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PLEISTOCENE EAST AFRICAN RHINOCEROSES

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INTRODUCTION

Though a good few names have been given, there are virtually only two species of rhinoceroses in the Quaternary of East and South Africa. These are the black rhinoceros *Diceros bicornis* (L.) and the white rhinoceros *Ceratotherium simum* (Burchell). The former a browser, the latter a grazer, the skulls appear markedly distinct; yet from the specializations among the Pontian (Early Pliocene) forms of *Diceros* it seems likely that the emergence of *Ceratotherium* from the *Diceros* stock took place only in the Pliocene (Thenius, 1955). By Early Pleistocene times the two living forms had already diversified, and their teeth are nearly as distinct as those in modern skulls. The distinction is most easily made in the permanent upper dentition, and the milk dentition shows progressive divergence in pattern as we pass backward along the series (Hooijer, 1959). *Ceratotherium simum* is the hypsodont form, with much cement on the teeth, and with the transverse lophs in the upper

molars (protoloph and metaloph) obliquely placed, recurved backward. This does not show in *Diceros bicornis*, which also has less high-crowned teeth.

In the Early Pleistocene form of *Ceratotherium simum* protoloph and metaloph are less oblique, the metaloph in fact still transverse in its course, and there is evidence that the crowns were not quite as high as those at present either. This has already been demonstrated by various authors. As we shall see in the present paper *Diceros bicornis* also displays a trend toward progressive hypsodonty in the course of the Quaternary. The evidence is scanty, resting upon a few isolated observations, and we could do with a great deal more material, but the trends are evident. There is subspecific advance at least in the teeth of both of the extant African species of rhinoceros. The history of them is one sad story of slaughter, intensified by the demand for their horns which are highly valued for their supposedly aphrodisiac properties in the Far East, where the Asiatic species of rhinoceros are so rapidly becoming exterminated that horns are much harder to come by.

Diceros bicornis, the least threatened species with a number of individuals of well over 10,000, shows some geographic variation, which has recently been reported by Groves (1967, p. 270) thus: "A single widespread race is indicated, distributed from Transkei in the south to Lake Victoria in the north, with a very large race at the Cape, another large one on the Chobe river, two smaller ones respectively in East Africa to the east of the Rift Valley and in West Africa, and a large broad-skulled one to the northwest of the Kenya distribution." Such a pattern of geographic subspeciation must have existed at any time in the Pleistocene as well, but most of the meagre material that we have in the way of fossils are teeth, in which these racial differences do not show.

Ceratotherium simum, not even 2,000 individuals of which survive today, has a discontinuous historic distribution area: south of the Zambesi, and then again in Equatorial Africa west of the Nile (maps in Heller, 1913, pl. 10, and Guggisberg, 1966, p. 79). There is remarkably little difference between these recent geographical forms: this concerns mainly the greater depth of the dorsal concavity of the adult skull in the South African specimens (at least 60 mm as compared with 50 mm or less in the Lado Enclave specimens), and further the greater length of the permanent toothrow in the South African specimens, averaging about 300 mm as against 270 mm in the northern skulls (Heller, 1913, p. 30). An adult Leiden Museum skull from the Cape (cat. ost. b) bridges the gap, with a depth of dorsal skull concavity of 55 mm. The difference in average length P^2–M^3 is trivial, and no indication of general size, as the overall length of the toothrow decreases during life as a result of interproximal wear. A subadult skull from the Cape in the Leiden Museum (cat. ost. a, Van Horstok, August, 1831) has 250 mm for the length P^2–M^2 in a slightly worn state (M^3 erupting), whereas in cat. ost. b, in which the teeth are well worn (including M^3) the length P^2–M^2 has reduced to 210 mm, a difference of 40 mm. Such differential characters as have been advanced are hardly worthy of subspecific distinction, yet

the two subspecific names, *C. simum simum* (Burchell) for the southern, and *C. simum cottoni* (Lydekker) for the northern form, are being universally upheld in the literature to this day.

The South African remains of Quaternary rhinoceroses known to date have been revised by Cooke (1950), and the Late Pleistocene remains of the black and the white rhinoceros from Hopefield, Cape Province, have been described by Hooijer and Singer (1960). In Late Pleistocene deposits the black rhinoceros is the common form, and the white rhinoceros rare. Contrariwise, in the Early Pleistocene Makapansgat Limeworks Cave collection (Hooijer, 1959) the white rhinoceros predominates. The collection from this australopithecine site is very remarkable in that it consists almost exclusively of milk molars, most of them unworn or hardly touched by wear. This is an indication that it was mainly sucklings that became fossilized in this cave; such a concentration of milk teeth has not before been recorded from any rhino site, in Africa or elsewhere. To me it seems evidence that *Australopithecus* was capable of a high level of cooperative behaviour for hunting; this only corroborates the views on the cultural status of the australopithecines currently based on other evidence. No differences between the Pleistocene and the Recent teeth were found apart from a tendency for the fossil teeth to be larger than the corresponding modern, which is a common phenomenon (Hooijer, 1950).

Turning now to the East African Pleistocene record, both the black and the white rhinoceros have been found at Olduvai Gorge, Tanzania. *Diceros bicornis* does not occur in the lower portion, the Early Pleistocene Bed I and Lower Bed II, but is found only higher up. It does occur in the Early Pleistocene of Makapansgat in South Africa, though sparingly, and, as we shall see in the sequel, we now have evidence of its presence in the Early Pleistocene deposits of the Omo Basin in Ethiopia as well. This early form of *D. bicornis* differs from the extant form only in being slightly larger-toothed, and less hypsodont. We know nothing of its skull characters yet. The modern genus *Diceros* appears first in the Early Pliocene, in North Africa as well as in Europe. I have recently described a small, extinct rhinoceros from the Late Miocene of Fort Ternan, Kenya, that appears to be a collateral development of a browsing, bicorn rhinoceros, differing from *Diceros* in a combination of primitive and progressive features: *Paradiceros mukirii* Hooijer (1968). It is more advanced than the Early Miocene forms previously described (Hooijer, 1966).

The white rhinoceros ranged all over the African continent in the Pleistocene. The North African "*Rhinoceros mauritanicus*" of Pomel's, as Arambourg (1938, p. 22) has shown, is inseparable from *Ceratotherium simum*. The name *mauritanicum* should, however, remain available and used if and when a find of an entire skull of the Moroccan white rhinoceros would eventually prove it to be distinguishable from the living (sub)species. Arambourg (l.c.) stated it to be closer to the typical (southern) than to the Equatorial form in its great toothrow length (one observation: 300 mm), but this does not carry any weight as indicating any closer actual

relationship of the Moroccan fossil with the South African rather than with the northern recent form, the size difference between which is trivial at any rate, as we have seen above. Moreover, Pleistocene remains of living mammalian species generally being on the large side, their measurements are bound to agree better with the larger than with the smaller of the observations on the living forms.

One of the new fossil forms described from Olduvai Gorge as a result of the German expedition of 1913 was *Rhinoceros simus germanoafricanus* Hilzheimer (1925), based on an incomplete skull and mandible. As has already been shown by Zeuner (1934, p. 63), the Olduvai white rhino is not more primitive in cranial features than the extant form. It is not known from which level at Olduvai the type specimen came; Leakey (1965, p. 25) writes that from the illustrations it seems that it may have come from deposits younger than Bed IV. However, the upper molars of *germanoafricanum* do differ from those of the living white rhinoceros: the metaloph is transverse in its course, and the protoloph at its origin is nearly perpendicular to the ectoloph and recurved backward only distally.

These peculiar characters clearly shown in Hilzheimer's illustration (reproduced in Arambourg, 1947, p. 299, fig. 24) are just the same as those found by Dietrich (1942, 1945) to be typical of the Early Pleistocene rhinoceros from Laetolil, Tanzania, which was baptized *Serengeticeros efficax* Dietrich. The resemblance in molar structure has been noticed by Arambourg (1947, p. 300) in his discussion of the Omo white rhinoceros, which also differs from the modern form in being less plagiolophodont, and he refers to the Omo form as *Atelodus* cf. *germanoafricanus*. Dietrich (1945, p. 56) based his diagnosis on the upper molars exclusively, the cranial characters being unknown, and did not fail to mention (Dietrich, 1945, p. 68) that the molars of Hilzheimer's skull could very well belong to *Serengeticeros*. A comparison between Dietrich's 1945 illustrations of the upper molars and Hilzheimer's figure indicates the virtual identity in molar patterns of the Olduvai and the Laetolil fossil rhinoceros.

These are not the only Early Pleistocene sites whence this primitive type of *Ceratotherium simum* molar comes: Hopwood (1926) described as *Rhinoceros scotti* an M^2 sin. from the Kaiso Beds of Uganda that is indistinguishable from *C. simum* but displays the primitive characters of the Laetolil and Omo molars (Hopwood, 1926, p. 17, fig. 3), as remarked by Dietrich (1945, p. 51) and by Arambourg (1947, p. 301).

Neither Arambourg (1947, p. 300) nor Leakey (1965, p. 25) deem it necessary to uphold the genus *Serengeticeros* of Dietrich's. Neither do I consider the difference between the (Early) Pleistocene and the living white rhinoceros to be of generic, or even specific value. It seems that subspecific distinction is the most that can be accredited to the Early Pleistocene stage of *C. simum*, which has been recognized, as we have seen, under three different names, at Kaiso, Laetolil, Olduvai, and Omo. The name that has priority is *germanoafricanum* Hilzheimer, 1925, antedating *scotti* Hopwood by one, and *efficax* Dietrich by seventeen years.

In his preliminary report on the Olduvai fauna, Leakey (1965, p. 25) writes that some Bed I and lower Bed II specimens seem to be *Ceratotherium efficax*, whereas a number of specimens from upper Bed II and Bed IV are placed under *Ceratotherium simum germanoafricanum*. I believe we cannot really differentiate the two, and that the name by which the primitive, Early Pleistocene stage should be known is *Ceratotherium simum germanoafricanum* (Hilzheimer), the name *efficax* Dietrich falling away as a synonym. Besides in being less plagiolophodont than the recent form, it is also slightly less hypsodont: Dietrich (1945, p. 59) mentions that the height of M^3 of "*Serengeticeros*" (reconstructed) is 85 mm as opposed to some 120–130 mm in the Late Quaternary *Ceratotherium*. Dietrich's reconstruction may be a little too low, although there remains a difference. An Omo M^3 is stated by Arambourg (1947, p. 297) to be close to 10 cm in height.

Rhinoceros specimens from Olduvai Gorge are present in great numbers at the National Museum Centre for Prehistory and Palaeontology in Nairobi, where I had the opportunity to study them in the summer of 1967 through the courtesy of Dr. L. S. B. Leakey. This study was aided by a grant from the Wenner-Gren Foundation for Anthropological Research, Inc., New York. N.Y. I have also included Olduvai material in the British Museum (Natural History) in London; Dr. A. J. Sutcliffe and Mrs. S. C. Coryndon, F. L. S., kindly made these specimens available. Surface material that cannot be allocated to any level in particular has been left out of account, unless the specimen is particularly well-preserved.

There is further rhinoceros material from the Early Pleistocene of Laetolil, Tanzania, at the Nairobi Centre as well as at the British Museum (Natural History). The rhinoceros specimens obtained in the Omo Basin, southern Ethiopia, by the Kenyan, French, and American parties working there in the summer of 1967 have also been studied by me; preliminary accounts of the results of the field work, with some faunal data, have recently been published (Arambourg *et al.*, 1967; Howell, 1968). Dr. W. W. Bishop has allowed me to study the rhino material from the Chemeron Formation, Lake Baringo, Kenya (see Martyn and Tobias, 1967). Finally, some material has been included originating from Kanam West, Naivasha, and Olorgesailie. I am grateful to all who have made this material available for study, and to Mrs. J. G. Ament who made the photographs.

CHEMERON FORMATION, LAKE BARINGO, KENYA

A skull of *Ceratotherium* found *in situ* in the Basal Beds of the Chemeron Formation, Lake Baringo (J.M.91) and a maxillary portion holding the much worn M^{1-3} sin. from the Lower Fish Beds of the same Formation (J.M.507) have been examined by me at the Nairobi Centre in 1967 through the courtesy of Dr. W. W. Bishop. The mammalian fauna as a whole, as Leakey (in Martyn and Tobias, 1967, p. 477) observed, is strongly suggestive of that from strata attributed to the Early Villa-

franchian. Both the skull and the palate indeed display the features of the primitive *Ceratotherium simum* described by Dietrich from Laetolil, here named *C. simum germanoafricanum* (Hilzheimer).

The skull (Pl. **1**, figs. 1–2) unfortunately is rather distorted, and lacks the front part; P^3 dext. is the foremost tooth preserved. The palate is broken, and the left molar series pushed inward, M^1 mostly so, but the posterior border of the palate is on a level with that of M^2, as in the modern form. Only the right zygomatic arch and the right half of the occiput are preserved. The postglenoid processes are present, but the posttympanic processes broken off. The dorsal surface of the skull is missing. Very few measurements can be taken from a skull in this state of preservation (Table VIII); the bicondylar width is no larger than in recent skulls of *C. simum*, and the zygomatic width, which can be approximately taken, is about as large as in the largest recent skulls measured by Heller (1913: 373 mm and 384 mm, both old with M^3 worn). Despite the deformations, the fossil skull appears to have the same backwardly inclined occiput by which the modern form is characterized, and cranial differences from recent *C. simum* are not apparent.

With the molars, however, it is a different matter. As can be seen most distinctly in the M^1 but also in the premolars and M^2 the metaloph is not oblique but rather transversely placed, while the backward recurvation of the protoloph is less marked than that in modern dentitions, i.e., the "*Serengeticeros*" characteristics discussed above. Moreover, the slightly worn M^3 of the Chemeron skull appears to be less hypsodont than that of the modern form. Although the outer surface is exposed only for a height of 45 mm, it can be compared with other specimens and this comparison tends to show that the sides of the crown converge more markedly crownward in the Chemeron sample than in the others.

The outer surface of M^3 of skull J.M.91 has an anteroposterior length at the alveolar border of 68 mm (this is not the actual base of the crown yet). The length at the occlusal surface, which is 45 mm higher up the crown, is only 38 mm, giving a decrease in outer surface length of 30 mm. Two recent M^3 of *Ceratotherium simum* examined show that the crownward taper of the sides of the outer surface over a height of 45 mm is decidedly less, as follows. The M^3 of a southern skull (Leiden Museum, cat. ost. b) has an exposed portion of just 45 mm in height, and the anteroposterior diameter of the outer surface is 73 mm basally, and 62 mm apically, giving a decrease of 11 mm. Another recent M^3, in a skull from the Western Nile District, Uganda (Leiden Museum, reg. no. 13120), has an anteroposterior diameter of the outer surface at base of 68 mm, which has reduced to 58 mm 45 mm higher up, giving a decrease of 10 mm. Thus, although actual crown heights cannot be given, the fossil M^3 is seen to be less hypsodont than the modern.

It is of interest to note that two Olduvai Bed II specimens of M^3, which will be listed later, when measured in the same way, prove to be intermediate between the Chemeron M^3 and the recent in degree of crownward taper, while a Bed IV Olduvai

specimen conforms to the recent type. The Bed II specimens are M.14810, an M^3 dext., and OLD/57, SHK II, 181, an M^3 sin., with a decrease in outer surface length over 45 mm of height of 20–22 mm. The Bed IV specimen, OLD/55, BK II, 95, an M^3 sin., tapers only 5 mm in anteroposterior outer surface length over a height of 45 mm. These few observations point to progressive heightening of the crown of M^3 of *C. simum* from Early Pleistocene to Recent.

The maxillary portion from the Chemeron Formation (J.M.507) holds only the three molars, from the left side, and in M^2 the transverse position of the metaloph is clearly seen (Pl. **2**, fig. 1). While it is characteristic of *C. simum* molars for the crochet to unite with the crista so as to form a medifossette, exceptions do occur, and the present specimen is such an exception: the crochet extends across the medisinus without uniting with the crista. The molar is very much worn down, and the medisinus is cut off from the internal border of the crown. Of the M^3 in the same specimen, worn down to a few mm from the crown base, only the central part and a small portion of the anterior face remain. The medisinus is likewise closed off internally, but the crochet extends completely across the valley, making for an elongated fossette. No further observations on this specimen can be given.

The Chemeron specimens, therefore, in their transverse position of the metaloph of the upper molars, agree with the Laetolil form, and can be identified as *C. simum germanoafricanum* just as the Olduvai, Omo, and Kaiso material discussed above. Although no cranial differences between the fossil and the living form have been observed, the degree of hypsodonty in the fossil form is less advanced than in the recent, as the observations on M^3 have shown.

OLDUVAI GORGE, TANZANIA

Remains of rhinoceroses come from all levels at Olduvai. Most of it is teeth or parts of teeth of *Ceratotherium simum*; some specimens represent *Diceros bicornis*, and this has been marked as such in the lists that follow. The postcranial bones I have been unable to identify specifically; the two recent species are extraordinarily close osteologically although the white is the larger, which is of little help when dealing with Pleistocene bones. Tables of measurements of the postcranial skeletal remains are given at the end of the present paper; the recent skeletons of *C. simum* and *D. bicornis* compared are in the National Museum Centre for Prehistory and Palaeontology Department of Osteology, and their measurements have been given also in cases in which there were no corresponding bones in the fossil collection; they may be needed later.

The Olduvai material originates from the following sites (M. D. Leakey, 1965, and personal communication):

DK I—Lower Bed I; FLK NN—Mid Bed I; KK I—Bed I; MTK I—Bed I; MTK—Bed I or II; HWK(E)II—Lower Bed II; FLK II—Upper Bed II; EF-HR—Upper

Bed II; FC II—Upper Bed II; MNK II—Upper Bed II; SHK II—Upper Bed II; BK II—Upper Bed II; TK II—Upper Bed II; JK2, Geol. Pit 8—Bed III; JK2/A—Bed III or IV; JK2/B—Bed III or IV; MRC—Bed IV; Rhino Korongo—Bed IV; CMK—Bed IV.

The lower part of Bed II is separated from the upper part by a geological break; the lower part of Bed II belongs with Bed I to the Early Pleistocene (Late Villafranchian), and the upper part of Bed II up to Bed IV represents the Middle Pleistocene (Leakey, 1965, p. 78). It has been found that some upper teeth from Bed I agree full well with the primitive type of *C. simum* as described from Laetolil by Dietrich (and earlier by Hilzheimer from Olduvai), and that the dentition of the Bed IV skull is of the same advanced type as that in modern skulls of *C. simum*. The transformation of the Early Pleistocene *Ceratotherium simum germanoafricanum* teeth into those of the modern form was in all probability a gradual process, taking perhaps several hundred thousand years. The material that we have covering this time interval, in the succession of deposits at Olduvai, is extensive, but limb bones and lower teeth as well as fragmentary uppers are of no avail in determining the stage of evolution of the white rhinoceros. Relatively few specimens remain that are characteristic one way or another. It has been shown that two specimens of M^3 from Olduvai Bed II are intermediate between that of the Early Pleistocene Baringo white rhino on the one hand, and the modern M^3 on the other. One of the Bed II specimens comes from the upper part of Bed II, while the position of the other M^3 in Bed II is unknown. Should such specimens be referred to *C. simum germanoafricanum* to *C. simum simum*, or should they be given a new name to designate an intergrading form between the two? I do not consider it expedient to follow the last course. As always in studies of clinal variations in time, the problem arises of how to name the intermediate stages, in so far as they can be recognized in the material available. I believe the best we can do is to indicate the forms transitional between *germanoafricanum* and *simum*, if need be, by a bifid racial terminal (cf. Harrison, 1945), thus:

Ceratotherium simum — *C. s. simum* (Burchell)
Ceratotherium simum — *C. s. germanoafricanum* (Hilzheimer)

Bed I

OLD/60, FLK NN, M^1 or M^2 sin., damaged anteriorly and at the corners. The medifossette is closed by the union of crochet and crista, the postfossette closed off behind, and the medisinus still open internally. The metaloph is transverse, as in the Laetolil molars figured by Dietrich (1945, Pl. XIII, figs. 1 and 6). The greatest (anterior) basal width of the molar is about 85 mm, at least 10 mm more than that in any recent skull in which this measurement can be taken (Pl. **2**, fig. 2).

OLD/63, DK I, 4199, portion of DM^2 sin.
OLD/63, DK I, III/10, ectoloph fragment.
B.M. (N.H.), M.14805, P^2 dext. and sin. (1931).
OLD/63, DK I, II/1, 3068, DM_3 dext., length ca. 40 mm.
B.M. (N.H.), M.14808, right mandibular ramus with broken molars.
OLD/41, S.I, F 496, scaphoid sin.
OLD/55, FLK, scaphoid sin., incomplete anteriorly.
OLD/41, S.I, F 520, scaphoid sin., incomplete basally.
OLD/62, DK I, 259, cuneiform dext., incomplete laterally.
OLD/59, KK I, 298, unciform sin.
OLD/62, DK I, 449, unciform dext.
OLD/61, DK I, 28, unciform dext.
OLD/41, S.I, F 861, metacarpal II dext.
OLD/59, MTK I, 97, metacarpal III dext.
OLD/59, MTK I, 98, metacarpal III sin., incomplete proximally.
OLD/41, S.I, F 850, metacarpal III sin., distal end missing.
OLD/62, S.I, a little west of THC, metacarpal III sin., damaged proximally.
OLD/59, FLK, 523, proximal portion of metacarpal III dext.
OLD/62, DK I, 403, metacarpal IV dext.
OLD/61, FLK NN, phalanx I, median digit, length 45 mm, prox. width 63 mm.
OLD/59, KK I, 493, phalanx I, lateral digit, length 41 mm, prox. width 40 mm.
OLD/41, S.I, F 822, phalanx III, median digit, length 26 mm, prox. width 86 mm.
OLD/60, FLK NN, astragalus dext.
OLD/59, FLK, 522, astragalus sin.
OLD/41, S.I, F 486, calcaneum dext., incomplete.
OLD/60, FLK NN, cuboid dext., incomplete.
OLD/60, FLK NN, Tr.II, navicular dext.
OLD/62, FLK NN, Tr.IV, 8849, ectocuneiform sin.
OLD/41, S.I, F 514, ectocuneiform dext.
OLD/52, DK I, 69, metatarsal III dext. without distal end.

Bed I or II

OLD/59, MTK, 105, scaphoid dext.
OLD/41, S.2, 781A, astragalus dext.
OLD/59, FLK I–II, 637, distal portion of lateral metapodial.

Bed II

B.M. (N.H.), M.14810, M^3 dext., marked Bed II, has a length of outer surface at base of 78 mm. It is worn to a height of 90 mm from the base, and the occlusal length is 48 mm. The level of 68 mm outer surface length is half way up the crown (45 mm from the occlusal edge), giving a decrease in length of 20 mm over a height

of 45 mm (30 mm in the Baringo, and 10–11 mm in two recent M^3, see p. 76). B.M. (N.H.), DM_4 dext., marked II S, 15/5/35, has a length of 49 mm.

Bed II, Lower part

OLD/62, HWK E II, 581, fragment of right upper molar.
OLD/62, HWK E II, 843, atlas, associated with some other cervical vertebrae. The atlas is only slightly damaged apart from lacking part of the left wing. The greatest height is 145 mm, the width over the condyle facets 155 mm. The axis (no. 804) has an anterior articular facet width of 150 mm and a greatest (posterior) height of 190 mm; the transverse processes are for the most part missing. The third cervical vertebra (no. 805) is in two parts: the dorsal arch detached from the body. Cervicals 4 and 5 (nos. 812 and 799) are in one piece though their processes are incomplete. The specimens articulate very well and would seem to represent a single individual. They conform in shape and gradation in characters to those in recent skeletons.
OLD/54, HWK II, 400, radius dext., without the distal end.
OLD/62, HWK E II, 247, metacarpal III sin.
OLD/62, HWK II, 791, left half of pelvis, with the ilium partially preserved, the acetabulum entire, and the symphysial border of the obturator foramen missing. Of the right half (no. 795) the acetabular portion and the ischial branch only are preserved.
OLD/59, HWK II, 432, distal end of fibula sin.
OLD/–, HWK E II, 820, patella sin.
OLD/62, HWK E II, 234, astragalus dext.

Bed II, Upper part

Diceros bicornis. OLD/63, MNK II I/1, 460, internal portion of an M^1 dext. This specimen, in the transverse position of the protoloph, absence of medifossette, and shallow postsinus clearly belongs to the black rhinoceros.
Diceros bicornis. OLD/63, MNK II III/1, 2365, unworn crown of DM_4 sin. Length 45 mm, width at base ca. 23 mm, conforming to its homologue in the black rhino.
Diceros bicornis. B.M. (N.H.), P^4 dext., marked FLK II S, 2/7/35, anterior width ca. 65 mm, evidently represents the black rhinoceros.
Diceros bicornis. OLD/52, BK II, 281, anterior outer fragment of left upper molar the paracone style development of which shows that it represents this species.
OLD/59, FLK II, 705C, P^3 sin., incomplete behind.
OLD/59, FLK II, 705D, fragment of left upper molar.
OLD/63, FLK II, Tr.I, ectoloph portion.
OLD/59, FLK, S.23, proximal portion of metacarpal III dext.
OLD/59, FLK, 522, astragalus sin.
OLD/63, FC II, P^3 dext., anterior width 63 mm, posterior width 60 mm (Pl. **2** fig. 5).

OLD/63, EF-HR, 211, fragment of right lower molar.
OLD/63, MNK II SK, 140, shaft and distal end of humerus dext.
OLD/63, FC II, 108A, proximal part of humerus sin.
OLD/63, MNK II SK, 1, ulna dext., olecranon incomplete.
OLD/63, MNK II, 3295, calcaneum sin., incomplete.
OLD/57, SHK II, 181, M^3 sin., slightly worn, actual height 102 mm externally. The length of the outer surface at base is 71 mm. At 45 mm above the level of 68 mm anteroposterior length (cf. p. 76) the length of the outer surface is 46 mm, giving a decrease of 22 mm (Pl. **5**, fig. 3).
OLD/63, BK II, 1064, M^1 sin., damaged antero-externally. Basal width 73 mm anteriorly, and 60 mm posteriorly (Pl. **2**, fig. 3).
OLD/63, TK II, 2622, M^1 or M^2 dext., incomplete internally and externally; anterior width ca. 70 mm (Pl. **2**, fig. 4).
OLD/63, TK II, 2833, P^3 dext., anterior width 60 mm.
OLD/–, BK II, M^3 sin., incomplete behind.
OLD/57, SHK II, 161, central portion of upper molar.
OLD/53, BK II, area C, posterior portion of M^3 sin.
OLD/52, BK II, 280, portion of left upper premolar.
OLD/57, BK II, 650, incomplete P^2 sin., width ca. 40 mm.
OLD/67, BK II, P^1 dext.
OLD/57, BK II, 1015, P^3 sin., incomplete antero-externally; width 60 mm.
OLD/57, BK II, 980, P^3 dext., anterior width 54 mm.
OLD/52, BK II, 279, P^2 sin., incomplete; width ca. 40 mm.
OLD/63, TK II, 2075, P^2 sin., width ca. 40 mm.
OLD/63, BK II, 785, anterior portion of DM^3 dext.
OLD/53, BK II Ex., 367, DM^3 sin., good specimen. The medifossette and postfossette pits, exposed at the broken base of the crown, are of the same depth. Although the tooth is worn, the greatest ectoloph length can be taken, and this is within the variation limits of the Makapansgat DM^3 of *C. simum*, exceeding that in a recent specimen (Table I).

TABLE I

Measurements of DM^3 of *Ceratotherium* (mm)

	Makapansgat	OLD/53, BK II 367	Recent
Greatest length ectoloph	54–61	59	53
Anterior width	48	52	46
Posterior width	46	42	44

OLD/63, BK II, 764, P^2 dext., width ca. 40 mm.
OLD/63, TK II, 2472, DM^1 sin.
OLD/57, SHK II, 112, fragment of upper molar.
OLD/63, BK II, 830, ectoloph portion.
OLD/63, BK II, 630, ectoloph portion.
OLD/63, BK II, area C, fragment of upper molar.
OLD/57, SHK II, S421, medifossette of upper molar.
OLD/53, SHK II, 298, P_{3-4} dext., much worn, in jaw fragment.
OLD/57, BK II, 487, left lower premolar, much worn down.
OLD/57, BK II, 488, M_2 dext., length 54 mm.
OLD/55, BK II, 59, P_3 sin., length 38 mm.
OLD/53, BK II, 366, left lower premolar, worn down to base.
OLD/63, TK II, 2356, incomplete right lower molar.
OLD/57, SHK II, 106, P_1 dext., length 28 mm.
OLD/57, SHK II, 296, fragment of lower molar.
OLD/63, TK II, 2463, fragment of left lower premolar.
OLD/57, SHK II, 245, broken lower molar.
OLD/57, BK II, 1451, juvenile mandible with DM_{1-4} *in situ*.
OLD/63, BK II, 2295, right half of mandible with DM_{2-4}, M_1 erupting. Length from condyle to front 490 mm, height of body at DM_4 130 mm. Tooth measurements hardly differ from those of the foregoing specimen (Table II).

TABLE II

Measurements of lower milk teeth of *Ceratotherium* (mm)

	BK II 1451	BK II 2295
DM_1, ant. post.	25	—
transv.	13	—
DM_2, ant. post.	34	32
transv.	17	17
DM_3, ant. post.	41	38
transv.	22	21
DM_4, ant. post.	48	48
transv.	27	23

OLD/63, TK II, 2452, proximal portion of scapula dext.
OLD/53, BK II Ex., 438, proximal portion of scapula sin.
OLD/63, BK II, 3122, proximal portion of scapula dext., utilized.
OLD/63, BK II, 1974, humerus dext., incomplete at either end.
OLD/63, BK II, 3014B, medial distal condyle of humerus dext.
OLD/53, BK II, Ex., proximal portion of radius dext.

OLD/55, BK II, 127, unciform dext., posterior process incomplete.
OLD/57, SHK S, 95, phalanx I, median digit, length 34 mm, prox. width 44 mm.
OLD/52, BK II, 324, phalanx II, median digit, length 27 mm, prox. width 41 mm.
OLD/53, SHK II, 298, phalanx III, median digit, length 23 mm, prox. width 64 mm.
OLD/52, BK II, 323, phalanx I, lateral digit, length 32 mm, prox. width 34 mm.
OLD/52, BK II, 325, phalanx I, lateral digit, length 29 mm, prox. width 27 mm.
OLD/63, BK II, 878, tibia sin. without proximal end.
OLD/52, SHK II, 692, astragalus dext.
OLD/63, TK II, 2492, astragalus dext.
OLD/53, SHK II, 287, astragalus dext.
OLD/57, BK II, 661, astragalus dext.
OLD/63, TK II, 2407, calcaneum sin.
OLD/55, BK II, 22, cuboid dext.
OLD/53, BK II Ex., 131, navicular sin.
OLD/57, BK II, 520, ectocuneiform dext.
OLD/53, SHK II, 288, ectocuneiform sin.

Bed III

Diceros bicornis. B.M. (N.H.), M.14799, M^3 dext., is one of the few specimens from Bed III belonging to this species. It measures 48 mm anteroposteriorly (on the inner side); the anterotransverse diameter is 58 mm, and the length of the outer surface 57 mm. It is indistinguishable from recent M^3 of *D. bicornis*, but as it is worn the crown height cannot be determined.

In the collection at the National Museum Centre for Prehistory, Nairobi, there are rhinoceros specimens from JK2, Geol. Pit 8, an excavation made by Miss Dr. Maxine Kleindienst (now Mrs. Haldemann-Kleindienst), to whom I am indebted for information relating to the stratigraphical distribution of the finds (in litt., July 29, 1967). As noted in a published report (Kleindienst, 1964) various Beds are exposed, but the material from Trench 8 is the only excavated material from Bed III that can be considered to belong to that formation and not to be derived. One of the most interesting specimens of this dig is an upper milk molar of the common species, *Ceratotherium simum*, larger than a recent specimen but not quite as large as its homologues from the Makapansgat Limeworks Cave in South Africa (Hooijer, 1959):
OLD/62, JK2, Geol. Pit. 8, section 5, no. 1618, DM^2 dext. The parastyle is rather raised, and there is no cingulum along the internal face but only a small tubercle at the medisinus entrances, springing from the base of the hypocone. The crista is bifid, and one arm joins the crochet, forming a medifossette.
OLD/62, JK2, Geol. Pit 8, section 6, no. 1593, P_3 dext., length 37 mm.
OLD/62, JK2, Geol. Pit 8, section 1, no. cem. 178, humerus dext., slightly damaged proximally.
OLD/62, JK2, Geol. Pit 8, no. 379, unciform dext.

TABLE III

Measurements of DM^2 of *Ceratotherium* (mm)

	Makapansgat	OLD/62, JK2 1618	Recent
Greatest length ectoloph	42–51	42	41
Anterior width	39–41	39	36
Posterior width	39–43	38	35

OLD/62, JK2, Geol. Pit 8, section 5, no. 1612, acetabular portion of left innominate. OLD/62, JK2, Geol. Pit 8, no. 1961, proximal end of metatarsal III sin. Some specimens in B.M. (N.H.), marked Bed III, also represent the common *Ceratotherium*: M.14807, left mandibular ramus with M_{2-3} and right ramus with P_2 (broken) through M_3, height at M_1 130 mm; M.14809, right ramus of the mandible with broken molars, and (unnumbered) an M_3 sin., 17/5/35, with a length of 65 mm.

Bed III or IV

Here belong various specimens from JK2, Trenches A and B, which are either from Bed III or from Lower Bed IV, excavated by Miss Kleindienst in 1962:

Diceros bicornis. OLD/62, JK2/A, no. 1025, DM^2 dext. It lacks the outer portion but shows the continuous internal cingulum by which it is distinguished from its homologue in *Ceratotherium*. No medifossette is formed as there is no crista. Unfortunately no measurements can be given (Pl. **3**, fig. 6).

Diceros bicornis. OLD/62, JK2/B, floor, square M4, no. 13, central fragment of left upper molar. The small crochet does not extend across the medisinus, and part of the postsinus is present, showing it to be much shallower than the medisinus. These are characters that stamp this specimen, incomplete as it is, as belonging to the black rhinoceros.

OLD/62, JK2/A, no. 2806, P^3 sin., incomplete internally; width ca. 58 mm.
OLD/62, JK2/A, no. 3269, upper portion of P^3 sin., incomplete behind (Pl. **3**, figs. 1–2).
OLD/62, JK2/A, no. 3172, ectoloph portion.
OLD/62, JK2/A, no. 3056, ectoloph portion.
OLD/62, JK2/A, no. 2446, M_{1-3} in ramus fragment; length of M_3 at alveolus 65 mm.
OLD/62, JK2/B, floor N4–21, M_2 dext., length 54 mm.
OLD/62, JK2/B, P_2 dext., length 35 mm.
OLD/62, JK2/A, no. 832, left lower premolar, much worn down.
OLD/62, JK2/A, no. 1687, magnum dext., downward process incomplete.
OLD/62, JK2/B, no. 1127, metacarpal III dext., incomplete at both ends.
OLD/62, JK2/A, no. 484, base of trochanter tertius of femur dext.

There are further some *Ceratotherium* specimens in the 1961 Olduvai collection marked JK2/B, including an M_1 dext., length 50 mm, and some molar fragments with the characteristic medifossettes and parastyles.

Bed IV

Diceros bicornis. B.M. (N.H.), CMK IV S, 20/5/35, is an M^3 sin. displaying all the distinctive characters of the modern black rhinoceros.

B.M. (N.H.), M.14812, P^3 sin., marked IV '31; width 50 mm.

OLD/55, BK II, 95, originating from Bed IV, is a damaged M^3 sin. The crown was probably unworn; the greatest height preserved is 85 mm. The anteroposterior length of the outer surface at base is 68 mm, and that 45 mm higher up is 63 mm, giving a decrease of only 5 mm (30 mm in the Baringo, 20–22 mm in two Bed II, and 10–11 mm in two recent M^3, see p. 76).

OLD/52, MRC, 641, M_2 sin., much worn down.

OLD/62, Rhino Korongo, the greater part of the left half of a skull, together with an entire mandible. The nasal bones and the top of the occiput are missing as well as most of the palate and the skull base apart from the left inferior squamosal processes and the occipital condyles. The full left cheek teeth series P^2–M^3 is preserved (Pl. **6**, figs. 1–2). There is nothing in the structure of the teeth that distinguishes them from those in modern *C. simum*: the transverse lophs of the P and M are as obliquely placed as those in recent skulls. Skull characters likewise are those of the modern white rhinoceros, but the skull is impressive because of its great size (Table VIII). The condylo-basal length, which can be exactly taken, exceeds that in all of the modern *C. simum* skulls recorded by Heller (1913: maximum 750 mm), and the total length of the mandible is greater than in all but one of Heller's specimen's, viz., the old male from South Africa that has the maximum skull length: its mandibular length is 635 mm.

To the same skull belongs the right M^2 with a portion of the palate, showing the lateral palatine foramen and part of the posterior palatine notch (Pl. **3**, fig. 8). The right M^2 differs from the left M^2 of the skull in that the medifossette is not closed off internally but remains confluent with the medisinus, an individual aberration occasionally seen in recent molars as well.

LAETOLIL, TANZANIA

All the rhinoceros specimens from this site that I have seen belong to *Ceratotherium simum*, and some of the best specimens show the differential characters on which Dietrich (1942, 1945) based his *Serengeticeros efficax*.

In the 1959 Laetolil collection at the Nairobi Centre there is a DM^3 sin. (no. 116), much worn down (Pl. **3**, fig. 7) measuring 48 mm anterotransversely and 46 mm

posterotransversely, as do Makapansgat specimens (Hooijer, 1959). An incomplete DM^3 dext. (no. 119) is 50 mm wide anteriorly. A P^3 sin. (no. 582) is much worn, and incomplete internally; the only enamel pit left on the occlusal surface is that of the medisinus. The anterior width of another P^3 sin. (no. 418) is 51 mm; that of a P^4 sin. (no. 346), 61 mm, the same as that in the anterior half of a left tooth (no. 439) that may represent P^4.

A P^3 and P^4 dext. in the 1935 Laetolil collection in the British Museum (Natural History) both incomplete anteroexternally, show the metaloph to be transversely placed, and not oblique as in the modern white rhino. The P^3 is 61 mm transversely at base, the P^4, 66 mm. Unfortunately, the height is not known in any of the Laetolil teeth as they are all worn.

A right M^3 in the Nairobi Centre collection (no. 194) lacks all the corners except for the anterointernal one; hence, no measurements can be given.

There is, in the Nairobi collection, a mandible from Laetolil in a rather fragmentary state; the symphysial portion with the much worn crowns of the premolars, and further part of the right ramus with root stumps of some of the molars. In the British Museum (Natural History) collection there is a left mandible with P_3–M_3 (length 235 mm); the height at M_1 is only 100 mm, and the symphysis is broken.

OMO BASIN, S. ETHIOPIA

A well-preserved skull of *Ceratotherium simum* from the Upper Series of the Omo Basin (with *Loxodonta africana* and *Phacochoerus aethiopicus*) (AP 671–1), found at a site called " Rhino Canyon ", was sent to Nairobi through the courtesy of Professor Clark Howell in July 1967. It is stated to come from probably near the known lower limits of the Upper Series of the Omo Basin. The skull (Pl. **4**, figs. 1–2) is laterally crushed, and lacks the tip of the nasal bones. The full left dentition P^2–M^3 is *in situ* as well as the right P^3–M^3. The last molar is just touched by wear. From the few measurements that can be given (Table VIII) the specimen does not appear to be particularly large, less so than the largest in Heller's series from South Africa. The tooth patterns conform to those in the modern white rhino.

An isolated P_3 sin. of *C. simum*, measuring 48 by 28 mm, is no. 70 of the collection from the Omo Upper Level made by R. Leakey in 1967.

A palatal portion of the skull, with M^{2-3} sin., and a broken P^4 sin. (no. 24) of the Omo 1967 collection made by R. Leakey, is from the lower level, and shows the Early Pleistocene features (Pl. **5**, figs. 4–5).

The following specimens of *Ceratotherium simum* originate from the White Sands of the Omo Basin (cf. Howell, 1968):

no. 591, unworn crown of P^3 sin., base incomplete. Greatest length of ectoloph 58 mm, height over 85 mm (Pl. **3**, figs. 4–5).

no. 333, M_3 sin., length 64 mm, width 35 mm.

no. 492, right lower molar, length 57 mm, height of posterior loph (barely worn), 78 mm.

no. 409, left lower molar, incomplete in front.

no. 332, P_3 dext., much worn, and

no. 549, central fragment of left upper molar.

There is an astragalus sin., no. 491, slightly damaged, from the Omo White Sands; measurements in Table XXIII.

All the remaining Omo rhino teeth collected by the 1967 parties listed below belong to *Diceros bicornis*, a species not recorded before from Omo. There are two unworn specimens of M^3 that show the most distinctive character of the fossil *D. bicornis* as compared with the modern form. The outer surface of an M^3 sin. from the White Sands (no. 12; Pl. **5**, fig. 1), as well as an M^3 dext. collected by the French party, have the height just slightly greater than the basal length of the outer surface. The French specimen comes from a level provisionally regarded as Upper Villafranchian (Arambourg *et al.*, 1967, p. 1895, as *Diceros* cf. *bicornis*), and the American specimen is Early Pleistocene as well.

TABLE IV

Measurements of M^3 of *Diceros bicornis* (mm)

	Omo sin. unworn	Omo dext. unworn	Nairobi Recent unworn	Nairobi Recent worn
Ant. post. (internally)	—	50	50	49
Anterotransverse	—	52	51	55
Length of outer surface	55	58	54	60
Height of ectoloph	56	59	64	—

In the modern *D. bicornis* the unworn M^3 has the outer surface distinctly higher than wide; in a specimen recorded by Cooper (1934, p. 581) the height from the level between the roots to the peak of the crown is 84 mm, and the maximum breadth 71 mm. An unworn M^3 in the osteological collection at the Nairobi Centre (no. 6)

TABLE V

Measurements of DM^3 of *Diceros bicornis* (mm)

	Omo	Makapansgat	Recent
Greatest length ectoloph	47	47–52	45–49
Anterior width	45	46–60	40–49
Posterior width	42	43–47	37–43

has the height of the ectoloph exceeding the basal length by 10 mm (Table IV). An outer view of the recent specimen is given in Pl. **5**, fig. 2.

A specimen in the Omo collection of 1967 made by R. Leakey is a DM^3 sin. (no. 135) from the Lower Level, which is on the small side compared with its homologues of *Diceros bicornis* from Makapansgat (Hooijer, 1959).

Apart from the outer surface of the unworn M^3 sin. there are two more specimens of *Diceros bicornis* originating from the Omo White Sands, viz.,

no. 461, inner portion of protoloph and medisinus of P^3 sin. with heavy internal cingulum, and

no. 598, M_3 sin., length 57 mm, width 36 mm.

KANAM WEST, KENYA

From Kanam West there are rhinoceros teeth representing the two recent species. This site is considered Early Pleistocene.

In the British Museum (Natural History) collection there is an M^3 dext. of *Ceratotherium simum*, M.15888, which measures 84 mm at the base of the outer surface. The height of the slightly worn crown is just over 100 mm. The outer surface is 74 mm in length half way up the crown, and then reduced to 50 mm at the top due to the convexity of the anterior edge. This specimen is rather higher than Dietrich (1945, p. 59) would admit for the Early Pleistocene form from Laetolil, but close to an Omo M^3 of *C. simum germanoafricanum* (Arambourg, 1947, p. 197).

M.15892 is an upper dentition of *Diceros bicornis* from Kanam West, embedded in plaster and lacking only the left M^3. They represent an old individual, and their dimensions do not exceed those in the Recent or the Upper Pleistocene Hopefield *Diceros bicornis* specimens (Hooijer and Singer, 1960).

TABLE VI

Measurements of upper teeth of *D. bicornis* from Kanam West (mm)

P^2, ant. transv.	38	M^1, ant. post	ca. 47
post. transv.	41	ant. transv.	63
P^3, ant. post.	34	post. transv.	60
ant. transv.	52	M^2, ant. transv.	62
post. transv.	—	post. transv.	55
P^4, ant. post.	40	M^3, ant. post.	49
ant. transv.	58	ant. transv.	56
post. transv.	56	length outer surface	57

In the Nairobi Centre collection there is a DM^4 dext. from Kanam West, F.3516, a surface find (Pl. **3**, fig. 3) which is entire and about half worn down (the greatest length of the ectoloph, therefore, cannot be taken). It is similar in size to the

Makapansgat DM^4 of *D. bicornis* (Hooijer, 1959), and somewhat larger than its homologue in extant *D. bicornis* (Table VII).

TABLE VII

Measurements of DM^4 of *Diceros bicornis* (mm)

	Kanam	Makapansgat	Recent
Ant. post.	45+	—	49–55
Ant. transv.	54	52–53	45–52
Post. transv.	49	51	40–47

There is further a worn DM^4 sin., with the antero-external angle missing, with a postero-transverse diameter of likewise 49 mm, and two upper molar fragments (F.3520 and F.2517).

NAIVASHA

In the collection at the National Museum Centre for Prehistory and Palaeontology in Nairobi there is a mandible of *Ceratotherium simum* found by Mr. J. K. Ker on his farm near Knights, about 10 miles from Naivasha, at a depth of four feet in white soil, on top of an escarpment. The specimen, brought in by Wakeford Thompson, is hardly fossilized in appearance. It is the only white rhinoceros specimen thus far from this site (Naivasha is some 50 miles N.W. of Nairobi) and determination of its geological age would be of considerable interest.

The symphysial portion is incomplete and the ascending rami missing; the teeth present are P_3–M_2 on either side, and the right M_3. The mental foramen is below the P_3–P_4 junction. The premolars have both valleys closed off from the lingual margin; M_1 has the anterior valley worn out and only the posterior remaining. M_2 has the enamel figures of metalophid and hypolophid just joining occlusally, while M_3 is only touched by wear. The M_3 is 66 mm long by a height of ca. 70 mm. The teeth do not differ in size from Recent specimens and the stage of wear corresponds with that of the old female mandibles nos 8 and 9 on Plate **28** of Heller (1913).

OLORGESAILIE

An entire tibia dext., marked Olorgesailie, site 10, Basal Beds B (surface) August 1944. Measurements in Table XXII.

TABLE VIII

Measurements of skull and mandible of *Ceratotherium simum* subsp. (mm)

	Leiden Museum cat. b	Nairobi Centre no. 34	Olduvai Bed IV	Baringo J.M.91	Omo AP671–1
Occipito-nasal length	780	825	ca.920	—	—
Condylo-basal length	700	720	780	—	ca. 700
Zygomatic width	345	340	—	ca. 380	—
Lacrymal width	315	280	—	—	—
Postorbital constriction	120	115	—	—	—
Width at occipital crest	225	220	—	—	—
Bicondylar width	165	155	175	160	155
Depth of dorsal concavity	55	45	—	—	—
Least depth of zygoma	80	70	—	—	—
From foramen magnum to occipital crest	170	170	—	—	ca. 180
Width of nasal boss	160	195	—	—	—
Separation inferior squamosal processes	5	10	10	—	—
Length P^2–M^2	210	260	270	—	250
Mandible, total length	595	585	630	—	—
Length of symphysis	155	135	ca. 165	—	—
Width at symphysis	115	105	ca. 130	—	—
Height of body at M_1	125	115	140	—	—
Width of ramus at angle	160	155	165	—	—
Length P_2–M_2	190	250	275	—	—

TABLE IX

Measurements of scapula (mm)

	bicornis	*simum*	TK II 2452	BK II 438	BK II 3122
Ant. post. diam. of glenoid cavity	85	100	110	110	ca. 110
Transv. diam. of idem	80	95	—	—	95
Transv. diam. tuber scapulae	45	55	75	60	—

TABLE X

Measurements of humerus (mm)

	bicornis	*simum*	BK II 1974	MNK II 140	JK2 178
Length, caput to medial condyle	350	400	380	—	350
Width over caput and post. part of lateral tuberosity	145	180	—	—	ca. 155
Width at deltoid tuberosity	130	170	—	—	140
Least width of shaft	60	85	80	75	70
Greatest distal width	150	180	—	—	150
Width of trochlea	100	120	110	105	100

TABLE XI

Measurements of radius (mm)

	bicornis	*simum*	HWK II 400	BK II
Median length	345	380	—	—
Proximal width	100	120	115	ca.100
Mid-shaft width	55	70	65	—
Distal width	95	120	—	—

TABLE XII

Measurements of ulna (mm)

	bicornis	*simum*	MNK II
Greatest length	450	510	—
Width at semilunar notch	90	110	90
Mid-shaft width	45	60	50
Greatest distal width	75	90	70

TABLE XIII

Measurements of scaphoid (mm)

	bicornis	*simum*	S.I. F 496	MTK 105	FLK	S.I. F 520
Posterior height	50	62	65	ca. 65	60	60
Anterior height	60	65	70	60	—	—
Proximal width	55	60	75	70	—	—
Max. diam. distal facets	70	73	85	83	ca. 70	—

TABLE XIV

Measurements of lunar (mm)

	bicornis	*simum*
Anterior height	48	60
Proximal width	48	58
Max. ant. post. diameter	68	75

TABLE XV

Measurements of cuneiform (mm)

	bicornis	*simum*	DK I 259	F 836*
Anterior height	50	58	70	52
Distal width	38	45	—	43
Prox. ant. post. diameter	40	48	ca. 55	48
Max. horizontal diameter	53	66	ca. 80	57

* Olduvai, no site or level given, but entire (right) specimen.

TABLE XVI

Measurements of magnum (mm)

	bicornis	*simum*	JK2 1687
Anterior height	32	38	34
Anterior width	49	58	ca. 45
Prox. ant. post. diameter	67	70	67
Greatest diameter	85	84	90

TABLE XVII

Measurements of unciform (mm)

	bicornis	*simum*	KK I 298	BK II 127	DK I 449	DK I 28	JK2 379
Anterior height	51	55	66	54	68	73	56
Greatest width	63	74	ca. 90	74	97	110	70
Greatest ant. post. diam.	90	99	ca. 110	—	122	134	93

TABLE XVIII

Measurements of metacarpals (mm)

Mc. II	*bicornis*	*simum*	S.I F 861
Median length	147	160	183
Proximal width	32	45	47
Proximal ant. post. diameter	46	49	58
Middle width	33	40	44
Middle ant. post. diameter	19	24	30
Greatest distal width	39	50	53
Width of distal trochlea	33	40	48
Distal ant. post. diameter	41	45	58
Ratio middle width/length	0·22	0·25	0·24

Mc. III	*bicornis*	*simum*	HWK II 247	S.I w.THC	MTK 97	I 98	S.I 850	FLK 523
Median length	162	176	193	210	205	208	—	—
Proximal width	59	68	86	—	84	—	ca.90	70
Proximal ant. post. diameter	48	52	66	—	66	—	70	ca. 70
Middle width	46	58	66	68	64	65	67	—
Middle ant. post. diameter	22	28	34	34	33	32	33	—
Greatest distal width	61	71	84	—	83	86	—	—
Width of distal trochlea	51	59	71	—	66	68	—	—
Distal ant. post. diameter	44	48	54	59	57	60	—	—
Ratio middle width/length	0·28	0·33	0·34	0·32	0·31	0·31	—	—

TABLE XVIII—(*continued*)

Mc. IV	*bicornis*	*simum*	DK I 403
Median length	136	143	166
Proximal width	43	54	65
Proximal ant. post. diameter	43	50	54
Middle width	33	41	48
Middle ant. post. diameter	18	23	31
Greatest distal width	43	52	59
Width of distal trochlea	37	42	52
Distal ant. post. diameter	38	45	51
Ratio middle width/length	0·24	0·29	0·29

TABLE XIX

Measurements of pelvis (mm)

	bicornis	*simum*	HWK II 791	JK2 1612
Diameter of acetabulum	90	115	120	ca. 95
Greater diam. of obturator for.	105	115	125	—
Least width of ilium shaft	70	90	110	—

TABLE XX

Measurements of femur (mm)

	bicornis	*simum*
Greatest length	440	530
Proximal width	195	225
Least width of shaft	60	80
Greatest distal width	120	150
Distal ant. post. diameter, medial side	160	190
Diameter of caput	80	95

TABLE XXI

Measurements of patella (mm)

	bicornis	*simum*	HWK II 820	OLD*
Length	95	107	107	125
Width	87	93	105	110

*Olduvai, no site or level given, but particularly large specimen.

TABLE XXII

Measurements of tibia (mm)

	bicornis	*simum*	BK II 878	F 3312*	F 3313*	Olorgesailie
Greatest length	335	380	—	—	—	370
Proximal width	110	135	—	—	—	115
Distal width	85	95	85	110	90	90
Distal ant. post. diameter	70	80	70	85	70	67

* Two OLD/41 specimens, marked S 4 and S 2, respectively, both distal ends of tibiae sin.

TABLE XXIII

Measurements of astragalus (mm)

	bicornis	*simum*	HWK II 234	FLK NN	S2 781A	SHK II 692
Lateral height	71	74	100	91	88	84
Medial height	70	75	99	88	90	84
Total width	83	95	118	108	109	106
Ratio medial height/total width	0·84	0·79	0·84	0·81	0·83	0·79
Trochlea width	78	83	108	101	93	96
Width of distal facets	72	85	103	93	90	86

	TK II 2429	SHK II 287	BK II 661	FLK 522	Omo White Sands
Lateral height	—	73	ca. 75	—	66
Medial height	90	72	79	ca. 95	65
Total width	108	82	99	ca. 115	74
Ratio medial height/total width	0·83	0·88	0·79	ca.0·83	0·88

TABLE XXIV

Measurements of calcaneum (mm)

	bicornis	*simum*	TK II 2407	S.I F 486	MNK II 3295
Lateral height	110	125	140	ca. 140	120
Greatest width	70	80	95	—	—
Ant. post. diameter	65	75	80	80	70

TABLE XXV

Measurements of cuboid (mm)

	bicornis	*simum*	BK II 22	FLK NN	OLD/51* 403
Anterior height	37	43	46	50	46
Anterior width	44	52	46	—	42
Greatest ant. post. diameter	65	80	80	—	75

* No site or level given: entire cuboid sin.

TABLE XXVI

Measurements of navicular (mm)

	bicornis	*simum*	FLK NN Tr. II	BK II 131
Anterior height	24	29	31	23
Total width	45	55	—	45
Ant. post. diameter	56	62	64	52

TABLE XXVII

Measurements of ectocuneiform (mm)

	bicornis	*simum*	FLK NN 8894	S.I F 514	SHK II 288	BK II 520
Anterior height	24	27	31	31	25	28
Anterior width	45	57	67	70	43	57
Ant. post. diameter	53	54	66	65	46	56

TABLE XXVIII

Measurements of metatarsals (mm)

Mt. II	*bicornis*	*simum*
Median length	129	151
Proximal width	25	34
Proximal ant. post. diam.	42	47
Middle width	25	28
Middle ant. post. diam.	19	24
Greatest distal width	33	39
Width of distal trochlea	29	36
Distal ant. post. diameter	36	40
Ratio middle width/length	0·20	0·19

TABLE XXVIII—(*continued*)

Mt. III	*bicornis*	*simum*	DK I 69	JK2 1961
Median length	148	169	—	—
Proximal width	48	55	74	57
Proximal ant. post. diameter	48	49	ca. 55	52
Middle width	40	48	67	—
Middle ant. post. diameter	21	25	38	—
Greatest distal width	54	66	—	—
Width of distal trochlea	47	51	—	—
Distal ant. post. diameter	42	47	—	—
Ratio middle width/length	0·27	0·28	—	—

Mt. IV	*bicornis*	*simum*
Median length	125	146
Proximal width	42	49
Proximal ant. post. diameter	40	45
Middle width	26	29
Middle ant. post. diameter	24	28
Greatest distal width	36	39
Width of distal trochlea	33	37
Distal ant. post. diameter	38	41
Ratio middle width/length	0·21	0·20

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LEGENDS TO PLATES

PLATE 1

Ceratotherium simum germanoafricanum (Hilzheimer)

FIG. 1. Skull, Chemeron Formation, Lake Baringo, J.M.91, palatal view. × 1/5.
FIG. 2. Same, right view. × 1/5.

PLATE 2

Ceratotherium simum germanoafricanum (Hilzheimer)

FIG. 1. Maxillary with M^{1-3} sin., Chemeron Formation, Lake Baringo, J.M.507, crown view. × 2/3.
FIG. 2. M^1 or M^2 sin., OLD/60, FLK NN, crown view. × 2/3.

Ceratotherium simum (Burchel) subsp.

FIG. 3. M^1 sin., OLD/63, BK II, 1064, crown view. × 2/3.
FIG. 4. M^1 or M^2 dext., OLD/63, TK II, 2622, crown view. × 2/3.
FIG. 5. P^3 dext., OLD/63, FC II, crown view. × 2/3.

PLATE 3

Ceratotherium simum (Burchell) subsp.

FIG. 1. P^3 sin., OLD/62, JK2/A, no. 3269, crown view. × 2/3.
FIG. 2. Same, outer view. × 2/3.
FIG. 4. P^3 sin., Omo White Sands, 1967, 591, crown view. × 2/3.
FIG. 5. Same, outer view. × 2/3.
FIG. 7. DM^3 sin., Laetolil, 1959, 116, crown view. × 2/3.
FIG. 8. M^2 dext., OLD/62, Rhino Korongo, crown view. × 2/3.

Diceros bicornis (L.) subsp.

FIG. 3. DM^4 dext., Kanam West, F.3516, crown view. × 2/3.
FIG. 6. DM^2 dext., OLD/62, JK2/A, no. 1025, crown view. × 2/3.

PLATE 4

Ceratotherium simum (Burchell) subsp.

FIG. 1. Skull, Omo, Upper Series, 1967, Rhino Canyon, palatal view. × 1/5.
FIG. 2. Same, right view. × 1/5.

PLATE 5

Diceros bicornis (L.) subsp.

FIG. 1. M^3 sin., Omo White Sands, 1967, 12, outer view. × 2/3.
FIG. 2. M^3 sin., Recent, Dept. of Osteology, Nairobi, no. 6, outer view. × 2/3.

Ceratotherium simum (Burchell) subp.

FIG. 3. M^3 sin., OLD/57, SHK II, 181, outer view. × 2/3.

Ceratotherium simum germanoafricanum (Hilzheimer)

FIG. 4. Palatal portion of skull with M^{2-3} sin., Omo, Lower Level, 1967, crown view. × 1/3.
FIG. 5. Skull fragment with broken P^4 sin., Omo, Lower Level, 1967, no. 24, crown view. × 2/3.

PLATE 6

Ceratotherium simum (Burchell) subsp.

FIG. 1. Skull, OLD/62, Rhino Korongo, left view. × 1/5.
FIG. 2. P^2–M^3 sin. of same skull, crown view. × 1/2.

PLATE 1

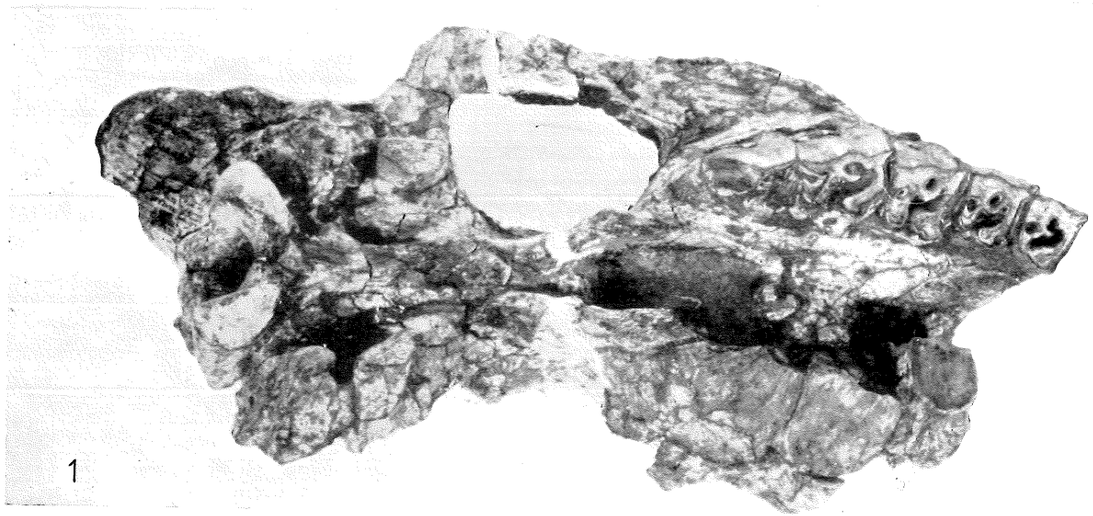

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PLATE 2

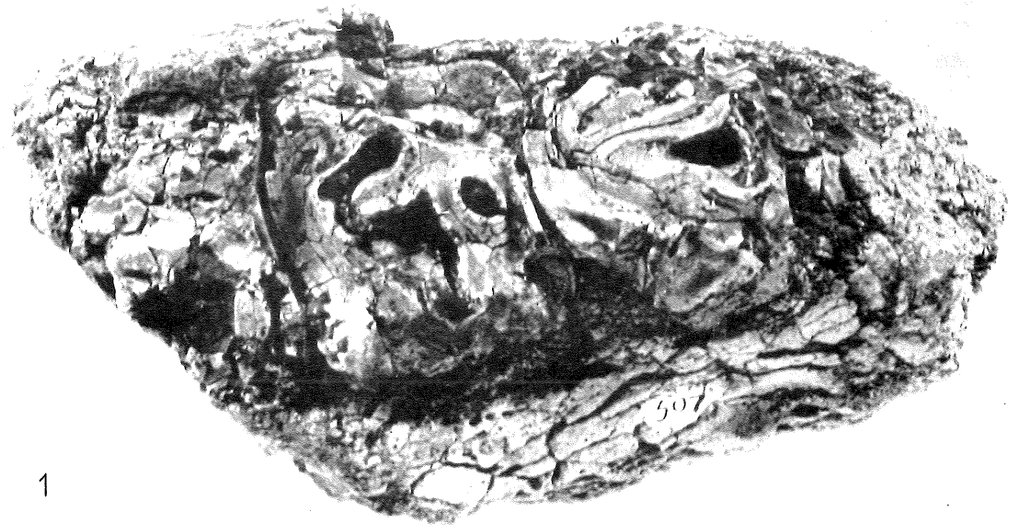

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Plate 3

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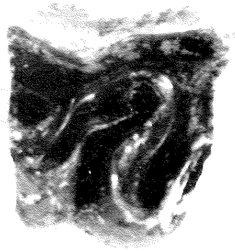

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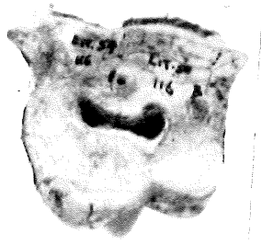

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Plate 4

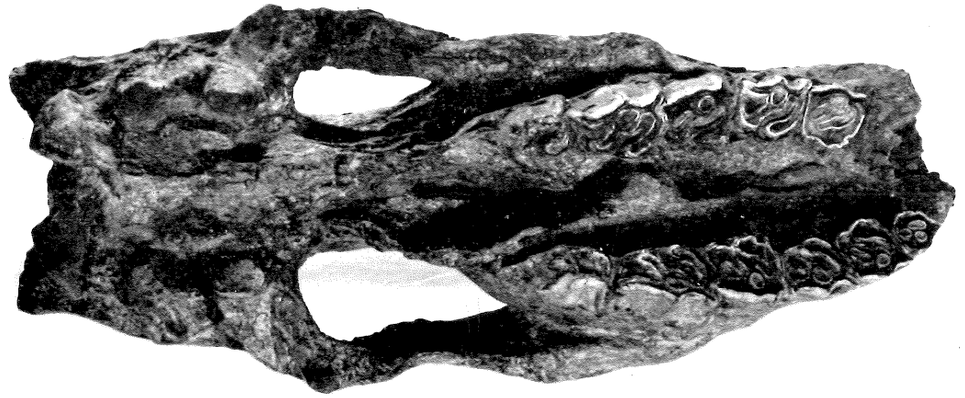

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PLATE 5

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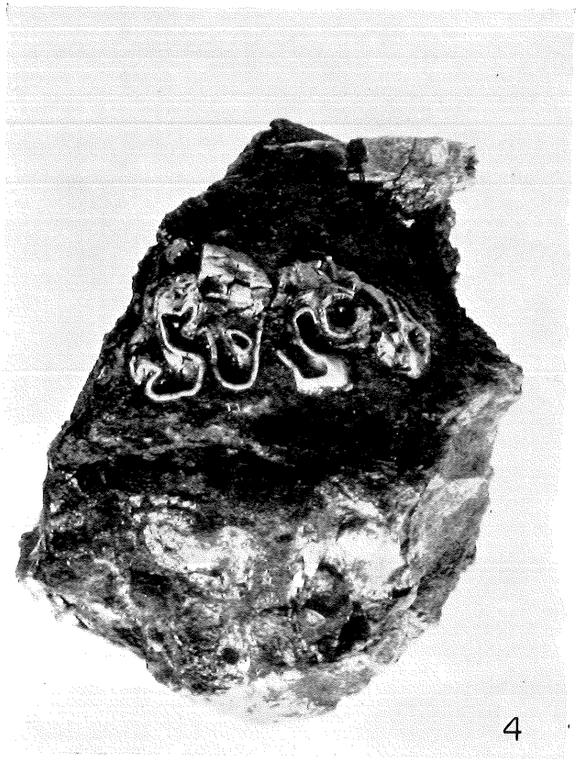

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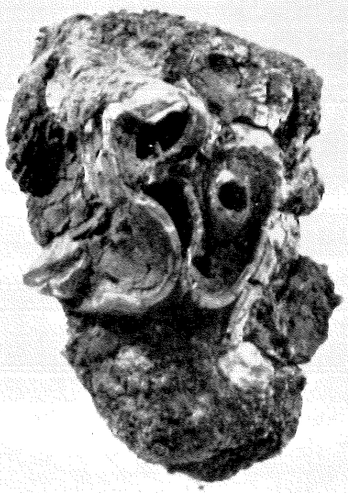

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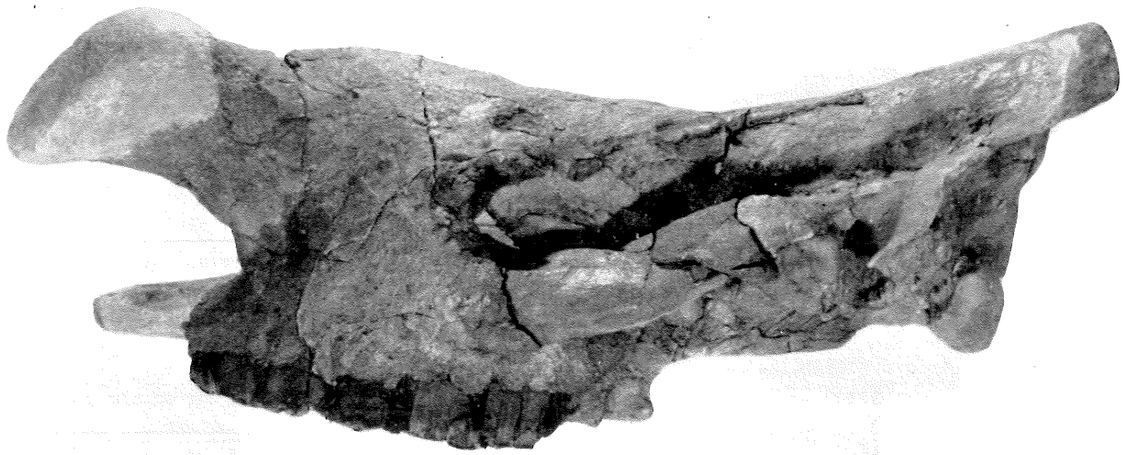
PLATE 6



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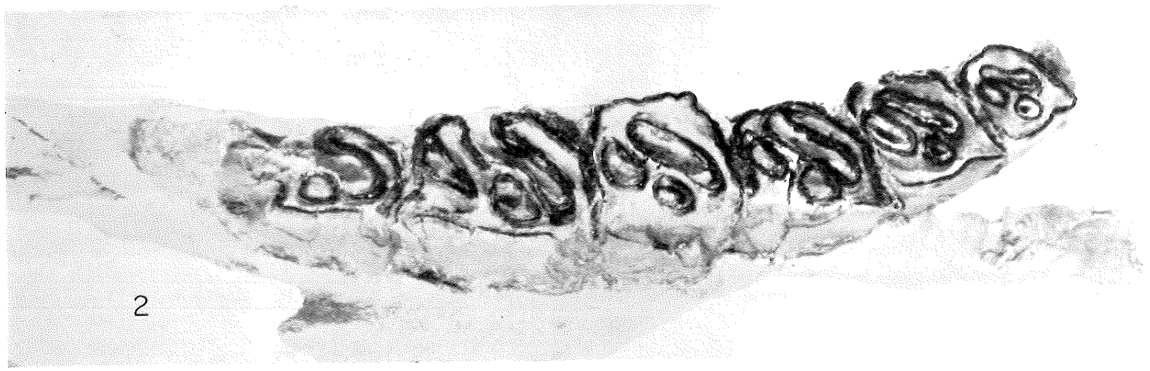

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