KOOBI FORA RESEARCH PROJECT

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THE FOSSIL UNGULATES: PROBOSCIDEA, PERISSODACTYLA, AND SUIDAE

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FAMILY RHINOCEROTIDAE

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Although it is often the case that surface prospecting results in the collection of larger components of fossil faunas at the expense of the smaller, the rhinos have proved particularly elusive and remain rare elements in the collections of Plio-Pleistocene mammals from east of Lake Turkana. There is a very marked contrast between these Plio-Pleistocene assemblages and that from the nearby early Miocene locality of Buluk, 50 km northeast of Koobi Fora base camp (Harris and Watkins 1974) in which rhinos form a significant proportion of the recoverable fauna. Such a pronounced difference in relative frequency of fossil rhinos between the early Miocene and Early Pleistocene is not, however, unique to the region to the east of Lake Turkana but is typical of other East African localities of similar age. The apparent scarcity of rhinos in the Koobi Fora assemblages appears real in that, while rhinos have not been preferentially sought, I am unaware of any instance in which rhino remains were identified in the field but not collected. Thus of the more than 2500 mammalian fossils collected from 1974 onwards, only 34 specimens of rhinos were retrieved (17 of which were unmeasureable tooth fragments) to add to the material described by Harris (1976). In all, three species have been identified in the succession. *Ceratotherium praecox* is present in the Kubi Algi Formation and becomes replaced by the extinct white rhino subspecies *Ceratotherium simum germanoafricanum* in the Koobi Fora Formation. A black rhino, virtually indistinguishable from the extant *Diceros bicornis*, also makes an appearance in the Koobi Fora Formation.

Rhinos are unknown in Africa prior to the Miocene but four genera—*Brachypotherium*, *Aceratherium*, *Dicerorhinus*, and *Chilotheridium*—are each represented by one or more species in the early Miocene (Hooijer 1978). The first three of these genera have Eurasian representatives but these are specifically distinct from their African counterparts. The extant African rhinos belong to a group (*Diceros*, *Paradiceros*, *Ceratotherium*) which appears to have been of African origin (Hooijer 1978). *Paradiceros mukirii* from the Middle Miocene of Fort Ternan in Kenya is the earliest representative of this group. Hooijer (1972, 1978) interprets *Paradiceros* as a collaterally developed browser from the same ancestral stock as *Diceros* while Guerin (1976) concludes that *Paradiceros* shares a number of features with the Eurasian *Dicerorhinus*. Hooijer (1978) suggests that *Diceros* and *Ceratotherium* spread from southern to northern Africa, although the earliest African example of the genus *Diceros* appears to be *Diceros douarensis* from the Late Miocene of northern Tunisia (Guerin 1966). Other species of *Diceros* have been reported from the Late Miocene and Pliocene of Europe but all are specifically distinct from *Diceros bicornis* which is so far the only black rhino species reported from East Africa. Thenius (1956) suggested that *Ceratotherium* diverged from *Diceros* during the Pliocene and his estimate seems substantiated by the relatively recent (1972) recognition of *Ceratotherium praecox* from Pliocene localities in East and North Africa (Hooijer and Patterson 1972; Hooijer 1972). *C. praecox* possesses features common to both genera but patently belongs to the most progressive lineage of the group which adopted a grazing rather than browsing diet. Both *Diceros* and *Ceratotherium* occur in the Laetolil Beds of Tanzania (Leakey and Hay 1979) that are dated at about 3·6 Ma. However, *Ceratotherium* seems to be a more common element of the Late Pliocene and Early Pleistocene faunas of East Africa than *Diceros* (Guerin 1976; Harris 1976; Hooijer 1976), though this might merely reflect the environments sampled by the known fossiliferous localities. Towards the end of the Pliocene *C. praecox* apparently gave rise to *C. simum germanoafricanum*, which in turn ultimately and perhaps imperceptibly evolved into the extant white rhino. The black rhinos from Laetoli have not yet been fully studied, but examples younger than 3 Ma are virtually indistinguishable from their modern counterparts.

***Ceratotherium* Gray 1867**

Diagnosis. A genus of the subfamily Dicerorhininae having an elongate cranium with a high face and an occiput that is enlarged and protrudes behind the occipital condyles. The angle of the mandible is reduced and the symphysis short. First premolars variable; molars subhypsodont with cement; protoloph and metaloph transverse to very oblique; postfossette on M^3 (after Piveteau 1958).

***Ceratotherium praecox* Hooijer and Patterson 1972**

- *1969 *Ceratotherium simum germanoafricanum* (Hilzheimer); Hooijer: 77, 86, Plate 2, Fig. 1; Plate 5, Figs. 4–5
- 1970 *Ceratotherium* sp. nov.; Patterson, Behrensmeyer and Sill: 921
- 1972 *Ceratotherium praecox* Hooijer and Patterson: 19–25, Figs. 9–10
- 1972 *Ceratotherium praecox* Hooijer and Patterson; Hooijer: 152–191, Plates 21–34
- 1973 *Ceratotherium praecox* Hooijer and Patterson; Hooijer: 168–170
- 1975 *Ceratotherium praecox* Hooijer and Patterson; Hooijer: 188–189, Plate 1

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^3 and no fossetids in lower cheek teeth, internal cingula in upper cheek teeth variable (Hooijer and Patterson 1972).

Holotype. KNM-KP 36, incomplete skull with damaged Lt M^{2-3} and Rt P^4–M^3, lacking anterior portion, left zygomatic arch, basicranium and much of skull roof; specimen from the Pliocene locality of Kanapoi and housed at the National Museums of Kenya.

KOOBI FORA MATERIAL

The species is only poorly represented in the lower part of the Kubi Algi Formation. The best specimen comprises an immature individual of *C. praecox* (KNM-ER 5555) from Area 117 in which the deciduous dentition was erupted and in wear and the first permanent molars were beginning to erupt. The cranium, mandible, and skeleton of this specimen were originally preserved in articulation. Unfortunately by the time the specimen was discovered a *Commiphora* bush had become rooted in the skull and physical and biological weathering had combined to leave the skeleton in an advanced state of disintegration. Portions of the cranium, mandible, and skeleton were recovered but have not yet been completely prepared. Both the cranium and mandible are, at the time of writing, in small fragments providing little information other than that the mandibular ramus was relatively deep even in such an immature specimen.

Only the deciduous teeth from this specimen were in a reasonable state of preservation. The specimen was identified as *C. praecox* on the basis that the antero-internal corners of the upper cheek teeth were not rounded, the lophs were less oblique than in *C. simum germanoafricanum*, and the premolars (but not molars) had well developed internal cingulae.

Although the skeleton has yet to be completely repaired and reassembled, there were some obvious differences from that of extant white rhinos. Despite the immaturity of the individual, the postcranial elements provide the impression of an animal rather larger than extant white rhinos in the osteological collections of the National Museums of Kenya. The atlas vertebra, for example, has a more massive neural arch with much larger and more concave facets for articulation with the axis. The transverse process, on the other hand, extends less far laterally and is shorter anteroposteriorly.

Both the humerus and ulna were longer but more slender than in *C. simum*. The lateral tuberosity of the proximal end of the humerus was more gracile, and the deltoid tuberosity less prominent, than in the extant species. In the ulna the medial facet for articulation with the humerus was deeper (more concave), longer, and broader than in *C. simum*. The shaft was distinctly more slender and the distal epiphysis narrower.

Only the distal portions of the shaft and distal epiphyses of the femur have been fully prepared. The shaft is apparently more elongate and the third trochanter larger, much more massive, and sited higher on the shaft. The supracondyloid fossa is larger but less deeply excavated than in *C. simum*. The tibia is longer but proportionately more slender than in *C. simum* but otherwise similar in morphology.

Only the immature skeleton from Area 117 may be confidently assigned to *Ceratotherium praecox*. The remaining specimens from Areas 117 and 250 (an

* Abbreviated synonymy.

PLATE 4.1. *Ceratotherium praecox* immature right mandible (KNM-ER 5555).

astragalus, KNM-ER 2924, and some isolated teeth) are less diagnostic but are undoubtedly *Ceratotherium* rather than *Diceros* and are provisionally assigned to *C. praecox* pending the recovery of further remains from the Kubi Algi Formation. The relatively large size of the postcranial elements of the immature skeleton is in accordance with the recent findings of Guerin (1979) that *C. praecox* was significantly larger than *C. simum germanoafricanum*.

Ceratotherium simum (Burchell) 1817

*1817 *Rhinoceros simus* Burchell: 97
1827 *Rhinoceros camus* Griffith: 292
1827 *Rhinoceros burchelli* Lesson: 332
1853 *Rhinoceros oswelli* Gray: 46
1895 *Rhinoceros (Atelodus) mauritanicus* Pomel: 13
1945 *Serengeticeros efficax* Dietrich: 56
1926 *Rhinoceros scotti* Hopwood: 17

Diagnosis. Skull markedly dolichocranial, with backward-leaning occipital crest; no incisors or canines; jaws abbreviated in front; mandibular symphysis broad, spatulate; nasal bones broad, short, high; ascending ramus of mandible backward-leaning; no marked angulation at gonion. Cheek teeth hypsodont; protoloph and metaloph strongly curved back, showing early fusion with wear; much cement on crown. Thoracic vertebra 17 or 18 is anticlinal, forming a presacral eminence well separated from sacral eminence (after Groves 1972).

Groves (1972) listed two extant and two fossil subspecies of the white rhinoceros *Ceratotherium simum*. Of the extant taxa, the type subspecies *C. simum simum* is from southern Africa while *C. simum cottoni* has its type locality in the Sudan. Although the present ranges of the two subspecies are separated by about 2000 km (Groves 1972, Fig. 2) the differences upon which the division is justified are relatively minor, the type subspecies having a slightly longer tooth row, a deeper concavity of the skull, thicker body hair and a tendency to associate in larger groups (10–14 versus 4 or less). Of the fossil subspecies, that from East Africa, *C. simum germanoafricanum*, is distinctive and is common at localities of latest Pliocene and early Pleistocene age. *C. simum mauritanicum* from North Africa does not appear to be well founded. White rhinos from southern Africa appear to belong either to the extinct species *C. praecox* or the extant subspecies; the apparent absence of *C. simum germanoafricanum* probably reflects the paucity of samples of Late Pliocene and Early Pleistocene age in this part of the continent.

* Abbreviated synonomy.

Ceratotherium simum germanoafricanum (Hilzheimer) 1925

- *1925 *Rhinoceros simus germanoafricanus* Hilzheimer: 50
- 1926 *Rhinoceros scotti* Hopwood: 16
- 1942 *Serengeticeros efficax* Dietrich: 297
- 1947 *Atelodus* cf. *germano-africanus* Arambourg: 295

Diagnosis. An extinct subspecies of *Ceratotherium simum* differing from extant forms by having a shorter cranial vault, an occiput that is less tall and less backwardly inclined and in which the upper cheek teeth are less hypsodont and less plagiolophodont.

KOOBI FORA MATERIAL

The white rhinoceros is a little more common than the black in the Koobi Fora Formation but it is by no means a common constituent of the individual local faunas. Remains include an adult and two immature skulls, several mandibles and a few postcranial elements.

The only adult skull (KNM-ER 328C) is virtually complete but lacks the anterior portion of the premaxilla, the anterior cheek teeth, and the tip of the left postglenoid process. The specimen was encased in an indurated sandstone matrix and has still to be thoroughly prepared. The skull is of similar size to that of extant white rhinos but is smaller than a skull reported by Hooijer (1969) from Olduvai Bed IV that apparently belonged to the extant subspecies. Morphologically the complete Koobi Fora skull is very similar to extant examples in most respects. The most obvious difference concerns the angle between the plane of the occiput and that of the cranial vault. In modern white rhinos this angle is acute, the nuchal crest overhanging or lying behind the level of the occipital condyles, whereas in the Koobi Fora specimen the angle between these two planes is nearly at right angles. Other minor differences exhibited by the Koobi Fora specimen 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 crania, 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 just erupting, showing wear on its most elevated portion. The nasal boss of this specimen is lower, more rounded, narrower anteriorly and wider posteriorly than that of KNM-ER 328. The external nares and orbital region are both more compressed dorsoventrally than in the adult skull, and the zygomatic arch is straighter and more gracile. Supratemporal ridges are not obvious; their absence may be due to erosion but perhaps also to the relative immaturity of the specimen.

The second incomplete immature cranium, KNM-ER 2320, was recovered from the *Not. scotti* 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 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 unworn. In both immature skulls the palatonarial border is opposite M^1 whereas in the adult skull it is opposite M^2. 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 its occipital region it appears to be less elongate then 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 329 and the apparent discrepancy in both size and robustness is therefore quite impressive. The differences may reflect the 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 (*Met. andrewsi* or *Met. compactus* 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 (2164, 2278, 5649) exhibit similar differences from the mandibles of extant white rhinos.

A number of isolated *Ceratotherium* teeth have been

* Abbreviated synonomy.

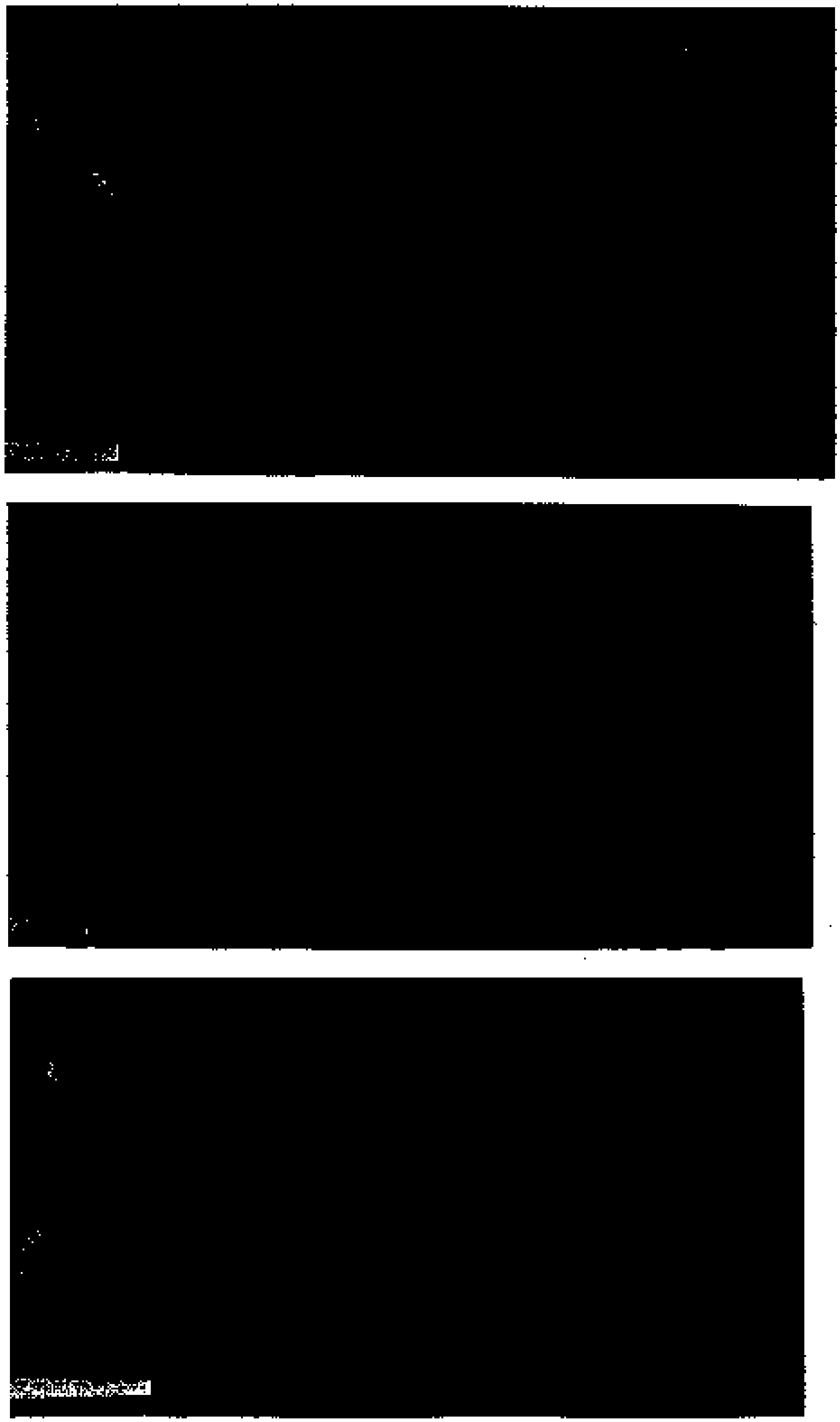


PLATE 4.2. *Ceratotherium simum germanoafricanum* adult cranium (KNM-ER 328C). Top: right lateral view. Centre: occlusal view. Bottom: dorsal view.

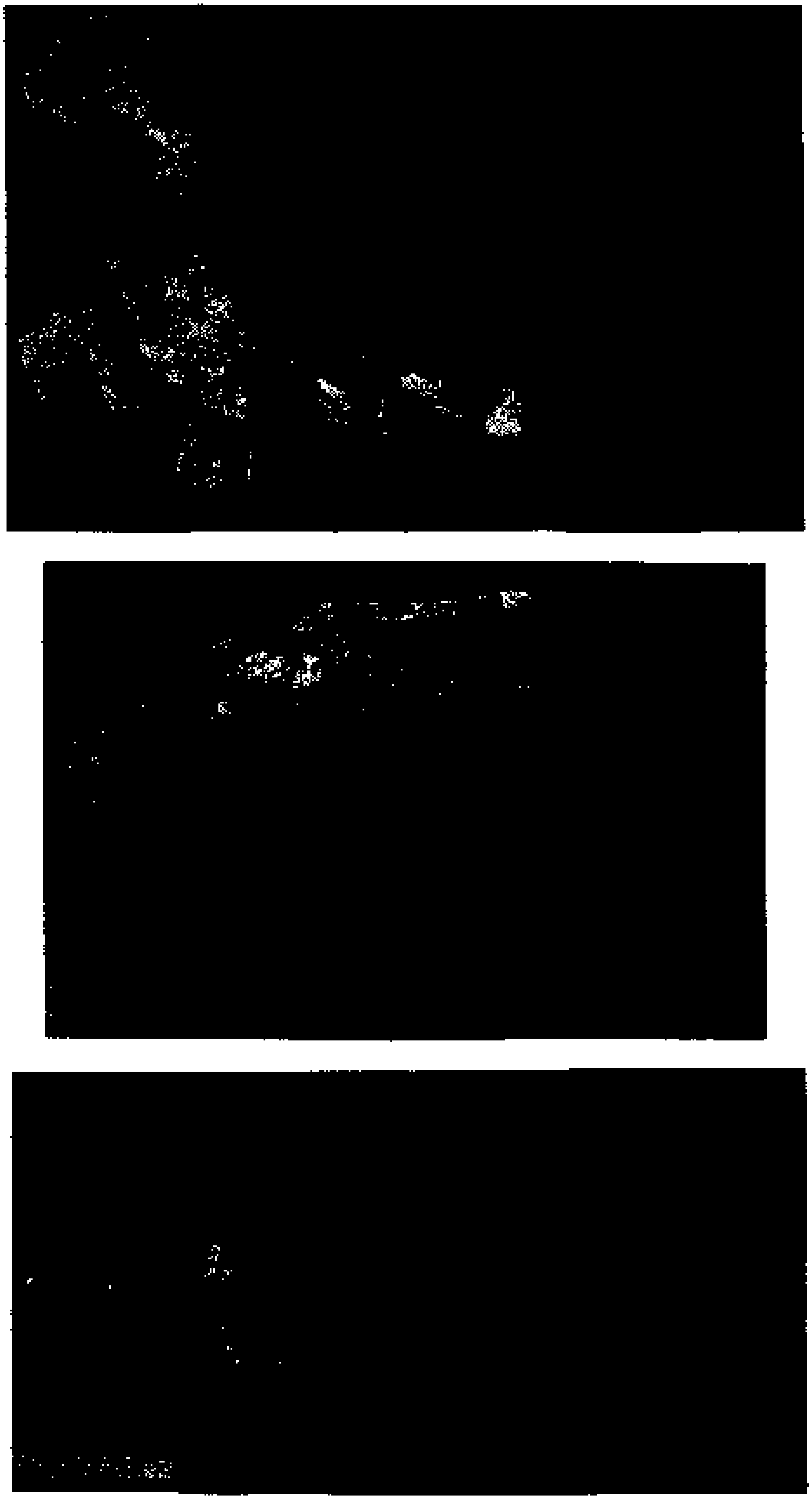
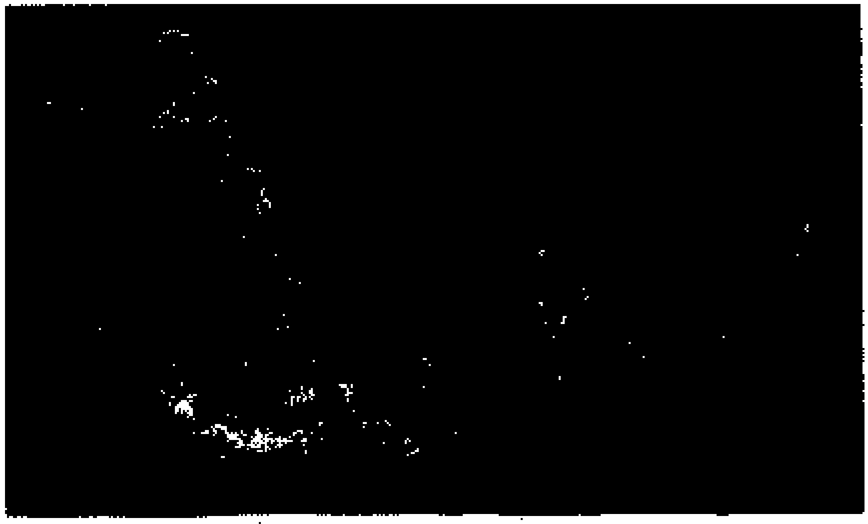


PLATE 4.5. *Ceratotherium simum germanoafricanum* immature crania.
Top: KNM-ER 2320, left lateral view; Centre: occlusal view. Bottom: KNM-ER 309, left lateral view



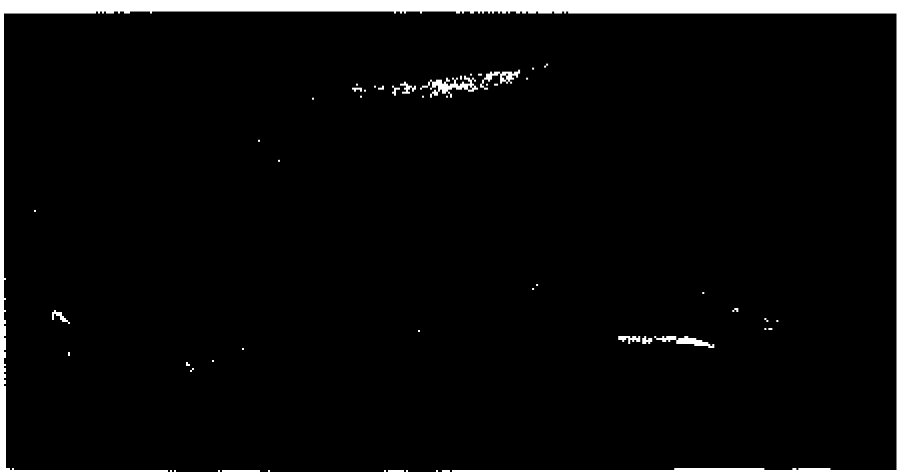


PLATE 4.4. *Ceratotherium simum germanoafricanum*.
Top: KNM-ER 328B, right mandible, lateral view; Centre: occlusal view. Bottom: KNM-ER 329, immature cranium, occlusal view.

collected from the Koobi Fora Formation. Inferior cheek teeth are virtually identical to those of extant examples but there are some differences in the upper cheek teeth between the extinct and extant subspecies. The upper cheek teeth of *C. simum germanoafricanum* appear relatively wider although they are of similar anteroposterior length. Although many of the isolated specimens are greatly worn or incomplete, they appear slightly less hypsodont than those of modern examples. I have found no discernible trend involving increase in hypsodonty upwards through the section as was used by Maglio (1972) in the definition of his faunal zones. The main morphological difference of the teeth concerns the metaloph, that of the fossil specimens being orientated more transversely than in extant examples.

Postcranial remains of *C. simum germanoafricanum* are uncommon. Hooijer (1969, p. 77) pointed out that caution should be exercised in allocating African Plio-Pleistocene rhino postcranials to *Ceratotherium* or *Diceros*, preferring not to do so for material from Olduvai. The specimens allocated below to *C. simum germanoafricanum* have been so identified with reference to their large size and overall morphological similarity with the postcranials of extant white rhinos in the osteological collections of the National Museums of Kenya. Such attributions achieve a measure of support from the relative frequency of white versus black rhino dental remains in the sequence. All the postcranial material considered here derives from the *Met. andrewsi* zone. Most belongs to a single partial skeleton KNM-ER 2278.

The sole incomplete head of a left scapula (2278B) indicates that the head of the scapula of the extinct subspecies was of similar dimensions to that of the extant white rhino but somewhat less concave. A left radius (2278C) is of similar length to that of the extant white rhino but is proportionately wider 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 those of 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.

Unfortunately, for comparative purposes, the only manus and pes elements of an extant white rhino in the Nairobi collections were of an immature individual although these are closely comparable in size to those quoted by Hooijer (1969) for the extant subspecies. The left cuneiform (2278D) was larger and proportionately wider than in the extant form. The ulnar facet of this specimen is relatively wider anteriorly. The unciform facet is wider posteriorly and assumes a more triangular shape than in recent examples.

A fragment of acetabulum (2278E) is less concave than in the pelvis of an extant white rhino. The patella (2278F) is larger and proportionately broader. A right fibula (2278G) is virtually complete but lacks the proximal end. The specimen could only have been marginally longer than in recent white rhinos but is appreciably more massive. The tibial facet of the distal epiphysis is of similar size to 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 Koobi Fora (1195 and 2278J). They are both larger and proportionately deeper than in recent examples. A medial facet for articulation with the calcaneum is contiguous with the ventrolateral calcaneal facet and with the cuboid and navicular facets; the medial calcaneal facet is isolated from the three remaining articular surfaces in *C. s. simum*. The articular facets for the navicular and cuboid are proportionately less wide laterally and deeper craniocaudally than in extant white rhino astragali.

A right navicular (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 (2278L) is larger than in *C. simum simum*. The dorsal facet that articulates with the calcaneum and astragalus is rectangular (longer than wide) in the Koobi Fora specimen but square in recent examples. That part of the facet that articulates with the astragalus is narrower in 2278L while in modern examples 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 (2278M) is larger than in modern examples and contrasts morphologically in that it tapers posteriorly rather than anteriorly. The metatarsal facet on the distal surface shows a greater concavo-convex curvature. The facet that articulates with the lateral cuneiform does not extend to become contiguous with the metatarsal facet as 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 the atlas (2278N) constitutes 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 were associated with the same skeleton (2278 P-S). Unfortunately these all lack neural arches and all but the bases of the transverse processes. They are somewhat larger than the equivalent examples in the extant white rhinos. 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 (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 rhino and the anterior articular surface of the centrum is less dorsoventrally flattened.

The specimens of *Ceratotherium* from the Koobi Fora Formation are assigned to *Ceratotherium simum germanoafricanum* on the basis of the transverse orientation of the metaloph in the upper cheek teeth, and the less backward inclination of the occiput. The Koobi Fora *C. simum germanoafricanum* teeth are less hypsodont than those of modern white rhinos but too few suitably preserved specimens are known from the Koobi Fora Formation to permit deductions on size or hypsodonty changes through the succession. Postcranial elements from this formation tend to be larger than equivalent examples of extant white rhinos. It is unfortunate that those postcranial elements preserved of the *C. praecox* skeleton from Area 117 are not (with the exception of the atlas vertebra) preserved in the skeleton of *C. s. germanoafricanum* from Area 123. Although few comparable measurements are possible between these two specimens it would appear that the (immature) axis of *C. praecox* is slightly larger than that of the adult *C. simum germanoafricanum* specimen. Guerin (1979) has shown there is a progressive decrease in size in the *C. praecox–C. s. germanoafricanum–C. s. simum* lineage.

White rhinos are present as infrequent elements of local faunas throughout much of the mammal-bearing portion of the succession east of Lake Turkana. That more specimens have been retrieved from the *Met. andrewsi* zone probably reflects only that this is the most fossiliferous (and most heavily collected) portion of the sequence, but palaeoecological inferences (Chapter 7) also suggest more optimal conditions for supporting white rhinos. *Ceratotherium praecox* occurs initially in the Pliocene sediments of Kanapoi and Ekora and persists until Member B of the Omo Shungura Formation. It is therefore not unexpected that *C. praecox* should be represented also in the Kubi Algi Formation which, from other evidence, coincides with the later part of the known range of the species. *Ceratotherium simum germanoafricanum* is restricted to the Koobi Fora Formation. The *praecox*-like appearance of the immature skull from the *Not. scotti* zone (KNM-ER 2320) is probably due to its juvenile state rather than indicative of a form transitional between *C. praecox* and *C. simum*. Hooijer (1969) and Maglio (1972) recognize an increase in hypsodonty in the teeth of *C. simum germanoafricanum* from 2–1 Ma, but too few appropriately preserved specimens are known from Koobi Fora to verify satisfactorily such a trend.

White rhinos are today entirely graminiferous (Groves 1972) and there seems little doubt that despite reports of their slightly lesser hypsodonty *C. praecox* and *C. simum germanoafricanum* were also specialized grazers. Other contemporary elements of the faunal assemblages indicate the nearby presence of grassland in the ancient Lake Turkana basin. The low frequency of white rhinos in the preserved assemblages might indicate that conditions immediately adjacent to areas of sediment accumulation were not optimally suited to support populations of white rhinos but that tolerable conditions existed at some distance from the lake and the rivers that drained into it.

Diceros Gray, 1821

Diagnosis. Cranium inclined upwards towards the rear; orbit low, open posteriorly. Postglenoid and post-tympanic processes in contact or only slightly separated. Nasals round, thick, truncated anteriorly, with rugosities anteriorly. Angle of mandible reduced. Horns converge. Molars brachyodont but with a thin layer of cement (after Piveteau 1958).

Only one species of *Diceros* (the type species) occurs in sub-Saharan Africa today and the features that distinguish black from white rhinos at the generic level suffice to differentiate the species. Black rhinos are reported to be commoner than white in the upper portions of the Olduvai sequence (Hooijer 1969) but they are less frequent at other and earlier levels in eastern Africa. Crania have now been recovered from Koobi Fora (Harris 1976), Omo (Hooijer 1973) and Laetoli (Leakey and Hay 1979) but remains other than incomplete dentitions are rare. Extinct Pliocene species of *Diceros* have been reported from North Africa and the eastern Mediterranean (Hooijer 1976) but detailed comparisons have yet to appear in the literature. Whether such northern species were ancestral to the extant black rhino or whether the latter evolved from the Middle Miocene *Paradiceros* (Hooijer 1976) must await detailed study of the Laetoli and other material.

Diceros bicornis (Linn.), 1758

The living black rhinoceros exhibits considerable geographic variation with regard to overall size (Zukowsky 1964; Groves 1967). Whether such variation was characteristic of Pliocene and Pleistocene representatives cannot be ascertained until appreciably larger fossil samples are available for study. This possibility must, however, be borne in mind during any future evaluation of fossil material. It appears generally accepted that *Diceros* and *Ceratotherium* shared a common ancestry and that *Diceros* is the less progressive of the two. There is some evidence to suggest that the teeth of *Diceros* became slightly more hypsodont through time (Hooijer 1976) but that there was an overall decrease in body size (Guerin 1979).

KOOBI FORA MATERIAL

Diceros bicornis has been recorded from a number of localities of Late Pliocene and Early Pleistocene age (Guerin 1976; Hooijer 1969, 1976; Leakey *et al.* 1976). At Koobi Fora it is even less common than *Ceratotherium* and remains, most of which are partial dentitions or isolated teeth, are apparently restricted to the *Not. scotti* and *Met. andrewsi* zones. There is no evidence to suggest it could not have occurred at earlier or later horizons and the number and provenance of the Koobi Fora specimens probably reflects the overall scarcity of rhinos from this locality.

The cranium (KNM-ER 696) was originally reported as from the *Met. compactus* zone (Harris 1976) but is now known to be from the *Met. andrewsi* zone (P. Abell, personal communication). It is of interest in that it was the first relatively complete fossil black rhino skull ever collected. Other crania have subsequently been recovered from older sediments at Omo (Hooijer 1973) and Laetoli (Leakey and Hay 1979). In most respects the Koobi Fora cranium is morphologically similar to that of modern examples of *D. bicornis*; differences are minor and mainly restricted to the cranial region. The specimen was not fully mature, third molars being present but incompletely erupted, and many of the sutures can be distinguished. Groves (1967) recognized large and small races of extant black rhinos in Africa; the Koobi Fora specimen would appear to be representative of a small race.

The premaxilla and 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 from the osteological collections of the National Museums of Kenya, including the infraorbital canal which appears to be 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 extant *D. bicornis*. The zygomatic arch of the Koobi Fora 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 appears to be 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 Koobi Fora specimen is defined by lateral processes from the paramastoid. The paroccipital process is of similar size and shape to that of the modern skulls in the Nairobi collections but the paramastoid appears wider and deeper. This may, however, be due to the

PLATE 4.5. *Diceros bicornis* cranium (KNM-ER 636).
Above: left lateral view. Below: occlusal view.

different shape of the occiput of the fossil cranium. The posterior face of the paroccipital process is less concave at its base in the fossil specimen, 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, the paramastoid bears both lateral and ventral protuberances. The lateral protuberance is more clearly defined and projects farther than in modern examples. The ventral protuberance is sited farther from the lateral process in the fossil cranium and its tip has a concave rather than a convex facet.

In the auditory region the hyoid process of the fossil cranium is a little larger than in 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 specimen are of similar size to modern examples but bear a keel from the posterolateral edge extending to the

PLATE 4.6. *Diceros bicornis* cranium (KNM-ER 636).
Top: dorsal view. Bottom left: anterior view. Bottom right: occipital view.

anteroventral tip of the process. The distal tip of the postglenoid process appears narrower than in extant skulls in which the postglenoid processes are rounded posteriorly. The glenoid fossa is less concave and less posteriorly orientated than in modern crania but is of similar size.

An immature mandible KNM-ER 472 attributed to *D. bicornis* by Harris (1976) has proved on subsequent re-examination to belong to *C. simum germanoafricanum*. The most complete black rhino mandible from Koobi Fora, KNM-ER 2139, is deeper and stouter than many examples of extant black rhinos and has a wider but shorter mandibular symphysis, an attribute confirmed by a second partial symphysis (KNM-ER 5650).

There appears to be no difference in dental morphology between the *D. bicornis* specimens from Koobi Fora and extant examples. Most of the fossil teeth are worn but appear slightly less hypsodont than in modern examples.

A left astragalus, KNM-ER 1196, is larger than that of modern examples of *D. bicornis*. It differs morphologically in that the lateral edge of the calcaneal facet is not produced distally and in that there is no large posterior projection on the medial edge of the astragalus below the medial edge of the trochlea. The specimen is, however, appreciably smaller than others here attributed to *C. simum germanoafricanum* and is clearly closer in overall shape to black rather than white rhinos. It is therefore

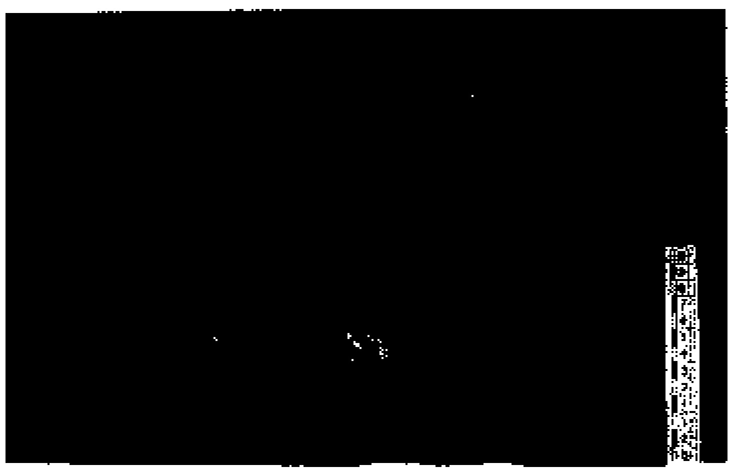


PLATE 4.7. *Diceros bicornis* mandible (KNM-ER 2139). Above: left lateral view. Below: occlusal view.

tentatively identified as *D. bicornis* pending the recovery of material other than white rhino from the *Not. scotti* zone. Guerin (1979) has pointed out that extant black rhinos are significantly smaller than Pleistocene representatives, which is borne out by the Koobi Fora astragalus.

Groves (1967) recognized seven modern subspecies of *D. bicornis* that could be differentiated on length and breadth parameters of the skull. These fall into larger and smaller size groups. Groves noted the presence of two extant subspecies in northern Kenya—the larger *D. bicornis ladoensis* and the smaller *D. b. michaeli*. Records were not available to Groves of rhinos from the vicinity of Lake Turkana although they were not uncommon here at the turn of the century. Indeed one was sighted by Kamoya Kimeu in 1974 and fresh footprints and dung were observed in 1977. The poached carcase of a black rhino was discovered north-east of Area 123 by Dr Frank Brown in 1981. A relatively fresh skull was collected from the Nderati waterhole by the 1968 expedition and on detailed examination this proves to be *D. bicornis brucii* (not *D. b. michaeli* as recorded by Harris 1976). Using Groves' parameters, the Koobi Fora cranium, although subadult, is also closer to *D.*

b. brucii than to the other recognized subspecies. The less complete but earlier skull from Omo Shungura Member C (Hooijer 1973) appears to be rather larger.

The bulk of the diet of black rhinos is comprised of herbs and shrubs, grasses providing a minor to negligible component. In consequence black rhinos tend to occur at higher density in bushland and woodland than in more open habitats. The overall scarcity of rhinos in the Plio-Pleistocene assemblages from east of Lake Turkana may well be a result of their patterns of behaviour. That fewer black than white rhinos are known from most assemblages may reflect further the prevailing types of habitat. One puzzling feature is that white rhinos appear to be far more common than black at most localities during the early Pleistocene, and persist in eastern African assemblages until the late Pleistocene or early Holocene, but today are restricted in distribution to a belt to the west of the western Rift Valley and to southern Africa. The black rhino was more common than the white in recent and historic times. Perhaps the life style of the black rhino is less conducive to its preservation in fossil assemblages.

DISCUSSION

The fossil material from Koobi Fora has contributed appreciably to our knowledge of the cranial anatomy of black and white rhinos during the Early Pleistocene but in contrast to other groups, such as the elephants and suids, only minor evolutionary changes took place during the course of the Pliocene and Pleistocene. While rhinos were eminently successful large herbivores during the African Miocene, the ecological changes that brought about the spread of grassland habitats during the latter part of the Neogene, and the evolution or immigration of mammals better adapted to live in them, contributed to the subsequent decline of this superfamily in Africa. By the middle Pliocene the extant African genera had appeared in substantially their present form. Thereafter two progressive evolutionary trends were manifest in both lineages—slight increase in hypsodonty and size of the cheek teeth and decrease in overall body size. The former presumably reflected an increasing dependence on a siliceous and abrasive diet; the latter was perhaps symptomatic of the comparatively greater success of the elephants and larger artiodactyls and their subsequent effect on and interaction with the environment. Thus although the influence of man has significantly contributed to the decline of the rhinos in recent years, it appears that this group was already past its zenith by the time that man's technological and aggressive efficiency became documented in the archaeological record.

Available evidence suggests that the extant African genera shared a common ancestry towards or shortly after the end of the Miocene. The subsequent fossil record of *Ceratotherium* documents its progressive adaptation to a graminiferous diet, initially by increase in hypsodonty and later by slight modification of the orientation of the lophs of the upper molars. The wide mouth, from which the vernacular name is derived, is eminently suitable for grazing and progressive elongation of the cranium (rather than the neck) enabled the animal to reach grass at the preferred height of less than 10 cm (Kingdon 1979). In contrast *Diceros* appears to have had a relatively more conservative history although the detailed investigation of the earliest material (from Laetoli) has yet to be published. Black rhinos today consume a wide variety of plants and are highly selective for herbs, shrubs, and legumes; there is no evidence that a different diet was preferred in the past. Both white and black rhinos are sedentary and territorial, factors which may well contribute to their relative scarcity in the fossil record. While the white rhino appears to be water-dependent (Foster 1967, p. 170), black rhinos are known to be able to survive in habitats lacking permanent water (Goddard 1968, p. 16). This plus the more solitary nature of the black rhino may partially explain its lesser frequency in fossil assemblages. The white rhino is very rarely aggressive towards man (Foster 1967), a factor which may have contributed to its demise in eastern and southern Africa in historic times.

SPECIMEN LISTS AND TABLES

ABBREVIATIONS TO TABLES

†	approximate measurement	ht	height
|	maximum measurement on incomplete specimen	hyp	width at hypolophid
( )	estimated measurement	int	internal
ap	anteroposterior length	met	width at metaloph
ant	anterior	post	posterior
dist	distal	prot	width at protoloph(id)
epic	width at lateral epicondyle	prox	proximal
ext	external	tr	transverse width

Ceratotherium praecox

	KNM-ER No.	Area	Specimen
Zone A	3185	250	Rt M1/2
	3186	250	Upper molar frags
Zone B	2924	117	Rt astragalus frag
	4655	117	Lt P_2 frag
	5555	117	immature cranium and skeleton

Table 4.1.
Ceratotherium praecox deciduous dentition measurements (mm)

	KNM-ER	5555 (Rt)	5555 (Lt)
dP^1	ap	23·2	—
	prot	22·5	—
	met	19·8	—
dP^2	ap	33·4	33·0
	prot	33·5	33·6
	met	36·4	34·3
Rt M^2	ap	64·2	—
	prot	58·3	·
	met	51·0	—
dP_1	ap	18·1	17·5
	tr	13·3	13·0
dP_2	ap	28·0	28·2
	prot	19·0	20·0
	met	21·7	20·1 +
dP_3	ap	39·0	-
	prot	38·2	—
	met	30·3	-

TABLE 4.2. *Ceratotherium praecox* postcranial measurements (mm)

	KNM-ER No.	5555 (Lt)	5555 (Rt)	5555	*OM 2186
Humerus	Length	430	—		450
	Prox ap	160	—		180
	Prox tr	182	—		212
	Dist ap	116	—		126
	Dist tr	114	—		120
	Dist epic	167	161		178
Ulna	Length	528	—		510
	Width coronoid process	112	—		108
	Dist ap	56	—		57
	Dist tr	41			42
Femur	Dist ap	195	—		186
	Dist tr	126	140		125
Tibia	Length	428	450		400
	Prox ap	136	141		158
	Prox tr	135	151		194
	Dist ap	78	80		82
	Dist tr	98+	95		102
Atlas vertebra	Length neural arch			64	47
	Width lt side atlas			139	177
	Length transverse process			104	121
	Width axis facet			74	57
	Depth axis facet			45	33

* Osteology Collections, National Museums of Kenya.

Ceratotherium simum germanoafricanum

	KNM-ER No.	Area	Specimen
Notochoerus scotti zone	1190	130	Rt P^3
	2145	100	Rt M_2
	2320	105	immature cranium
	2700	105	Rt M^{1-2}
	2755	14	Lt M_3
	4649	100	Rt mandible frag
	4651	14	Rt $\underline{P}$
	4653	12	Rt $P^?$ and $\underline{M}$ frags
Metridiochoerus andrewsi zone	1167	103	Rt $P^?$
	1188	6A	Rt mandible (P_2–M_3), Lt P_2 and Lt M_2
	1189	103	isolated upper teeth
	1191	8	Rt $M^{?-?}$
	1192	102	Lt M_3
	1193	102	Rt M_3, Rt P_4
	1194	6A	Lt M_1
	1195	8B	Lt astragalus
	2156	102	Rt mandible frag
	2164	130	Rt mandible (P_2–M_3)

Ceratotherium simum germanoafricanum cont.

	KNM-ER No.	Area	Specimen
	2257	105	prox. Lt radius
	2278	123	mandible and postcranial frags
	2623	130	Lt mandible frag (M_1)
	4648	105	Rt mandible frag (M_2)
	4654	105	intermediate phalanx
	4656	102	Rt M_3
	5647	123	Rt P_4
	5649	106	Lt mandible
Metridiochoerus compactus zone	4650	103	Lt P^2
Horizon indet.	328	Ileret	cranium
	329	Ileret	cranium
	472	KF III	Rt and Lt mandible
	659	KF IIB	Lt M^3
	686	KF IIB	Lt M_2
	687	KF IIB	isolated teeth

TABLE 4.3. *Ceratotherium simum germanoafricanum* cranial measurements (mm)

KNM-ER No.	328C	329	2320	*OM 2184
Maximum length	800	(635)	(500)	825
Minimum length nasal boss to nuchal crest	733	633	—	756
Length nasal boss to external auditory meatus	632	540	459	—
Basilar length	752	(635)	—	713
Length palatonarial border to occipital condyles	431	400	(308)	427
Width nasal boss	182	161	82	194
Maximum width cranium at orbit	302	(240)	166	180
Minimum width cranial vault at temporal fossa	120	115	103	112
Width dorsal edge nuchal crest	275	(208)	—	216
Maximum width occiput	283	—	—	216
Width occipital condyles	151	(158)	—	154
Depth foramen magnum to nuchal crest	156	(98)	—	162
Maximum width cranium at zygoma	373	(320)	(286)	335
Width palate at M^1	65	106	69	100
Width palate at M^3	82		113	—

* Osteology Collections, National Museums of Kenya.

TABLE 4.4. *Ceratotherium simum germanoafricanum* upper dentition measurements (mm)

	KNM-ER No.	*OM No.	ap ext.	ap int	prot	met	tr
P^2	4650		34·7	—	40·8	38·8	
	4653		30·1+	—	—	34·9+	
		2184	38·9	36·3	38·5	40·0	
P^3	1187		—	—	51·6		
	1190		49·4	46·4	51·5	48·8+	
		2184	46·0	46·4	51·9	47·0	
		2216	38·0	30·4	34·7	31·0	
P^4	328(Lt)		51·0	43·9	63·8	62·2	
	328(Rt)		54·5	41·1	63·6	56·5	
	1189(Rt)		46·1	43·4	59·2	55·3	
		2184	55·2	51·2	51·2	44·6	
		2216	44·6	39·0	39·0	35·8	
M^1	328(Lt)		48·5	41·0	70·0	61·9	
	328(Rt)		50·0	39·8	70·0	64·5	
	329		71·0	48·2	57·1	33·8	
	2700		48·6	—	60·1	55·5	
		2184	50·5	52·5	58·0	55·1	
		2216	46·1	37·9	42·6	36·2	
M^2	328(Lt)		65·5	50·4	(75·5)	61·3	
	328(Rt)		64·0	56·0	77·2	64·8	
	1191		58·4	54·8	67·6	54·9	
		2184	73·2	60·2	51·6	45·7	
		2216	46·4	43·8	51·0	40·5	
M^3	328(Lt)		70·3	60·2			59·3
	328(Rt)		64·4	61·3			59·8
	659		68·2	65·6			61·2
	1189(Lt)		63·4	62·1			54·9
	1189(Rt)		77·4	69·4			54·7
		2216	58·9	46·3			42·3

* Osteology Collections, National Museums of Kenya.

TABLE 4.5. *Ceratotherium simum germanoafricanum* mandible measurements (mm)

KNM-ER No.	328A	328B	472	1188	2164	2278	5649	*OM 2184
Total length	616	622	—	—	—	—	—	583
Length symphysis	92	121	68	—	87	—		83
Max. width at symphysis	71	79	91	—	74	—	—	65
Height ramus at M_1	144	135	102	—	128	150	124·8	115
Height ramus at M_3	130	125	·	·	(119)	145	122·2	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	244	233	207		—	244
Length P_4–M_3	251	247	-	231	242	246+	243·8	260
Length P_2–M_3	278	286	—	306	283	—	—	296

* Osteology Collections, National Museums of Kenya.

TABLE 4.5. *Ceratotherium simum germanoafricanum* lower dentition measurements (mm)

KNM-ER No.	328A	328B	472(Lt)	472(Rt)	686	687	1188(Lt)	1188(Rt)	1192	1193	1194	2145	2164	2278	2755	4648	4656	5647	5649	*OM 2184
P_2 ap	—	36·3	35·6	38·9	—	36·6	35·3	35·4	—	—	—	—	32·9	—	—	—	—	—	—	37·6
prot		29·8	21·1	17·7	—	20·9	19·3	19·4	—	—	—	—	19·2	—	—	—	—	—	—	24·0
hyp	—	24·3	19·1	18·6	—	21·0	20·3	20·2	—	—	—	—	20·0	—	—	—	—	—	—	23·7
P_3 ap	43·5	38·7	43·5	42·5	—	41·6+	—	42·6	—	—	—	—	36·6	—	—	—	—	—	41·6	48·4
prot	28·4	28·1	20·7	20·4	—	24·1	—	23·9	—	—	—	—	27·3	—	—	—	—	—	22·0	28·3
hyp	29·1	16·9	20·3	19·6	—	25·5	—	24·3	—	—	—	—	29·0	29·2	—	—	—	—	24·6	29·2
P_4 ap	49·3	41·2	—	—	—	46·3+	—	46·4	—	50·2	—	—	43·4	41·6	—	—	—	43·1	46·8	50·5
prot	30·8	32·8	—	—	—	28·7	—	25·7	—	28·7	—	—	30·6	32·5	—	—	—	27·0	26·4	31·9
hyp	33·0	33·2	—	—	—	31·3	—	27·6	—	31·2	—	—	32·9	33·0	—	—	—	29·3	—	30·9
M_1 ap	41·0	46·5	50·0	49·7	—	46·2	—	48·8	—	—	50·6	—	40·4	—	—	—	—	—	47·5	54·0
prot	41·3	35·3	24·7	27·8	—	27·3	—	26·4	—	—	40·2	—	31·8	—	—	—	—	—	—	32·4
hyp	34·2	32·8	25·4	30·0	—	31·7	—	30·6	—	—	36·0	—	30·6	—	—	—	—	—	—	33·2
M_2 ap	53·6	54·6	58·2	60·6	53·0	55·0	62·1	65·0	—	—	—	48·7	50·2	48·1	—	60·2	—	—	50·3	61·5
prot	34·6	34·4	20·6	24·3	36·9	26·8	29·9	29·2	—	—	—	32·6	31·9	35·6	—	39·1	—	—	—	31·8
hyp	34·6	32·2	20·2	22·7	35·5	36·4	32·3+	33·6	—	—	—	28·6	31·9	33·2	—	32·0	—	—	—	30·2
M_3 ap	56·2	60·4	—	—	—	60·0	—	65·7	55·9	56·5+	—	—	61·0	65·5	62·6	—	55·5	—	51·6	58·1
prot	34·8	31·6	—	—	—	29·6	—	29·2	36·6	29·0+	—	—	31·3	38·2	32·6	—	31·3	—	—	29·6
hyp	31·8	30·1	—	—	—	27·4	—	26·8	30·9	30·0	—	—	30·4	33·2	30·6	—	26·4	—	—	22·2

* Osteology Collections, National Museums of Kenya.

TABLE 4.7.
Ceratotherium simum germanoafricanum deciduous dentition measurements (mm)

KNM-ER No.	329(Rt)	472(Rt)	472(Lt)	2320
dP¹ ap ext	30·0			25·9
ap int	29·6			22·6
tr	26·9			19·2
dP² ap ext	39·8			40·7
ap int	36·1			32·8
prot	37·0			37·2
met	43·6			31·6
dP³ ap ext	48·7			48·2+
ap int	41·0			42·0
prot	53·6			46·6
met	55·7			38·2

KNM-ER No.	329(Rt)	472(Rt)	472(Lt)	2320
dP⁴ ap ext	61·8			56·5
ap int	54·8			43·6
prot	56·6			41·5
met	53·3			43·0
dP_4 ap ext		44·2		
ap int		22·4	—	
prot		22·4	(22·7)	
hyp		24·5	24·7	

TABLE 4.8.
Ceratotherium simum germanoafricanum postcranial measurements (mm)

	Radius		
	KNM-ER 2257	2278C	OM 2744*
Max. length	—	417	410
Prox epiphysis ap	90	85+	74
Prox epiphysis tr	134	142+	119
Min. width midpoint shaft	—	83	63
Dist epiphysis ap	·	87	73
Dist epiphysis tr	—	144	119

	Cuneiform		Patella	
	KNM-ER 2278D	OM 2186*	KNM-ER 2278F	OM 2186
Max. length (dorsoventral)	67	60	93	87
Max. prox width (mediolateral)	54	47	87	68
Max. prox depth (craniocaudal)	46	38	—	..
Max. distal width	54	42	121	95
Max. distal depth	57	48	—	—
Max. depth (craniocaudal)	—	—	63	54

	Fibula	
	KNM-ER 2278G	OM 2186
Max. length	335 †	325 †
Width distal epiphysis	65	45
Depth distal epiphysis	36	24
Max. width tibial facet	17	20
Max. width astragalus facet	48	32

(continued overleaf)

TABLE 4.8. *cont.*

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

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

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

	Navicular KNM-ER 2278K	Navicular OM 2186	Middle cuneiform KNM-ER 2278M	Middle cuneiform OM 2186
Max. length (craniocaudal)	72	60	50	44
Width cranial edge	70	57	27	18
Width (mediolateral) caudal edge	57	51	19	22
Max. depth (proximodistal)	37	33	25	17

TABLE 4.8. *cont.*

	Intermediate phalanx KNM-ER 4654
Length	38·7
Prox ap	—
Prox tr	52·8
Dist ap	27·2
Dist tr	53·6

	Atlas vertebra KNM-ER 2278N	OM 2744
Length ventral edge neural canal from ant surface to post edge spine	94	76
Ht left occipital condylar facet	59	52
Width left occipital condylar facet	98 †	84
Ht left axis facet	48	31
Width left axis facet	54	42 †

	3rd cervical vertebra		4th cervical vertebra			5th cervical vertebra		
	KNM-ER 2278P	OM 2186	KNM-ER 2278Q	OM 2186	OM 2744	KNM-ER 2278R	OM 2186	OM 2744
Max length centrum	94	75	112	87	80	98	85	72
Ht ant epiphysis centrum	82	63	83	73	64	82	71	68
Width ant epiphysis centrum	53	47	54	47	46	56	49	42
Ht post epiphysis centrum	92	81		79	75	90	79	79
Width post epiphysis centrum	89	64	—	64	89	85	73	59

	6th cervical vertebra			1st sacral vertebra	
	KNM-ER 2278S	OM 2186	OM 2744	KNM-ER 2278T	OM 2744
Max length centrum	61	78	79	81	54 †
Ht ant epiphysis centrum	83	67	68	71	41
Width ant epiphysis centrum	58	50	44	87	90
Ht post epiphysis centrum	85	77	76	58	—
Width post epiphysis centrum	84 †	78	65	91	79

* Osteology Collections, National Museums of Kenya.

Diceros bicornis

	KNM-ER No.	Area	Specimen
Notochoerus scotti zone	1196	131	Rt astragalus
Metridiochoerus andrewsi zone	369	104	Lt P^1
	636	1A	cranium
	1186	105	maxilla frags
	1194	6A	Lt M_1
	2139	119	Rt and Lt mandible frags
	4646	104	Lt M_2
	4657	104	Rt M_2
	5650	123	mandible symphysis
Horizon indet.	327	119/123	Rt maxilla frag
	691	KF IIB	isolated teeth

TABLE 4.9. *Diceros bicornis* cranial measurements (mm)

	KNM-ER 636	*OM 2178	**UB 20133
Length nasals to nuchal crest	524	547	505
Max. width cranium at ant edge orbit	230	258	258
Min. width cranium at temporal fossa	107	117	112
Max. width cranium at post edge of zygomatic arch	305	325	300
Min. width supratemporal ridges	77	72	54
Width dorsal edge of nuchal crest	167	189	170
Max. width of occiput	218	236	219
Depth ant portion of zygoma	42	55	68
Depth post portion of zygoma	50	50	47
Max. depth zygoma	50	60	69
Width foramen magnum	46	44	47
Depth foramen magnum	38	40	48
Width occipital condyles	116	126	114
Length palatonarial border to occipital condyles	303	318	273
Length ant edge orbit to glenoid fossa	216	231	204
Width pterygoid to 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	160
Max. width lateral edges of paroccipital processes	218	217	—
Depth left paroccipital below mastoid foramen	86	88	—
Max. length left paroccipital	60	53	—
Max. length right paroccipital	60	56	—

* Osteology Collections, National Museums of Kenya.
** Collections of the University of Bristol, Dept. of Geology.

TABLE 4.10. *Diceros bicornis* upper dentition measurements (mm)

KNM-ER No.		327	369	636(Lt)	636(Rt)	691(Lt)	691(Rt)	1186(Lt)	1186(Rt)	*OM 2180
P^1	ap ext	—	30·4	20·6	—	—	—	—	—	21·8
	ap int	—	29·4	26·3	—	—	—	—	—	22·5
	tr	—	36·5	21·6	—	—	—	—	—	21·5
P^2	ap ext	—	—	32·4	33·3	36·4		—	—	32·2
	ap int	·	—	25·2	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	53·1	47·0
	ap int	42·2	·	37·4	40·0	44·1	43·3	42·5	41·8	39·7
	prot	57·1	—	59·4	63·0	60·2	55·8	66·0	69·0	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	42·6
	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	63·9	—	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

* Osteology Collections, National Museums of Kenya.

TABLE 4.11. *Diceros bicornis* mandible measurements (mm)

	KNM-ER 2139	KNM-ER 5650	*OM 2180	**UB 23310
Length of symphysis	73	96 +	92	101
Max. width of ant end symphysis	67	—	48	43
Max. width of symphysis	121	115	114	104
Height of body at M_1	84	75	72	79
Length P_1–M_3	195	—	220	216

* Osteology Collections, National Museums of Kenya.
** Collections of the University of Bristol, Dept. of Geology.

TABLE 4.12. *Diceros bicornis* lower dentition measurements (mm)

KNM-ER No.		2139	4646	5650(Rt)	5650(Lt)	*OM 2180	*OM 2181
P_3	ap ext	—	—		34·0	39·4	37·0
	ap int	—	—	—	31·9	39·5	36·8
	prot	—	—		20·6	24·5	25·0
	hyp		—	—	22·9	38·5	27·3
P_4	ap ext	40·9	—	39·8 †	40·4	45·6	39·7
	ap int	—	—	38·3	35·5	41·6	34·2
	prot	29·3 †		27·5	26·7	30·0	28·1
	hyp	33·3 †	—	31·4	30·5	33·3	29·9
M_1	ap ext	42·5	—	—	—	48·0	50·4
	ap int	44·2	—	—	—	43·8	43·1
	prot		—	—	—	30·0	27·7
	hyp	—	—		—	32·3	32·1
M_2	ap ext	48·8	—	—	—	47·3	51·7
	ap int	—	—	—	—	52·1	52·7
	prot	—	—	—		30·1	29·3
	hyp	—		—	—	32·0	30·1
M_3	ap ext	—	54·0		—	—	—
	ap int	—	—	—	—	—	—
	prot	—	28·6	—	—	—	—
	hyp	—	27·0	—	—	—	—

* Osteology Collections, National Museums of Kenya.

TABLE 4.13.
Diceros bicornis astragalus measurements (mm)

	KNM-ER 1196	*OM 2185
Max. length	90·8	84·1
Medial length	80·4	78·7
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

* Osteology Collections, National Museums of Kenya.

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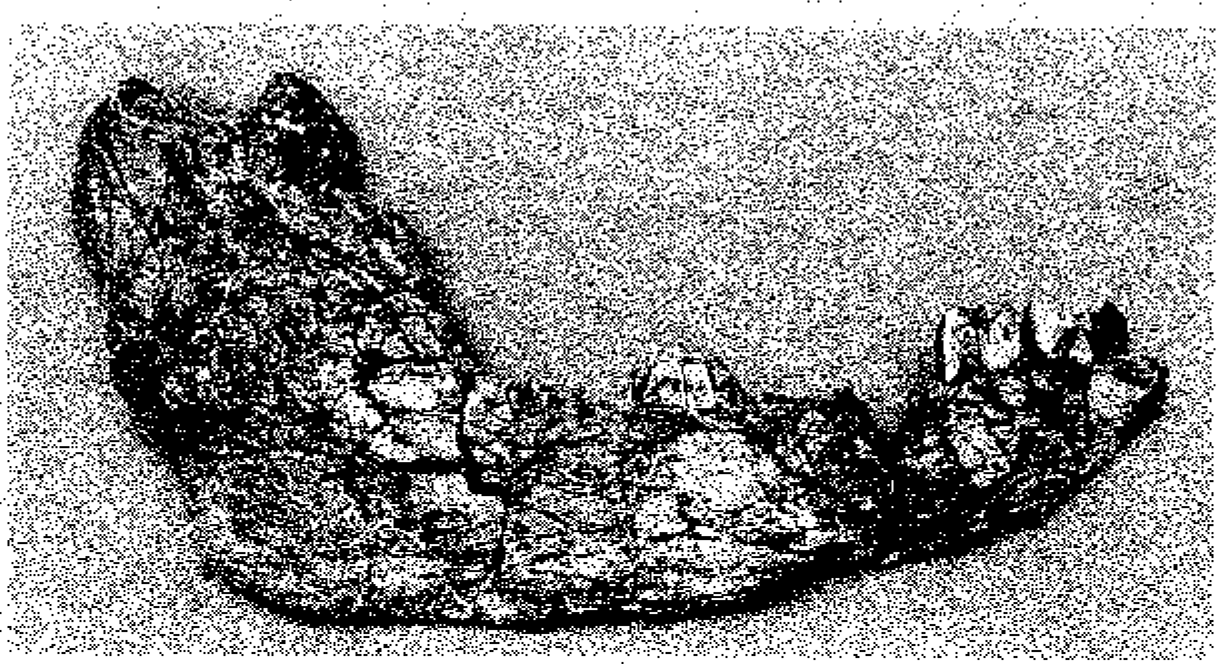


PLATE 9.1. *Ceratotherium praecox* immature right mandible (KNM-ER 3555).

astragalus, KNM-ER 2924, and some isolated teeth) are less diagnostic but are undoubtedly *Ceratotherium* rather than *Diceros* and are provisionally assigned to *C. praecox* pending the recovery of further remains from the Kubi Algi Formation. The relatively large size of the postcranial elements of the immature skeleton is in accordance with the recent findings of Guerin (1979) that *C. praecox* was significantly larger than *C. simum germanoafricanum*.

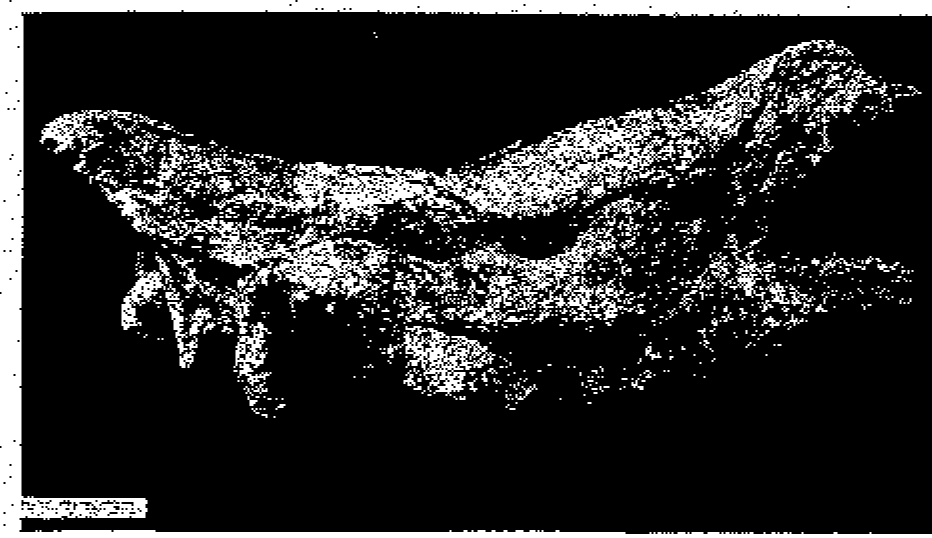
Ceratotherium simum (Burchell) 1817

- *1817 *Rhinoceros simus* Burchell: 97
- 1827 *Rhinoceros camus* Griffith: 292
- 1827 *Rhinoceros burchelli* Lesson: 332
- 1853 *Rhinoceros oswelli* Gray: 46
- *1895 *Rhinoceros (Atelodus) mauritanicus* Pomel: 13
- 1945 *Serengeticeros efficax* Dietrich: 56
- 1926 *Rhinoceros scotti* Hopwood: 17

Diagnosis. Skull markedly dolichocranial, with backward-leaning occipital crest; no incisors or canines; jaws abbreviated in front; mandibular symphysis broad, spatulate; nasal bones broad, short, high; ascending ramus of mandible backward-leaning, no marked angulation at gonion. Cheek teeth hypsodont; protoloph and metaloph strongly curved back, showing early fusion with wear; much cement on crown. Thoracic vertebra 17 or 18 is anticlinal, forming a presacral eminence well separated from sacral eminence (after Groves 1972).

Groves (1972) listed two extant and two fossil subspecies of the white rhinoceros *Ceratotherium simum*. Of the extant taxa, the type subspecies *C. simum simum* is from southern Africa while *C. simum cottoni* has its type locality in the Sudan. Although the present ranges of the two subspecies are separated by about 2000 km (Groves 1972, Fig. 2) the differences upon which the division is justified are relatively minor, the type subspecies having a slightly longer tooth row, a deeper concavity of the skull, thicker body hair and a tendency to associate in larger groups (10–14 versus 4 or less). Of the fossil subspecies, that from East Africa, *C. simum germanoafricanum*, is distinctive and is common at localities of latest Pliocene and early Pleistocene age. *C. simum mauritanicum* from North Africa does not appear to be well founded. White rhinos from southern Africa appear to belong either to the extinct species *C. praecox* or the extant subspecies; the apparent absence of *C. simum germanoafricanum* probably reflects the paucity of samples of Late Pliocene and Early Pleistocene age in this part of the continent.

* Abbreviated synonymy.



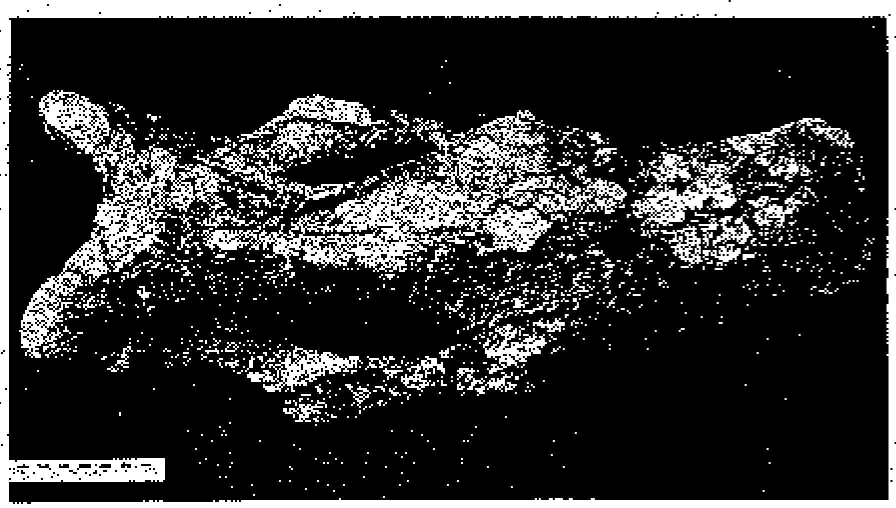


PLATE 4.2. *Ceratotherium simum germanoafricanum* adult cranium (KNM-ER 3[illegible]).
Top: right lateral view. Centre: occlusal view. Bottom: dorsal view

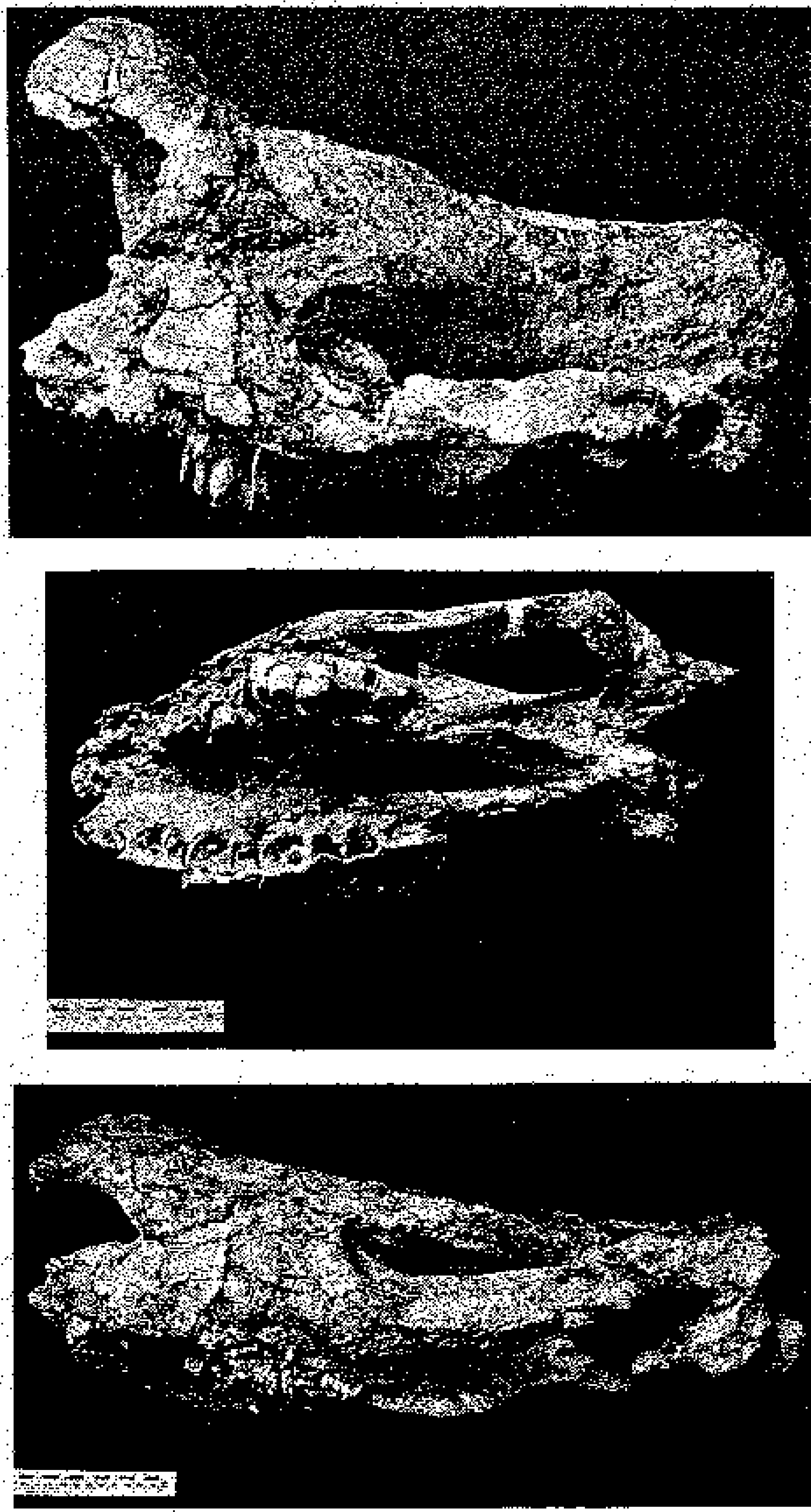


PLATE 4.3. *Ceratotherium simum germanoafricanum* immature crania.
Top: KNM-ER [illegible], left lateral view, Centre: occlusal view. Bottom: KNM-ER 329, left lateral view

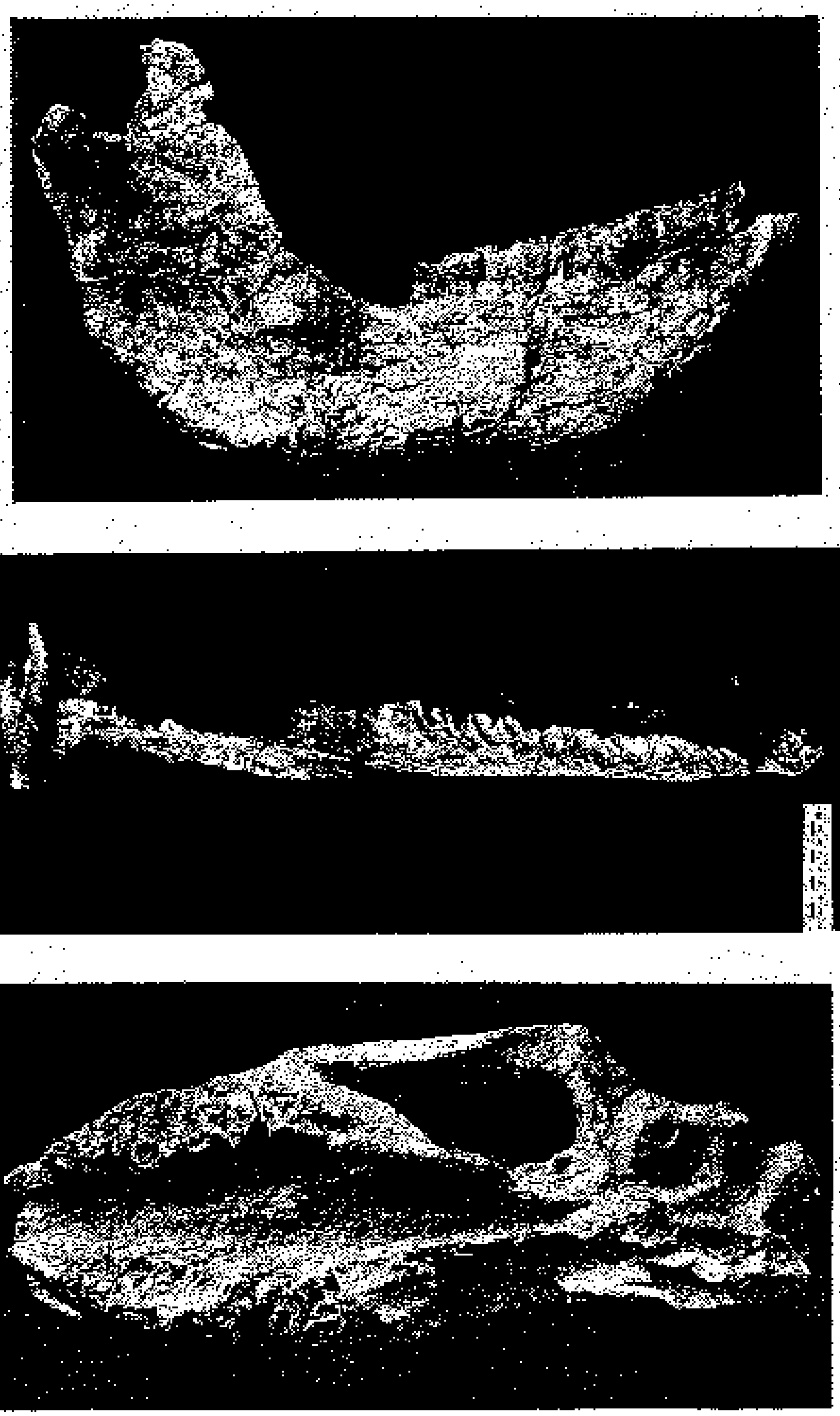
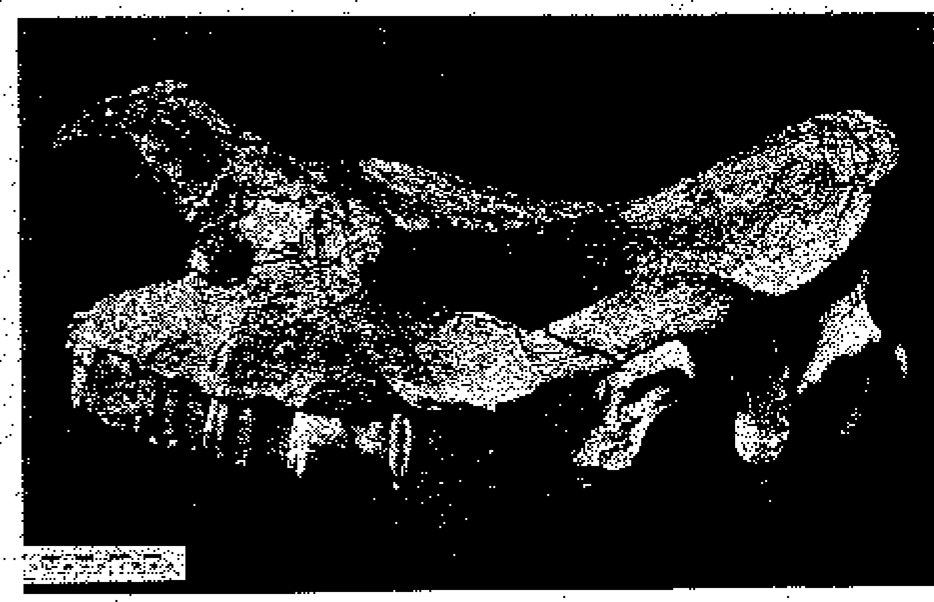


PLATE 4.4. *Ceratotherium simum germanoafricanum*.
Top: KNM-ER 328B, right mandible, lateral view. Centre: occlusal view. Bottom: KNM-ER 329, immature cranium, occlusal view.



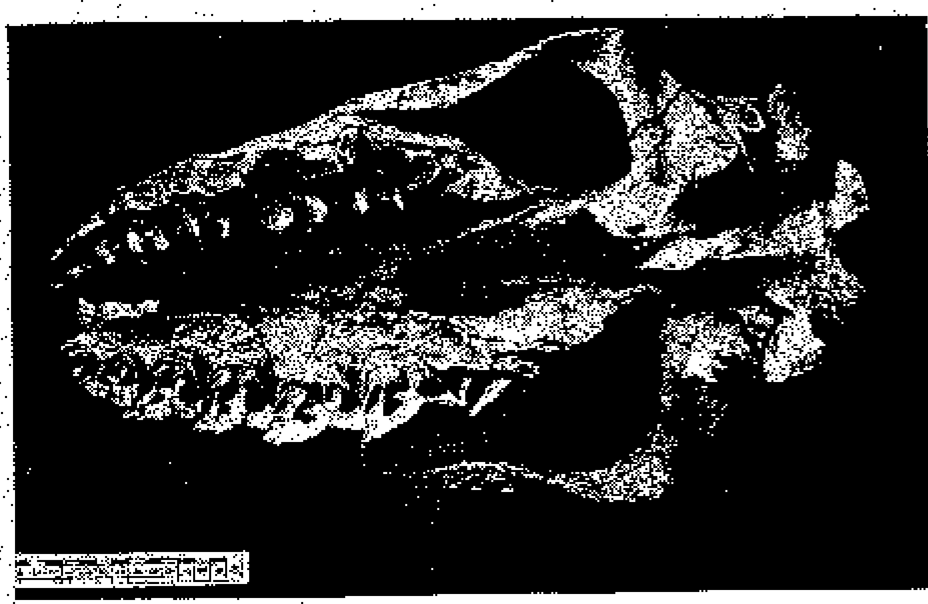
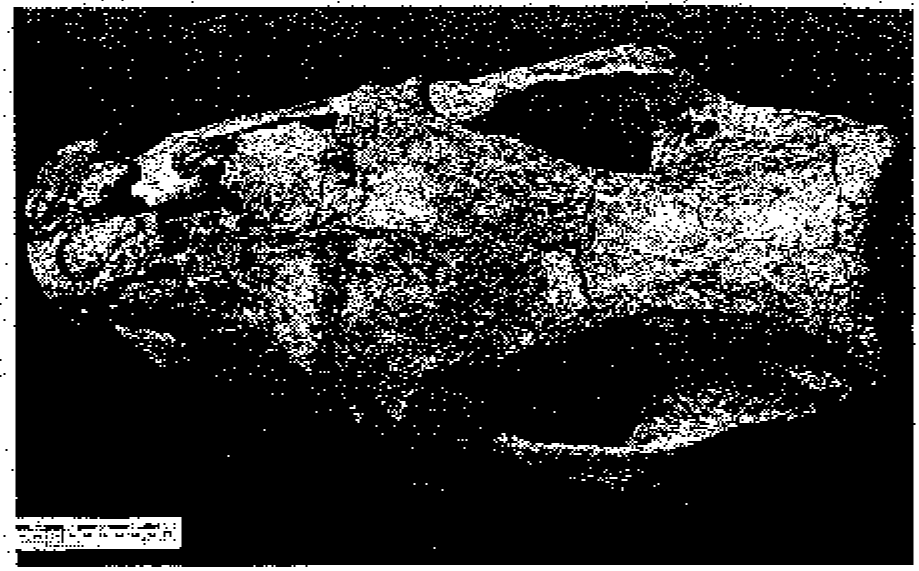


PLATE 5.9. *Diceros bicornis* cranium (KNM-ER-636).
Above: left lateral view. Below: occlusal view.

different shape of the occiput of the fossil cranium. The posterior face of the paroccipital process is less concave at its base in the fossil specimen, 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, the paramastoid bears both lateral and ventral protuberances. The lateral protuberance is more clearly defined and projects farther than in modern examples. The ventral protuberance is sited farther from the lateral process in the fossil cranium and its tip has a concave rather than a convex facet.

In the auditory region the hyoid process of the fossil cranium is a little larger than in 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 specimen are of similar size to modern examples but bear a keel from the posterolateral edge extending to the



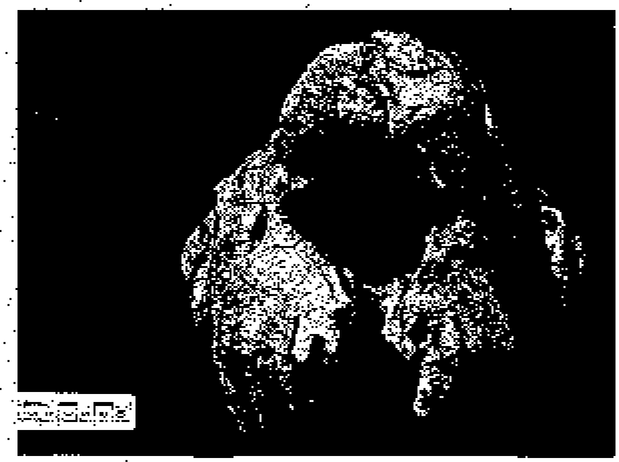


Plate 4.6: *Diceros bicornis* cranium (KNM-ER 696).
Top: dorsal view. Bottom left: anterior view. Bottom right: occipital view.

anteroventral tip of the process. The distal tip of the postglenoid process appears narrower than in extant skulls in which the postglenoid processes are rounded posteriorly. The glenoid fossa is less concave and less posteriorly orientated than in modern crania but is of similar size.

An immature mandible KNM-ER 472 attributed to *D. bicornis* by Harris (1976) has proved on subsequent re-examination to belong to *C. simum germanoafricanum*. The most complete black rhino mandible from Koobi Fora, KNM-ER 2139, is deeper and stouter than many examples of extant black rhinos and has a wider but shorter mandibular symphysis, an attribute confirmed by a second partial symphysis (KNM-ER 5650).

There appears to be no difference in dental morphology between the *D. bicornis* specimens from Koobi Fora and extant examples. Most of the fossil teeth are worn but appear slightly less hypsodont than in modern examples.

A left astragalus, KNM-ER 1196, is larger than that of modern examples of *D. bicornis*. It differs morphologically in that the lateral edge of the calcaneal facet is not produced distally and in that there is no large posterior projection on the medial edge of the astragalus below the medial edge of the trochlea. The specimen is, however, appreciably smaller than others here attributed to *C. simum germanoafricanum* and is clearly closer in overall shape to black rather than white rhinos. It is therefore

PLATE 4.7. *Diceros bicornis* mandible (KNM-ER 2139).
Above: left lateral view. Below: occlusal view.

tentatively identified as *D. bicornis* pending the recovery of material other than white rhino from the *Nst. scotti* zone. Guerin (1979) has pointed out that extant black rhinos are significantly smaller than Pleistocene representatives, which is borne out by the Koobi Fora astragalus.

Groves (1967) recognised seven modern subspecies of *D. bicornis* that could be differentiated on length and breadth parameters of the skull. These fall into larger and smaller size groups. Groves noted the presence of two extant subspecies in northern Kenya—the larger *D. bicornis ladoensis* and the smaller *D. b. michaeli*. Records were not available to Groves of rhinos from the vicinity of Lake Turkana although they were not uncommon here at the turn of the century. Indeed one was sighted by Kamoya Kimeu in 1974 and fresh footprints and dung were observed in 1977. The poached carcase of a black rhino was discovered north-east of Area 123 by Dr Frank Brown in 1981. A relatively fresh skull was collected from the Nderati waterhole by the 1968 expedition and on detailed examination this proves to be *D. bicornis brucii* (not *D. b. michaeli* as recorded by Harris 1976). Using Groves' parameters, the Koobi Fora cranium, although subadult, is also closer to *D.*