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ADDITIONAL MIOCENE TO PLEISTOCENE RHINOCEROSES OF AFRICA

by

D. A. HOOIJER

Rijksmuseum van Natuurlijke Historie, Leiden

(With 2 plates)

The purpose of the present paper is to place on record data on fossil Rhinocerotidae from Africa not included in earlier papers. Material has turned up in Africa in great quantities over the last decade, much from beautifully calibrated sequences especially in Ethiopia and the Baringo area of Kenya. Dreary descriptions of fossil teeth and bones are simply a prerequisite to construct, as is my aim, a sort of phylogeny of the rhinoceroses of Africa comparable to those long established for Europe or America. We have at this moment seven genera and a dozen or so species of Rhinocerotidae from the Neogene and the Quaternary, which will be dealt with below. My research in East and South Africa has been supported by grants-in-aid from the Wenner-Gren Foundation for Anthropological Research, Inc., in New York City.

Brachypotherium heinzelini Hooijer

This species, first recorded from Sinda, Congo (Hooijer, 1963), and afterwards from Rusinga, Karungu, and Napak II (Hooijer, 1966), is characteristic of the Early Miocene of East Africa. Recently, the lower jaw fragment from the Miocene of Langental in Southwest Africa described but unnamed by Stromer (1926: 112) was identified as *Brachypotherium heinzelini* by Heissig (1971); the first southern African record of the species. I agree with this identification, but it is not correct to state that flattened external grooves such as seen in the Langental P_4-M_2 appear first in *Brachypotherium* only at the base of the Vindobonian (Heissig, 1971: 127): *Brachypotherium stehlini* Viret of the Upper Burdigalian and Lower

Vindobonian already has them (Hooijer, 1966: 145). The external grooves and cingula are variable in *B. heinzelini* as well as in *B. snowi* (Fourtau) of Egypt and *B. aurelianense* (Nouel) of Europe.

There are a few specimens of the present species from Napak II C collected in 1965 and not recorded in Hooijer (1966); these, like the 1964 Napak II C P^4 (Hooijer, 1966: 143) have been sent to me by Dr. W. W. Bishop. There is an M^3 dext. in two portions: the protoloph, and the outer surface (ecto-metaloph), without a metacone bulge (pl. 1 figs. 11-12). The dimensions are: ant. transv. ca. 67 mm; length outer surface ca. 74 mm, very much as in *Brachypotherium brachypus* (Lartet) (Hooijer, 1966: 144); the two species are very close in dental dimensions. There is further an M_3 dext. from Napak II C, 1965 (pl. 1 figs. 7-8), which measures ant. post. 60 mm, ant. transv. and post. transv. both 33 mm, mentioned but not figured in Hooijer & Patterson, 1972. Fine, horizontal striations can be seen on the enamel; this is typical of these as well as other *Brachypotherium* cheek teeth. The full external crown height of the M_3 is ca. 40 mm. A Napak II C 1965 M_2 dext. measures 33, and 34 mm transversely in front and behind, slightly smaller than an M_2 from Napak II A, 1964 already recorded (Hooijer, 1966: 146).

From Rusinga and Bukwa we now have astragali that conform nicely to those of Singa, Congo, and Rusinga recorded in 1963 and 1966: a cast of an astragalus dext. from Rusinga (R. 76, Kiahera Formation) and one of an astragalus sin. from Bukwa, found in 1971, have been kindly sent to me by Dr. Peter Andrews. Measurements are in table 1; the Sinda, Congo specimen was figured (Hooijer, 1963, pl. 5 fig. 10, pl. 8 fig. 7) as well as the Gumba, Rusinga specimen (Hooijer, 1966, pl. 14 fig. 3); further figures of brachypothere astragali are deemed unnecessary.

Table 1

Measurements of astragalus of *Brachypotherium heinzelini* (mm)

	Rusinga, Gumba	Rusinga, Kiahera	Bukwa	Sinda, Congo
Medial height	60	60	64	68
Lateral height	57	64	63	—
Total width	82	88	90+	102
Ratio medial height / total width	0.73	0.68	0.71—	0.67
Trochlea width	68	71	68	—
Width distal facets	71	76	77	—

The ratio medial height/total width is of importance to distinguish between the various rhinocerotid astragali, as is the excess of the trochlea width over the medial height. It will be seen from table 1 that the ratio medial height/total width in *B. heinzelini* varies from 0.67 to 0.73, and that the trochlea width is distinctly greater than the medial height, except in the Bukwa specimen, which has a height/width ratio of less than 0.71 as the total width is over 90 mm but exactly how much I cannot tell.

There is further evidence of the presence of *Brachypotherium heinzelini* at the Bukwa site: an M_2 dext. found in 1971, a cast of which was sent to me by Dr. Peter Andrews in 1972, shows the external cingulum, which is diagnostic of *Brachypotherium* although it does not always show. The measurements (ant. post. 59 mm, ant. transv. 36 mm, post. transv. 38 mm) are very similar to those of the Napak II A M_2 previously recorded (Hooijer, 1966: 146, pl. 8 fig. 2).

Thus, Bukwa is a new locality for *Brachypotherium heinzelini*, as was Napak in 1966. These two Miocene sites are exceedingly similar faunistically to Rusinga. In an earlier paper I briefly mentioned that among material from Napak sent to me by Dr. Bill Bishop there is a very characteristic upper molar of *Brachyodus aequatorialis* MacInnes (Hooijer, 1966: 186), which enhances the faunal likeness between Napak and Rusinga. It is an M^2 dext. from Napak II C, 1964, which measures ant. post. 36 mm, ant. transv. 40 mm, and post. transv. 34 mm, only slightly larger than the Rusinga, even the Gumba M^2 of *Brachyodus aequatorialis* (MacInnes, 1951: 7), which certainly does not indicate a specific difference. The Bukwa site, put on the map by Walker (1968, 1969), also yields *Brachyodus aequatorialis* but this material I have not seen. Likewise, I do not know on what basis "*Dicerorhinus* sp." is included in the faunal list of Bukwa (Walker, 1968: 153). Bukwa has *Chilotheridium* (Hooijer, 1971: 358, 360) as shown by casts that Dr. Alan Walker has provided. The astragali of this genus are rather close to those of *Brachypotherium heinzelini* (which, as shown above, is also present at Bukwa), but the medial height/total width ratio is 0.72-0.77 and the trochlea width is only slightly greater than the medial height (Hooijer, 1971: 377).

A very characteristic phalanx II of a median digit in the British Museum (Natural History) collection, M. 29390, originates from Arongo Uyoma, 18/10/35. The length is 21 mm, the proximal width ca. 60 mm (cf. Hooijer, 1966: 149). A site is listed as Chianda Uyoma in Le Gros Clark & Leakey (1951: 5) and Bishop (1967: 47); there is also Arongo Chianda, 25/10/39, with a generically uncertain but non-brachypothere astragalus (Hooijer, 1966: 172), not listed as such by Le Gros Clark & Leakey (1951) and probably not the same site. At any rate, Arongo Uyoma is an addition to the Miocene rhinocerotid sites in Kenya.

There are two teeth from the Chemeron Formation that cannot but belong to *Brachypotherium heinzelini*: an M_3 dext., KNM/BC/414 (pl. 1 figs. 5-6), and a P_2 dext, KNM/BC/415 (pl. 2 figs. 5-6). The first mentioned specimen is only slightly worn and shows the external cingulum along the anterior portion of the metalophid, while the external groove between metalophid and hypolophid is flattened out at least basally. The full external crown height is ca. 40 mm. It measures 56 mm at base anteroposteriorly, 34 mm anterotransversely, and 33 mm posterotransversely, as the Napak II C specimen recorded above. This is not *Brachypotherium lewisi* Hooijer & Patterson, the post-Miocene form, which is larger: basal widths of M_3 38-40 mm (Hooijer & Patterson, 1972, table 3). The P_2 dext. is unworn, at least 38 mm high externally at the hypolophid, and the basal crown diameters are: ant. post. 33 mm, ant. transv. 18 mm, post. transv. 20 mm. No P_2 of *B. heinzelini* of East Africa is available, but *B. snowi* (Fourtau) of Moghara, Egypt, is very close in tooth size and its P_2 is of the same size; that of *B. lewisi* is larger (Hooijer & Patterson, 1972, table 3). Both the M_3 and the P_2 show the fine horizontal striations on the enamel seen in *Brachypotherium* cheek teeth.

The Chemeron Formation (Bishop, 1972: 242) has an age greater than 2.0 million years and less than 5.4 million years: the presence of unquestionable *Brachypotherium heinzelini* teeth in this Plio/Pleistocene deposit may only be explained if we accept them as secondarily deposited, reworked Miocene specimens.

In the Chemeron we have not only *Brachypotherium heinzelini*, but also *Dicerorhinus leakeyi* Hooijer as a Miocene element (see under that head in the present paper). A specimen, however, that definitely is Plio-Pleistocene in age and that comes from the Chemeron Formation, locality J. M. 511 (KNM/BC/376) is an upper right fourth premolar of *Ancylotherium hennigi* (Dietrich), three views of which are given in the present paper (pl. 2 figs. 7-9). Chalicothere teeth are rare in the Pleistocene of Africa; none have been reported from Olduvai Gorge, but there is a Laetolil M^2 described by Dietrich (1942: 105). The Chemeron P^4 and the Laetolil M^2 are in the same size category: the P^4, 28 mm anteroposteriorly and 31 mm transversely, is one-sixth smaller in linear dimensions than its homologue in *Ancylotherium pentelicum* (Gaudry & Lartet) (Thenius, 1953: 105, fig. 1), and so is the (holotype) M^2 of *A. hennigi* (Dietrich, 1942: 105, 55 by 40 mm). As to the identity of the Chemeron chalicothere there can be no doubt; it was mentioned in an earlier paper (Hooijer, 1972: 188) as adding to the younger elements of the fauna from the Chemeron Formation, nearer to the 2 million-year-limit than to the 5+ million-year-limit as given by Bishop (1972: 242) [1]).

Brachypotherium lewisi Hooijer & Patterson

This large species, the terminal form of the *Brachypotherium* lineage in Africa, fully described in Hooijer & Patterson (1972), is found at Lothagam-1, Members B and C; fragmentary remains originate from Ngorora and Sahabi and are recorded as *B.* cf. *lewisi* although there is little doubt that the Lothagam species is represented at these sites. I have now an additional specimen from Ngorora, a P_3 or P_4 sin., marked 2/14a, incomplete anteriorly, with the external groove flattened out, the external cingulum present but weakly developed, and a posterotransverse diameter of 33 mm (cf. Hooijer & Patterson, 1972, table 3). From the Mpesida Beds comes an M_1 or M_2 sin., KNM/MP/131 (pl. 1 fig. 13). It is the anterior portion of the tooth, with an external cingulum, the characteristic horizontal enamel striations, and an anterior basal width of at least 37 mm. The great width excludes the Miocene *B. heinzelini*. The Mpesida Beds, age ca. 7 million years (Bishop, 1972: 241), fill the gap between Ngorora (12— m.y.) and Sahabi, Libya (6 m.y.), and there is no shade of doubt that the Lothagam-1 species *B. lewisi* is here represented: this adds to the faunal list of Mpesida presented by Bishop (1972: 241), who lists „Rhinocerotidae" without generic or specific allocation.

Aceratherium acutirostratum (Deraniyagala)

From the Alengerr Beds in Kenya, between 14 and 12 million years old, Bishop (1972: 240) cites *Dicerorhinus leakeyi* Hooijer, but *Aceratherium acutirostratum* is present as well. A P^3 sin. is very slightly worn. The external surface is missing, the ant. post. diameter ca. 32 mm. The protocone constriction is marked, crochet and crista very small, and the antecrochet is narrow but prominent. The internal cingulum is 7 mm high and forms a ledge extending from protocone to metaloph; between it and the antecrochet there is a pit. These characters point to *Aceratherium acutirostratum* (cf. Hooijer, 1966: 138). The species in question occurs at Moruaret Hill, whence the type came (Deraniyagala, 1951), Sinda, Congo (Hooijer, 1963), and at Napak I, Karungu and Rusinga sites (Hooijer, 1966). It is usually

1) In the U.S.A. Omo collections sent to me in 1972 I found another P^4 of *Ancylotherium hennigi*. It is from locality 11, no. 28, Shungura Member D5, 28 mm anteroposteriorly and 29 mm transversely, and from the left side. Two fragments of upper molars of the same species, L. 697-2 and P. 923-22, are from Shungura Member G, likewise at the 2 million-year-level (cf. Cooke & Maglio, 1972: 306).

associated with *Dicerorhinus leakeyi* from which it is well-nigh indistinguishable postcranially (Hooijer, 1966: 152-154). A typical *D. leakeyi* tooth from Alengerr will be recorded below, but there is a third rhinoceros tooth from the Alengerr Beds, a P_3 dext., that may belong to either one of the genera and species. It has a sharply defined external groove between meta- and hypolophid, no external cingulum, and measures: ant. post. 30 mm, ant. transv. 20 mm, and post. transv. 23 mm (cf. Hooijer, 1966: 131, 141).

Beside *Brachypotherium snowi* (Fourtau) there is at Moghara, Egypt, some rhinoceros material that may be *Aceratherium*. Andrews (1900) recorded an incomplete atlas measuring 140 mm across the articular cavities for the occipital condyles, the size of that of *A. acutirostratum* (Hooijer, 1966: 158), as well as an incomplete scapula approximately 360 mm in height, and with a glenoid surface 77 by 62 mm in diameters, not larger than *Dicerorhinus sumatrensis* (Hooijer, 1966: 158) that is smaller than *D. leakeyi*. It is impossible to determine the species on these poor remains, but they may well represent *Aceratherium* (cf. also Arambourg, 1933: 131). There is a lot of postcranial material from Ombo, a site in Kenya from which we have *Dicerorhinus leakeyi* as well as *Chilotheridium pattersoni* Hooijer, which is too large for *Chilotheridium pattersoni*: this may be either *Aceratherium acutirostratum* or *Dicerorhinus leakeyi* and will be enumerated in the following pages. Ombo (Bishop, 1967: 46), at 34° 34′ E., 00° 04′ S., has a fauna including Rhinocerotidae (l.c.: 50), and in my 1966 paper I recorded just one distal end of a median metapodial from that site (M. 18836), which I now think may belong to *Chilotheridium pattersoni* (vide infra). The specimens from Ombo are in the Archdeacon W. E. Owen collection, purchased by the British Museum (Natural History) in May, 1938, as follows: cuneiform dext. (A), magnum dext. (A), unciform dext. (A), proximal part of Mc. III dext. (G), distal part of idem (H), proximal part of Mc. IV dext. (B), distal part of idem (C), astragalus sin., medial portion only, navicular dext. (B), phalanx I of median digit (D), and phalanx I of lateral digit. Measurements are presented in table 2.

These bones, as comparison with the various tables in Hooijer (1966) shows, belong to non-brachypothere forms and are different from those of *Chilotheridium pattersoni* as recorded in Hooijer (1971).

Dicerorhinus leakeyi Hooijer

An unworn P^4 and part of M^1 sin. from Ombo, M. 29426 (pl. 2 fig. 1) belong to the present species represented at Rusinga and Napak V and VI (Hooijer, 1966). Of the P^4 we see the wall, at least 10 mm high, at the

Table 2

Measurements of bones of *A. acutirostratum* or *D. leakeyi*, Ombo (mm)

Cuneiform, anterior height	44	Mc. IV, proximal width	43
distal width	32	proximal ant. post. diameter	45
proximal ant. post. diameter	29	greatest distal width	44+
greatest horizontal diameter	38	width of distal trochlea	43
Magnum, greatest anterior height	30	distal ant. post. diameter	40
greatest anterior width	45+	Astragalus, medial height	78
proximal ant. post. diameter	72	Navicular, greatest ant. height	23
Unciform, greatest ant. height	ca. 50	total width	43
greatest width	ca. 66	ant. post. diameter	53
greatest ant. post. diameter	87	Phalanx I, median digit, length	36
Mc. III, proximal width	60	proximal width	53
proximal ant. post. diameter	ca. 55	Phalanx I, lateral digit, length	28
greatest distal width	ca. 60	proximal width	32+
width of distal trochlea	49		
distal ant. post. diameter	ca. 45		

medisinus entrance, and no anterior or posterior protocone folds, or antecrochet. M^1 has a wide medisinus entrance blocked by a cingular ridge; the protocone is hardly marked off, the crochet weak; there is a small crista and no antecrochet. P^4, 50 mm high at the unworn ectoloph, is 56 mm anterotransversely and 52 mm posterotransversely. M^1 measures ca. 60 mm anterotransversely. These Ombo teeth have all the characteristics of those of *D. leakeyi* and are but slightly larger than their Rusinga homologues (Hooijer, 1966: 126-129).

An M^3 sin. from the Alengerr Beds, much worn down, shows the very marked metacone bulge, which makes the crown trapezoid rather than triangular in outline; the protocone constriction is slight. The ant. post. (internal) diameter is 43 mm, the ant. transv. 51 mm, and the length of the outer surface 53 mm, all within the limits of the Rusinga M^3 (Hooijer, 1966: 128-129).

Then, in the Chemeron Formation, we find three dental elements that do belong to *D. leakeyi,* although this is a Miocene species; the remarks in connexion with the Chemeron *Brachypotherium heinzelini* teeth apply here as well.

An upper molar, KNM/BC/416, 5/8/67, is from the right side and moderately worn. The paracone style is well defined, the metastyle raised; there is no metacone style but a concavity instead. No inner cingulum is apparent, the medisinus entrance low and wide, the protocone folds (anterior and posterior), crochet, and antecrochet very weak; a crista is absent. Measurements: ant. post. ca. 42 mm, ant. transv. 56 mm, post. transv. 49

mm (cf. Hooijer, 1966: 129) make this most probably an M^2. The specimen is presented in crown view in pl. 2 fig. 2.

A left upper premolar, unfortunately incomplete externally as well as behind, is KNM/BC/375. This Chemeron tooth, the internal base of which is broken off below the bottom of the medisinus, has no protocone constriction or antecrochet, a very small crochet and no crista. Incomplete though it is, it appears inseparable from the P^2 in *Dicerorhinus leakeyi* (ant. post. 26-31 mm, ant. transv. 34-35 mm: Hooijer, 1966: 127). A crown view of the specimen is in pl. 2 fig. 3.

Finally, the last Chemeron tooth referable in my opinion to *D. leakeyi* is but a fragment, KNM/BC/374 (pl. 2 fig. 4). It holds the medisinus, obstructed by a projection from the metaloph, and three fossettes. The anterior cingulum is preserved, and no protocone constriction is evident. The external and posterior borders of the crown are missing, and the internal metaloph portion is incomplete. The specimen represents a left upper premolar, and the three fossettes appear to be, from front to back, the deepest portion of the medisinus cut off by the crochet, a true medifossette, formed by the union of crochet and crista, and the postfossette. The medisinus entrance obstruction, the condition of the protocone, and the size are as in P^2 of *Dicerorhinus leakeyi*. A medifossette is not usually found in the premolars of this species, but they are present occasionally in species in which they are normally absent, and its presence in the Chemeron P^2 does not militate against its belonging to *D. leakeyi*.

The rolled condition, especially of the two second upper premolars, would be in harmony with the view, which I hold, that the *D. leakeyi* teeth are intrusions in the Chemeron Formation and come from a Miocene deposit.

Chilotheridium pattersoni Hooijer

The species occurs in abundance at Loperot (Hooijer, 1971), but has also been found at (and described as *Chilotherium* from) Rusinga (Hooijer, 1966: 151-152). The genus, perhaps not the same species, occurs at Kirimun and Bukwa II (Hooijer, 1971: 358, 360). At Ngorora there is not only dental but also postcranial material (Hooijer, 1971: 360, 362, 364, 365 and pl. 11) proving the specific identity of the Ngorora form with *C. pattersoni*. Now we have some material originating from Ombo, dental as wel as postcranial, proving the existence of *C. pattersoni* at this site. Ombo is a Miocene site in Kenya (see Bishop, 1967: 46, 50).

There is first part of a right upper molar, marked Ombo 9/3/35, M. 15049, much worn down (pl. 1 fig. 9). It has a markedly constricted, internally flattened, protocone, a very marked antecrochet curving inward toward the medisinus entrance at base, a weak crochet, and no crista. This tooth has all the unmistakable characteristics of *C. pattersoni.* The symphysial portion of a mandible with the right tusk, diameter ca. 27 mm vertically and ca. 37 mm horizontally at crown base, belongs here also: the tusk dimensions are close to those of the Kirimun specimen (Hooijer, 1971: 358). There is the back portion of a skull, but not in a very good condition, and a right and left M^{2-3}, evidently of the same individual. The M^{2-3} dext. from Ombo are figured in pl. 1 fig. 10. The antero-external corners are incomplete (the left M^{2-3} lack the postero-internal corners). Part of the outer surface of M^3 sin. is misplaced, but M^3 dext. is better preserved. In M^2 the medisinus is closed off by the antecrochet that extends all across it. The marked protocone constrictions, the internal flattening of the protocones, the anterior hypocone folds, the downward and inward curve of the antecrochet, ending basally at the medisinus entrance, and the metacone bulge at the base of the outer surface of M^3, all these features are as in *Chilotheridium pattersoni.* The measurements are given in table 3.

Table 3

Measurements of upper molars of *Chilotheridium pattersoni* (mm)

	Ombo	Loperot
M^2, ant. post.	—	ca. 55-57
ant. transv.	65	ca. 70
post. transv.	60	ca. 65
M^3, ant. post. (internally)	52	ca. 55-57
ant. transv.	55	ca. 60
length outer surface	—	61-62

The distal end of a median metapodial from Ombo, M. 18836, left unidentified in 1966, may now be referred to *C. pattersoni.* The greatest distal width (ca. 53 mm) and the trochlea width (ca. 44 mm) are approximate because of damage, but the distal ant. post. diameter can be exactly given (41 mm). These dimensions are within the range of those in median metapodials from Loperot (Hooijer, 1971: 384, table 32 A). Ombo, therefore, may be added to the list of sites yielding *Chilotheridium pattersoni* proper.

In my *Chilotheridium* paper I said that *Chilotheridium* differs from *Chilotherium* in that the former has pneumatized frontals and parietals, whereas in *Chilotherium* frontals and parietals are not pneumatized (cf. Ringström, 1924). However, in her study of the natural cast of the brain, nasal, and accessory cavities of *Chilotherium* Edinger (1937) observed that there are small air sinuses in these bones, although they are certainly not as extensive as those in *Chilotheridium*. The table of distinguishing characters of *Chilotherium*, *Chilotheridium*, and *Diceratherium* in Hooijer (1971: 387) should be amended accordingly.

Diceros bicornis (L.) subsp.

This, the modern species of black rhinoceros of Africa, actually dates back to about 4 million years. At this stage the molar crowns were not quite as high as those in modern skulls, a difference that appears to be of subspecific scope only, although the cranial characters at this stage are as yet unknown. In my paper on the Pleistocene East African rhinoceroses (Hooijer, 1969) I mentioned this fact for M^3 originating from Ethiopia, the Usno Formation, placed around the 3 million year level (Cooke & Maglio, 1972: 306), but the same evidence obtains for a tooth from the Mursi Formation of Ethiopia, 4 million years old.

The tooth in question, which forms part of the American Omo collection entrusted to me by Dr. F. Clark Howell, is a slightly worn DM^4 dext., the only *Diceros bicornis* tooth from the Mursi Formation, marked Y. 4-47 and collected in 1969. The greatest anteroposterior diameter of the ectoloph can be taken, and it shows the maximum of the recent DM^4 of *D. bicornis* (table 4).

Table 4

Measurements of upper milk molars of *Diceros bicornis* (mm)

	L. 116-6	Recent
DM^3, greatest length ectoloph	48	43-49
ant. transv.	44	40-49
post. transv.	ca. 40	37-43
	Y. 4-47	
DM^4, greatest length ectoloph	55	49-55
ant. transv.	48	45-52
post. transv.	45	40-47

In the early stage of wear, the tooth shows all the characters seen in modern *Diceros bicornis*: a prominent paracone style, slight median elevation of the ectoloph apically but a depressed area basally between the roots, no metacone style, a slightly raised metastyle, a horizontal, well-developed anterior cingulum terminating on the internal face of the protocone, a postsinus markedly shallower than the medisinus, a large crochet, no trace of a crista. These characters serve to distinguish the upper cheek of *D. bicornis* from those of *Ceratotherium simum* (Burchell), the modern white rhinoceros of Africa (cf. Hooijer, 1959). The two species occur together throughout the Pleistocene of Africa: there is much material, postcranial as well, in the collections from the Shungura Formation, Omo valley, Ethiopia, given to me for study by Dr. F. Clark Howell. Since we have stratigraphic control on the specimens collected by the American missions to Ethiopia it seems best to start with the material from the oldest level represented in the Omo succession, and this happens to be the DM^4 of the Mursi Formation. The rhinoceros collection from Makapansgat, South Africa (Hooijer, 1959) consists almost exclusively of deciduous teeth, and there are several specimens of DM^4 of *D. bicornis* in this lot one of which (in M 2107, Hooijer, 1959: 10, and fig. 4) slightly exceeds the recent in width. Other than that, no differences between the Makapansgat milk teeth and those in recent skulls can be found.

One of the recent DM^4 of *D. bicornis* available to me (Leiden Museum, cat. ost. c) is worn even less than that from the Mursi Formation, and also shows the anterior and posterior bulges over which the greatest ectoloph length can be taken. When the tooth wears down to below that level this measurement cannot be taken any more. There is another, unworn DM^4 of *D. bicornis* (in Leiden Museum, cat. ost. d), which is not yet calcified all the way to the base, so that the height of the ectoloph cannot be taken, but the apical portion of the crown is perfect. The greatest anteroposterior ectoloph length is 55 mm in cat. ost. c, and 50 mm in cat. ost. d (cf. table 4 of the present paper: this is almost the total range of variation, based on six specimens).

The posterior metastyle bulge is just above (apically of) the posterior cingulum in the recent as well as the fossil teeth, and the distance from the top of the cingulum laterally of the incision behind the postsinus and the base of the incision between metacone and hypocone (not yet reached by wear in the fossil DM^4) is 26-27 mm in both of the recent DM^4 against only 21 mm in the fossil. Since the height of the lateral portion of the posterior cingulum above the base of the metacone is the same in all the teeth (27 mm) it follows that the total crown height of the Mursi Formation DM^4 is less than that in its recent counterparts. The anterior parastyle bulge, less marked than the posterior, metastyle bulge, is at the level of the (nearly horizontal) anterior cingulum in the fossil as well as in the recent DM^4. Unfortunately, the anterior height of the Mursi Formation DM^4 cannot be determined as both protocone and paracone are worn, and nothing of the apical rim of the protoloph remains. The height of the top of the anterior cingulum in the depression for the metastyle of the tooth in front (DM^3) above the enamel base of the paracone is exactly the same in the teeth (24 mm). This confirms the observation made above in the posterior part of the tooth, viz., that the difference in total crown height between the fossil and the recent teeth is restricted to the apical portion of the crown, above the ectoloph bulges, fore and aft.

Thus, when a tooth is worn to below (rootward of) its greatest antero-posterior ectoloph extension we can see no difference between the fossil, less hypsodont, and the recent, more hypsodont, specimens. What we need to establish a difference (if any) in total crown height, are unworn, or very slightly worn, specimens.

From the Mursi Formation (4 million years old) I have further only one astragalus, marked Y. 4-48. It is from the right side and conforms in all respects to the astragalus in the living *D. bicornis* (see table 5), no difference of any kind being apparent.

Table 5

Measurements of astragalus of *D. bicornis* and *C. simum* (mm)

	Y. 4-48	L. 1-27	491	*D. bicornis*	L. 5/6-46A	*C. simum*
Lateral height	67	70	66	65-71	78	74-76
Medial height	68	66	65	68-70	86	75-84
Total width	83	81	74	83-86	95	95-104
Ratio medial height/ total width	0.82	0.81	0.88	0.79-0.84	0.91	0.79-0.81
Trochlea width	68	65	66	75-78	86	83-87
Width of distal facets	71	66	64	70-73	84	85-88

Of the astragali in table 5, that marked Y. 4-48 is the oldest in the Ethiopian succession (Mursi Formation); L. 1-27 is from the left side and comes from Shungura Member B 11 (just above the 4 m.y. level); no. 491 is also from the left side and is from the Usno Formation (around the 3 m.y. level), while L. 5/6-46A is left again, and from Shungura Member E (only a little older than 2 m.y.). The three specimens that I refer to *D. bicornis* (the first three columns in table 5) are rather on the small side, all of them, while the specimen marked L. 5/6-46A is rather largish, and stands out rather markedly when the series of astragali is laid out on a table. The impression is strongly made that the difference is that which we see between recent *D. bicornis* and *C. simum,* the latter being the larger form. Even though, as I pointed out a number of times in earlier papers, Pleistocene remains of living species tend to be on the large side when compared with corresponding recent material (this holds good for Africa as well as other parts of the world), there is no species other than *D. bicornis* to which the smallish astragali may be referred, and the large Shungura Member E astragalus fits in very nicely with *C. simum* (the variation ranges in the column under *D. bicornis* and those in the terminal column under *C. simum* are derived from earlier papers; mainly Hooijer, 1972, 1969, and Hooijer & Singer, 1960).

I now proceed to the next younger specimens of *D. bicornis* in the Omo succession, which are those from near the 3 m.y. level, Shungura Member C. It is from this level that we have a very fine skull, without the mandible; it is marked L. 68-1. The skull is laterally compressed, has lost the condyles and the right zygomatic arch, and all the teeth are worn to such an extent that the full crown heights cannot be determined. It is, therefore, fully adult. It has all the visible characters of the skull in modern *D. bicornis*: the occiput inclination is the same, the dorsal profile, the horn bosses on frontals and nasals, the naso-maxillary notch extending backward to above the anterior border of P^3, the anterior border of the orbit being placed above the anterior border of M^2, the teeth in the state into which they are worn; everything is as in modern *D. bicornis*. From the few measurements that can actually be taken (table 6) it is evident that the Shungura Member C skull is well within recent limits of size; the Cape race of *D. bicornis* (Leiden Museum, cat. ost. a) is the largest of them all (first column), and in columns 2, 3, and 4 follow the skull measurements one each of the races *D. bicornis bicornis, D. bicornis holmwoodi,* and *D. bicornis somaliensis* in the British Museum (Natural History), after Hopwood (1939). The Leiden Museum skull no. 5738 is a zoo specimen of unknown provenance, *D. bicornis* subsp. Its teeth are in a good stage of wear, with the M^3 worn down about one-sixth of its height, and M^1 half worn down.

Table 6

Skull measurements of *Diceros bicornis* (mm)

Specimen	L.M. a	British Museum			L.M. 5738	Shungura C
Occipito-nasal length	640	590	550	555	570	580
Condylo-basal length	635	560	555	530	565	—
Zygomatic width	365	360	330	305	335	—
Lacrymal width	300	275	255	240	265	—
Postorbital constriction	125	120	120	110	115	—
Width at occipital crest (dorsally)	210	205	195	175	195	—
Greatest occipital width	250	—	—	—	245	—
Bicondylar width	140	—	—	—	135	—
Foramen magnum to occipital crest	160	160	150	145	155	—
Width of nasal boss	150	145	150	130	150	ca. 130
Separation inferior squamosal proc.	10	—	—	—	5	—
Length P^2-M^3	295	260	265	210	250	270

The teeth (the left tooth series is rather well-preserved) do not appear to differ from those in modern skulls, but, as said above, a possible difference in full crown height, of course, does not show. That there is a difference in crown height between the 3 million-year-old *D. bicornis* and the modern black rhinoceros molars is shown by an unworn M^3 from the Usno Formation (White Sands in Hooijer, 1969: 87, pl. 5 fig. 1), the formation from which comes the *D. bicornis* astragalus no. 401 in table 5 above, and which is round the 3 m.y. level.

The specimen, then, which is marked W. 12 and which comprises just the outer surface of an M^3 sin., originates from the White Sands (now included in the Usno Formation, cf. Howell, 1972: 350) and has an ectoloph height of 56 mm by a basal anteroposterior outer surface length of 55 mm. In the recent M^3 used for comparison (Hooijer, 1969, pl. 5 fig. 2) the crown height is 64 mm by a basal length of 54 mm. The difference would not have been detected had the crown been worn to an external height of 35 mm, for the tapering of the crown, especially the swing backward of the parastyle in front, is visible only in the top 20 mm of the fossil molar. Above this level, 35 mm from the base, the recent molar continues the very gradual backward curve of the parastyle, without a break, and the rounding off of the crown begins only at 45 mm from the base. Though the rim of the ectometaloph is placed nearly 10 mm higher in the recent than in the fossil molar, the basal 35 mm of the two crowns look exactly the same.

We have, therefore, evidence that even at the 3 million year level the hypsodonty of *D. bicornis* was not yet what it is today. The skull characters of the 3 million year old *D. bicornis* were already what they are at present, witness the Shungura Member C skull above described. And the astragali mentioned above (table 5) tend to show that postcranially, too, the 4-3 million-year-old *D. bicornis* was indistinguishable from the living form. It is only the teeth that were not quite as high as they are today. In basal diameters the Shungura Member C cheek teeth tally well with the recent (table 7).

Continuing the description of the remains of *D. bicornis* in the Omo succession we come to specimens from the Usno Formation and Shungura Member C that are less important, although they should be placed on record as well (a very incomplete humerus from Shungura Member B11 is included in a later table with other, later humeri).

B. 366, Usno Formation, is a P^3 sin. of *D. bicornis*, damaged antero-externally only. Measurements: ant. transv. 50 mm, post. transv. 48 mm, just as in a recent skull (see table 7, last column).

W. 461, Usno Formation, is a P^3 sin. again, but comprises only the internal portion of protoloph and the external and posterior walls of the medisinus. The crochet is bifid, there is no crista, and no measurements can be given.

Table 7

Measurements of upper teeth of *Diceros bicornis* (mm)

	Shungura C	L.M. cat. a	L.M. cat. e	L.M.5738
P^2, ant. transv.	35	39	40	—
post. transv.	41	44	42	37
P^3, ant. transv.	49	61	58	50
post. transv.	47	58	53	48
P^4, ant. transv.	55	70	67	62
post. transv.	53	65	—	58
M^1, ant. transv.	66	69	66	61
post. transv.	62	64	61	56
M^2, ant. transv.	—	72	69	59
post. transv.	ca. 56	63	—	54
M^3, ant. post. (int.)	56	—	—	53
ant. transv.	59	64	—	59
l. outer surface	65	—	—	—

W. 13, Usno Formation, is a fragment of a left upper molar, showing the paracone style and hence referable to the present species. The state of preservation is exactly the same as that of the M^3, W. 12, and the two teeth may have belonged to the same dentition.

W. 598, Usno Formation, is an M_3 sin. with the anterior lophid incomplete internally. Measurements: ant. post. 57 mm, post. transv. 36 mm. Height of posterior lobe, barely worn, 43 mm internally. Mentioned by Hooijer (1969: 88).

L. 27-20, Shungura Member C, worn ectoloph of M^2 sin., para- and metastyles broken off. *D. bicornis.*

L. 27-21, Shungura Member C, anterior fragment of left upper molar, *D. bicornis.*

L. 58-2, Shungura Member C, an entire trapezoid sin.; small part chipped off above anteriorly. In table 8 the specimen may be compared with its homologues in the recent species; it seems evident that it is closer to *D. bicornis* than to *C. simum.*

Table 8

Measurements of trapezoid of *D. bicornis* and *C. simum* (mm)

	Shungura C	*Diceros bicornis*		*C. simum*
	L. 58-2	L.M.	S.A.M.	S.A.M.
Anterior width	30	27	30	35
Anterior height	—	32	31	32
Posterior height	31	32	29	36
Ant. post. diameter	42	40	41	49

L. 12-17, Shungura Member D2, is a mandible wanting the ascending portions, and damaged in the symphysial region. The premolars and molars are very much worn down: the length P_4-M_3 is only 170 mm, and the height of the mandible at M_1, 95 mm. In individually younger adults of *D. bicornis*, with M_3 slightly to moderately worn, the length P_4-M_3 runs from 220 to 190 mm by a body height at M_1 of 85-95 mm.

Table 9

Measurements of lower teeth of *Diceros bicornis* (mm)

	Shungura D	L.M. cat. e	L.M. cat. b
P_2, ant. post.	28	30	31
ant. transv.	18	19	19
post. transv.	20	24	22
P_3, ant. post.	38	39	41
ant. transv.	27	26	26
post. transv.	30	33	32
M_1, ant. post.	53	52	53
ant. transv.	33	33	34
post. transv.	35	36	35
M_2, ant. post.	57	56	58

L. 314-1, Shungura Member D, is the left half of a mandible with P_4 erupting and M_3 not yet protruding beyond the alveolar rim. The coronoid process has broken off, and the condyle is incomplete internally. The P_{2-3} and the incomplete M_2 are but slightly worn, and they conform in size to those of *D. bicornis* (table 9). The outer base of the crown of the P_4 has been exposed, and the full external crown heights, at the anterior and at the posterior lophid, have been measured (table 10). They are practically the same as in a recent P_4 that has the same anteroposterior outer surface length. It is, therefore, evident that the fossil *D. bicornis* subsp. had already caught up in crown height of its teeth with the living form by the time of deposition of Shungura Member D, which is about 2½ million years ago (cf. Cooke & Maglio, 1972: 306).

Table 10

Measurements of unworn P_4 of *Diceros bicornis* (mm)

	Shungura D	L.M. cat. e
Greatest length, externally	44	44
Height of metalophid	62	63
Height of hypolophid	54	55

L. 76-25, Shungura Member D, several upper molar fragments of *D. bicornis*.

L. 122-21, Shungura Member D, P_3 dext., incomplete.

There are no specimens of *Diceros bicornis* in the American collection from Shungura Member E.

L. 116-5, Shungura Member F, is a P^3 dext., incomplete antero-externally. The measurements (ant. transv. 56 mm, post. transv. 52 mm) are as in recent *D. bicornis* (see table 7).

L. 116-6, Shungura Member F, is a DM^3 dext., moderately worn; postero-internal angle incomplete so that the greatest anteroposterior ectoloph length cannot be taken. It is indistinguishable for size from its recent homologues (see table 4).

L. 465-72, Shungura Member F, a lower molar fragment of *D. bicornis.*

L. 398-449, Shungura Member F, outer part of DM^4 sin.

L. 16-115, Shungura Member G, is an M^1 sin. of *D. bicornis,* rather worn, antero-external angle broken off. It measures 56 mm postero-transversely, as in L.M. no. 5738 (table 7).

L. 628-94, Shungura Member G, is a much abraded DM^3 sin. of *D. bicornis,* measuring 40 mm antero-transversely, within recent limits (see table 4).

L. 628-216, Shungura Member G, postero-internal fragment of DM^3 sin.; no measurements.

L. 43-22, Shungura Member G, central fragment of right upper P, *D. bicornis.*

L. 628-93, Shungura Member G, antero-external fragment of upper P or M dext.

Two damaged proximal humerus portions, from the right side: L. 7-24, Shungura Member G, and L. 16-42, Shungura Member G, conform to recent *D. bicornis* rather than to *C. simum* (table 11). Also in this table a very incomplete specimen, L. 1-80, from Shungura Member B11, slightly smaller than the others but referable to *D. bicornis* as well.

Table 11

Measurements of humerus of *D. bicornis* and *C. simum* (mm)

	L. 7-24	L. 16-42	L. 1-80	*D. bicornis*	*C. simum*
Width over caput and posterior part of lateral tuberosity	155	150	145	145-160	180-190
Width at deltoid tuberosity	140	140	—	130-150	165-175

This brings the list of Ethiopian material of *D. bicornis* to a close. At the 2 million year level (Shungura Members F and G) *D. bicornis* has all the characters of the living form; by 2½ million years ago the hypsodonty is already that of the living form, and around the 3 million year level (Shungura

Member C, and Usno Formation) we observe that the tooth crowns are not quite as high as they are at present, although the skull characters are already modern. The oldest *D. bicornis* in the Ethiopian succession, the Mursi Formation specimens (ca. 4 million years), is less high-crowned in its molars than the living, but its astragaline features are modern.

There is a *Diceros* in Africa much older than *D. bicornis*, viz., *Diceros douariensis* Guérin (1966), which comes from the Mio-Pliocene of Tunesia. It is stated by its describer (Guérin, 1966: 33, 44) to be more hypsodont than recent *D. bicornis*, which surprised me. Guérin gives no height/length indices of the molars of the recent species, but presents those for M^1 and M^2 of his *D. douariensis*. These indices, however, are based on ectoloph height at origin of metaloph, and the basal anteroposterior ectoloph length: 112 for M^1, and 90 for M^2. Since Guérin also gives the basal anteroposterior ectoloph lengths (53 mm for M^1 sin., and 62 mm for M^2 sin.) the ectoloph heights can be calculated, and these are 59 mm for M^1 sin., and 56 mm for M^2 sin. Height/length indices for unworn upper molars given by me in previous papers (Hooijer, 1972; Hooijer & Patterson, 1972) are based on the maximum, not the basal, anteroposterior ectoloph lengths, not given in Guérin's paper. At my request Dr. Guérin kindly sent me the greatest antero-posterior ectoloph lengths, which are 61.5 mm for M^1 sin., and 67.5 mm for M^2 sin. (in litt., December 22, 1971). This gives 96 for the height/length index of M^1 of *D. douariensis*, and 83 for the height/length index of M^2 of *D. douariensis*. These figures are lower than those for the M^2 of modern *D. bicornis*: I found height/length indices for M^2 of *D. bicornis* of 104, and 109 (Hooijer, 1972: 160).

The unworn M^1 of *Paradiceros mukirii* Hooijer (1968) from the Late Miocene of Fort Ternan has an ectoloph height of 42 mm, and a greatest anteroposterior ectoloph length of 49 mm, which gives a heigh/length index of 86, again, lower than that in the recent species of *Diceros*.

Consequently, contrary to Guérin's statement, *Diceros douariensis* is less hypsodont than the modern form, just as is *Paradiceros mukirii*, the earliest member of the *Diceros* group anywhere (see Hooijer & Patterson, 1972, fig. 11).

Diceros bicornis is also present in the Kapthurin Formation, a faunal list of which is presented by Bishop (1972: 244). The Kapthurin Formation is placed quite high in the Baringo sequence, just pre-Holocene (Bishop, 1972: 228). *D. bicornis* should be added to the faunal list of that Formation, for in 1963 Professor Bryan Patterson and his party found a rather complete skull at exposures of the Kapthurin Formation west of Lake Baringo. The skull is indistinguishable from recent *D. bicornis* (Hooijer & Patterson, 1972, Appendix).

Besides *Ceratotherium simum germanoafricanum,* Maglio (1971) records *Diceros bicornis* from the faunal zones Koobi Fora II and III, East Rudolf. These zones, which are less than 2.6 million years old (a tuff dated at this is at the bottom of Koobi Fora II: Vondra, Johnson, Bowen & Behrensmeyer, 1971, fig. 3 at KBS; cf. Isaac, Leakey & Behrensmeyer, 1971, table 1), have yielded a number of *D. bicornis* specimens including a subadult skull (M^3 unerupted) and several unworn premolar and molar crowns. I studied this material at the Centre for Prehistory and Palaeontology in Nairobi in the summer of 1971.

The subadult skull of the Koobi Fora II and III faunal zones comes from Ileret in the north and bears the number KNM-ER 636. The Ileret section has not been radiometrically dated but is roughly contemporaneous with the entire Koobi Fora II and III sequence (Maglio, 1971). It has been stated by Maglio that the East Rudolf *Diceros bicornis* has proportionally longer molars and larger premolars than the living, but my examination of the material does not bear this out. The Koobi Fora *Diceros bicornis* differs in no way from the recent. The skull is compared with recent skulls of the same dental age in table 12.

Table 12

Skull measurements of *Diceros bicornis* (mm)

	Ileret 1 A	Nairobi MPE 1DB6	L.M. cat. b	L.M. cat. e
Occipito-nasal length	525	530	575	570
Zygomatic width	305	315	340	350
Lacrymal width	230	225	240	260
Postorbital constriction	110	110	115	130
Width at occipital crest (dorsally)	170	180	200	220
Greatest occipital width	215	210	250	250
Bicondylar width	115	130	150	—

The transverse diameters of the premolars and molars cannot be given as the ectoloph bases are not exposed yet, but the premolars are no larger than those in the two subadult Leiden Museum skulls (cat. b and e), and the greatest anteroposterior ectoloph length of the slightly worn M^2 in the Ileret skull (66 mm) is within recent limits (61, 68, and 70 mm in the three recent examples). Unfortunately, the full crown heights cannot be determined in any of the Ileret teeth.

In KNM-ER 691, Koobi Fora II B, there are P^2 sin., P^3-P^4, both sides, the slightly worn M^1, both sides, and M^2, both sides, very slightly worn. The P^2 dext. evidently belonging to the same dentition bears the number 369, matching the P^2 sin. which is in with the P^{3-4} and M^{1-2} of number 691. Tooth measurements are presented in table, together with the height/length indices, based on the greatest (not basal) anteroposterior ectoloph lengths. In this way the data are comparable to those given for *D. bicornis* given in earlier papers (Hooijer, 1969; Hooijer & Patterson, 1972; Hooijer, 1972).

Table 13

Measurements of unworn upper P and M of *Diceros bicornis* (mm)

	P^2	P^3	P^4	M^1	M^2
Greatest anteroposterior length	37	47	53	60	66
Height of ectoloph	50	68	72	70+	75
Antero-transverse diameter (base)	38	55	64	62+	68
Postero-transverse diameter (base)	40	54	57	58	59
Height/length index	135	145	136	117+	114

The transverse diameters of the Koobi Fora upper P and M tally well with those given in table 7. The height/length index of a P^4 in a recent Leiden Museum skull is 145 (Hooijer, 1972: 160), as in the Koobi Fora P^3. In the upper molars the index is not quite as high as that in the premolars; as already stated above two M^2 of recent *D. bicornis* have indices of 104-109, and an M^3 gives 119 for the height/length index.

The Olduvai Gorge specimens of *Diceros bicornis* have been recorded by Hooijer (1969); it should be noted that the species is not represented in Bed I and Lower Bed II, where we have only *Ceratotherium simum*. *D. bicornis* is also absent at Chemeron and at Later Kaiso (ca. 2-3 m.y.: Cooke & Coryndon, 1970: 184, 217). The Ethiopian record shows it to be present already 4 million years ago (Mursi Formation); the absence of *D. bicornis* at some later sites is probably ecological.

Ceratotherium praecox Hooijer & Patterson

Although recently described at length (Hooijer & Patterson, 1972; Hooijer, 1972) there are a few more data to be recorded. Too late for inclusion in my 1972 paper I found in the collection at Bedford College, London, a metapodial originating from the Mpesida Beds, age 7 million years (Bishop, 1972: 241). This is an Mt. IV, KNM/MP/132, from the right side, and there is no species to which the bone could be referred but *Ceratotherium praecox*. In every dimension and in the width/length ratio it is within the variation limits of sixteen fourth metatarsals of *C. praecox* from Langebaanweg (Hooijer, 1972, table 47), as shown in table 14 of the present paper. It tends to show that *C. praecox* is even more precocious than we thought it to be, for the Mpesida record is a million years earlier than the earliest *C. praecox* so far, which is from Lothagam-1 (Hooijer & Patterson, 1972), also from the Aterir Beds and Mursi (Hooijer, 1972). As at Lothagam, *Ceratotherium praecox* at the Mpesida Beds is associated with *Brachypotherium lewisi* (see under that head in the present paper).

Table 14

Measurements of Mt. IV of *Ceratotherium praecox* (mm)

	Mpesida	Langebaanweg
Median length	167	152-174
Proximal width	58	45-65
Proximal ant. post. diameter	ca. 55	42-56
Middle width	35	27-35
Middle ant. post. diameter	36	32-48
Greatest distal width	46	37-47
Width distal trochlea	ca. 41	34-41
Distal ant. post. diameter	ca. 48	39-49
Ratio middle width/length	0.21	0.17-0.22

Two upper teeth, a metapodial, and a proximal sesamoid of *Ceratotherium praecox* from the Aterir Beds (ca. 4 m.y.) have already been recorded (Hooijer, 1972: 189). Three teeth of the present species from the Aterir Beds are figured in the present paper. A P^3 sin., KNM/AT/155, is shown in pl. 1 fig. 1; the measurements conform to those of the Langebaanweg P^3 (Hooijer, 1972: 162). The crown of an M^1 dext., wanting the external part, KNM/AT/156, is in pl. 1 fig. 2. These specimens show the characteristically angular antero-internal crown corner, the marked protocone fold, internally indented protocone, absence of medifossette, and (in the premolar) the very weak paracone style. Then, a very much worn right upper molar, M^1 dext., KNM/AT/157, incomplete externally and behind, is in pl. 1 fig. 3. The anteroposterior diameter of the protocone is 28 mm; the pronounced antero-internal crown angle is well seen in this specimen.

From the Plio-Pleistocene Chemeron Formation I recorded a maxilla with M^{1-3} originally (Hooijer, 1969, pl. 2 fig. 1) referred to *C. simum germano-africanum* (Hilzheimer), which afterwards turned out to represent *Ceratotherium praecox* (Hooijer, 1972: 187). This specimen is from locality J. M. 507. I have one more specimen, a P^4 dext. from locality J. M. 493, KNM/BC/417, wanting the ectoloph (pl. 1 fig. 4). The internal crown face is 46 mm anteroposteriorly, 28 mm of which are occupied by the protocone.

There are further two phalanges from the Chemeron likewise belonging to *C. praecox*, viz., the second phalanx of a median digit marked 5/1 Q, length 28 mm, proximal width ca. 60 mm, and a third phalanx of a lateral digit marked 5/1 Q as well, 30 mm in length and 60 mm in maximum transverse diameter; cf. table 49 and p. 187 in Hooijer (1972).

Ceratotherium praecox is held by us to be direct ancestor of the living white rhinoceros, *Ceratotherium simum* (Burchell) (Hooijer & Patterson, 1972, fig. 11). It has here been shown to date back 7 million years (the Mpesida metapodial), and its transformation into *C. simum* took place 4 to 3 million years ago.

Ceratotherium simum (Burchell) subsp.

There is a lot of material of this species from Olduvai Gorge (Hooijer, 1969); it is represented at all levels there. In the Omo succession it is present in abundance, but the Mursi Formation (Omo, Lower Level of 1967 in Hooijer, 1969) specimens have been relegated to *Ceratotherium praecox* (Hooijer, 1972: 187). The American Omo collections given to me for study by Dr. F. Clark Howell show that *C. simum* is present in Shungura Members B and D-G and in the Usno Formation. The earliest specimens (Shungura Member B, a little higher than the 4 million year level) are not complete or characteristic enough to decide whether perhaps the early subspecies, *C. simum germanoafricanum* (Hilzheimer) is present. This form occurs in the Chemeron Formation (locality J. M. 91, Hooijer, 1969: 76, pl. 1) and does not differ from the living species in cranial characters; only the teeth are somewhat less high-crowned and the lophs stand a little less oblique than in the living species although they already have the rounded antero-internal crown angles of the living species.

A good skull, with the mandible, clearly representing *C. simum germanoafricanum* comes from the lower part of the section at Ileret, East Rudolf, and was examined by me at the Nairobi Centre for Prehistory and Palaeontology in the summer of 1971. Unfortunately, the exact level at which it occurred is uncertain, but the Ileret Lower Unit is roughly contemporaneous with the entire Koobi Fora II and III sequence farther to the south (Maglio, 1971), younger than 2.6 million years (see Vondra, Johnson, Bowen & Behrensmeyer, 1971, fig. 3: the tuff shown in this figure at KBS, level of Koobi Fora II A, is the one dated at 2.6 m.y., cf. Isaac, Leakey & Behrensmeyer, 1971, table 1). The measurements are given in table 15.

Table 15

Measurements of skull and mandible of *Ceratotherium simum germanoafricanum* (mm)

	KNM-ER 328
Condylo-basal length	770
Zygomatic width	370
Lacrymal width	285
Postorbital constriction	120
Width at occipital crest	275
Bicondylar width	150
Depth of dorsal concavity	55
From foramen magnum to occipital crest	160
Width of nasal boss	180
Separation between inferior squamosal processes	5
Length P^2-M^2	ca. 220
Mandible, total length	620
Length of symphysis	145
Width at symphysis	—
Height of body at M_1	ca. 140
Width of ramus at angle	170
Length P_2-M_2	220

The Ileret skull is longer than any of the recent skulls of *C. simum* recorded by Heller (1913: maximum condylobasal length 750 mm); the Ileret mandible is longer than all but one of Heller's 1913 specimens (which has a length of 635 mm); the Chemeron Formation (loc. J. M. 91) skull recorded before (Hooijer, 1969: 76, pl. 1) is very slightly larger (zygomatic width ca. 380 mm, bicondylar width 160 mm).

An M_3 sin. in KNM-ER 687 (Koobi Fora II B) has a crown height of 90 mm; an M^3 sin., KNM-ER 659 (Koobi Fora II B), slightly worn, is 81 mm high. In living *C. simum* full crown heights of last molars are 100 mm or over; Dietrich (1945: 59) gives 120-130 mm for M^3.

L. 1-37, Shungura Member B, is an M_1 sin., the internal base incomplete, greatest observed height ca. 70 mm, anteroposterior diameter 57 mm at top, but 45 mm at base.

L. 374-3, Shungura Member B, outer fragment of lower right premolar.

L. 1-84, Shungura Member B 11, DM^3 sin., wanting the ectoloph, no measurements.

No material being present from Shungura Member C, the Usno Formation specimens, which are likewise round the 3 million year level, will be mentioned now.

W. 332, Usno Formation, is a P^2 dext., much worn, showing much cement and a large, concave interproximal wear facet behind. Measurements: ant. transv. 23 mm, post. transv. 27 mm.

W. 591, Usno Formation, unworn crown of P^3 or P^4 sin., unfortunately not calcified all the way down to the base. Figured in Hooijer (1969, pl. 3 figs. 4-5). The bottoms of medi- and postsinus are still open. The suppression of the paracone style, formation of a medifossette, and rounded antero-internal crown angle leave no doubt as to its belonging to *C. simum*, not *C. praecox* that we find at the 4 million year level (Mursi Formation). The height of the ectoloph as preserved is 85 mm, but full calcification may have given 20-25 mm more, which, with a greatest anteroposterior ectoloph length of 58 mm, would give a height/length index of 180-190 for this premolar. A slightly worn P^4 of the living *C. simum* from the Cape (L.M., cat. ost. a) has an ectoloph height of 95 mm; the protoloph is not quite confluent with the ectoloph on the occlusal surface and probably no more than 10 mm is worn off. This, by 55 mm greatest anteroposterior ectoloph length, gives a height/length index of 173 as preserved, and ca. 190 if the crown had been unworn. A completely unworn P^4 of the living *C. simum* in the South African Museum has an ectoloph height of 103 mm by a greatest anteroposterior ectoloph length of only 46 mm, giving a height/length index of 224 (Hooijer, 1972: 160). The Usno P^4, therefore, is almost fully, or even fully as high-crowned as its counterpart in recent skulls of *C. simum*.

The transition from *C. praecox* to *C. simum*, we might say, took place between 4 and 3 million years ago.

W. 409, Usno Formation, M_1 sin., incomplete antero-internally; cement coating partially retained, 43 mm anteroposteriorly at base.

W. 333, Usno Formation, M_3 sin., worn, much cement. Measurements: ant. post. 64 mm, ant. transv. 35 mm, post. transv. 31 mm.

W. 7.442, Usno Formation, right lower molar, incomplete anteriorly at base, ant. post. diameter 57 mm at top; height of slightly worn posterior lophid 78 mm.

W. 549, Usno Formation, fragment of left upper molar; height as preserved 80 mm.

All the Usno Formation molars can be matched in recent skulls of *C. simum*.

L. 9-3, Shungura Member D5, M_1 sin., incomplete antero-externally. Ant. post. diameter at base ca. 45 mm.

L. 21-25, Shungura Member D, entire entocuneiform sin. The entocuneiform was not present among the material of *Ceratotherium praecox* from Langebaanweg (Hooijer, 1972), but comparisons may be made with the entocuneiform of *Chilotheridium pattersoni* from Loperot of which there are three specimens (Hooijer, 1971: 382). In the Shungura bone the facets for mesocuneiform and metatarsal II are separated by a non-articular groove, or fossa; these facets are continuous in the entocuneiform of *Diceros bicornis*. However, in *Chilotheridium* the mesocuneiform facet and the metatarsal II facet are either united or separate so that this does not seem to be a matter of great moment. The measurements are given in table 16.

Table 16

Measurements of entocuneiform in *C. simum, D. bicornis*, and *Chilotheridium* (mm)

	C. simum	*D. bicornis*	*Chilotheridium*		
	L. 21-25	L.M.	1	2	3
Anterior height	44	36	42	43	31
Proximal ant. post. diameter	34	26	33	31	29
Distal ant. post. diameter	36	29	44	41	—
Proximal width	23	17	18	17	14
Greatest height, with post. tuberosity	57	57	51	47	—

The posterior tuberosity of the entocuneiform projects less backward and further downward in *Diceros* and the Shungura bone than it does in *Chilotheridium*, as shown in the distal ant. post. diameter (which includes the posterior tuberosity) and in the greatest height. Except in its greatest height, the Shungura entocuneiform presents the same excess in size over its homologue in *D. bicornis* as do the L. 5/6 astragalus and calcaneum, and the Shungura bone may be confidently referred to *C. simum*.

L. 5/6-8, Shungura Member E, M^2 sin. The paracone style is completely suppressed, the parastyle raised. The protoloph is incomplete at the base of the medisinus, and most of the metaloph is missing. The height of the ectoloph is 102 mm, by a greatest anteroposterior length, high up the crown, of 60 mm, giving a height/length index of 170. The height/length index of M^2 in recent *Diceros bicornis* is 104-109; that of M^2 of *Ceratotherium praecox* (Lothagam-1 and Langebaanweg) 117-134 (Hooijer, 1972: 160). The Shungura M^2 is clearly as hypsodont as is that in modern *C. simum*: in height/length index it exceeds its homologue in *C. praecox* by one-third, as is also the case in P^4 and P_4 (Hooijer, 1972: 160, 161).

L. 5/6-46B, Shungura Member E, calcaneum sin. associated with the astragalus L. 5/6-46A of *C. simum* already recorded in table 5 of the present paper. In its measurements (table 17) it shows the same excess in size over its homologue in *D. bicornis* as does that of *C. simum*, to which it may be referred.

L. 210-22, Shungura Member E, P^4 sin., slightly worn, ectoloph height 94 mm, greatest anteroposterior ectoloph length 55 mm, indistinguishable from that in the living species.

Table 17

Measurements of calcaneum of *D. bicornis* and *C. simum* (mm)

	D. bicornis	L. 5/6-46B	*C. simum*
Greatest height	110-114	130	125
Greatest width	65-70	76	80-82
Ant. post. diameter	60-66	73	66-75

L. 465-71, Shungura Member F, fragment of left upper molar, showing medi- and postsinus of equal depth and marked posterior protocone extension.

L. 467-45, Shungura Member F, crown portions of right upper and left lower molars, like L. 465-71 indistinguishable from recent *C. simum* specimens.

L. 628-190, Shungura Member G, DM_2 dext., unworn crown, preserved height of ectoloph 41 mm; internal base incomplete. Measurements: ant. post. 35 mm, ant. transv. ca. 15 mm, post. transv. ca. 17 mm, as in *C. simum* (cf. Hooijer, 1972: 168).

L. 597-15, Shungura Member G, P_3 dext., incomplete behind basally; crown height, as worn, 70 mm. Base embedded in jaw bone, ant. post. diameter 43 mm. *C. simum*.

There remain in the Omo collection some fragmentary upper teeth without a record for the exact level: a left P^3 or P^4 and a right M^1 (?), incomplete internally. No paracone styles, medifossettes formed, medi- and postsinuses equal in depth. Greatest anteroposterior ectoloph diameter of P, at 65 mm from base (not the greatest diameter) 50 mm. These conform to the recent *C. simum*.

From Karmosit, a locality about 3.4 million years old (or a little older), Rhinocerotidae are listed by Bishop (1972: 243) without further identification. I have seen from this site a large portion of the frontal bone with a low but extensive horn boss, and also a humerus dext. lacking the part proximally of the deltoid tuberosity (the two specimens, in the collection at Bedford College, London, are marked M/800 and M/730, respectively). Both of the specimens suggest *Ceratotherium simum*: the frontal portion is of the right shape, and the humerus (table 18) conforms to *C. simum* as well.

Table 18

Measurements of humerus of *D. bicornis* and *C. simum* (mm)

	Karmosit	*D. bicornis*	*C. simum*
Least width of shaft	ca. 80	60-65	70-85
Greatest distal width	170	150-155	180
Width of trochlea	120	100-105	120

Several incomplete lower molars from Chesowanja, age probably less than 1.2 million years (Bishop, 1972: 243) represent *C. simum*. These are KNM/CE/55-57; the width can be taken only in the last: ca. 30 mm.

Paradiceros mukirii Hooijer

Very little must needs be added to what I said about this unique genus and species of the Late Miocene of Fort Ternan in Kenya (Hooijer, 1968). It is a small, two-horned, browsing rhinocerotid that differs from *Diceros bicornis* in a peculiar combination of primitive as well as progressive characters. In the former category come the teeth, which are lower-crowned (as is also the case in the Mio-Pliocene *Diceros douariensis* as we have seen above), and in the latter the more abbreviated mandibular symphysis. The humerus of *Paradiceros* is decidedly shorter than that in *Diceros* (all species), which suggests that *Paradiceros* was more of a running rhinoceros, a more swift-moving type, than is *Diceros*, another generalized feature of the Miocene form. It is, therefore, clear that *Paradiceros* does not stand in a simple, direct ancestor-descendant relationship to *Diceros*, which emerged only several millions of years later (in the classical "Pontian"), but rather represents a collateral development from the same ancestral stock as *Diceros*. This, then, strongly suggests that the origin of the *Diceros* group of rhinocerotids was in Africa, and this has been brought out in a diagram in Hooijer & Patterson (1972, fig. 11). This diagram needs just a slight correction now that we know that *Ceratotherium praecox* (see above under that head) was already there in the 7 million-year-old Mpesida Beds, antedating the appearance of this, the first *Ceratotherium*, at Lothagam-1 by a million years.

Rhinocerotidarum incertae sedis

For the sake of completeness I mention here a few fragmentary bones that defy identification beyond the family level. From the Lukeino Beds, age less than 6.7 million years, possibly older than 6 million years (Bishop, 1972: 241), no Rhinocerotidae have so far been recorded, but I found in the collection at Bedford College, London, a distal fragment of a rhinocerotid humerus, marked KYI, 21/7/67. It comprises only the medial condyle and epicondyle of a humerus dext.; the anteroposterior diameter of the condylus medialis is 115 mm, larger than in *Diceros bicornis* and possibly referable to *Ceratotherium praecox*. This is, however, clearly too little upon which to base a specific identification, and in the absence of teeth the allocation of the Lukeino Beds rhinocerotid must remain uncertain. From Arongo Uyoma, the site whence comes a brachypothere second phalanx of a median digit, there is a proximal sesamoid of a median digit (M. 29393) 45 mm long and 23 mm wide. A very similar proximal sesamoid comes from Chianda Uyoma (Hooijer, 1966: 182). These do not seem to be brachypothere, and may be associated with the non-brachypothere astragalus from Arongo Chianda that belongs to either *Aceratherium* or *Dicerorhinus* (Hooijer, 1966: 172), but a bone such as this must be left as "rhinocerotid" for the time being. An incomplete magnum sin. also from Arongo Uyoma (M. 29397) falls in the same broad category.

References

Andrews, C. W., 1900. Fossil Mammalia from Egypt. — Geol. Mag., n.s., dec. 4, 7: 401-403.

Arambourg, C., 1933. Mammifères Miocènes du Turkana (Afrique Orientale). — Ann. de Paléont., 22: 121-147, 1 pl., 5 figs.

Bishop, W. W., 1967. The Later Tertiary in East Africa — Volcanics, Sediments, and Faunal Inventary, in: W. W. Bishop & J. D. Clark (editors), Background to Evolution in Africa. Chicago & London (Univ. of Chicago Press): 31-56, 3 figs.

——, 1972. Stratigraphic succession 'versus' calibration in East Africa, in: W. W. Bishop & J. A. Miller (editors), Calibration of Hominoid Evolution. Edinburgh (Scottish Academic Press): 219-246, 7 figs.

Cooke, H. B. S., & S. C. Coryndon, 1970. Pleistocene mammals from the Kaiso Formation and other related deposits in Uganda. — Fossil Vertebrates of Africa, 2: 107-224, 18 pls., 17 figs.

Cooke, H. B. S., & V. J. Maglio, 1972. Plio-Pleistocene stratigraphy in East Africa in relation to proboscidean and suid evolution, in: W. W. Bishop & J. A. Miller (editors), Calibration of Hominoid Evolution. Edinburgh (Scottish Academic Press): 303-329, 8 figs.

Deraniyagala, P. E. P., 1951. A hornless rhinoceros from the Mio-Pliocene deposits of East Africa. — Spolia Zeylanica, 26 (2): 133-135, 1 pl.

Dietrich, W. O., 1942. Ältestquartäre Säugetiere aus der Südlichen Serengeti, Deutsch-Ost-afrikas. — Palaeontographica, 94A: 43-133, pls. III-XXIII, 2 figs.

——, 1945. Nashornreste aus dem Quartär Deutsch-Ostafrikas. — Palaeontographica, 96A: 46-90, pls. XIII-XIX, 1 fig.

Edinger, T., 1937. Ein Steinkern der Gehirn-, Nasen- und Nebenhöhlen von Chilotherium. — Bull. Geol. Inst. Uppsala, 27: 32-41, 4 figs.

Guérin, C., 1966. Diceros douariensis nov. sp., un Rhinoceros du Mio-Pliocène de Tunisie du Nord. — Doc. Labo. Géol. Fac. Sci. Lyon, 16: 1-50, 12 figs.

Heissig, K., 1971. Brachypotherium aus dem Miozän von Südwestafrika. — Mitt. Bayer. Staatssamml. Paläont. hist. Geol., 11: 125-128, 2 figs.

Heller, F., 1913. The white rhinoceros. — Smithson. Misc. Coll., 61: 1-77, 31 pls.

Hooijer, D. A., 1959. Fossil rhinoceroses from the Limeworks Cave, Makapansgat. — Pal. Africana, 6: 1-13, 4 figs.

——, 1963. Miocene Mammalia of Congo (with a chapter by A. Gautier and J. Lepersonne). — Ann. Mus. Royal de l'Afrique Centrale, Tervuren, Belgique, Sci. Géol., 46: I-IX + 1-77, 10 pls., 8 figs.

——, 1966. Miocene rhinoceroses of East Africa. — Bull. Brit. Mus. (Nat. Hist.), Geol., 13: 117-190, 15 pls.

——, 1968. A rhinoceros from the Late Miocene of Fort Ternan, Kenya. — Zool. Med., Leiden, 43: 77-92, pls. 1-3.

HOOIJER, D. A., 1969. Pleistocene East African rhinoceroses. — Fossil Vertebrates of Africa, 1: 71-98, 6 pls.

——, 1971. A new rhinoceros from the Late Miocene of Loperot, Turkana District, Kenya. — Bull. Mus. Comp. Zool., 142: 339-392, 11 pls., 1 fig.

——, 1972. A Late Pliocene rhinoceros from Langebaanweg, Cape Province. — Ann. S. A. Museum, 59 (9): 151-191, pls. 21-34.

HOOIJER, D. A., & B. PATTERSON, 1972. Rhinoceroses from the Pliocene of Northwestern Kenya. — Bull. Mus. Comp. Zool., 144: 1-26, 11 figs.

HOOIJER, D. A. & R. SINGER, 1960. Fossil rhinoceroses from Hopefield, South Africa. — Zool. Med., Leiden, 37: 113-128, pl. XI.

HOPWOOD, A. T., 1939. Contributions to the study of some African mammals. II. The subspecies of the Black Rhinoceros, Diceros bicornis (Linnaeus), defined by the proportions of the skull. — Journ. Linn. Soc. (Zool.), London, 40: 447-457, 2 pls.

HOWELL, F. C., 1972. Pliocene/Pleistocene Hominidae in Eastern Africa, absolute and relative ages, in: W. W. Bishop & J. A. Miller (editors), Calibration of Hominoid Evolution. Edinburgh (Scottish Academic Press): 331-368, 8 figs.

ISAAC, G. L., R. E. F. LEAKEY & A. K. BEHRENSMEYER, 1971. Archaeological traces of Early Hominid Activities, East of Lake Rudolf, Kenya. — Science, 173: 1129-1134, 4 figs.

LE GROS CLARK, W. E., & L. S. B. LEAKEY, 1951. The Miocene Hominoidea of East Africa. — Fossil Mammals of Africa, 1: I-V + 1-117, 9 pls., 28 figs.

MACINNES, D. G., 1951. Miocene Anthracotheriidae from East Africa. — Fossil Mammals of Africa, 4: 1-24, 4 pls., 2 figs.

MAGLIO, V. J., 1971. Vertebrate faunas from the Kubi Algi, Koobi Fora and Ileret areas, East Rudolf, Kenya. — Nature: 231 (no. 5300, May 28): 248-249.

RINGSTRÖM, T., 1924. Nashörner der Hipparion-Fauna Nord-Chinas. — Pal. Sinica, C, 1 (4): 1-156, 12 pls., 92 figs.

STROMER, E., 1926. Reste Land- und Süsswasser-bewohnender Wirbeltiere aus den Diamantfeldern Deutsch-Südwestafrikas, in: E. Kaiser, Die Diamantenwüste Sudwest-Afrikas. Berlin (D. Reimer), 2: 107-153, pls. 40-42, 6 figs.

THENIUS, E., 1953. Studien über fossile Vertebraten Griechenlands. III. Das Maxillargebiss von Ancylotherium pentelicum Gaudry und Lartet. — Ann. Geol. Pays Helléniques, 5: 97-106, 1 fig.

VONDRA, C. F., G. D. JOHNSON, B. E. BOWEN & A. K. BEHRENSMEYER, 1971. Preliminary stratigraphical studies of the East Rudolf Basin, Kenya. — Nature, 231 (no. 5300, May 28): 245-248, 3 figs.

WALKER, A., 1968. The Lower Miocene fossil site of Bukwa, Sebei. — Uganda Journ., 32: 149-156, 1 pl., 2 figs.

——, 1969. Fossil mammal locality on Mount Elgon, Eastern Uganda. — Nature, 223 (no. 5206, Aug. 9): 591-593.

Explanation of the Plates

Plate 1

Ceratotherium praecox Hooijer & Patterson

Fig. 1. P^3 sin., KNM/AT/155, Aterir Beds, crown view. × 0.6.
Fig. 2. M^1 dext., KNM/AT/156, Aterir Beds, crown view. × 0.5.
Fig. 3. M^1 dext., KNM/AT/157, Aterir Beds, crown view. × 0.6.
Fig. 4. P^4 dext., KNM/BC/417, Chemeron Fm., crown view. × 0.6.

Brachypotherium heinzelini Hooijer

Fig. 5. M_3 dext., KNM/BC/414, Chemeron Fm., crown view. × 0.6.
Fig. 6. Same, external view. × 0.5.
Fig. 7. M_3 dext., Napak II C, 1965, external view. × 0.5.
Fig. 8. Same, crown view. × 0.6.
Fig. 11. M^3 dext., Napak II C, 1965, external view. × 0.5.
Fig. 12. Protoloph of M^3 dext., Napak II C, 1965, posterior view. × 0.5.

Chilotheridium pattersoni Hooijer

Fig. 9. Right upper molar, M. 15049, Ombo, crown view. × 0.5.
Fig. 10. M^{2-3} dext., M. 29427, Ombo, crown view. × 0.6.

Brachypotherium lewisi Hooijer & Patterson

Fig. 13. Part of lower molar, KNM/MP/131, Mpesida Beds, external view. × 0.5.

Plate 2

Dicerorhinus leakeyi Hooijer

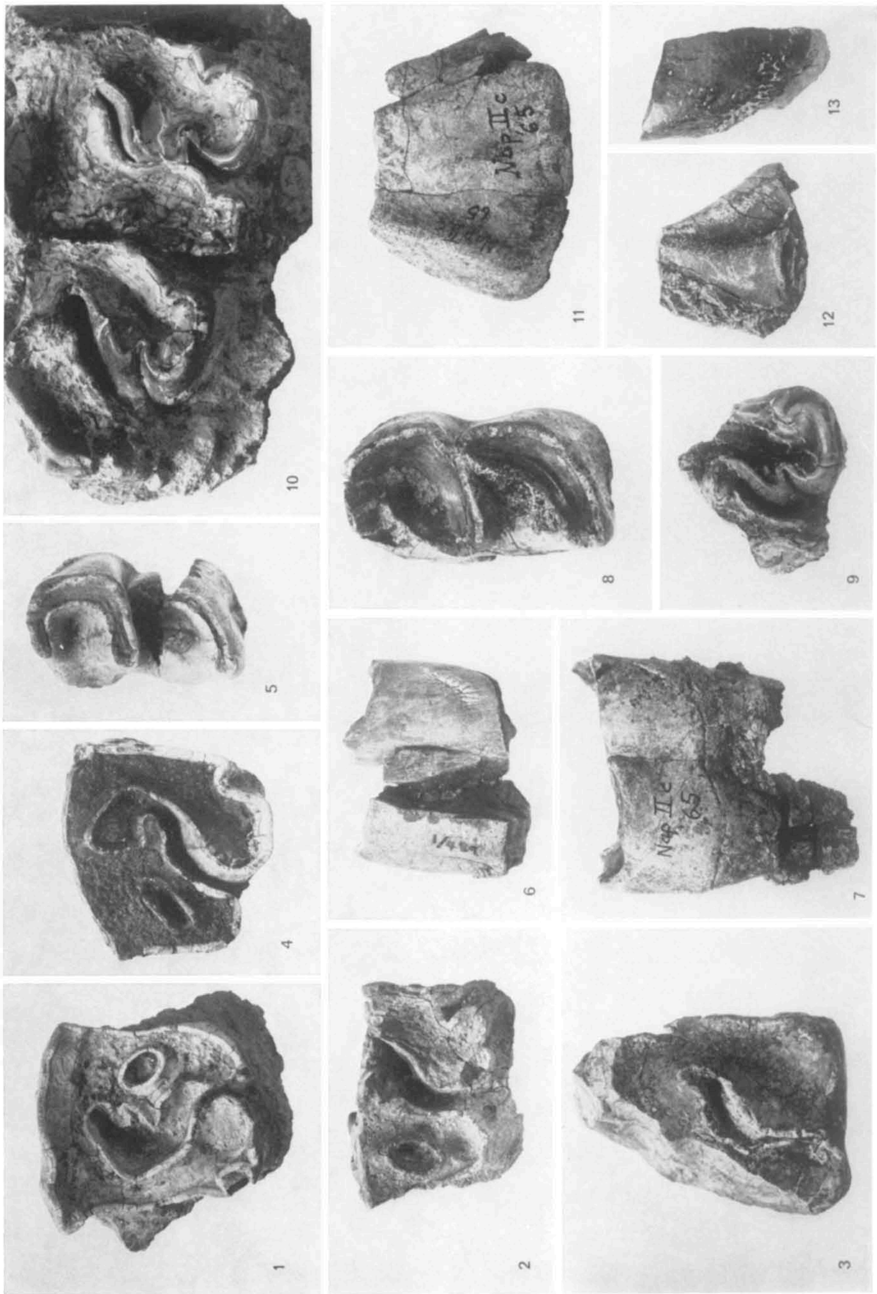
Fig. 1. P^4-M^1 sin., M. 29426, Ombo, crown view. × 0.7.
Fig. 2. M^2 dext., KNM/BC/416, Chemeron Fm., crown view. × 0.8.
Fig. 3. P^2 sin., KNM/BC/375, Chemeron Fm., crown view. × 0.7.
Fig. 4. P^2 sin., KNM/BC/374, Chemeron Fm., crown view. × 1.0.

Brachypotherium heinzelini Hooijer

Fig. 5. P_2 dext., KNM/BC/415, Chemeron Fm., crown view. × 0.7.
Fig. 6. Same, external view. × 0.7.

Ancylotherium hennigi (Dietrich)

Fig. 7. P^4 dext., KNM/BC/376, Chemeron Fm., external view. × 0.7.
Fig. 8. Same, crown view. × 0.7.
Fig. 9. Same, internal view. × 0.7.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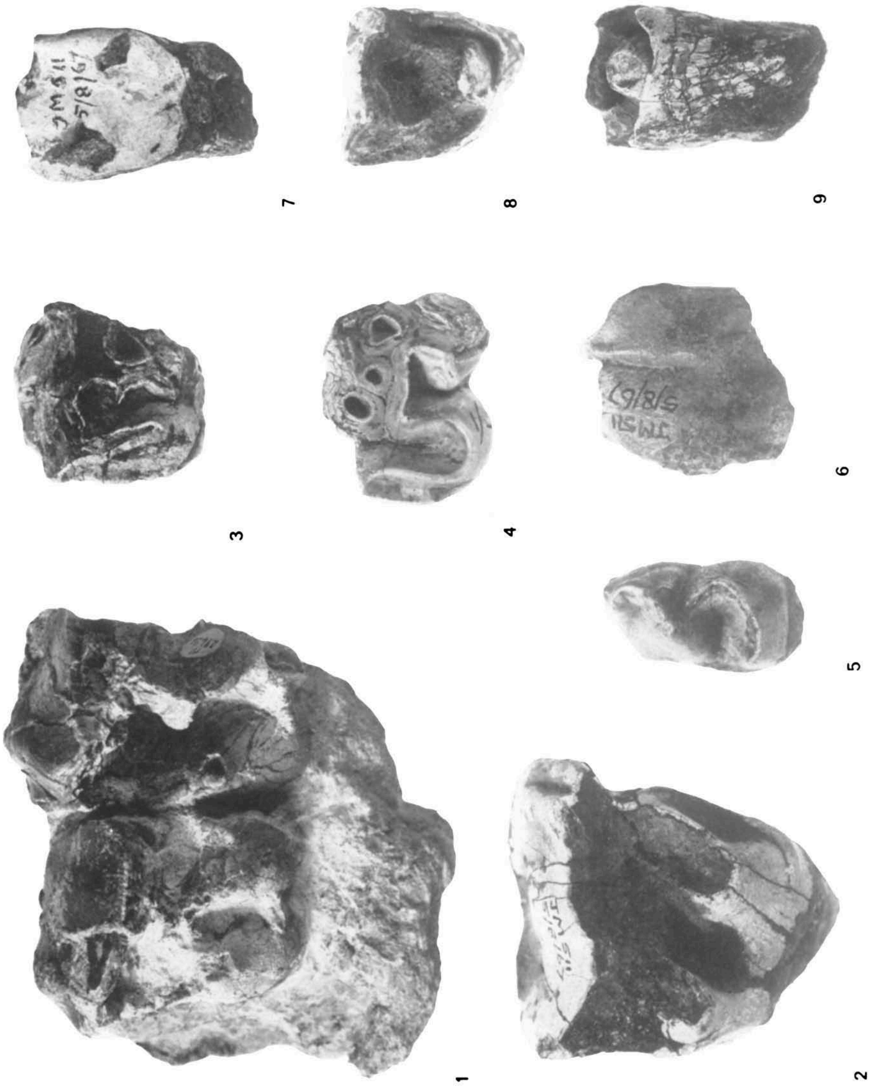
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