ZOOLOGISCHE MEDEDELINGEN

UITGEGEVEN DOOR HET

RIJKSMUSEUM VAN NATUURLIJKE HISTORIE TE LEIDEN

(MINISTERIE VAN CULTUUR, RECREATIE EN MAATSCHAPPELIJK WERK)

Deel 43 no. 6 25 september 1968

A RHINOCEROS FROM THE LATE MIOCENE OF FORT TERNAN, KENYA

by

D. A. HOOIJER

Rijksmuseum van Natuurlijke Historie, Leiden

With 3 plates

SYNOPSIS

A rhinoceros from the Fort Ternan site, Kenya, Late Miocene in age, represents a form distinctly more advanced than the genera and species known from the Early Miocene although it is not directly ancestral to the Quaternary forms. It is a collaterally developed tuskless, two-horned, browsing species from the same ancestral stock as the modern *Diceros bicornis* (L.), and it is named *Paradiceros mukirii*. This is the first rhinocerotid filling the gap between the African Early Miocene and the Pleistocene rhinocerotids.

Through the courtesy of Dr. L. S. B. Leakey the writer has been priviliged to study the rhinocerotid remains of the Fort Ternan site, housed in the Centre for Prehistory and Palaeontology, National Museum, Nairobi. The site, whence came *Kenyapithecus wickeri* Leakey (1962), has been K/A dated younger than East African sites yielding a fauna tentatively accepted as correlative with the European Burdigalian, or Early Miocene. The study of the Fort Ternan fauna is in progress. What is emerging is compatible with a Late Miocene (Vindobonian) age (cf. Leakey, 1967: 9).

It is a pleasure to thank Dr. Leakey for his unfailing interest in the matter and for courtesies extended to me. My journey to East Africa, in the summer of 1967, has been made possible by a grant from the Wenner-Gren Foundation for Anthropological Research in New York, New York. Photographs have been kindly taken by Mr. E. J. Rundle.

The generic and specific diagnosis of the Fort Ternan rhinocerotid is as follows:

RHINOCEROTIDAE

Paradiceros nov. gen.

Diagnosis. — Two horns, placed on nasals and frontals respectively. Inferior squamosal processes separate. Occiput vertical. Mandibular symphysis abbreviated but not widened; edentulous in the adult. Cheek teeth brachyodont, protocone constricted, antecrochet prominent. Last upper molar subtriangular. Upper molars with wide and low medisinus entrance, upper premolars with high internal pass. Limbs and some of the foot bones more shortened than in *Aceratherium* or *Dicerorhinus* though not to the extent seen in *Brachypotherium* or *Chilotherium*.

Genotype. — *Paradiceros mukirii* nov. spec.

Paradiceros mukirii nov. spec.

Diagnosis. — A species of *Paradiceros* with the following characters: shallow naso-maxillary notch (over P^2); mesostyle in DM^2; protocone constricted and antecrochet prominent in milk and first molars rather than in last and pre-molars. Limb bones moderately short; astragalus not shortened.

Holotype. — A juvenile skull from Fort Ternan, 1963, 3113, preserved in the Centre for Prehistory and Palaeontology, National Museum, Nairobi, Kenya.

Horizon. — Late Miocene.

Derivation of the new names. — The specific name has been given in honour of the senior field officer for Dr. Leakey, Heslon Mukiri, in charge of the Fort Ternan, and other, excavations for many years past. The generic name implies that the Fort Ternan form is a representative of a group of species parallel, but not linked, to the lineage of *Diceros bicornis*.

Description of the holotype specimen. — The most complete specimen in the Fort Ternan collection pertaining to rhinoceroses is a juvenile skull lacking only the nasal and basi-occipital bones (pl. 1). Most conspicuous is a median rugose horn boss placed just behind the level of the postorbital processes of the frontal bones. The cranial sutures are still open, and the full milk dentition, DM^{1-4}, is present on both sides and in wear, with the first permanent molar, M^1, just appearing at the alveolar rim but not yet having cut the gum. A skull of *Diceros bicornis* in the Department of Osteology of the Nairobi Centre has the same dental age as the fossil specimen and has been used for direct comparison.

The skull in itself is not entirely unlike that of *Diceros*, but differs

in a number of obtrusive characters, such as the more developed median frontal boss, the slenderness of the zygomatic arches, the more marked temporal crests (not smoothly rounded as in the recent specimen), the more sudden fronto-parietal contraction in dorsal view, the more forward position of the infraorbital foramina (distance from anterior border of orbit 7 cm instead of 5 cm in the larger *Diceros* skull); in side view moreover the less prominent occiput and apparently less upturned nasals (although these bones are lost along their sutures with the frontals and the maxillaries). The two inferior squamosal processes, viz., the post-glenoid and the post-tympanic, do not join below the subaural channel but remain free, a character of the modern African genera *Diceros* and *Ceratotherium* in contradistinction to *Rhinoceros* and *Dicerorhinus* wherein the channel is closed below. Although the exoccipitals as well as the basioccipital are missing it is clear from the remainder of the squama occipitalis that the Fort Ternan rhinoceros had a vertical occiput like *Diceros* and other browsing genera, not a backwardly inclined occiput like *Ceratotherium* and other grazing genera.

The Fort Ternan skull as a whole has a more "mature" look, so to say, than that of *Diceros bicornis* in the same growth stage although the latter is larger overall.

Some metrical comparisons may be given (those of the juvenile *Diceros* skull in parentheses); median length from basisphenoid-basioccipital suture to front of DM^1 255 mm (280 mm); zygomatic width 200 mm (240 mm); width of palate across outer borders of DM^4 130 mm (140 mm); least width of maxillaries in front of DM^1 ca. 40 mm (50 mm); width of frontals over postorbital processes 140 mm (170 mm); least width of cranium 90 mm (100 mm); greatest superior width of occiput ca. 120 mm (130 mm); height of skull from anterior part of frontals to posterior part of palate 85 mm (105 mm); height of occiput above basisphenoid 120 mm (150 mm).

The premaxillaries are missing in the Fort Ternan skull as is usual even in recent museum specimens; it is unknown therefore whether they bore teeth. The naso-maxillary notch extends to above the junction DM^1-DM^2, and the posterior border of the palate is on a level with the posterior border of DM^4 both in the fossil and in the recent *Diceros* specimen.

The four milk molars, excellently preserved, on the whole resemble those of the modern *Diceros* except for the following differences:

(1) the more marked parastyle, parastyle fold, and paracone style in DM^{3-4} as compared with modern *Diceros*;

(2) the well-developed mesostyle in DM^2, not normally present in *Diceros* but present in *Dicerorhinus* and the Asiatic forms;

(3) the more weakly developed internal cingula, which are virtually absent

except along the protocone of DM^2, whereas in *Diceros* a cingulum is continuous in DM^2 and present at least anteriorly and at the medisinus entrance in DM^{3-4};

(4) the constriction of the protocone by folds both anteriorly and posteriorly in the protoloph is much more strongly marked in the Fort Ternan form than in *Diceros,* a character distinctive of a number of Miocene genera. As is usual in rhinocerotid molars that have the protocone constricted off there is also a fold in the anterior surface of the metaloph: this is most marked in the posterior milk molar, and all but absent in *Diceros*;

(5) the antecrochet is rather marked in the milk molars and becomes more conspicuous with wear; it does not show in the contrasted *Diceros* specimens except occasionally in DM^2;

(6) the crochet is less well developed than in *Diceros,* in which it may even be bifid apically and longer than in the Fort Ternan form, recurving outward and almost blocking the medisinus; and

(7) the crista is also less developed in the Fort Ternan teeth than in *Diceros*; it is absent or very weak in DM^{3-4}, and present but slender in DM^2, cutting off the medifossette with the crochet.

TABLE 1

Measurements of upper milk teeth of *Paradiceros* (mm)

No. of specimen	3113 dext.	3113 sin.	3	3135	777	130	*Diceros bicornis* (6 specimens)
DM^1, ant. post.	19	19	23	—	—	—	21-25
transv.	17	17	ca. 19	—	—	—	20-22
DM^2, ant. post.	ca. 27	27	—	28	26	ca. 29	37-40
ant. transv.	—	28	ca. 28	26	24	27	31-35
post. transv.	30	30	30	27	26	ca. 30	35-40
DM^3, ant. post.	—	36	ca. 36	—	—	—	43-49
ant. transv.	—	34	35	—	—	ca. 35	40-49
post. transv.	—	34	36	—	—	—	37-43
DM^4, ant. post.	39	39	45+	—	—	—	49-55
ant. transv.	39	39	43	—	—	—	45-52
post. transv.	38	38	41	—	—	—	40-47

In all these seven points the Fort Ternan milk teeth differ from those of *Diceros*; the distinctive features of the skull have already been outlined above. The measurements of the deciduous teeth are given in table 1 along with those of other Fort Ternan specimens, F.T. (= Fort Ternan) 1962, 3, a set of milk molars from the right side in a maxillary fragment, two isolated DM^2, unworn, left (F.T. 1963, 3135) and right (F.T. 1961, 777), and a left DM^{2-3} in a maxillary fragment (F.T. 1962, 130). In the right

DM^2 as well as in the left DM^2 associated with a DM^3 the mesostyle, so characteristic of the Fort Ternan form, is even duplicated.

The skull fragment carrying the right DM^{1-4} (no. 3) likewise shows the nasomaxillary notch exending to over the front of DM^2, and the infraorbital foramen to lie only slightly behind it, as in the type specimen. There is further in the collection an adult fragment holding P^{2-4} sin. (F.T. 1963, 3376) that has DM^1 persisting on the right side, measuring 18 mm anteroposteriorly. The milk dentition of the Fort Ternan rhinocerotid is represented further by tiny fragments of maxillary teeth, but there are a DM_{2-4} of a left mandible (F.T. 1962, 2044) just coming into use, plus an isolated and incomplete DM_3 dext. (F.T. 1961, 321). Neither of the two lower third milk molars show the bilobed anterior portion of the metalophid typical of the Asiatic forms and present in a Uganda specimen of *Dicerorhinus leakeyi* Hooijer (1966: 135, pl. 4 fig. 1). Like the upper, the lower milk molars of *Paradiceros mukirii* are approximately equal in size to those of *Dicerorhinus leakeyi* but for the third, which is longer (36-40 mm, Hooijer, 1966, table 8) in *D. leakeyi* because of an anterior development absent in *Paradiceros*.

TABLE 2

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

No. of specimen	2044	321	*Diceros bicornis*
DM_2, ant. post.	27	—	27
ant. transv.	12	—	13
post. transv.	—	—	15
DM_3, ant. post.	30	—	38
ant. transv.	15	16	19
post. transv.	16	—	20
DM_4, ant. post.	34	—	41
ant. transv.	19	—	22
post. transv.	19	—	23

Of the permanent dentition there is a splendid, unworn M^1 sin. (F.T. 1963, 3379), that shows an important feature, the relative height of the crown (pl. 2 fig. 4). The differential characters of the molar are the same as those of DM^4, and the anterior and posterior basal widths are 48 mm, and 46 mm, respectively, just below the variation limits of M^1 in *Dicerorhinus leakeyi* (Hooijer, 1966: 129), which differs from the Fort Ternan molar in the protocone constriction and antecrochet being weakly developed. However, the height of the unworn ectoloph of the Fort Ternan M^1, measured at the paracone, is 42 mm against a full length of the ectoloph of 49 mm, or one-sixth more. This is a crown to which the term brachyodont

may be applied (cf. Cooper, 1934: 578/579). The *Paradiceros* molar is even relatively lower than that of *Dicerorhinus sumatrensis* (Fischer), the most primitive or generalized among the extant rhinocerotids (Cooper 1934, fig. 4A). The crown of M^1 of *Diceros bicornis* (Cooper, 1934, fig. 4B) is markedly higher than wide, and thereby is on the hypsodont side, taking *Rhinoceros sondaicus* Desmarest as the standard to which the term mesodont may be applied. There is another M^1 (F.T. 1963, 3109), of the right side, very much worn down, which measures 47 mm antero-transversely and 44 mm postero-transversely. The cingular development at the entrance to the medisinus is slightly more pronounced than that in the unworn M^1.

An isolated and worn last upper molar, M^3 dext. (F.T. 1963, 3489), lacks only a chip of enamel antero-internally (pl. 2 figs. 5-6). In this molar the protocone constriction and the antecrochet are not manifested, yet the wide, low medisinus entrance and the general size of the two upper molars are similar enough to suggest conspecificity. Fortunately, an entire upper dentition in the Fort Ternan collection (F.T. 1964, 133-135) proves the protocone fold to be very much more strongly marked in M^1 than in M^3, thus settling the problem. *Paradiceros* thus appears to be much closer to *Dicerorhinus* in its M^3 than it is in its M^1 in the lack of constriction of the protocone and of the resulting prominence of the antecrochet.

Nevertheless, it remains an easy matter to tell an M^3 of *Paradiceros* from one of *Dicerorhinus,* for *Dicerorhinus* last upper molars, even in the living Sumatran species, have a peculiar trapezoid outline instead of the more advanced subtriangular outline. This is caused by the strong development of the metacone in *Dicerorhinus,* supported even by a root of its own, causing a bulge at the junction of ectoloph and metaloph; in forms in which the metacone has been submerged in the outer surface no such bulging is seen. *Paradiceros* has an M^3 without a metacone bulge just as the Miocene *Aceratherium, Brachypotherium,* and *Chilotherium* (vide Hooijer,. 1966: 139, 144, 150, pl. 7). In the Fort Ternan M^3 the internal cingulum manifests itself along the hypocone only; this doubtless will prove variable when larger samples become available in the future.

The upper premolars of *Paradiceros* are well preserved in a fragment of the skull (F.T. 1963, 3376, pl. 2 fig. 2). The (left) series P^{2-4} is much worn down but shows the protocone to be constricted to a limited extent, and the antecrochet to be not very prominent. The inner entrance to the medisinus forms a high pass, at least 15 mm from the enamel margin of the crown in P^3 and P^4, in which respect these teeth are similar to the dicerorhine rhinoceros teeth from Rusinga. The inner cingulum is developed posteriorly, sharply rising along the hypocone from a point some 7-8 mm

from the gingival line where protoloph and metaloph meet. It joins the posterior cingulum. In P^2, as usual, the anterior cingulum is very prominent, forming a kind of prefossette; this tooth is narrower in front than behind instead of the reverse as in P^3 and P^4. In *Dicerorhinus leakeyi,* which comes closer to *Paradiceros mukirii* in size than the other East African Miocene genera and species thus far recognized, the internal cingulum is also present, though feebly, on the protoloph of the upper premolars. Other available upper premolars in the Fort Ternan collection are an isolated P^2 sin. (F.T. 1961, 219), without the external enamel and very much worn down, and a similarly used P^4 dext. (F.T. 1961, 1029), incomplete anteriorly. The former is slightly smaller, the latter larger, than its homologue in no. 3376 (table 3).

TABLE 3

Measurements of upper P and M of *Paradiceros* (mm)

No. of specimen	3376	219/1029	133/135	3379/3489
P^2, ant. post.	23	23	—	—
ant. transv.	30	ca. 28	25	—
post. transv.	33	ca. 30	29	—
P^3, ant. post.	28	—	26	—
ant. transv.	42	—	37	—
post. transv.	41	—	37	—
P^4, ant. post.	30	—	28	—
ant. transv.	46	48	39	—
post. transv.	44	46	38	—
M^1, ant. post.	—	—	36	40
ant. transv.	—	—	47	48
post. transv.	—	—	46	46
M^2, ant. post.	—	—	ca. 42	—
ant. transv.	—	—	48	—
post. transv.	—	—	44	—
M^3, ant. post. (int.)	—	—	40	39
ant. transv.	—	—	47	47
length outer surface	—	—	ca. 46	48

Whereas the complete but crushed *Paradiceros* skull no. 133/35 allows of nothing but dental measurements to be taken, it shows the size relations of the premolars and molars in a single individual, and demonstrates that P^{2-4} are smaller, M^1 and M^3 of the same size as the others available to date from the Fort Ternan site. All these teeth present the distinguishing characters detailed above. The skull fragment no. 3376 shows an important feature, viz., the depth of the nasomaxillary notch in the adult, which is shown on the left side (pl. 2 fig. 3) and extends to over P^2. Its full depth, from the nasal tips, is 11 cm. The height of the adult skull, from the lower border of the maxillaries at the roots of the premaxillaries (incomplete) to

the top of the nasals, is likewise 11 cm. The nasal notch is comparatively shallow, as in the juvenile type specimen; in other genera like *Aceratherium* it may extend backward to over the front of M^1 (Hooijer, 1966: 136). The nasal notch in the skull of *Dicerorhinus leakeyi* from Rusinga is again shallow, extending only to DM^1 (Hooijer, 1966: 123). The infraorbital foramen in *Paradiceros mukirii* is placed 15 mm behind the notch, over P^3. In *D. leakeyi* it is over P^2 (Hooijer, 1966: 123).

The configuration of the nasals is well shown in no. 3376 as well as in another specimen (F. T. 1962, 2345). The nasal bones are wide and strong, supporting an undoubtedly well-developed horn for which the rugosity is very marked. The tips of the nasals are slightly down-bent. Their width is 11 cm, and even 12 cm in the second specimen. In no. 3376 the dorsal surface of the skull is preserved for a length of 26 cm behind the tips of the nasals, and it just shows the boss for the frontal horn, which was evidently smaller. Unfortunately the distortion that the specimen has undergone does not allow of an exact dorsal profile to be taken. Neither do the remains of the premaxillaries, preserved only for a few cm in front of the persisting anterior milk molar, suffice to settle whether or not they bore tusks. The mandible of *Paradiceros mukirii* is, however, decisive: the absence of front teeth differentiates *Paradiceros* from all genera at present known from the East African Miocene.

A very well preserved mandible lacking only the ascending portions of the rami (F. T. 1962, 3209) has the symphysial portion complete; the full dentition P_2-M_3 is in wear. The symphysis is edentulous, showing milk incisor alveoli but no traces of permanent canines or incisors. The anterior premolar is lacking, in contrast to the modern *Diceros* which sports this little tooth. However, in view of the variability in this respect of *Dicerorhinus leakeyi*, which in one specimen has a P_1 and in another has not, without any accompanying difference in the lower dentition, this does not appear to be a matter of great moment. In modern *Diceros* mandibles P_1 is usually present, and the anterior end of the symphysis with its small pits looks just like that in *Paradiceros*. However, an important difference is observed in the length of the symphysis: in the Fort Ternan form it is more abbreviated than it is in the living black rhinoceros. Beside the mandible no. 3209 we have an incomplete, deformed left ramus of the mandible (F. T. 1962, 3503), which has the symphysis preserved and the last molar well in use (pl. 2 fig. 1). In the Fort Ternan symphyses the median length is the same (83 mm); it is one-fourth longer in modern mandibles of *Diceros* used for comparison (see table 4). The two specimens of *Paradiceros* differ, however, in the extent to which the symphysis projects forward beyond P_2:

in one the pre-P_2 part is more than twice as long as it is in the other, occupying more than one-half the total symphysis length. There is a constriction of the symphysis just in front of the anterior premolar, and a slight expansion at the end, which is less pronounced in *Diceros* but would not have been if P_1 had not been present. The position of the mental foramina is the same in the two *Paradiceros* mandibles: below the P_2/P_3 junction, rather like that in *Diceros* (in *Ceratotherium* the mental foramen is placed further back and the symphysis is wider). The premolars and the molars all show an external groove where metalophid meets hypolophid, not the flattening that we find in (advanced) brachypotheres. The measurements presented in table 5 do not include the individual anteroposterior diameters as so often enamel is lost fore and aft as a result of interproximal wear. Specimens included in table 5 are a P_3 dext. (F.T. 1964, 381), a P_4 sin. (F.T. 1965, 778), and an M_3 dext. (F. T. 1961, 929).

TABLE 4

Measurements of mandibular symphysis of *Paradiceros* (mm)

No. of specimen	3209	3503	*Diceros bicornis*	
Median length	83	83	102	102
Length in front of P_2	20	45	39	32
Least width	54	48	51	49
Greatest anterior width	ca. 60	58	54	51

TABLE 5

Measurements of lower P and M of *Paradiceros* (mm)

No. of specimen	3209	3503	381/778/929
P_2, ant. transv.	13	—	—
post. transv.	15	—	—
P_3, ant. transv.	19	18	18
post. transv.	22	21	20
P_4, ant. transv.	23	23	22
post. transv.	26	25	22
M_1, ant. transv.	26	24	—
post. transv.	29	28	—
M_2, ant. transv.	28	26	—
post. transv.	29	28	—
M_3, ant. transv.	25	24	24
post. transv.	28	—	28
Length P_2-M_3	205	—	—
Length P_4-M_3	155	ca. 150	—
Length M_1-M_3	120	ca. 120	—

Of the vertebrae, only one Fort Ternan specimen, of the atlas, is sufficiently well preserved for comparison purposes. It has the wings incomplete,

and is F.T. 1963, 3497. There is no intervertebral foramen ventrally but an anterior notch, laterally of the articular surface for the occipital condyle, present on either side. This is just as in *Dicerorhinus* (Arambourg, 1959: 63/64; Hooijer, 1966: 158), and unlike *Diceros* (*pachygnathus* as well as *bicornis*, Arambourg, 1959: 63, fig. 25 B) in which there is a large ventral foramen instead of merely a notch. The median ventral tubercle is well-developed on the Fort Ternan specimen as it is in *Diceros* as well as in *Dicerorhinus*. The greatest length of the Fort Ternan atlas, ca. 90 mm, is less than that in a specimen of *Diceros bicornis* at hand (110 mm); the greatest width cannot be given. The width across the occipital articular facets is 110 mm (140 mm), that between the dorsal intervertebral foramina 70 mm (80 mm), whereas the greatest (posterior) height is ca. 120 mm, fully equal to that in the recent form.

The non-vertebral postcranial elements in the Fort Ternan collection pertaining to rhinoceroses include the highly characteristic metapodials and astragalus, but there are also some limb bones and a carpal and tarsal bones.

A very nearly perfect right humerus (F.T. 1961, 1132; pl. 3 fig. 1) is more shortened than that in *Dicerorhinus* and *Diceros* (in which latter the humerus is one-fifth longer by the same widths), yet it is not as short as the bone in *Brachypotherium*, which is markedly broadened distally (cf. Hooijer, 1966: 160).

TABLE 6

Measurements of *Paradiceros* humerus (mm)

Greatest length (laterally)	330
Length from caput to medial condyle	300
Width over caput and posterior part of lateral tuberosity	132
Width at deltoid tuberosity	125
Least width of shaft	60
Greatest distal width	132
Trochlea width	93

The distal epiphysis of a left radius (F.T. 1963, 3375) measures 75 mm transversely. A left ulna (F.T. 1964, 72) has a maximum length (table 7)

TABLE 7

Measurements of *Paradiceros* ulna (mm)

Greatest length	335
Length from proc. anconaeus (beak)	290
Length of olecranon from same	ca. 120
Width at semilunar notch	ca. 70
Middle width	ca. 45
Greatest distal diameter	50

very similar to the lateral length of the humerus, as in various *Dicerorhinus* skeletons (Hooijer, 1966: 160/161).

A left os magnum (F.T. 1963, 3447) is very similar to a Rusinga specimen (Hooijer, 1966: 164), which does not imply any generic identity as the Rusinga bone on itself cannot be assigned to any genus in particular.

TABLE 8

Measurements of *Paradiceros* metapodials (mm)

Greatest anterior height	25
Greatest anterior width	42
Proximal ant. post. diameter	61
Greatest overall diameter	76

Rhinocerotid metapodials have been found to be of great value, indicating the degree of elongation or abbreviation of the feet; typical brachypothere metapodials are easily distinguished from those of long-limbed and -footed forms like *Aceratherium* or *Dicerorhinus*. Progressive metapodial shortening is what we observe in rhinocerotid lineages, though a metapodial as such does not suffice for generic determination among the dolichopodal forms and should ideally be associated with cranial and dental material. In the Fort Ternan collection there are four entire metapodials, as follows:

metacarpal III dext., F.T. 1963, 1932 (pl. 3 fig. 2),
metatarsal II sin., F.T. 1962, 200,
metatarsal III dext., F.T. 1962, 3504 (pl. 3 fig. 4), and
metatarsal III sin., F.T. 1963, 204.

The dimensions and width/length ratios of these bones (table 9) indicate a marked variability in middle metatarsals. The middle metacarpal is nearly as slender as that in *Dicerorhinus* or *Aceratherium* (Hooijer, 1966: 165/166), and the metatarsals are shorter than those in these genera, nearly as much

TABLE 9

Measurements of *Paradiceros* metapodials (mm)

	Mc. III	Mt. II	Mt. III	Mt. III
Median length	152	116	132	115
Proximal width	56	26	45	43
Proximal ant. post. diameter	ca. 43	36	41	36
Middle width	42	24	45	31
Middle ant. post. diameter	21	21	19	20
Greatest distal width	52	33	53	40
Width of distal trochlea	47	32	42	37
Distal ant. post. diameter	ca. 37	ca. 30	36	33
Ratio: middle width/length	0.28	0.21	0.34	0.27

as in *Brachypotherium* or *Chilotherium* (Hooijer, 1966: 179, 147, 152). In *Dicerorhinus leakeyi* the metatarsals are very long indeed, the metacarpals of the same individual unfortunately not available, but in skeletons of *Dicerorhinus primaevus* Arambourg (1959) and of *Dicerorhinus sumatrensis* (Fischer) Mc. III is longer than Mt. III (Hooijer, 1966: 166 and 179), just as in *Paradiceros mukirii*. The proximal portion of an Mc. III dext. (F.T. 1963, 3480) has a proximal width of only 45 mm and a width approximately at the middle of 38 mm; what its length was we do not know.

Three phalanges of one and the same lateral digit (F.T. 1961, 719-721) are definitely close to the non-brachypothere *Dicerorhinus/Aceratherium* type. It is most likely that they belong to the manus. There are even smaller second phalanges in the Rusinga collection (Hooijer, 1966: 182).

TABLE 10

Measurements of *Paradiceros* phalanges (mm)

	I	II	III
Length	27	24	30
Proximal width	35	31	54

None of the Fort Ternan rhinocerotid femora is completely preserved, hence few dependable metrical data are available. A right femur (F.T. 1962, 2720) lacks the distal end, another (F.T. 1964, 480) the proximal end and has an incomplete patellar articular surface besides. Both lack the third trochanter. Since the two bones are equally massive their approximate maximum length can be given, which is some 420 mm, or four-fifths that in *Dicerorhinus leakeyi* (Hooijer, 1966: 169), nearly the same length ratio as that found for the humerus.

TABLE 11

Measurements of *Paradiceros* femur (mm)

No. of specimen	2720	480
Greatest length	?420	?420
Transverse diameter of caput	90	—
Proximal width	170	—
Least width of shaft	70	70
Greatest distal width	—	115

Of the tibia we have from Fort Ternan one left specimen with the fibula attached but with the greater part of the proximal surface missing (F.T. 1962, 2004). The greatest length is approximately 320 mm, or three-fourths that in the *Dicerorhinus leakeyi* skeleton (Hooijer, 1966: 171). The distal

width of the Fort Ternan tibia is 80 mm, four-fifths that in *D. leakeyi*. Hence, this is again a limb bone of dolichopodal proportions: in *Brachypotherium* the distal tibial width would be about one-third the greatest length instead of merely one-fourth.

Five specimens of the astragalus are in the Fort Ternan collection, as follows:

astragalus sin., F.T. 1963, 3006,
astragalus sin., F.T. 1961, 162,
astragalus sin., F.T., 1962, 2009,
astragalus dext., F.T. 1962, 2448, and
astragalus dext., F.T. 1964, 524 (pl. 3 fig. 3).

These bones are fully within the limits of variation of those of the *Dicerorhinus*/*Aceratherium* class, which vary in medial height/total width ratio from 0.80 to 0.97 (Hooijer, 1966: 173). In the East and Central African *Brachypotherium* we find for this ratio 0.73 or less (Hooijer 1966: 148).

TABLE 12

Measurements of *Paradiceros* astragali (mm)

No. of specimen	3006	162	2009	2448	524
Lateral height	59	62	61	61	69
Medial height	ca. 60	64	—	63	74
Total width	70	79	80	ca. 70	81
Ratio medial height/total width	ca. 0.86	0.81	—	ca. 0.90	0.91
Trochlea width	63	65	68	69	75
Width of distal facets	57	69	62	59	66

Calcanea number three specimens, one right (F.T. 1961, 972), and two left (F.T. 1964, 393, and F.T. 1961, 971).

TABLE 13

Measurements of *Paradiceros* calcanea (mm)

No. of specimen	972	393	971
Lateral height	110	115	105
Greatest width	58	55	60
Ant. post. cuboid facet	39	40	46
Transv. diam. of idem	25	25	27
Greatest diameter of tuber	52	61	52
Transv. diameter of idem	39	41	41

There remains a right cuboid in the collection (F.T. 1964, 525), which is almost certainly of the same individual as the astragalus no. 524. Its

anterior height (43 mm) is almost equal to its anterior width (41 mm), which places this bone outside the *Brachypotherium* group in which the cuboid is distinctly wider than high anteriorly. The greatest anteroposterior diameter is 64 mm. Although all the Rusinga rhinocerotids are larger than the Fort Ternan form, there are a few among the number of Rusinga cuboids that are smaller (Hooijer, 1966: 176).

This completes the description of the rhinocerotid material from the Fort Ternan site at present available. In the absence of any evidence to the contrary I have accepted all this material to represent but one genus and species.

In considering the probable relationships of our new form, it is clear that the Fort Ternan rhinocerotid cannot be accommodated in any of the known African Miocene genera *Aceratherium, Brachypotherium, Chilotherium,* or *Dicerorhinus. Chilotherium* is so aberrant in its mandibular symphysial development as to bear no comparison with *Paradiceros*; comparisons with the other genera have been made. It is of importance to state once more that *Paradiceros* is set apart from all these genera in its complete loss of mandibular tusks. In this respect it approaches the Pleistocene/Recent genera *Diceros* and *Ceratotherium.* The rhinocerotid tooth from Sahabi in Cyrenaica described by d'Erasmo (1954) as belonging to *Teleoceras* (an American genus that has even more abbreviated metapodials than the Old World *Brachypotherium*) is so huge in comparison with the Fort Ternan form as to be excluded at once; in my opinion the Sahabi rhinocerotid represents the genus *Indricotherium,* and as such, as already noted by Savage (1967: 281), it is the second record of *Indricotherium* outside Asia and in beds which are otherwise dated as Late Miocene (the Asiatic records being Late Oligocene and Early Miocene, as is the European: Petronijevic & Thenius, 1957).

Paradiceros mukirii as we now know it links the tusked and protocone-constricted, hornless or horned, Miocene forms with the tuskless, protocone-unbound, two-horned Quaternary forms (*Ceratotherium* sprang from *Diceros* only in the Pliocene: Thenius, 1955). In its marked symphysial abbreviation, as in its shortened limbs and feet, *Paradiceros* cannot be considered directly related to modern *Diceros* but rather to represent the result of a parallel development from the early stock (pre-Miocene rhinocerotids are still deplorably unknown from Africa), an evolutionary product, indeed, like *Diceros,* but along a different line. The genus *Diceros,* known since the Early Pliocene in Europe as well as in Africa (with *Diceros douariensis* Guérin (1966) of northern Tunisia), comprises large forms not dissimilar to *Diceros bicornis.* The recent species appears first in the Early Pleistocene,

though sparingly, alongside *Ceratotherium simum* (Burchell) in the Limeworks Cave deposits, Makapansgat, South Africa (Hooijer, 1959).

There is scanty evidence concerning extra-African rhinocerotids that may be close to *Paradiceros mukirii*. The Bugti beds of Baluchistan, whose fauna is linked up with that of the African Miocene, features a great variety of rhinocerotids, but the smaller forms, variously referred to "*Ceratorhinus tagicus*" or "*Aceratherium albigense*" or simply left unnamed, are poorly known. The P^{2-3} sin. figured by Cooper (1934: 601, pl. 64 fig. 24) measure 27 mm, and 34 mm, respectively, in width; they possess heavy internal cingula, and an unobstructed medisinus entrance, unlike *P. mukirii*. Still smaller are the M^{1-2} dext. (Cooper, 1934, pl. 65 fig. 26) and two M^3 sin. (Cooper, 1934, pl. 65, fig. 27 and 29), which are some 30 to 32 mm in greatest transverse diameters, or two-thirds that of the Fort Ternan M^{1-3}. On the other hand, the DM^{2-4}, M^1, and P^3 dext. placed with *Diceratherium shahbazi* Pilgrim (Cooper, 1934: 602, pl. 67 figs. 37-38) tally well in size and in morphology (protocone constriction, antecrochet, weak inner cingula, high internal pass to medisinus in P^3) with *Paradiceros mukirii*. The skull and limb and foot bones of the very same Dera Bugti form are unknown. If correctly assigned to *Diceratherium,* strictly a Late Oligocene and Early Miocene North American genus which is characterized by a transverse pair of nasal horns, the Baluchi teeth do not represent *Paradiceros*. A skull with a transverse nasal horn pair has long been known from the Late Oligocene (Aquitanian) of Gannat, France, as "*Rhinoceros*" *pleuroceros* Duvernoy, currently placed in *Diceratherium* which, thus, would occur in the Old World as well as the New. *Diceratherium shahbazi* has been placed by Breuning in the genus *Paracaenopus,* typified by tusks in both jaws and a trapezoid M^3, again unlike the Fort Ternan form here described. Yet, the possibility that Bugti rhinocerotids of one description or another do represent the genus *Paradiceros* should be left open for the time being.

In the collection at the Nairobi Centre there is a cast of a worn P^2 sin. collected in 1963 east of Maralal, Kenya, by the Harvard Expedition (numbered 15-63K). It is exceedingly similar to its homologue in *Paradiceros mukirii,* and its posterior width is 29 mm. The tooth is incomplete in front, but strongly suggests a form closely related to or identical with that of Fort Ternan. Antelopine horn core fragments and an astragalus comparable to Fort Ternan species have recently been reported from Maralal by Dr. A. W. Gentry. Thus, Maralal could possibly prove to be a second locality for *Paradiceros mukirii*, and perhaps even contemporaneous.

REFERENCES

ARAMBOURG, C., 1959. Vertébrés continentaux du Miocène supérieur de l'Afrique du Nord. — Publ. Serv. Carte Géol. de l'Algérie, n.s., Paléontologie, 4: 1-161, pls. 1-18, figs. 1-52.

COOPER, C. F., 1934. The extinct rhinoceroses of Baluchistan. — Phil. Trans. Royal Soc. London, (B) 223: 569-616, pls. 64-67, figs. 1-21.

ERASMO, G. D', 1954. Sopra un molare di Teleoceras del giacimento fossilifero di Sahabi in Cirenaica. — Rendiconti Accad. dei XL, (4) 4 & 5: 89-102, 1 pl., figs. 1-14.

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

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

——, 1966. Miocene rhinoceroses of East Africa. — Fossil Mammals of Africa, 21: 117-190, pls. 1-15.

LEAKEY, L. S. B., 1962. A new lower Pliocene fossil Primate from Kenya. — Ann. Mag. Nat. Hist., (13) 4: 689-696, pl. 18.

——, 1967. Notes on the mammalian faunas from the Miocene and Pleistocene of of East Africa. In: W. W. BISHOP & J. D. CLARK (editors), Background to evolution in Africa: 7-29.

PETRONIJEVIC, Z., & E. THENIUS, 1957. Über den ersten Nachweis von Indricotherien (= Baluchitherien, Rhinocerotidae, Mammalia) im Tertiär von Europa. — Anz. math.-naturw. Klasse Österr. Akad. Wiss., 1957: 153-155.

SAVAGE, R. J. G., 1967. Early Miocene mammal faunas of the Tethyan Region. In: C. G. ADAMS & D. V. AGER (editors), Aspects of Tethyan Biogeography. — Syst. Ass. Publ. 7: 247-282, figs. 1-3.

THENIUS, E., 1955. Zur Kenntniss der unterpliozänen Diceros-Arten (Mammalia, Rhinocerotidae). — Ann. Naturhist. Mus. Wien, 60: 202-211, figs. 1-6.

EXPLANATION OF THE PLATES

Plate 1

Paradiceros mukirii nov. spec. Fig. 1. Juvenile skull, holotype, F.T. 1962, 3113, palatal view, × 1/3; fig. 2. Same, left view, × 1/3; fig. 3. Same, top view, × 1/3; E. J. Rundle phot.

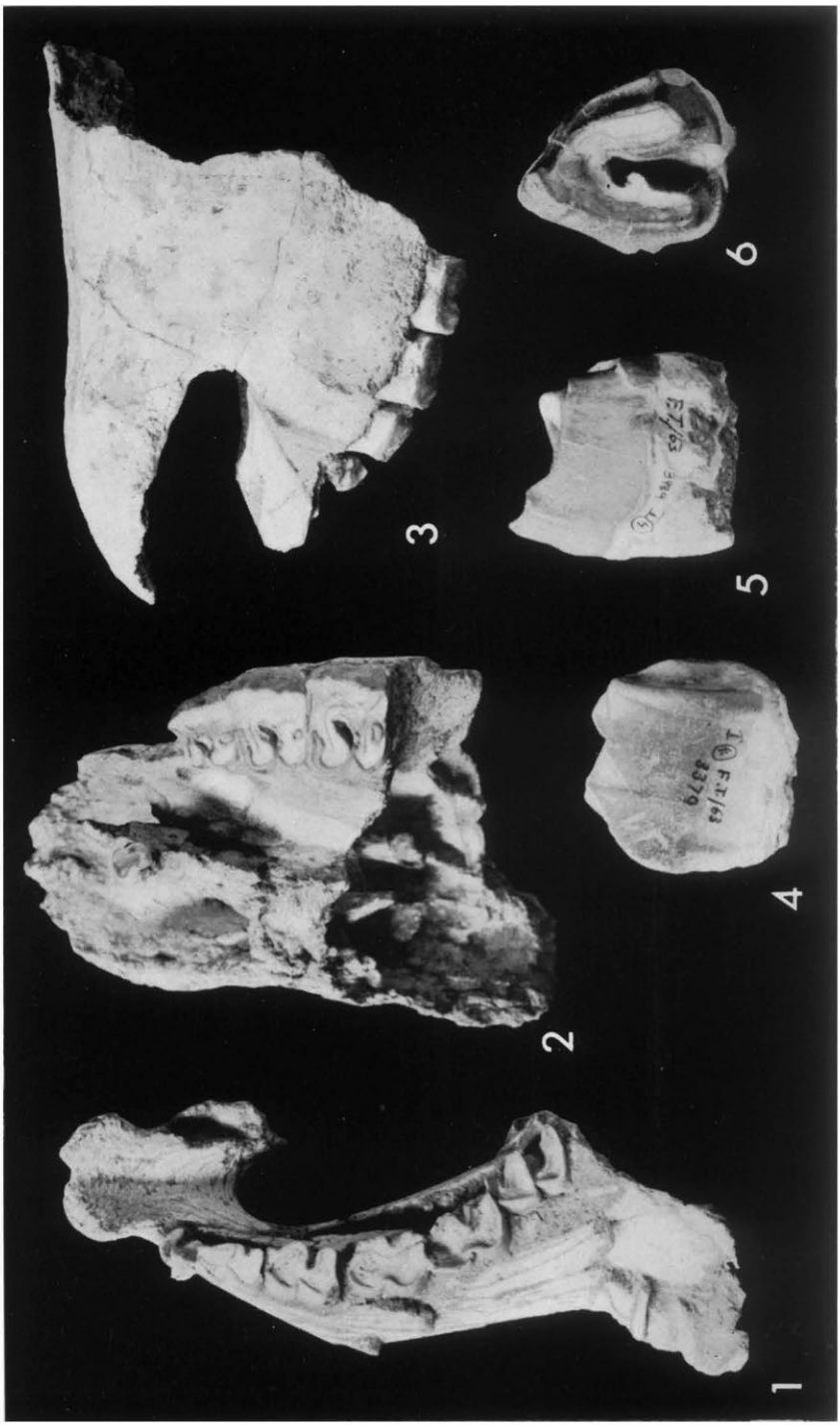
Plate 2

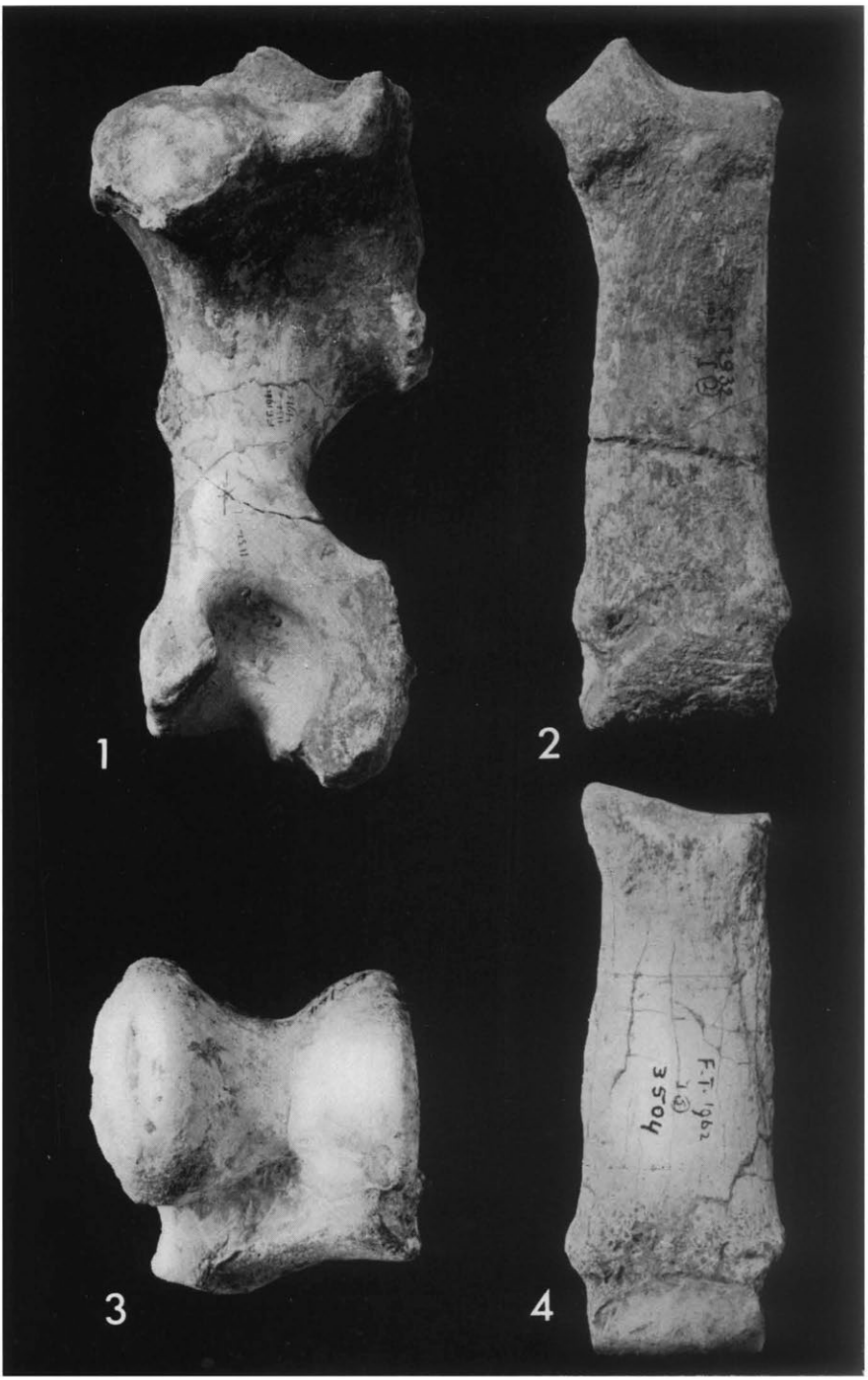
Paradiceros mukirii nov. spec. Fig. 1. Left mandible, F.T. 1962, 3503, top view, × 1/3; fig. 2. Skull portion with palate holding P^{2-4}, F.T. 1963, 3376, palatal view, × 1/3; fig. 3. Same, left view, × 1/3; fig. 4. M^1 sin., F.T. 1963, 3379, external view, × 3/5; fig. 5. M^3 dext., F.T. 1963, 3489, external view, × 3/5; fig. 6. Same, crown view, × 3/5; E. J. Rundle phot.

Plate 3

Paradiceros mukirii nov. spec. Fig. 1. Humerus dext., F.T. 1961, 1132, postterior view, × 1/3; fig. 2. Metacarpal III dext., F.T. 1963, 1932, front view, × 5/9; fig. 3. Astragalus dext., F.T. 1964, 524, front view, × 5/9; fig. 4. Metatarsal III dext., F.T. 1962, 3504, front view, × 5/9; E. J. Rundle phot.


1
2
3


1
2
3
4
5
6


1
2
3
4