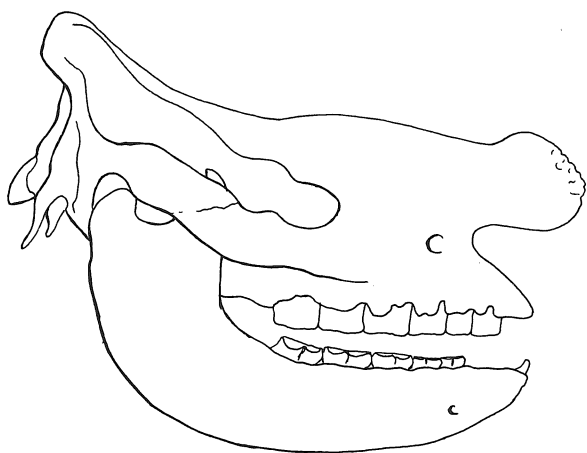


## 19

## Rhinocerotidae

Dirk A. Hooijer



Hitherto there has been no attempt at construction of a phylogeny of African Rhinocerotidae comparable to that of European rhinoceroses as given by Osborn (1900). But then, until some 10 years or so ago very little African rhinocerotid material earlier than Pleistocene was available in the literature, and even this was either not specifically identified or incorrectly named<sup>1</sup>.

In the last decade fossil rhinocerotids have turned up in Africa in ever increasing numbers, most of them Miocene in age, such as the Congo species *Aceratherium acutirostratus* (Deraniyagala) and *Brachypotherium heinzellini* Hooijer (1963). Both of these also occur in the East African Miocene as does *Dicerorhinus leakeyi* Hooijer (1966). From the Miocene of Fort Ternan, Kenya, comes *Paradicerus mukirii* Hooijer (1968) and the Miocene rhinocerotid from Loperot, Kenya, originally described on a single tooth as *Chilotherium* spec. (Hooijer 1966, p. 150), proved to be a new genus, *Chilotheridium pattersoni* Hooijer (1971). Then followed two Mio-Pliocene species from Lothagam Hill, Kanapoi and Ekora in Kenya: *Brachypotherium lewisi* Hooijer and Patterson (1972) and *Ceratotherium praecox* Hooijer and Patterson (1972); the latter is also present at Langebaanweg, South Africa (Hooijer 1972). Both *Ceratotherium simum* (Burchell), the modern white rhinoceros, and *Diceros bicornis* (L.), the modern black rhinoceros, proved to date back several million years in well-calibrated sequences of deposits in Kenya, Tanzania, and Ethiopia (Hooijer 1969, 1973). The classical "Pontian" as I use it in this paper is the modern Vallesian and Turolian, around the 10 m.y. level (cf Van Couvering 1972, p. 249).

## The Fossil Rhinoceroses

### Family Rhinocerotidae Owen 1845

#### Genus *Brachypotherium* Roger 1904

The ancestral stock from which came the African *Brachypotherium* as well as *Aceratherium* seems to be the Oligocene aceratheres of Europe. It appears now that in the later Oligocene Africa received from

<sup>1</sup> *Rhinoceros* spec., Miocene of Moghara, Egypt (Andrews 1900); *Rhinoceros* spec. indet., Miocene of Karungu, Kenya (Andrews 1914); *Teleoceras snowi* Fourtau (1920), Miocene of Moghara, Egypt; *Rhinoceros* gen. et spec. indet., Miocene of Langental, Southwest Africa (Stromer 1926); *Aceratherium?* spec., Miocene of Losodok, Kenya (Arambourg 1933); *Turkanatherium acutirostratus* Deraniyagala (1951), Miocene of Losodok, Kenya; *Teleoceras* aff. *medicorutum* Osborn, Miocene of Sahabi, Cyrenaica (d'Erasmus 1954).

Eurasia a number of elements in exchange for the export of African stocks to Eurasia (see Cooke 1968 for a conspectus of the evolution of mammals of Africa). Although we have no evidence so far in Africa of any pre-Miocene rhinocerotids (none occur in the rich Fayum deposits), they must have been there already in the (late) Oligocene since the early Miocene African forms are full-fledged species different from other Old World forms of the same genera. The genus *Brachypotherium* is characterized by very brachydont upper molars with ectolophs that are flattened behind the paracone style, antecrochets that are only weakly developed, and very slightly marked protocone constrictions. External cingula and flattened external grooves are usually present on lower molars, and a large pair of central incisors is present in both jaws. In the postcranial skeleton the metapodials are very short, from whence the group gets its name.

When the earliest *Brachypotherium* species of Africa was described (as *Teleoceras snowi* Fourtau [1920] from Moghara in Egypt), the Eurasian brachypotheres were customarily placed in the American genus *Teleoceras* Hatcher of 1894, although already in 1904 Roger had created the genus *Brachypotherium* for them. The then accepted relationship between these two genera was expressed by Osborn (1910, p. 292) thus: "*Teleoceras medicornutus*, discovered in the Pawnee Creek region of Colorado, is a remarkably close successor to the *T. aurelianense* of the lower Miocene of France . . . one of the most brilliant illustrations of the migration theory between the New and Old Worlds." Today we believe that *Teleoceras* is a descendant of *Aphelops* Cope and that the similarity in teeth and brachypody to *Brachypotherium* is due to parallelism. "*Rhinoceros*" *aurelianensis* Nouel (1866), from the early Burdigalian of Europe, was followed in the late Burdigalian and early Vindobonian by *Brachypotherium stehlini* Viret (1961, p. 71), which is generally larger than *Brachypotherium aurelianense* and in which the external groove in the lower cheek teeth between the anterior and posterior lophids may be completely flattened, while the external cingulum is almost invariably present (cf Roman and Viret 1934, p. 33, pl. 10, figs. 7 and 8, as *Brachypotherium cf brachypus* [Lartet]). In *Brachypotherium stehlini* the metapodials are more shortened than in *B. aurelianense*, and in the late Vindobonian *Brachypotherium brachypus* proper, and in the "Pontian" *B. goldfussi* (Kaup), metapodial and limb shortening have reached an extreme.

The Moghara *Brachypotherium snowi*, as an early brachypother, varies in the flattening of the exter-

nal groove and external cingula of the lower molars. A more advanced species is *Brachypotherium heinzellini* Hooijer (1963, p. 45), which occurs in the Sinda Beds of Congo and was afterwards found at Rusinga and Karungu in Kenya, Napak in Uganda (Hooijer 1966, p. 142-150), and identified from Langental in southwestern Africa by Heissig (1971). All these sites in East Africa as well as Langental are considered to be early Miocene in age, tentative correlates of the European Burdigalian. The species was recently found to occur also at Bukwa, another early Miocene Uganda site (Hooijer 1973). From the radiometric dates given in table 19.1 it is evident that this species, *Brachypotherium heinzellini*, existed for at least some 4 m.y., from Bukwa II to Rusinga; we find even more impressive longevities in other Neogene African rhinocerotid species.

*Brachypotherium heinzellini*, an exclusively Miocene species, resembles the late Vindobonian *B. brachypus* of Europe in its metapodial shortening; only the lateral metacarpals are relatively shorter and wider. It is definitely more advanced than the Moghara *Brachypotherium snowi*, which has only reached the evolutionary stage of the late Burdigalian and early Vindobonian *Brachypotherium stehlini* of Europe.

Its dentition is characterized by variable external cingula and flattened external grooves in the lower cheek teeth, very large upper incisors, the upper cheek teeth by flattened ectolophs behind the paracone style, weak antecrochets, and but slightly constricted protocones. The enamel often displays fine, horizontal striations also seen in European *Brachypotherium*.

There is a gap in the African record of some 6 m.y., for the next *Brachypotherium* is known from the Ngorora Formation in Kenya (Hooijer 1971, p. 364), which is that much younger than the latest *B. heinzellini* at Rusinga (see table 19.1). The Ngorora milk molar is too large for this earlier Miocene species but could belong with *Brachypotherium lewisi* Hooijer and Patterson (1972) from Lothagam-1. There is an upper molar from Sahabi in Libya, originally published as *Teleoceras aff. medicornutum* Osborn by d'Erasmus (1954), that apparently represents this large *Brachypotherium* as well (Hooijer and Patterson 1972, p. 17), and we may have it also in the Mpesida Beds in Kenya (Hooijer 1973). *Brachypotherium lewisi* is the terminal form of the *Brachypotherium* lineage in Africa, carrying the genus on into the latest Miocene. (In Europe the genus became extinct already by "Pontian" times, with *B. goldfussi*.) *Brachypotherium lewisi* is very large indeed; the condylobasal length of the type skull is

Table 19.1 The rhinoceroses of Africa, distribution in time and space.

	Million years	<i>Brachypotherium</i>	<i>Aceratherium</i>	<i>Dicerorhinus</i>	<i>Chilotheridium</i>	<i>Diceros</i>	<i>Ceratotherium</i>	<i>Paradiceros</i>
Olduvai								
Beds upper II-IV	?1-0.5	.	.	.	.	x	x	.
Beds I-lower II	1.8	.	.	.	.	.	x	.
Chemeron Fm.	4-2	.	.	.	.	.	x	.
Omo								
Shungura Fm.	4-2	.	.	.	.	x	x	.
Mursi Fm.	4	.	.	.	.	x	x	.
Aterir Beds	< 4	.	.	.	.	.	x	.
Kanapoi	4	.	.	.	.	.	x	.
Langebaanweg, S.A.	4	.	.	.	.	.	x	.
Lothagam Hill	6	x	.	.	.	.	x	.
Sahabi, Libya	6	x	.	.	.	.	.	.
Mpesida Beds	7	x	.	.	.	.	x	.
Ngorora Fm.	< 12	x	x	or x	x	.	.	.
Kirimun	—	.	x	or x	x	.	.	.
Douaria, Tunisia	12	.	.	.	.	x	.	.
Alengerr Beds	14-12	.	x	x	.	.	.	.
Fort Ternan	14	.	.	.	.	.	.	x
Loperot	18	.	.	.	x	.	.	.
Sinda, Congo	—	x	x	?	.	.	.	.
Rusinga	18.5	x	x	x	x	.	.	.
Ombo	—	.	.	x	x	.	.	.
Napak	19	x	x	x	.	.	.	.
Bukwa II	23	x	.	?	x	.	.	.
Moghara, Egypt	—	x	?	.	.	.	.	.

over 70 cm. The upper molars are 90 mm transversely as opposed to 70 mm in *B. snowi* or *B. heinzelini*, from either one of which it may have descended. The nasals are hornless, slender, and not very long; the frontals are flat and hornless; and the inferior squamosal processes unite below the subaural channel.

### Genus *Aceratherium* Kaup 1832

The acerathere rhinocerotids (a contradiction in terms) started as Oligocene forms that retained tetradactyl forefeet up into the "Pontian." Metacarpal V (actually the fourth finger, as metacarpal I is but a vestige) remained surprisingly constant as a bone one-half as long as metacarpal IV all through the geological record, which spans some 20 m.y. The earliest representative in Africa may be the Moghara *Aceratherium*(?) spec. recorded by Andrews (1900), which occurs alongside *Brachypotherium snowi*; Dr. Roger Hamilton has indubitable *Aceratherium* material along with *Brachypotherium snowi* from the

early Miocene of Gebel Zelten in Libya. From Moruorot in Kenya, Deraniyagala (1951) described *Turkanatherium acutirostratus*, but this is an *Aceratherium* (Arambourg 1959, p. 74; Hooijer 1963, p. 43). *Aceratherium acutirostratum* (Deraniyagala) is rather widespread in the early Miocene of East Africa—Rusinga, Napak I, Karungu (Hooijer 1966, pp. 136-142)—and ranges up into the Alengerr Beds (Hooijer 1973), some 5 m.y. younger (see table 19.1). Either this species or *Dicerorhinus leakeyi* or both are present at Kirimun and in the Ngorora Formation, which would make for a record span for a single species of 7 m.y. Although the upper teeth and the skull can be told apart easily, it is difficult to distinguish between the lower teeth (except the tusks) and the postcranial material of *Aceratherium acutirostratum* and *Dicerorhinus leakeyi*. This makes identification especially difficult where the two species occur together, as at Napak, Rusinga, and in the Alengerr Beds (Hooijer 1966, 1973).

The skull of *Aceratherium acutirostratum* is

unique in the combination of a shallow nasomaxillary notch (back to above the middle of  $P^3$ , as in the Aquitanian *Aceratherium lemanense* [Pomel] of Europe) and an elevated occiput (as in the terminal, "Pontian" *Aceratherium incisivum* [Kaup] of Europe). The upper cheek teeth have markedly constricted protocones, prominent antecrochets, and the premolars have strong internal cingula, which distinguish them from those of *Dicerorhinus leakeyi*. The upper incisors are much larger than those in *Dicerorhinus*, as in *Brachypotherium*, but are longer rooted than those in the latter. Both *Aceratherium* and *Dicerorhinus* are non-brachypothere, longer limbed, and longer footed than *Brachypotherium* (Hooijer 1966, 1973).

#### Genus *Dicerorhinus* Gloger 1841

The Miocene species of this genus, *Dicerorhinus leakeyi* Hooijer (1966, pp. 122–136) from Rusinga, Songhor, and Napak, (afterwards also found at Ombo and in the Alengerr Beds [Hooijer 1973]) combines characters found in different species in Europe. It has the skull shape of *Dicerorhinus sansaniensis* (Lartet) of the Vindobonian, and the teeth of *Dicerorhinus schleiermayeri* (Kaup) of the "Pontian."

The European lineages, from *Dicerorhinus tagicus* (Roman) of the Aquitanian and continuing up into the Pleistocene, are quite distinct from the African forms, which also include *Dicerorhinus primaevus* Arambourg (1959, p. 56) from the "Pontian" of Wadi el Hammam in Algeria and *Dicerorhinus africanus* Arambourg (1970, p. 79) of the North African Villafranchian (Lac Ichkeul). Thus the genus presumably persisted longer in Europe and North Africa than it did in East Africa, where the last occurrence known is in the Alengerr Beds and possibly at Kirimun and Ngorora (see table 19.1). The African forms are two-horned, with upper teeth that have weakly constricted protocones and a basal metacone bulge to  $M^3$  giving it a trapezoidal rather than subtriangular outline. The upper incisors, at least in *D. leakeyi*, are quite small and there are small incisors between the lower tusks; the latter differ from those of *Aceratherium* in being less bowed. The fifth metacarpal is reduced to a stump, unlike that in *Aceratherium*, in which it even carried some phalanges, but the articulation facet on metacarpal IV is of the same size in both genera so that even this metapodial cannot be generically identified when it occurs as an isolated bone. The longevity of *D. leakeyi* is similar to that of *Aceratherium acutirostratum*, that is, about 5 m.y.

#### Genus *Chilotheridium* Hooijer 1971

The genus *Chilotheridium* ranges from the early Miocene of Rusinga, Bukwa II (Hooijer 1971), and Ombo (Hooijer 1973) up into the late Miocene at Ngorora, and thus spans some 10 m.y. The type species, *Chilotheridium pattersoni* Hooijer (1971), comes from Loperot in Kenya. Quite characteristic of the genus are the tiny, horned nasals. The hypsodont teeth have sharply constricted protocones and large, inwardly curving antecrochets as in *Chilotherium* Ringström, with which it was confounded before the skull and postcranial skeleton were available. *Chilotherium* is a Eurasian genus ranging from Burdigalian to "Pontian," and I hold that *Chilotheridium* was its equivalent in Africa and originated from the same stock during the Eurasian Oligocene. But we have as yet no record of this in Africa. In the African *Chilotheridium* metacarpal V is a sizable bone; in *Chilotherium* it is much reduced, a progressive condition in *Chilotherium* as compared to *Chilotheridium*. *Chilotheridium* has a (small) nasal horn and large air sinuses in the frontal and parietal bones, whereas *Chilotherium* is hornless and has very small parietal and frontal air sinuses, which constitute generalized characters compared to *Chilotheridium*. There are no upper but large lower tusks, which are farther apart in *Chilotherium* than in the African *Chilotheridium*. The limb and foot bones of *Chilotheridium* are not as shortened as they are in *Chilotherium*.

#### Genus *Diceros* Gray 1821

This is the genus of the modern black rhinoceros of Africa, *Diceros bicornis* (L.). The genus as such goes back to the "Pontian" of Europe, southwestern Asia, and northern Africa with forms that are very close morphologically to *Diceros bicornis* and that have been placed in the same genus: *Diceros pachygnathus* (Wagner) from Samos and Maragha (Iran), and *Diceros douariensis* Guérin from Douaria, Tunisia. The modern species appears at the 4 m.y. level at Kanam West, East Africa (Hooijer 1969, pp. 88–89), and has recently been collected at Saragata Deare in the western Afar, Ethiopia, in deposits of about the same age (J. Kalb pers. comm.). The  $dM^4$  slightly exceeds its recent homologue in size, but the entire upper dentition is within recent size limits. As the teeth are worn we do not know whether they were as high-crowned as those in the living *D. bicornis*. That they were not at this early stage is shown by a slightly worn  $dM^4$  from the Mursi Formation (Hooijer 1973). Early *D. bicornis* has the dental pattern of the modern form: heavy internal

upper premolar cingula, marked paracone styles, produced anterointernal crown angles, proto- and metalophs transverse in position, crista and crochet usually separate, not forming a medifossette, post-sinus shallower than medisinus. By 2.5 m.y. ago, the time of deposition of Shungura Formation Member D (cf Cooke and Maglio 1972, p. 306), the molar crowns of *Diceros bicornis* have become as high as they are at present, and the skull from the 3 m.y. level (Shungura Member C) already has the modern characteristics (Hooijer 1973, 1975). We have *Diceros bicornis* from late Olduvai (Bed II, upper part, Bed III, and Bed IV), but not from early Olduvai (Bed I and lower part of Bed II) (Hooijer 1969). *D. bicornis* has not shown up in the Kaiso Formation, not even at later Kaiso, which is just below the 2 m.y. level (Cooke and Coryndon 1970; Cooke and Ewer 1972, p. 230), and neither is it present at Kanapoi (4 m.y. old, Hooijer and Patterson 1972) or in the 4 to 2 m.y. old Chemeron Formation (Hooijer 1969). In the latter, *Ceratotherium* is the only rhinocerotid genus found, which is probably ecological. In the Koobi Fora Formation, from about 3 m.y. ago on up to 1 m.y. ago, *D. bicornis* occurs in all three faunal zones. The molars appear slightly less hypsodont than in recent specimens and the skull shows a number of differences that suggest at least subspecific distinction (Harris 1976, p. 223.)

#### Genus *Ceratotherium* Gray 1867

*Ceratotherium praecox* Hooijer and Patterson is the earliest known species of the genus, and it occurs at Kanapoi, Lothagam-1, and Ekora, but also in the Chemeron Formation (locality J.M. 507), the Mursi Formation, the Aterir Beds (Hooijer 1972, pp. 187–189), and the Mpesida Beds (Hooijer 1973). The latter is its oldest occurrence, at the 7 m.y. level (see Cooke and Maglio 1972, p. 306; Bishop 1972, p. 231). It is a species characterized by four none-too-small upper incisors (these teeth have been lost in the modern white rhinoceros); a dorsal skull profile more concave, the posterior portion less extended behind; occiput less posteriorly inclined; and nuchal crest less thickened than in *Ceratotherium simum* (Burchell). The teeth are less high-crowned than those in the modern form, with angular anterointernal crown corners instead of rounded ones and hardly any or no medifossette formation. I believe that *C. praecox* is the immediate ancestor of *C. simum*, and it is most abundantly represented at Langebaanweg, Cape Province (Hooijer 1972), where it is the most common of the large mammals. A single upper molar comes from Swartlintjesfarm,

Hondeklipbaai, Namaqualand, about 160 km north of Langebaanweg.

The modern white rhinoceros of Africa first appears as *C. simum germanoaffricanum* (Hilzheimer) in the Shungura Formation Member B (a little more than 3 m.y. old, Hooijer 1973; Guerin 1976); the Chemeron Formation (locality J.M. 91, Hooijer 1969, p. 75); Kanam West (Hooijer 1969, p. 88), which is either at the 4 m.y. level or somewhat younger (Cooke and Maglio 1972, p. 306; Cooke and Ewer 1972, p. 230); and in all levels of the Koobi Fora Formation, from about 3 to 1 m.y. Its cranial characters show several distinct differences from the living white rhinoceros (Harris 1976, p. 223), and the teeth are slightly less hypsodont and the lophs slightly less obliquely placed, although they already have the rounded anterointernal crown corners in which the upper teeth of *C. simum* differ from those of *Diceros bicornis*. As a grazer, *C. simum* has higher crowned teeth than *D. bicornis* the browser, and further the teeth of the former have reduced paracone styles, wavy ectolophs, obliquely placed lophs and lophids, medifossettes formed by the union of crochet and crista, and postsinuses as deep as the medisinuses (Hooijer 1959). The skull of *D. bicornis* has a vertical occiput instead of a posteriorly inclined one as in *C. simum*. From the variations in the skulls of the "Pontian" *Diceros*, Thenius (1955) concluded that *Ceratotherium* split off from the *Diceros* stock probably in the Pliocene, a view that is fully substantiated by finds at Kanapoi, etc., of *Ceratotherium praecox* (for a diagram of the *Diceros* group, see Hooijer and Patterson 1972, fig. 11). The precocious *Ceratotherium* was spread over South Africa in the Mio-Pliocene just as *C. simum* and *D. bicornis* were in the Pleistocene (Makapansgat, Transvaal: Hooijer 1959; Hopefield, Cape Province: Hooijer and Singer 1960).

#### Genus *Paradiceros* Hooijer 1968

*Paradiceros mukirii* Hooijer (1968) occurs only at Fort Ternan in Kenya and clearly belongs to the *Diceros* group of genera but is much earlier than either *Diceros* proper or *Ceratotherium*. It is a rather small, two-horned, browsing type in which the molars are lower than those in *D. bicornis* (a primitive character) but with a more abbreviated mandibular symphysis (a progressive feature). The humerus is rather short, suggesting that the Fort Ternan form was a more swift-moving type, more of a generalized, running rhinocerotid than *Diceros* (all species). I hold *Paradiceros* to be a collaterally developed browser from the same ancestral stock as *Diceros*;

the *Diceros* group of genera probably originated in Africa (cf Hooijer and Patterson 1972, fig. 11).

## Conclusions

The distribution of the African rhinocerotids is plotted against the chronological sequence of sites in table 19.1. Within most genera there is more than one species, and each of them is different from those in the same genera in Eurasia, showing that evolution in Africa was independent from that in the rest of the Old World. In the early Miocene (Moghara, Bukwa, Napak), some 23 to 19 m.y. ago (van Couvering 1972), there are already in Africa distinct species of *Brachypotherium*, *Aceratherium*, *Dicerorhinus*, and *Chilotheridium*, which of course means that their ancestral stocks were there beforehand, in the Oligocene. The rhinocerotid record for this early arrival is a lamentable blank in Africa. *Chilotheridium* is even generically distinct and strictly African in appearance.

Africa further emerges as the continent of origin of the *Diceros* group of genera (*Paradiceros*, *Diceros*, and a fortiori *Ceratotherium*). *Ceratotherium* (both species) and *Diceros* were spread from southern to northern Africa in the Plio-Pleistocene and so was *Brachypotherium* already in the Miocene, linking up the South African fauna with those of the same period in Central and East Africa.

The species longevities that I have been able to establish (4 m.y. for *Brachypotherium heinzelini*, 7 m.y. for *Brachypotherium lewisi*, 5 m.y. for *Aceratherium acutirostratum* and *Dicerorhinus leakeyi*, and 5 m.y. for *Chilotheridium pattersoni*) are based upon radiometric age determinations, and these corroborate those obtained by means of sophisticated analysis of data in the literature on Neogene faunas of Spain, the Siwaliks, and China (Kurtén 1959). The mean species longevity for the Neogene is 5.2 m.y. This figure contrasts strikingly with the mean species longevity in the Pleistocene, also computed by Kurtén, which is 620,000 years, implying that the evolutionary rate was between eight and nine times faster in the Pleistocene than it was in the Neogene.

In most of the genera that I give in single columns in table 19.1 there is more than one species, but these do not necessarily represent single phyletic lineages even though the species may succeed each other in time (figure 19.1). In these Neogene rhinocerotids evolution was rather slow and even stagnant; two examples, in *Aceratherium* and in *Dicerorhinus*, stand out.

There is none or hardly any evolutionary change in the size of metacarpal V within the genus

*Aceratherium* right from the late Oligocene *A. lemanense* up into the "Pontian" *A. incisivum* (Hooijer 1966, p. 153), a time span of 10 m.y. at least. Here evolution seems to have come to a near standstill. The other case in point may be that in the genus *Dicerorhinus*, which is not a single lineage but several (Hooijer 1966, p. 120), the metacone bulge is retained in  $M^3$ , which gives this tooth its typical trapezoidal basal outline from the early Miocene East African *D. leakeyi* through the Pleistocene species and even into the Holocene *D. sumatrensis* (Fischer) (Hooijer 1966, pp. 128, 129).

In the genus *Brachypotherium*, which runs up only into the "Pontian" in Europe, there is progressive abbreviation of limbs and feet as well as size increase. *Brachypotherium lewisi* of the late Pliocene, the last survivor of its genus anywhere, is the greatest of them all and may well be the descendant of Miocene *B. heinzelini* or of *B. snowi*. However, there is a gap in the record of 6 m.y. or more (between Rusinga and Ngorora, table 19.1), and the specific advance took place during this interval. It would be of great interest to see if the limb and foot bones of *B. lewisi* are shortened even more than those in the European terminal species *B. goldfussi* of Eppelsheim, but we know next to nothing as yet of the postcranial skeleton of *B. lewisi*.

The closing of the "Pliocene gap" in Africa has given us an insight into the longevity of the living African species. The transformation of *Ceratotherium praecox* into *Ceratotherium simum* took place between 4 and 3 m.y. ago, and *Diceros bicornis* as a species is likewise about 4 m.y. old. There are not very many modern mammalian species that have such a long record; *Hippopotamus amphibius* L. and *Castor fiber* L. date back into the Villafranchian of Europe and are probably between 1 and 3 m.y. old, but some small mammals would seem to have appeared already in the Astian, over 3 m.y. ago (Kurtén 1968, p. 254). In the Plio-Pleistocene of East Africa the extant elephant and suids are not yet in evidence (Cooke and Maglio 1972, pp. 310, 318), which makes the white and the black rhinoceros old-timers by comparison.

My study of African fossil Rhinocerotidae would have been impossible without the cooperation of the late Louis Leakey and the following colleagues: Peter Andrews (Nairobi), T. H. Barry (Cape Town), W. W. Bishop (London), Frank Brown (Berkeley), P. M. Butler (Englefield Green, Surrey), L. Cahen (Tervuren), H. B. S. Cooke (Halifax, Nova Scotia), Yves Coppens (Paris), John van Couvering (Villa Park, California), P. E. P. Deraniyagala (Ceylon), A. Gautier (Ghent), Roger Hamilton (London), Jean de Heinzelin (Ghent), Brett Hendey (Cape Town), Andrew Hill (London), F. Clark Howell (Berkeley), Richard Leakey (Nairobi), J. Leper-

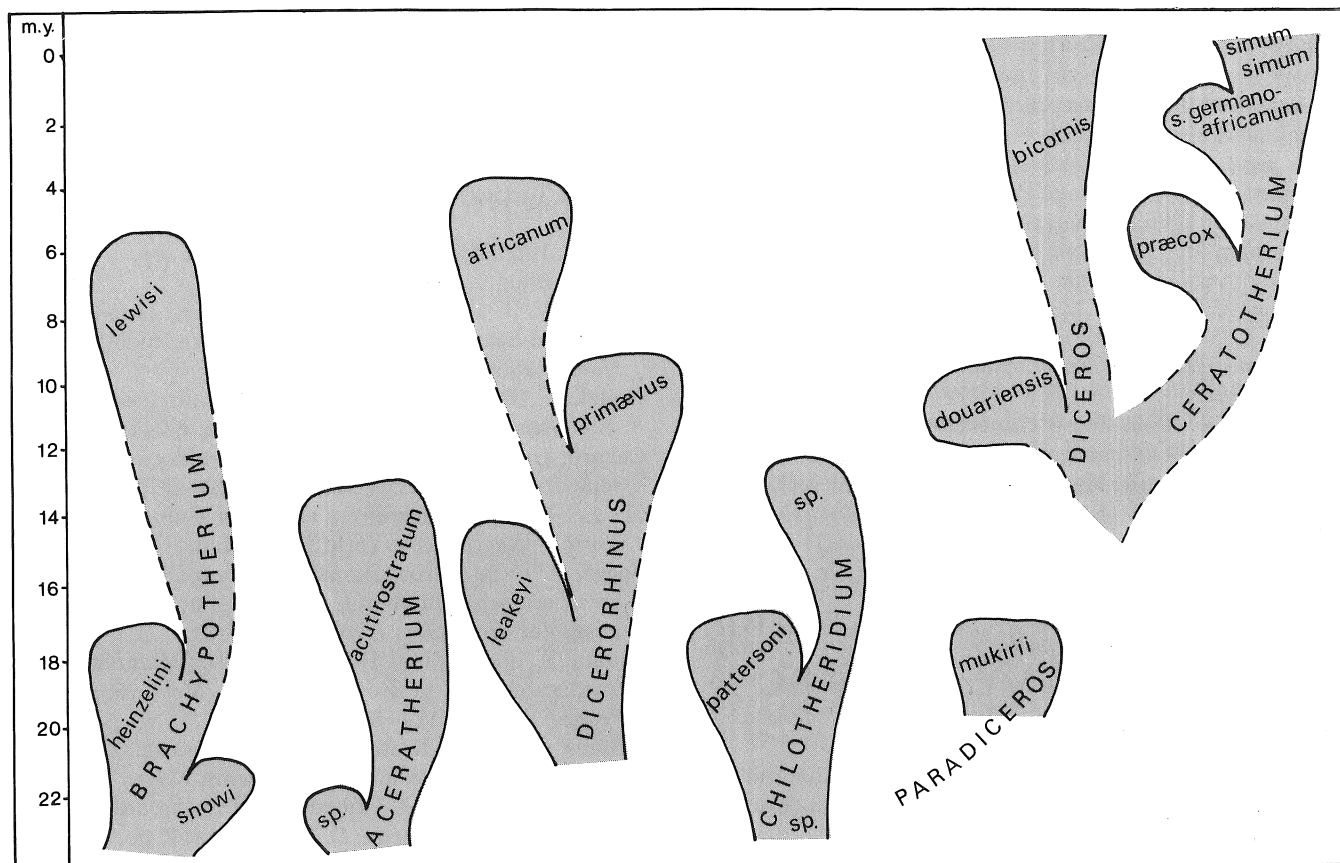


Figure 19.1 Proposed relationships among the fossil and recent species of African rhinoceroses.

sonne (Tervuren), Vincent Maglio (Princeton), Bryan Patterson (Cambridge, Mass.), Martin Pickford (London), Shirley Coryndon and R. J. G. Savage (Bristol), Anthony Sutcliffe (London), and Alan Walker (Nairobi).

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