

RHINOCEROSES FROM THE PLIOCENE OF NORTHWESTERN KENYA

DICK A. HOOIJER¹ AND BRYAN PATTERSON

ABSTRACT. A large brachypotherine, *Brachypotherium lewisi* sp. nov., is described from Lothagam-1; it is the last recorded member of the group. The genus has been present in Africa since the early Miocene and presumably immigrated from Eurasia somewhat before that time. Whether or not the African and Eurasian forms thereafter evolved in parallel is uncertain, but *B. lewisi* could have descended from the early Miocene *B. snoici* (Fourtau) of Egypt. Fragmentary remains from Ngorora and Sahabi are identified as *B. sp. cf. B. lewisi*. An upper molar from Lothagam-1 is referable to *Ceratotherium* and is the earliest record of the genus. This tooth is indistinguishable from those of specimens found in the later Kanapoi and Ekora sediments. *C. praecox* sp. nov. is based on this material. Fragments from the Mursi and the Chemeron (locality J. M. 507), previously identified as *C. simum*, are reassigned as *C. sp. cf. C. praecox*. The new species shows decided resemblances to *Diceros*, indicating that the white rhinoceroses diverged from the black during Pliocene time. Apart from the European Pontian *D. pachygynathus* (Wagner), the scantily recorded history of the *Diceros* group is wholly African. Quaternary specimens of *D. bicornis* and *C. simum simum* are recorded in an Appendix.

INTRODUCTION

Paleontological expeditions to Kenya from this Museum discovered and worked Pliocene deposits in southeastern Turkana District during the years 1965 to 1968. These deposits, Kanapoi (Patterson, 1966), Lothagam Hill and Ekora (Patterson, Behrensmeyer and Sill, 1970), have yielded a variety of vertebrates and molluses, in-

cluding the rhinocerotid remains here reported upon.

Two rhinoceroses are now known from Lothagam-1: a large *Brachypotherium*, represented by two incomplete skulls, two lower jaws, jaw fragments, isolated teeth, an atlas and portions of a femur, and an early form of *Ceratotherium*, known from a single incomplete upper molar. This is the only specimen in the Lothagam collection to reveal the presence of any relative of the living African forms. The Kanapoi and Ekora collections contain three incomplete skulls, three incomplete jaws, various teeth, and a humerus of a *Ceratotherium* that is inseparable on the evidence from the one occurring at Lothagam; it is less advanced than *C. simum* (Burchell) in skull structure and resembles *Diceros bicornis* (L.) in dental characters.

Specimens of *Brachypotherium* found *in situ* at Lothagam were in fine-grained sediments, those of *Ceratotherium* at Kanapoi and Ekora in coarse, including conglomeratic, ones.

The expeditions that collected these and other specimens were supported by National Science Foundation Grants GP-1188 and GA-425 to Patterson. We are also indebted to the Wenner-Gren Foundation for Anthropological Research for a grant to Hooijer. The drawings are by Miss Margaret Estey, the photographs by Drs. V. J. Maglio and R. C. Wood, and the drafting by Mr. Laszlo Meszoley. The abbreviation KNM stands for Kenya National Museum.

¹ Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands.

Family RHINOCEROTIDAE Owen

Genus *Brachypotherium* Roger*Brachypotherium lewisi* sp. nov.²

Diagnosis. Size very large: condylobasal length of type skull over 70 cm, antero-transverse diameters of M^1-2 some 90 mm as opposed to 70 mm in *B. brachypus* (Lartet) or *B. snowi* (Fourtau) from Miocene of Europe and Egypt, respectively. Nasals hornless, slender, not very long, deepest point of nasomaxillary notch above P^4 , anterior border of orbit above front of M^2 , frontals flat and hornless, inferior squamosal processes united below subaural channel. Upper incisors very large, upper cheek teeth brachydont, ectoloph flattened behind paracone style, antecrochet moderate, protocone constriction slight, external cingula often present. Lower canines present, brachydont cheek teeth with external groove between anterior and posterior lophids usually flattened out, external cingula often developed. Trochanter tertius of femur strongly developed.

Type. KNM LT 88, skull, crushed dorsoventrally, with cheek teeth and alveoli of incisors, lacking right zygomatic arch, right condyle and much of the occiput and roof of the cranium.

Hypodigm. The type and the following specimens: KNM LT 94, skull, crushed obliquely, with much of right side missing, LM^2 in place, LI^1 , RM^2 , parts of LM^1 and 3 and an incomplete atlas; KNM LT 91, left mandible with P_2-M_3 , lacking coronoid process; KNM LT 90, symphysis and incomplete horizontal rami with LP_{2-4} , RP_{2-3} , alveoli of C and P_1 ; KNM LT 84, incomplete R horizontal ramus of juvenile with dm_1-M_1 ; KNM LT 95, incomplete symphysis and portion of left ramus of juvenile with unerupted P_2 , M_2 , incomplete M_1 and alveoli of dc , dm_1 ; KNM LT 85, incomplete LI_1 ; KNM LT 87, RP^1 ; KNM

LT 99, RP^2 , incomplete LP^2 ; KNM LT 100, incomplete LP^2 and LM^2 ; KNM LT 80, incomplete RP^3 ; KNM LT 96, incomplete P_4 and M_1 ; KNM LT 93, incomplete RM^3 ; KNM LT 82, RM_1 ; KNM LT 84, incomplete RM_2 ; KNM LT 83, P_{2-4} ; KNM LT 86, portions of lower cheek teeth including LM_1 or 2 and RM_3 ; KNM LT 97, incomplete left femur, including a portion of the shaft at and distal to the third trochanter and parts of the distal end.

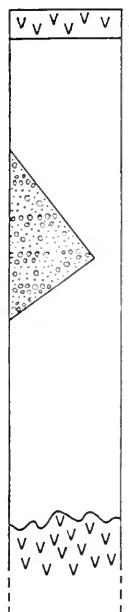
Horizon and locality. Late Pliocene, Lothagam-1, Members B and C (type from top of B, see Fig. 1 for details of stratigraphic distribution); Lothagam Hill, southeastern Turkana District, Kenya.

Description and discussion. The type skull (Fig. 2) is dorsoventrally crushed; the height of the left orbit being reduced to a bare centimeter. The depressed nasofrontal area of the skull is slightly displaced toward the left and shifted backward relative to the premaxillaries and the palate. The whole of the left zygomatic arch is preserved, however, and apparently only slightly distorted. The right orbit is less compressed than the left, but its anterior and upper borders are incomplete. The anterior border of the orbit is above the anterior border of M^2 . Behind the orbital region the whole of the top of the skull and the occiput is missing. The frontoparietal crests behind the postorbital processes of the frontals cannot be traced, and the least width of the cranium behind the orbits cannot be determined with any reasonable degree of accuracy. The temporal crest on the right side is partially preserved, and is rather thin. It is not clear from this specimen whether the two inferior squamosal processes unite below the external auditory meatus, but the second skull, KNM LT 94, described below, shows that they do.

The nasal bones are rather small, not more than 12 cm long, and tapering toward the tip, which remains some 15 cm behind the anterior ends of the premaxillaries. The distance from the nasal tip to

² Named for Mr. Arnold D. Lewis, member of three of the Museum's African expeditions and finder of the type specimens of both species here described.

KANAPOI



EKORA

KP 41

v v v v v

KP 32
KP 36 (type)KP 35
KP 30, KP 31
KP 34KP 33
KP 39

KP 40

v v v v v v v v

v v v v v v v v

v v v v v v v v

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LOTHAGAM-1



LT 83

LT 82, LT 97

LT 90

LT 85

LT 95, LT 96

LT 84

LT 91, LT 94

LT 80, LT 81, LT 87, LT 89

LT 86, LT 93

LT 99, LT 100

LT 88 (type)

C

B

A

Figure 1. Stratigraphic distribution of rhinoceros specimens in the Kanapoi, Ekora, and Lothagam-1 formations. All Kanapoi and Ekora specimens are *Ceratotherium praecox* sp. nov. All Lothagam-1 specimens are *Brachypotherium lewisi* sp. nov. except for LT 89, which is *Ceratotherium praecox* sp. nov. ref. Lothagam-1 is neither in scale nor in sequence with Kanapoi and Ekora. All numbers have the prefix KNM.

the front of the premaxillaries is, however, as a result of crushing clearly greater than it originally was. There is no indication of a nasal horn boss, nor does the frontal surface bear any indication of the former presence of a horn. The shape of the nasomaxillary notch cannot be made out in the specimen. The infraorbital foramen, however, can be seen on the left side; it is placed above P^4 .

The premaxillaries are short and wide; they show two alveoli for the upper incisors, partially filled with matrix. The interval between them is 25 mm, and both are distorted, with the borders damaged.

The right alveolus measures 55 mm anteroposteriorly and 30 mm transversely, the left 35 mm anteroposteriorly and 40 mm transversely. The true shape of the upper incisor or the length of its root cannot be made out from this, but KNM LT 94 has a well-preserved upper incisor that is described below.

The cheek teeth are excellently preserved although well worn. The posterior margin of the palate is damaged in the median line; the two lateral palatine foramina, however, are clearly seen and are on a level with the protolophs of M^3 . The width of the palate is 120 mm between the M^3 ,



Figure 2. *Brachypotherium lewisi* sp. nov. KNM LT 88, type. Ventral view of skull. $\times 0.25$.

TABLE 1. SKULL MEASUREMENTS OF *BRACHYPO-
THERIUM LEWISI* (mm)

	KNM LT 88	KNM LT 94
Length from occipital crest to nasal tip	—	ca. 580
Condylbasal length	710	—
Length from anterior border of orbit to external auditory meatus	300	345
Length from tip of premaxillaries to P^2	80	—
Width across premaxillaries	125	—
Width of frontals over superior borders of orbits	250	ca. 260
Width across zygomatic arches	ca. 520	—

and 80 mm between the P^3 . The right cheek tooth series is well aligned, with the internal borders forming a nearly straight line, whereas of the left tooth series P^1 and M^1 are somewhat displaced inward and P^2 is pushed outward a little. In both the right and the left cheek tooth series there is a longitudinal crack, 3–4 mm wide, running through P^3 to M^2 at about one-third of the crown widths from the external borders, leaving P^2 and M^3 unaffected.

P^2 is the foremost tooth present, but there is a trace of the alveolus for a small tooth in front of it, either a persistent milk tooth or a P^1 . P^2 is worn down to a height of 27 mm on the right, and of 34 mm on the left side, measured externally, at its maximum. There is neither a paracone nor a metacone style, the ectoloph being slightly convex anteroposteriorly as well as vertically. There is a faint external cingulum, most marked in the posterior part of the crown. The crown is wider behind than in front, and has a small crochet but no anterocheat or crista. The medisinus has a narrow, V-shaped entrance, as protocone and hypocone are closely approximated basally. There is a strong and continuous internal cingulum, 14 mm high, marking off a shallow pit at the end of the medisinus internal to the protocone-hypocone junction. The medisinus is very deep,

nearly 15 mm, much deeper than the postsinus, which is longer than wide. It is not quite cut off from the posterior crown border as the cingulum is indented behind the postsinus, and the deepest point of the notch has not yet been reached by wear.

P^3 , 34 mm high as worn externally on the right, against 32 mm on the left side, has a very slight paracone style and no metacone style, the external cingulum, shown posteriorly only, a weak crochet and no anterocheat or crista, as in P^2 . Unlike that tooth it is wider in front than behind. The internal cingulum is as well developed as that in P^2 . The pit closed off between it and the adjoining bases of proto- and hypocone is as in P^2 , and the postsinus is just isolated from the posterior crown margin. It is 7 mm deep, while the medisinus is just over 15 mm in depth, from the occlusal surface.

In P^4 , external height, as worn, 31 mm on both sides, the paracone style is slightly more marked than that in P^3 , and there is no metacone style. The external cingulum is virtually absent, while the anterior cingulum is strong, as in P^3 , but the internal cingulum is interrupted along the faces of protocone and hypocone, forming a strong ledge at the medisinus entrance that is 14 mm high from the crown base. The anterocheat begins to show, and the crochet is weaker than that in P^3 (an anterocheat increases, a crochet decreases toward the base of the medisinus). The postsinus is closed off behind and only 4–5 mm deep, half the depth of the medisinus.

M^1 is much worn down, to ca. 15 mm at the middle of the ectoloph. The anterocheat is weak but marked off by a groove (the posterior protocone fold). There are no traces of a crochet or crista in this advanced stage of wear. The internal cingulum shows as a 10 mm high ledge at the entrance to the medisinus only, while the external cingulum is present only along the posterior half of the base of the ectoloph. The paracone style is hardly visible, and the ectoloph behind it perfectly flat.

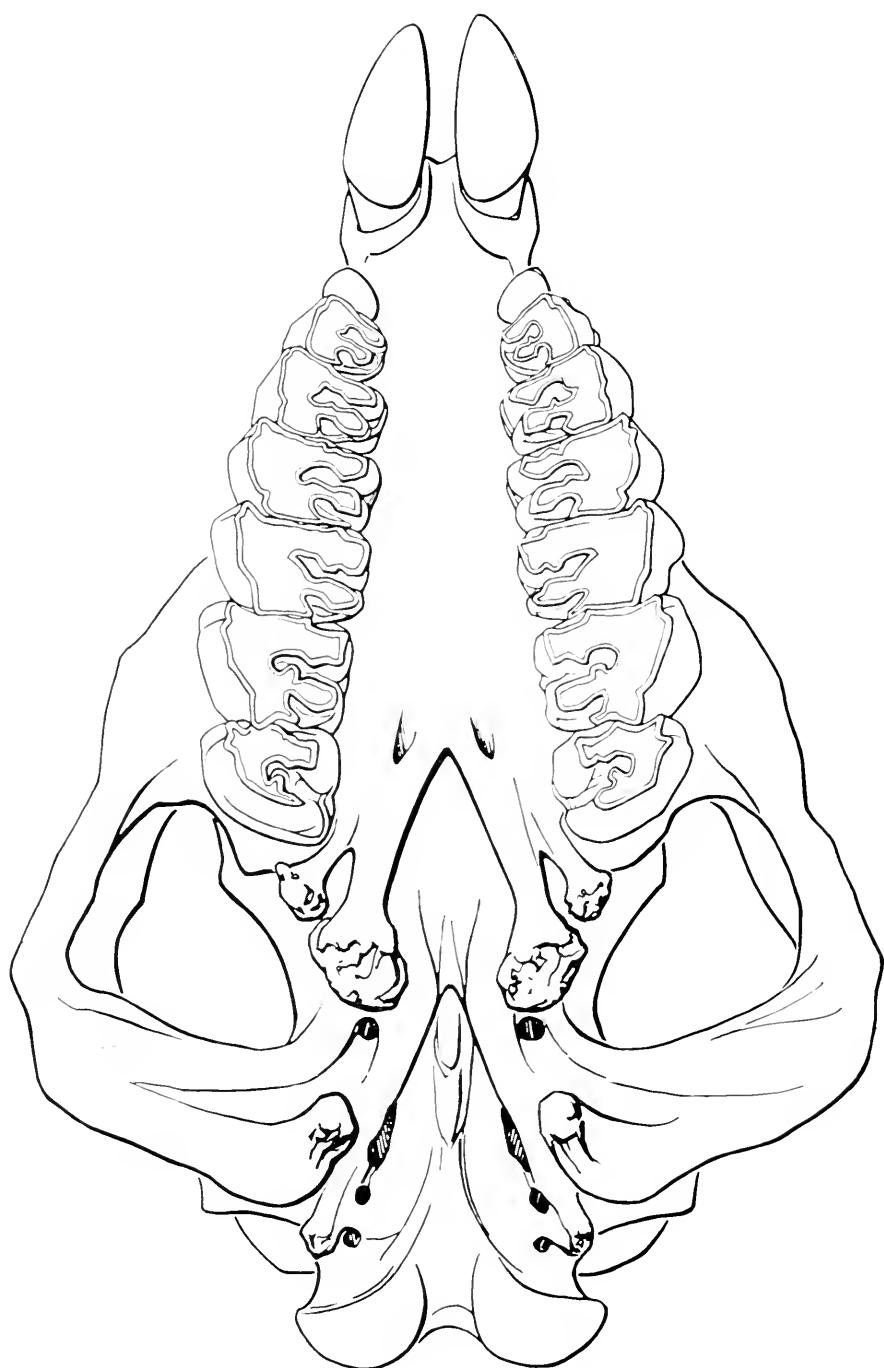


Figure 3. Restoration of ventral view of *Brachypatherium lewisi* sp. nov. based on KNM LT 88 (type) and KNM LT 94. $\times 0.25$.

TABLE 2. MEASUREMENTS OF UPPER TEETH OF *BRACHYPOTHERIUM** (mm)

	<i>B. aurelianense</i>	<i>B. snowi</i>	<i>B. goldfussi</i>	KNM LT 88	<i>B. lewisi</i> KNM LT 99	KNM LT 100	<i>B. sp. cf.</i> <i>B. lewisi</i> Sahabi
P ² , length	25	31	—	36	36	36	—
ant. width	35	43	—	48	49	50	—
post. width	—	45	—	51	51	52	—
P ³ , length	30	36	—	49	—	—	—
ant. width	46	60	—	72	—	—	—
post. width	—	56	—	67	—	—	—
P ⁴ , length	38	42	48	—	—	—	—
ant. width	55	69	65	84	—	—	—
post. width	—	61	59	73	—	—	—
M ¹ , length	42	48	ca. 51	ca. 65	—	—	—
ant. width	58	72	70	90	—	—	—
post. width	—	62	60	76	—	—	—
p. tr.: a. tr.	—	0.86	0.86	0.84	—	—	—
M ² , length	50	60	65	ca. 70	—	—	—
ant. width	60	74	69	86	—	87	99
post. width	—	64	57	72	—	71	92
p. tr.: a. tr.	—	0.86	0.82	0.84	—	0.82	0.93
M ³ , length	52	64	—	70	—	—	—
ant. width	55	—	—	80	—	—	—
Length ext. face	—	—	64	86	81	—	—
L P ² -M ³	240	275	—	330	—	—	—
L P ² -P ⁴	90	110	—	145	—	—	—

* Those of *B. snowi* taken from a cast kindly provided by Dr. Elwyn Simons.

M², worn externally to 30 mm from the crown base in the middle, shows both the antecrochet and the crochet; neither of these are very prominent but together they give the medisinus a sinuous course. The posterior as well as the anterior protocone fold are weakly developed, marking off the protocone; the cingulum is reduced internally to a mere knob, not more than 6 mm high, at the medisinus entrance. The paracone style, somewhat damaged in the left M², is more marked than that in M¹, showing a sharp parastyle fold in front that flattens out at the crown base. The ectoloph behind the paracone style is flattened. The medisinus is about 15 mm deep, the postsinus only half as deep as the medisinus.

M³ has a distinct paracone style, marked off in front by a sharp parastyle fold at the level reached by wear, which is 45 mm from the crown base in the middle of the external surface. The style and fold flatten out near the crown base. The external surface, or ecto-metaloph, shows no bulge at the base of the metacone but is regularly convex. The posterior cingulum is a marked ridge with a series of knobs, about 25-30 mm wide transversely. The crochet is prominent and rounded, extending half-way across the medisinus, the antecrochet internal to it on the opposite wall of the medisinus is not very prominent in this not very advanced stage of wear. The entrance to the medisinus is low and wide, the bases of proto- and hypocone being some 14 mm

apart; midway between these there is a marked ridge along the medisimus base, starting from the base of the crochet, and joining the internal cingulum. This internal cingulum forms a strong ridge, nearly 20 mm long, connecting the bases of protocone and hypocone, but absent along the flattened internal base of the protocone. The protocone constriction is marked by shallow anterior and posterior grooves. Measurements of the upper teeth are given in Table 2.

Although not a single molar is unworn, it is clear from the inward inclination of the ectolophs that the molars of the Lothagam rhinoceros are brachydont. This, coupled with the flattening of the ectolophs, the weak antecrochets, and slightly marked protocone constrictions, and the occasional presence of external cingula, stamp the molars as those of *Brachypotherium*. This is a genus of rhinocerotids known from the Burdigalian through Pontian of Europe, with two species previously known from Africa, viz., *B. snowi* (Fourtau) from the early Miocene of Moghra, Egypt (Fourtau, 1920), and *B. heinzelini* Hooijer (1963, 1966) from the Miocene of Congo, Kenya and Uganda. Measurements of the upper teeth of the Lower Burdigalian (earliest Miocene) *B. aurelianense* (Nouel) from France (Nouel, 1866) as well as *B. goldfussi* (Kaup) of the Pontian (after Kaup, 1854) are given in Table 2; the dentition of the Upper Vindobonian *B. brachypus* (Lartet) is very similar, in fact almost indistinguishable from that of *B. goldfussi*, and measurements of *B. brachypus* as well as of *B. heinzelini* upper teeth have already been given in Hooijer (1966: 144, Table 13). It is clear from Table 2 that the teeth of the Lothagam rhinoceros greatly exceed in size those of the other *Brachypotherium* species, including *B. snowi* from Egypt. As far as the structural characters go, the upper dentition of *B. brachypus* figured by Depéret (1887, pl. XXIII) shows continuous internal as well as external

cingula in P^2-M^2 (M^3 is only erupting and the base is not exposed). The antecrochets are weak and the crochets strong as may be expected in a dentition in such an early stage of wear. The ectolophs show the characteristic flattening. In *B. aurelianense*, which has the smallest tooth dimensions, the upper dentition has rather marked antecrochets in P^4-M^2 for the early wear stage; the internal cingular development is not shown in the illustration (Nouel, 1866, pl. 4). The upper jaw of *B. snowi* (Fourtau, 1920: 38) is that of an old individual, in which the medisimus is largely worn away. Both *B. aurelianense* and *B. snowi* possess large upper incisors by which the other brachypotherines are characterized. The skull characters of *B. aurelianense* will be dealt with after the description of the second Lothagam rhinoceros skull, KNM LT 94.

This specimen (Fig. 4, A and B) is crushed in a different way from the holotype, which helps in understanding what the original, undistorted, skull shape of *B. lewisi* may have been. The crushing has been such that the height was little affected although the dorsal surface slopes markedly down from right to left. Most of the right half of the skull is gone; the left half has the zygomatic arch, only slightly broken and distorted, and the orbito-frontal and parieto-occipital portions rather well preserved. The top of the occiput and a portion of the temporal crest are missing. The left premaxillary is broken off through the alveolus for I^1 , the tip of the nasals is slightly restored. The nasal bones are, again, slender and clearly hornless, and extend forward to above the anteriormost cheek tooth, for which only a small alveolus, 25 mm long and 20 mm wide, remains. The nasomaxillary notch is 15 cm deep from the nasal tip, and extends backward to above the alveolus for the last premolar. The infraorbital foramen is on the same level. The length from the deepest point of the nasomaxillary notch to the anterior border of the orbit is 11 cm, and

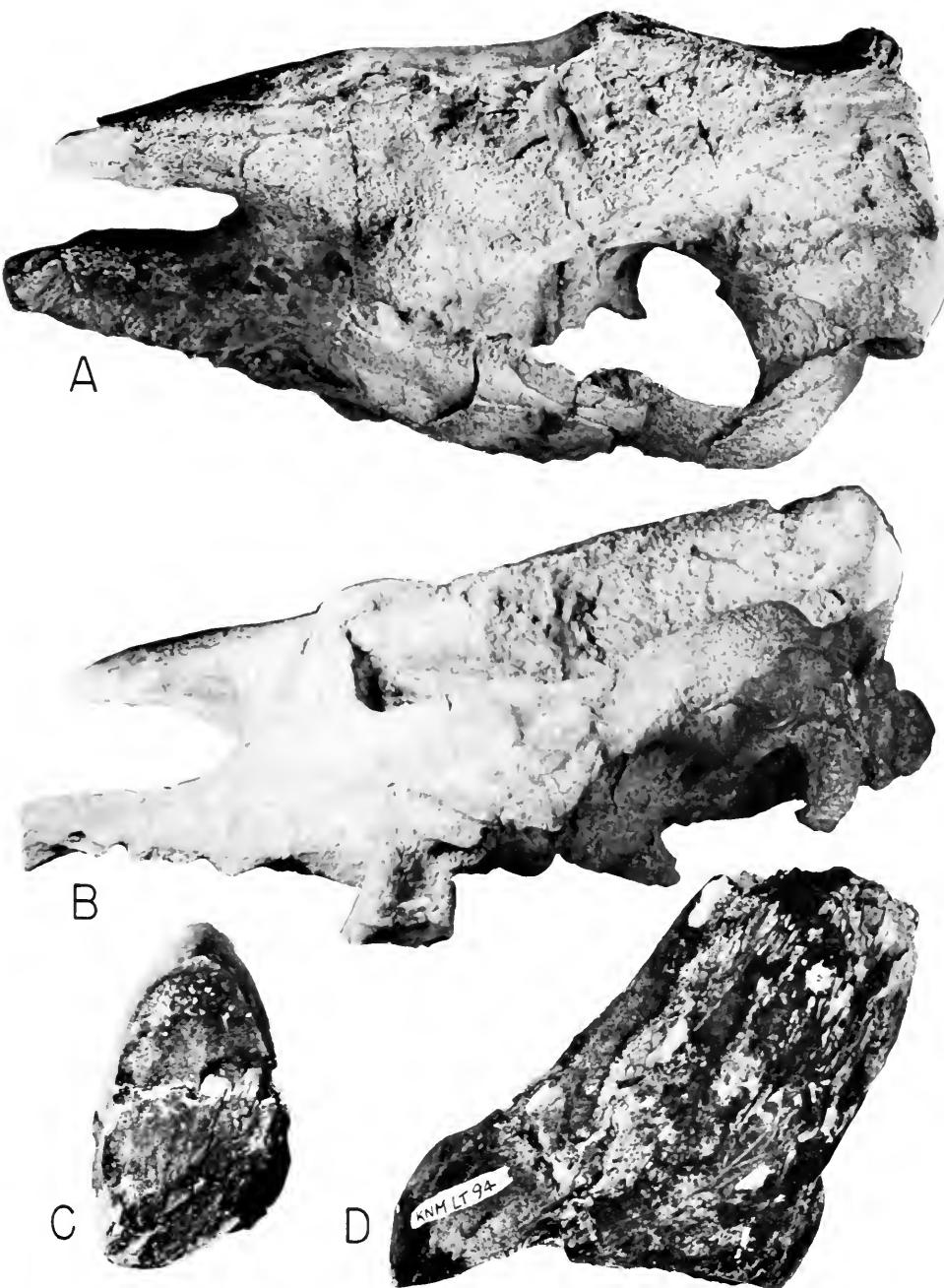


Figure 4. *Brachypatherium lewisi* sp. nov. KNM LT 94. A, dorsal, and B, left lateral views of skull. C, crown, and D, lateral views of left I^1 . A and B $\times 0.2$, C $\times 0.55$, and D $\times 0.61$.

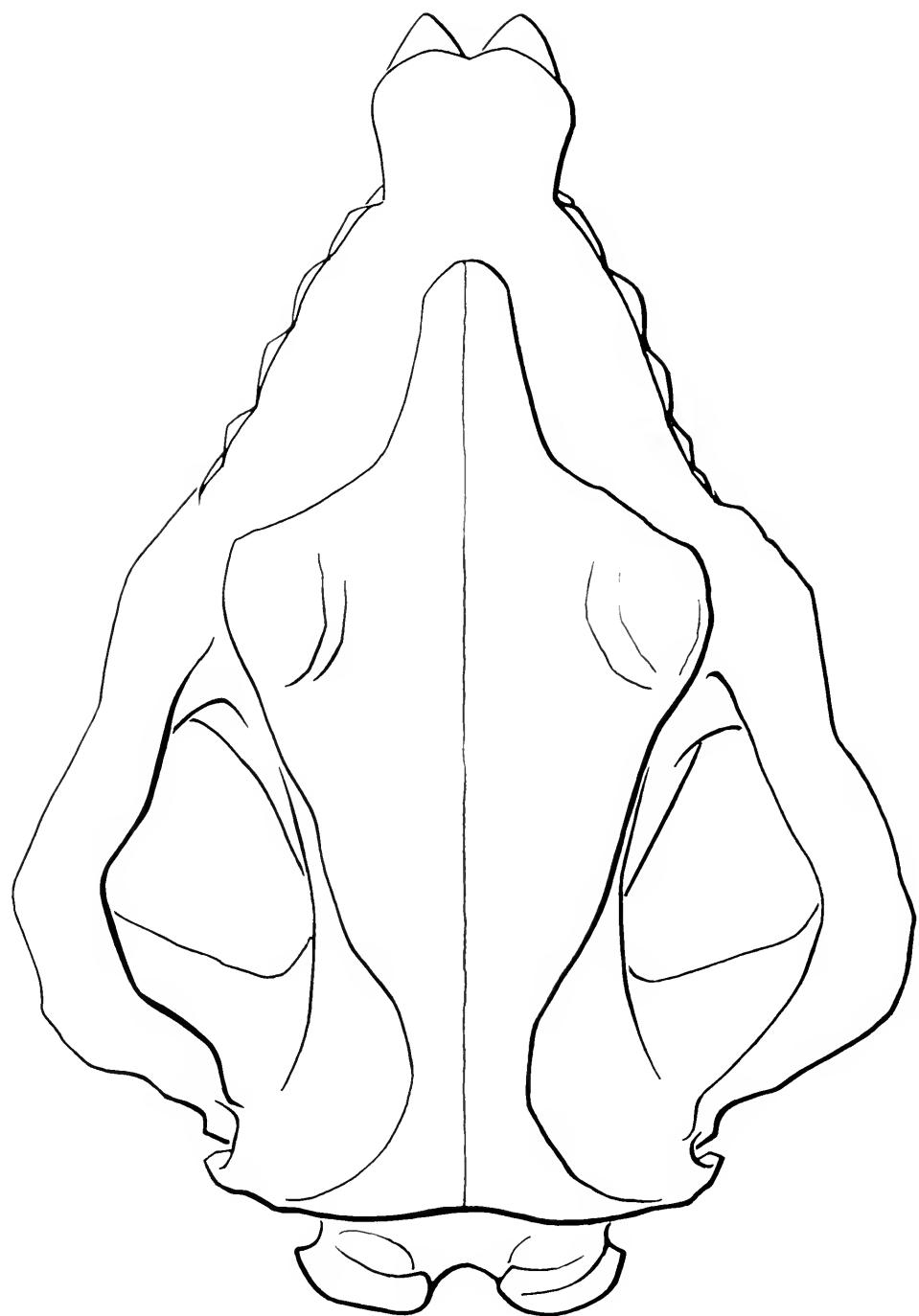


Figure 5. Restoration of dorsal view of *Brachypotherium lewisi* sp. nov. based on KNM LT 94 and KNM LT 88 (type). $\times 0.25$.

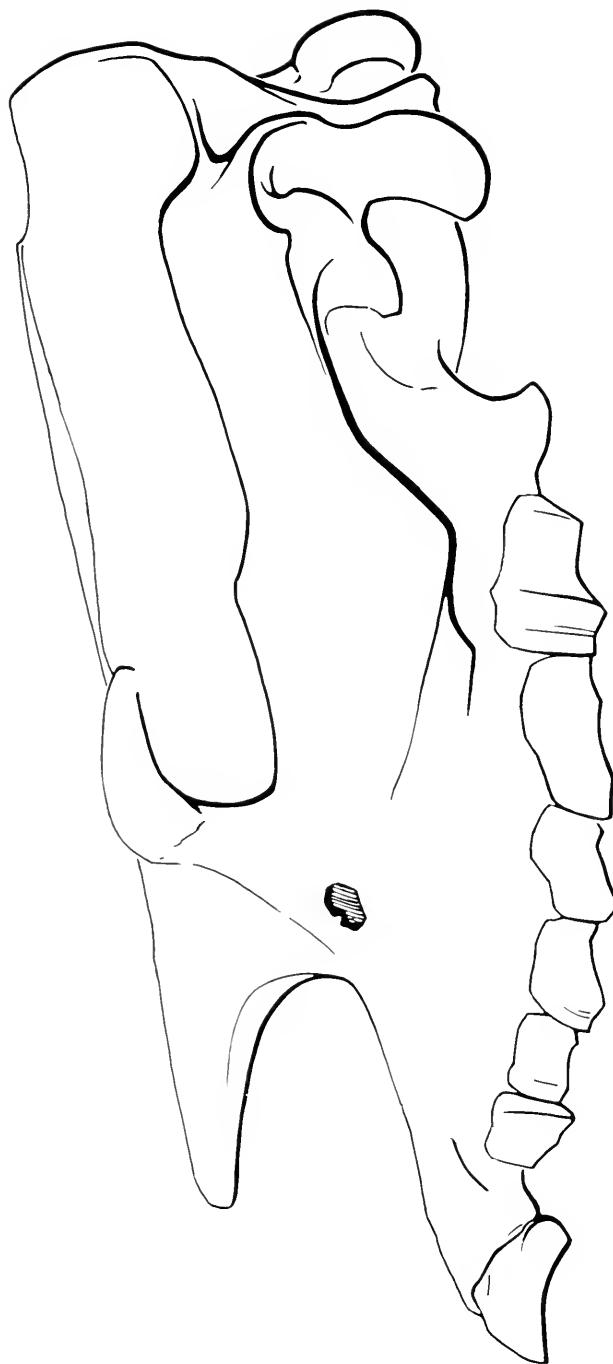


Figure 6. Restoration of left lateral view of *Brachypotherium lewisi* sp. nov. based on KNM LT 94 and KNM LT 88 (type). $\times 0.25$.

the anterior border of the orbit is above the front of M^2 . The superior border of the orbit is swollen, and the orbital cavity itself is 8 cm high. There is no indication of a frontal horn. The parieto-occipital crests converge behind, the least distance between them being only 45 mm. The upper portion of the occiput is missing, as it is in the type skull, and the left occipital condyle only is preserved. The distance from the posterior border of the condyle to the posterior border of M^2 on the same side of the skull is 35 cm, somewhat less than the same dimension in the type, which is otherwise smaller in the length from anterior border of orbit to external auditory meatus (see Table 1). The zygomatic widths are rather different in the two skulls, being greater in the shorter skull, but in either measurement some distortion has to be taken into account, and the actual widths most probably were not so dissimilar. The widths of the frontals over the upper borders of the orbits appear to differ hardly at all in the two specimens.

A composite reconstruction of the skull of *B. lewisi*, based on these differently crushed skulls, is given in Figures 3, 5, and 6.

The skull of *Brachypotherium aurelianense*, as described by Nouel (1866), measures only 50 cm from occipital crest to tip of nasals, and its zygomatic width is 35 cm; the skull, therefore, is relatively wider than that of the Lothagam species. The nasals, as measured from the nasofrontal suture (this suture does not show in the Lothagam skulls) are 20 cm long, and are thickened not far from the tip, which is taken by Nouel as evidence for the former presence of a narrow nasal horn. There is further a rounded elevation on the frontals indicating a second horn. The depth of the nasomaxillary notch from the tip of the nasals is 16 cm, and the distance from the deepest point of this notch to the orbit is 8 cm, shorter relative to the depth of the nasomaxillary notch than in the Lothagam species. The premaxillaries are

incomplete in the skull of *B. aurelianense*, but isolated large upper incisors have been found in the same deposits and there seems no doubt that *B. aurelianense* possessed incisors of this type, as do other species of *Brachypotherium*. The cheek teeth P^2-M^3 (P^1 is represented by an alveolus) are decidedly smaller than those of later *Brachypotherium* species (Table 2). The upper jaw of *B. snowi* has cheek teeth as large as those in *B. brachypus* or *B. goldfussi*, and shows a large alveolus for I^1 . The incisor, however, is placed more forward relative to the premolars in *B. snowi* than in *B. lewisi*: the interval between the incisor alveolus and the P^2 is nearly 90 mm, as opposed to some 40 mm in the larger Lothagam skull.

Of the dentition of KNM LT 94 only LM^2 is in place, although RM^2 , LI^1 and parts of LM^1 and 3 were found in the adjoining matrix. M^2 is more worn than that in the type skull, down to 25 mm from the crown base externally, but is otherwise exceedingly similar to it in both structure and dimensions (Table 2). The posterior cingulum of M^3 is somewhat weaker than in the type, forming a ridge only 15 mm wide; but the ridge along the mediusinus base is the same; the inner cingulum of M^1 is slightly more developed. The left upper incisor (Fig. 4, C and D) measures 65 mm anteroposteriorly and 45 mm transversely just below the crown at the base of the root. The root, as preserved, is 7 cm long and has a blunt apex, 45 by 35 mm in diameters. The distorted alveoli in the type skull would have lodged upper incisors of the same dimensions. The crown bulges out above the root and its antero-posterior and transverse diameters are 90 mm and 44 mm, respectively. An isolated anterior portion of LI^1 (KNM LT 85) is somewhat less worn; it shows a convex external and a flat internal surface, which form an edge in front that is distinct at the occlusal surface and fades away toward the crown base. The width of the crown is over 30 mm; the anterior crown height is

TABLE 3. MEASUREMENTS OF MANDIBLE AND LOWER TEETH OF *BRACHYPOTHERIUM* (mm)

	<i>B. snowi</i>	<i>B. goldfussi</i>		<i>B. lewisi</i>	
Length P_2 - M_3	—	—	—	295	KNM LT 91 290
P_1 to back of angle	—	—	—	540	—
Height of condyle	—	—	—	250	—
Height at M_3	95	—	—	110	—
Symphysis, length	126	—	—	ca. 140	125
Symphysis, least width	57	—	—	—	50
Symphysis, anterior width	72	—	—	—	60
Condyle, width	—	—	—	140	—
P_1 , length	15	—	—	26	—
width	11	—	—	15	—
P_2 , length	27	—	—	—	34
ant. width	19	—	—	20	19
post. width	22	—	—	25	25
P_3 , length	34	41	—	42	41
ant. width	25	—	—	26	24
post. width	27	26	—	32	31
P_4 , length	43	—	43	43	46
ant. width	—	—	—	31	31
post. width	28	—	35	40	36
M_1 , length	—	48	47	—	53
ant. width	—	—	—	41	—
post. width	—	39	33	45	—
M_2 , length	57	60+	52	62	KNM LT 84 65
ant. width	—	—	—	38	—
post. width	37	34	32	43	ca. 44
M_3 , length	62	61	58	55	—
ant. width	—	—	—	38	—
post. width	34	30	30	40	—

55 mm as preserved; of the massive root only the basal 4 cm are preserved. Like the other teeth, the upper incisor is larger than those of other known species of *Brachypotherium*; the complete upper incisor of *B. goldfussi* (Kaup, 1854: 2, pl. 1, fig. 13) has a crown 81 mm in length, while the width in other specimens varies from 23 to 33 mm. The upper I of *B. aurelianense* (Nouel, 1866, pl. 4, fig. 2) is 66 mm long as is the alveolus for the upper incisor in *B. snowi*. Upper incisors referred to *B.*

heinzelini Hooijer (1963: 47, pl. VII, fig. 2; 1966: 142) have crown diameters 76 to 80 mm long and 24 to 30 mm wide. Certain other teeth in the Lothagam-1 collection deserve mention. KNM LT 100 includes the inner and outer portions of LM^2 (anterior width ca. 90 mm), worn down externally to only 25 mm from the base, and LP^2 , worn to an external height of 20 mm. KNM LT 93, RM³ lacking most of the protoloph, bears a weak posterior cingulum, and the same, wide, ridged internal

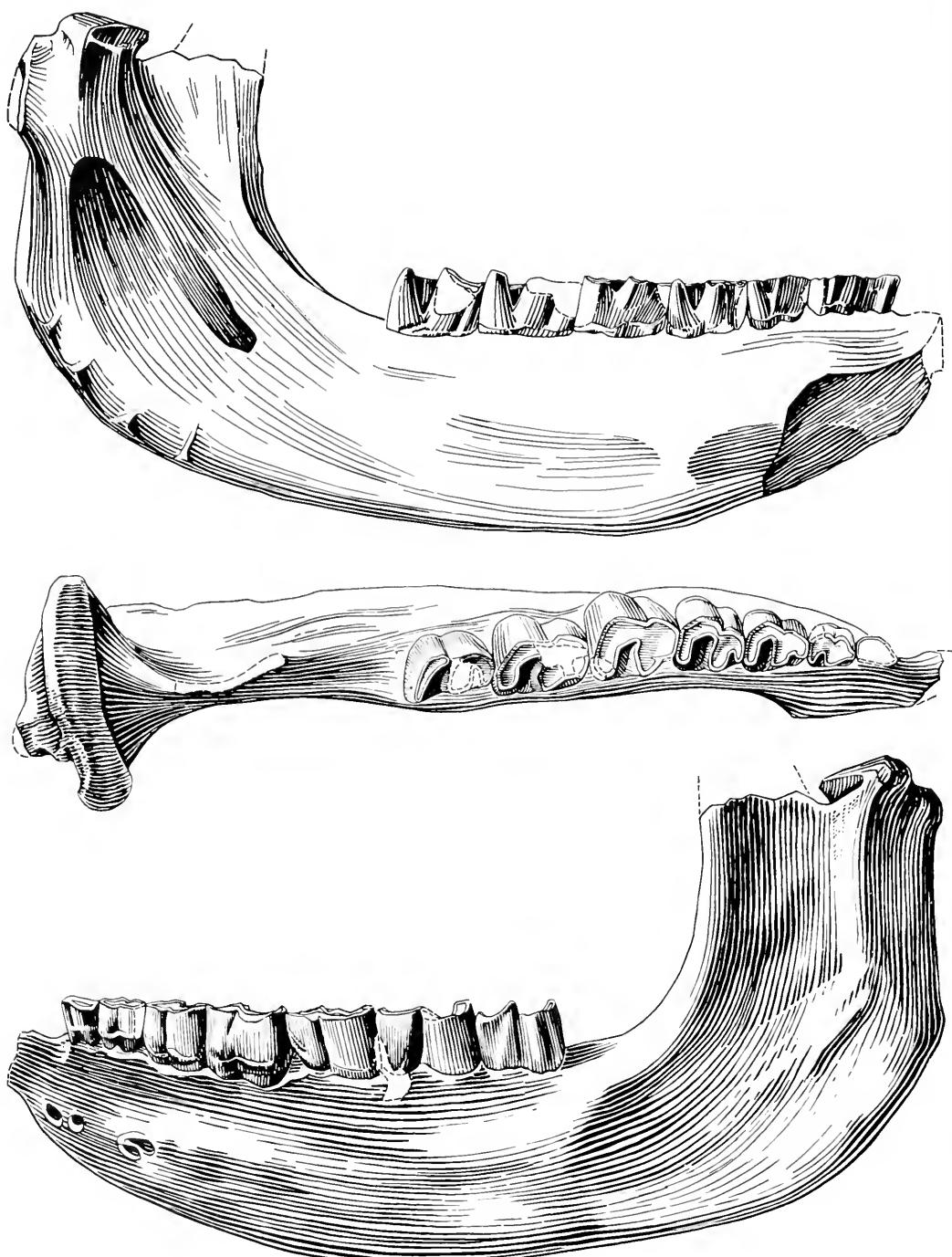


Figure 7. Left ramus of *Brachypatherium lewisi* sp. nov., KNM LT 91, in medial, dorsal and lateral views. $\times 0.25$.

entrance to the medisinus as do the other specimens of this tooth. An entire RP² and an LP² lacking the outer surface (KNM LT 99) agree closely in dimensions with the corresponding teeth in the type skull (Table 2). RP³ (KNM LT 80), lacking the outer surface, has a medisinus extending outward from the internal crown border for a length of 40 mm, exactly as in P³ of the type skull, which is worn to the same extent. We interpret as P₁ an isolated (KNM LT 87) tooth having a gently convex ectoloph 29 mm in length, a basal cingulum, a subtriangular crown, and a posterior width of 20 mm; the dimensions tally well with those of the alveolus for P¹ in skull KNM LT 94. The single root is pointed, slightly curved inward apically, and 4.5 cm long as preserved.

The left half of a mandible (KNM LT 91) includes part of an alveolus for the lower canine, the crowns of P₁ and worn P₂ to M₃ (Fig. 7; measurements in Table 3). The main feature of the cheek teeth is the flattening of the external groove between metalophid and hypolophid; external cingula occur in the premolars and also, although somewhat less distinctly developed, in the molars. These are, in the main, the characteristics of the lower cheek teeth in advanced brachypotherines (Hooijer, 1966: 145).

A second mandible, KNM LT 90 (Fig. 8A) has the symphysial region preserved and shows the alveoli of the two lower tusks, 30 by 20 mm in diameters. There are no traces of teeth between these alveoli; in the mandible of *B. snowi* (Fourtau, 1920: 42) there are two small ones between those of the canines. The length of the symphysis of KNM LT 90 and the length of P₂–M₃ are slightly less than those of KNM LT 91; the least and the anterior width of the symphysis are less than those in *B. snowi* (Table 3). There is no trace of an external cingulum in the teeth of this specimen, and the flattening out of the external groove is not so marked either, indicating a certain amount of individual

TABLE 4. MEASUREMENTS OF UNWORN LOWER PREMOLARS OF *BRACHYPOTHERIUM LEWISI* (mm)

	ant. post.	ant. transv.	post transv.	height, external
P ₂	35	—	24	47
P ₃	43	26	—	55
P ₄	—	33	—	56

variation in these characters. An isolated RM₂ (KNM LT 81), incomplete antero-externally, shows the completely flattened external groove as well as the external cingulum, and there is also a fragment of a lower molar (KNM LT 100) with the same features.

Unworn, although incomplete, lower premolars are known (KNM LT 83), and these reveal the full heights of the crowns (Table 4). KNM LT 86 includes external portions of lower molars with flattened external grooves and, occasionally, external cingula. The unworn hypolophid of RM₃ is 37 mm wide at the base, 34 mm high externally, and 27 mm high posterointernally. The unworn anterior lophid of LM₁ or ₂ is not less than 62 mm high; its width cannot be given.

The two lower molars of *Brachypotherium goldfussi* figured by Kaup (1834: 63, pl. XII, figs. 13 and 14) show the flattened external groove and the external cingulum. One of these molars, entire, is 61 mm long by 30 mm wide, and represents M₃; the other, incomplete behind, is at least 60 mm long, and its width is 34 mm. Other lower molars are recorded by Kaup (1854: 3, pl. 2, figs. 14–16), and their measurements, and those of a mandible figured by De Blainville, are given in Table 3. An M₂ of *B. heinzeli* from Napak, Uganda (Hooijer, 1966: 146, pl. 8, fig. 2), is shorter and wider, 56 by 37 mm, and an unrecorded M₃ from Napak (IIC, 1965) is 60 mm long by 33 mm wide; the Lothagam molars are wider than these.

The full lower milk dentition is preserved in an incomplete right ramus, KNM LT 84 (Fig. 10, C and D), which also contains

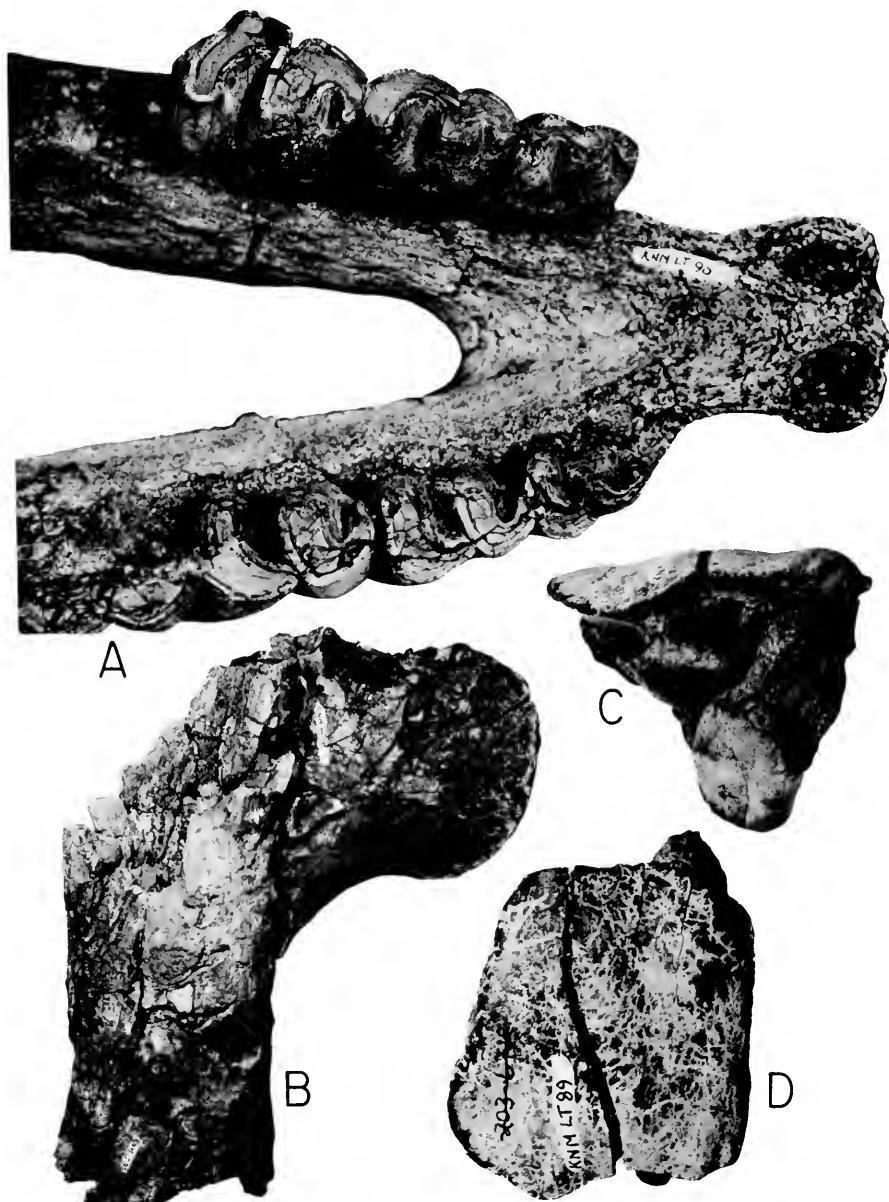


Figure 8. A and B, *Brachypotherium lewisi* sp. nov. A, KNM LT 90, dorsal view of anterior portion of mandible. $\times 0.5$. B, KNM LT 97, portion of shaft of left femur showing third trochanter, anterior view. $\times 0.3$. C and D, *Ceratotherium praecox* sp. nov. ref. KNM LT 89, crown and lateral views of right M^2 . $\times 0.6$.

M_1 and the alveolus for M_2 . The milk molars show moderately flattened external grooves and very weak external cingula.

As Table 5 shows, the milk molars of *B.*

lewisi from Lothagam exceed those of *B. brachypus* in size. DM_{2-4} and M_1 of this species (Upper Vindobonian of La Grive-Saint-Alban) have been figured by Depéret

TABLE 5. MEASUREMENTS OF LOWER MILK MOLARS OF *BRACHYPOTHERIUM LEWISI* (mm)

	<i>B. brachypus</i>	<i>B. lewisi</i>	<i>B. sp. cf. B. lewisi</i>
		KNM LT 84	Ngorora
DM ₁ , length	—	ca. 20	—
width	—	12	—
DM ₂ , length	25	32	—
ant. width	—	—	—
post. width	—	18	—
DM ₃ , length	36	43	46
ant. width	—	21	21
post. width	—	23	24
DM ₁ , length	39	46	—
ant. width	—	25	—
post. width	—	26	—

(1887, pl. XXIV), who believed them (p. 223) to be DM₁₋₄. Measurements were not given; the lengths of the crowns in Table 5 have been taken from his figures. The La Grive specimen has a strong external cingulum at the posterior lophid of DM₃. The length of DM₂-M₁ is 150 mm in *B. brachypus*, against no less than 172 mm in *B. lewisi*.

Of postcranial material from Lothagam-1 there is an incomplete atlas belonging to skull KNM LT 94. One of the wings is complete, indicating that the full width was some 36 cm. There is also a shaft of a left femur, KNM LT 97 (Fig. 8B), with a very large third trochanter, 11-12 cm high and projecting 11 cm beyond the shaft, the dimensions of which just below the process are 9 cm transversely and 7.5 cm antero-posteriorly. These bones indicate an animal nearly of the size of *Ceratotherium simum*, the full atlas width of which is 38 cm, and the corresponding shaft diameters of the femur are 9 by 6 cm. The third trochanter in *C. simum* is proportionately smaller, however, measuring only 9 cm in height and projecting but 7 cm beyond the shaft.

There is fragmentary evidence of very large brachypotherines in earlier Pliocene African deposits. D'Erasmo (1954) de-

scribed and figured a large M¹ or ², identified as *Teloceras* sp., from the Sahabi of Libya, which is somewhat older than Lothagam-1. Impressed by its size, Hooijer (1968: 90) suggested that this tooth might represent a species of *Indricotherium*. *B. lewisi* reveals its correct position. The Sahabi molar possesses an ectoloph that is flattened posterior to the paracone style, a weak antecrochet, a crochet that extends half way across the medisimus and, to judge from d'Erasmo's figure, a trace of an external cingulum; all these are characters seen in the Lothagam material. The specimen exceeds in size all M¹ and M² in our collection. Ngorora, Kenya, a deposit approximately 10 million years old, has yielded a large lower milk molar with an external cingulum that has been identified as *Brachypotherium* sp. (Hooijer, 1971). The dimensions of this tooth, L dm₃, are very close to those of *B. lewisi* (Table 5). More material is of course needed to settle the specific status of the Sahabi and Ngorora forms; for the present we may list them as *Brachypotherium* sp. cf. *B. lewisi*.

The genus has been present in Africa since early Miocene time. Presumably the group was an immigrant one, descendant from a Eurasian species close, or possibly ancestral to, the European *B. aurelianensis*. Whether, once established, the African species evolved in that continent in parallel to the Eurasian ones is an open question; descent of *B. lewisi* from *B. snowi* of Moghra could have taken place during the time available, however.

Ceratotherium Gray

In the Lothagam-1 collection there is one specimen of a rhinoceros that is not referable to *Brachypotherium lewisi*. This is KNM LT 89, a nearly unworn right M² lacking the lingual portion of the metaloph (Fig. 8, C and D).

This tooth differs from that of *B. lewisi* in being more hypsodont, with a very flattened ectoloph that bears only a faint

trace of a paracone style, a decided anterior protocone fold, a posteriorly bulging inner portion of the protocone but no antecrochet, a strong crochet, a small crista and a postsinus as deep as the medisinus. These are molar characters seen in the living African rhinoceroses, and it is clear that we have a specimen of this group in Lothagam-1.

The ectoloph is very gently undulating, being a little depressed at the base between the roots, slightly convex at the middle in the upper part of the crown and a little concave in the upper part of the posterior half. Wear on the ectoloph reaches back only to the place of origin of the crochet; the total height of the crown at the metaloph can thus be measured, as can the maximum length. The crown is higher than it is long. The anterior border of the ectoloph, the parastyle, is essentially straight; the posterior border, the meta-style, inclines posteriorly, from the root on, to form a posterior convexity in the upper third of the crown. The anterointernal corner of the crown is angular. The anterior cingulum is well developed but there is no cingulum around the flattened medial face of the protocone. What is preserved of the medisinus entrance shows no cingulum either. This entrance was clearly narrow and V-shaped. A sharp protocone fold is present in the anterior face of the protoloph above the cingulum. There is no indication of a posterior protocone fold such as would be involved in the formation of an antecrochet. On the contrary, the inner portion of the protoloph is swollen basally to give the effect of a backward curvature to the lingual portion of the loph. Within the medisinus, just buccal to the posterior bulge of the protocone, is a long, robust crochet that arises from the buccal end of the metaloph and extends almost fully across the sinus; it maintains its size to the base of the crown. A small, narrow crista, 5 mm in length at the stage of wear reached, projects from the ectoloph near the antero-external corner of the medisinus.

It falls well short of reaching the crochet and is confined to the upper part of the crown; had wear gone on for 6 or 7 mm more all trace of it would have disappeared. The postsinus is fully as deep as the medisinus.

This molar shows resemblances to both *Diceros* and *Ceratotherium*. Similarity to the former is seen in the angular, not rounded, anterointernal corner and non-oblique protoloph, and in the failure of crochet and crista to meet (this last is usual in *Diceros* while the reverse is usual in *Ceratotherium*, but occasional individuals of the one show the character of the other). Resemblances to *Ceratotherium* are the weakly undulating ectoloph with barely indicated paracone style, the greatest length of the ectoloph at the apical third and not at the middle, the V-shaped, not U-shaped, entrance of the medisinus, the depth of the postsinus equalling that of the medisinus and, strikingly, the degree of hypsodonty. An unerupted M^2 of a Recent *D. bicornis* (MCZ Dept. of Mammalogy, no. 51479) has an ectoloph height at the metaloph of 56 mm and an ectoloph length of 54 mm, whereas KNM LT 89 measures 74 mm in height and 63 mm in length. (The early stage of *D. bicornis* from the Usno and Shungura formations, Omo, no doubt had an even lower M^2 ; two unworn M^3 from these deposits have heights 1 mm greater than lengths, whereas in Recent specimens height exceeds length in this tooth by 10 mm, or more—Hooijer, 1969: 87).

We believe that KNM LT 89 represents a species that had departed from a *Diceros* ancestry in the direction of *Ceratotherium* and that it should be placed in that genus as the earliest representative so far known.

All rhinoceros remains from the Kanapoi and the Ekora are attributable to an extinct species of *Ceratotherium* that is also intermediate in many respects between the two living genera. The Lothagam specimen cannot be separated from it on the evidence available.

Ceratotherium praecox sp. nov.

Diagnosis. Skull differing from *C. simum* (Burchell) in greater concavity of skull roof, cranium less extended posteriorly, occiput more vertically inclined; cheek teeth not as hypsodont, lophs and lophids not markedly oblique, anterointernal corners of upper teeth not rounded, no medifossettes in P^4-M^2 and no fossettids in lower cheek teeth, internal cingula in upper cheek teeth variable.

Type. KNM KP 36, incomplete skull with damaged LM^2-3 and RP^4-M^3 , lacking anterior portion, left zygomatic arch, basiscranium and much of the skull roof.

Hypodigm. The type and the following specimens: KNM KP 30, occipital portion and nasals, numerous fragments; KNM KP 41, distorted skull with RP^2-M^3 , $L\ dm^1(?)-P^3$, lacking much of left side, palate and basiscranium; KNM KP 40, incomplete $L\ dm^2$; KNM KP 35, incomplete RP^2 ; KNM KP 32, incomplete rami with LP_2-M_3 , RP_3-M_3 ; KNM KP 33, portion of L ramus with part of unerupted P_3 , P_4 unerupted and unworn M_2 ; KNM KP 30, condylar region of L ramus; KNM KP 34, portion of L ramus with roots of molars; KNM KP 39, incomplete R humerus.

Horizons and localities. Kanapoi and Ekora formations (for details of stratigraphic distribution see Fig. 1); Kanapoi and Ekora, southeastern Turkana District, Kenya.

Referred specimen. KNM LT 89, little worn M^2 , lacking posterointernal portion. Lothagam-1, top Member B; Lothagam Hill, southeastern Turkana District, Kenya. Described above.

Previous finds of Plio-Pleistocene rhinoceroses in East Africa have been recorded by Hooijer (1969). *C. simum* is clearly present from the White Sands of the Usno formation (<3.3 m.y.) on. Two fragmentary specimens from earlier horizons that were referred to the living species in that paper demand reconsideration in the light of the evidence here presented.

These are the fragment of left maxillary with worn and damaged M^1-3 from the Chemeron Formation (locality J. M. 507) and the fragments of left maxillary with damaged P^4 and M^2-3 from the "lower level" (= Mursi formation) at Omo (Hooijer, 1969: 77, 86, pl. 2, fig. 1, pl. 5, figs. 4-5). The Chemeron and the Mursi correlate faunally with the Kanapoi, and we now suspect that these specimens are likely to be *C. praecox*. In support of this, M^2 lacks the medifossette and has an angulate anterointernal corner; the Mursi specimen has a medifossette in M^3 , but unfortunately our new material contains no well-preserved example of this tooth. Pending further knowledge, we list both as *C. sp.* cf. *C. praecox*.¹

Description and discussion. The type skull, KNM KP 36 (Fig. 9, A), lacks the anterior portion; the foremost tooth on the right side being P^4 and on the left M^2 . Both M^3 are badly broken and the remaining cheek teeth are either damaged or missing. The sides of the skull are very imperfect, especially the left, but on the right the anterior and lower border of the orbit is preserved, as is almost the entire zygomatic arch. The anterior border of the orbit is placed above the anterior border of M^2 , as in *D. bicornis*, rather than above that of M^3 , as in *C. simum*. The posterior elongation of the occipital portion of the cranium, so characteristic of Recent *Ceratotherium*, is likewise not in evidence. The pterygoid fossa and the median protuberance of the basisphenoid are shaped as in *Diceros*, the posterior zygomatic root is not placed so high above the palatal level as in Recent *Ceratotherium* nor so far behind the palate. The occipital surface is very

¹ A clearly recognizable *C. simum germano-africanum* does occur in the Chemeron but at locality J. M. 91, which is younger (ca. 2 m.y. — V. J. Maglio, personal communication). This subspecies occurs at Laetolil, probably from the upper level which has a similar age. A right M^3 of the same form comes from Kanam West. Part, at least, of Kanam correlates with Kanapoi, but it is uncertain that all of it does.

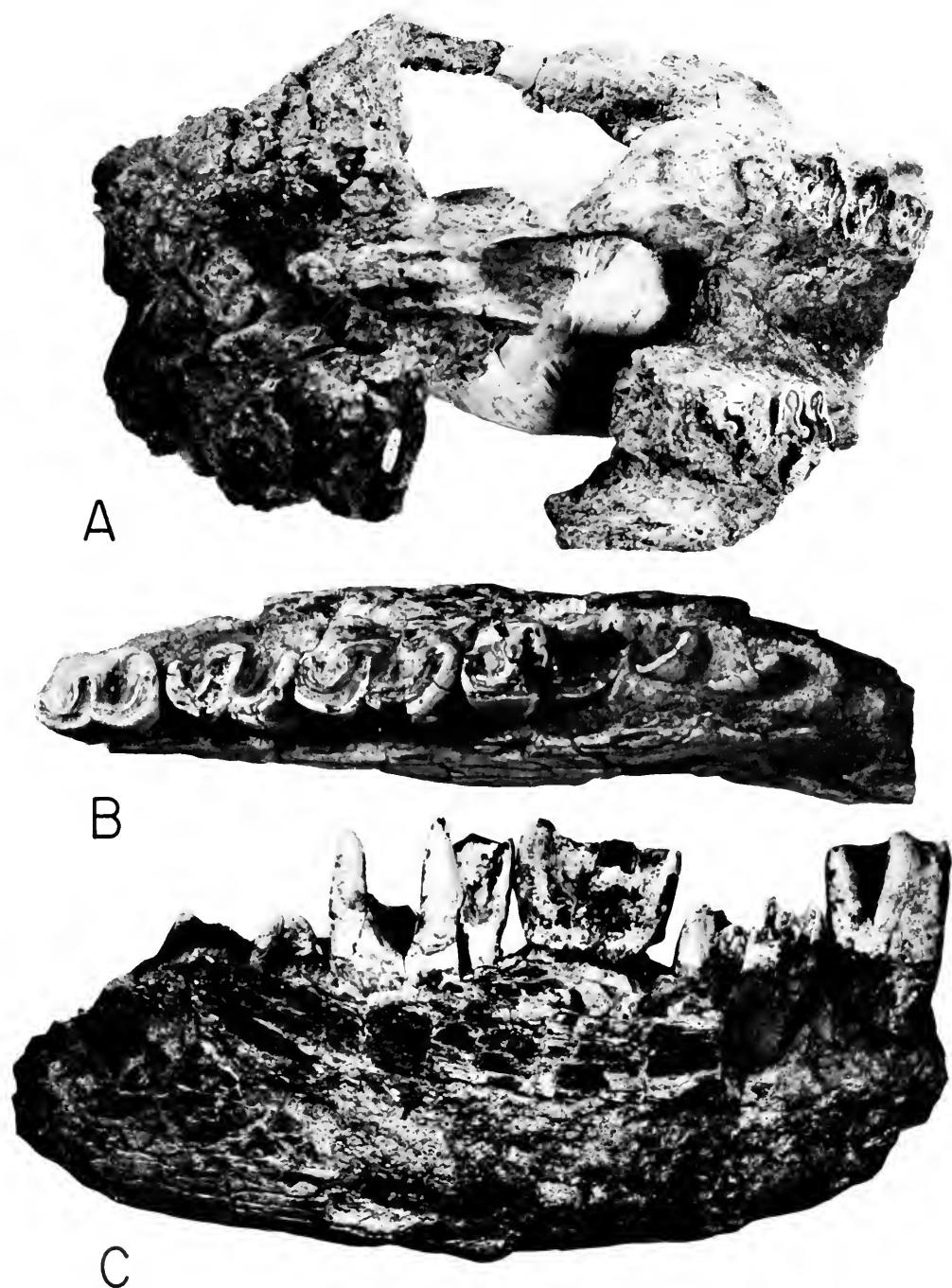


Figure 9. *Ceratatherium praecox* sp. nov. A, KNM KP 36, type, ventral view of incomplete skull. $\times 0.19$. B and C, KNM KP 32. Dorsal, B, and medial, C, views of portion of left ramus with P_3 - M_3 . $\times 0.4$.

TABLE 6. MEASUREMENTS OF SKULLS OF *DICEROS* AND *CERATOTHERIUM* (mm)

	<i>D. bicornis</i>			<i>C. praecox</i>		<i>C. simum</i>	
	MCZ 15693	MCZ 27135	MCZ 8397	KNM KP 36		MCZ 34850	MCZ 24917
Length of P^4 - M^3	185	180	180	205		205	190
From M^3 to back of postglenoid process	185	160	170	sin. 230	dext. 250	270	275
From ant. border of orbit to back of occip. crest	365	345	360	ca. 440		500	510
Zygomatic width	320	315	310	340		355	330
Least width of cranium	110	110	120	120		130	115
Width over both M^2	200	200	195	240		230	220

poorly preserved and the condyles are missing, but it is nevertheless clear that the inclination of the occiput is not nearly as marked as in the modern white rhino. The occipital crest is tolerably well preserved, and its posterior notch, although developed, is not as deep as in *C. simum*. In all these characters, therefore, the Kanapoi *Ceratotherium* is not far removed from *Diceros*. Most of the dorsal surface of the skull is missing, but the occipital portion, from about half-way between the anterior and the posterior zygomatic roots backward, is there and begins its rise only above the posterior zygomatic root, as in *D. bicornis*, rather than being weakly concave throughout as in *C. simum*. The cranial measurements that can be taken (Table 6) show that this skull is somewhat larger than Recent skulls of *D. bicornis* (MCZ, Dept. Mamm. nos. 15693, 27135, and 8397) and is also more elongated postdentally (cf. length P^4 - M^3 vs. length from M^3 to back of postglenoid process), although not to the extent seen in Recent *C. simum* (MCZ, Dept. Mamm., nos. 34850 and 24917). Since the occiput is superficially damaged above, only the approximate depth of the occipital notch can be given, which is 20 mm as against 20-30 mm in *D. bicornis*, and 50 mm in *C. simum*.

The dentition is very defective, but the internal crown portions preserved show that the metaloph is transverse in its

course, and that the protoloph bulges posteriorly in its lingual third, forming three-fifths of the internal surface, thus less obliquely placed than in *C. simum*. The postsinus is as deep as the medisinus, and there is no medifossette. The teeth thus present the same characters as does the Lothagam M^2 described above, typical of an emerging *Ceratotherium*. Because of advanced wear the crown heights cannot be determined. The internal cingulum is slight in P^4 , absent in the molars.

Skull KNM KP 30 from Kanapoi consists of a great many fragments, from which it has been possible to restore the occipital portion; this shows a sudden rise in profile from about 12 cm in front of the crest to the top, making the dorsal profile as a whole more deeply concave than in *C. simum*. The only dimensions that can be given are the least distance between the frontoparietal crests, 80 mm, and the least width of the cranium, ca. 140 mm; this was evidently a wider skull than the type. A very small portion of the occipital crest, on the left side, is preserved, showing that the posterior indentation of the crest was shallow, again as in the type. What little is preserved of the posterior occipital surface shows that the occiput, although more inclined posteriorly relative to the dorsal surface than in *D. bicornis*, is less posteriorly inclined relative to the dorsal surface than in *C. simum*. It is just possible to

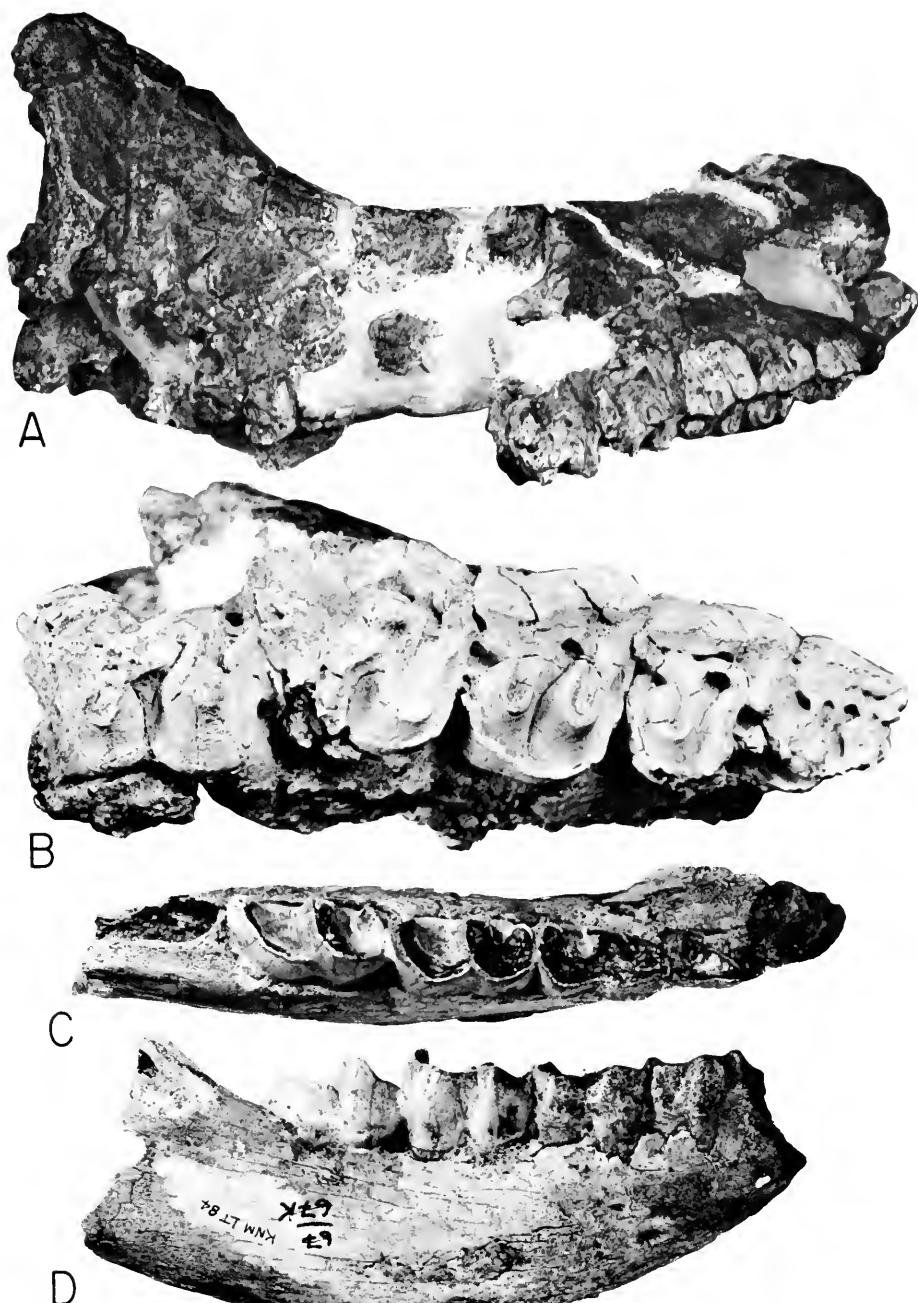


Figure 10. A and B, *Ceratotherium praecox* sp. nov. KNM KP 41. A, right lateral view of distorted skull (see p. 23). $\times 0.2$. B, crown view of right P^2-M^3 . $\times 0.52$. C and D, *Brachypotherium lewisi* sp. nov. KNM LT 84. Dorsal, C, and right lateral, D, views of juvenile right ramus with dm_{1-4} , M_1 . $\times 0.38$.

measure the angle between the dorsal plane, along the left temporal crest, and the occipital plane, of which a portion is preserved just below the nuchal crest where the temporal crest would have intersected it had it been straight instead of curving off laterally. The portion of the occipital surface preserved is part of a crest running from the nuchal crest downward, which converges with its fellow on the other side to a point in the median line above the occipital foramen. The angle that may thus be measured is 65 degrees; it is 65, 70, and 80 degrees in the three *D. bicornis* skulls, and 45 and 50 degrees in the two *C. simum* skulls used for comparison.

The only other portion of this specimen that could be restored from the fragments is the nasal, but it too is defective and mostly from the right side. The width cannot be determined exactly as the median line is not well marked off, but it would appear to have been *ca.* 160 mm, which is about as in *C. simum* (160–190 mm) and wider than in *D. bicornis* (125–145 mm), as would be expected in such a wide skull.

A third skull of this early *Ceratotherium* (Fig. 10, A, B) comes from the slightly younger Ekora formation (KNM KP 41) and has been crushed, distorted and partially fragmented in the ground. The dorsal profile, as preserved, is certainly too flat in the nasofrontal region and too steeply rising in the parieto-occipital region. Although the specimen is somewhat twisted lengthwise and only the right maxillary is in contact (the left being detached), it nevertheless shows the elongation of the postdental portion, which in this species surpasses *Diceros*. Nasal and frontal horn bosses do not appear to have been extensive. The angle between the dorsal and occipital surfaces of the occiput cannot be calculated. The naso-maxillary notch extends to a point above the anterior border of P^3 and the anterior border of the orbit is above the anterior border of M^2 , as in the type.

The anterior premolar, possibly a per-

TABLE 7. MEASUREMENTS OF UPPER TEETH OF *C. PRAECOX* AND *D. BICORNIS* (mm)

	<i>C. praecox</i>	<i>D. bicornis</i>
	KNM KP 41	
P^2 , length	30	29–32
ant. width	36	33–44
post. width	42	38–50
P^3 , length	40	36–44
ant. width	—	50–57
post. width	51	51–60
P^4 , length	—	43–51
ant. width	59	59–67
post. width	54	55–66
M^2 , length	67	58–70

sisting DM^1 , is *in situ* on the left side; it is considerably worn, with a transverse crown diameter of some 22 mm. P^2 is well preserved on the left side, P^3 incomplete anterointernally on both sides, and P^4 present on the right side. These premolars are in a good state of preservation, and compare very well with those of modern *D. bicornis* having heavy internal cingula and protolophs and metalophs in the transverse position, but differing in the absence of a paracone style, the ectolophs being as flattened and undulating as those in modern *Ceratotherium*. The postsinuses are as deep as, or only slightly shallower than, the medisinuses. All the premolars of KNM KP 41 have well-developed crochets, but only in LP^3 is the crochet joined by a crista to isolate a medifossette, which is usually present in all cheek teeth of *C. simum*. The molars, of which only the right series is preserved and of which the external parts are gone, have weak inner cingula, which is the only detectable difference from the Lothagam M^2 .

A left condylar portion of a mandible, KNM KP 31 is intermediate between living *Diceros* and living *Ceratotherium* in several respects: 1) the distance from dental foramen to base of posteromedial articular surface is somewhat greater than in *Diceros* but much smaller than in *Ceratotherium*,

TABLE 8. MEASUREMENTS OF LOWER TEETH OF *CERATOTHERIUM* AND *DICEROS* (mm)

	<i>C. praecox</i>	<i>D. bicornis</i>
KNM KP 32		
P ₂ , width	20	17-19
P ₃ , length	41	35-38
ant. width	27	21-23
post. width	28	25-27
P ₄ , length	47	41-44
ant. width	29	25-27
post. width	33	29-31
M ₁ , length	52	—
post. width	34	29-32
M ₂ , length	54	50-53
ant. width	34	28-32
post. width	34	31-34

indicating that the jaw orientation was evidently more nearly as in *Diceros*; 2) the condylar area is more massive and wider below the condyle than in our specimens of *Ceratotherium simum*; and, 3) the surface anterior to the medial portion of the condyle is flatter and more rugose than in *Diceros* and as flat but less rugose than in *Ceratotherium*. The medial surface beneath the condyle is more markedly concave than in either of the two living forms.

A right and a left (Fig. 9, B, C) ramus of the mandible (KNM KP 32) preserve LP₂, L and RP₃, erupting P₄, M₁₋₂, and erupting M₃. These teeth do not show any tendency to form the fossettids typical of *C. simum*. They are a little larger than in *D. bicornis*, and are higher-crowned. The height of the unworn posterointernal

column of M₂ is 51 mm, as against 36 mm in a Recent specimen of that species (MCZ, Dept. Mamm., no. 41993). In striking contrast to more advanced *Ceratotherium* there is no greater obliquity in the posterior portions of meta- and hypolophid in the fossil than in Recent *D. bicornis*. An erupting M₂ in a left mandibular ramus (KNM KP 33) has a posterior height of ca. 53 mm, showing once again the greater hypsodonty in the Kanapoi teeth as compared to Recent *D. bicornis*.

A somewhat imperfect right humerus (KNM KP 39) is the only posteranial element of a rhinoceros found thus far at Kanapoi. The caput and the proximal tuberosities, as well as the distal portion of the shaft and the trochlea and condyles, are superficially damaged, but the bone does not appear to differ in any major way from the humeri of modern *Diceros* and *Ceratotherium*; in dimensions it slightly exceeds the former but is notably less robust than the latter.

The *Diceros* group of rhinoceroses may have been essentially confined to Africa throughout their history, although their origin, if it occurred there, is at present wholly obscure. Until recently the earliest known species were the early Pliocene *Diceros pachygнатus* (Wagner) and *D. douardieus* Guérin from Europe and North Africa, respectively. On this basis a Eurasian origin could plausibly have been argued, but the discovery of the rather aberrant *Paradiceros mukirii* in the late Miocene Fort Ternan deposit (Hooijer, 1968) casts a different light on the matter, intimating, as it does, an African—not a

TABLE 9. MEASUREMENTS OF HUMERUS OF *CERATOTHERIUM* AND *DICEROS* (mm)

	<i>C. praecox</i>	<i>D. bicornis</i>	<i>C. simum</i>
KNM KP 39			
Length from caput to medial condyle	355	345-350	400-410
Width over caput and posterior part of lateral tuberosity ca. 160		145-160	180-190
Width at deltoid tuberosity	140	130-140	170-175
Greatest distal width	ca. 160	150-155	175-180

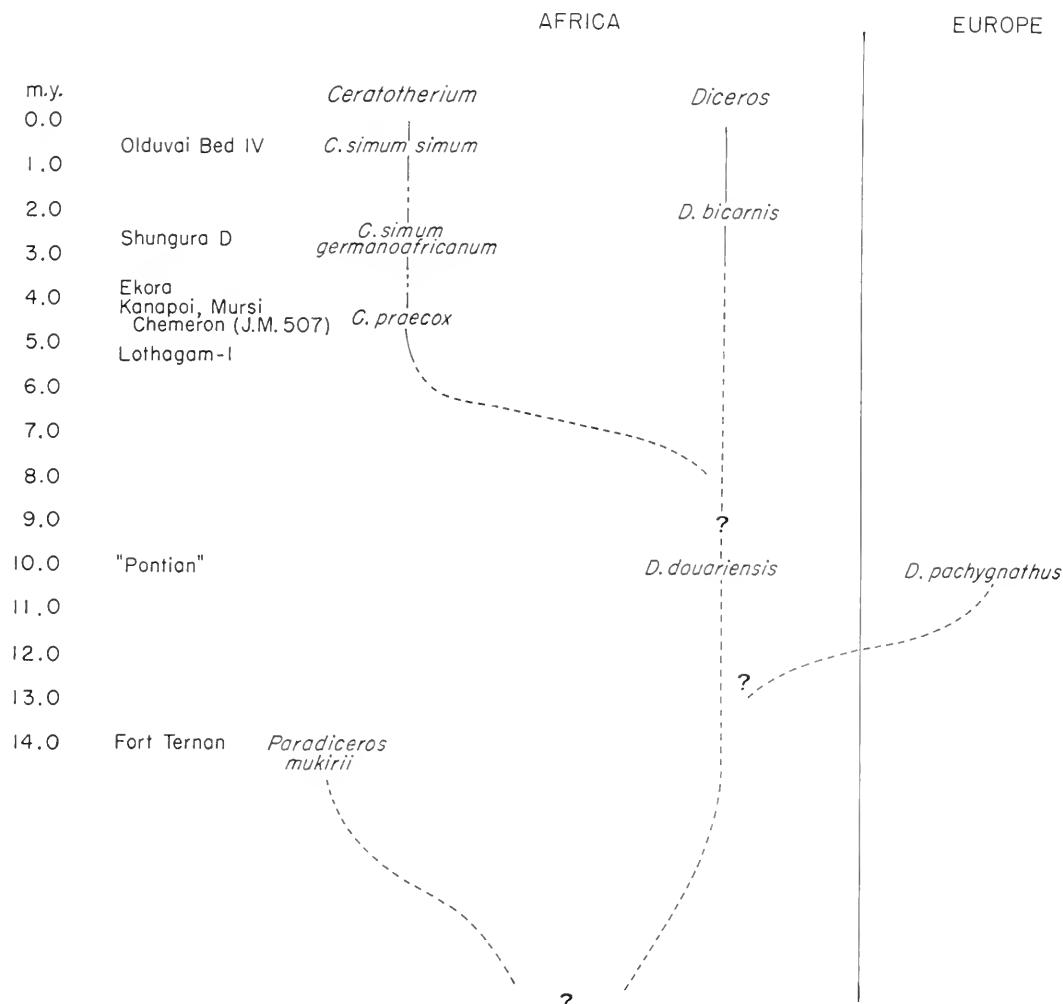


Figure 11. Chronology and geography of the Diceros group of the Rhinocerotidae.

Eurasian—Miocene history of which we are at present ignorant. Whatever the case, the later history, so far as known, is wholly African and *D. pachygnathus* is still the only extra-limital species (Fig. 11). Thenius (1955) has offered the suggestion that *Ceratotherium* diverged from *Diceros* in the course of the Pliocene; the discovery of *C. praecox* goes far toward confirming this.

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APPENDIX

Late Pleistocene Rhinoceros Remains

In order to round out the accounts given here and in Hooijer (1971) of the rhinoceros collected by the Museum's African expeditions, we append this note on two

late Pleistocene or, in the case of one, possibly Holocene, specimens obtained.

On the return trip from Turkana in 1963 a brief stop was made at exposures of the Kapthurin formation west of Lake Baringo and just south of the lava cliff that parallels the road near Kampi ya Samaki. Apart from two small fragments of a cranial roof of *Homo*, the only find of note made there was a rather complete skull of *Diceros*. Metrically and morphologically the specimen is indistinguishable from Recent specimens of *D. bicornis*.

Occasionally, isolated teeth of animals such as *Equus* can be picked up on the surface of Kanapoi (and Lothagam) exposures but have not been found *in situ* in the formation. Into this category falls an isolated P^4 of *Ceratotherium simum* lacking most of the protoloph and with superficial damage to the ectoloph (KNM KP 38). Mineralization apart, the specimen is indistinguishable from corresponding teeth of *C. s. simum*. As regards provenance of such surface finds, there are two possibilities. There recently have been, and in a few places still are, patches of sediment dating back to *ca.* 3,000 B. C. The artifacts found at Kanapoi are associated with these and the teeth may also be. The second possibility is that they have weathered out of coarse sediments thinly deposited in the Kanapoi area following a late Pleistocene period of erosion that preceded the present one. These sediments can be seen here and there in a few of the former gullies that have been exposed by the cutting of the current ones.