The protocone is still recognizable as a distinct entity on P3 and P4. The metaloph is slightly oblique, but short, being little more than a flattened cusp on the molars, and its lingual part is not curved posteriorly. A complete cingulum surrounds the lingual side of the premolars; it is weaker on P4. However, this cingulum is low, and the post-fossettes of the molars would not close before late wear, just before their disappearance. The labial side of P2 is evenly convex, but those of P3-M2 are more sinuous, with a distinct paracone fold in the upper part of the crown, which would vanish in later wear. The paracone fold is stronger on M3, which has a triangular outline. The occlusal surface consists of two distinct planes, indicating two distinct chewing phases, and the labial walls of the permanent teeth have sharp cusps in labial view.

Other Specimens from Hadar—An upper tooth row, AL-384-1 (SH4), is almost identical in size and morphology to AL-126-21, except that there is a small crista on M2. Most of the other specimens consist of isolated teeth or groups of two or three teeth that do not differ markedly from the ones described

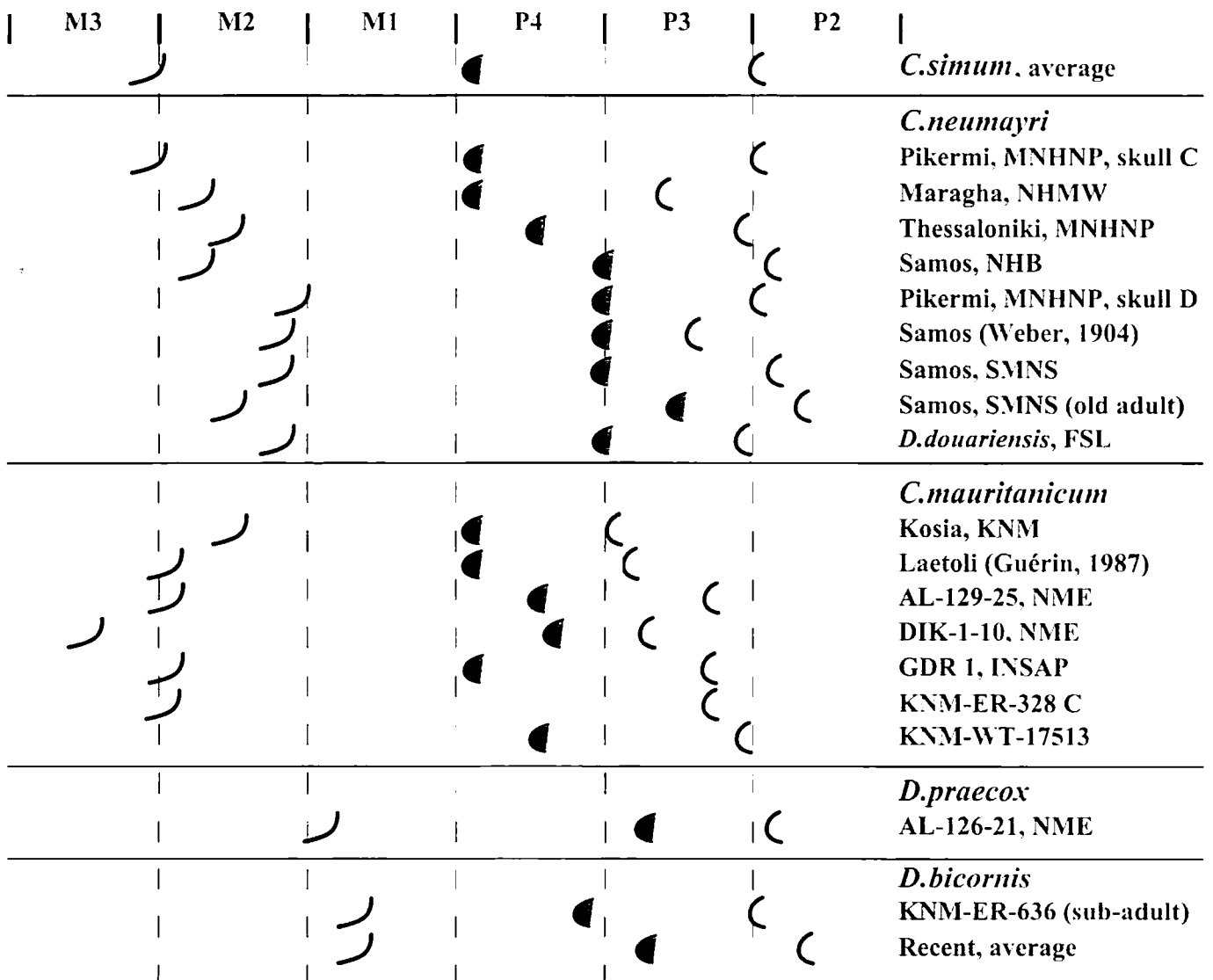


FIGURE 6. Positions (from left to right) of the anterior border of orbit, infraorbital foramen, and nasal notch, in various Dicerotini skulls.



FIGURE 7. *Diceros praecox*, juvenile left maxilla, AL-126-20, with DP1-M1, occlusal view. Scale equals 10 cm.

above. The associated M2 and M3, AL-313-1, are among the geologically youngest ones (sub-member DD2). Their large size (M2: 62 x 74 mm; M3: 70 x 68 mm) is outside the range of several tens of specimens of *D. bicornis* (Table 3; Guérin, 1980; table 5).

A juvenile skull fragment, AL-126-20 (SH1), consists of both tooth rows with DP1-DP4 in medium wear (right DP1 missing) and both unworn M1s (Fig. 7), the right zygomatic arch, and the glenoid fossa. This specimen can be referred confidently to *Diceros* by the characters of M1. The paracone fold is weaker than in *D. bicornis*, and there is a slight metacone fold on DP2. All milk teeth have a long crochet and a crista, but the antero-posteriorly elongated medifossette would not close in later wear, except on DP2. This tooth has a double crista, and a metaloph emerging posteriorly from the ectoloph, so that there is no postfossette. As on the permanent teeth, the metaloph is straight. There is no internal cingulum.

AL-274-2 is a fragment of maxilla with DP2-DP3 (stratigraphic level unknown). These teeth are similar to those of AL-126-20 in lacking a postfossette on DP2. This morphology is little changed in modern *D. bicornis*, except that there is often an incipient postfossette on DP2. Upper milk teeth of *D. praecox* can be distinguished from those of *C. mauritanicum* by the stronger paracone fold, straight metaloph not continuing into the distal cingulum, long and open medifossette, and frequent lack of postfossette, but the distinction is not easy without examining the actual specimens. It is therefore difficult to identify the two Omo DP2s illustrated by Hooijer (1975), which differ mainly in the lack of a cingulum in the specimen referred by him to *Ceratotherium*. However, the absence of a cingulum on AL-126-20 shows that this is not a reliable feature, and the Omo DP2s are better considered as *Dicerotini* indet.

The mandible AL-124-72 (BM) has a condyle which is inclined medio-ventrally, as in *D. bicornis*, in contrast to those of *C. simum* and *C. mauritanicum* (AL-125-1). However, the mandibles do not display any other specific feature.

Diceros bicornis (Linnaeus, 1758)

Diagnosis—Size smaller than *D. praecox*; face more angled on neurocranium, nuchal crest not expanded; cheek teeth narrower, lophs more transverse; premolar row shortened.

Range—Early Pleistocene to Recent, East and South Africa.

Referred Material—In the Lower Awash, most of the rhino material from the early middle Pleistocene of Asbole (Geraads et al., 2004) might represent this species, but it is too incomplete for definite specific identification.

Comparisons

All East African rhinos referred to *Diceros* had previously been included in *D. bicornis*, despite the fact that occurrence of an extant species in the earliest Pliocene (Nkondo Formation of Uganda, Guérin, 1994) would perhaps be unique among mammals. The skull AL-126-21 is significant because it links together tooth morphology that was referred previously to *D. bicornis* with an occiput that cannot be identified as such. This occipital is intermediate in morphology between the two living species and is, as a whole, similar to that of the late Miocene *C. neumayri*. The teeth are similar to those of *D. bicornis*, but the paracone fold is weaker than usual in the living species. The length of the molars (Table 3) approaches the upper limit of the range for this species, while their width often exceeds this limit. The premolars are also larger, the foremost teeth (P2 and the persistent DP1) being less reduced, a feature probably linked with a palate less narrowed anteriorly.

Some other late Pliocene East African specimens may also be referred to *D. praecox*. These include a crushed cranium from Laetoli briefly described and poorly illustrated by Guérin (1987:pl. 9.5). An unpublished skull (KNM-WT-41576) from the Upper Lomekwi Member of West Turkana has expanded lateral parts of the nuchal crest with a well-marked median notch; the premolars are large, like those from Hadar. The transition towards *D. bicornis* is illustrated by slightly younger specimens, such as the posterior part of the skull Omo-54-2090 from Shungura Formation Member D2 (NME), which has its maximum occipital width at mid-height rather than at the base as in *D. bicornis*. The skull KNM-ER-636 from the KBS Member of Koobi Fora is more like that of the living form and, although not identical, can best be identified as *D. bicornis* (Harris, 1976, 1983). These skulls are close in size to the mean of *D. bicornis*, but smaller than those from Hadar.

Few features can be observed on the type specimen of "*Ceratotherium*" *praecox*, KNM-KP-36 from Kanapoi. The dorsal profile is more concave than in all species of *Ceratotherium*, and this is clearly a derived feature of *Diceros*. The orientation of the occipital area is intermediate between both living species. The

TABLE 3. Occlusal lengths (maximum length for DP1-M3) of tooth-rows, and length x width of individual teeth, of the most complete Hadar specimens of *Diceros praecox* (measurements in mm; values above the maximum of *D. bicornis* are in bold)

	<i>Diceros praecox</i>				<i>Diceros bicornis</i>	
	AL-126-21	AL-313-1	AL-384-1	AL-720-1	Mean	Maximum
DP1-P4	158	—	161	—	131	161
P2-P4	135	—	135.5	—	—	—
M1-M3	148	—	148	—	148.5	174
DP1-M3	315	—	310	—	264	316
DP1	31 x 29.5	—	29.5 x 28	—	21.5 x 20	27.5 x 31
P2	46 x 47	—	42 x 46.5	39.5 x 42	34 x 38	41.5 x 45
P3	48 x 57.5	—	49 x 64.5	46.5 x 58	42.5 x 52	51.5 x 63
P4	51 x 63	—	51.5 x 72.5	—	48 x 59.5	56.5 x 69.5
M1	61 x 67.5	—	59 x 73.5	56.5 x 66	54.5 x 59.5	65 x 68
M2	61 x 67	62 x 74	59 x 72	—	59 x 60.5	71 x 71
M3	62 x 62.5	70 x 68	66 x 67.5	—	54.5 x 54.5	67.5 x 63

Mean of *D. bicornis* (N = 50-53 for the tooth-rows, N = 9-14 for individual teeth) from Guérin (1980).

orientations of the protoloph and metaloph are similar to those of *D. praecox* from Hadar, but the labial walls of the teeth are missing. KNM-KP-36 lacks all the apomorphic features of the *Ceratotherium* clade. The most complete skull used by Hooijer and Patterson (1972) in their definition of "*C.*" *praecox* was KNM-KP-41, from Ekora, a locality probably younger than Kanapoi but not precisely dated (Behrensmeyer, 1976). Crushing has accentuated the concavity of the skull profile and its resemblance to *D. bicornis*. Hooijer and Patterson (1972:23) correctly noted that the teeth are comparable to those of *D. bicornis*. They added that they differ by the weaker paracone fold, but this is not a valid difference, as this fold may vanish in moderate wear in the living form. The anterior premolars are small, as in *D. bicornis*. This skull is best identified as *D. bicornis*. It is unlikely to be older than late Pliocene. Other remains described by Hooijer and Patterson (1972) are fragmentary and do not add to the knowledge of this species. However, they show that some teeth (like those from Hadar) were slightly more hypsodont than those of *D. bicornis*.

The material from Lothagam here referred to *D. praecox* includes several skull elements: the most complete are KNM-LT-28563 and KNM-LT-23971 from the Apak Member. They are both referred to *D. bicornis* by Harris and Leakey (2003). They display the *Diceros*-like morphology of the skull, with a strong dorsal concavity, and a vertical occiput with the nuchal crest not extending behind the condyles. The teeth are brachyodont, with a paracone fold that is weaker than in *D. bicornis*, and are similar to those of *D. praecox* (including the type) from Kanapoi and Hadar. Hooijer and Patterson (1972) had previously reported the species from Lothagam on the basis of a single upper molar, KNM-LT-89, on which they noticed the lack of paracone fold.

DISCUSSION

Ceratotherium neumayri as the Stem Species of Living African Rhinoceroses

Morphological differences between *C. simum* and *D. bicornis* are mostly related to their diets, as explained by Zeuner (1934). The head of *C. simum*, which feeds on grasses, is held at an angle. It has a long skull, an occiput strongly inclined postero-dorsally with a nuchal crest extending beyond the condyles, a gently concave dorsal profile, and a neurocranium only slightly inclined relative to the face. *Diceros bicornis*, which is a browser, holds the head more horizontally, and the basicranial angle tends to close superiorly such that the neurocranium is tilted upward relative to the face. The extent of tilting is not, however, to the degree seen in the genus *Rhinoceros*, where the occiput is inclined even more anteriorly. Studies of the ontogeny of *Diceros* (Zeuner, 1934) strongly suggest that its skull shape is derived. Zeuner observed that during development the concavity of the upper skull profile increases, i.e., his angle *n* decreases (Fig. 8). Growth of the nuchal crest and horn bosses fail to fully explain this, because this decrease starts earlier in ontogeny (before Zeuner stage > 30 cm; Zeuner, 1934:44). He also showed that the occipito-palatal angle *po* decreases during the early stage (<30 cm). Thus, both the occipital and parietal profiles are less inclined forward (more *Ceratotherium*-like) during the early stages (<30 cm) than in the adult, which is certainly unlike the ancestral morphotype of both living species.

A likely ancestor for both living species is *Ceratotherium neumayri* (often incorrectly called *Diceros pachygnathus*; see Geraads, 1988), which is morphologically and ecologically intermediate between them. Zeuner (1934) showed that most of its cranial angles are also intermediate. *Ceratotherium neumayri* is well known in the eastern Mediterranean late Miocene, especially

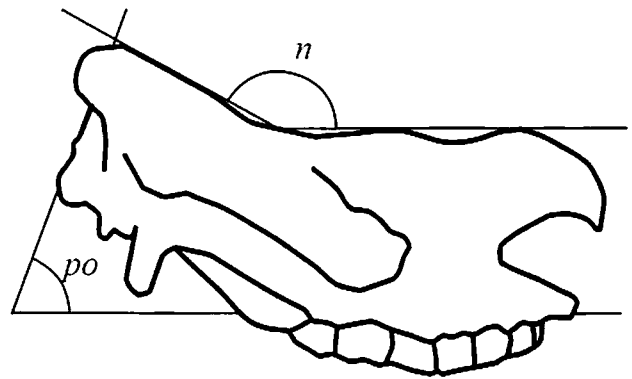


FIGURE 8. Zeuner's (1934) angles *n* and *po* in *Diceros bicornis*. Both are in the sagittal plane. Abbreviations: *n*, angle between the parietal and a tangent to horn bosses; *po*, angle between palate and occipital (opisthion to nuchal crest).

from Pikermi, Samos, Pentalophos, and Maragheh (Thenius, 1955; Geraads, 1988; Geraads and Koufos, 1990, and references therein). Related forms include late middle Miocene African representatives, such as *Paradiceros* from Fort Ternan, Kenya, and perhaps Beni Mellal, Morocco (Hooijer, 1968; Guérin, 1976). '*Dicerorhinus*' *primaevus* Arambourg, 1959, from the early late Miocene of Algeria (Arambourg, 1959; Geraads, 1986) could be the earliest member of this group. *Diceros australis* Guérin, 2000, from the middle Miocene of Namibia is not included because it is based upon a third metacarpal.

In *C. neumayri*, the nuchal crest and condyles are approximately at the same level, although this area is often crushed during fossilization, which prevents precise estimates. One of the best-preserved skulls (from Samos, NHB) has the nuchal crest clearly more posterior than the condyles. It should be noted that Gaudry's drawing (Gaudry, 1862–1867:pl.27, fig.2) showing the reverse relationship in a skull from Pikermi (MNHN: skull 'C' in Geraads, 1988) is incorrect: the nuchal crest is in fact level with the condyles in this specimen. *Ceratotherium neumayri* is also intermediate in basioccipital morphology, with a weak tubercle and open basioccipito-sphenoid angle. The same is true of the average position of the anterior orbital border and of the infra-orbital foramen (Fig. 6). The position of the nasal notch varies little among taxa, but it may be slightly more anterior in *D. bicornis* than in other species.

The difference in skull shape between the two living species is reflected in their skull measurements (Guérin, 1980); in Figure 2, *D. bicornis* (dashed line with asterisks) is compared to *C. simum* (used as a standard). The average measurements of ten skulls of *C. neumayri* from the Eastern Mediterranean late Miocene are plotted on the same diagram. Most of them fall between those of the living species. The less posteriorly expanded nuchal crest is reflected in the low value of (3) compared to *C. simum*, and in the short postorbital portion of the skull (8). However, the proportion of the anteorbital compared to the postorbital portion ([9] vs. [8]) is more similar to *C. simum* than to *Diceros*, which has a shortened maxillary region. *Ceratotherium neumayri* is also more like *C. simum* in having an occipital not much broader at the base than at the nuchal crest. The plesiomorphic state of a deep nasal notch (long nasal bones) distinguishes *C. neumayri* from both living species.

Ceratotherium neumayri was probably a mixed feeder because it is morphologically and metrically intermediate between both living species. Previous assignment of this species to *Diceros* (e.g., Guérin, 1966, 2000; Hooijer, 1978) was misleading because it implied it was a browser.

TABLE 4. Revised identification of some Pliocene African Dicerotini

Locality	Previously published identifications	Present identifications	Main specimens
Hadar	<i>Ceratotherium simum</i>	<i>Ceratotherium mauritanicum</i>	AL-129-25, AL-125-1
Omo	<i>Ceratotherium simum</i>	<i>Ceratotherium mauritanicum</i>	AL-126-21, AL-384-1
	<i>Diceros bicornis</i>	<i>Diceros praecox</i>	Omo 1b-69-4975
Koobi Fora	<i>Ceratotherium simum</i>	<i>Ceratotherium mauritanicum</i>	Omo 54-2090
	<i>Ceratotherium praecox</i>	<i>Diceros cf. praecox</i>	KNM-ER328C, KNM-ER-329
Lothagam	<i>Ceratotherium praecox</i>	<i>Diceros bicornis</i>	KNM-ER-5555
	<i>Diceros bicornis</i>	<i>Ceratotherium sp.?</i>	KNM-ER-636
Kanapoi	<i>Ceratotherium praecox</i>	<i>Diceros praecox</i>	KNM-LT-23970
	<i>Ceratotherium praecox</i>	<i>Diceros bicornis</i>	KNM-LT-28563, KNM-LT-23971
Ekora	<i>Ceratotherium praecox</i>	<i>Ceratotherium mauritanicum</i>	KNM-KP-36
Laetoli	<i>Ceratotherium praecox</i>	<i>Diceros bicornis</i>	KNM-KP-41
Langebaanweg	<i>Ceratotherium praecox</i>	<i>Diceros cf. praecox</i>	LAET-4979
	<i>Diceros bicornis</i>	<i>Ceratotherium sp.</i>	LAET-3065 L13035, L2519, L13747, L665

The Two Lineages of the African Pliocene

There are only a few late Miocene African sites with large mammals. The sole report of *C. neumayri* is a single tooth from Sahabi, Libya (Bernor et al., 1987), but some other African Dicerotini are of comparable morphology. "*Diceros*" *douariensis* Guérin, 1966, from Tunisia (Guérin, 1966; Geraads, 1989) could be conspecific with *C. neumayri*, but the only specimen definitely referable to this species is a skull (FSL-16749) too incomplete for its precise affinities to be assessed. An unpublished and poorly preserved maxilla from Lissasfa, Morocco, dated at close to the Miocene-Pliocene boundary (Raynal et al., 1999), is primitive in the high connection of the lingual tubercles of P2.

Two taxa can be identified in the SH1 submember, Lower Awash Valley (circa 3.3 Ma). One of them, *C. mauritanicum*, has teeth showing several of the apomorphic features of *C. simum*, and thus there is little doubt that they belong to the same lineage. The other has a dentition and skull morphology resembling *D. bicornis*, for which it is a likely ancestor. Despite the unambiguous phylogenetic position of this second species, *Diceros praecox*, it has been the subject of much confusion. In the literature, it was called either *D. bicornis* (at Lothagam, Hadar, and perhaps West Turkana) or *Ceratotherium praecox* (at Kanapoi and perhaps Koobi Fora). The former identification ignores the morphological differences between the two species of *Diceros*, but is phylogenetically sensible. The latter, originally used by Hooijer and Patterson (1972), assumes that it is the ancestor of later *Ceratotherium*. However, teeth similar to those of the type of '*C.*' *praecox* from Kanapoi display none of the apomorphic features of *Ceratotherium*, and are associated with *Diceros* skulls. There is little doubt that they belong to the *Diceros* clade. Attribution of the middle Pliocene *D. praecox* to *Ceratotherium* was the starting point of the confusion, which was further increased by the assignment of the late Pliocene true *Ceratotherium* to the same species. Revised identifications of the most diagnostic specimens are given in Table 4.

Available evidence suggests that the two lineages split soon after the Miocene-Pliocene boundary, leading from an ancestral mixed feeder, to a lineage of grazers (*Ceratotherium*) and a lineage of browsers (*Diceros*). The increased adaptation of the *Ceratotherium* clade to open grasslands and savannas led the *Diceros* clade to shift its ecological niche towards more closed habitats. This was associated with character displacement. Several features of *Diceros* evolved in directions opposite to those followed by *Ceratotherium*: smaller size, stronger paracone fold, more transverse lophs, triangular M3, and holding the head less inclined, with the associated features of anterodorsally inclined occipital, more concave skull profile, and stronger basioccipital

crest and tubercle. Evolution from mixed feeding to browsing is opposite to what has almost universally been documented for ungulates (e.g., Jernvall and Fortelius, 2002), but has been demonstrated in elephants (Cerling et al., 1999), and probably occurred in *Diceros* as well.

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