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A New Rhinoceros from the Late Miocene of Loperot, Turkana District, Kenya

D. A. HOOIJER

HARVARD UNIVERSITY
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A NEW RHINOCEROS FROM THE LATE MIOCENE OF LOPEROT, TURKANA DISTRICT, KENYA

D. A. HOOIJER[1]

CONTENTS

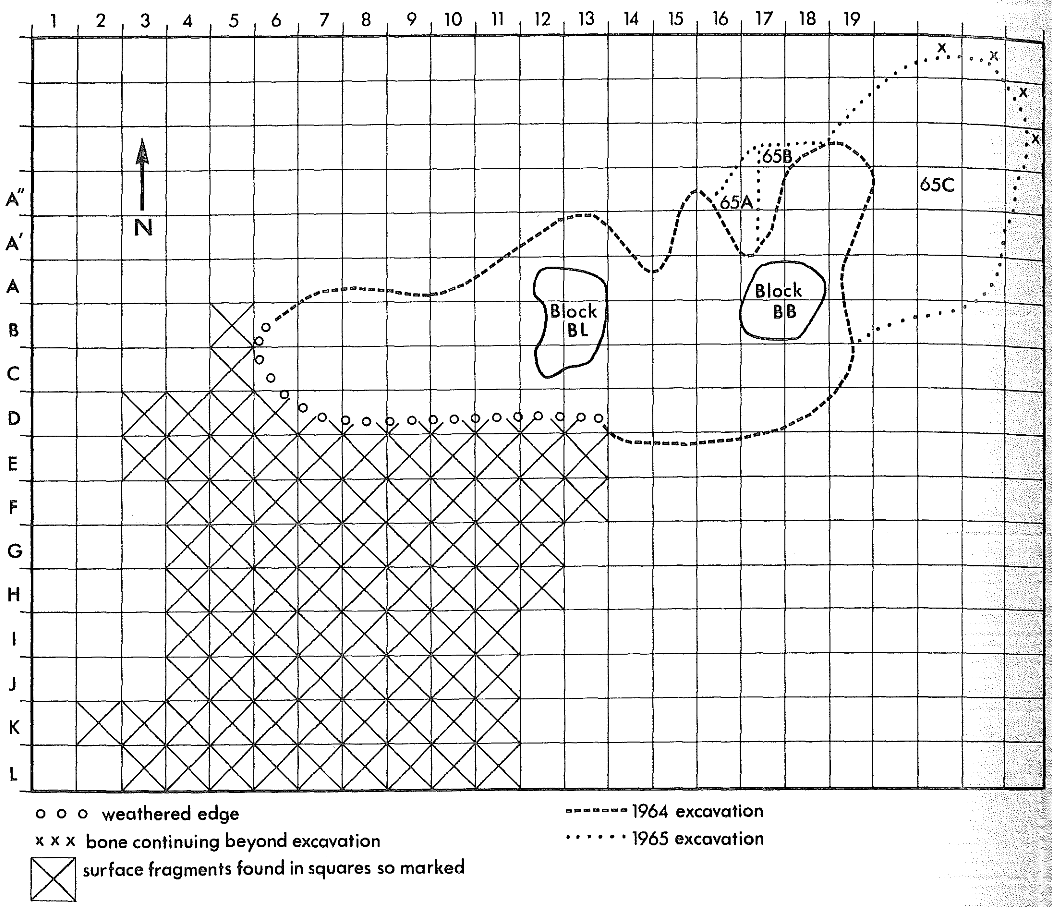
ABSTRACT. *Chilotheridium pattersoni*, a new genus and species of Rhinocerotidae from the late Miocene, Vindobonian, Turkana Grit Formation of northwestern Kenya, is described and compared with its close relatives *Chilotherium* and *Diceratherium*. The species also occurs at Ngorora. Fragments of *Chilotheridium* sp. from Bukwa II, Rusinga and Kirimun, of *Aceratherium* sp. or *Dicerorhinus* sp. from Kirimun and Ngorora, and of *Brachypotherium* sp. from Ngorora are recorded. Phalanges of a hippopotamid were mingled with the rhinoceros remains from the Turkana Grit; these constitute the earliest record of the family.

INTRODUCTION AND ACKNOWLEDGMENTS

In a paper on Miocene rhinoceroses of East Africa (Hooijer, 1966), a single last upper molar from the Turkana Grit Formation near Loperot, Turkana District, Kenya, collected in 1948 and preserved in the National Museum Centre for Prehistory and Palaeontology in Nairobi, was referred to the genus *Chilotherium* Ringström. To the same genus, and likewise without specific allocation, I referred two incomplete upper molars from Gumba and Wakondu on Rusinga Island. Teeth indistinguishable from those of *Chilotherium* have since been found at Bukwa II, Uganda (Walker, 1968), and at Ngorora, Kenya (collected by Dr. W. W. Bishop in 1968), early Miocene and early Pliocene, respectively. The Loperot rhinoceros has been cited as *Chilotherium* sp. by Leakey (1967: 15) and by Maglio (1969: 2).

In the years 1964 and 1965 Professor Bryan Patterson led field parties of the Harvard Museum of Comparative Zoology to the Loperot area, which is at latitude 02° 20′ N, and longitude 35° 50′ E, or 50 miles SSE of Lodwar and 45 miles SW of Lake Rudolf. The rhinoceroses collected were generously offered to me for description. The Loperot area has been geologically mapped by Joubert (1966), and three Potassium/Argon dates are available for the lava overlying the fossil-bearing Turkana Grit, 17.5 ± 0.9 m.y. for a sample five feet above the contact with the Turkana Grit at the rhinoceros quarry, 16.7 ± 0.8 m.y. for a sample approximately 200 feet above the contact with the Turkana Grit in the Auwerwer Hills, and 15.8 ± 1.2 m.y. from a basalt boulder in the Turkana Grit at the base of the Auwerwer

[1] Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands.



Text-figure 1. Map of the *Chilotheridium pattersoni* quarry, 70–64 K. The squares measure two feet to a side. Redrawn from expedition field notes.

Hills, 40 feet below the contact with the lava (Patterson, personal communication). The fossil-bearing beds at Loperot may be taken as early Vindobonian, late Miocene. They are older than those at Fort Ternan (*ca.* 14 m.y.). The rhinoceros of Fort Ternan, *Paradiceros mukirii* Hooijer (1968b), is widely different from that of Loperot in being bicorn, without lower canines, and with brachyodont cheek teeth, but its metapodials, so far as available, show a remarkable resemblance to those from the Loperot locality, as will be remarked upon in the proper places in the present monograph. A new genus and species of rhinoceros should ideally be based on skulls and teeth, as well as bones: I think we have such an ideal situation with the Loperot collection of Harvard. Rhinoceros remains make up the great bulk of the material collected from the Turkana Grit by the museum expeditions. All of them were found at the same level in the formation and in essentially the same spot. This locality is three and one-eighth miles north of the Kamuthia waterhole near the head of a dry wash known as Laminkwais (see map in Joubert, 1966), and the level is 55 feet below the overlying basalts of the Tvb_1 series. The great majority of the

rhinoceros remains come from one quarry in a bed of light brownish pink, jointed mudstone, in which the other specimens were also found. The state of preservation is poor: most of the teeth and bones are crushed and broken and the broken surfaces are not clean and sharp, being abraded as a result of postdepositional movements in the sediment. Nearly all of them were entirely dissociated and piled against or upon each other. The one exception is a right pes from the quarry, which is represented by most of its elements. Remains of at least twelve (and probably many more) individuals are represented, eight of them in the quarry. This mass occurrence with very little in the way of other animals is reminiscent of conditions at the famous Agate Springs *Diceratherium* quarry in the Miocene of Nebraska. Numbers of rhinoceroses evidently perished at these localities, perhaps along the courses of streams and rivers that were drying up during a prolonged dry season, the bones being subsequently swept by floods into a catchment area. Professor Patterson informs me that the *Chilotheridium* quarry was not exhausted when excavation of it was stopped in 1965. Parties working the area in the future should be able to collect additional material there.

The associated fauna of the Turkana Grit has as yet been mentioned only in part. Maglio (1969) records a tusk fragment of a shovel-tusked gomphothere, a very early member of the group, which suggests that Africa may have been the continent of origin of the amebelodontines. A similar conclusion may be drawn as to the hippopotamids: serendipitously, during the study of the Loperot collection it was found that there are a number of phalanges in 68–64K and 70–64K not or hardly distinguishable from those of the modern *Hippopotamus amphibius.* As the oldest remains of hippopotamids known to date are from the early Pliocene (Pontian) of Sicily and Spain (Hooijer, 1946; Aguirre, 1963), the Loperot hippopotamus is the earliest in the world. Maglio (1969) cites as elements of the Loperot fauna *Deinotherium hobleyi* Andrews, *Chilotherium* sp. (now *Chilotheridium*), *Brachyodus* (?) sp., *Dorcatherium* cf. *pigotti* Whitworth, and a hyracoid aff. *Prohyrax.*

As I was studying the collection, it became increasingly evident that the cranial and postcranial skeletal remains of this rhinoceros differed rather markedly from those of the genus *Chilotherium,* no matter how closely the dentition resembled that of this genus. In fact, had cranial and postcranial material not been found in association with the teeth, the East African form of rhinoceros described in the present paper would still have been called *Chilotherium.* As the material other than dental cannot be placed in any genus of rhinoceroses at present known, the Loperot rhinoceros is here referred to a new genus and species, *Chilotheridium pattersoni* gen. et sp. nov.

It has been necessary to use the original field numbers in this paper. Thus, 68–64K means the sixty-eighth specimen or lot collected in Kenya by the 1964 expedition of the museum. The quarry bears the collective number 70–64K and combinations following this number, such as BB and A17, denote the position of a bone in the quarry (see Fig. 1). In addition, the various elements, skull, mandible, scapula, humerus, etc., have been consecutively numbered for each kind. All specimens are the property of the National Museum of Kenya and will in due course receive the permanent catalogue numbers of that institution.

I am greatly indebted to Professor Bryan Patterson for offering me the Loperot rhinoceros remains for study and report. I am likewise grateful to Dr. L. S. B. Leakey for allowing me to describe the Kirimun tusk of *Chilotheridium,* to Dr. W. W. Bishop for permission to record the Ngorora *Chilotheridium,* and to Dr. Alan Walker for sending me casts and data on the Bukwa II *Chilotheridium.* Professor Patterson's field work was supported by

National Science Foundation Grant No. G.P. 1188.

Family *Rhinocerotidae* Owen, 1845
Chilotheridium gen. nov.

Diagnosis. Small single nasal horn in both sexes; premaxillaries weak, no upper I; frontals and parietals pneumatized; orbit not placed so near upper contour of skull as in *Chilotherium;* cranium and occiput rather narrow; parietal crests not widely separated; inferior squamosal processes not united below; symphysial portion of mandible narrow, slightly expanding anteriorly. Cheek teeth fully hypsodont as in *Chilotherium* and with the same pattern: uppers with paracone style fading away basally and posterior portion of ectoloph flattened; protocone well set off by folds and flattened internally; anterior fold in metaloph, marking off hypocone; antecrochet prominent basally, curving inward to medisinus entrance; crochet usually well developed, and crista weak or absent; metacone bulge at base in M^3; anterior cingulum strong, internal cingulum weak and usually forming cusp at medisinus entrance. Lower canine subtriangular in cross section, depressed dorsoventrally, internal edge sharpened by wear, outer lower edge rounded, and outer upper edge ridged. Scapula low and wide; limb and foot bones not much shortened; radius and ulna, and tibia and fibula not ankylosed; radius with cuneiform facet; lunar without facet for ulna; metacarpal V present, three-fifths the length of metacarpal IV; lateral metapodials somewhat divergent posteriorly; femur with small third trochanter; calcaneum without tibia facet; navicular nearly rectangular; cuboid wider than high; metatarsal III with small cuboid facet.

Type species. Chilotheridium pattersoni sp. nov.

Chilotheridium pattersoni sp. nov.

Diagnosis. As for the genus.

Type. Skull No. 2 described and figured in the present paper (70–64K, B12).

Hypodigm. The type and numerous other elements (see Appendix, p. 390).

Horizon and locality. Turkana Grit; vicinity of Loperot, Turkana district, Kenya.

Age. Late Miocene, Vindobonian.

Name. The specific name is given in honor of Professor Bryan Patterson, who let me have the Loperot material for study.

SKULL AND DENTITION OF *CHILOTHERIDIUM PATTERSONI* GEN. ET SP. NOV.

Two skulls from the Loperot rhinoceros quarry, with most of the dentition, establish the uniqueness of the rhinoceros from this site; they will be described in the following pages.

Loperot skull No. 1 (70–64K, C9–10), four views of which are given, (Pl. 2, figs. 1–3, Pl. 3, fig. 1) is a much deformed specimen that is broken into innumerable small pieces. Plaster has been applied wherever needed to hold the skull parts together, evidently in the position in which they were found. Most of the right side of the skull is concealed by a thick mass of plaster, exposing only part of the occiput (both occipital condyles are there, but too close together and displaced to the right of the median line of the skull), part of the temporal fossa, the nasal, and the premolars and molars, which lack their outer portions. Of the skull base we find the body of the sphenoid embedded in plaster and lying obliquely to the right.

The left side of skull No. 1 is better preserved; it is, however, much depressed because of crushing in the middle, and the top of the occiput is missing. The frontoparietal crest does not meet its fellow on the right side but remains a few centimeters distant from it. The postglenoid process is heavy, and does not unite with the posttympanic process below the external auditory meatus. The glenoid cavity is partially restored with plaster. The zygomatic arch is pressed downward and has been restored from fragments that do not

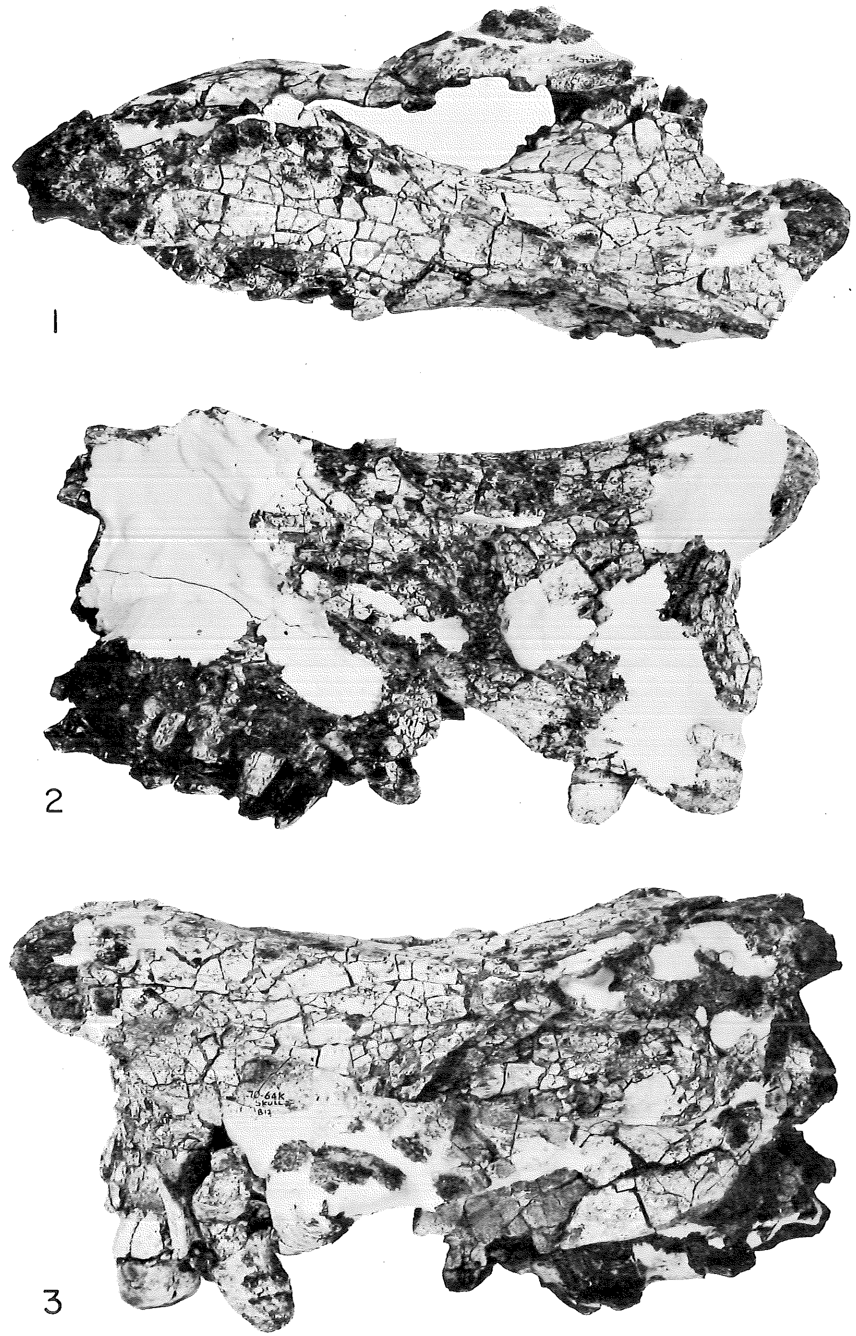


Plate 1. *Chilotheridium pattersoni.* Skull No. 2 (70–64K, B12), type. Fig. 1, top view; fig. 2, left view; fig. 3, right view. X 0.25.

fit very well. The orbitotemporal fossa is so crushed that the position of the orbit cannot be made out. Because of crushing, the anterior frontonasal region of the skull lies much higher than the middle part of the skull, and holds most of the nasals, which show a rugose area for a horn. The nasals, about 55 mm wide and only 25 mm high at a point about 10 cm in front of the nasomaxillary notch, suddenly expand vertically to a height of 43 mm, where there begins a rugose horn boss 60 mm long and 35 mm wide, with a weak median groove. The nasals diminish to a width of 48 mm and a height of 30 mm at the front end of the horn boss, and are broken off 1 cm in front of the boss. The ventral surface of the nasal bones is flat (Pl. 5, figs. 1–2).

The depth of the nasomaxillary notch is considerable (the portion of bone embedded in the plaster above the P^2 on the left side does not belong there). As seen on the right side the nasals are free for about 10 cm behind the horn boss, that is, to above the P^4–M^1 junction.

The dentition of skull No. 1, at least that on the left side, is rather well preserved, considering the state of preservation of the cranium. The right toothrow lacks P^2 and M^3 entirely and the outer parts of P^3–M^2. The inner columns of these teeth are nearly all broken.

P^2 is worn to a height of 17 mm from the crown base externally, and has medisinus as well as postsinus closed off as fossettes. The entrance to the medisinus forms an indentation. There is a very weak internal cingulum. The ectoloph is regularly convex with no styles showing.

P^3, the worn crown of which is 28 mm high externally, has the same two fossettes, and a trace of a cingulum at the base of the internal indentation representing the entrance to the medisinus. On the ectoloph there is only one style, the paracone style, more distinct above than at the base of the crown.

P^4, 45 mm high externally, as worn, has the antecrochet touching the metaloph, just about to close off the medisinus, in which a weak crista and a bifurcated crochet are seen. The postsinus is still open behind as the level of the posterior cingulum has not yet been reached by wear. The internal cingulum is manifest as a weak ridge along the bases of proto- and metaloph, and at the medisinus entrance. On the ectoloph, the paracone style, again, is seen to flatten out basally, while there is no metacone style. At this stage of wear, the anterior and posterior protocone folds, and the anterior hypocone fold, can be seen distinctly.

M^1, about 40 mm high as worn at the ectoloph (part of it is plaster), is not very well preserved: most of the metaloph is missing. The crochet, however, is there; it is well developed but does not block the medisinus. In the protoloph, the constriction of the protocone is very marked, and the antecrochet can be seen distinctly. The internal cingulum is barely indicated.

M^2, worn externally to a height of 60 mm, has the metaloph displaced upward and forward, making the medisinus too narrow. It has the same characters as M^1, but shows in addition that the paracone style disappears in the basal part of the crown, which is depressed only between the roots.

M^3 is unfortunately broken at the junction of proto- and ectoloph; the protoloph is displaced somewhat inward, with the cleft filled with plaster, so that the anterotransverse diameter cannot be given. The top of the ecto-metaloph (outer surface) internal to the large crochet is broken off. The crown is worn to a height of 70 mm, and there has not been very much wear, as seen from the narrow worn edges of the lophs. The unworn crown of M^3 would not have been more than some 5–10 mm higher. As the basal length of the outer surface is 62 mm, this is a decidedly hypsodont crown. At 50 mm above the base the length of the outer surface still amounts to 52 mm.

The M^3 of *"Chilotherium* spec." from Loperot described earlier (Hooijer, 1966:

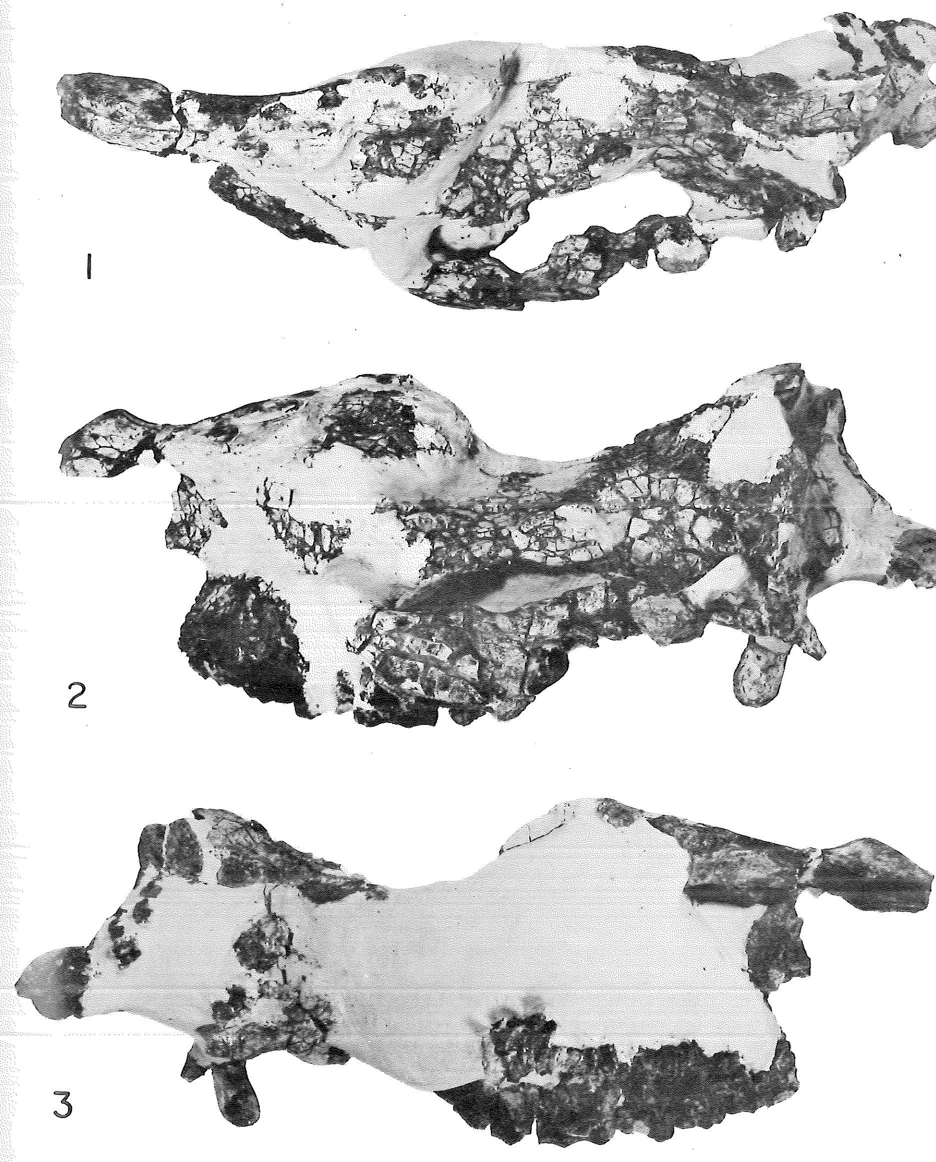


Plate 2. *Chilotheridium pattersoni.* Skull No. 1 (70–64K, C9–10). Fig. 1, top view; fig. 2, left view; fig. 3, right view. X 0.17.

150–152) is only a trifle smaller, and more worn, but resembles that in skull No. 1 very closely indeed. The paracone style, fading away basally; the internally flattened, constricted protocone; the basally prominent antecrochet (the medisinus base is broken and filled with plaster); the metacone bulging out basally; and, the posterior cingulum forming a point some 20 mm high, are all very much as in the 1948 Loperot specimen.

Loperot skull No. 2 (70–64K, B12) is better preserved than skull No. 1, and is the holotype of *Chilotheridium pattersoni* gen. et sp. nov. Four views of the specimen are given (Pl. 1, figs. 1–3; Pl. 3, fig. 2). Although this specimen, too, is broken into numerous small fragments held together by matrix, plastic, or plaster, there is not as much distortion. Most of the right side of the skull is there; the nasals and the premolar-bearing part of the palate are broken off but are preserved separately. On the left side the palate, zygomatic arch and occiput are missing, and the temporal fossa is pushed inward. This side of the skull is much fortified with plaster.

Seen from the right side, then (Pl. 1, fig. 3), the dorsal surface of skull No. 2 is weakly concave anteroposteriorly and flat transversely, with no trace of a horn boss on the frontals. The postorbital processes of the frontals are damaged, but the width over these can be given approximately. The two frontoparietal crests converge behind the orbit to a least distance of 25 mm, and then diverge into the temporal crests, of which only that on the right side is preserved. The occiput is notched in the median line above, and projects backward slightly beyond the occipital condyle. The occipital surface, of which only the right half (without the paroccipital process) remains, has been restored with plaster just above the beginning of the depression for the nuchal ligament. The zygomatic arch bears a slight postorbital process, behind which it is heavily restored with plaster. As it is, the arch is much extended along the fractures, and it ends below the glenoid cavity, which is distorted, too. The postglenoid process is, however, well preserved, and does not unite with the posttympanic process but remains a few millimeters distant from it below the external auditory meatus. The anterior border of the orbit is placed above the anterior border of M^2. Because of superficial damage the infraorbital foramina cannot be located. The nasomaxillary notch extends backward to above the anterior border of M^1. The nasals have broken off a few centimeters from the deepest point of the notch. Fortunately, however, there were many fragments of the nasal bones, and it has been possible to restore them; although they do not fit on to the skull, they doubtless belong to the same individual.

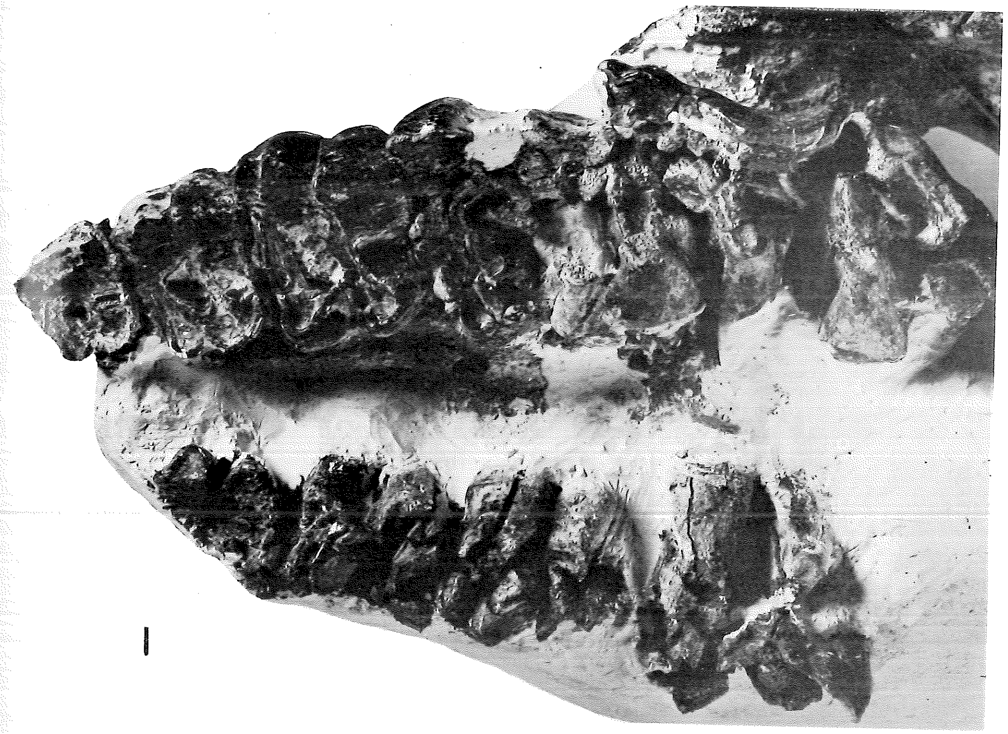
The portion of the nasals preserved (Pl. 4, figs. 2–3) is 14 cm long, and shows the weak median horn boss, 55 mm long and 35 mm wide, grooved in the middle. The height of the nasals from the top of the boss is 42 mm behind, and over 30 mm in front. Anterior to the horn boss the nasals form a projection about 45 mm long and 33 mm wide, bluntly pointed.

The premolars (in the maxillary portion: Pl. 4, fig. 1) and the molars are more worn than those in skull No. 1. Whether or not there was a persistent DM^1 cannot be made out in this specimen. Very little is preserved of the premaxillaries, which seem rather weak and were in all probability edentulous.

P^2, worn down to 8 mm from the crown base, shows only two small enamel pits of the medisinus and the postsinus, and a weak internal cingulum.

P^3 shows the same two pits, and an inner cingulum forming a point at the indentation representing the entrance to the medisinus. Its crown is worn down to 15 mm from the base.

In P^4, of which the outer portion is missing, the crown is still 20 mm high internally. The deep grooves delimiting the protocone (which is split vertically, the cleft being



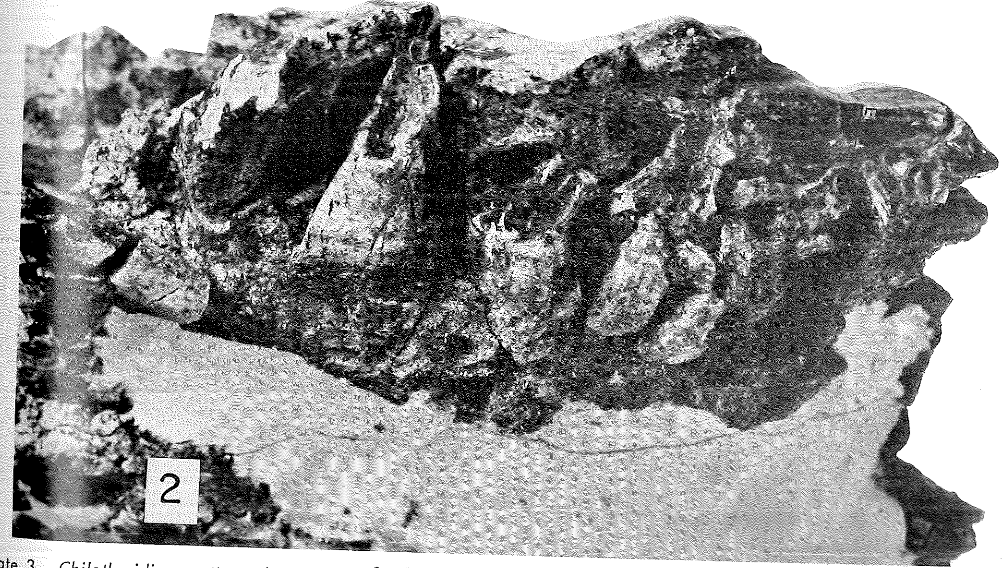


Plate 3. *Chilotheridium pattersoni*. Fig. 1, LP^2–M^3, RP^3–M^2 of skull No. 1 (70–64K, C9–10), crown view. × 0.50. Fig. 2, RM^1 (part)–RM^3 of skull No. 2 (70–64K, B12), type, crown view. × 0.70.

filled with matrix) are well shown, as is also the antecrochet next to it, which extends across the medisinus and joins the metaloph, cutting off the medisinus as a fossette. There is no trace of a crista or a crochet. The postsinus is closed off, too. The inner cingulum is continuous and well developed; it forms a conspicuous ridge at the medisinus entrance.

There is an anterior-internal fragment of the M^1 attached to the maxillary portion, showing neatly the anterior protocone fold. This portion belongs to the M^1 in the skull, but it cannot be replaced because of distortion of the bone. M^1, the outer surface of which is restored with plaster, is poorly preserved, having the metaloph with the crochet broken and distorted.

In M^2 the ectoloph (height as worn *ca.* 40 mm) is broken. Its structure is well shown: the strong antecrochet, the constricted protocone (split again, as in P^4), as well as the crochet, which extends forward externally of the antecrochet. There is no crista. The paracone style is weak, and fades out in the basal portion of the crown. The internal cingulum is continuous. There is an anterior fold in the metaloph opposite the protocone.

M^3, worn to 55 mm above the base, has the portion of the outer surface internal to the crochet broken and displaced, so that the length of the outer surface cannot be given. The protocone is flattened internally and well marked off by folds; the antecrochet is prominent basally and curves inward to the medisinus entrance. The outer surface is flattened especially toward the base, where the paracone style fades away. The metacone forms a bulge at the base, near the internal angle. The internal cingulum is present along the protocone, and, as a prominent cusp, at the medisinus entrance; it joins the posterior cingulum, which forms a point 28 mm high.

Apart from the more developed cingula and the absence of a (weak) crista in all the teeth, there is no difference between the dentition of skull No. 2 and that of skull No. 1.

There is further in the Loperot collection a right maxillary holding DM^1, P^{2-3}, DM^4 and M^1 (70–64K, 65B), representing a third individual (Pl. 7, fig. 3). The anteriormost tooth in this specimen is small, much worn down, and subtriangular, evidently a persisting anterior milk molar, DM^1. Its dimensions are *ca.* 25 mm anteroposteriorly, and *ca.* 20 mm transversely. In the middle of its broken worn surface it shows the base of the medisinus.

P^2 is broken, and the anterior part of its ectoloph is displaced forward, flanking the crown of the DM^1. It is 33 mm high externally, and not much worn; the protocone constriction can be seen clearly, but the metaloph (in part restored with plaster) is badly preserved.

P^3 is 42 mm high at the worn ectoloph, which is split vertically in the middle and distended along the fracture. A very small crista and a crochet are present, and the protocone constriction is very marked. The anterotransverse diameter of P^3 is 41 mm (less than that in skulls 1 and 2: Table 2), and the posterior width cannot be taken, as the metaloph is incomplete internally.

DM^4, the last milk molar, is rather worn but not broken: its greatest crown height is 25 mm. It shows all the characters of the first and second molars in skulls Nos. 1 and 2: the prominent antecrochet external to the constricted protocone, the anterior metaloph fold, the well-developed crochet, a trace of a crista, and the weak inner cingulum. The enamel is, of course, thinner, and the size less (anterotransverse 49 mm, posterotransverse 46 mm).

M^1 in the maxillary fragment is broken and incomplete internally. The external height of the worn crown is just about 60 mm.

The left maxillary belonging to the same individual as the right (70–64K, 65B) has a broken P^3, a DM^4 the ectoloph of which is displaced anteriorly but which is other-

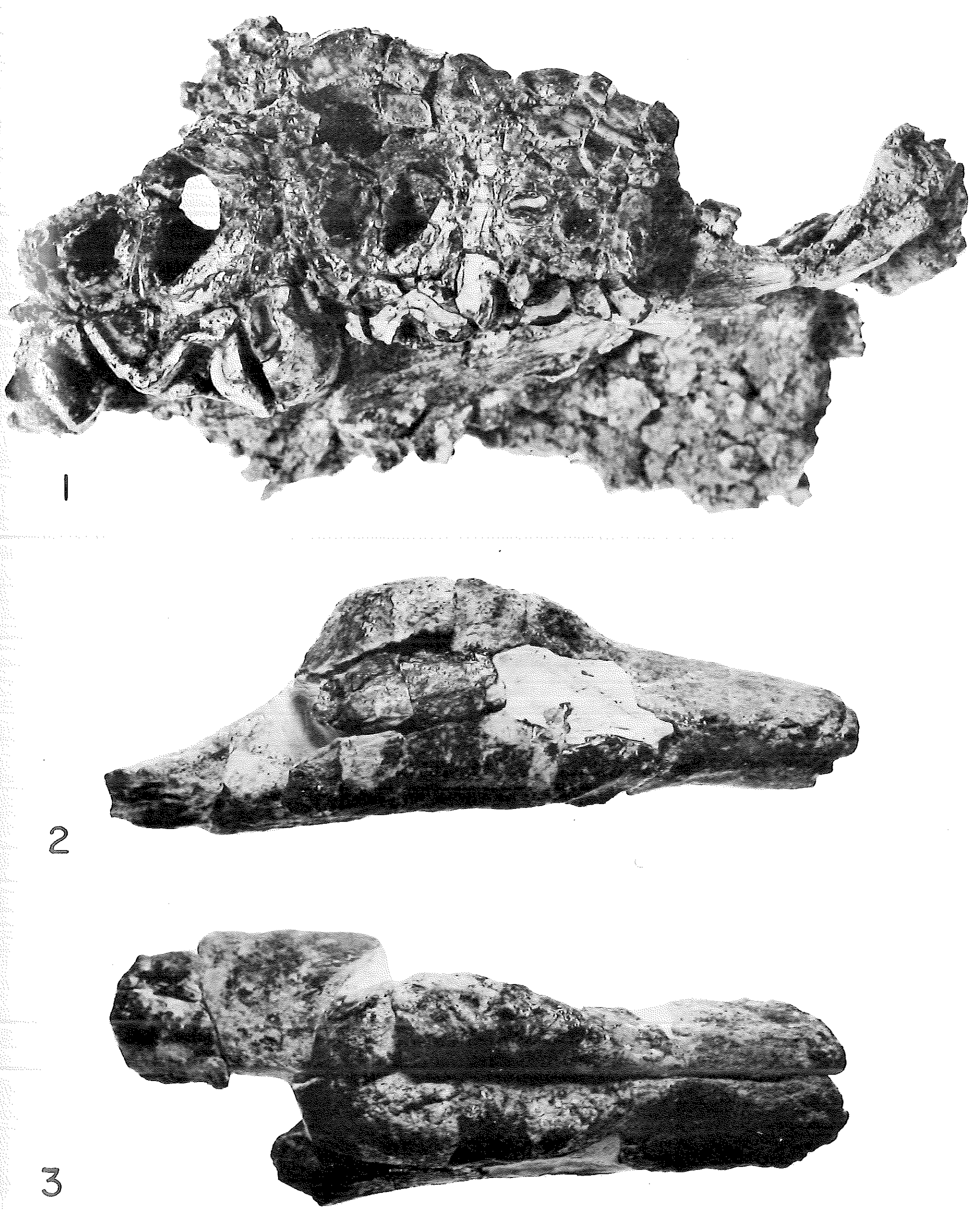


Plate 4. *Chilotheridium pattersoni.* Fig. 1, RP^2–M^1 (part) of skull No. 2 (70–64K, B12), type, crown view. × 0.80. Figs. 2–3, nasals of same skull in right and top views. × 0.70.

TABLE 1. Measurements of the skull from Loperot (in mm)

	Loperot No. 2	*Chilotherium* China (Ringström, 1924)
Greatest length from occipital to tip of nasals	*ca.* 520	*ca.* 445–*ca.* 520
From occipital crest to front of orbit	360	290–322
Least distance between parietal crests	25	45–63
Width over postorbital processes of frontals	*ca.* 125	129–169
Distance from nasal notch to front of orbit	65	65–78
Width of nasals at 3 cm from tip	32	35–52
Height of occiput from lower border of foramen magnum	*ca.* 190	160–*ca.* 205
Greatest width of upper portion of occiput	*ca.* 115	*ca.* 135–175

wise a mirror image of RDM^4, and M^{1-2} both transversely compressed. The M^2 is unworn and the ectoloph height of this molar is exactly 71 mm by a greatest anteroposterior ectoloph length of 62 mm, demonstrating the marked hypsodonty of the Loperot form.

Among the surface finds at 70–64K, C9–10, there are a number of tooth fragments making up a considerable part of an RM^3, similar to those described above. Its worn ectoloph is 63 mm high.

There is also a nasal portion in 70–64K, A″ 18, very much like those of skulls Nos. 1 and 2. The height of the nasals at the highest (posterior) portion of the horn boss is 52 mm, and the basal width at that level is 51 mm. The boss is shorter and wider than the others: length 50 mm, and width 38 mm. In front of it the nasals are only 34 mm high and wide; they taper to their blunt tip for a length of about 50 mm (Pl. 5, figs. 3–4).

Now that we have the skull as well as the upper dentition of the Loperot rhinoceros, it is easy to see that this form cannot be referred to *Chilotherium* as defined by Ringström (1924). *Chilotherium* has hornless, straight nasals, frontals and parietals not pneumatized, and the orbit placed just below the upper contour of the skull. The Loperot form, as we have seen, has a single, weak nasal horn boss, and the nasals are straight only as far as the ventral surface is concerned. The frontals and parietals are pneumatized: many air cells are seen on the broken surfaces. In keeping with this condition, found in most rhinoceroses except in *Teleoceras*, the orbit is not placed as high in the Loperot rhinoceros as in *Chilotherium*. As far as the hornlessness of *Chilotherium* is concerned, Bohlin (1937: 92) points to an indistinct, rugose structure on the nasal tips of a skull of *Chilotherium habereri* var. *laticeps* from Shansi that may perhaps be interpreted as a horn boss. Ringström also states in his diagnosis of *Chilotherium* that the frontal region is depressed, but this is not a constant character among the *Chilotherium* species. Among the Chinese Pontian *Chilotherium* species there is one, *Chilotherium planifrons* Ringström (1924: 47), in which the frontal region is flat, not depressed. The parietal crests are farther apart in the Chinese chilotheres than in the Loperot form, and the occiput is wider above (see Table 1). The premaxillaries of the Loperot rhinoceros are rather weak, and there are no remains of upper tusks in the collection, so that they were apparently edentulous, as is also the case in *Chilotherium*.

The Loperot skulls agree with those of the Chinese *Chilotherium* in the small distance between, and the position relative to the molars of, the orbit and nasomaxillary notch. Further they agree with *Chilotherium* in their separation of the inferior squamosal processes, and, above all, in the details of their dental structure, such as the hypsodonty combined with flattening of the ectolophs, the marked constriction

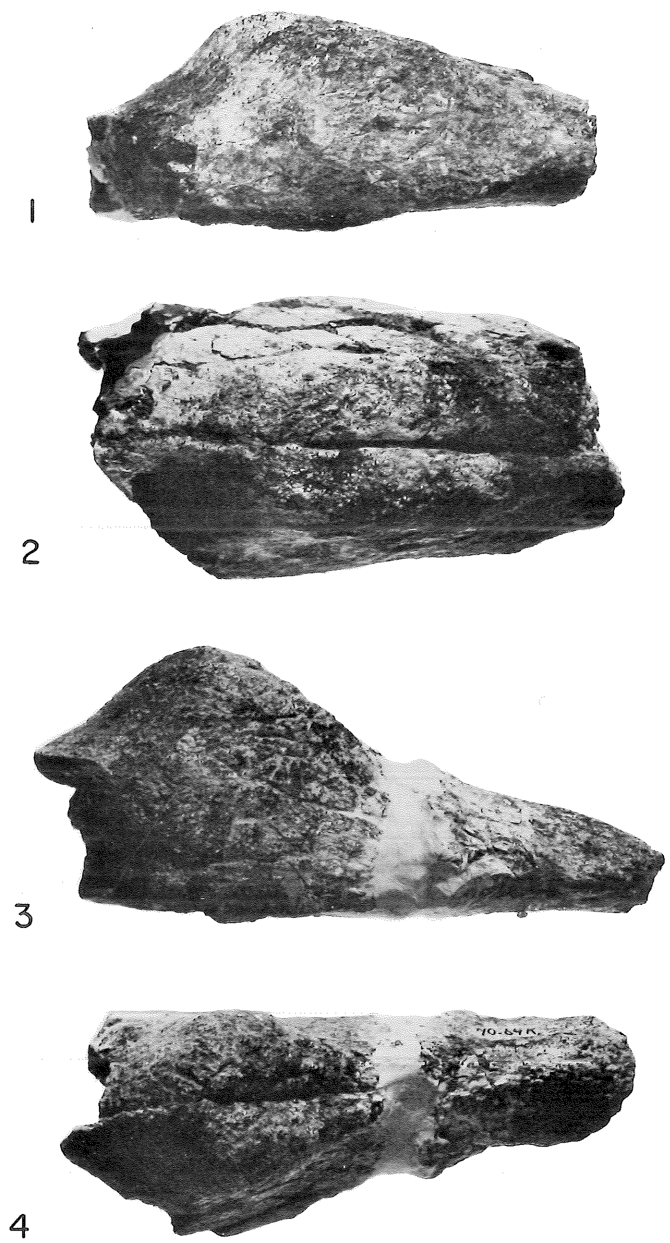


Plate 5. *Chilotheridium pattersoni*. Figs. 1–2, nasals of skull No. 1 (70–64K, C9–10); figs. 3–4, isolated nasals (70–64K). Right and top views. × 0.70.

TABLE 2. Measurements of the upper dentitions from Loperot (in mm)

	Skull No. 1	Skull No. 2	
P^2, a.-p.	31	—	
tr., ant.	31	*ca.* 35	
tr., post.	35	*ca.* 40	
P^3, a.-p.	33	—	
tr., ant.	45	*ca.* 45	
tr., post.	48	—	
P^4, a.-p.	42	—	
tr., ant.	58	—	
tr., post.	56	—	
M^1, a.-p.	—	—	
tr., ant.	64	*ca.* 60	
tr., post.	—	—	
M^2, a.-p.	57	*ca.* 55	
tr., ant.	—	*ca.* 70	
tr., post.	—	*ca.* 65	Loperot 1948
M^3, a.-p. (internally)	*ca.* 57	*ca.* 55	56
tr., ant.	—	*ca.* 60	60
length outer surface	62	—	61

of the protocone, the antecrochet development, the weakness of the crista, if any, and the metacone bulge in M^3.

The great length from occipital crest to front of orbit, as seen in Table 1, would seem to differentiate the Loperot skull from those recorded by Ringström. However, the relative length in the Loperot form is not greater than that in all of the Chinese species. It is true that in two skulls of *Chilotherium anderssoni* Ringström fully as long as the Loperot skull (*ca.* 510–*ca.* 520 mm in occipitonasal length), the distance from occipital crest to front of orbit is only 310–322 mm, as opposed to 360 mm in Loperot skull No. 2. However, in the skull of *Chilotherium planifrons* the occipitonasal length is *ca.* 445 mm, and the length from occipital crest to front of orbit is 300 mm (Ringström, 1924: 54), that is, two-thirds the occipitonasal length (*ca.* 0.67), equal to that in the Loperot skull (*ca.* 0.69).

There remain, therefore, several important cranial differences between the Loperot rhinoceros and the Chinese species of *Chilotherium.* In the Loperot form a weak median nasal horn is present in three out of three specimens, whereas in the chilotheres, nasal horns, if any at all, are the exception rather than the rule. The unpneumatized frontals and parietals, and the wider occiput and greater distance between the parietal crests set *Chilotherium* off from the Loperot form.

It is of interest to observe that the Loperot rhinoceros, with respect to the narrowness of the skull, rather resembles the Chinese forms referred to the genus *Diceratherium* (*palaeosinense* Ringström, 1924, and *tsaidamense* Bohlin, 1937). The width of the upper portion of the occiput is 98–129 mm in *Diceratherium,* and the least width between the parietal crests 10–31 mm (Bohlin, 1937: 64–65), both ranges that include the observations on the Loperot form (cf. Table 1). However, the Loperot rhinoceros cannot be referred to *Diceratherium* because it is not hornless (? female), nor does it have a transverse pair of horns on its nasals (? male). The dentition of the Loperot form is fully as hypsodont as in *Chilotherium,* and not subhypsodont as in *Diceratherium.* In the latter genus, moreover, the inferior squamosal processes enclose the subaural chan-

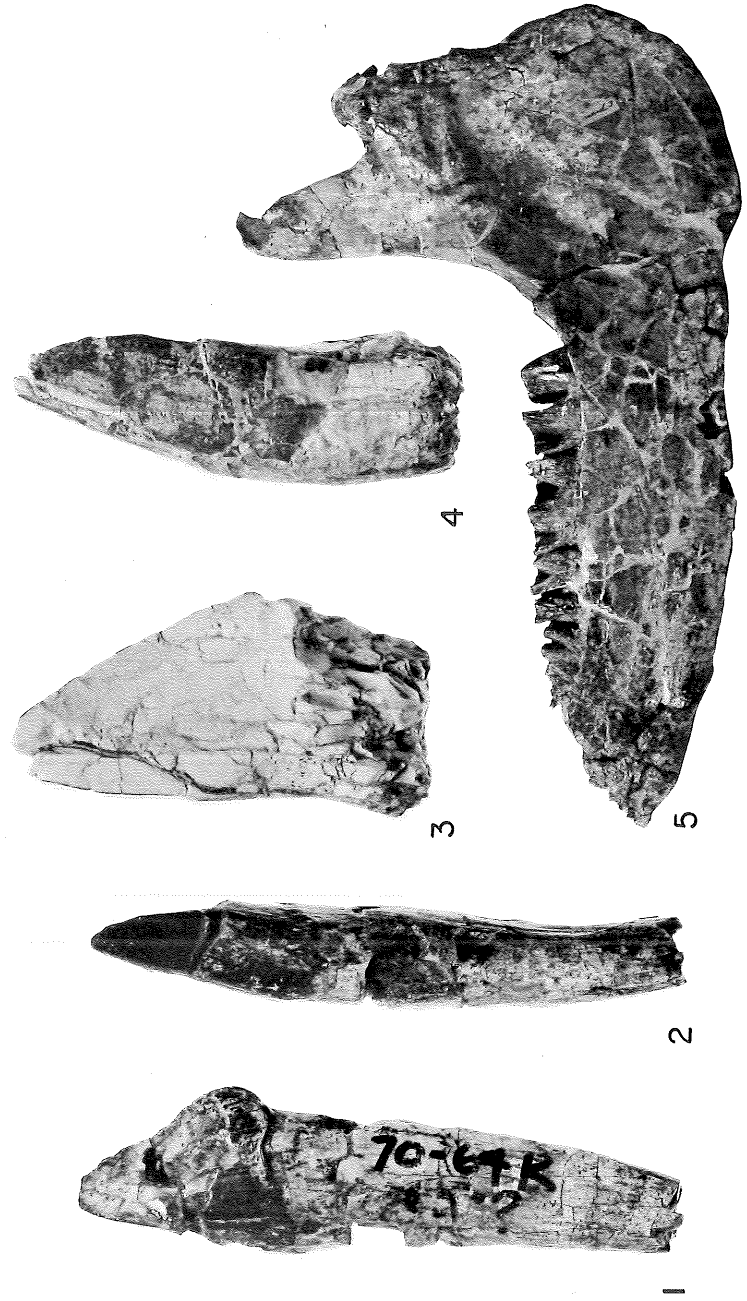


Plate 6. *Chilotheridium pattersoni.* Figs. 1–2, left lower canine (70–64K, 65), top and outer views, × 0.73. Fig. 5, right half of mandible No. 3 (70–64K, B11), inner view, × 0.22. *Chilotheridium* sp. cf. *C. pattersoni,* Kirimun, Kenya. Figs. 3–4, left lower canine (N.M.K. no. 33, 1949), top and outer views, × 0.69.

nel. This all apart from the fact that the reference of the Chinese forms to *Diceratherium* is provisional and subject to revision (Ringström, 1924: 120; Bohlin, 1937: 98).

There are no mandibles in the Loperot collection associated with the crania described, but there are three isolated ones, all broken in the symphysial region, as well as two halves and two isolated lower canines. The mandibles, like the skulls, are extremely fragmented and distorted; plaster and plastic have been used to hold the specimens together in one piece. Some of the specimens of the lower jaw have been crushed sideways, and the symphysis is so deformed that width measurements cannot be given. Only in two specimens is enough of the symphysis preserved to permit measurements to be taken.

Mandible No. 1, labelled 70–64K, has been crushed from above downward; the ascending rami lack the coronoid process, and the condyle has been pressed down into the fragmented ramus so that its height above the lower border of the angle of the mandible is only some 185 mm, or roughly two-thirds that in the other mandibles, in which the height has not been so visibly reduced. The right canine of the mandible is lost, but its alveolus remains, while the left is broken off just inside its alveolar border. The cross section seen is a transverse oval, approximately 22 by 17 mm in diameter. The two canines are placed quite laterally in the symphysis, and there are no incisors or traces of alveoli between them. The symphysis widens to the front, but exact measurements cannot be given. The premolars and molars are all broken. An inner view of the left ramus with the distorted symphysis is given in Plate 7, figure 2.

Mandible No. 2 (70–64K, 65) has the symphysis laterally compressed, and shows parts of the two canine alveoli, although it is impossible to measure them. The space between the two rami is only a centimeter or two, and the ascending portions, restored from fragments, are very unequal: the right is a full 7 cm higher (from condyle to angle) than the left. The cheek teeth are characterized by the smallness of P_2, the external groove between the lophids of P_3–M_3 being well defined, and the absence of an external cingulum.

Mandible No. 3 (70–64K, B11) lacks the ascending ramus on the left side. The symphysial region is deformed, but a few measurements can be given. The symphysis widens slightly to the front, as it does in mandible No. 1 as well. The left ramus with the symphysis is presented in Plate 7, figure 1; the anterior two premolars from the right side are attached to this portion. An inner view of the right half of this mandible is given in Plate 6, figure 5.

Mandible No. 4 (70–64K, 65C) is quite complete on the right side, but it lacks the condyle. Of the left half of the same specimen only the portion bearing P_3 and P_4 is preserved. The forwardly expanding symphysis is incomplete in front, but the least width, at P_2, can be given.

Mandible No. 5 (70–64K, A18) consists of part of the left ramus, with P_2 and two complete molars.

The lower canine marked 70–64K, 65–? is well preserved (Pl. 6, figs. 1–2). It is of the left side, and the crown, worn to a height of 44 mm, is subtriangular in section. The internal edge is very sharp because of wear, the outer lower edge is rounded, and the upper outer edge marked by a longitudinal ridge. The base of the crown is slightly swollen lateroventrally. The dimensions at the crown base are 30 mm horizontally and 18 mm vertically. The enamel is very thin, especially on its upper surface. The root, a transverse oval 25 by 18 mm in cross section below the crown, becomes nearly round in section at the (broken) apex (15 by 14 mm); its length as preserved is 70 mm. This is just about the size of the smallest three lower canines of *Chilotherium anderssoni* as recorded by Ringström (1924: 37: 28–30 by 18–19 mm).

The other isolated lower canine (70–64K,

Plate 7. *Chilotheridium pattersoni.* Fig. 1, left half of mandible No. 3 (70–64K, B11), outer view, × 0.31. Fig. 2, left half of mandible No. 1 (70–64K), inner view, × 0.19. Fig. 3, right maxillary with dm^1, P^{2-3}, dm^4, M^1, crown view, × 0.38.

TABLE 3. Measurements of the mandible from Loperot (in mm)

	No. of specimen 1	2	3	4	*Chilotherium* China (Ringström, 1924)
Height from condyle to lower border of angle	—	*ca.* 265	*ca.* 250	—	215–231
Length from posterior border of C to that of angle	*ca.* 530	*ca.* 520	*ca.* 490	*ca.* 480	415–485
Height of ramus at M_3	—	*ca.* 90	*ca.* 95	*ca.* 100	76–*ca.* 90
Width of ramus at M_1	—	*ca.* 40	*ca.* 40	—	40–50
Median length of symphysis	*ca.* 150	—	*ca.* 130	—	104–137
Width of symphysis at P_2	—	—	—	*ca.* 80	98–128
Anterior width of symphysis	*ca.* 100	—	*ca.* 110	—	130–*ca.* 190
Distance between C at alveoli	*ca.* 45	—	*ca.* 60	—	75–93
Diastema C–P_2	—	—	*ca.* 50	—	55–96

A16) is not as well preserved. It is from the right side, measures 30 by 15 mm at the crown base, and is, therefore, more depressed from above downward than the left canine. The worn crown is 55 mm high, and there is a basal cingulum and a ridge along the dorsolateral edge. The inner edge of the crown is, again, sharp because of wear on the upper surface.

TABLE 4. Measurements of the lower dentitions from Loperot (in mm)

	No. of specimen 1	2	3	4	5
P_2, a.-p.	—	22	25	—	23
tr.	—	15	—	—	14
P_3, a.-p.	—	34	—	—	—
tr., ant.	—	20	—	18	—
tr., post.	—	21	—	21	—
P_4, a.-p.	—	38	—	—	—
tr., ant.	—	26	—	25	—
tr., post.	30	26	—	28	—
M_1, a.-p.	—	—	—	—	46
tr., ant.	—	*ca.* 26	—	28	—
tr., post.	—	—	—	29	26
M_2, a.-p.	—	58	57	53	—
tr., ant.	—	29	28	28	—
tr., post.	32	31	32	30	—
M_3, a.-p.	—	57	60	53	—
tr., ant.	—	29	30	27	—
tr., post.	29	28	28	27	—

It will be observed that, in keeping with its narrow cranium, the Loperot rhinoceros has a mandible that is narrower than that in the Chinese chilotheres. Further, although the height and the length of the jaw, as well as the symphysial length, may be greater in the Loperot form than in *Chilotherium* from China, there is no difference in proportions. The ratio of the height to the length of the mandible in Nos. 2 and 3 (the only ones in which both of these dimensions can be given approximately) is *ca.* 0.51; two mandibles of *Chilotherium anderssoni* give 0.48 (218:445) and 0.52 (231:443) respectively (Ringström, 1924: 54). The length of the symphysis in mandibles No. 1 and 3 is 0.27–0.28 (approximately) of the total length; in the Chinese chilotheres this ratio varies from 0.25 (in *Chilotherium habereri* var. *laticeps* 104:415) to 0.29 (in *Chilotherium anderssoni* 128:443) (Ringström, 1924: 54). In the narrow symphysis the Loperot rhinoceros approaches the Chinese *Diceratherium* (distance between C at alveoli 24–45 mm; width of symphysis 75–95 mm: Bohlin, 1937: 70), but in these Chinese forms the symphysis does not widen to the front, P_2 is relatively larger, and the coronoid process is stronger (cf. Ringström, 1924: 109–110; Bohlin, 1937: 71).

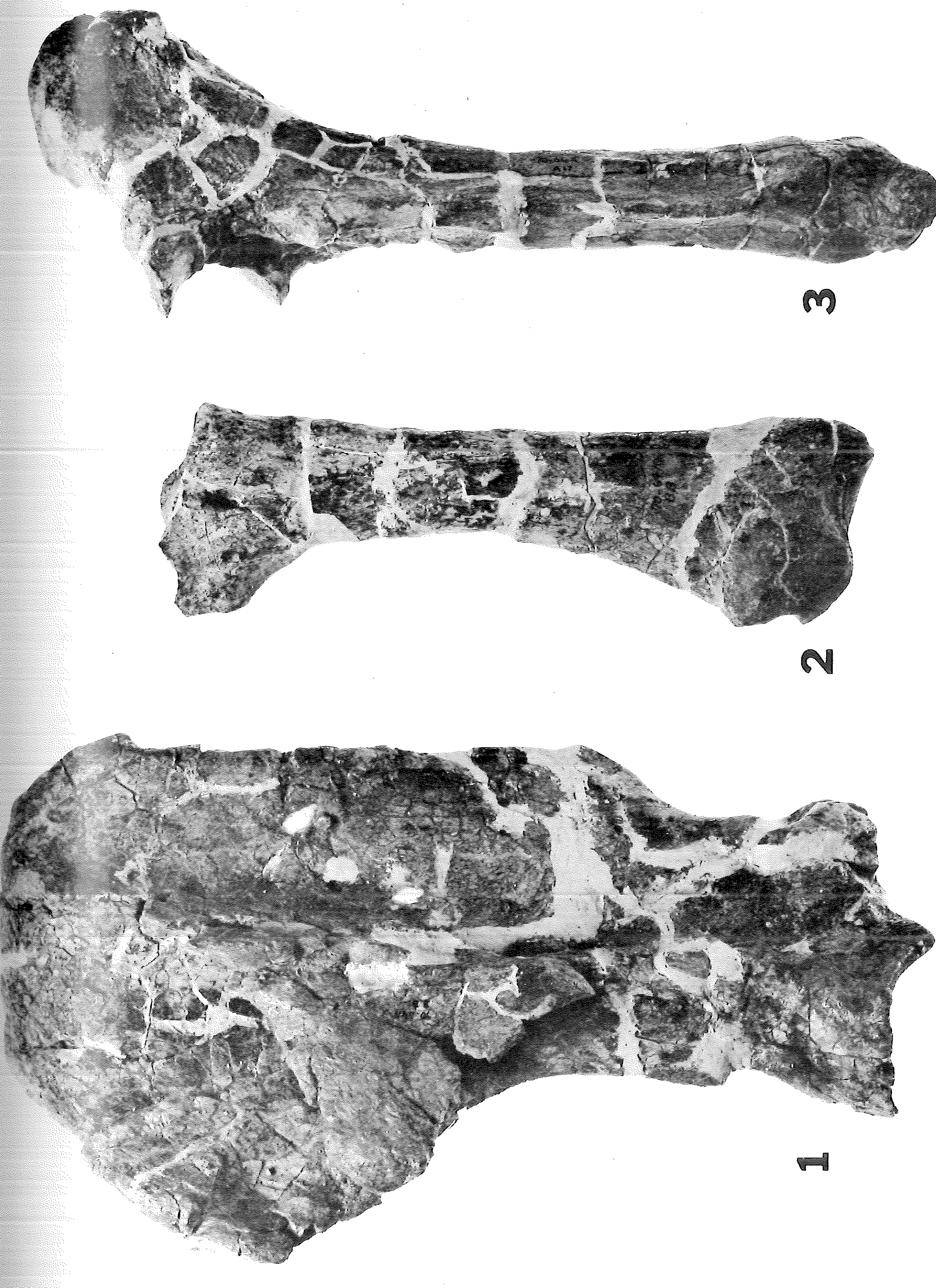


Plate 8. *Chilotheridium pattersoni*. Fig. 1, right scapula, No. 2 (70–64K, BB), lateral view. Fig. 2, right radius, No. 1 (70–64K, BB), front view. Fig. 3, right ulna, No. 1 (70–64K, A17), lateral view. × 0.33.

CHILOTHERIDIUM FROM EAST AFRICAN SITES OTHER THAN LOPEROT

Rusinga Island: Gumba and Wakondu

Two incomplete upper molars in the National Museum Centre for Prehistory and Palaeontology, Nairobi, originating from Gumba and Wakondu, respectively, have been described as *Chilotherium* sp. (Hooijer, 1966: 151, pl. 6, figs. 10 and 11), an identification that in the light of the Loperot discoveries may now be changed to *Chilotheridium* sp. Whether the Rusinga molars are specifically the same as those from Loperot must remain uncertain. While most of the vertebrate fossils from Rusinga come from strata about 18 m.y. old, age estimations of the formations on the Gumba Peninsula must be deferred until the completion of the study by Van Couvering and Miller (1969).

Kirimun, Kenya

The tip of a lower left canine from Kirimun in the collection at the National Museum Centre for Prehistory and Palaeontology, Nairobi (no. 33, 1949), is heavily worn and rather flattened horizontally (Pl. 6, figs 3–4). The vertical diameter at crown base is 25 mm, the horizontal diameter at least 40 mm. At the inner edge wear has produced a sharp angle. The enamel is thin but is present externally and ventrally. The tip is broken; the crown length as far as preserved is 60 mm. Very little more than the crown is preserved, but the root seems to assume a round cross section. The shape of the crown is as in *Chilotheridium* from Loperot, but the Kirimun specimen is larger; in size it is larger than all but one of the lower canines of *Chilotherium anderssoni* recorded by Ringström (1924: 37), which measures 47 by 26 mm.

Chilotheridium is not the only genus of rhinoceroses present at Kirimun. Among the bits of teeth from this site, collected during the Harvard Kenya Expedition of 1963 and sent to me for identification by Professor Bryan Patterson, there are part of an M_3 and part of a DM^3 or DM^4 referable to either *Aceratherium* or *Dicerorhinus*. The posterior half of an RM_3 (39–63K) from Kirimun, 27 mm wide, is worn to a height of 24 mm. Direct comparison with M_3 of *Aceratherium acutirostratum* (unworn height 30 mm) shows the same marked crownward taper of the sides of the postero-internal column and the same marked postero-external angle of the crown. In the Loperot M_3 the crown is higher (unworn height 50 mm), and, consequently, the crownward taper is less; the postero-external crown angle is less angular, too. The antero-external portion of a DM^3 or LDM^4 from Kirimun (25–63K), having thin enamel and showing the parastyle fold and paracone style, can be matched in the homologous teeth of *Dicerorhinus leakeyi* and *Aceratherium acutirostratum* from Rusinga described before (Hooijer, 1966: 134 and 142). Whether the second species of rhinocerotids from Kirimun represents *Aceratherium* or *Dicerorhinus* cannot be made out on the basis of this meagre material.

The Kirimun locality, at latitude 00° 43′N, and longitude 36° 54′E, is considered either late Miocene or early Pliocene by Leakey (*in* Bishop, 1967: 47).

Bukwa II, Uganda

Early in 1969 Dr. Alan Walker sent me casts of a number of teeth in the Uganda Museum, Kampala, excellently prepared by him and identified as *Chilotherium* sp. nov. (Walker, 1968, 1969). The specimens originate from the site Bukwa II on the northeast slopes of Mt. Elgon (Masaba), at latitude 01° 17′N, longitude 34° 47′E, and the capping lava has been dated at 22 m.y. The teeth, illustrated in Walker (1968), do agree with their homologues in the Loperot collection in all their diagnostic characters. There are teeth evidently of a single individual: a RP^2 incomplete internally and a LP^2 lacking the posterior outer corner and an inner portion of the protoloph; a RP^4 with an external height of 25

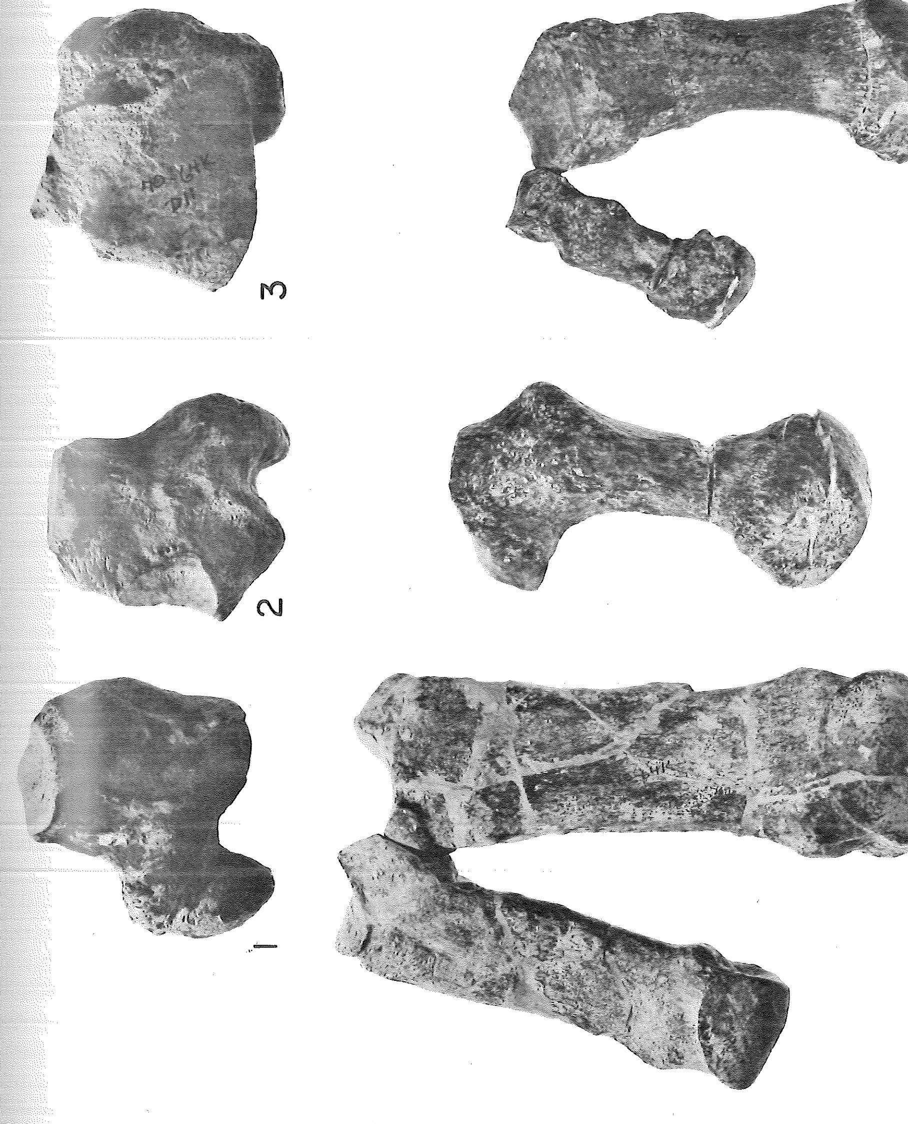


Plate 9. *Chilotheridium pattersoni*. Figs. 1–2, right entocuneiform, No. 1 (70–64K), and left entocuneiform, No. 2 (70–64K, D11), lateral views, × 0.70. Fig. 3, left metatarsal IV, No. 3 (70–64K), proximal view, × 0.90. Fig. 4, left metacarpal II, No. 2 (70–64K, A17), and left metacarpal III, No. 4 (70–64K, A17), articulated; front view, × 0.50. Fig. 5, right metacarpal V, No. 1 (70–64K, B14), lateral view, × 0.73. Fig. 6, the same articulated with right metacarpal IV, No. 1 (70–64K, B14), front view, × 0.50.

TABLE 5. Measurements of teeth of *Chilotheridium* from Bukwa II (in mm)

P^2, a.-p.	29	M^1, a.-p.	52	P_3, a.-p.	34
tr., ant.	34	tr., ant.	67	tr., ant.	20
tr., post.	*ca.* 39	tr., post.	64	tr., post.	23
P^4, a.-p.	40	M^2, a.-p.	61	P_4, a.-p.	37
tr., ant.	58	tr., ant.	74	tr., ant.	25
tr., post.	56	tr., post.	63	tr., post.	28

mm as worn, with the medisinus just closed off internally, very marked protocone folds as well as an anterior fold in the metaloph, an inner cingulum just a little less developed than that in P^4 of Loperot skull No. 2; an RM^1 worn down to 20 mm from the base externally, and an RM^2 nearly 30 mm high at the ectoloph, both showing an internally flattened, constricted protocone and an anterior metaloph fold, the powerful antecrochet, and the flattened ectoloph behind the (only) style, the paracone style, very weak so near the base, and the internal cingulum barely indicated at protoloph and metaloph but present at the medisinus entrance as a cusp. The P^2, as observed by Walker (1968: 155), has an anterior contact facet indicating the presence of a tooth, which must have been DM^1 also demonstrable in Loperot skull No. 1. Both P^4s (illustrated in the position of P^3 in Walker, 1968, plate) and the M^1 show what appears to be a very weak external cingulum, almost invisible on the casts. Of the mandible there are $RP_{3\text{-}4}$ and the posterior portion of LM_3. Measurements of the Bukwa II teeth (Table 5) are very close indeed to those of the Loperot teeth (cf. Tables 2 and 4). The M_3 fragment has a posterior width of 31 mm, slightly greater than that in Loperot specimens (27–29 mm). The Bukwa site may be taken as early Miocene, even very early at that (Walker, 1968: 155).

The Bukwa II material described above is indistinguishable from that of Loperot, but although the generic position is certain (*Chilotheridium*) the specific identity of the two forms is a matter of conjecture. There is a second genus of rhinoceros at Bukwa II, identified by Walker (1968, 1969) as *Dicerorhinus* sp. (I have not seen this material). An incomplete right astragalus is all we have of postcranial material of rhinocerotids at Bukwa II, and a cast of it has been kindly sent to me by Dr. Walker. It lacks the medial ridge of the trochlea as well as the medial portion of the facet for the navicular, so that the medial height, the total width, and the widths of the trochlea and of the distal facets cannot be taken. The lateral height of the Bukwa II astragalus is 63 mm. It is impossible, even by direct comparison with the astragali of *Chilotheridium* of Loperot (this paper, p. 377) and with those of *Dicerorhinus* and *Aceratherium* (Hooijer, 1966: 173), to determine to which of these genera the Bukwa II bone should be referred. So, pending the discovery of postcranial material at Bukwa II that will prove to be identical with that of Loperot, the specific identity of the Bukwa II *Chilotheridium* with that of Loperot must remain uncertain.

Ngorora, Kenya

Late in 1968 Dr. W. W. Bishop entrusted to me the rhinoceros remains collected by him that year in the Ngorora Formation, Kenya, at latitude 00° 53′N, longitude 35° 51′E, approximately 10 m.y. old, i.e., early Pliocene. The rhinoceros remains were all picked up from the surface and are rather fragmentary. However, there is material of *Chilotheridium* again in this lot, dental as well as postcranial, which justifies the inclusion of the Ngorora material in the present paper.

To begin with, there is a right maxilla with DM^1, P^{2-4} and M^1, marked in the field 2/13.S. The tooth crowns are much worn and damaged internally as well as externally. No measurements can be given of either DM^1 or P^2. P^3 is *ca.* 45 mm anterotransversely, and P^4 is *ca.* 55 mm wide anteriorly, and *ca.* 52 mm wide behind, close to the Loperot teeth (Table 2). In

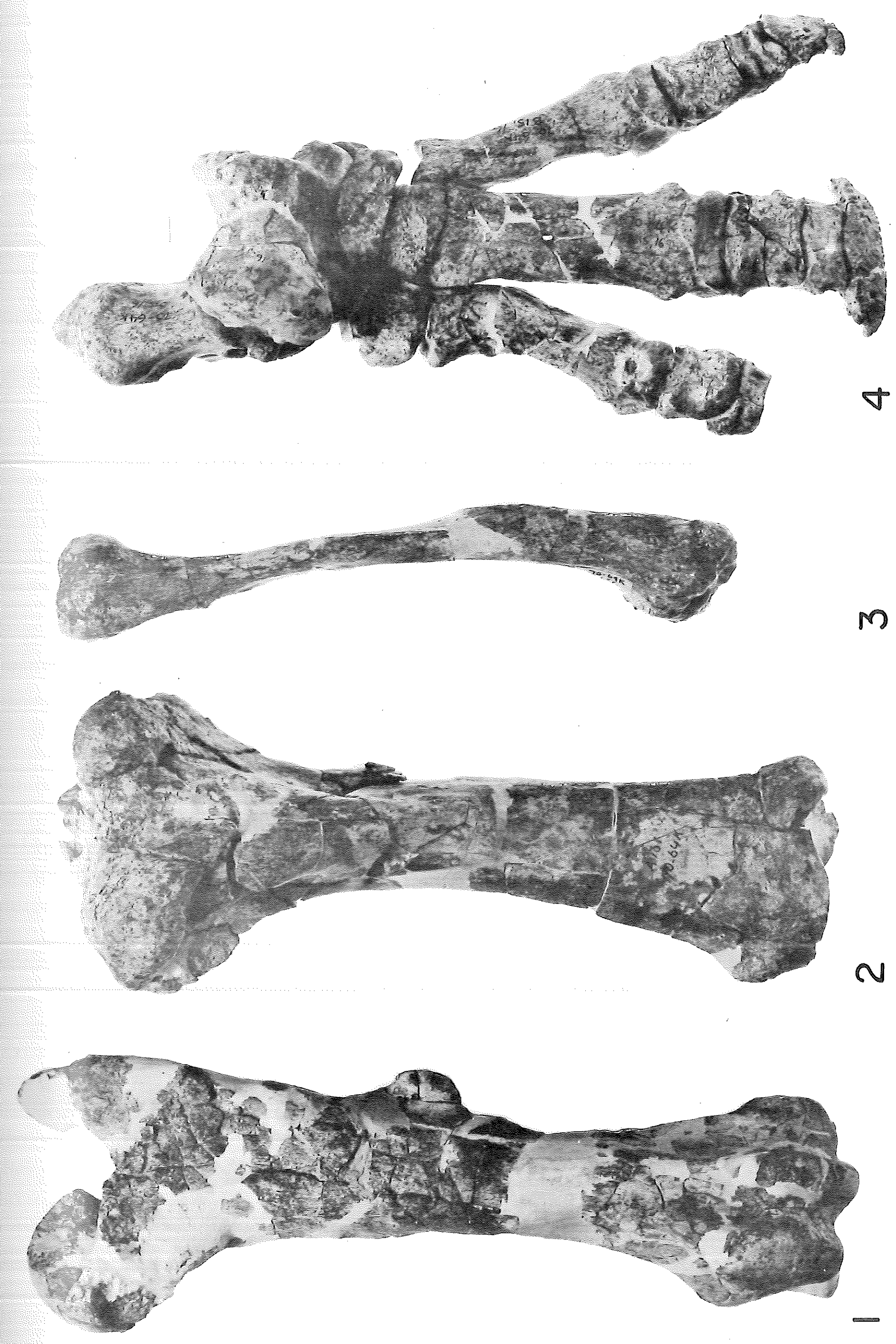


Plate 10. *Chilotheridium pattersoni*. Fig. 1, left femur, No. 1 (70–64K), front view, × 0.24. Fig. 2, right tibia, No. 1 (70–64K, A16), front view, × 0.32. Fig. 3, right fibula, No. 1 (70–64K, 65C), lateral view, × 0.32. Fig. 4, right pes, No. 1 (70–64K, B15–16), front view, × 0.32.

P^3 the medisinus remains only as an enamel island, the postsinus having been worn off completely. In P^4 both the medisinus, showing a weak crochet, and the postsinus remain as enamel islands. The posterior portion of the ectoloph is preserved in P^4, and it shows the flatness characteristic of *Chilotheridium* molars, there being no metacone style. The entrance to the medisinus has a cingular cusp slightly less developed than that in Loperot skull No. 1; the internal cingulum is weakly developed along the protoloph, too. The posterior protocone fold as well as the anterior metaloph fold can be seen distinctly; the antecrochet extends all across the medisinus. The M^1 is so much worn down and incomplete externally and internally that no measurements can be given; it shows, however, the anterior protocone fold (Pl. 11, fig. 1).

In the lot labelled 2/13.S there are further a number of fragments of an upper dentition, some of which are more characteristic than others. The RP^4 is the most complete specimen; it comprises most of the ectoloph and the external portion of the protoloph, and further, the inner portion of the metaloph not fitting on to the remainder of the crown. The ectoloph of P^4 is worn to a height of 49 mm and measures 42 mm anteroposteriorly. The paracone style is there, but effaced near the crown base, and there is no metacone style, the posterior half of the outer surface being flat, just as in the P^4 of Loperot skull No. 1 that is slightly more worn down. The portion of the protoloph preserved bears a well-developed cingulum. The anterior metaloph or hypocone fold is seen in the detached fragment; the protocone is not preserved in this specimen.

To the same individual appear to belong the posterior portions of the ectolophs or RM^1 and RM^2, both showing the absence of the metacone style. This makes the posterior portion of the ectoloph flat or even concave apically. The antero-external portion of an unworn LM^3 fortunately is present in the collection as well. The Ngorora cheek teeth show the hypsodonty by which *Chilotheridium* is characterized, notably the M^2 (Pl. 11, fig. 4). This dentition as a whole is a little less worn down than that of Loperot skull No. 1, the (worn) heights of P^4, M^1 and M^2 (49, 43, and 68 mm, respectively) being somewhat greater than those in Loperot skull No. 1 (45, 40, and 60 mm, respectively). The portion of LM^3 lacks the base, so that the full height cannot be determined; it is broken off anteriorly along the cingulum, which is highest in the depression into which fits the metastyle of M^2, 20 mm below (rootward of) the unworn edge. In the slightly worn M^3 of Loperot skull No. 1 the anterior cingulum is about 15 mm below the worn edge so that some 5 mm may be added to get the full crown height, which may be, then, 75 mm. Among the smaller fragments in lot 2/13.S there is one showing the posterior protocone fold being curved inward toward the base, as is characteristic of *Chilotheridium* molars. The other bits preserved are not characteristic one way or the other. In the lot 2/11.S there is an internal fragment of LM^3, rather worn, with the characteristic antecrochet, limited by the posterior protocone fold curving inward basally. In lot 2/11A.S there is a protoloph portion of a left upper molar with the strong anterior cingulum as well as the anterior protocone fold, and the inner surface of the protocone shows the characteristic flattening.

Although at the moment of writing we do not have any better preserved upper molars from Ngorora, the marked hypsodonty as seen in M^2, the flattened posterior ectoloph portions, the strong anterior cingulum, the inwardly curving posterior protocone folds, and the internal flattening of the protocone are absolutely diagnostic of *Chilotheridium*. In *Aceratherium* we find constricted protocones, too, but these are not flattened internally, and the molars are low crowned, the height of the outer surface of M^3 (unworn) in *Aceratherium*

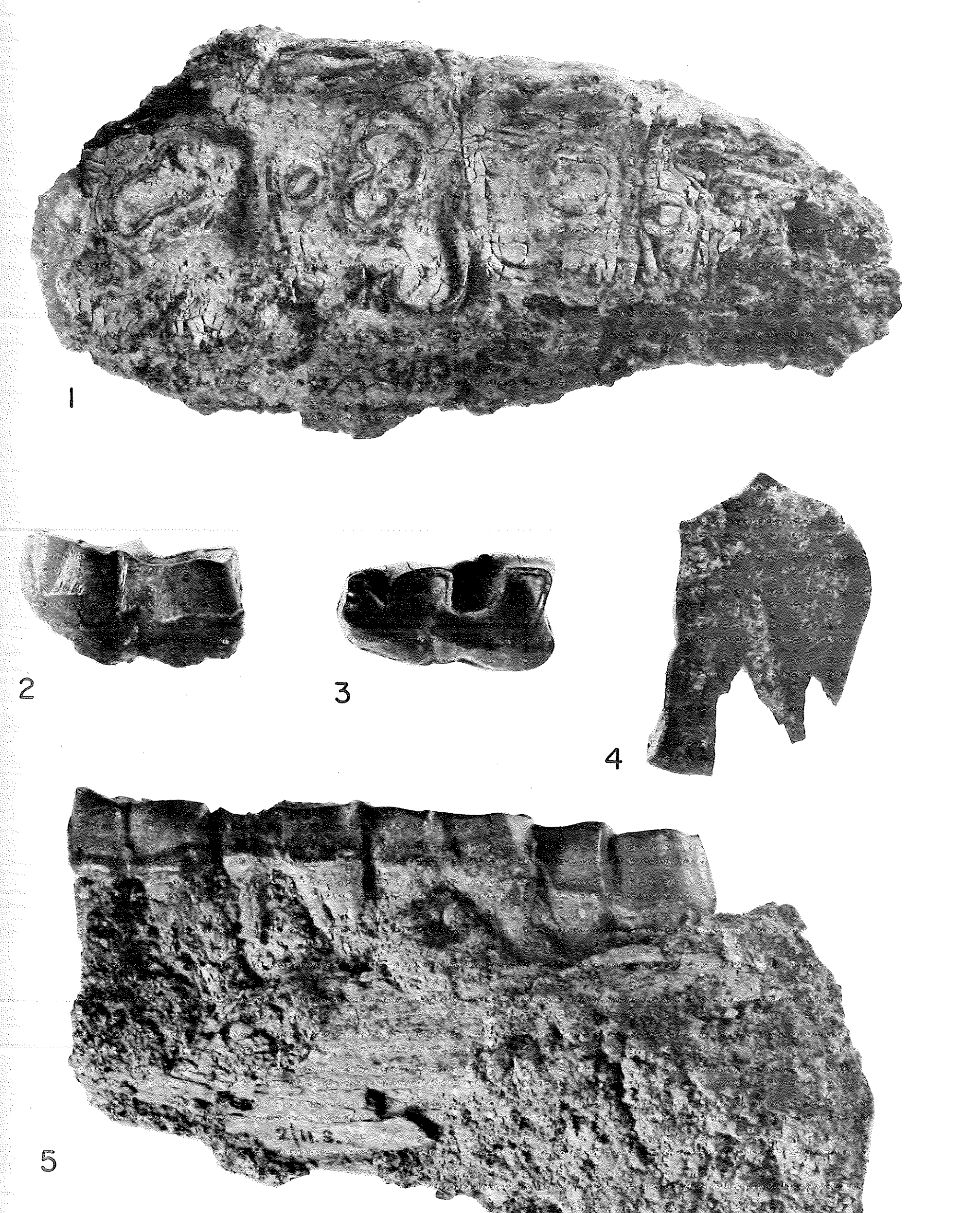


Plate 11. *Chilotheridium pattersoni*. Fig. 1, right maxillary with dm^1, P^2–M^1 (2/13.S), crown view, × 0.75. Fig. 4, RM^2, posterior portion of ectoloph (2/13.S), outer view, × 0.60. *Brachypotherium* sp. Figs. 2–3, L dm_3 (2/2.S), outer and crown views, × 0.67. *Aceratherium* c. q. *Dicerorhinus* sp. Fig. 5, left ramus with P_4–M_3 (2/11.S), outer view, × 0.55. All from Ngorora, Kenya.

TABLE 6. Measurements of lower teeth of *Aceratherium* and *Dicerorhinus* (in mm)

	Ngorora 2/11.S	Ngorora 2/14.S	Ngorora 2/1.SL	Rusinga, Karungu, and Moruorot
P_2, a. -p.	—	25	26	26–28
tr.	—	18	18	17–22
P_3, tr., post.	—	25	—	22–24
P_4, a. -p.	38	37	—	35–39
tr., ant.	26	25	24	24–26
tr., post.	29	28	27	25–30
M^1, a. -p.	—	—	—	41–44
tr., ant.	28	—	—	26–29
tr., post.	30	30	—	28–31
M_2, a. -p.	45	49	—	41–50
tr., ant.	29	29	—	26–32
tr., post.	30	31	—	27–31
M_3, a. -p.	47	—	—	44–53
tr., ant.	28	—	—	27–31
tr., post.	28	28	—	26–29

acutirostratum being only 49 mm by a length of 65 mm (Hooijer, 1963: 43).

Lower teeth in the Ngorora collection at present available do not show the hypsodonty by which *Chilotheridium* is characterized: in the lot 2/14.S an unworn posterior lophid of RM_3 is only 30 mm high, against 50 mm in mandible No. 3 from Loperot. In lot 2/11.S there are a left ramus of the mandible with P_4–M_3 and a right ramus with $M_{2\text{-}3}$ of the same individual (Pl. 11, fig. 5). All the teeth are worn, and there are external cingula in the groove between the lophids of P_4, M_1 and M_2, which are short ridges placed 7–8 mm above the crown bases. The external grooves are well marked as in *Aceratherium* or *Dicerorhinus*, unlike what we find in advanced brachypotheres, where the external grooves are flattened out. In lot 2/14.S there are, all isolated but evidently belonging to one individual, P_2 from both sides, RP_3 incomplete in front, RP_4, the posterior part of RM_1, RM_2, and the posterior portion of RM_3. In this lot there are no external cingula except in M_2, a few cusplets down near the base of the external groove. There are further a RP_2 and a LP_4 in lot 2/1.SL, the external part of a lower P in 2/1.SU, and the posterior portion of a left lower molar, either M_1 or M_2, in lot 2/11.A.S., the latter unworn and with a full height of 40 mm. In Loperot mandible No. 3 a worn M_2 has just this height, and therefore was higher when unworn. Measurements (Table 6) show the Ngorora lower teeth to be similar to those of Loperot (Table 4) in size, except for the lengths of M_2 and M_3, which are greater in the Loperot mandibles. The Ngorora teeth, of course, are also less high crowned than those of Loperot, as stated above. As shown in Table 6 the Ngorora teeth are well within the variation limits of the mandibular teeth of *Aceratherium* and *Dicerorhinus* previously recorded from Rusinga, Karungu, and Moruorot (after Hooijer, 1966: 131, 133 and 141; 1968a: 234).

The lower teeth of *Dicerorhinus leakeyi* and *Aceratherium acutirostratum* are indistinguishable, and there are no differences between these and the Ngorora lowers. The lower teeth from Loperot are more hypsodont, as we have seen, and M_2 and M_3 are somewhat longer than those from Ngorora.

There is a lower milk molar in the Ngorora collection, a left DM_3 marked 2/2.S (Pl. 11, figs. 2–3) characterized by its thin enamel and the presence of a weak but continuous cingulum externally. External cingula may develop in *Brachypotherium* lower molars (see Roman and Viret, 1934: pl. X). Our *Brachypotherium heinzelini* from Congo, Kenya, and Uganda does not show a cingulum on its lower molars so far as known, and lower milk molars of this species have not yet been found. In size the Ngorora DM_3 exceeds that of *Brachypotherium brachypus* (Lartet) from La Grive-Saint-Alban; dentally there is no great difference between this species and *B. heinzelini* (Hooijer, 1966: 144), and therefore the Ngorora milk molar would seem to be too large to be referred to the latter species. In a collection from Lothagam Hill, Kenya, shortly to be published upon by Professor Patterson and myself, and dating back approximately 5 million years, there is a large species of *Brachypotherium,* and its DM_3 is rather similar in dimensions and has a weak external cingulum as well. Measurements are given in Table 7.

TABLE 7. Measurements of DM_3 of *Brachypotherium* sp. (in mm)

	Ngorora	Lothagam Hill
DM_3, a. -p.	46	43
tr., ant.	21	21
tr., post.	24	23

The postcranial material from Ngorora, scanty as it is, belongs to *Chilotheridium* only. There are the proximal and distal parts of a right radius and a phalanx, both labelled 2/11.S. The radius is *ca.* 90 mm wide proximally by a shaft width of *ca.* 46 mm, and a width of the distal facets of 80 mm. These dimensions are as in *Chilotheridium* from Loperot (Table 8), and the presence of a small, lateral facet for the cuneiform unequivocally shows the Ngorora radius to belong to this genus. The phalanx is the first of a median digit, with a length of 33 mm and a proximal width of 46 mm, of the same size and proportions as in the Loperot *Chilotheridium* (p. 385).

Since we have both dental and postcranial material from Ngorora that is indistinguishable from that of Loperot, it would seem justified to accept not only generic but also specific identity of the rhinoceros from the two localities.

POSTCRANIAL SKELETON OF *CHILOTHERIDIUM PATTERSONI* GEN. ET SP. NOV.

There are two specimens of the atlas in the Loperot collection, one (70–64K, 65B) nearly complete, the other (70–64K, C1) lacking the dorsal arch and much distorted. The greatest width of the first specimen is 285 mm, the width across the occipital articular facets 130 mm, the distance between the intervertebral foramina in the dorsal arch 93 mm, and the mid-ventral length (including the median posterior tubercle *ca.* 20 mm long and wide) *ca.* 65 mm. These data do not differ much from those of the atlas of *Chilotherium anderssoni* (Ringström, 1924: 55; Bohlin, 1937: 72), but the atlas of *Aceratherium acutirostratum* (Hooijer, 1966: 158) is not so very different either.

Of the scapula we have a series of five specimens, two of which are rather complete although they are fragmented (70–64K, A18, and 70–64K, BB, from the left and from the right side, respectively), and three specimens all from the right side (70–64K, BL, 70–64K, 65B, and 70–64K, BB) lacking most of the borders and of the spine; the last specimen is a proximal portion only.

The thickened vertebral or upper border is best preserved in scapula No. 2; it is highest at the point where the spina scapulae ends and is regularly convex. It forms an angle behind, at two-thirds of the height from the anterior border of the glenoid cavity, where it passes into the thin posterior border, which is concave throughout. The anterior border of the scapula is likewise thin. It is straight for the most part in the reconstructed specimen No. 2 but was probably weakly convex in its upper three-fourths, the basal part being concave, forming the "neck," and becoming very thick where it ends in the massive tuber scapulae. The spina scapulae, running from the neck to the upper border, gives off a large, triangular, posteriorly directed tuber spinae, which extends just beyond the posterior border with its thick, rough extremity a little distance above the middle of the height of the bone. It is broken into fragments that are held together with plastic and plaster and is pressed against the infraspinous fossa, but it originally extended outward as well as backward. Its anteroposterior extent is 130–140 mm (the upper portion of the

TABLE 8. Measurements of radius from Loperot (in mm)

	No. of specimen									
	1	2	3	4	7	8	9	10	11	14
Median length	315	310	280	290	—	—	—	—	—	—
Proximal width	94	96	90	90	—	92	86	—	—	—
Middle width	*ca.* 50	*ca.* 45	*ca.* 45	*ca.* 45	—	—	—	—	—	—
Greatest distal width	95	95	—	*ca.* 100	—	—	—	—	—	—
Width distal facets	87	86	88	*ca.* 90	82	—	—	85	80	80

tuber spinae, preserved in scapula No. 1, is slightly longer than that in specimen No. 2). The total height, from the anterior border of the glenoid cavity to the end of the spine at the upper border, is 440 mm in No. 2; in No. 1 it is *ca.* 470 mm, but this measurement is too great because of the spaces between the fragments, filled with plaster. Likewise, the anteroposterior diameter of the neck, over 120 mm in No. 2, is too large; in No. 1 this diameter is 100 mm, which must be very nearly correct as there are no spaces between the bone fragments in this portion. The anteroposterior diameter over the glenoid cavity and tuber scapulae reads 120 mm in No. 1, and the anteroposterior and transverse diameters of the glenoid cavity are 80 mm and 70 mm in No. 2. The greatest anteroposterior diameter of the scapula is over 240 mm, as seen in No. 2. No more exact measurements can be given.

The scapula of *Chilotherium* from China, originally stated to be *ca.* 400 mm high and 93 mm wide at the neck (Ringström, 1924: 60/61), as a more complete specimen showed, is 478 mm high and 88 mm wide at the neck (Bohlin, 1937: 80). Our Loperot scapulae are less high, and wider at the neck (see above), while the tuber spinae is more developed than in *Chilotherium,* longer than the width of the neck. The scapula of *Dicerorhinus leakeyi* is likewise higher and slenderer than those of Loperot (Hooijer, 1966: 158), with a less developed tuber spinae, only 75 mm long and not extending to the posterior margin of the bone. A lateral view of Loperot scapula No. 2 is given in Plate 8, figure 1. The proportions of the Loperot scapula are very similar to those in the slightly smaller *Diceratherium* from China, of which the greatest height is 404 mm, the neck width 77–? 85 mm, and the greatest anteroposterior diameter 200–204 mm (Bohlin, 1937: 80 and fig. 120).

Humeri in the Loperot collection are very poorly preserved. There are three bones from the right side: 70–64K, A18, 70–64K, BB, and 70–64K. In No. 1 both ends are preserved, but no exact measurements can be given because of the crushing of the specimen. Number 2 lacks the proximal end, and in No. 3 the distal end is shattered. There is, in addition, No. 4, the distal trochlea of a right humerus, 70–64K.

The humerus of the Chinese *Chilotherium* (Ringström, 1924: 55 and 61) is shorter than that in fossil *Dicerorhinus* (Hooijer, 1966: 160), but less broad as well except in the greatest width at the distal end, which is proportionally greater in *Chilotherium* than in *Dicerorhinus.* It is unfortunate that the Loperot bones cannot be exactly measured; the length from caput to medial condyle in No. 1 would have been about 340 mm, like that in *Chilotherium* (345–353 mm), but the greatest distal width would not have exceeded 130 mm, which is less than that in the *Chilotherium* humeri (150 mm) but proportionally as great as that in *D. orientalis* and *D. primaevus* with a length of 370–400 mm and a greatest distal width of 160–167 mm.

TABLE 9. Measurements of ulna from Loperot (in mm)

	No. of specimen				
	1	2	3	5	9
Greatest length	420	*ca.* 400	*ca.* 390	—	—
Length from proc. anconaeus ("beak")	355	*ca.* 350	—	—	—
Length of olecranon from "beak"	145	*ca.* 125	*ca.* 125	135	—
Width at semilunar notch	90	80	—	*ca.* 80	—
Greatest distal diameter	62	60	66	—	60

The width of the distal trochlea is 90 mm in Loperot humerus No. 4, not greater than that in *Chilotherium.*

The following specimens of the radius are in the Loperot collection: 1) right radius, 70–64K, BB; 2) left radius, 70–64K, A16; 3) and 4) right and left radius, 70–64K, C14; 5) right radius without distal end, 70–64K, BB; 6) left radius without distal end, 70–64K, A17; 7) right radius in three parts, 70–64K, BB; 8) proximal portion of right radius, 70–64K; 9) proximal portion of left radius, 70–64K, E10; 10) distal portion of right radius, 70–64K; 11) distal portion of right radius, 70–64K, B16; 12) idem, 57–64K; 13) idem, 70–64K, C12; 14) distal portion of left radius, 70–64K, BB; and, 15) distal fragment of right radius comprising only part of the facet for the scaphoid, 70–64K. Measurements are given in Table 8.

These radii, especially Nos. 3 and 4, agree very well with those of *Chilotherium anderssoni, Diceratherium palaeosinense,* and *D. tsaidamense* in length and proximal and distal width (Ringström, 1924: 55 and 113; Bohlin, 1937: 82). The mid-shaft width is greater in *Chilotherium* (55–57 mm) than in *Diceratherium* (41–46 mm); in this respect the Loperot radii are nearer to *Diceratherium.* All the specimens in which the lateral portion of the distal end is well preserved show a very small facet for the cuneiform, set off at an obtuse angle from that for the lunar (Nos. 1–4, 7, 10–12, and 14). Such a facet, only 1 cm wide and 1½ to 2 cm anteroposteriorly, is found in *Chilotherium* as well as in the Chinese *Diceratherium* and in the American diceratheres (Ringström, 1924: 46 and 111; Bohlin, 1937: 82). It does not show in *Aceratherium* or *Dicerorhinus* (which have longer radii: Hooijer, 1966: 161), and not in the recent rhinoceroses either. Radius No. 1 is shown in Plate 8, figure 2.

The ulna is represented in the Loperot collection by the following specimens: 1) left ulna, 70–64K, A17; 2) right ulna broken at mid-shaft, 70–64K; 3) right ulna broken at mid-shaft, 70–64K, BB; 4) right ulna without distal end, 70–64K, BB?; 5) left ulna without distal end, 70–64K, C14; 6) left ulna, much broken, distal end missing, 70–64K, C14; 7) left ulna, olecranon and distal end missing, 70–64K, BB; 8) right ulna, olecranon and distal epiphyses missing, 70–64K, A17; 9) distal portion of right ulna, 70–64K, BB; 10) distal portion and part of shaft of right ulna, 57–64K; and, 11) distal portion of left ulna, 70–64K, BB. Few of these bones can be measured exactly.

Entire ulnae are not available either in the Chinese *Chilotherium* or in the Chinese *Diceratherium;* Ringström (1924: 55) gives the length of the ulna of *Chilotherium anderssoni* as 370–390 mm, with a least width of 33 mm. Our most complete specimen (No. 1) has a least width of *ca.* 45 mm; the specimen is figured in Plate 8, figure 3. It should be remarked that among the Loperot material there is no case of ankylosis of radius and ulna as we see in *Chilotherium* (Ringström, 1924: 56).

TABLE 10. Measurements of scaphoid from Loperot (in mm)

	No. of specimen					
	1	2	3	4	5	6
Posterior height	59	55	55	—	—	60
Anterior height	47	43	46	44	—	47
Proximal width	43	40	—	—	39	43
Distal width	52	43	—	—	—	52
Greatest distal diameter	71	*ca.* 67	—	—	—	70

Six specimens of the scaphoid[1] are in the Loperot collection, Nos. 1–5 are from the right side (marked consecutively 70–64K, A16; 70–64K; 70–64K, BB; 70–64K, D11; and 70–64K, BB), and No. 6 is from the left side (70–64K). Number 3 is incomplete laterally, No. 4 lacks the posterior half, and No. 5 is incomplete distally. Numbers 1 and 6 may well have belonged to one and the same individual. Measurements are in Table 10.

The Loperot scaphoids differ from those of *Aceratherium* and *Dicerorhinus* (Hooijer, 1966: 162) in that the distal outward projection, which bears on its distal surface the facet for the magnum, extends beyond the proximal radius facet, thus making the distal width greater than the proximal. This is most marked in Nos. 1 and 6, and less in No. 2. Further, the proximal projection behind the radius facet is much developed in Nos. 1 and 6, and not so in Nos. 2 and 3. In none of the specimens does the distal projection behind the trapezium facet extend downward beyond this facet, as it does in *Aceratherium* and *Dicerorhinus* to a certain extent. In all the fossil specimens the posterior height exceeds the anterior height (the latter measured over the convex anterior portion of the radius facet and the ridge between the facets for the trapezoid and the magnum), while these heights are nearly equal in *Dicerorhinus sumatrensis.* In this recent species the ratio of anterior height (55 mm) to greatest distal diameter (79 mm) is 70, which shows that the scaphoid is relatively higher than that in *Dicerorhinus ringstroemi* (see Hooijer, 1966: 162), in which this ratio is 66. In a specimen of *Diceratherium palaeosinense* this ratio is 62, and in a specimen of *Chilotherium* it is only 51 (Bohlin, 1946: 222). Our Loperot specimens give *ca.* 64–67 for this ratio, and therefore are not as low as the scaphoid in *Chilotherium* but appear to agree better with *Diceratherium* and *Dicerorhinus* in this respect.

The lunar is represented in the Loperot collection by four specimens, but none of these is entire, unfortunately. All lack the posterior downward projection. In No. 1, a right lunar (70–64K), there are at least the greater parts of the upper and lower lateral facets for the cuneiform, of the distal facet for the unciform, and of the medial facets for the scaphoid (anteriorly) and the magnum (posteriorly). The medial part of the proximal facet for the radius is broken off, and hence the proximal width cannot be given. Number 2, a right lunar (70–64K) is damaged anteriorly as well, but its proximal width can be given. Number 3, a right lunar (70–64K) consists merely of a lateral portion, and is injured posteriorly, lacking most of the radius facet. Number 4, a left lunar (70–64K), is nearly complete proximally but lacks the distal unciform facet. In all of these specimens there is no facet for the ulna, the proximal lateral facet for the ulna that we find in *Aceratherium* and *Dicerorhinus* (Hooijer, 1966: 162). As stated above, in these genera the radius does not show a distal lateral facet for the cuneiform, the ulna articulating (for a very small part) with the lunar, cutting off the radius from contact with the cuneiform. The condition seen in the Loperot lunars is like that in *Chilotherium* and *Diceratherium* (Ringström, 1924: 56 and 111; Bohlin, 1937: 82).

[1] In the nomenclature of the carpal bones British usage is adopted. The terms used are in the first column, below, and those used by Ringström (1924) and Bohlin (1937, 1946) appear in the second column.

scaphoid	Radiale
lunar	Intermedium
cuneiform	Ulnare
pisiform	Pisiforme
trapezium	Carpale I
trapezoid	Carpale II
magnum	Carpale III
unciform	Carpale IV & V

TABLE 11. Measurements of lunar from Loperot (in mm)

	No. of specimen			
	1	2	3	4
Anterior height	38	*ca.* 35	30+	—
Proximal width	—	36	—	40

Of the cuneiform we have twelve specimens in the Loperot collection; Nos. 1–7 are from the right side, and Nos. 8–12 from the left: 1) 57–64K; 2) 57–64K; 3) 70–64K, damaged proximally; 4) 68–64K, posterior half missing; 5) 68–64K, incomplete proximally and laterally; 6) 70–64K, incomplete distally; 7) 70–64K, A16, incomplete behind; 8) 68–64K; 9) 57–64K, incomplete behind; 10) 70–64K, BB; 11) 70–64K, incomplete behind; and, 12) 70–64K, incomplete in front and distally.

The cuneiform of *Chilotherium* as described by Bohlin (1946: 224) does not appear to have very distinctive characters: the depressions and swellings on the nonarticular surfaces vary individually, and so do the heights of the two facets for the lunar and the shape of the distal unciform facet. It is stated that the unciform facet is quadrangular rather than triangular because the anterolateral side of the bone is so strongly convex, but this varies individually, too: in No. 1 the facet is subtriangular, and in No. 2 it is rather quadrangular. In *Dicerorhinus* the cuneiform varies in these respects also.

Three proximal ends of pisiforms, marked 57–64K, 70–64K, and 70–64K, display the two small facets for the ulna and the cuneiform, set at right angles to each other, or slightly less than 90°. Bohlin (1946: 226) states that the angle between these two facets on the pisiform is distinctly obtuse in *Chilotherium,* whereas it is less than 90° in the American *Diceratherium.* Since the main part is missing in the Loperot pisiforms, the diameter over the two proximal facets may be given, which is 26 mm, 23 mm, and 24 mm in Nos. 1–3.

No trapezium has been recognized in the collection.

The trapezoid is represented in the Loperot collection by seven specimens, as follows: 1) right trapezoid, 70–64K, H11, incomplete posteriorly; 2) right trapezoid, posterior half only, 70–64K; 3) right trapezoid, 70–64K, damaged at both ends; 4) left trapezoid, 57–64K; 5) left trapezoid, 70–64K, A16; 6) left trapezoid, 57–64K; and, 7) left trapezoid, 70–64K, incomplete behind. Ringström (1924: 57) mentions the trapezoid of *Chilotherium* to be of the ordinary type; it is mentioned by Bohlin (1937: 82) to differ from that of the Chinese *Diceratherium* in the markedly oblique posterior surface. This *Chilotherium* feature does not show in the Loperot trapezoids. As seen in Table 13 the anterior width and height are nearly equal in Nos. 1 and 7, and very different in Nos. 4–6; the two trapezoids of *Diceratherium* (Bohlin, 1937: 84) vary in the same way. In *Chilotherium* (2 specimens:

TABLE 12. Measurements of cuneiform from Loperot (in mm)

	No. of specimen											
	1	2	3	4	5	6	7	8	9	10	11	12
Anterior height	45	42	—	47	—	—	43	45	42	43	42	—
Distal width	43	34	36	—	34	—	34	39	35	33	38	34
Proximal ant. post. diam.	33	31	—	—	29	32	—	34	—	30	—	—
Greatest horizontal diam.	51	44	49	—	47	—	—	48	—	46	—	—

TABLE 13. Measurements of trapezoid from Loperot (in mm)

	No. of specimen					
	1	2	4	5	6	7
Anterior height	*ca.* 26	—	30	29	30	26
Anterior width	28	—	24	22	25	25
Greatest ant. post. diam.	—	—	41	39	46	—
Posterior height	—	27	28	27	33	—
Posterior width	—	18	16	16	17	—

Bohlin, 1937: 84) anterior width and height of the trapezoid are nearly the same, and in one specimen the width exceeds the height, as in Loperot trapezoid No. 1.

In the earlier Miocene East African rhinoceros collection (Hooijer, 1966) the trapezoid was not represented; the trapezoid of *Dicerorhinus primaevus* Arambourg (1959: 67) has the same anterior height and anteroposterior diameter as Loperot No. 5, while the trapezoid of *Dicerorhinus sumatrensis* (same skeleton as that used in the 1966 paper) in anterior height and width (34 mm and 28 mm) as well as in posterior height and width (33 mm and 21 mm) exceeds all the fossil specimens, even though its anteroposterior diameter is only 38 mm.

The magnum is represented in the Loperot collection by no less than ten specimens, but none of these is entire. The posterior downward process is missing in all the specimens; it is separately preserved in Nos. 1 and 2 but cannot be fitted on to the remainder of the bone. The convex posterior facet for the lunar is broken off in all specimens except Nos. 1, 2 and 8, leaving just the front portion of the bone. In No. 10 this portion is incomplete laterally. Numbers 1–7 are from the right side, Nos. 8–10 from the left. They are marked as follows: 1) 70–64K, BB; 2) 70–64K, B14; 3) 70–64K; 4) 70–64K; 5) 57–64K; 6) 70–64K; 7) 70–64K; 8) 70–64K; 9) 68–64K; and, 10) 70–64K, H11. Measurements are given in Table 14.

The magnum of *Chilotherium* is described by Ringström (1924: 57) as large and wide with a small height; the magnum of *Diceratherium palaeosinense* is wider still (45 mm against 36–37 mm) by nearly the same height (23 mm against 20–22 mm), and that of *Diceratherium tsaidamense* is 36 mm wide and 26 mm high (Bohlin, 1937: 84). The ratio of height to width in the Loperot magnum series varies from 0.63 (in No. 1) to 0.75 (in No. 9); in *D. tsaidamense* and *D. palaeosinense* these ratios are 0.72, and 0.51, respectively, and in two *Chilotherium* specimens these values are 0.61 and 0.54. Thus, the *Chilotherium* magnum appears to be relatively wider than those from Loperot, and so is that of *Diceratherium palaeosinense,* while *D. tsaidamense* resembles the Loperot bones in relative height of the magnum. It is further worthy of note that two Rusinga magna (Hooijer, 1966: 164) are very close to that of *D. tsaidamense* in height (25–27 mm) and width (36–38 mm) but exceed it in greatest length (75–82 mm against only 67 mm).

Twelve specimens of the unciform are in the Loperot collection; all except No. 1 and No. 9 lack the posterior process. Numbers 2, 4 and 11 are incomplete laterally, and No. 8 is merely a mediodistal fragment. Numbers 1–8 are from the right side, and Nos. 9–12 from the left. Numbers 5 and 9 almost certainly belong to a single individual. The markings on the bones are as follows: 1) 70–64K, A17; 2) 57–64K; 3) 70–64K, J7; 4) 70–64K, A16, 17; 5) 70–64K; 6) 57–64K; 7) 57–64K; 8) 70–64K; 9) 70–64K, A16; 10) 70–64K, E11; 11) 70–64K; and, 12) 70–64K, D10.

TABLE 14. Measurements of magnum from Loperot (in mm)

	No. of specimen									
	1	2	3	4	5	6	7	8	9	10
Greatest anterior height	31	32	32	33	32	33	30	30	33	32
Greatest anterior width	49	44	48	47	47	45	44	44	44	—
Proximal ant. post. diam.	59	59	—	—	—	—	—	57	—	—

TABLE 15. Measurements of unciform from Loperot (in mm)

	No. of specimen										
	1	2	3	4	5	6	7	9	10	11	12
Greatest anterior height	47	45	38	43	43	42	42	42	45	43	39
Greatest width	57	—	47	—	47	47	51	46	51	—	54
Greatest ant. post. diameter	83	—	—	—	—	—	—	71	—	—	—

The measurements in Table 15 indicate the variability in the Loperot series. In comparing these data with those of *Chilotherium* and *Dicerorhinus* as given by Bohlin (1946: 225), it should be remarked that the height anteriorly as given by this author and as shown in his illustrations is taken at right angles to the proximal facet for the lunar, which corresponds to what I use as greatest width. I take the greatest anterior height perpendicular to the straight portion of the distal surface articulating with metacarpal III and the medial portion of metacarpal IV, and from there to the top of the bone, which is the lateral end of the facet for the cuneiform. As can be seen from the front views of the bones in Bohlin (1946: 225, fig. 81), the greatest height is only *ca.* 35 mm in the largest of the two *Chilotherium* unciforms with a greatest width of 46 mm and a greatest anteroposterior diameter of 86 mm. The greatest height in an unciform of *Dicerorhinus ringstroemi* Arambourg (1959: 73; for *D. orientalis* Ringström, non Schlosser) from the Chinese Pontian is *ca.* 65 mm by a greatest width of 78 mm and a greatest anteroposterior diameter of 108 mm.

The ratio of anterior height to anterior width is *ca.* 0.76 in the *Chilotherium,* and *ca.* 0.83 in the *Dicerorhinus* specimen, a difference of no significance; in our Loperot series this height/width ratio varies from 0.72 in No. 12 to 0.92 in No. 5. The difference between *Chilotherium* and *Dicerorhinus* unciforms can be demonstrated in ratio of anterior width to greatest anteroposterior diameter; this was already shown by Bohlin (1946: 225, table). In *Chilotherium* (two specimens) the ratio is 0.53 and 0.57, whereas in *Dicerorhinus ringstroemi* this ratio is 0.71 and 0.72; in Recent *Dicerorhinus sumatrensis* (Hooijer, 1966: 164) the ratio is even 0.79. In their ratio of greatest width to greatest anteroposterior diameter the two entire Loperot unciforms are intermediate and even nearer to *Dicerorhinus* than to *Chilotherium,* the ratio being 0.65 in No. 9, and 0.69 in No. 1. It should finally be noted that the two Rusinga unciforms previously recorded (Hooijer, 1966: 164) are within the variation limits of the *Dicerorhinus* specimens, their ratios being 0.72 and 0.75.

In the Loperot collection there are a number of specimens of all four metacarpals, as follows:

Metacarpal II, 9 specimens: 1) right Mc. II, 70–64K, B13; 2) left Mc. II, 70–64K, A17; 3) right Mc. II, proximal portion, 70–64K, BB; 4) right Mc. II, proximal portion, incomplete laterally, 70–64K; 5) right Mc. II, proximal portion, incomplete behind, 70–64K; 6) right Mc. II, proximal portion, incomplete laterally, 57–64K; 7) left Mc. II, proximal portion, incomplete laterally, 70–64K; 8) left Mc. II, proximal portion, 70–64K, B14; and, 9) left Mc. II, proximal portion, 70–64K.

Metacarpal III, 5 specimens: 1) right Mc. III, 70–64K; 2) right Mc. III, proximal portion, incomplete behind, 57–64K; 3)

TABLE 16. Measurements of Metacarpals II–V from Loperot (in mm)

	No. of specimen				
Mc. II	1	2	3	7	8
Median length	123	123	—	—	—
Proximal width	41	42	43	43	47
Proximal ant. post. diameter	36	37	43	42	39
Middle width	33	*ca.* 33	36	—	—
Middle ant. post. diameter	17	15	18	18	—
Greatest distal width	43	37	—	—	—
Width of distal trochlea	37	32	—	—	—
Distal ant. post. diameter	37	37	—	—	—
Ratio middle width/length	0.27	*ca.* 0.27	—	—	—

	No. of specimen				
Mc. III	1	2	3	4	5
Median length	140	—	—	143	154
Proximal width	49	61	57	52	61
Proximal ant. post. diameter	38	—	—	40	44
Middle width	39	—	—	40	43
Middle ant. post. diameter	17	—	—	18	21
Greatest distal width	52	—	—	51	61
Width of distal trochlea	45	—	—	45	49
Distal ant. post. diameter	39	—	—	38	40
Ratio middle width/length	0.28	—	—	0.28	0.28

	No. of specimen				
Mc. IV	1	2	3	4	5
Median length	115	116	—	126	118
Proximal width	37	34	39	—	35
Proximal ant. post. diameter	44	41	43	—	42
Middle width	26	—	—	31	23
Middle ant. post. diameter	18	16	—	18	17
Greatest distal width	41	40	—	46	39
Width of distal trochlea	36	34	—	38	34
Distal ant. post. diameter	33	37	—	36	36
Ratio middle width/length	0.23	—	—	0.25	0.19

	No. of specimen				
Mc. V	1	2	3	4	5
Median length	71	71	70	82	—
Proximal width	18	20	17	22	18
Proximal ant. post. diameter	35	34	28	35	*ca.* 30
Middle width	17	18	15	19	—
Middle ant. post. diameter	12	13	12	15	—
Greatest distal width	28	28	26	32	29
Width of distal trochlea	25	25	21	31	24
Distal ant. post. diameter	25	24	23	25	23
Ratio middle width/length	0.24	0.25	0.21	0.23	—

right Mc. III, proximal portion, incomplete behind, 70–64K, B14; 4) right Mc. III, 70–64K, A17; and, 5) left Mc. III, 70–64K, A17.

Metacarpal IV, 5 specimens: 1) right Mc. IV, 70–64K, B14; 2) right Mc. IV, 70–64K, C14; 3) right Mc. IV, proximal portion, 57–64K; 4) left Mc. IV, damaged proximally, 70–64K, A17 (proximal half), and A16, 17 (distal half); and, 5) left Mc. IV, facet for Mc. V damaged, 70–64K, C14.

Metacarpal V, 5 specimens: 1) right Mc. V, 70–64K, B14; 2) left Mc. V, 70–64K, BB; 3) left Mc. V, 70–64K, C14; 4) left Mc. V, BB; and, 5) left Mc. V, portion at midshaft missing, 70–64K.

Of the Fort Ternan rhinoceros, *Paradiceros mukirii* (Hooijer, 1968b: 87), the only metacarpal available, Mc. III, is hardly distinguishable from its homologue in the Loperot *Chilotheridium pattersoni*, showing that metapodials alone are unreliable for specific (or generic) differentiation (see Hooijer, 1966: 153/54, and above, p. 340).

The metacarpals of the Loperot rhinoceros, as shown in Table 16, are not at all as short and wide at mid-shaft as are those of the Chinese *Chilotherium;* the measurements of a set of metacarpals of *Chilotherium anderssoni* as given by Ringström (1924: 58) give the following data for the ratio middle width/length: Mc. II, 0.34; Mc. III, 0.34, and Mc. IV, 0.28. We shall find the same difference in the metatarsals, of which more material of *Chilotherium* is available for comparison. Moreover, in *Chilotherium* the fifth metacarpal is reduced to the same extent as in *Diceros bicornis,* resembling a rounded sesamoid bone about 25 mm in diameter (Ringström, 1924: 57). In a Recent skeleton of this species in the Leiden Museum (Reg. No. 5738) the rudiment of Mc. V is 35 mm long and pointed distally; the proximal facet for the unciform is convex anteroposteriorly and measures 25 by 20 mm in diameter, that for Mc. IV is much smaller, 20 by 7 mm. The fifth metacarpal of the Loperot rhinoceros is small, but has a fully developed distal articular surface. Metacarpal V No. 1 doubtless belonged to the same individual as Mc. IV No. 1, and its median length is three-fifths that of Mc. IV. When the interproximal facets are placed on each other, the Mc. V is seen to be directed backward, its shaft forming an angle of 45° with that of Mc. IV. The proximal end of Mc. V is much extended anteroposteriorly, and bears a large convex facet for the unciform that projects much behind the shaft. The proximal medial facet for Mc. IV is placed along the posterior half of the unciform facet, at right angles to it, and measures only 20 by 10 mm against 30 by 17 mm for the unciform facet. The anterior projection of the proximal end of Mc. V is formed by a protuberance below the unciform facet, which brings the bone on a level with Mc. IV. The shaft of Mc. V, then, diverges distally from that of Mc. IV at an angle of 45°. The distal end of Mc. V with the trochlea is turned outward (away from Mc. IV): the rather asymmetrical trochlea has its median posterior ridge set at an angle of 35° to the anteroposterior long axis of the proximal end. One of the specimens of Mc. V (No. 4) is decidedly longer than the others; unfortunately this specimen cannot be associated with any other metacarpal. In its width/length ratio this bone is within the limits of the three shorter Mc. V Nos. 1–3. Undoubtedly the small Mc. V in the Loperot rhinoceros carried some phalanges, and some of these have been found.

There are very few associations among the metacarpals, but Mc. II No. 2 belonged to the same individual as Mc. III No. 4, and when these bones are held together with their interproximal facets on each other, the Mc. II is seen to be not parallel to Mc. III but directed backward from it at an angle of 15–20°. In the same way, Mc. IV was probably directed backward relative to Mc. III, but there are no associated bones to prove this. The backward divergence of the lateral metacarpals relative to the

TABLE 17. Measurements of metacarpal II in various genera (in mm)

	Brachypotherium	*Chilotherium*	*Diceratherium*	*Chilotheridium*	*Dicerorhinus*
Median length	125	106	122–123	123	136
Proximal width	52	(44)	43–46	41–42	35
Proximal ant. post. diameter	47	39	38–39	36–37	37
Middle width	45	36	34	33	34
Middle ant. post. diameter	25	13	13	15–17	18
Greatest distal width	50	37	33–34	37–43	47
Ratio middle width/length	0.36	0.34	0.28	0.27	0.25

median metacarpal is seen in *Chilotherium* as well (Ringström, 1924: 57). The metacarpals discussed above are presented in Plate 9, figures 4–6.

Of the metacarpals of the Chinese *Diceratherium* only Mc. II is known by entire specimens (Bohlin, 1937: 84). Bohlin gives the greatest length of two Mc. II of *Diceratherium tsaidamense* as 127–129 mm, which makes for a median length of 122 or 123 mm (the greatest length of Mc. II Nos. 1 and 2, both 123 mm in median length, is 129–130 mm). Therefore, the Loperot Mc. II are closely comparable in length to those of *D. tsaidamense*. Bohlin (1937: 85) gives also the dimensions of an Mc. II of *Chilotherium;* the median length of this specimen is only 106 mm by a middle width of 36 mm (Ringström, 1924: 58). In Table 17 the comparisons of Mc. II are extended to include *Brachypotherium heinzelini* Hooijer (1966: 147) from Rusinga, the Mc. II of which, again closely comparable to those of *Diceratherium tsaidamense* in median length, is much more massive at mid-shaft, surpassing *Chilotherium* in this respect. Unfortunately, there are as yet no entire specimens of Mc. II of the African *Aceratherium* or *Dicerorhinus,* but it is conceivable that these would not differ much in proportions from the Mc. II of *Dicerorhinus sumatrensis* (Hooijer, 1966: 166), the measurements of which are given in the last column of Table 17.

Although in the slenderness of the metacarpal the Loperot rhinoceros (*Chilotheridium*) is nearest to *Diceratherium* and *Dicerorhinus,* and far removed from *Chilotherium* and *Brachypotherium* in the peculiar contact of the radius with the cuneiform, not seen in the Recent genera, *Chilotheridium* agrees only with *Chilotherium* and *Diceratherium.* Whether the Chinese *Diceratherium* had an Mc. V is not known; in the American diceratheres it is represented only by a rudiment, as in the living species (Peterson, 1920: 445, pl. LXIII, fig. 1). A small Mc. V, about three-fifths the length of the adjoining Mc. IV, is found in various species of *Aceratherium* (see references in Hooijer, 1966: 153). In a typical *Aceratherium lemanense* of the Aquitanian (Roman, 1924: 52, figs. 23–24) Mc. V is 85 mm long, and Mc. IV 125 mm. In the old illustration of the manus of *Aceratherium tetradactylum* in Duvernoy (1853, pl. VII, fig. 1a), the fifth metacarpal has two phalanges assigned to it, one as wide as the metacarpal itself and squarish, the terminal phalanx narrow and pointed.

Isolated phalanges abound in the Loperot collection, but, with the exception of those of the pes marked 70–64K, B15, 16, they cannot be assigned to any metapodial in particular, and the only categories that can be made are phalanges I, II, and III of either a median or a lateral digit. Some few of the isolated phalanges are decidedly smaller than those of digits II or IV, and these are the ones that I regard as belonging to metacarpal V. The specimens are marked as follows: 1) phalanx I and II (associated), 57–64K; 2) phalanx I, 57–64K; 3) phalanx I, 70–64K; 4) phalanx I, 70–64K, BB; 5) phalanx II, 70–64K, D7; 6) phalanx I, 70–64K, A16; and, 7) phalanx I and II (associated), 70–64K. Measurements are given in Table 18.

TABLE 18. Measurements of phalanges of Mc. V from Loperot (in mm)

	No. of specimen						
	1	2	3	4	5	6	7
Phalanx I, length	19	19	21	21	19	18	18
Proximal width	25	24	23	23	21	21	20
Phalanx II, length	14	—	—	—	—	—	11
Proximal width	24	—	—	—	—	—	17

Among the rib fragments there is one, marked 70–64K, 65A, preserving the vertebral end and measuring 60 cm along the curve. The greatest width of the rib is *ca.* 50 mm. In the configuration of the head and tubercle it agrees best with the 5th to 7th rib, right side, in Recent skeletons.

The greater part of a left os coxae, marked 70–64K, A16, has the acetabulum and the shaft and most of the wing of the ilium. The specimen is broken into numerous small fragments that have been somewhat forced apart; the spaces between them are filled with plastic and plaster. The ilium is flattened to such an extent that the natural curvations of the gluteal and pelvic surfaces are almost gone. Pubis and ischium are broken off along the borders of the acetabulum, the diameter of which can be given only as 7–8 cm. The naturally three-sided shaft of the ilium is flattened, and measures about 9 cm in least width between the medial and the lateral borders. The concave lateral border of the ilium, up the tuber coxae, is relatively well preserved. Of the anterior border only the convex and thickened lateral half of the iliac crest is there. The tuber sacrale is preserved, but the concave medial border, from there on to the acetabulum, is rather damaged. The diameter of the ilium from acetabulum to the middle of the iliac crest is about 50 cm, and the greatest diameter of the wing from tuber coxae to tuber sacrale is about 55 cm. Both measurements are at least 5 cm too large, considering the filled-in cracks of the bone.

The following specimens of the femur are in the Loperot collection: 1) left femur, 70–64K; 2) left femur, incomplete distally, 70–64K; 3) right femur, immature shaft only, 70–64K, BB; 4) distal epiphysis of right femur, possibly belonging to No. 3, 70–64K; 5) distal end of left femur, 70–64K, A16; and, 6) proximal part of shaft of left femur, 70–64K, BB. Because of the crushing of the specimens very few measurements can be given (Table 19).

The most striking character of the Loperot femora is the small size of the third trochanter. This is shown in No. 1 (Pl. 10, fig. 1) as well as in Nos. 2, 3, and 6. The trochanter tertius is placed just at the middle of the height, is not more than 50 mm vertically at base, and does not project outward and forward for more than 20 mm. The femur of *Dicerorhinus leakeyi* from Rusinga (Hooijer, 1966: 169, pl. 13, fig. 1), 545 mm in greatest length, has a trochanter tertius in the right (unfigured)

TABLE 19. Measurements of femur from Loperot (in mm)

	No. of specimen				
	1	2	3	4	6
Greatest length	*ca.* 470	*ca.* 470	—	—	—
Proximal width	—	*ca.* 180	—	—	—
Width over third trochanter	90	90	75	—	*ca.* 80
Least width of shaft	—	*ca.* 60	55	—	—
Greatest distal width	*ca.* 120	—	—	110	—
Distal ant. post. diameter, medial side	145	—	—	155	—

TABLE 20. Measurements of patella from Loperot (in mm)

	No. of specimen		
	1	2	3
Length	89	89	72
Width	90	93	77

specimen that measures 100 mm high vertically at its base and projects outward and forward, extending the width across this process to 130 mm in contrast to the least width of the shaft below it of 75 mm. In Recent *D. sumatrensis* the third trochanter is likewise well developed; a femur not very much shorter than the Loperot specimens (greatest length 423 mm) has a width over the third trochanter of 115 mm by a least shaft width of 56 mm. The femora of *Chilotherium* do show a large and prominent third trochanter; Ringström (1924: 62, pl. IX, fig. 4) figures a specimen of *Chilotherium* from China only 430 mm in greatest length but with a width over the third trochanter of 128 mm, and a least width of shaft (estimated) of *ca.* 60 mm, while the *Chilotherium* femur from the Middle Siwaliks figured by Colbert (1935: 211, fig. 96) is likewise twice as wide over the third trochanter as its least shaft width.

It is in *Diceratherium tsaidamense* that we find a third trochanter on the femur that is just as small as that in the Loperot rhinoceros (Bohlin, 1937: 87, pl. IX, fig. 4); the width over the third trochanter is only one-half greater than the least shaft width. However, in the other Chinese *Diceratherium, D. palaeosinense,* the femur is nearer to that of *Chilotherium,* and its third trochanter is even somewhat larger than that in the latter genus (Bohlin, 1937: 87).

Of the patella there are three entire specimens in the Loperot collection as well as parts of five others. Number 1 is a right patella, 70–64K; No. 2 a right patella, 57–64K; No. 3 a left patella, 70–64K, E10;

TABLE 21. Measurements of tibia from Loperot (in mm)

	No. of specimen			
	1	2	3	4
Greatest length	320	*ca.* 360	—	—
Medial length	285	*ca.* 320	—	—
Proximal width	118	—	—	—
Middle width	45	*ca.* 55	—	—
Distal width	88	95	93	96
Distal ant. post. diameter	69	*ca.* 75	—	71

whereas the fragments come from 70–64K, D11 (surface), D12, and BB. The Loperot patellae are slightly wider than long (Table 20), the Rusinga patellae longer than wide (Hooijer, 1966: 170), but this difference is most probably insignificant. A patella of *Chilotherium anderssoni* (Ringström, 1924: 58) is 90 mm long and 87 mm wide; a specimen of *Diceratherium tsaidamense* (Bohlin, 1937: 88) measures 79 mm in length.

The following specimens of the tibia are in the Loperot collection: 1) right tibia, 70–64K, A16; 2) right tibia, damaged at both ends, 70–64K; 3) right tibia, proximal part flattened, 70–64, BB; 4) distal end of right tibia, 57–64K; 5) proximal end of shaft of left tibia, 70–64K, BB?; and, 6) lateral distal fragment of left tibia, 70–64K, E10. Measurements (Table 21) show that the most complete specimen is the smallest; yet it is longer than the tibia in *Chilotherium* by the same middle and distal widths (Ringström, 1924: 58 and 63; length 275–*ca.* 280 mm, middle width 47–48 mm, distal width 84–86 mm). The greatest length of the Middle Siwalik *Chilotherium* tibia is only 245 mm by a middle width of 43 mm (Colbert, 1935: 212).

The difference between proximal and distal width is less in *Chilotherium* (105 and 92 mm, respectively) than in *Diceratherium tsaidamense* (95 and 69 mm, respectively); in the latter species (measurements taken from Bohlin, 1937: 89) the proximal width is one-third greater than the distal width,

TABLE 22. Measurements of fibula from Loperot (in mm)

	No. of specimen					
	1	2	3	5	6	7
Length	290	*ca.* 300	255	—	—	—
Greatest proximal diameter	44	45	40	—	—	—
Mid-shaft diameters	21 × 14	—	19 × 14	—	—	—
Greatest distal diameter	48	—	41	45	38	38

as it is in Loperot tibia No. 1 (see Pl. 10, fig. 2).

Although there are seven specimens of the fibula in the Loperot collection none of these appears to belong to any of the tibiae. Nor is there any case of ankylosis of these bones, in contradistinction to what we find in *Chilotherium* (Ringström, 1924: 58). The specimens are as follows: 1) right fibula, 70–64K, 65C; 2) left fibula, 70–64K, 65C; 3) right fibula, 70–64K, B15, 16; 4) proximal portion of right fibula, 70–64K; 5) distal end of left fibula, 70–64K; 6) distal end of right fibula, 70–64K; and, 7) distal end of left fibula, 70–64K.

Bohlin (1937: 89) found a fibula of *Diceratherium tsaidamense* to be more rounded in section at mid-shaft (17 × 17 mm) than one of *Chilotherium* (24 × 14 mm). If this is a good distinguishing character the Loperot bones are closer to *Chilotherium* than to *Diceratherium* (Table 22). The best preserved Loperot fibula is figured in Plate 10, figure 3.

There is most of a right pes in the Loperot collection; all bones are marked 70–64K, B15, 16, and fit together so well that there

TABLE 23. Measurements of astragalus from Loperot (in mm)

	No. of specimen				
	1	2	3	4	5
Lateral height	65	71	—	72	63
Medial height	65	—	64	72	67
Total width	89	—	89	93	89
Ratio medial height/ total width	0.73	—	0.72	0.77	0.75
Trochlea width	70	75	67	76	71
Width of distal facets	73	—	—	79	73

is no doubt as to their belonging to a single individual. There are the astragalus, calcaneum, navicular, cuboid, ectocuneiform, and all three metatarsals with their three phalanges each except for the third phalanx of the fourth digit; there is even one sesamoid. Thus, the tarsals missing are the mesocuneiform and the entocuneiform, but of these there are several specimens of other individuals in the collection. The bones in this right pes (Pl. 10, fig. 4) are all No. 1 in their series.

The series of Loperot astragali is as follows: 1) right astragalus, 70–64K, B15, 16; 2) right astragalus, 70–64K; 3) right astragalus, 70–64K, A16, 17; 4) left astragalus, 70–64K, A18; and, 5) left astragalus, 70–64K, C12. Numbers 2–5 are incomplete distally. In addition there are seven fragments of right, and four fragments of left astragali; of these no measurements can be given.

In the Loperot astragali (Table 23) the ratio of medial height to total width (0.72–0.77) is intermediate between that in *Brachypotherium* (0.64–0.73) on the one hand and that in *Dicerorhinus* and *Aceratherium* (0.80–0.97) on the other (Hooijer, 1966: 148 and 173). The trochlea width is slightly greater than the medial height, as may be the case in *Dicerorhinus* and *Aceratherium* (Hooijer, 1966: 174); in *Brachypotherium* the difference between these two measurements is greater. Ringström (1924: 58) mentions that in a large number of entire *Chilotherium* astragali the three calcaneum facets are separate, whereas in the astragalus of *Diceratherium* (Ringström, 1924: 111) the medial and the distal

TABLE 24. Measurements of calcaneum from Loperot (in mm)

	No. of specimen									
	1	2	3	4	5	6	7	8	9	10
Lateral height	112	126	132	—	—	113	—	—	—	—
Greatest width	74	—	*ca.* 75	—	—	68	—	—	—	—
Ratio width/height	0.66	—	*ca.* 0.57	—	—	0.60	—	—	—	—
Ant. post. diam. cuboid facet	42	—	40	—	—	42	—	—	—	—
Transverse diam. of same	25	—	22	—	21	22	—	—	—	—
Greatest diameter of tuber	59	62	72	61	59	70	—	59	*ca.* 60	51
Transverse diam. of same	42	42	48	40	45	43	47	42	41	40

calcaneum facets are confluent. I do not consider this difference to be of any significance (cf. Hooijer, 1966: 174, footnote). As follows from Ringström's illustrations the astragalus of *Diceratherium* is relatively higher than that of *Chilotherium;* measurements are given only by Bohlin (1946: 228), and they show that in *Diceratherium palaeosinense* the medial height exceeds the trochlea width, whereas in *Chilotherium* the trochlea width slightly exceeds the medial height. Both conditions are found in *Dicerorhinus* and *Aceratherium.* The total width of the *Chilotherium* and *Diceratherium* astragali is not recorded, but I have measured an astragalus of the Middle Siwalik *Chilotherium* recorded by Colbert (1935: 212) and found the medial height to be 60 mm and the total width 77 mm, giving a ratio of 0.78, very much as in the Loperot astragali and in those of *Dicerorhinus* and *Aceratherium.* It is clear that not only are the Loperot astragali not as much shortened as in *Brachypotherium* but they are also not as long as in *Dicerorhinus* and *Acertherium* on the whole; they are nearer to *Chilotherium* than to *Diceratherium* in that the trochlea width slightly exceeds the medial height, admittedly a variable feature. The relative height of the Loperot astragali is more like that in *Chilotherium* than in *Diceratherium* (cf. Ringström, 1924: text-figs. 40 and 71–72), the approximate medial height/total width ratio as taken from the figures being 0.75 in the former against 0.81 in the latter.

The calcaneum is again well represented in the collection from Loperot, although in the majority of the specimens the transverse process, the sustentaculum tali, has broken off, and the proximal portion with the cuboid facet is missing in one-half the number of specimens (Nos. 4 and 7–10). In No. 1 the sustentaculum tali is preserved separately and there has been some loss of substance so that it does not fit on to the remainder of the calcaneum, but the associated astragalus fits the calcaneum so perfectly that the greatest width can nevertheless be taken. The series is as follows: 1) right calcaneum, 70–64K, B15, 16; 2) right calcaneum, 70–64K, BL; 3) right calcaneum, 70–64K, A18; 4) right calcaneum, 70–64K, A16, 17; 5) right calcaneum, 68–64K, tuber portion and proximal portion separate; 6) left calcaneum, 70–64K, BB; 7) left calcaneum, 70–64K, A16; 8) left calcaneum, 70–64K, E10; 9) left calcaneum, 70–64K, E12; and, 10) left calcaneum, 70–64K.

The calcaneum of *Chilotherium* is rather short and massive (Ringström, 1924: 58, pl. VIII, fig. 7), and has the three astragalar facets separate, whereas in *Diceratherium palaeosinense* the two lower astragalar facets are confluent. In the few Loperot calcanea in which this can be checked there is no fusion of the two lower facets for the astragalus (and neither is there any fusion of the two corresponding facets for the calcaneum on the astragali of Loperot). This feature is variable in *Diceratherium* (Bohlin, 1937: 89), and is evidently not a very reliable character. In the Loperot

TABLE 25. Measurements of navicular from Loperot (in mm)

	No. of specimen			
	1	2	3	4
Greatest anterior height	22	20	19	*ca.* 19
Total width	49	50	*ca.* 50	—
Ant. post. diameter	61	—	63	—

astragali there is no trace of a facet for the tibia behind and lateral to the upper facet for the astragalus; this facet is mentioned by Bohlin as most characteristic of *Chilotherium.* There remains a slight difference in relative height of the calcaneum: in the Loperot calcanea (Table 24) the ratio width/length is *ca.* 0.57–0.66, while in two *Chilotherium* calcanea this ratio is 0.67 and 0.74, but in four specimens of *Diceratherium tsaidamense* and *D. palaeosinense* the width/length ratio is 0.61–0.71 (cf. Bohlin, 1937: 90). The development of the tuber calcanei is too variable to be of any value for specific distinction. Thus, the Loperot calcanea are slightly longer than those in *Chilotherium,* but differ in not having a facet for the tibia; on the whole they are nearer to *Diceratherium* from China.

The navicular of the right pes from 70–64K, B15, 16, is not complete; it has a cut in the anterior face and lacks a portion posterolaterally. The other naviculars are not complete either. The series is: 1) right navicular, 70–64K, B15, 16; 2) right navicular, incomplete posteromedially, 57–64K; 3) right navicular, lacking the posterolateral portion, 70–64K; and, 4) left navicular, all borders except the lateral incomplete, 70–64K, C11. In *Chilotherium anderssoni* this bone (called Centrale) is wider behind than in front; it has an obtuse anteromedial angle (Bohlin, 1937: 90, fig. 155). That of *Diceratherium tsaidamense* (Bohlin, 1937: 90, fig. 156) is not as wide behind and is more nearly rectangular (it should be noted that in the upper [proximal] views of the navicular given by Bohlin [1937: figs. 155 and 156] the anterior side is above, and the medial to the right). Our Loperot naviculars (Table 25) are decidedly more rectangular than is that of *Chilotherium* (the width of the latter, given as 59 mm by Ringström [1924: 60], as Bohlin's figure 155 shows, is only 50 mm behind and 30 mm in front), and agree with the navicular in *Diceratherium tsaidamense* in that anteroposterior diameters are about one-fifth greater than the width (46 mm, and 38 mm); in *Chilotherium* the anteroposterior diameter is very nearly equal to the (posterior) width (52 mm, and 53 mm: Bohlin, 1937: 90).

There are two facets for the cuboid laterally on the navicular, a small and low anterior one, and a larger posterior facet that is not vertical but oblique, facing downward and outward. Between these two facets there is a nonarticular groove or fossa. We find, of course, the corresponding facets on the cuboid, the posterior facet facing upward and inward. The latter facet is bordered below by a nearly vertical facet that articulates with the ectocuneiform, for which there is also an anterior medial facet on the cuboid, placed below the anterior navicular facet and separated from it by a nonarticular groove. A third element that articulates with the medial surface of the cuboid is metatarsal III, situated, of course, below the ectocuneiform: there is a very small but yet distinct facet proximally and anteriorly on the lateral surface of metatarsal III, placed between the large proximal ectocuneiform facet and the anterior of the two lateral metatarsal IV facets. On the cuboid itself this little facet is practically indistinguishable; in the articulated pes, the cuboid facet on metatarsal III forms just a small downward extension of the cuboid facet on the ectocuneiform.

The relations of the contact facets between cuboid on the one hand, and navicular, ectocuneiform, and metatarsal III on the other, described in the preceding paragraph, exist in the Loperot rhinoceros and

Table 26. Measurements of cuboid from Loperot (in mm)

	No. of specimen			
	1	2	3	4
Anterior height	32	35	32	35
Anterior width	41	41	36	39
Greatest ant. post. diameter	60	63	—	56

in Recent *Diceros bicornis* and *Dicerorhinus* (Recent and fossil) as well. Admittedly the facet for the third metatarsal on the cuboid is hardly discernible, but when the associated metatarsal III is examined, we find the little cuboid facet, which truncates the edge between the ectocuneiform facet and the metatarsal IV facet on the middle metatarsal. In *Dicerorhinus sumatrensis* as well as in both *Dicerorhinus leakeyi* (Hooijer, 1966: pl. 13, fig. 3) and *Diceros bicornis* there is a contact between cuboid and metatarsal III as well as a contact between cuboid and ectocuneiform. I am mentioning this specially because Ringström (1924: 59) states that in the Recent forms there is a distinct facet on the cuboid (Tarsale IV & V) for metatarsal III, but none or only a very indistinct one for the ectocuneiform (Tarsale III). This is not in accord with my own observations; on the contrary, the ectocuneiform facets are much more clearly seen than the metatarsal III facets. This reverse situation is the one that obtains in *Chilotherium;* Ringström states that in that genus the ectocuneiform facet on the cuboid is large, whereas there is no metatarsal III facet on the cuboid. As far as I know this is the condition in the nonchilothere rhinoceroses as well, and no reliance can be placed on this for the distinction between genera.

Ringström (1924: 59) further mentions that in *Chilotherium* the two proximal facets for astragalus and calcaneum meet at an obtuse angle in the middle of the cuboid and are separated by a ridge, a condition elsewhere found only in *Teleoceras.* The obtuse angle and a smooth ridge (not a very sharp one) is seen in the Recent forms as well as in the Loperot cuboids. Of these cuboids we have four specimens, as follows: 1) right cuboid, 70–64K, B15, 16; 2) right cuboid, 70–64K, D11; 3) right cuboid, incomplete behind, 70–64K; and, 4) right cuboid, idem, 70–64K, A16, 17. The measurements are given in Table 26.

All four of the Loperot cuboids are wider than high anteriorly; this is, however, much more marked in the cuboid of *Chilotherium anderssoni,* with a height of 27 mm and a width of 46 mm (Ringström, 1924: 60). The great width in the Loperot cuboids, it seems, is caused by the presence of a lateral outgrowth of bone that is well separated from the proximal (calcaneum) and distal (metatarsal IV) facets. This outgrowth is a very distinctive feature of the Loperot specimens, and does not show in the cuboids of *Dicerorhinus* and *Aceratherium* (Hooijer, 1966: 176, pl. 13, figs. 5 and 6). In the cuboids of these two genera anterior height and width are either nearly equal, or the height exceeds the width. The cuboid of *Chilotherium* is seen to project laterally much beyond the fourth metatarsal (Ringström, 1924: pl. IX, fig. 3); it does not do so in the Loperot rhinoceros as the articulated pes (Pl. 10, fig. 4) shows. Unfortunately there is no cuboid of the Chinese *Diceratherium* on record.

Five ectocuneiforms are in the Loperot collection: 1) right ectocuneiform, 70–63K, B15, 16; 2) right ectocuneiform, 70–64K; 3) right ectocuneiform, 70–64K, A16; 4) left ectocuneiform, 70–64K, incomplete medially; and, 5) left ectocuneiform, 70–64K, D11. This bone, the cuboid facets of which have already been mentioned, has two medial proximal facets for metatarsal II, and a small, high-placed posterior medial facet for the mesocuneiform. The width anteriorly is very nearly twice the anterior height (Table 27), in which it contrasts with the ectocuneiform of *Chilotherium,* with a width (44 mm) nearly three times the height (15 mm) (Ringström, 1924: 60). The ectocuneiform of the Chinese *Diceratherium* has not been described.

Table 27. Measurements of ectocuneiform from Loperot (in mm)

	No. of specimen				
	1	2	3	4	5
Anterior height	21	23	21	21	23
Anterior width	42	44	43	—	45
Ant. post. diameter	44	48	46	43	48

Table 28. Measurements of mesocuneiform from Loperot (in mm)

	No. of specimen		
	1	2	3
Height	13	12	15
Width	21	20	22
Anteroposterior diameter	32	33	34

The mesocuneiform, a bone missing in the right pes from 70–64K, B15, 16, fits on to metatarsal II and has a correspondingly shaped distal facet, transversely convex anteriorly, elongated anteroposteriorly, ending narrow behind. There are three specimens: 1) right mesocuneiform, 68–64K; 2) right mesocuneiform, 70–64K, D11; and, 3) left mesocuneiform, 70–64K. The bone has a facet for the ectocuneiform proximally on the lateral side, and another one for the entocuneiform posteromedially. The latter facet is either limited to the proximal part and is then continuous with the entocuneiform facet on the navicular, or the facet on the mesocuneiform may extend along the full height and, in that case, it is continuous with both the facet on the navicular and that on metatarsal II. The first-mentioned condition is seen in mesocuneiforms 1 and 3, whereas the second condition obtains in mesocuneiform 2. The entocuneiform facets on mesocuneiforms 1 and 3 differ much in size. Although No. 3 is larger than No. 1, the entocuneiform facet is smaller in No. 3, in which it is confined to the proximal third of the height, than in No. 1, in which it occupies the proximal half of the height. The measurements (Table 28) indicate that the Loperot mesocuneiforms are not as wide relative to their height as the mesocuneiform of *Chilotherium,* which has a height of 12 mm by a width of 23 mm (Ringström, 1924: 60: Tarsale II). The difference is rather small.

Of the entocuneiform we have three specimens in the Loperot collection: 1) right entocuneiform, 70–64K; 2) left entocuneiform, 70–64K, D11; and, 3) left entocuneiform, 70–64K. The posterior tuberosity is missing in the last specimen. This bone, which is placed behind the mesocuneiform, has a large, nearly horizontal facet proximally for the navicular. At right angles to it (nearly vertical) is a small facet for the mesocuneiform, which may, or may not, be continuous with the facet for metatarsal II. Ringström (1924: 59) and Bohlin (1937: 90), who refer to the entocuneiform as the large sesamoid bone, mention these three facets in *Chilotherium anderssoni* and *Diceratherium tsaidamense* but do not mention whether the mesocuneiform and metatarsal II facets are separate or united. In Loperot No. 1 these two facets are continuous, but in Nos. 2 and 3 the facets for mesocuneiform and metatarsal II are separated by a nonarticular fossa (among the mesocuneiforms treated above the same variation occurs, No. 2 showing the entocuneiform facet to be continuous with that on metatarsal II, Nos. 1 and 3 showing these to be separate). The proximal facet for the navicular is the largest of all facets, the facet for the mesocuneiform is low and wide, and only in entocuneiform No. 1 it is continuous with the vertical, narrow facet for metatarsal II. In Table 29 I give the measurements of the Loperot specimens as well as those of *Chilotherium* and *Diceratherium* of China; the anteroposterior diameter (width in the table of Bohlin, 1937: 90) is taken above, thus not including the posterior hook-

TABLE 29. Measurements of entocuneiform from Loperot (in mm)

	No. of specimen				
	1	2	3	*Chilotherium*	*Diceratherium*
Height	42	43	31	50	40
Anteroposterior diameter	33	31	29	32	26
Width	18	17	14	15	18

shaped process, and the width (thickness in Bohlin's table) is transverse.

The variability in the Loperot series is so great as to make the intergeneric differences in size and proportions appear meaningless; lateral views of Loperot Nos. 1 and 2 are given in Plate 9, figures 1–2.

Apart from the right Mt. II–IV of the associated pes there are only two entire metatarsals, and, further, some proximal portions of metatarsals in the Loperot collection, as follows:

TABLE 30. Measurements of metatarsals II–IV from Loperot (in mm)

	No. of specimen			*Chilotherium*
Mt. II	1	2	3	Siwaliks
Median length	110	119	—	94
Proximal width	28	31	*ca.* 24	*ca.* 23
Proximal ant. post. diameter	39	—	—	*ca.* 33
Middle width	23	27	—	23
Middle ant. post. diameter	21	26	—	18
Greatest distal width	35	42	—	*ca.* 30
Width of distal trochlea	34	38	—	*ca.* 26
Distal ant. post. diameter	38	43	—	32
Ratio middle width/length	0.21	0.23		0.24

	No. of specimen	
Mt. III	1	
Median length	124	104
Proximal width	43	41
Proximal ant. post. diameter	40	*ca.* 40
Middle width	37	34
Middle ant. post. diameter	19	*ca.* 18
Greatest distal width	49	44
Width of distal trochlea	43	39
Distal ant. post. diameter	36	—
Ratio middle width/length	0.30	0.33

	No. of specimen				
Mt. IV	1	2	3	4	
Median length	109	107	—	—	87
Proximal width	39	39	41	44	*ca.* 37
Proximal ant. post. diameter	*ca.* 40	43	—	—	41
Middle width	23	22	—	—	24
Middle ant. post. diameter	21	21	—	—	16
Greatest distal width	33	34	—	—	—
Width of distal trochlea	33	35	—	—	*ca.* 28
Distal ant. post. diameter	36	35	—	—	—
Ratio middle width/length	0.21	0.21	—	—	0.28

TABLE 31. Measurements of metatarsal IV in various species (in mm)

	Chilotherium anderssoni	*Diceratherium palaeosinense*	*Diceratherium tsaidamense*	*Chilotheridium pattersoni*	*Dicerorhinus leakeyi*
Median length	89–90	83	—	107–109	166
Proximal width	36–37	34	29	39	44
Proximal ant. post. diameter	39	41	31	*ca.* 40–43	46
Middle width	25	29	20	22–23	29
Middle ant. post. diameter	—	—	—	21	—
Greatest distal width	—	—	—	33–34	38
Ratio middle width/length	0.28	0.35	—	0.21	0.18

Metatarsal II, 3 specimens: 1) right Mt. II, 70–64K, B15, 16; 2) right Mt. II, damaged proximally, 70–64K, BB; and, 3) right Mt. II, proximal portion only, 70–64K.

Metatarsal III, 1 specimen: 1) right Mt. III, 70–64K, B15, 16.

Metatarsal IV, 5 specimens: 1) right Mt. IV, damaged proximally, 70–64K, B15, 16; 2) left Mt. IV, 70–64K, 65B; 3) left Mt. IV, proximal portion, incomplete behind, 70–64K, D11; 4) left Mt. IV, proximal portion, incomplete medially, 70–64K, A16, 17; and, 5) right Mt. IV, proximal end, incomplete anteriorly and laterally, 70–64K, D12.

When the measurements and indices of the Loperot metatarsals are compared with those of *Paradiceros mukirii* of Fort Ternan (Hooijer, 1968b: 87), it is seen that the Loperot Mt. II is nearly identical with that of Fort Ternan, and that the single Loperot Mt. III is perfectly intermediate between the two Mt. III of *Paradiceros mukirii* on record. I found the same to be true for Mc. III. Yet the two forms are widely different cranially and dentally (above, p. 340).

The metatarsals from Loperot are longer and relatively more slender than those of *Chilotherium;* the measurements in the last column of Table 30 are those of the pes from the Middle Siwaliks recorded by Colbert (1935: 212) and taken by me on a visit to the American Museum of Natural History in New York in September 1965. The difference in relative length is greatest in metatarsal IV. The metatarsals of *Chilotherium anderssoni,* the length and middle width of which are given by Ringström (1924: 60), are very similar to those of the Middle Siwalik *Chilotherium:* Mt. II, 24–25 mm; Mt. III, 36–37 mm, and Mt. IV, 27–29 mm. As already mentioned above, the Loperot Mt. III has a small cuboid facet; according to Ringström (1924: 72) *Chilotherium* does not have a cuboid facet on its metatarsal III.

According to measurements recorded by Bohlin (1937: 91), metatarsal IV of the Chinese *Chilotherium* (two specimens) has a middle width/length ratio of 0.28, but that of *Diceratherium palaeosinense* is incomplete but seems to be much slenderer. The measurements are given in Table 31, together with those of the Loperot *Chilotheridium* and those of *Dicerorhinus leakeyi* (Hooijer, 1966: 179), which has the slenderest shaft of all Mt. IV recorded here.

Metatarsal IV of the Loperot species is nearest to *Dicerorhinus* in relative shaft width (in Recent *D. sumatrensis* the ratio is 0.20). The proximal facet (for the cuboid) is almost flat, as it is in *Chilotherium* as well as in *Diceratherium palaeosinense;* in *D. tsaidamense* (according to the incomplete specimen referred to this species by Bohlin, 1937: 91, figs. 159 and 160) the cuboid facet is raised laterally, and, further, the posterior of the two facets for metatarsal III is placed lower than the anterior. In the Loperot form the posterior metatarsal II facet is placed slightly lower than the anterior, as in fossil

Table 32. A. Distal ends of median metapodials from Loperot (in mm)

No.		Greatest width	Trochlea width	Ant. post. diameter
1	70–64K, E10	59	48	—
2	70–64K, B16	47	43	37
4	70–64K	*ca.* 54	48	—
5	70–64K	—	—	44
6	68–64K	—	43	—
7	70–64K, A16, 17	52	—	39
8	70–64K, D11	—	43	36
	B. Distal ends of lateral metapodials			
1	57–64K	42	37	37
3	70–64K	48	38	39
4	70–64K, BB	42	38	—
5	70–64K	46	35	36
6	70–64K	—	*ca.* 30	35
7	70–64K	45	38	—
8	57–64K	38	37	38
9	70–64K	—	32	36
10	70–64K	36	34	39
11	70–64K	40	35	—
12	70–64K, A16, 17	30	31	—
13	70–64K	41	35	41
14	70–64K	—	35	—
15	70–64K, D11	—	31	38
16	70-64K, D11	33	33	—

Table 33. Measurements of posterior phalanges from Loperot (in mm)

	Digit		
	II	III	IV
Phalanx I, length	30	31	30
Proximal width	34	45	32
Phalanx II, length	22	20	18
Proximal width	33	42	31
Phalanx III, length	34	31	—
Greatest diameter	45+	70	—

and Recent *Dicerorhinus.* In the articulated pes (70–64K, B15, 16) there is only a slight posterior divergence of the lateral metatarsals relative to the median; this is more marked in *Chilotherium* (Ringström, 1924: 60, pl. IX, fig. 3). What the position of the lateral metatarsals in the Chinese *Diceratherium* is I do not know.

As seen in the proximal views of Mt. IV of *D. tsaidamense* and *Chilotherium* (Bohlin, 1937: 91, figs. 159 and 161), the bone extends laterally beyond the cuboid facet, which is sharply marked off laterally. Such a collar of bone is also found lateral to the proximal cuboid facet in the Loperot specimens; it is particularly well developed in No. 3 (Pl. 9, fig. 3), which is from the left side as are Bohlin's specimens. In the articulated pes this bone prominence is placed just below the lateral bone development on the cuboid, serving for attachment of ligaments. We do not find such a development in Recent *Dicerorhinus,* and in *D. leakeyi* it is present, but placed posteriorly rather than laterally.

Measurements of a number of distal ends of median as well as of lateral metapodials are given below.

The phalanges I–III of digits II and III, and phalanges I and II of digit IV of the right pes (70–64K, B15, 16) are available, and their measurements are given in Table 33.

The measurements of the first phalanx of digit III agree very well with those in *Diceratherium tsaidamense* (length 29 mm, width 45 mm: Bohlin, 1937: 86), and those of the first phalanx of digit II are the same as those in this species as well as in *Chilotherium* (length 30 mm, width 34 mm: Bohlin, 1937: 85). In *Brachypotherium heinzelini* the proximal phalanges of these digits are shorter and wider (length 28 mm, proximal width 55 mm in digit III, and length 28 mm, proximal width 43 mm in a lateral digit: Hooijer, 1966: 149), while in *Dicerorhinus leakeyi* the proximal phalanges of these digits are much longer (length 40 mm, proximal width 55 mm in digit III, and length 37 mm, proximal width 40 mm in digit II: Hooijer, 1966: 180).

There remain a fair number of isolated phalanges in the Loperot collection; whether they belong to the fore or to the hind foot is impossible to tell. These specimens are enumerated below.

Of the third phalanges of the median digit only one specimen is entire (70–64K, BB?). It is 31 mm high and the greatest (transverse) diameter is 78 mm. Of the third phalanges of lateral digits there are only incomplete specimens varying in greatest length from 33 to 41 mm; the transverse diameter cannot be taken in any of the specimens. These terminal phalanges, which belong either to digit II or to digit IV, manus or pes, are as rough and porous, with many perforations on or near the distal border, as the end phalanges of digit III. I find this also in the living rhinoceroses. Ringström (1924: 63) found the terminal phalanx of a lateral digit of *Chilotherium* to be much less rough on the surface, with few, small perforations showing, and states that this is probably because the lateral digits diverge backward and are functional only to a very slight extent.

To round off the account of the remains of the Loperot rhinoceros I have to mention the sesamoid bones. One, a proximal sesamoid of the median digit, is associated with the right pes marked 70–64K, B15, 16; there are eleven more sesamoids of digit III (manus or pes), and there are twenty entire proximal sesamoids of lateral digits (II or IV), as listed below.

Table 34. Phalanx 1, median digit from Loperot (in mm)

No.		Length	Proximal width
1	70–64K, E10	29	50
2	70–64K	33	49
3	70–64K	30	46
4	70–64K	31	47
5	68–64K	31	48
6	70–64K, BB	29	51
7	68–64K	31	49
8	70–64K	33	46
9	70–64K, A16, 17	33	43
10	70–64K	31	41
11	70–64K, A16, 17	31	43
12	68–64K	31	45
13	57–64K	28	52
14	57–64K	30	49
15	70–64K	29	42
	Phalanx 2, median digit		
1	70–64K, E12	24	49
2	57–64K	20	52
3	70–64K, A16	19	53
4	70–64K	20	43
5	70–64K	21	43
6	70–64K	19	49
7	70–64K	21	*ca.* 53
8	70–64K, A16, 17	20	44
9	68–64K	21	*ca.* 55
10	70–64K, EM	21	48
11	57–64K	23	49

Phalanx 1, lateral digit

No.		Length	Proximal width
1	70–64K, E10	31	37
2	70–64K, A17	30	*ca.* 33
3	70–64K	32	38
4	70–64K, A16	32	34
5	57–64K	30	40
6	70–64K, BB	32	39
7	70–64K	32	36
8	70–64K, H10	30	33
9	70–64K	31	34
10	57–64K	29	34
11	70–64K	28	30
12	70–64K	33	41
13	70–64K	30	32
14	70–64K	30	35
15	70–64K	31	35
16	57–64K	28	37
17	70–64K, B14	30	33
18	70–64K, D11	30	37
19	70–64K	29	33

Table 34. (Continued)

Phalanx 2, lateral digit

1	70–64K	21	37
2	70–64K, D11	20	33
3	70–64K, D11	20	34
4	70–64K, D12	21	39
5	70–64K	22	32
6	70–64K, A16, 17	21	34
7	70–64K, A16, 17	18	37
8	70–64K	28	41
9	57–64K	19	35
10	70–64K, H11	20	37
11	70–64K	20	32
12	70–64K	20	34
13	57–64K	21	41
14	70–64K, B14	18	30
15	57–64K	19	41
16	68–64K	19	33
17	70–64K, A16, 17	21	34
18	70–64K	19	32

TABLE 35. Proximal sesamoids from Loperot (in mm)

No.		Length	Width
	median digit		
1	70–64K, B15, 16	38	19
2	57–64K	46	24
3	70–64K, A16	38	18
4	70–64K	45	22
5	57–64K	37	19
6	70–64K	43	22
7	70–64K	45	24
8	57–64K	48	22
9	70–64K	39	18
10	70–64K	41	21
11	70–64K	40	21
12	70–64K	41	22
	lateral digit		
1	70–64K, D11	35	18
2	70–64K	36	18
3	70–64K, A16	31	15
4	70–64K	35	19
5	70–64K	32	16
6	70–64K, D11	27	15
7	70–64K	34	17
8	70–64K	27	16
9	70–64K	33	17
10	70–64K	31	15
11	57–64K	34	18
12	70–64K	31	16
13	70–64K	34	17
14	70–64K	29	15
15	70–64K	29	14
16	70–64K	30	16
17	70–64K	32	15
18	70–64K	29	16
19	70–64K	32	17
20	70–64K	34	16

TABLE 36. Distinguishing characters of *Chilotherium*, *Chilotheridium*, and *Diceratherium*[1]

Chilotherium	Chilotheridium	Diceratherium
Hornless in both sexes	Small single nasal horn in both sexes	Small terminal nasal pair of horns (♂) or hornless (♀)
Frontals and parietals not pneumatized	Frontals and parietals pneumatized	Frontals and parietals pneumatized
Orbit placed very high, just below upper skull contour	Orbit not placed so very high	Orbit not placed so very high
Cranium and occiput not narrowed	Cranium and occiput rather narrow	Cranium and occiput rather narrow
Parietal crests widely separated	Parietal crests not widely separated	Parietal crests not widely separated
Inferior squamosal processes not united below	Inferior squamosal processes not united below	Inferior squamosal processes united below
Mandibular symphysis much widened anteriorly	Mandibular symphysis narrow, slightly expanded anteriorly	Mandibular symphysis narrow, not widening to the front
Lower C widely separated	Lower C not so widely separated	Lower C not so widely separated
Cheek teeth hypsodont	Cheek teeth hypsodont	Cheek teeth subhypsodont
Scapula high and slender	Scapula low and wide	Scapula low and wide
Humerus, radius, femur, and tibia shortened	Humerus, radius, femur, and tibia not much shortened	Humerus, radius, femur, and tibia not much shortened

TABLE 36. (Continued)

Ulna ankylosed with radius	Ulna not united with radius	Ulna not united with radius
Fibula ankylosed with tibia, and not rounded in mid-shaft section	Fibula not united with tibia, and not rounded in mid-shaft section	Fibula not united with tibia, and rounded in mid-shaft section
Femur with large third trochanter	Femur with small third trochanter	Femur (in *D. tsaidamense* only) with small third trochanter
Manus and pes tridactyl	Manus tetradactyl, pes tridactyl	Manus probably tridactyl, pes tridactyl
Astragalus moderately long	Astragalus moderately long	Astragalus longer
Calcaneum short, with facet for tibia behind upper facet for astragalus	Calcaneum somewhat longer, without tibia facet	Calcaneum somewhat longer, without tibia facet
Navicular wider behind than in front	Navicular nearly rectangular	Navicular nearly rectangular
Cuboid much wider than high, ridged between astragalus and calcaneum facets	Cuboid wider than high, with lateral bone prominence, smooth ridge between astragalus and calcaneum facets	(Cuboid unknown)
Metapodials short, lateral metapodials diverging posteriorly	Metapodials longer, lateral metapodials somewhat divergent posteriorly	Metapodials longer, but (in *D. palaeosinense*) Mt. IV rather short
Metatarsal III without facet for cuboid	Metatarsal III with small facet for cuboid	(Metatarsal III unknown)

[1] The three genera agree in the following characters: premaxillaries weak, no upper I, radius with cuneiform facet, and lunar without facet for the ulna.

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APPENDIX

Hypodigm of *Chilotheridium pattersoni*
Hooijer, gen. et sp. nov.

Field No. 70–64K, found by B. Patterson.

Skull, C9–10 (No. 1)
" , TYPE, B12 " 2
Right and left maxilla, 65B
Nasal bones, A″18
M^3, right, C9–10
Mandible (No. 1)
" , 65 " 2
" , B11 " 3
" , right ramus, part of left, 65C " 4
" , part of left ramus, A18 " 5
Lower canine, left, 65
" " , right, A16
Atlas, 65B
" , C1
Left scapula, A18
Right " , BB
" " , BL
" " , 65B
" " , BB
Right humerus, A18 (No. 1)
" " , BB " 2
" " , — " 3
" " , distal end, — " 4
Right radius, BB (No. 1)
Left " , A16 " 2
Right " , C14 " 3
Left " , C14 " 4
Right " , BB " 5
Left " , A17 " 6
Right " , BB " 7
" " , proximal end, — " 8
" " , " " , E10 " 9
" " , distal end, — " 10
" " , " " , B16 " 11
" " , " " , C12 " 13
Left " , " " , BB " 14
Right " , " " , — " 15
Left ulna, A17 (No. 1)
Right " , — " 2
" " , BB " 3
" " , BB " 4
Left " , C14 " 5
" " , C14 " 6
" " , BB " 7
Right " , A17 " 8
" " , distal end, BB " 9
Left " , " " , BB " 11
Right scaphoid, A16 (No. 1)
" " , — " 2
" " , BB " 3
" " , D11 " 4
" " , BB " 5
Left " , — " 6

Right lunar, — (No. 1)
" " , — " 2
" " , — " 3
Left " , — " 4
Right cuneiform, — (No. 3)
" " , — " 6
" " , A16 " 7
Left " , BB " 10
" " , — " 11
" " , — " 12
Pisiform, proximal end, —
" , " " , —
Right trapezoid, H11 (No. 1)
" " , — " 2
" " , — " 3
Left " , A16 " 5
" " , — " 7
Right magnum, BB (No. 1)
" " , B14 " 2
" " , — " 3
" " , — " 4
" " , — " 6
" " , — " 7
Left " , — " 8
" " , — " 9
" " , H11 " 10
Right unciform, A17 (No. 1)
" " , J7 " 3
" " , A16 " 4
" " , — " 5
" " , — " 8
Left " , A16 " 9
" " , E11 " 10
" " , — " 11
" " , D10 " 12
Right metacarpal II, B13 (No. 1)
" " " , proximal part, " 2
BB " 3
" " " , proximal part, — " 4
" " " , " " , — " 5
Left " " , " " , — " 7
" " " , " " , B14 " 8
" " " , " " , — " 9
Right metacarpal III, — (No. 1)
" " " , proximal part, B14 " 3
Left " " , A17 " 5
Right metacarpal IV, C14 (No. 2)
Left " " , A16, 17 " 4
" " " , C14 " 5
Left metacarpal V, BB (No. 2)
" " " , C14 " 3
" " " , BB " 4
" " " , mid-shaft missing, — " 5
Left metacarpal II (No. 2) and left metacarpal III (No. 4) of one individual, A17.
Right metacarpal IV (No. 1) and the right metacarpal V (No. 1) of one individual, B14.
Rib, 65A
Partial sacrum and part of left os innominatum, A16.

Left femur, — (No. 1)
" " , — " 2
Right " , shaft only, juv., BB " 3
" " , distal epiphysis, — " 4
Left " , distal end, A16 " 5
" " , proximal part of shaft, BB " 6
Right patella, — (No. 1)
Left " , E10 " 3
Parts of five others, D11, D12, BB
Right tibia, A16 (No. 1)
" " , incomplete at end, — " 2
" " , BB " 3
Left " , proximal end of shaft, BB " 5
" " , lateral distal fragment, E10 " 6
Right fibula, 65C (No. 1)
Left " , 65C " 2
Right " , B15, 16 " 3
" " , proximal part, — " 4
Left " , distal end, — " 5
Right " , " " , — " 6
Left " , " " , — " 7
Most of right pes of one individual, including astragalus (No. 1), calcaneum (No. 1), navicular (No. 1), cuboid (No. 1), ectocuneiform (No. 1), mt. II (No. 1), mt. III (No. 1), mt. IV (No. 1), all phalanges except IV 3, and one sesamoid (No. 1); B15, 16.
Right astragalus, incomplete distally, — (No. 2)
" " , " " , A16, 17 " 3
Left astragalus, incomplete distally, A18 " 4
" " , " " , C12 " 5
Right calcaneum, BL (No. 2)
" " , A18 " 3
" " , A16, 17 " 4
Left " , BB " 6
" " , A16 " 7
" " , E10 " 8
" " , E12 " 9
" " , — " 10
Right navicular, — (No. 3)
Left " , C11 " 4
Right cuboid, D11 (No. 2)
" " , — " 3
" " , A16, 17 " 4
Right ectocuneiform, — (No. 2)
" " , A16 " 3
Left " , D11 " 4
" " , D11 " 5
Right mesocuneiform, D11 (No. 2)
Left " , — " 3
Right entocuneiform, D11 (No. 2)
Left " , — " 3
Right metatarsal II, BB (No. 2)
" " " , proximal part, — " 3
Left metatarsal IV, 65B (No. 2)
" " " , proximal part, D11 " 3
" " " , " " ,
A16, 17 " 4
Right " " , proximal end, D12 " 5
Median metapodial, distal end, E10 (No. 1)
" " , " " , B16 " 2
" " , " " , — " 3
" " , " " , — " 4
" " , " " , — " 5
" " , " " , A16, 17 " 7
" " , " " , D11 " 8
Lateral metapodial, distal end, — (No. 2)
" " , " " , — " 3
" " , " " , BB " 4
" " , " " , — " 5
" " , " " , — " 6
" " , " " , — " 7
" " , " " , — " 9
" " , " " , — " 10
" " , " " , — " 11
" " , " " , A16, 17 " 12
" " , " " , — " 13
" " , " " , — " 14
" " , " " , D11 " 15
" " , " " , D11 " 16
Phalanx 1, median digit, E10 (No. 1)
" , " " , — " 2
" , " " , — " 3
" , " " , — " 4
" , " " , BB " 6
" , " " , — " 8
" , " " , A16, 17 " 9
" , " " , — " 10
" , " " , A16, 17 " 11
" , " " , — " 15
Phalanx 2, median digit, E12 (No. 1)
" , " " , A16 " 3
" , " " , — " 4
" , " " , — " 5
" , " " , — " 6
" , " " , — " 7
" , " " , A16, 17 " 8
" , " " , — " 10
Phalanx 3, median digit
Phalanx 1, lateral digit, E10 (No. 1)
" , " " , A17 " 2
" , " " , — " 3
" , " " , A16 " 4
" , " " , BB " 6
" , " " , — " 7
" , " " , H10 " 8
" , " " , — " 9
" , " " , — " 11
" , " " , — " 12
" , " " , — " 13
" , " " , — " 14
" , " " , — " 15
" , " " , B14 " 17
" , " " , D11 " 18
" , " " , — " 19

Phalanx 2, lateral digit, —	(No. 1)
" , " " , D11	" 2
" , " " , D11	" 3
" , " " , D12	" 4
" , " " , —	" 5
" , " " , A16, 17	" 6
" , " " , A16, 17	" 7
" , " " , —	" 8
" , " " , H11	" 10
" , " " , —	" 11
" , " " , —	" 12
" , " " , B14	" 14
" , " " , A16, 17	" 17
" , " " , —	" 18

Phalanx 3, lateral digit; several incomplete specimens.

Proximal sesamoid, median digit, B15, 16	(No. 1)
" " , " " , A16	" 3
" " , " " , —	" 4
" " , " " , —	" 6
" " , " " , —	" 7
" " , " " , —	" 9
" " , " " , —	" 10
" " , " " , —	" 11
" " , " " , —	" 12
Proximal sesamoid, lateral digit, D11	(No. 1)
" " , " " , —	" 2
" " , " " , A16	" 3
" " , " " , —	" 4
" " , " " , —	" 5
" " , " " , D11	" 6
" " , " " , —	" 7
" " , " " , —	" 8
" " , " " , —	" 9
" " , " " , —	" 10
" " , " " , —	" 12
" " , " " , —	" 13
" " , " " , —	" 14
" " , " " , —	" 15
" " , " " , —	" 16
" " , " " , —	" 17
" " , " " , —	" 18
" " , " " , —	" 19
" " , " " , —	" 20

At least eight individuals are represented. Numerous other bones were also collected from this quarry but are not listed since they do not add to knowledge of the species.

Field No. 57–64K, approximately 50 yards southeast of 70–64K and at same level. Found by B. Patterson. (This may be a continuation of the 70–64K quarry.)

Right radius, distal part	(No. 12)
Left ulna, distal part	(No. 10)
Right cuneiform	(No. 1)
" "	" 2
Left "	" 9
Pisiform, proximal end	
Left trapezoid	(No. 4)
" "	6
Right magnum	(No. 5)
Right unciform	(No. 2)
" "	" 6
	" 7
Right metacarpal II, proximal part	(No. 6)
Right metacarpal III, proximal part	(No. 2)
Right metacarpal IV, proximal part	(No. 3)
Right patella	(No. 2)
Right tibia, distal end	(No. 4)
Right navicular	(No. 2)
Lateral metapodial, distal end	(No. 1)
" " , " "	(No. 8)
Phalanx 1, median digit	(No. 13)
" , " "	" 14
Phalanx 2, median digit	(No. 2)
" , " "	" 11
Phalanx 1, lateral digit	(No. 5)
" , " "	" 10
" , " "	" 16
Phalanx 2, lateral digit	(No. 9)
" , " "	" 13
" , " "	" 15
Proximal sesamoid, median digit	(No. 2)
" " , " "	" 5
" " , " "	" 8
Proximal sesamoid, lateral digit	(No. 11)

At least two individuals are represented.

Field No. 64–64K, approximately 20 yards east of and at same level as 70–64K. Found by C. T. Williams.
Incomplete mandible.

Field No. 68–64K, as for 64–64K. Found by W. D. Sill.

Right cuneiform	(No. 4)
Right calcaneum	(No. 5)
Right mesocuneiform	(No. 1)
Median metapodial, distal end	(No. 6)
Phalanx 1, median digit	(No. 5)
" , " "	7
" , " "	12
Phalanx 2, median digit	(No. 9)
Phalanx 2, lateral digit	(No. 16)

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TYSON R. ROBERTS

HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS, U.S.A.

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