Plate 4

FOSSIL RHINOCEROTIDAE (MAMMALIA, PERISSODACTYLA) FROM EAST RUDOLF, KENYA

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ABSTRACT

Two rhinocerotid taxa, *Diceros bicornis* subsp. and *Ceratotherium simum germanoafricanum* have been retrieved from the Plio/Pleistocene sediments to the east of Lake Rudolf, Kenya. Both taxa are known from relatively complete skulls and mandibles and both occur throughout the fossiliferous sequence of the Koobi Fora Formation. The East Rudolf material further documents morphological differences shown by Plio/Pleistocene representatives of the extant black and white rhinoceroses.

INTRODUCTION

During the past five years Plio/Pleistocene sediments from the north eastern shore of Lake Rudolf, Kenya, have yielded a wealth of vertebrate fossils, early hominid remains and associated artefacts. Provisional faunal lists have been published

(Leakey, 1970 ; Maglio, 1971, 1972) as have accounts of the geology (Behrensmeyer, 1970 ; Vondra *et al.*, 1971 ; Bowen and Vondra, 1973), the chronostratigraphy (Fitch and Miller, 1970 ; Brock and Isaac, 1974) and the archaeology (Leakey, M. D. 1970 ; Isaac *et al.*, 1971 ; Leakey and Isaac, 1972). Descriptions and provisional identifications of many of the hominid remains have appeared in press (Day and Leakey, 1973, 1974 ; Leakey, 1970, 1971, 1973, 1974 ; Leakey *et al.*, 1971, 1972 ; Leakey and Walker, 1973 ; Leakey and Wood, 1972). Of the remaining mammalian groups, an account of the colobine monkeys has been published previously (Leakey and Leakey, 1973) and descriptions of three further groups appear in this volume.

Maglio (1972) recognized four distinct faunal assemblages from the East Rudolf region and consequently designated four faunal zones. Few fossil rhinoceroses have been recovered from the oldest assemblage — the *Notochoerus capensis* zone of the Kubi Algi Formation in the Kubi region. The bulk of the East Rudolf fauna, and of the fossil rhinos, has been collected from three successive faunal zones of the Koobi Fora Formation in the Koobi Fora and Ileret regions.

The earliest of the three fauna zones in the Koobi Fora Formation — the *Mesochoerus limnetes* zone — occurs in the Lower Member of the Koobi Fora Formation at horizons up to 35m below the KBS Tuff. Very few specimens have so far been collected from earlier levels in the Lower Member.

The *Metridiochoerus andrewsi* zone fauna has been derived from the Upper Member of the Koobi Fora Formation at levels between the KBS and Koobi Fora Tuffs. Relatively few specimens have been collected from levels immediately above the Koobi Fora Tuff in the Koobi Fora region. The *M. andrewsi* zone also occurs in the Ileret Member of the Koobi Fora Formation at levels between the KBS and Middle Tuffs.

The *Loxodonta africana* zone fauna is so far confined to the Ileret region. Here it occurs in the Ileret Member of the Koobi Fora Formation at horizons between the Middle and Chari Tuffs (Fig. 1).

Rhinoceroses are not prolific members of the fauna in any of the three faunal zones of the Koobi Fora Formation (Harris, in press) and are similarly scarce from contemporary and earlier horizons in the nearby Omo Basin (Hooijer, 1973 ; Guerin, in press). The relative scarcity of the rhinocerotid material severely limits the use of this group for internal correlation within the East Rudolf sequence although evolutionary changes within and between the faunal zones are exhibited by other mammalian groups, particularly the proboscideans, suids and bovids (Maglio, 1972 ; Cooke, in press ; Harris, in press). Fossil remains of both the black and white rhinoceroses occur throughout the Koobi Fora Formation and specimens include virtually complete skulls and mandibles of the two taxa represented. They thereby provide important information on the cranial morphology of Early Pleistocene rhinoceroses. The most common rhinocerotid specimens comprise isolated teeth and jaw fragments. Very few postcranial elements have been recovered to date.

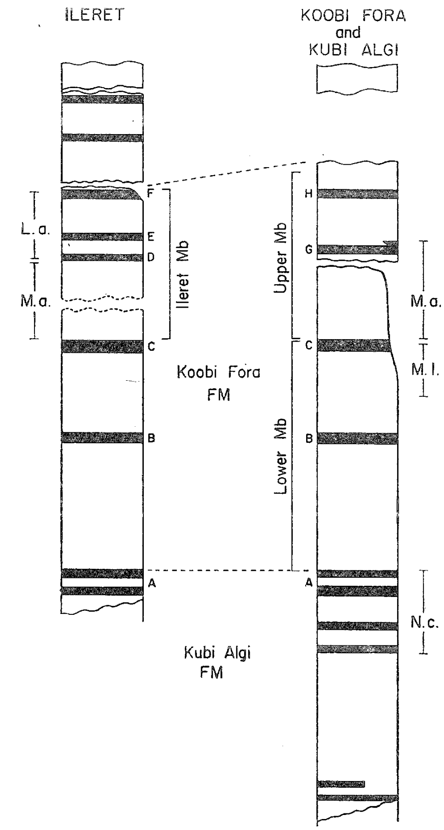

FIG. 1. Diagram of the sequence of tuffs and faunal zones in the East Rudolf succession. The total thickness of the sediments is about 300 m but thicknesses of the tuffs and other units in the diagram are not to scale. Recent geological investigations have shown the *M. andrewsi* zone to extend upwards to the Middle Tuff (E).

A : Suregei Tuff Complex ; B : Tulu Bor Tuff ; C : KBS Tuff ; D : Lower Tuff ; E : Middle Tuff ; F : Chari Tuff ; G : Koobi Fora Tuff ; H : Karari Tuff.

N.c.: *Notochoerus capensis* zone; M. L.: *Mesochoerus limnetes zone*; M.a.: *Metridiochoerus andrewsi* zone; L.a.: *Loxodonta africana* zone.

Abbreviations

Specimen numbers with the prefix KNM-ER are fossils from East Rudolf in the collection of the National Museum of Kenya, Nairobi. Specimen numbers with the prefix OM are recent rhinoceroses from the osteological collections of the National Museum of Kenya. The specimen designated U.B.R.C. in Table I is a modern black rhinoceros skull collected from the east shore of Lake Rudolf in 1968 and now in the recent osteology collection of the Department of Geology, University of Bristol.

SYSTEMATIC DESCRIPTIONS

Superfamily **RHINOCEROTOIDEA** Gill 1872

Family ***RHINOCEROTIDAE*** Owen 1845

Subfamily **Dicerorhininae** Simpson 1945

Genus ***Diceros*** Gray 1821

Diceros bicornis (Linnaeus) 1758. ***Diceros bicornis*** subsp.

Material referred

KNM-ER 636, virtually complete skull; KNM-ER 327, fragmentary R maxilla (P^3–M^3); KNM-ER 1186A, fragmentary R maxilla (P^3–M^1); KNM-ER 1186B, fragmentary R maxilla (M^{2-3}); KNM-ER 1186C, fragmentary L maxilla (P^3–M^1); KNM-ER 1187, fragmentary L maxilla (P^3); KNM-ER 472, immature mandible (L and R P_{2-3}, DP_4; M_{1-2}); KNM-ER 2139, mandible (LP_4–M_2, RM_2); KNM-ER 2156, fragment edentulous R mandible; KNM-ER 691, isolated teeth (LP^2–M^2, RP^3–M^2), KNM-ER 2145 ($L\bar{M}$); KNM-ER 1196, R astragalus.

Horizon

The skull (KNM-ER 636) was collected from the *Loxodonta africana* zone. A fragmentary maxilla (KNM-ER 1186) and the astragalus (KNM-ER 1196) came from the *Mesochoerus limnetes* zone. The remaining specimens were recovered from the *Metridiochoerus andrewsi* zone in the Koobi Fora region.

Description

The skull of the East Rudolf black rhinoceros (KNM-ER 636) is of particular interest in that it is one of very few fossil skulls of this species yet known. In most respects the skull is morphologically similar to that of modern examples of *Diceros bicornis*; the differences are minor and restricted mainly to the cranial region. The specimen is not fully mature, the third molars being present but incompletely erupted. In length the skull matches modern examples of *D. bicornis* but is less wide, though the latter feature may be due to the relative immaturity of the specimen. Many of the sutures, especially those of the facial region, can be distinguished.

The premaxillae and the right anterior premolar are missing. The nasal region was broken and crushed dorsoventrally but has now been restored to its original position. All the foramina of the facial and cranial regions are smaller than in modern skulls, including the infraorbital canal which is sited somewhat higher above the P^4 alveolus than in recent examples. Above the lacrimal canal there is

a large traction epiphysis which is separated from the traction epiphysis of the frontal bone as in immature specimens of the extant *D. bicornis*. The zygomatic arch of the East Rudolf specimen is less massive than in modern skulls and the orbital region of the face is less concave in its dorsal portion and less convex below the orbit.

The occipital region of the modern black rhinoceros is wide and rounded whereas that of the East Rudolf skull appears taller, squarer and narrower. The widest part of the occiput in modern skulls is formed by the ventral portion of the nuchal crest whereas the widest point on the occiput of the East Rudolf specimen is defined by lateral processes from the paramastoid. The paroccipital process is of similar size and shape to that of modern skulls but the paramastoid appears wider and deeper. This may, however, be due to the different shape of the occiput of the East Rudolf skull. The posterior face of the paroccipital process is less concave at its base in the East Rudolf skull, the process itself being directed anteriorly rather than vertically and the long axis of the tip of the process points anteromedially rather than posteromedially. As in modern skulls of *D. bicornis*, the paramastoid bears both lateral and ventral protruberances. The lateral protruberance is more clearly defined and projects farther than in modern examples. The ventral protruberance is sited farther from the lateral process in the East Rudolf skull and its tip has a concave rather than a convex facet.

In the auditory region the hyoid process of the East Rudolf skull is a little larger than that of modern skulls and is also more markedly concave at its distal extremity. The muscular process is large, long and stout, and is apparently more anteriorly orientated than in modern skulls.

The postglenoid processes of the fossil skull are of similar size to modern examples but bear a keel from the posterolateral edge extending to the anteroventral tip of the process. The distal tip of the postglenoid process of the East Rudolf skull appears narrower than in modern skulls, in which the postglenoid processes are rounded posteriorly. The glenoid fossa of the East Rudolf skull is less concave and less posteriorly orientated than in modern skulls but is of similar size.

Both mandibles (KNM-ER 472, 2139) lack ascending rami. The horizontal ramus is deeper and stouter than modern black rhino examples and that of KNM-ER 472 is particularly more robust. Both fossil specimens have wider but shorter mandibular symphyses than modern examples.

There is no difference in dental morphology between the East Rudolf fossil black rhinoceros and recent examples of *D. bicornis*. Most of the fossil teeth are worn but appear slightly less hypsodont than those of extant representatives.

The left astragalus (KNM-ER 1196) is larger than that of modern examples of *D. bicornis*. It differs morphologically from modern examples in that the lateral edge of the lateral calcaneal facet is not produced distally and in that there is no

TABLE I

Skull measurements of *Diceros bicornis* subsp.

	KNM–ER 636	OM 2178	U.B.R.C.
Length nasals to nuchal crest	524	547	502
Max. width skull at anterior edge of orbit	230	258	—
Min. width skull vault at temporal fossa	107	117	—
Max. width skull at posterior edge of zygomatic arch	305	325	297
Min. width supratemporal ridges	77	72	—
Width dorsal edge of nuchal crest	167	189	—
Max. width of occiput	218	236	112
Depth anterior portion of zygoma	42	55	—
Depth posterior portion of zygoma	50	50	—
Max. depth zygoma	50	60	—
Width foramen magnum	46	44	—
Depth foramen magnum	38	40	—
Width occipital condyles	116	126	—
Width left occipital condyle	36	44	—
Depth left occipital condyle	47	52	—
Width right occipital condyle	37	46	—
Depth right occipital condyle	48	53	—
Length palatonarial border to occipital condyles	303	318	—
Length anterior edge orbit to glenoid fossa	216	231	—
Width pterygoid at humular process	91	104	—
Length right postglenoid process	64	62	—
Width right postglenoid process	37	37	—
Depth right postglenoid process	33	32	—
Width between lateral edges of hypoglossal foramen	68	75	—
Max. width lateral edges of paroccipital processes	218	217	—
Depth left paroccipital below mastoid foramen	86	88	—
Depth right paroccipital below mastoid foramen	88	80	—
Max. length left paroccipital	60	53	—
Max. length right paroccipital	60	56	—

large posterior projection on the medial edge of the astragalus below the medial edge of the trochlea.

Discussion

Groves (1967) recognized seven modern subspecies of *D. bicornis* that he defined on length and breadth parameters of the skull. A modern skull collected from East Rudolf in 1968 belongs to the smallest subspecies *Diceros bicornis michaeli*. According to Groves' criteria, the East Rudolf fossil black rhino skull is closest to *Diceros bicornis brucii* (the Somali black rhinoceros) and is thus intermediate in size between the two modern subspecies of black rhino common to northern Kenya – *D. b. michaeli* and *Diceros bicornis ladoensis*. A rather older but incomplete fossil skull of *D. bicornis* has been recovered from Shungura Member C in the Omo Basin (Hooijer, 1973 : 164). It is unfortunate that this specimen may be too distorted laterally to provide an adequate comparison between it and the East Rudolf specimen on one hand and modern subspecies on the other.

Both the East Rudolf *D. bicornis* mandibles are from the *Metridiochoerus andrewsi* zone. KNM–ER 472 is slightly deeper than a mandible from Shungura Member D2 of the Omo Basin and than modern mandibles quoted by Hooijer (1973 : 164). KNM–ER 2139 is more slender than the Omo mandible and falls within the range of variation of the recent examples. It is unlikely, however, that the depth of the horizontal ramus is a crucial diagnostic or evolutionary feature.

Upper teeth of *D. bicornis* subsp. from the *Mesochoerus limnetes* zone are slightly larger than those from later horizons. However more specimens are needed to establish the range of individual variation at different levels before any tentative conclusions on evolutionary trends within the East Rudolf succession can be formulated.

The astragalus (KNM–ER 1196) comes from the *Mesochoerus limnetes* zone and is larger than modern examples. It is closer in size to an astragalus from Shungura Member E (Hooijer, 1973 : 160) than it is to other specimens from earlier horizons in the Omo Basin.

TABLE II

Mandible measurements of *Diceros bicornis* subsp.

	KNM–ER 472	KNM–ER 2139	OM 2180
Length of symphysis	68	73	92
Max. width of anterior end symphysis	91	67	48
Max. width of symphysis	91	121	114
Height of body at M_1	102	84	72
Length P_2–M_2	244	195	220

TABLE III

Measurements of upper teeth of *Diceros bicornis* subsp.

	b KNM-ER 327	c KNM-ER 636(l)	c KNM-ER 636(r)	b KNM-ER 691(l)	b KNM-ER 691(r)	a KNM-ER 1186(l)	a KNM-ER 1186(r)	OM 2180
P^1 ap. ext.	—	20·6	—	—	—	—	—	21·8
ap. int.	—	26·3	—	—	—	—	—	22·5
tr.	—	21·6	—	—	—	—	—	21·5
P^2 ap. ext.	—	32·4	33·3	36·4	—	—	—	32·2
ap. int.	—	25·1	25·4	27·0	—	—	—	28·0
prot.	—	38·3	37·3	37·2	—	—	—	37·3
met.	—	42·0	39·4	34·2	—	—	—	42·5
P^3 ap. ext.	38·0†	45·6	45·9	44·4	43·1	50·0	46·5	42·2
ap. int.	35·0*	35·2	35·0	40·2	40·5	38·0	37·0	33·7
prot.	47·2	53·0	54·8	49·5	49·1	50·5	53·0	54·6
met.	50·0†	50·3	51·7	50·4	48·4	49·6	49·1	53·2
P^4 ap. ext.	41·9*	49·3	50·0	49·2	49·2	50·0	53·4	47·0
ap. int.	42·4	37·4	40·0	44·1	43·3	42·5	41·8	39·7
prot.	57·1	52·4	63·0	60·2	55·8	66·0	63·0	62·5
met.	57·1	54·8	65·7	50·7	52·5	56·0	54·6	58·2
M^1 ap. ext.	49·3	52·7	53·5	49·5	54·0	58·7	59·1	52·6
ap. int.	44·4	39·3	41·6	43·0	45·5	45·5	43·8	42·2
prot.	58·5	60·5	60·0	51·7	54·0	67·7	66·7	59·2
met.	53·1	54·2	52·7	49·6	45·5	51·7†	54·2	55·3
M^2 ap. ext.	55·7	62·8	61·9	56·7	58·7	62·7	—	58·0
ap. int.	48·8	42·7	46·2	48·8	49·2	57·0	—	48·5
prot.	63·3	63·2	62·1	63·3	65·0	67·6	—	59·5
met.	51·5	40·2	41·6	51·2	48·0	41·9†	—	45·5
M^3 ap. ext.	41·1*	—	—	—	—	60·8	—	52·1
ap. int.	41·2	—	—	—	—	56·3*	—	50·0*
tr.	51·3	—	—	—	—	40·0†	—	49·6

a = *M. limnetes* zone; b = *M. andrewsi* zone; c = *L. africana* zone; ap. = anteroposterior; ext. = external; int. = internal; tr. = transverse; prot. = protoloph; met. = metaloph; † = maximum measurement on incomplete specimen; * = approximately.

TABLE IV

Measurements of lower teeth of *Diceros bicornis* subsp.

	KNM-ER 472(l)	KNM-ER 472(r)	KNM-ER 2139	OM 2180	OM 2181
P_2 ap. ext.	31·4	34·5	—	28·6	28·6
ap. int.	35·6	38·3	—	28·3	25·5
prot.	21·1	17·7	—	18·7	16·8
hyp.	19·1	18·6	—	20·0	20·0
P_3 ap. ext.	43·5	42·5	—	40·3	36·4
ap. int.	43·1	42·0	—	36·0	31·6
prot.	20·7	20·4	—	35·5	24·7
hyp.	20·3	19·6	—	27·7	27·3
DP_4 ap. ext.	—	44·2	—	—	—
ap.int.	—	22·4	—	—	—
prot.	22·7*	22·4	—	—	—
hyp.	24·7	24·5	—	—	—
P_4 ap. ext.	—	—	40·9	45·6	39·7
ap. int.	—	—	—	41·6	34·2
prot.	—	—	29·3†	30·0	28·1
hyp.	—	—	33·3†	33·3	29·9
M_1 ap. ext.	50·0	49·7	42·5	48·0	50·4
ap. int.	47·2	46·9	44·2	43·8	43·1
prot.	24·7	27·8	—	30·0	27·7
hyp.	25·4	30·0	—	32·3	32·1
M_2 ap. ext.	58·2	59·2	48·8	47·3	51·1
ap. int.	58·2	60·6	—	52·1	52·7
prot.	20·6	24·3	—	30·1	29·3
hyp.	20·2	22·7	—	32·0	30·1

ap. = anteroposterior; ext. = external; int. = internal; prot. = protolophid; hyp. = hypolophid; † = maximum measurement on incomplete specimen; * = approximately.

TABLE V

Measurements of astragalus of *Diceros bicornis* subsp.

	KNM-ER 1196	OM 2185
Max. length	90·8	84·1
Medial length	80·4	73·7
Lateral length	80·4	79·7
Max. width	96·6	91·0
Proximal width	74·9	78·8
Distal width	88·1	76·2
Depth trochlea	60·5	58·0
Depth navicular facet	50·0	50·4

Genus *Ceratotherium* Gray 1867

Ceratotherium simum (Burchell) 1817. ***Ceratotherium simum germanoafricanum*** (Hilzheimer) 1925

Material referred

KNM-ER 328C, adult cranium; KNM-ER 329, incomplete immature cranium; KNM-ER 2320, incomplete immature cranium; KNM-ER 328A, L mandible (P_3–M_3); KNM-ER 328B, R mandible (P_2–M_3); KNM-ER 2164, R mandible (P_2–M_3); KNM-ER 2278, fragmentary mandible; KNM-ER 686, LM_2; KNM-ER 687, isolated teeth (LP_2–M_3); KNM-ER 1188, mandible fragments (RP_2–M_3, LP_2, LM_2); KNM-ER 1192, LM_3; KNM-ER 1193, RP_4; KNM-ER 1193B, RM_3 frag; KNM-ER 1194, LM_1; KNM-ER 369, RP^2; KNM-ER 659, LM^3; KNM-ER 1189, isolated teeth (RP^4, RM^3, LM^3); KNM-ER 1190, RP^3; KNM-ER 1191 (RM^2); KNM-ER 1195, L astragalus; KNM-ER 2278B–T, postcranial elements (B = head L scapula; C = L radius; D = L cuneiform; E = acetabulum frag.; F = R patella; G = L fibula; H = R calcaneum; J = R astragalus; K = R navicular; L = R cuboid; M = L middle cuneiform; N = atlas vertebra frag.; P–S = centra of cervical vertebrae III–VI; T = sacral vertebra I frag.).

Horizon

KNM-ER 328 and 329 were collected in 1968 from the Ileret region but the precise locality and horizon remain unknown. KNM-ER 1190 and 2320 are from the *Mesochoerus limnetes* zone. KNM-ER 1188, 1191 and 1194 are from the *L. africana* zone. The remaining specimens are from the *Metridiochoerus andrewsi* zone.

Description

The white rhinoceros is more abundantly represented in the Koobi Fora Formation than the black rhinoceros but it is still not a common element of the East Rudolf fauna. Remains include an adult and two immature skulls, several mandibles, isolated teeth and a limited number of postcranial elements. The East Rudolf white rhinoceros specimens are allocated to the subspecies *Ceratotherium simum germanoafricanum* which was discussed in some detail in an earlier volume of this series (Hooijer, 1969).

The adult skull (KNM-ER 328C) is virtually complete but lacks the anterior portion of the premaxillae, the anterior cheek teeth and the tip of the left postglenoid process. The specimen was encased in an indurated sandstone matrix and in consequence could not be as thoroughly prepared as the *D. bicornis* subsp. skull for fear of damaging the specimen. The adult skull is of similar size to that of the extant white rhinoceros but is smaller than a skull reported by Hooijer (1969: Table VIII) from Olduvai Gorge, Tanzania. In most respects the East Rudolf skull is very similar to that of modern examples. The most important difference concerns the angle between the plane of the occiput and the plane of the cranial vault in front of the nuchal crest. This angle is acute in modern white rhinos but nearly at right angles in the East Rudolf specimen. More minor differences shown by the East Rudolf skull include shorter and less massive postglenoid processes, a more slender paroccipital region and a lesser elevation of the nuchal crest above the foramen magnum.

One of the immature skulls (KNM-ER 329) lacks the premaxillae, the right zygomatic arch, part of the dorsal edge of the cranial vault and much of the lateral and dorsal region of the occiput. The left tooth row has been badly broken and eroded. All the deciduous premolars of the right tooth row are worn and the anterior molar is erupting and shows wear on the most elevated portion. The nasal boss of KNM-ER 329 is less tall, more rounded, narrower anteriorly and wider posteriorly than that of the adult skull (KNM-ER 328). The external nares and the orbital region are both more compressed dorsoventrally than in the adult skull. The zygomatic arch of KNM-ER 329 is straighter and more slender. Supratemporal ridges are not obvious; their absence may perhaps be due to erosion but perhaps also to the relative immaturity of the specimen.

A second incomplete and immature skull, KNM-ER 2320, was recovered from the *Mesochoerus limnetes* zone. It has suffered slight lateral compression and lacks premaxillae, the anterior portion of the right maxilla, the right zygomatic arch and most of the cranial region of the skull behind the external auditory meatus. DP^{2-4} are erupted and worn. DP^1 is not fully erupted but shows wear on the ectoloph. M^1 is partly erupted but is unworn. In both immature skulls the palatonarial border is opposite M^1 whereas in the adult skull it is opposite M^3. The nasal boss stands high above the palate, as in the adult skull, but is proportionately narrower than in either KNM-ER 328 or 329. Although KNM-ER 2320 has lost most of the occipital region it appears to be less elongate than either of the other skulls and this is reflected in the distance between the anterior tip of the nasals and the external auditory meatus. The zygomatic arch is relatively more slender than in KNM-ER 329 and the supraorbital process of the frontal is less massive. KNM-ER 2320 is only slightly less mature than KNM-ER 329 and the apparent discrepancy both in skull size and robustness is therefore quite impressive. The differences may reflect the different horizons from which the specimens were collected. The precise localities and horizons of KNM-ER 328 and 329 are not known but they were both collected from the Ileret region and are likely, therefore, to be from younger horizons (*Metridiochoerus andrewsi* or *L. africanana* zones) than KNM-ER 2320.

The mandible (KNM-ER 328A and B) associated with the adult skull is longer, deeper and wider than that of recent specimens and has a longer symphysis. The anterior edge of the ascending ramus is more nearly vertical and the coronoid process is taller, more slender, and sited more anteriorly in relation to the condyle. The masseteric fossa is less deeply excavated than in modern examples. Other less complete specimens from East Rudolf (KNM-ER 2164 and 2278) exhibit similar differences from mandibles of recent white rhinos.

A number of *Ceratotherium* upper teeth have been collected from East Rudolf sites in addition to those belonging to the skulls. They are of similar length to teeth of *C. simum* in the Osteology collections of the National Museum of Kenya but are relatively wider. Many of the East Rudolf specimens are heavily worn or incomplete but in general appear less hypsodont than those of recent white rhinos. The only major morphological difference between the upper teeth of East Rudolph specimens and those of modern examples is in the orientation of the metaloph, that of the fossil specimens being orientated more transversely. The inferior dentition of the East Rudolf *Ceratotherium* is very similar to modern examples.

Postcranial elements of *Ceratotherium* are rare at East Rudolf and to date are restricted to a partial skeleton from the Koobi Fora region and an isolated astragalus from the Ileret region. Both specimens are from the *Metridiochoerus andrewsi* zone. The partial skeleton includes fore and hind limb elements together with a few vertebrae.

An incomplete head of a left scapula (KNM-ER 2278B) was found associated with the partial skeleton. From this fragment it may be determined that the scapular head of *C. s. germanoafricanum* was of similar size to that of the extant white rhino but somewhat less concave.

The left radius from East Rudolf (KNM-ER 2278C) is of similar length to that of the extant white rhino but is proportionately wide and more massive. The proximal and distal epiphyses are not completely preserved but the lateral and medial surfaces that articulate with the humerus are more equal in size than in the extant white rhino. The articular facets for the scaphoid and lunar are subequal in size whereas in *Ceratotherium simum simum* the scaphoid facet is appreciably larger than the lunar facet.

It is regretted that the only manus and pes elements of the extant white rhinocerus in the osteological collection of the National Museum of Kenya were not from a fully mature individual.* A left cuneiform of *C. s. germanoafricanum* was larger and proportionately wider than available specimens from modern white rhinos. The ulnar facet of this specimen (KNM-ER 2278D) is relatively wider anteriorly than in the extant white rhino. The unciform facet is wider posteriorly and assumes a more triangular shape than in recent examples.

* The measurements are, however, comparable to those quoted for the extant white rhinoceros by Hooijer (1969, 1973).

The only East Rudolf example of a fossil white rhino pelvis comprises a fragment of acetabulum (KNM-ER 2278E). This is less concave than in the pelvis of extant white rhinos.

The patella of *C. s. germanoafricanum* (KNM-ER 2278F) is larger and proportionately broader than recent examples but is otherwise similar in morphology.

A right fibula (KNM-ER 2278G) is virtually complete but lacks the proximal end. The specimen could only have been slightly longer than in recent white rhinos but is appreciably more massive. The tibial facet of the distal epiphysis is of similar size to that of the extant white rhino and is thus relatively smaller, in contrast to the astragalus facet, than in the extant form.

A right calcaneum (KNM-ER 2278H) is larger than that of the modern white rhino and has a proportionately stouter tuber calcis. There are three separate facets for articulation with the astragalus in the extant white rhino — a large concavo-convex dorsolateral facet, a smaller convex medial facet and a small elongate and concave ventrolateral facet that adjoins the cuboid facet. In the fossil example the medial facet is proportionately larger and less concave. It is also contiguous with both the (larger) ventrolateral facet and the cuboid facet.

Two examples of *C. s. germanoafricanum* astragali are known from East Rudolf (KNM-ER 1195 and 2278J). They are both larger and proportionately deeper than recent examples. A medial facet for articulation with the calcaneum is contiguous with a ventrolateral calcaneal facet and with the cuboid and navicular facets; the medial calcaneal facet is isolated from the remaining three articular surfaces in *C. s. simum*. The articular facets for the navicular and cuboid are proportionately less wide laterally and deeper craniocaudally than in modern white rhino astragali.

A right navicular (KNM-ER 2278K) is larger but otherwise similar to that of modern white rhinos except that the facet for the medial cuneiform is confined to the anterior edge of the distal surface and does not therefore extend posteriorly to become contiguous with the cuboid facet.

A right cuboid (KNM-ER 2278L) is larger than in *C. s. simum*. The dorsal facet that articulates with the calcaneum and astragalus is rectangular (longer than wide) in the East Rudolf specimen but square in recent examples. That part of the facet that articulates with the astragalus is narrower in the East Rudolf specimen than it is in modern examples (in which it is of similar width to the calcaneal facet). On the distal surface the metatarsal facet tapers more abruptly from the cranial surface in the fossil specimen.

A left middle cuneiform (KNM-ER 2278M) is larger than modern examples and contrasts morphologically in that it tapers posteriorly rather than anteriorly. The metatarsal facet on the distal surface shows a greater concavoconvex curvature.

The facet that articulates with the lateral cuneiform does not extend to become contiguous with the metatarsal facet as it does in recent examples.

The axial skeleton is represented by five cervical vertebrae and a portion of the sacrum. A fragment of the left side of an atlas vertebra (KNM–ER 2278N) comprises that portion from the central posteroventral spine to the lateral edge of the axis and condylar facets. The left condylar articular surface is incomplete medially but is seen to be less concave than in recent specimens. The neural arch is missing. The axis facet is taller but less wide than in recent white rhinos and is separated from the odontoid articular facet by some 15 mm at the ventral edge and by a well defined ridge at the dorsal edge. In the extant white rhino atlases examined, the axis and odontoid facets are continuous and undemarcated.

Centra of the third to sixth cervical vertebrae have been collected at East Rudolf (KNM–ER 2278P–S). Unfortunately these lack neural arches and all but the bases of the transverse processes. They are somewhat larger than equivalent examples of neck vertebrae of the modern white rhino. The centra of the fossil specimens differ morphologically from recent examples in that, except in the third cervical vertebra, the ridge that extends posteriorly along the ventral edge from the anterior articular surface does not continue on to the posterior centrum epiphysis.

Also associated with the partial *C. s. germanoafricanum* skeleton was a portion of the first sacral vertebra (KNM–ER 2278T) lacking the neural spine, the left transverse process and much of the right transverse process. It is somewhat larger than the equivalent vertebra of the modern white rhinoceros and the anterior articular surface of the centrum is less dorsoventrally flattened.

Discussion

Thenius (1955) suggested that *Ceratotherium* diverged from *Diceros* during the course of the Pliocene and more recent descriptions of fossil rhinocerotid material from East and South Africa (Hooijer, 1972, 1973; Hooijer and Patterson, 1972) have tended to confirm this. A tooth showing similarities to both *Diceros* and *Ceratotherium*, but placed in the latter genus, was recorded by Hooijer and Patterson (1972: 17–18) from Lothagam, Kenya (dated older than 4·5 million years). From the nearby but younger sites of Kanapoi and Ekora (4·0 m.y.) the type specimens of a primitive species of *Ceratotherium* (*C. praecox*) have been retrieved. *C. praecox* is believed to be directly ancestral to *C. simum* (Hooijer and Patterson, 1972: fig. 11; Hooijer 1973: 170). *C. praecox* has been show to occur at sites in East and South Africa from about 7 million years (Hooijer, 1972, 1973) and evolved directly into *C. simum* between 3–4 million years ago (Hooijer, 1973: 170).

C. praecox is apparently absent from the sequence at East Rudolf although so far only fragmentary remains have been retrieved from the Kubi Algi Formation. The immature skull from the *Mesochoerus limnetes* zone (KNM–ER 2320) is assigned to

C. s. germanoafricanum but the specimen has a shorter cranial region than other skulls attributed to this taxon and a short cranial region is a diagnostic feature of *C. praecox* (Hooijer and Patterson, 1972: 19). It is, however, entirely likely that the *C. praecox*–*C. simum* transition was a similarly gradual process to that effecting the transition from *C. s. germanoafricanum* to the recent subspecies.

C. s. germanoafricanum is confined to late Pliocene and early Pleistocene localities. It has been recorded from Laetolil and Bed I at Olduvai (Hooijer, 1969) and in the Shungura and Usno Formations of the Omo Basin (Hooijer, 1973) as well as at East Rudolf (Hooijer, 1973; Harris, in press). It has also been reported from locality JM 91 in the Chemeron Formation of the Lake Baringo region (Hooijer, 1969) although an earlier locality (JM 507) of the same formation has yielded *C. praecox* (Hooijer, 1973: 169).

TABLE VI

Measurements of *Ceratotherium simum germanoafricanum* skulls

	KNM–ER 328C	KNM–ER 329	KNM–ER 2320	OM 2184
Max. length	800	635†	500†	825
Min. length nasal boss to nuchal crest	733	633	—	756
Length nasal boss to external auditory meatus	652	540	459	—
Basilar length	752	635†	—	713
Length palatonarial border to occipital condyles	431	400	308†	427
Width nasal boss	182	161	82	194
Max. width skull at orbit	302	240*	166	180
Min. width cranial vault at temporal fossa	120	115	103	112
Width dorsal edge nuchal crest	275	208*	—	216
Max. width occiput	283	—	—	216
Width occipital condyles	151	158*	—	154
Depth foramen magnum to nuchal crest	156	98*	—	162
Max. width skull at zygoma	373	320*	286*	335
Width palate at M^1	65	106	69	100
Width palate at M^3	82	—	113	—

† = maximum measurement on incomplete specimen. * = approximately.

The East Rudolf specimens are assigned to *C. s. germanoafricanum* on the bases of the transverse orientation of the metaloph in the upper teeth and of the less backward inclination of the occiput. The East Rudolf *Ceratotherium* teeth are apparently less hypsodont than those of recent white rhinos but too few suitably preserved specimens are known to permit deductions on size or hypsodonty changes within the sequence of the Koobi Fora Formation. Postcranial elements from East Rudolf tend to be larger than equivalent specimens of extant white rhinos. Attempts to correlate East Rudolf postcranial remains with those from Olduvai (Hooijer, 1969) or the Omo (Hooijer, 1973) on the basis of size have so far proved unsatisfactory, probably because too few specimens are known to be able to gain a measure of individual variation at any one level.

TABLE VII

Measurements of *Ceratotherium simum germanoafricanum* mandibles

	KNM–ER 328A	KNM–ER 328B	KNM–ER 1188	KNM–ER 2164	KNM–ER 2278	OM 2184
Total length	616	622	—	—	—	583
Length symphysis	92	121	—	87	—	83
Max. width at symphysis	71	79	—	74	—	65
Height ramus at M_1	144	135	—	128	150	115
Height ramus at M_3	130	125	—	119*	145	116
Max. width ramus at angle	69	78	—	—	—	60
Width condyle	121	129	—	—	101†	122
Height coronoid above ventral edge of body	—	381	—	—	—	298
Length P_2–M_2	217*	219	233	207	—	244
Length P_3–M_3	251	247	231	242	246†	260
Length P_2–M_3	278	286	306	283	—	296

† = maximum measurement on incomplete specimen. * = approximately.

TABLE VIII

Upper dentition measurements of *Ceratotherium simum germanoafricanum*

		KNM–ER 328(l)	KNM–ER 328(r)	KNM–ER 329	b KNM–ER 369	b KNM–ER 659	b KNM–ER 1189(l)	b KNM–ER 1189(r)	a KNM–ER 1190	c KNM–ER 1191	OM 2184	OM 2216
P^2	ap. ext.	—	—	—	38·4	—	—	—	—	—	38·9	—
	ap. int.	—	—	—	29·4	—	—	—	—	—	36·3	—
	prot.	—	—	—	36·5	—	—	—	—	—	38·5	—
	met.	—	—	—	35·8	—	—	—	—	—	40·0	—
P^3	ap. ext.	—	—	—	—	—	—	—	49·4	—	46·0	38·0
	ap. int.	—	—	—	—	—	—	—	46·4	—	46·4	30·4
	prot.	—	—	—	—	—	—	—	51·5	—	51·9	34·7
	met.	—	—	—	—	—	—	—	48·8†	—	47·0	31·0
P^4	ap. ext.	51·0	54·5	—	—	—	—	46·1	—	—	55·2	44·6
	ap. int.	43·9	41·1	—	—	—	—	43·4	—	—	42·5	37·0
	prot.	63·8	63·6	—	—	—	—	59·2	—	—	51·2	39·0
	met.	62·2	56·5	—	—	—	—	55·3	—	—	44·6	35·8
M_1	ap. ext.	48·5	50·0	71·0	—	—	—	—	—	—	50·5	46·1
	ap. int.	41·0	39·8	48·2	—	—	—	—	—	—	52·5	37·9
	prot.	70·0	70·0	57·1	—	—	—	—	—	—	58·0	42·6
	met.	61·9	64·5	33·8	—	—	—	—	—	—	55·1	36·2
M_2	ap. ext.	65·5	64·0	—	—	—	—	—	—	58·4	73·2	46·4
	ap. int.	50·4	56·0	—	—	—	—	—	—	54·8	60·2	43·8
	prot.	75·5*	77·2	—	—	—	—	—	—	67·6	51·6	51·0
	met.	61·3	64·8	—	—	—	—	—	—	54·9	45·7	40·5
M_3	ap. ext.	70·3	64·4	—	—	68·2	63·4	77·4	—	—	—	58·3
	ap. int.	60·2	61·3	—	—	65·6	62·1	69·4	—	—	—	46·3
	tr.	59·3	59·8	—	—	61·2	54·9	54·7	—	—	—	42·3

a = *M. limnetes* zone; b = *M. andrewsi* zone; c = *L. africana* zone; ap. = anteroposterior; ext. = external; int. = internal; prot. = protoloph; met. = metaloph; tr. = transverse; † = maximum measurement on incomplete specimen; * = approximately.

TABLE IX

Lower dentition measurements of *Ceratotherium simum germanoafricanum*

		KNM-ER 328A	KNM-ER 328B	b KNM-ER 687	c KNM-ER 1188(l)	c KNM-ER 1188(r)	b KNM-ER 1192	b KNM-ER 1193	b KNM-ER 1194	b KNM-ER 2164	b KNM-ER 2278	OM 2184
P_2	ap.	—	36·3	36·6	35·3	35·4	—	—	—	32·9	—	37·6
	prot.	—	22·8	20·3	19·3	19·4	—	—	—	19·2	—	24·0
	hyp.	—	24·3	21·0	20·3	20·2	—	—	—	20·0	—	23·7
P_3	ap.	43·5	38·7	41·6†	—	42·6	—	—	—	36·6	—	48·4
	prot.	28·4	28·2	24·1	—	23·9	—	—	—	27·3	—	28·3
	hyp.	29·1	26·9	25·5	—	24·3	—	—	—	29·0	29·2	29·2
P_4	ap.	49·3	41·2	46·3†	—	46·4	—	50·2	—	43·4	41·6	50·5
	prot.	30·8	32·8	28·7	—	25·7	—	28·7	—	30·6	32·5	31·9
	hyp.	33·0	33·2	31·3	—	27·6	—	31·2	—	32·9	33·0	30·9
M_1	ap.	41·0	46·5	46·2	—	48·8	—	—	50·6	40·4	—	54·0
	prot.	41·3	35·3	27·3	—	26·4	—	—	40·2	31·8	—	32·4
	hyp.	34·2	32·8	31·7	—	30·6	—	—	36·0	30·6	—	33·2
M_2	ap.	53·6	54·6	55·0	62·1	65·0	—	—	—	50·2	48·1	61·5
	prot.	34·6	34·4	26·8	29·9	29·2	—	—	—	31·9	35·6	31·8
	hyp.	34·6	32·2	36·4	32·3†	33·6	—	—	—	31·9	33·2	30·2
M_3	ap.	56·2	60·4	60·0	—	65·7	55·9	56·5†	—	61·0	65·5	58·1
	prot.	34·8	31·6	29·6	—	29·2	36·6	29·0†	—	31·3	38·2	29·6
	hyp.	31·8	30·1	27·4	—	26·8	30·3	30·0	—	30·4	33·2	22·2

b = *M. andrewsi* zone ; c = *L. africana* zone ; ap. = anteroposterior ; prot. = protolophid ; hyp. = hypolophid ; † = maximum measurement on incomplete specimen.

TABLE X

Deciduous dentition measurements of *Ceratotherium simum germanoafricanum*

		KNM-ER 329(r)	KNM-ER 2320
DP^1	ap. ext.	30·0	25·9
	ap. int.	29·6	22·6
	tr.	26·9	19·2
DP^2	ap. ext.	39·8	40·7
	ap. int.	36·1	32·8
	prot.	37·0	37·2
	met.	43·6	31·6
DP^3	ap. ext.	48·7	48·2†
	ap. int.	41·0	42·0
	prot.	53·6	46·6
	met.	55·7	38·2
DP^4	ap. ext.	61·8	56·5
	ap. int.	54·8	43·6
	prot.	56·6	41·5
	met.	53·3	43·0

ap. = anteroposterior ; ext. = external ; int. = internal ; tr. = transverse ; prot. = protoloph ; met. = metaloph ; † = maximum measurement on incomplete specimen.

TABLE XI

Measurements of radius of *Ceratotherium simum germanoafricanum*

	KNM-ER 2278C	OM 2744
Max. length	417	410
Width proximal epiphysis	142†	119
Depth proximal epiphysis	85†	74
Min. width midpoint shaft	83	62
Width distal epiphysis	144	119
Depth distal epiphysis	87	73

† = Maximum measurement on incomplete specimen.

TABLE XII

Measurements of cuneiform of *Ceratotherium simum germanoafricanum*

	KNM–ER 2278D	OM 2186
Max. length (dorsoventral)	67	60
Max. proximal width (mediolateral)	54	47
Max. proximal depth (craniocaudal)	46	38
Max. distal width	54	42
Max. distal depth	57	48

TABLE XIII

Measurements of patella of *Ceratotherium simum germanoafricanum*

	KNM–ER 2278F	OM 2186
Max. length (dorsoventral)	93	87
Max. proximal width (mediolateral)	87	68
Max. distal width	121	95
Max. depth (craniocaudal)	63	54

TABLE XIV

Measurements of fibula of *Ceratotherium simum germanoafricanum*

	KNM–ER 2278G	OM 2744
Max. length	335*	325*
Width distal epiphysis	65	45
Depth distal epiphysis	36	24
Max. with tibial facet	17	20
Max. width astragalus facet	48	32

* = approximately.

TABLE XV

Measurements of calcaneum of *Ceratotherium simum germanoafricanum*

	KNM–ER 2278H	OM 2186
Max. length	160	132
Max. width (mediolateral) of articular surface	98	82
Max. depth (dorsoventral) of articular surface	101	86
Max. width tuber calcis	67	54
Max. depth tuber calcis	84	79

TABLE XVI

Measurements of astragalus of *Ceratotherium simum germanoafricanum*

	KNM–ER 1195	KNM–ER 2278J	OM 2186
Max. length	109	108	88
Length lateral edge	100	107	77
Length medial edge	98	92	75
Max. width	112	119	92
Proximal width	97	87	77
Distal width	101	118	85
Depth at trochlea	70	70	63
Depth at navicular facet	67	61	45

TABLE XVII

Measurements of navicular of *Ceratotherium simum germanoafricanum*

	KNM–ER 2278K	OM 2186
Max. length (craniocaudal)	72	60
Width cranial edge	70	57
Width caudal edge	57	51
Max. depth (proximodistal)	37	33

TABLE XVIII

Measurements of cuboid of *Ceratotherium simum germanoafricanum*

	KNM–ER 2278L	OM 2186
Length (craniocaudal) of proximal surface	61	48
Width (mediolateral) of proximal surface	50	51
Depth (proximodistal) of cranial edge	51	42
Length of distal surface	82	70
Width of distal surface	56	53
Depth of caudal edge	86	75

TABLE XIX

Measurements of middle cuneiform of *Ceratotherium simum germanoafricanum*

	KNM–ER 2278M	OM 2186
Max. length (craniocaudal)	50	44
Width (mediolateral) of caudal edge	19	22
Width of cranial edge	27	18
Max. depth (proximodistal)	25	17

TABLE XX

Measurements of vertebrae of *Ceratotherium simum germanoafricanum*

Atlas vertebra	KNM–ER 2278N	OM 2744
Length ventral edge of neural canal from anterior surface to posterior edge of spine	94	76
Height left occipital condylar facet	59	52
Width left occipital condylar facet	98*	84
Height left axis facet	48	31
Width left axis facet	54	43*

continued

TABLE XX (*continued*)

Third cervical vertebra	KNM–ER 2278P	OM 2186
Max. length centrum	94	75
Height anterior epiphysis centrum	82	63
Width anterior epiphysis centrum	53	47
Height posterior epiphysis centrum	92	81
Width posterior epiphysis centrum	89	64

Fourth cervical vertebra	KNM–ER 2278Q	OM 2744	OM 2186
Max. length centrum	112	80	87
Height anterior epiphysis centrum	83	64	73
Width anterior epiphysis centrum	54	46	47
Height posterior epiphysis centrum	—	75	79
Width posterior epiphysis centrum	—	55	66

Fifth cervical vertebra	KNM–ER 2278R	OM 2744	OM 2186
Max. length centrum	98	72	85
Height anterior epiphysis centrum	82	68	71
Width anterior epiphysis centrum	56	42	49
Height posterior epiphysis centrum	90	79	79
Width posterior epiphysis centrum	85	59	73

Sixth cervical vertebra	KNM–ER 2278S	OM 2186	OM 2744
Max. length centrum	61	78	79
Height anterior epiphysis centrum	83	67	68
Width anterior epiphysis centrum	58	50	44
Height posterior epiphysis centrum	85	77	76
Width posterior epiphysis centrum	84*	78	65

First sacral vertebra	KNM–ER 2278T	OM 2744
Max. length centrum	81	54*
Height anterior epiphysis centrum	71	41
Width anterior epiphysis centrum	87	90
Height posterior epiphysis centrum	58	—
Width posterior epiphysis centrum	91	79

* = approximately.

SUMMARY

Two rhinocerotid taxa, *Diceros bicornis* subsp. and *Ceratotherium simum germanoafricanum*, occur in the Plio/Pleistocene fauna from East Rudolf. Both are known from relatively complete skulls and dentitions and both occur throughout the fossiliferous sequence of the Koobi Fora Formation. More specimens of *Ceratotherium* have been collected but too few specimens of either taxon are known to be able to determine whether this reflects the actual proportion of the two taxa in northern Kenya during the period of time in question or is merely due to fortuitous collecting.

TABLE XXI

Chronological distribution of East Rudolf *Rhinocerotidae*

	M. limnetes zone	*M. andrewsi* zone	*L. africana* zone	Indet.
Diceros bicornis subsp.	2	7	1	—
Ceratotherium simum germanoafricanum	2	11	3	2

The skull of *D. bicornis* from East Rudolf was collected in 1970 and was the first fossil black rhino skull ever found although another, earlier, skull has subsequently been collected from the Omo Basin (Hooijer, 1973). The East Rudolf skull differs from the modern forms only in minor features of the cranial region and of the dentition. The East Rudolf material confirms evidence from other African Plio/Pleistocene sites that the evolution of the modern black rhinoceros had essentially been accomplished by the early Pleistocene. Further similarly complete skulls from East Rudolf and other sites are needed before geographic variation such as that described by Groves (1967) for modern black rhinoceroses can also be confirmed in the Pleistocene.

The East Rudolf white rhinoceros belongs to the fossil subspecies *C. s. germanoafricanum*. The latter taxon changed gradually and almost imperceptibly into the extant white rhino by the late Pleistocene. The East Rudolf material assists in the documentation of the differences between the fossil and extant subspecies. Perhaps material as yet uncollected from the Kubi Algi Formation will similarly assist in documenting the change from *C. praecox* to *C. simum*.

The fossil rhinoceroses from East Rudolf do not conflict with the correlation of the *Metridiochoerus andrewsi* zone with Bed I at Olduvai and with Member G of the Shungura Formation in the Omo Basin. However, because evolutionary changes in African rhinoceroses during the Pleicestocene appear to be minimal, and because of the current scarcity of complete rhinoceros remains from other Pleistocene sites, other mammalian groups would appear to be more useful than rhinocerotids as tools for attempting faunal correlation.

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LEGENDS TO PLATES

PLATE 1

Upper : KNM–ER 636, *Diceros bicornis* subsp. skull, right lateral view.
Lower : KNM–ER 472, *Diceros bicornis* subsp. mandible, right lateral view.

PLATE 2

Upper : KNM–ER 636, *Diceros bicornis* subsp. skull, ventral view.
Lower : KNM–ER 472, *Diceros bicornis* subsp. mandible, occlusal view.

PLATE 3

(a) : KNM–ER 636, *Diceros bicornis* subsp. skull, posterior view.
(b) : KNM–ER 328C, *Ceratotherium simum germanoafricanum* skull, posterior view.

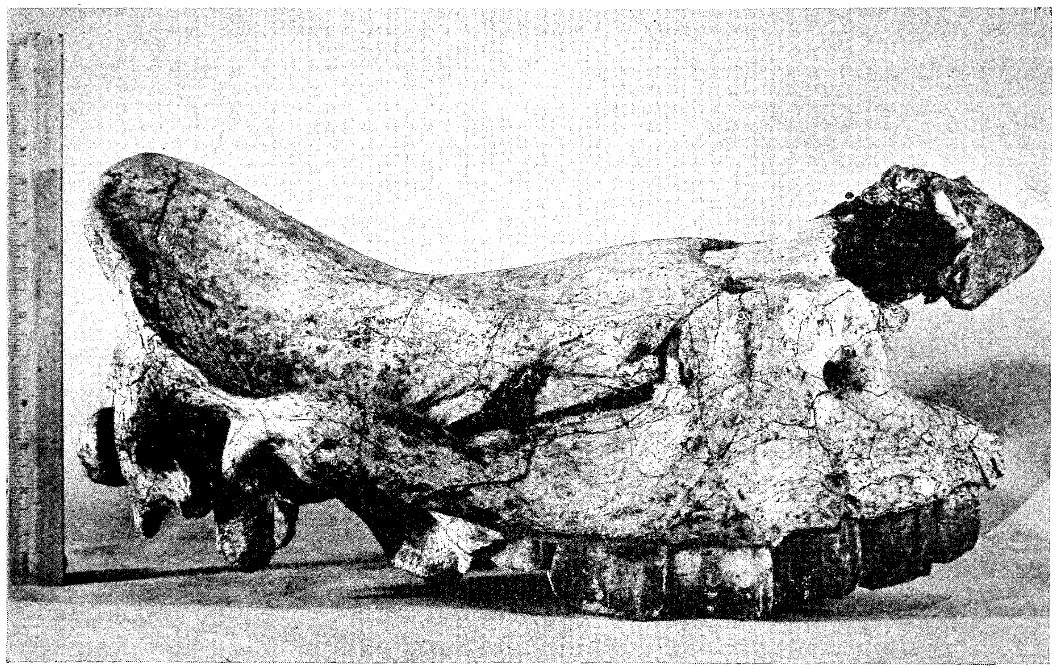
PLATE 4

Upper : KNM–ER 329, *Ceratotherium simum germanoafricanum* immature skull, left lateral view.
Lower : KNM–ER 328C, *Ceratotherium simum germanoafricanum* skull, left lateral view.

PLATE 5

Upper : KNM–ER 328B, *Ceratotherium simum germanoafricanum* right mandible, lateral view.
Lower : KNM–ER 328C, *Ceratotherium simum germanoafricanum* skull, ventral view.

PLATE I



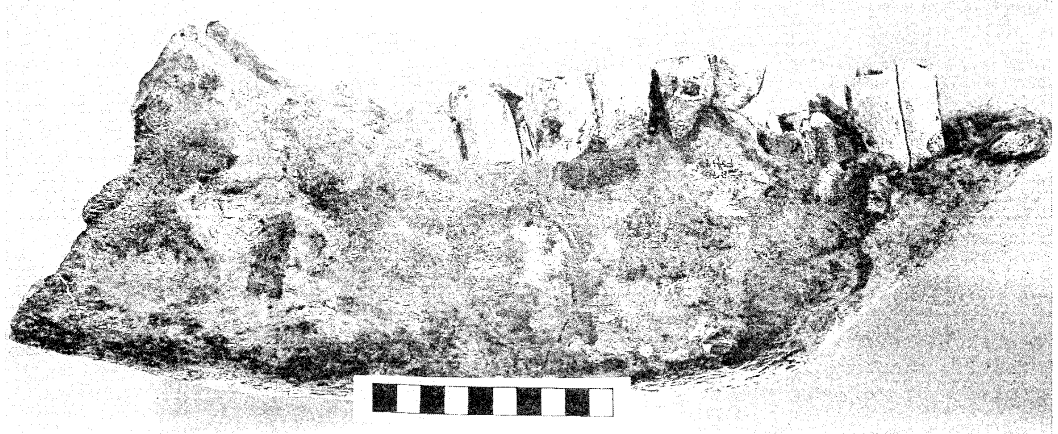
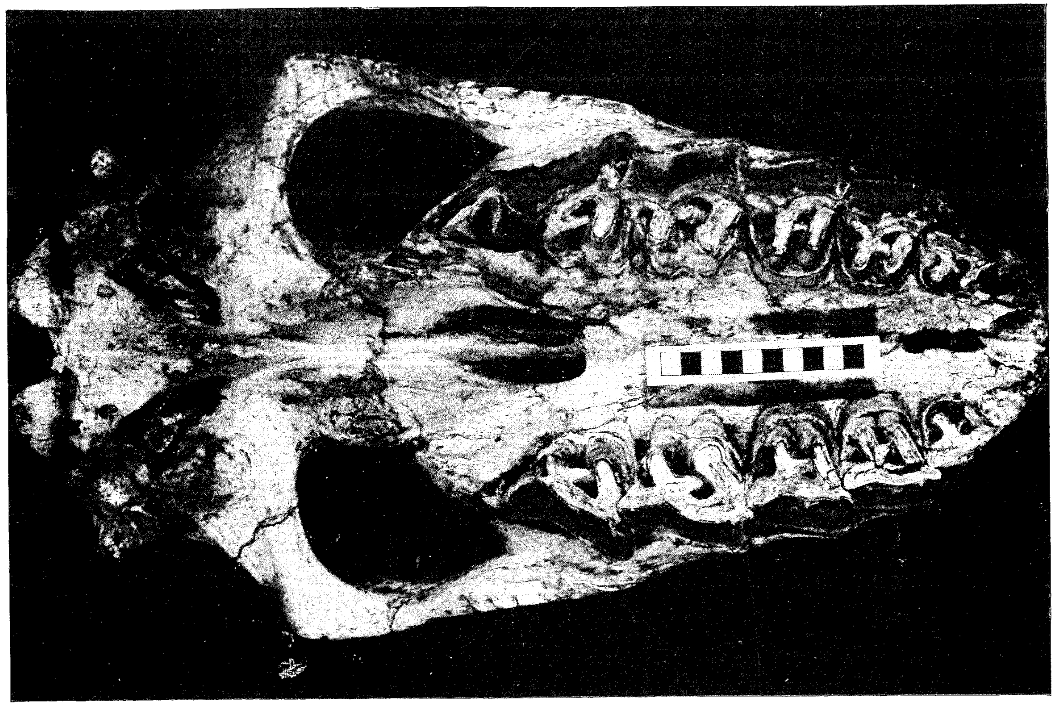


PLATE 2



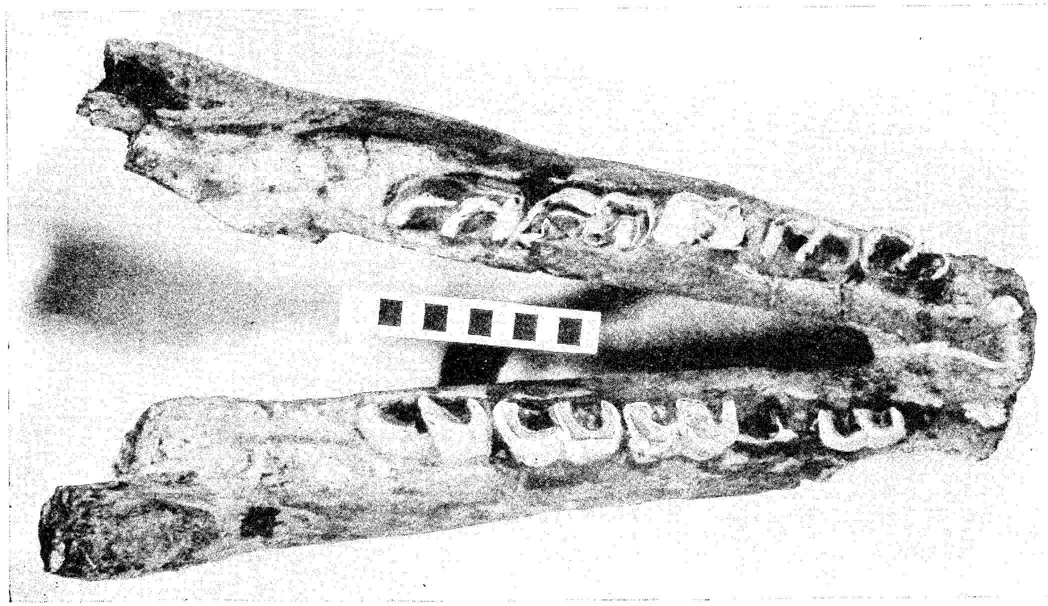
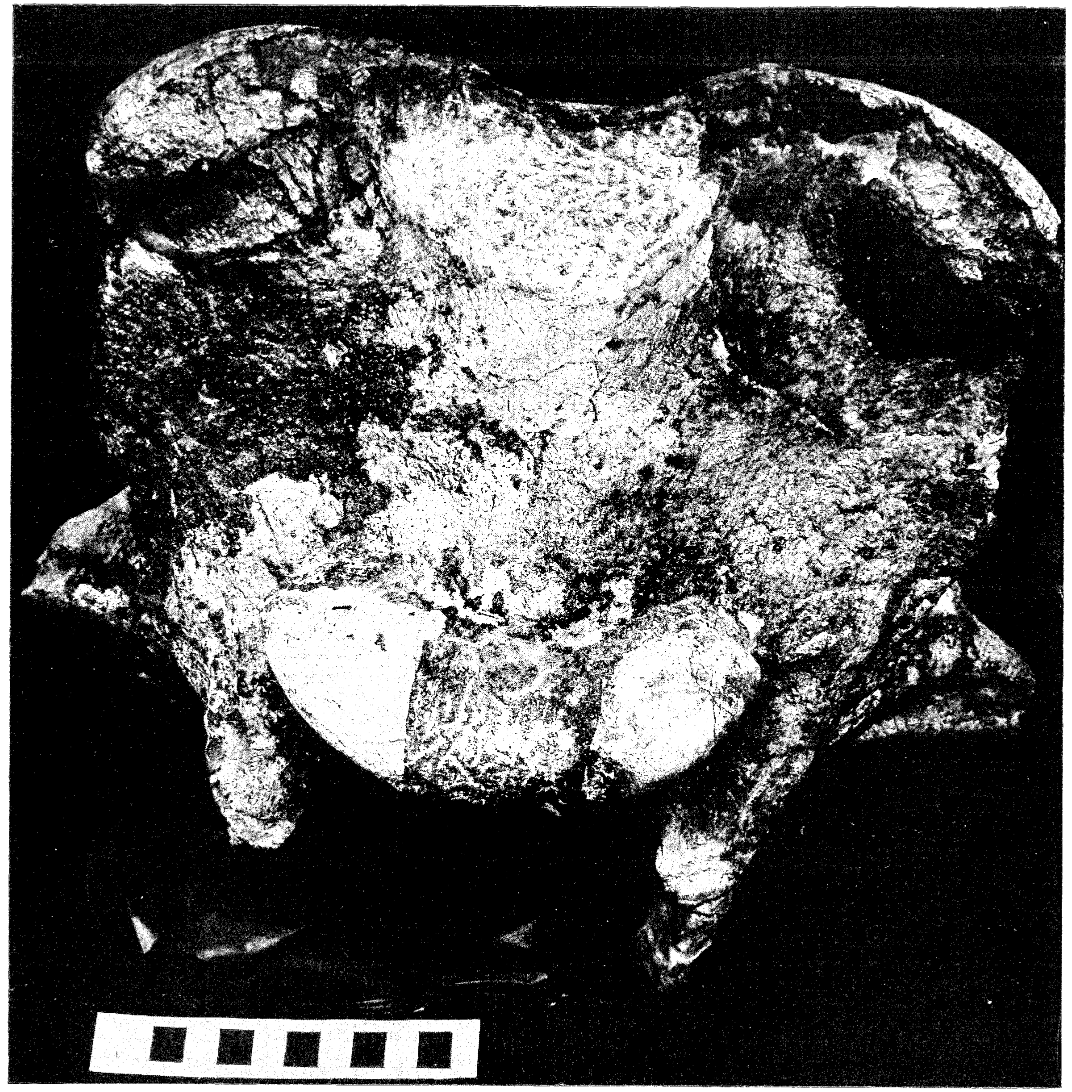


PLATE 3a



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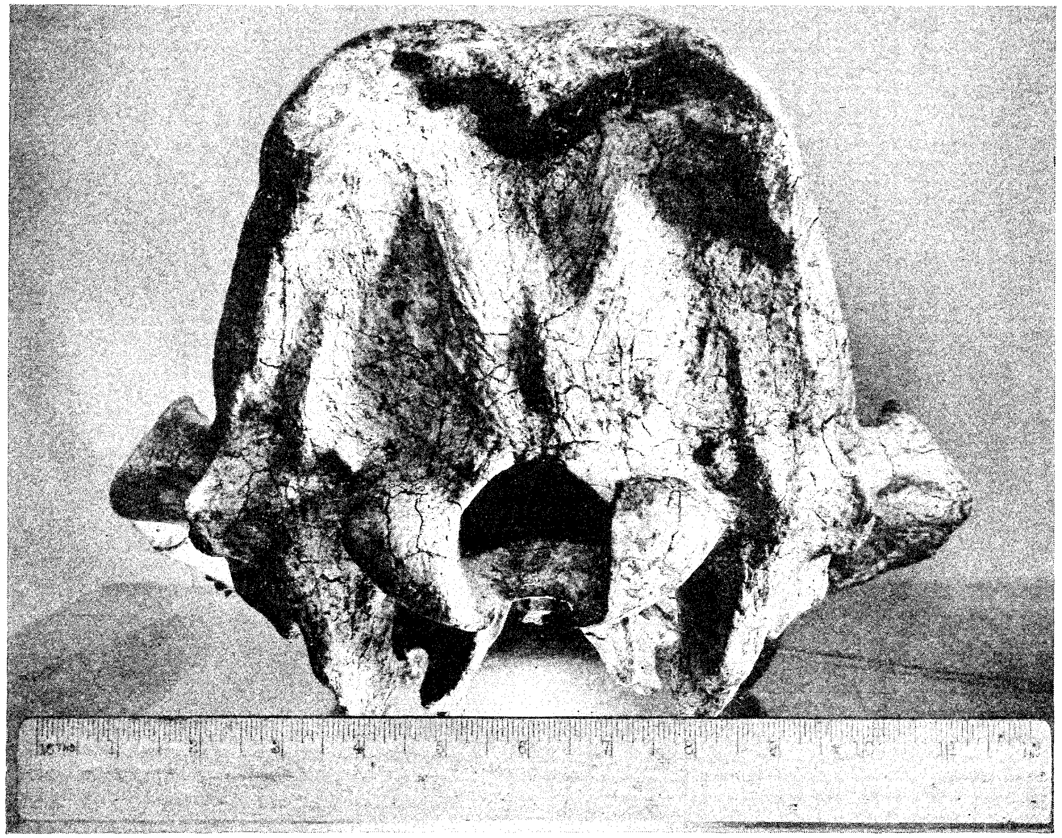
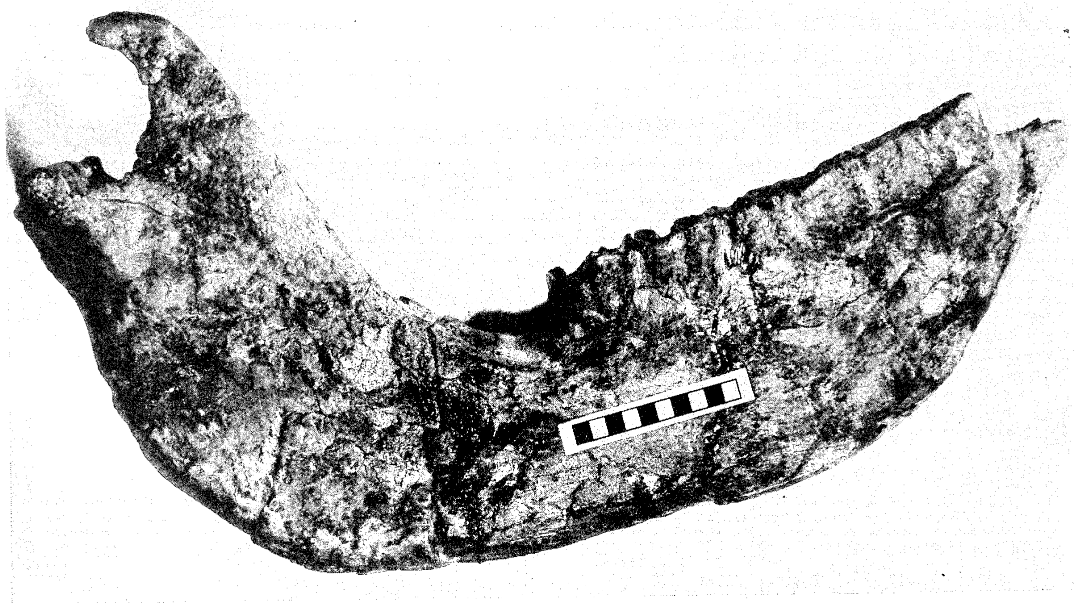


Plate 4

Plate 5



THE LOWER MIOCENE SUIDAE OF AFRICA

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