9.1

Lothagam Rhinocerotidae

John M. Harris and Meave G. Leakey

Three rhino species are represented in the Lothagam succession. *Brachypotherium lewisi* is the common rhino from the Nawata Formation, which in recent years has yielded additional dental and postcranial remains of this species. *Ceratotherium praecox* is present in both the Lower and Upper Nawata, and *Diceros bicornis* occurs in the Upper Nawata. Both *Ceratotherium* and *Diceros* occur in the Apak Member, but only *C. praecox* has been recovered from the Kaiyumung Member. Isotopic analysis of tooth enamel suggests that *B. lewisi* was primarily a browser and that *C. praecox* started exploiting C_4 grasses in the Upper Nawata.

The 1967 collection of rhinoceroses from Lothagam comprised a score of specimens, about half of which were believed to have derived from Lothagam Member 1B and the remainder from Member 1C. They were described by Hooijer and Patterson (1972), who recognized two new species—*Brachypotherium lewisi* and *Ceratotherium praecox*, the latter being better known from Kanapoi (Hooijer and Patterson 1972) and Langebaanweg (Hooijer 1972). The material was of interest in that it contained the largest and latest representative of the *Brachypotherium* lineage, and this evidently coexisted with the earliest known individual of *Ceratotherium*. These specimens were described in great detail by Hooijer and Patterson and need not be redescribed here. The only other Lothagam rhino specimen predating the 1990s collections is an incomplete upper molar of *Ceratotherium* (KNM-LT 396) that was recovered in 1972 and is now believed to be from surficial Holocene (Galana Boi) beds.

The Lothagam rhino hypodigm was more than doubled during the early 1990s by field parties from the National Museums of Kenya. During this project, the (sparse) field documentation of the 1967 specimens was reexamined and, where possible, the provenance of the earlier material was confirmed or refined. The new information helped clarify the distribution of *Brachypotherium*, now known to be mainly restricted to the Nawata Formation, and documented the presence of a third genus—*Diceros*. Teeth of the three genera may be distinguished by the criteria provided in table 9.1.

Using the criteria from table 9.1, it now appears evident that three of Hooijer and Patterson's original identifications were erroneous. Two incomplete lower dentitions, LT 82 from the Upper Nawata and LT 83 from the Apak Member, are now seen to belong to *Ceratotherium praecox*, whereas LT 84, an immature mandible from the Upper Nawata, is better identified as *Diceros*.

Systematic Description

Brachypotherium lewisi
Hooijer and Patterson, 1972
(Figures 9.1–9.4; tables 9.2, 9.3)

Diagnosis

Size very large: condylobasal length of skull over 70 cm, antero-transverse diameters of M^{1-2} some 90 mm as opposed to 70 mm in *B. brachypus* (Lartet) or *B. snowi* (Fourtau) from Miocene of Europe and Egypt, respectively. Nasals hornless, slender, not very long, deepest point of nasomaxillary notch above P^4; anterior border of orbit above front of M^2, frontals flat and hornless, inferior squamosal processes united below subaural

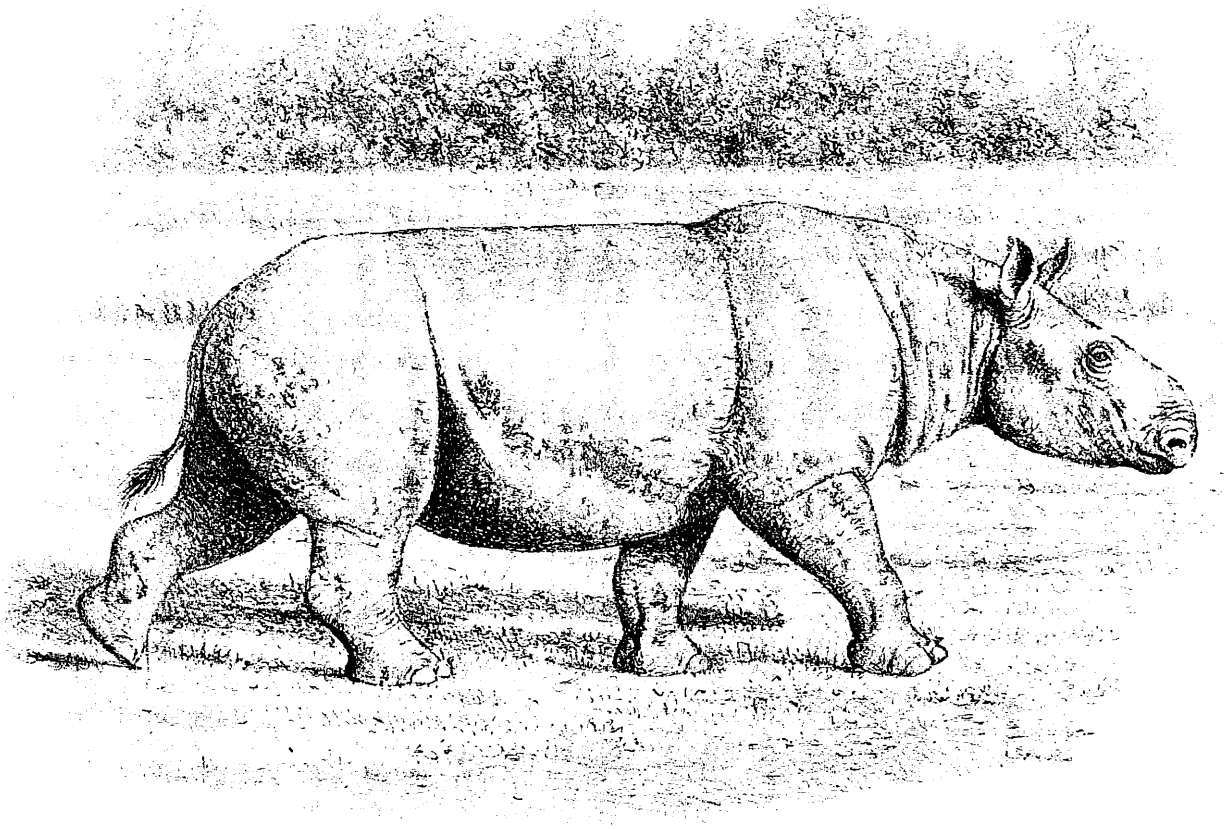

Figure 9.1 Restoration of *Brachypotherium lewisi* by Mauricio Antón. Shoulder height = 150 cm.

channel. Upper incisors very large, upper cheek teeth brachyodont, ectoloph flattened behind paracone style, antecrochet moderate, protocone constriction slight, external cingula often present. Lower canines present, brachyodont cheek teeth with external groove between anterior and posterior lophids usually flattened out, external cingula often developed. Trochanter tertius of femur strongly developed.

Holotype

KNM-LT 88, cranium (Lt. and Rt. P^2–M^3) from the Lower Nawata.

Lothagam Material

- *Lower Nawata:* holotype; 80, Rt. P^3; 87, Rt. P^1; 94, crushed cranium (Lt. M^2, Lt. I^1, Rt. M^2, partial M^1 and M^3); 81, partial lower molar; 86, lower molar fragments; 93, Rt. M^3; 99, Lt. and Rt. P^2; 100, partial Lt. P^2 and P^3; 22874, Rt. M^2; 22961, Rt. P^2; 23800, Lt. Mc III; 23960, lower or upper I^1, I^2 and M fragments; 23963, Lt. P^2; 23964, Lt. Mt II. Lt. Mt IV; 23965, upper molar fragments; 24290, Lt. M^3, tooth fra ments; 26280, broken Lt. $M_{?2}$; 26286, Rt. Mc 26300, distal Lt. Mc II or IV; 28735, Lt. and Rt. low molar fragments.
- *Upper Nawata:* 85, partial Lt. I^1; 91, Lt. mandil (P_1–M_3); partial atlas; 95, Lt. juvenile mandible fra ment and symphysis (P_2 and M_2, fragment M 22872, Lt. upper P^2; 23962, Rt. P_1; 23967, Rt. 1 26279, partial Lt. mandible (M_3); 26281, proximal I Mt III; 26301, sixth cervical vertebra; 26312, Lt. M IV.
- *Apak Member:* 90, mandible (Rt. P_2–M_3, Lt. P_2–M 97, distal Lt. femur including third trochanter.
- *Horizon indet.:* 12686, Lt. humerus

Brachypotherium species comprise a group of large ar heavy-bodied rhinoceroses characterized by the pre ence of upper tusks (I^1) and short limbs and feet (Han ilton 1973); they exploited riparian and forested hab tats (Guérin 1980). *Brachypotherium lewisi* was a lar hornless species that constituted the termination of t *Brachypotherium* lineage, outlasting *B. goldfussi* fro the Pontian of Europe (Hooijer 1978). Initially reco nized from Lothagam, the species is also represented the Kenyan localities of Ngorora (Hooijer 1971) ar

Mpesida (Hooijer 1973), as well as at Sahabi in Libya (Hooijer 1978). Twenty new specimens have been recovered from Lothagam by the National Museums of Kenya expeditions, mostly isolated teeth and limb bones (figure 9.2)—all of which were from the Nawata Formation and most from its lower member. The 1967 expedition, however, collected two specimens (LT 90, 97) that appear to be from the Apak Member.

A posterior cervical vertebra (C6?), LT 26301, lacks all but one of the articular processes but is identified as *Brachypotherium* because of its large size and slight differences from cervical vertebrae of the two extant species (such as two small protruding rugosities on the ventral surface). The articular facets for the ribs are relatively large. The maximum ventral anteroposterior length of 105 mm and the dorsal length of 88 mm are larger than in either extant species. Both anterior and posterior articular facets of the centrum are almost circular in profile; mediolateral and dorsoventral measurements of the strongly concave anterior articular surface are 81 by 80 mm; those for the strongly convex posterior facet are 80 by 75 mm.

Figure 9.2 *Brachypotherium lewisi* premolars and metacarpals: top tooth = KNM-LT 22961, Rt. P^2; bottom tooth = KNM-LT 80, Rt. P^3. Left metacarpal = KNM-LT 26286, Rt. metacarpal II; center metacarpal = KNM-LT 23800, Lt. metacarpal III, right metacarpal = KNM-LT 26312, Lt. metacarpal IV; all three quarters of their natural size. Top row metacarpals = lateral view; bottom row = medial view.

A weathered left humerus attributable to *Brachypotherium*, LT 12686, lacks the lateral portion of the distal epiphysis, so that details of the relative proportions of the lateral epicondyle and radial articular surface have been lost. Bone is also lost proximally from the greater tuberosity. As in both extant rhino species, the medial epicondyle is only lightly developed. The proximal portion of the diaphysis is more strongly compressed than in the modern species. The greater tuberosity is rugose but rather less so than is typical of *Ceratotherium simum*. There is a sharp waisting of the shaft distal to the tuberosity that is evident in both anterior and posterior view.

Brachypotherium metacarpals of lengths comparable to those of modern species are proportionately stouter and more robust. The second and fourth metacarpals are distinctly "waisted" in the mid-portion of the diaphysis, a feature also present but less pronounced in Mc III (figure 9.3).

Metacarpal II of *Brachypotherium* is more symmetrical and has relatively broader epiphyses and a more waisted diaphysis than is characteristic of the modern

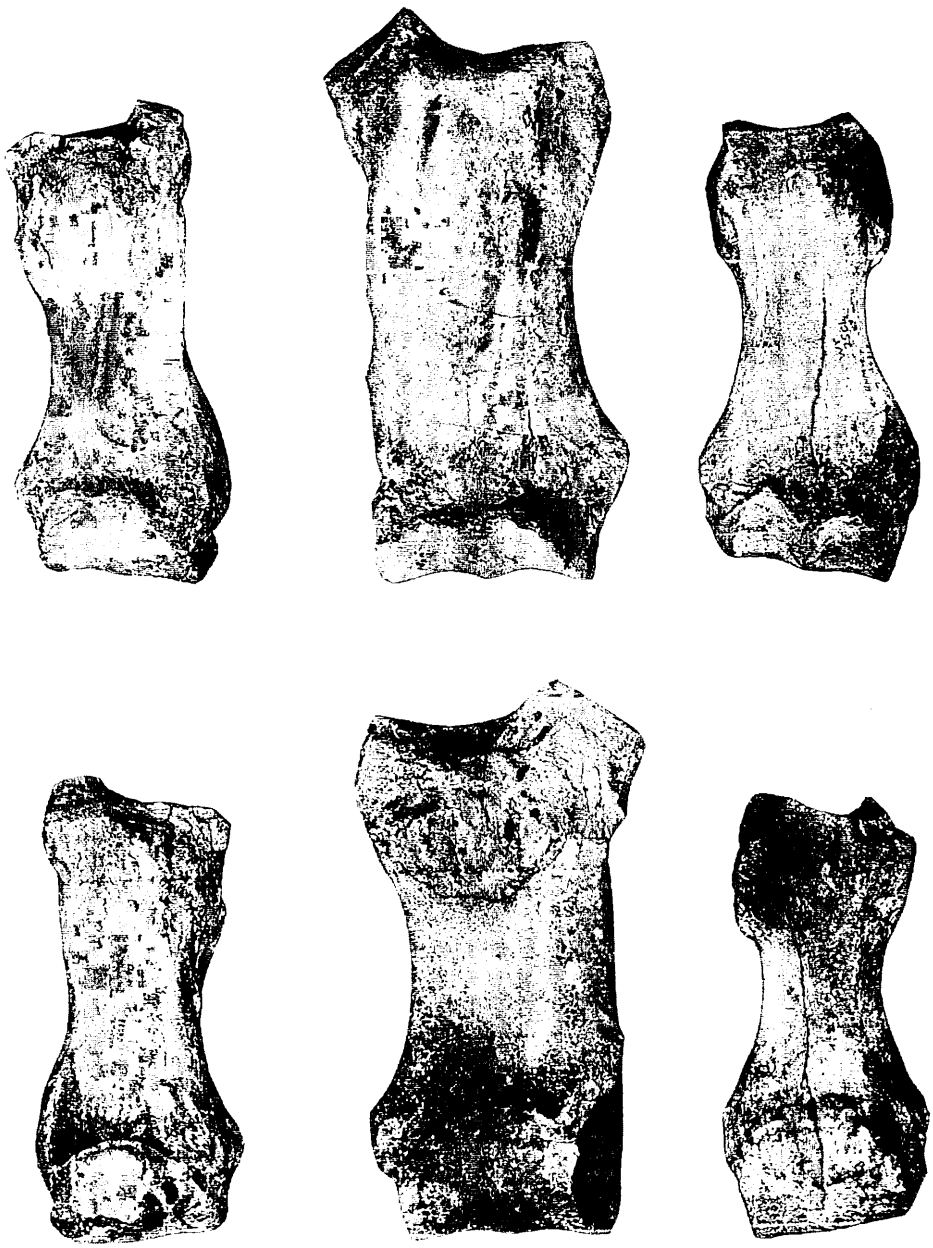

Figure 9.3 *Brachypotherium lewisi* metacarpals: left = KNM-LT 26286, Rt. metacarpal II; center = KNM-LT 23800, Lt. metacarpal III; right = KNM-LT 26312, Lt. metacarpal IV; all half of their natural size. Top row = posterior view; bottom row = anterior view.

species. Laterally, as in both modern species, the narrow facet for articulation with Mc III extends the entire length of the lateral surface. Proximally, in contrast to the modern species, the trapezoid facet is large and almost square, being almost as wide mediolaterally as it is deep anteroposteriorly.

Metacarpal III has a very anteroposteriorly compressed diaphysis but with stout carinate ridges that extend distally from the magnum facet along the lateral and medial margins to enclose a deeply excavated proximal hollow. The medial of these two ridges is the better developed. Proximally, the posterior portion of the large magnum facet is convex anteroposteriorly, whereas the anterior portion, although broken, appears to have been concave. Laterally, there is a clearly defined anterior facet for articulation with the unciform, and this is proportionately larger and more steeply angled than the concave facet of the extant species. The broken, proportionately small facet for articulation with Mc IV is located at the anterolateral corner of the magnum facet. There is no posterior facet for articulation with Mc IV, in contrast to the large circular posterior facets present for this purpose in both extant species. Medially, the small triangular-shaped anteromedial facet for articulation with Mc II is proportionately larger than in *Diceros* and comparable in relative size to that of *C. simum*.

Metacarpal IV has a distal epiphysis that is stouter and more symmetrical than in both extant species. The proximal epiphysis is also more symmetrical, with the proximal triangular facet for the trapezoid being much broader mediolaterally. Medially, the narrow facet for articulation with Mc III extends almost the length of the medial surface, although its posterior extent cannot be determined because of bone damage. There is no posterior facet for the third metacarpal, in contrast to both extant species where this facet is large and circular. There is a small, narrow, obliquely oriented facet for articulation with the magnum between the larger trapezoid facet and that for Mc III.

The metatarsals of *Brachypotherium* (figure 9.4) are much broader than those of *Ceratotherium simum*. Metatarsal II has a waisted diaphysis (though it is less pronounced than in the metacarpals), whereas Mt IV narrows proximally. The preserved portion of the proximal shaft of Mt III is markedly flattened from back to front and broadens distally. The proximal epiphyses of all three metatarsals are of comparable size to the extant species, although, except for Mt IV, they are mediolaterally broader, but the preserved distal epiphyses are much stouter.

Metatarsal II has very robust epiphyses and an elongated rugosity on the posterior face of the diaphysis. The proximal facets for the middle and external cuneiform are broader than in either extant species, and that for the internal cuneiform is circular and is angled obliquely to the diaphysis axis rather than parallel to it as in *D. bicornis* and *C. simum*. There is a large posterior internal cuneiform facet as in *Ceratotherium* (this facet is absent in *Diceros*).

Metatarsal III is represented only by its proximal portion, which is wider mediolaterally but shallower back to front than in *C. simum* and has a distinctly L-shaped proximal internal cuneiform facet. Laterally, there is only a very small anterior Mt IV facet (in contrast to both modern species); the posterior Mt IV facet, although present and large in the modern species, is absent. Medially, the posterior Mt II facet is absent. Because bone is missing in the area of the anterior Mt II facet, it is not possible to assess whether this facet was present in Mt III; however there is no corresponding facet on Mt II.

Metatarsal IV has a distal epiphysis that is larger than that of the extant species, and the proximal and distal epiphyses are in the plane of the axis of the shaft, which lacks torsion. In both modern species there is some torsion, so that the two epiphyses are offset. Proximally, the cuboid facet profile is broader posteriorly than in *C. simum* and extends to the posterior edge of the epiphysis. The medial margin is almost at a right angle to the dorsal margin, whereas in the modern species the angle between the two margins is closer to 45°. In contrast, the lateral margin meets the anterior margin at a right angle in the modern species but is closer to 45° in the fossil. Laterally, the anterior facet for Mt III is more elongated back to front than that of the modern species, and there is no posterior Mt III facet, although this facet is well developed in both modern species.

In general, the *Brachypotherium* metapodials are broader and without the tightly fitting joints (characteristic of the modern species) that occur both between the adjoining proximal epiphyses and between the proximal epiphyses and the podials.

A few *Brachypotherium* lower teeth were retrieved from the Namurungule Formation; these were evidently of similar size to *B. heinzeli* and thus smaller than those of *B. lewisi* (Nakaya et al. 1984).

Ceratotherium praecox Hooijer and Patterson, 1972

(Tables 9.4, 9.5)

Diagnosis

Skull differing from *C. simum* (Burchell) in greater concavity of skull roof, cranium less extended posteriorly, occiput more vertically inclined; cheek teeth not as hypsodont, lophs and lophids not markedly oblique, anterointernal corners of upper teeth not rounded, no

Figure 9.4 *Brachypotherium lewisi* metatarsals: left = KNM-LT 23964A, Lt. metatarsal II; center = KNM-LT 26281, Rt. metatarsal III; right = KNM-LT 26964B, Lt. metatarsal IV; all half natural size. Top row = posterior view; center row = lateral view; bottom row = anterior view.

medifossettes in P^2–M^2 and no fossettids in lower cheek teeth, internal cingula in upper cheek teeth variable.

Lothagam Material

- *Lower Nawata:* 89, Rt. M^2; 26289, Rt. ulna.
- *Upper Nawata:* 82, Rt. M_1; 23772, Lt. P^2 or P^3, and tooth fragments; 23970, partial cranium; 23972, Lt. astragalus; 26278, Rt. $M_{1?2}$.
- *Apak Member:* 83, P_{2-4} and partial molars; 23966, Lt. calcaneum; 26296, sixth cervical vertebra.
- *Kaiyumung Member:* 23968, Lt. mandible fragment (P_2); 23969, Rt. maxilla (P^{1-2}); 26283, Rt. mandible (P_2–M_3); 26284, proximal phalanx III.
- *Galana Boi:* 96, Rt. P^4.

Nine new white rhino specimens were added to the Lothagam hypodigm, most from the upper part of the sequence. The record of *Ceratotherium* from the Lower Nawata is sparse, comprising an ulna collected recently and an upper molar collected in 1967, but the provenance data appear secure. According to Hooijer (1972), *C. praecox* is directly ancestral to the extant white rhino but differs from it cranially by having a more concave dorsal surface, a less extended posterior portion, a less posteriorly inclined occiput, and a less thick nuchal crest. The sole cranial specimen from Lothagam, LT 23970, derives from the Upper Nawata. The most readily recognizable parts constitute portions of the left and right zygomatic arches, the nasal boss, and fragments of the rear portion of the cranial vault. The zygomatic fragments are comparable in size to equivalent portions of an extant white rhino skull (OM 2184) from the osteology collections of the National Museums of Kenya. The nasal boss is closely comparable in shape but a little larger than that of the same modern white rhino specimen and appreciably larger than that of *Diceros bicornis* fossil cranium LT 23971 from the Apak Member. The occipital fragment includes much of the right and part of the left nuchal crest. In contrast to that of the extant white rhino, the nuchal crest of the fossil specimen extends laterally rather than posterolaterally. The upper part of the occiput also appears steeply angled backward as in the extant *C. simum* and in contrast to both fossil and extant examples of *D. bicornis*. However, more complete white rhino crania from Kanapoi and Kosia (and hence about 4 Ma in age) have occiputs that are less steeply angled than in extant crania. In addition, the dorsal surface of the rear portion of the cranial vault is almost horizontal, whereas that of fossil and recent examples of the black rhino rise steeply upward in front of the nuchal crest. The mandibular symphysis is narrower than in *C. simum* and more similar to that of *Diceros*. The cheek teeth are more hypsodont than those of *D. bicornis* but decidedly less so than those of *C. simum*. The transverse lophs of the upper cheek teeth are less backwardly inclined in *C. praecox* than in *C. simum*, and present a superficial resemblance to those of *Diceros*.

Several postcranial elements attributable to *Ceratotherium praecox* have been recovered. A posterior cervical vertebra, LT 26296, is almost complete and very similar to the C6 of *C. simum*. Its maximum ventral anteroposterior length is 93 mm, and its dorsal length is approximately 82 mm. Both articular surfaces of the centrum are almost circular in profile; dorsoventral and mediolateral measurements of the strongly concave anterior articular surface are 66 by 64 mm whereas those of the strongly convex posterior surface are 63 by 62 mm.

A right ulna, LT 26289, is almost indistinguishable from that of the extant *C. simum* except for its larger size and a larger degree of retroflexion of the diaphysis that gives it a more strongly concave curvature of the posterior surface. A left astragalus (LT 23972), a left calcaneum (LT 23966), and a proximal phalanx (LT 26284) are all indistinguishable morphologically from those of the extant species.

Postcranially, *C. simum* is larger than *D. bicornis* and has more massive metapodials, but otherwise the limb elements of the two extant species are remarkably similar; the abundant postcranial elements of *C. praecox* from Langebaanweg are rather larger than those of extant white rhinos (Hooijer 1972), but *C. praecox* foot elements from Lothagam are comparable in size to those of *C. simum*, and the limb bones fall within the range of variation of the living species.

Diceros bicornis (Linnaeus)

(Figure 9.5; table 9.6)

Lothagam Material

- *Upper Nawata:* 84, Rt. juvenile mandible (dP_1–M_1); 23665, Rt. M^1; 23961, Lt. $P^{2 \text{ or } 3}$; 26285, /M, Lt. P_3.
- *Apak Member:* 23971, partial cranium, Rt. M^{2-3}, Lt. M^3; 28563, cranium; 28762, Lt. M_1.

The earliest representatives of the genus *Diceros* are *D. pachygnathus* (Wagner) from the Pontian of Samos and Maragha and *D. douariensis* Guérin from the Late Miocene of Tunisia (Hooijer 1978). However, the presence of teeth indistinguishable from those of the extant *D. bicornis* in the Upper Nawata appear to represent the oldest specimens of the extant species. As previously observed by Guérin (1987), remains of the black rhinoceros have now been recovered from numerous localities of Late Pliocene and Pleistocene age in Africa

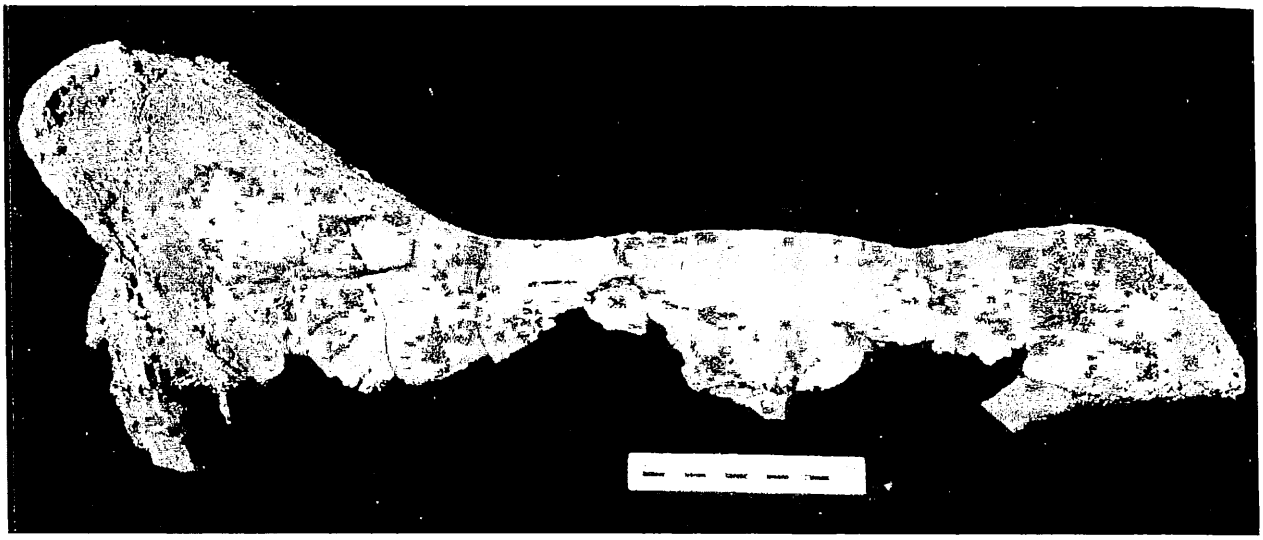

Figure 9.5 *Diceros bicornis* partial cranium KNM-LT 23971, right lateral view.

but not in sufficient quantities to document major anatomical (and hence taxonomic) differences from the extant species. The Lothagam hypodigm comprises two partial crania (KNM-LT 23971 and 28563), an immature mandible (LT 84), and several isolated teeth. The more complete of the two partial crania, LT 28563, is comparable in size to that of an extant black rhino, but it is missing much of the surface bone, which thus precludes a detailed description. The specimen is evidently an elderly adult because the associated teeth are worn almost to their roots. The rear of the cranial vault seems to rise more steeply than in extant black rhinos, but this may be because much of the surface bone is missing from the anterior part of the cranium. The nuchal fossa is more deeply excavated than in extant specimens; the paroccipital process is stouter, but the occiput is similarly vertically oriented. The other specimen, LT 23971, preserves the dorsal surface of the cranium from the nasals to the nuchal crest. It is identical in shape to extant black rhinos but is larger and with proportionately stouter nasals; however, its associated teeth are of identical size to extant representatives. In contrast, the crania of *Ceratotherium* are longer, and the cranial vault rises less abruptly anterior to the nuchal crest. The teeth appear identical in both size and morphology to those of extant representatives. Despite their larger size, it seems prudent to interpret the Lothagam crania as belonging to the extant species until such time that more complete material provides support for taxonomic differentiation.

Discussion

The lack of detailed locality information for the original (1967) collection is unfortunate because most of the better specimens were collected at that time. The provenance of the more recently collected material is, however, well substantiated. Of these, all of the recently collected *Brachypotherium* specimens are restricted to the Nawata Formation, whereas *Diceros* specimens hail from the Upper Nawata and Apak, and *Ceratotherium* comes from the Upper Nawata and Kaiyumung Members. Thus the change in the Lothagam rhino assemblage from that characteristic of the Miocene to essentially modern forms took place in the upper part of the Nawata Formation. Thenius (1955) proposed that *Ceratotherium* split off from *Diceros* stock somewhere in the Pliocene. Hooijer (1972) regarded *C. praecox* as little removed from the point of divergence. The presence of both the earliest representatives of *C. praecox* and *Diceros* in the Upper Nawata extends the timing of the dichotomy back into the Late Miocene.

The isotopic data are interesting in this respect. Some samples were taken from accessioned and identified specimens and some from rhino tooth fragments recovered at the outcrop. The *Brachypotherium* teeth sampled from the Nawata Formation (LT 86, 95, 100) were evidently C_3 browsers, but the sole *Brachypotherium* tooth from the Apak Member (LT 90) indicated a diet of mixed C_3 and C_4 vegetation. In contrast, a *Ceratotherium* individual from the Lower Nawata (LT 89) evidently browsed on C_3 vegetation, but others from the Upper Nawata (LT 23772) and Kaiyumung Members (LT 26283) were C_4 grazers. Of the unidentified rhino enamel fragments, those from the Lower Nawata were all C_3 browsers, whereas one sample from the Apak Member was from a C_3 browser (perhaps *Diceros?*) but five others were C_4 grazers (perhaps *Ceratotherium?*). The implications appear to be that there was a distinct ecological change between the lower and upper mem-

bers of the Nawata Formation and that the diet of the white rhinos reflected this change.

Isotopic analyses of mammalian enamel from the Samburu Hills indicate that C_4 vegetation was present at the time that sequence accumulated and that some of the rhinoceroses were exploiting it. However, none of the rhino genera reported by Nakaya (1994) from the Samburu Hills assemblages (*Paradiceros, Chilotheridium, Kenyatherium,* iranotheriine) are present in the Lothagam sequence. It seems entirely possible, therefore, that at the Samburu Hills C_4 vegetation formed a significant portion of the biomass somewhat earlier than at Lothagam and was exploited there by taxa that are not represented in the Lothagam assemblages.

Acknowledgments

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Table Abbreviations

ant = anterior
ap = anteroposterior length
dist = distal
dt = maximum depth
dv = dorsoventral depth
E = estimated measurement
lat = lateral
Lr = lower
Lt = left
lt = length
med = medial
post = posterior
prox = proximal
Rt = right
tc = tuber calcis
tr = transverse width
Ur = upper

TABLE 9.1 Distinguishing Features of the Lothagam Rhino Genera

Brachypotherium	*Diceros*	*Ceratotherium*
Teeth large and brachyodont	Teeth smaller and brachyodont	Teeth hypsodont
Thick enamel	Enamel of intermediate thickness	Thin enamel
Large upper, small lower incisors	No incisors	Moderate upper incisors
Labial edge of upper tooth oriented at wide angle to tooth row axis	Labial edge of upper teeth at lesser angle to tooth row axis	Labial edge of upper teeth at lesser angle to tooth row axis
Ectoloph very wide	Ectoloph narrow	Ectoloph narrow
Paracone style present	Paracone style present	No paracone style
Metacone style absent	Metacone style present	No metacone style
Wear surface at metacone forms ridge (consistent with transverse chewing)	Wear surface at metacone forms ridge	No metacone ridge (consistent with sagittal chewing)
Protolophs and metalophs transversely oriented	Protolophs and metalophs more diagonally orientated	Protolophs and metalophs most posteriorly orientated
Ectoloph behind metacone not reflected buccally	Ectoloph behind metacone reflected buccally	Ectoloph behind metacone not reflected buccally
Crotchet weak, never meeting protoloph	Crotchet stronger	Crotchet strong and crista present (but not connected as in extant white rhinos)

TABLE 9.2 Measurements (in mm) of Teeth of *Brachypotherium lewisi*

	LT 22872 Ur Nawata	LT 93 Lr Nawata	LT 24290 Lr Nawata	LT 99 Lr Nawata	LT 22961 Lr Nawata	LT 22874 Lr Nawata
P^2 ap	42.42	—	—	37.95	37.04	—
ant tr	46.42	—	—	46.08	43.02	—
post tr	50.29	—	—	49.0	45.0	—
M^2 ap	—	—	—	—	—	63.59
ant tr	—	—	—	—	—	—
post tr	—	—	—	—	—	65.78
M^3 ap	—	—	61.57	—	—	—
ant tr	—	—	70.25	—	—	—
post tr	—	79.4	76.84	—	—	—

	LT 94 Rt Lr Nawata	LT 94 Lt Lr Nawata	LT 88 Lt Lr Nawata	LT 88 Rt Lr Nawata	LT 23963 Lr Nawata
P^2 ap	—	—	39.67	38.89	40.88
ant tr	—	—	41.94	45.31	39.4
post tr	—	—	47.5	51.59	45.34
P^3 ap	—	—	42.17	50.04	—
ant tr	—	—	73.1	71.92	—
post tr	—	—	71.27	69.03	—
P^4 ap	—	—	44.71	56.95	—
ant tr	—	—	85.91	88.59	—
post tr	—	—	80.59	77.74	—
M^1 ap	—	—	63.55	65.25	—
ant tr	—	—	92.45	91.75	—
post tr	—	—	77.56	82.25	—
M^2 ap	76.28	80.58	75.81	76.07	—
ant tr	88.56	90.2	90.34	89.84	—
post tr	73.19	71.22	77.06	77.91	—
M^3 ap	—	—	73.58	70.32	—
ant tr	—	—	79.22	76.18	—
post tr	—	—	84.72	79.0	—

	LT 23962 Ur Nawata	LT 23967 Ur Nawata	LT 90 Lt Apak	LT 90 Rt Apak
P_1 ap	25.5	26.0	—	—
ant tr	13.93	15.15	—	—
post tr	20.39	20.45	—	—
P_2 ap	—	—	32.28	33.1
ant tr	—	—	19.64	19.45
post tr	—	—	22.82	26.14E

continued

TABLE 9.2 Measurements (in mm) of Teeth of *Brachypotherium lewisi* (Continued)

	LT 23962 Ur Nawata	LT 23967 Ur Nawata	LT 90 Lt Apak	LT 90 Rt Apak
P_3 ap	—	—	38.22	41.67
ant tr	—	—	24.97	25.94
post tr	—	—	30.4	33.09
P_4 ap	—	—	49.37	49.29
ant tr	—	—	31.04	32.96
post tr	—	—	36.17	35.92
M_1 ap	—	—	—	50.72
ant tr	—	—	—	—
post tr	—	—	—	—
M_2 ap	—	—	—	48.7
ant tr	—	—	—	—
post tr	—	—	—	—

	LT 26279 Ur Nawata	LT 81 Lr Nawata	LT 26280 Lr Nawata	LT 91 Ur Nawata	LT 28735 Lr Nawata
P_1 ap	—	—	—	20.23	—
ant tr	—	—	—	—	—
post tr	—	—	—	—	—
P_2 ap	—	—	—	28.57	—
ant tr	—	—	—	20.8	—
post tr	—	—	—	24.52	—
P_3 ap	—	—	—	36.2	—
ant tr	—	—	—	27.05	—
post tr	—	—	—	31.37	—
P_4 ap	—	—	—	45.17	—
ant tr	—	—	—	32.86	—
post tr	—	—	—	38.27	—
M_1 ap	—	—	—	50.12	—
ant tr	—	—	—	37.52	—
post tr	—	—	—	41.96E	—
M_2 ap	—	—	—	59.3E	—
ant tr	—	—	—	—	—
post tr	—	—	45.96	41.99E	—
M_3ap	72.03	—	—	54	—
ant tr	38.45	—	—	35.24	37.4
post tr	—	—	—	34.92	—

TABLE 9.3 Postcranial Measurements of *Brachypotherium lewisi*

	lt	prox ap	prox tr	dist ap	dist tr
Lt. Mt II 23964A	111	45	37	43	44
Rt. Mt III 26281	—	—	54	—	—
Lt. Mt IV 23964B	101	47	44	47	50
Rt. Mc II 26286	129	40	34	30	37
Lt. Mc III 23800	170	40	70	31	47
Dist Mc II or IV 26300	—	—	—	31	41
Lt. Mc IV 26312	140	46	54	43	59

TABLE 9.4 Measurements (in mm) of Teeth of *Ceratotherium praecox*

	LT 89 Lr Nawata	LT 23969 Kaiyumung	LT 23772 Ur Nawata
P^1 ap	—	22.67	—
ant tr	—	13.67	—
post tr	—	17.69E	—
P^2 ap	—	—	—
ant tr	—	—	—
post tr	—	—	—
P^3 ap	—	—	—
ant tr	—	—	35.87
post tr	—	—	48.89
M^2 ap	58.0	—	—
ant tr	63.78	—	—
post tr	—	—	—

	LT 26278 Ur Nawata	LT 26283 Kaiyumung	LT 23968 Kaiyumung	LT 82 Ur Nawata	LT 83 Apak
P_2 ap	—	30.33	—	—	—
ant tr	—	17.69	—	—	—
post tr	—	21.2	—	—	—
P_3 ap	—	37.55	43*	—	34.66
ant tr	—	25.2	—	—	—
post tr	—	—	—	—	23.43
P_4 ap	—	—	—	—	43.67
ant tr	—	—	—	—	27.09
post tr	—	—	—	—	—
M_1 ap	—	—	—	37.9	—
ant tr	—	—	—	22.79	—
post tr	—	—	—	25.93	—
M_2 ap	60.5	58.88	—	—	—
ant tr	45.0	42.43	—	—	30.34
post tr	46.0	42.66	—	—	—

TABLE 9.5 Postcranial Measurements of *Ceratotherium praecox*

	Astragalus	lat lt	med lt	prox tr	dist tr	dt
Upper Nawata	LT23972	865	82	85	77	65

	Calcaneum	lt	prox dv	prox tr	tc dv	tc tr
Apak Member	LT23966	133	72	89	70	55

	Proximal phalanx III	lt	prox ap	prox tr	dist ap	dist tr
Kaiyumung Member	LT26284	33	29	47	23	41

TABLE 9.6 Measurements (in mm) of Teeth of *Diceros bicornis*

	LT 84 Ur Nawata	LT 2397 Lt Apak	LT 23665 Ur Nawata	LT 23961 Ur Nawata	LT 28563 Apak
P^1 ap	—	—	—	—	—
ant tr	12.5	—	—	—	—
post tr	—	—	—	—	—
P^2 ap	24.57	—	—	31.45	35.12
ant tr	—	—	—	19.65	—
post tr	17.68	—	—	23.41	—
P^3 ap	37.77	—	—	—	43.79
ant tr	21.1	—	—	—	—
post tr	23.72	—	—	—	—
P^4 ap	41.26	—	—	—	49.76
ant tr	24.85	—	—	—	—
post tr	25.84	—	—	—	—
M^1 ap	50.22	—	53.21	—	—
ant tr	25.59	—	53.45	—	—
post tr	~26.0	—	53.32	—	—
M^2 ap	—	—	—	—	65.73
ant tr	—	—	—	—	—
post tr	—	—	—	—	63.72
M^3 ap	—	47.08	—	—	—
ant tr	—	56.12	—	—	—
post tr	—	58.09	—	—	—

	LT 23971 Rt Apak
M^1 ap	48.66
ant tr	60.7
post tr	58.57
M^3 ap	48.14
ant tr	55.2
post tr	57.48

	LT 28762 Apak
M_1 ap	48.22
ant tr	—
post tr	27.77

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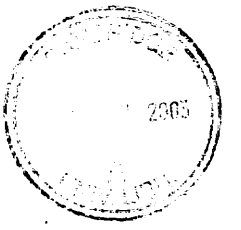

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