LAETOLI

A PLIOCENE SITE IN NORTHERN TANZANIA

EDITED BY

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9.4 Fossil Rhinocerotidae (Mammalia, Perissodactyla) from Laetoli

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INTRODUCTION

The first exhaustive study of fossils from the Laetoli region was by W. O. Dietrich (1942*a*) who recorded the presence of rhinocerotid remains. He interpreted the dental remains to be close to those of *Ceratotherium simum* (the extant white rhinoceros) but the recovered postcranial elements could not be assigned to either this species or to *Diceros bicornis* until the diagnostic characters had been better established (Dietrich 1942*a*, pp. 104–5). However, in the same work Dietrich made allusion to a predecessor ('Vorfahr') of *C. simum* (p. 133, legend to pl. XXIII, fig. 189) which was to be described in a later work. A brief note published the same year (Dietrich 1942*b*) defined the Laetoli rhino as *Serengeticeros efficax* gen. and sp. nov., a detailed study of the remains of which was published in 1947. Arambourg (1947) demonstrated that *Seren-*

geticeros was a junior synonym of *Ceratotherium* (although he used *Atelodus*) and assimilated the Laetoli species into the white rhino subspecies found at Olduvai—*C. simum germanoafricanum* Hiltzheimer.

Faunal lists published subsequently cited *C. simum germanoafricanum* as the only rhinoceros from Laetoli until M. D. Leakey *et al.* (1976) noted the presence of both *Ceratotherium* and *Diceros* in the Laetolil Beds. Both genera were subsequently cited by Harris (1977) and Leakey and Hay (1979) but without attributing them to species.

At the invitation of Mary Leakey, I undertook the study of the Laetoli rhinoceroses during two field seasons in 1977 and 1979 and I am most grateful to Dr Leakey and her associates for the generous hospitality and facilities with which I was provided. By mid-September of 1979 about 245 rhinocerotid specimens had been recovered of which 144 could be identified to species. These belonged to two species known from East and South Africa during the terminal Pliocene and earliest Pleistocene—*Ceratotherium praecox* Hooijer and Patterson and *Diceros bicornis* (Linn.). All this material came from the Laetolil Beds except for the cranium LAET 81/74 from the Upper Ndolanya Beds at Loc. 14 attributed to *C. simum*.

I have compared the rhinocerotid material from the Laetolil Beds with samples of extant *C. simum* and *D. bicornis* (Guérin 1980*a*), with fossil *D. bicornis* material from Omo, Afar, Koobi Fora and Olduvai (Guérin 1979), with remains of *C. simum germanoafricanum* from Omo, the Denen Dora Member of the Hadar Formation, Koobi Fora and Olduvai (Guérin 1979), and with specimens (or casts) of *C. praecox* from the Sidi Hakoma Member of the Hadar Formation, the Chemeron Formation of Kenya and from Langebaanweg in South Africa. These comparisons were made possible through the kind cooperation of the staff of the National Museum of Ethiopia in Addis Ababa (Omo and Hadar material), and of Richard Leakey and John M. Harris at the National Museum of Kenya (Koobi Fora, Chemeron and Olduvai material). To avoid discrepancies arising from different measurement techniques, I used only those specimens that I had myself measured. The methods I used are described in detail in Guérin (1980*a*).

SYSTEMATIC DESCRIPTION

Ceratotherium praecox Hooijer and Patterson, 1972

Abbreviated synonymy

1942a cf. *Ceratotherium simum* (partim); Dietrich: 104–5
1942a Vorfahr des *Ceratotherium simum*; Dietrich: 133, pl. XXIII fig. 189
1942b *Serengeticeros efficax*; Dietrich: 297–300, fig. 2
1947 *Serengeticeros efficax*; Dietrich: 45–90, pls. XXIII (figs. 1, 3, 4, 6), XIV (8, 10), XV (11–20), XVI (21–3), XVII (28, 32), XVIII (36), XIX (42)
1947 *Atelodus germanoafricanus*; Arambourg: 299–301
1969 *Ceratotherium simum germanoafricanum*; Hooijer: 85
1972 *Ceratotherium simum germanoafricanum*; Hooijer: 153
1976 *Ceratotherium* sp.; M. D. Leakey *et al.*: 464
1977 *Ceratotherium* sp.; Harris, table 1
1979 *Ceratotherium praecox*; Guérin: 285 *et seq.*
1979 *Ceratotherium* sp.; Leakey and Hay: 4

The species was defined in 1972 on material from Kanapoi and Ekora and was also recorded from Lothagam. Hooijer (1972) described abundant material from Langebaanweg which he attributed to the same species. Strict application of the law of priority would make *C. praecox* a junior synonym of *C. efficax* (Dietrich, 1942). In order not to complicate matters while awaiting an eventual decision from the International Commission for Zoological Nomenclature, I am using *C. praecox* as this name has wider recognition.

The material described below was recovered by Dr Mary Leakey and her colleagues during the 1974 and subsequent field seasons at Laetoli. Previously recovered material includes specimens described by Dietrich in 1942 and 1947 (partial palate with tooth-row, 11 upper tooth-rows, 4 mandibles, 192 isolated teeth, 5 limb bone fragments and 34 foot bones); this material forms part of the Kohl-Larsen collections now in the University of Berlin. There are also the remains which were at first attributed to *C. simum* by Hooijer (1969, p. 85): a mandible fragment and five isolated upper teeth in the collection of the National Museum of Kenya and also a half mandible plus two upper teeth in the British Museum (Natural History). A list of the recently recovered rhinoceros material is provided at the end of the chapter.

Description

Cranium. In lateral view (pl. 9.4A) the cranium is very bulky. The nasal-occipital distance measured on LAET 74/323 is less than the mean for extant *C. simum* but LAET 78/4979 is more robust (length anterior maxillae to occipital condyles = 655 mm, length anterior maxillae to occipital crest = 725 mm) and its size approaches that of *C. simum germanoafricanum*.

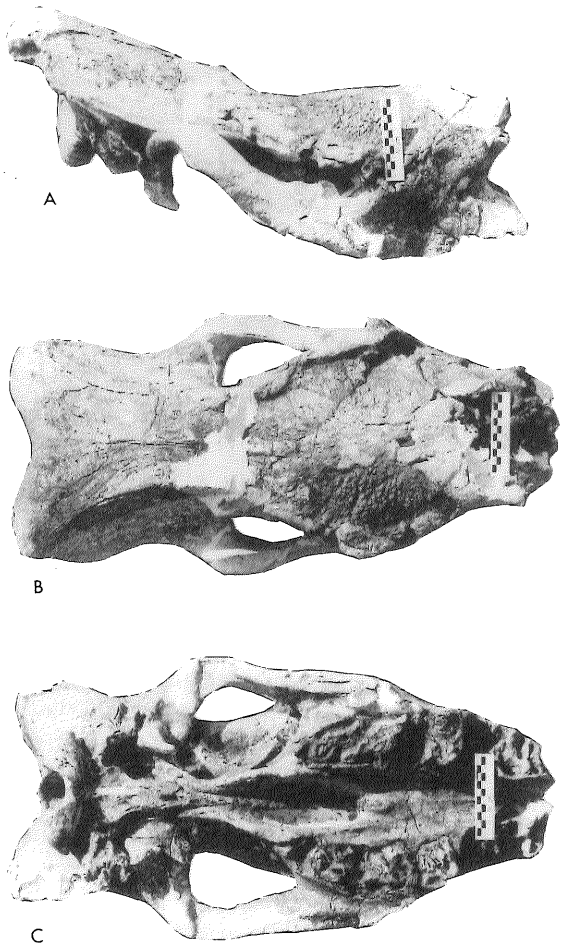

PLATE 9.4. *Ceratotherium praecox* cranium (LAET 4979) from Laetoli. A: Lateral view; B: Dorsal view; C: Ventral view. (Photographs by John Reader)

The nasal is very thick and the insertion of the two horns is well marked. The cranial vault, as described by Hooijer and Patterson (1972, pp. 19, 21), is markedly concave. The height of the occiput is close to the mean for extant and fossil *C. simum* but the cranial vault is lower and more strongly curved. The occiput is less drawn out posteriorly than in *C. simum* and the distance between the nuchal crest and the postorbital processes is shorter than the mean for extant *C. simum* (Table 9.3). Similarly, the length from the rear of M^3 to the occipital condyle is shorter than in fossil and recent *C. simum*. The external auditory pseudo meatus is not completely closed ventrally; the postglenoid process is thin with its distal part recurved anteriorly, while the short and massive post-tympanic process extends much less ventrally than the postglenoid and is not contiguous with the latter. The nasal aperture is located above the interval between P^3–P^4 and is thus more posteriorly sited than in extant *C. simum* or *C. simum germanoafricanum* (above P^2 or P^3), or than in Hadar specimens of *C. praecox* (in front or above P^3). In a cranium from Ekora, it is sited in front of P^3 (Hooijer and Patterson 1972, p. 23).

The infraorbital foramen is located above the rear of P^4, as in *C. praecox* from Hadar and in recent and fossil *C. simum*. The anterior edge of the orbit is above the rear of M^2, again as in the Hadar *C. praecox* and in *C. simum*, although it is sited in front of M^2 in the type specimen from Kanapoi and in the Ekora cranium (Hooijer and Patterson 1972, pp. 19, 23).

In dorsal view (Pl. 9.4B), one may observe the short and broad nasal bones that are rounded at their extremity, the preorbital process which is not distinct from the suborbital one, and the less well marked constriction of the cranium behind the orbits than in *C. simum*. The nuchal crest is very wide (exceeding the maximum observed in *C. simum*) and displays a shallow but wide U-shaped notch in the midline; this notch is a generic character although, as noted by Hooijer and Patterson (1972, p. 21), it is deeper in *C. simum*. The width of the zygomatic arch is the same as that of three *C. praecox* specimens from Hadar and of one specimen of *C. simum germanoafricanum* from Koobi Fora; it is close to the maximum observed in 26 extant *C. simum* crania.

In posterior view, the contour of the occipital surface is rather complex. The maximum width is sited above the level of the mastoid processes, another generic characteristic. The width of the occiput at the level of the mastoid processes is the same as the mean for extant *C. simum* but the maximum width is greater than in extant specimens. The occiput is depressed in the middle of its upper portion with a small boss in the centre of the depression.

In ventral view (Pl. 9.4C), the post-palatine notch is level with the interval between M^2 and M^3 as in *C. praecox* from Hadar or in extant and fossil *C. simum*.

The two Laetoli crania of *C. praecox* agree with the diagnostic cranial descriptions provided by Hooijer and Patterson (1972).

Mandible. There is only one measurable fragment, comprising a horizontal ramus of which the dimensions are close to the lower limit observed in specimens of *C. praecox* from Hadar. The specimen is smaller than extant and fossil specimens of *C. simum* (Table 9.4).

Dentition. A well-preserved DP^2 shows a well developed crochet, a double crista and a closed medifossette. There is a continuous internal cingulum and no

trace of constriction of the protocone. This morphology is very close to that seen in specimens from Langebaanweg (Hooijer 1972, p. 166) and in the Mursi Formation at Omo (Hooijer 1975, p. 187), the former having a simple crista and the latter a double closed medifossette. There is hardly any difference from the DP^2 of extant *C. simum* except for the profile of the ectoloph which is more clearly and regularly rounded at the levels of the paracone fold, the mesostyle and the metacone fold in the extant species (Guérin 1980*a*). As Hooijer has stated (1972, p. 167), the upper milk molars of *C. praecox* are intermediate in size between those of *C. simum* and *D. bicornis* but combine the morphological characters of both.

Two specimens of P^1 are known. The ectoloph is weakly but regularly convex. A crochet and antecrochet are present but do not touch. There is a clear internal cingulum.

Seven specimens of P^2 have been recovered, all on average a little larger than the three examples from Hadar. The crochet is always present (double in one specimen), a crista is present in four specimens. There is no example of a true closed medifossette but in two specimens the medifossette is nearly closed. The protocone is weakly constricted. The internal cingulum is present and continuous. On one specimen a fold of enamel extends from the hypocone.

In material available for comparison, the medifossette is closed in two out of three P^2s from Hadar but not in the specimen from Langebaanweg; the internal cingulum is absent in one Hadar specimen. For the Langebaanweg material Hooijer (1972, pp. 153–5, 157, 161) noted that as a general rule there was a strong internal cingulum and a small crochet, the crista could be present or absent, 3 out of 9 teeth showed a closed medifossette, and in one case the crochet was bifid while in another it was double. In *C. simum germanoafricanum* the P^2 is of similar size and the medifossette is usually closed.

The five available examples of P^3 have an ectoloph with a weak paracone fold, the crochet is always present (double in one case), the crista is present in four specimens but weak in one of these, and one specimen shows a partially closed medifossette. In two specimens the protocone is weakly constricted. The internal cingulum is continuous in two specimens, absent in two and weakly developed in one. In one specimen there is a weak external cingulum. In all specimens the medial extremity of the protoloph extends posteriorly after the middle part of the tooth.

In *C. praecox* from Hadar the P^3 is on average a little wider but shows the same morphological characters with a closed medifossette in two out of six specimens, a crista in five out of six, no internal cingulum and variable constriction of the protocone. The P^3 from Langebaanweg has no crista but has a strong internal cingulum. Hooijer (1972) describes 19 specimens of P^3 which generally have a strong internal cingulum, a weak crochet, no crista and a constriction of the hypocone that becomes a groove; two of the 19 specimens have a bifid crochet and two others a small crista. In *C. simum germanoafricanum* the P^3 is of similar size, the medifossette is closed and there is no constriction of either protocone or cingulum.

The two Laetoli examples of M^1 show a clear paracone fold, a strong crochet, a variable crista—weak in one case but strong in the other where it contributes to the closed medifossette. There is no internal cingulum. The protocone is constricted. The postero-internal extremity of the protoloph extends towards the rear of the level of the crochet.

In eight upper dentitions of *C. praecox* (6 from Hadar, one from Chemeron and one from Langebaanweg) the crochet is always present, the crista is absent only from the Langebaanweg specimen, and the medifossette is closed except in the Langebaanweg specimen and in one side of a cranium from Hadar (but not the other). The protocone is constricted except in one tooth from Hadar while another Hadar tooth has a discontinuous internal cingulum. In the very abundant material from Langebaanweg, Hooijer (1972, pp. 154, 156, 157, 163) records one case of a double crochet and several cases of a constricted hypocone. In *C. simum germanoafricanum* there is usually no constriction of the protocone, no internal cingulum and the crista is often absent.

Only one well preserved M^2 is known from Laetoli. The crochet and crista are present and fused into a double closed medifossette. The protocone is constricted. Comparative material of *C. praecox* from Hadar, Chemeron and Langebaanweg shows similar characters with minor variations: one Langebaanweg specimen lacks a crista, in one each from Langebaanweg and Hadar the medifossette is not closed. Hooijer (1972, p. 163) noted that of 24 M^2s from Langebaanweg only two had crista and closed medifossettes. In *C. simum germanoafricanum* the M^2 is usually clearly larger, the crista may be weak and there is often no medifossette. There may be a weak constriction of the protocone and traces of an internal cingulum. The profile of the ectoloph is flatter and more regular than in *C. praecox*.

Three good examples of M^3 are known from Laetoli of which two are very worn. Crochet and crista are present, the medifossette is closed in only one specimen. The protocone is only faintly constricted and

there is no internal cingulum. Comparative material of *C. praecox* from Hadar includes four M^3s with a crista and closed medifossette but those from Chemeron or Langebaanweg have neither crista nor closed medifossette. The internal cingulum is absent and the constriction of the protocone varies from none to strong. In *C. simum germanoafricanum* the M^3 is a little larger and may have more of a trapezoidal outline than a triangular one. In half of the observed specimens the crista is absent, there may be traces of an internal cingulum, and the protocone constriction is as variable as in *C. praecox*.

Lower deciduous teeth from Laetoli include one DP_1, one DP_2, two DP_3s, and one DP_4. These are of similar size to specimens from Hadar. One of the DP_3 specimens is little worn and shows sharp V-shaped internal valleys with a strong difference in level. There are no labial or lingual cingula. Size and morphology are close to specimens of *C. simum germanoafricanum*.

There are three P_1s, two P_2s, a P_3, and a P_4 from Laetoli which are close to those of *C. praecox* from Hadar in size. There are no internal or external cingula. Although the species diagnosis stipulates no fossetids in the lower cheek-teeth (Hooijer and Patterson 1972, p. 17) the P_3 from Laetoli has a closed posterior valley. In *C. simum germanoafricanum* the premolars appear more hypsodont and are on average a little larger.

One specimen of M_1, three of M_2 and one of M_3 were available for study but the M_1 and M_3 were very worn. The dimensions are of the same order as teeth from Hadar, the lengths of the Laetoli teeth are, however, a little smaller. The internal valleys have a sharp V-shaped transverse profile with a generally strong though sometimes moderate difference in level. One of the Laetoli M_2s shows traces of internal and external cingula which I have noticed in only one of 17 Hadar M_2s. On average, the lower teeth of *C. simum germanoafricanum* are a little wider.

Skeleton. The radius is a little longer than that of the largest extant *C. simum* and has a more massive proximal epiphysis (Table 9.9). In contrast, the distal epiphysis is comparable in size to that of an average *C. simum* radius. The proximal articulation bears a transversely elongate external facet whose anterior border is very retracted in relation to the anterior border of the internal facet. The posterior edge of the external facet is more or less regular, weakly concave and very oblique in such a way that the posterior border of the articulation forms a very obtuse angle. The anterior border of the articular surface is very strongly undulating with a large re-entrant angle at the level of the coronoid process. The distal epiphysis bears a distinct lateral external facet. The radius of *C. simum* is characterized by a strong extension of the external facet of the proximal epiphysis and by a very undulating anterior border with a strong re-entrant angle at the level of the coronoid process (Guérin 1980*a*).

The scaphoid (Table 9.10) is longer, as broad and a little taller than that of extant *C. simum*; the proximal articulation is about the same size but the distal is longer on average. The scaphoid of fossil *C. simum* specimens is larger in all dimensions. The anterior surface of the *C. praecox* scaphoid has a medial edge that is rounded, thick and strongly convex with the point of maximum convexity sited at about mid height. The lateral edge is short, convex in its proximal portion, depressed at mid-height and subrectangular in its distal portion. The contour of the proximal border is asymmetrically hollowed out and more elevated on its medial side. The medial height is taller than the lateral height. The proximal articular surface is short and broad, and trapezoidal with its greatest width along the medial edge. The scaphoid of *C. simum* is characterized by its size, its spherical appearance, its medial height being taller than its lateral, and the asymmetry of the contour of the proximal edge of the anterior surface—the medial edge of this surface being very rounded and spherical (Guérin 1980*a*).

Seven semilunars have been recovered from Laetoli of which three are complete or nearly so. They are similar in size (Table 9.11) to those of extant *C. simum* but smaller, and particularly narrower, than in *C. simum* fossils. The anterior surface has a pointed distal extremity, the point being sited near the midline. The proximal edge is wide with, on its lateral edge, a clear facet for the ulna which makes an obtuse angle with the remainder of this edge. On the lateral surface the two facets for the cuneiform are both long, low and elliptical; the distal facet is taller than the proximal. In extant *C. simum* the anterior surface of the semilunar has a rounded distal extremity (Guérin 1980*a*); this is the sole character separating the semilunars of the two species.

The eight known cuneiforms (= pyramidals) are of similar size to those of extant *C. simum* (table 9.12) but differ in proportions; in *C. praecox* this bone is a little longer and a little taller but a little less wide. The antero-external surface is a little wider than tall. On the postero-internal surface the proximal articular facet is very elongate transversely but is not very high; the distal articular facet is L-shaped but taller laterally than medially. The proximal articular facet is trap-

ezoidal with a lateral edge shorter than the medial edge. The distal articular facet is trapezoidal in shape but with rounded corners. The cuneiform of extant *C. simum* is very similar morphologically (Guérin 1980a).

The pisiform (Table 9.13) is a little larger than that of extant *C. simum*. In lateral view this bone is racket-shaped (as in all rhinocerotids) but the racket is very spherical (as for all Dicerotinae). The posterior edge is not appreciably taller than the anterior edge, the superior and inferior edges are depressed in their centre, the posterior edge is convex.

Three adult trapezoids are well preserved (Table 9.14). The dimensions are as in a large extant *C. simum*. On the medial surface the facet for the trapezium only occupies part of the height of the bone.

Only one complete magnum is known but six others provide some measurements (Table 9.15). The magnum is on average a little longer, narrower and taller than that of extant *C. simum*. The anterior surface has a rounded pentagonal outline that is asymmetrical distally. The medial transverse extension is sharp but not very strong. The proximal articulation is wide. On the lateral surface the unciform facet is rectangular and clearly taller than long. Other than by its size, the magnum of extant *C. simum* differs by the stronger transverse extension on the anterior surface (Guérin 1980*a*).

The unciform is on average a little larger than that of extant *C. simum* but smaller than in fossil *C. simum* specimens (Table 9.16). The anterior surface is taller on the lateral side than on the medial. The distal edge is rectilinear, becoming strongly and regularly convex in its lateral portion. In superior view the facet for the cuneiform is continuous with the facet for metacarpal V. The medial articulation is kidney-shaped. The morphology is close to that of *C. simum* except for the outline of the medial articulation which is more quadrangular in the latter, and for the lack of separation (at least anteriorly) between the cuneiform and Mc V facets (Guérin 1980*a*).

Metacarpal III is longer than that of the largest extant *C. simum* (Table 9.17) but the other dimensions are, on average, smaller. The Mc III of fossil *C. simum* specimens is larger and much more massive. The proximal articulation is very wide with a slightly curving anterior edge. On the lateral surface of the proximal epiphysis the anterior facet has a rounded trapeze shape and is nearly as large as the posterior which is kidney-shaped and located lower than the anterior. The distal part of the anterior facet is smaller than the proximal. In transverse section the diaphysis is trapeze-shaped, the long edge on the anterior surface is slightly convex while the short edge is concave. The Mc III of extant *C. simum* has a wider proximal articulation with a more concave anterior edge but the other morphological characters are identical to that of *C. praecox*.

In *C. praecox* Mc IIIs from Langebaanweg, Hooijer (1972, p. 176) noted that the ratio between the transverse diameter of the diaphysis and its length included values that were found in two extant *C. simum* specimens but my observations do not support this. Perhaps the cause of this discrepancy is that he used a different method of measuring and had a smaller sample of *C. simum*? The third metacarpals from Laetoli, like those from Hadar, are much larger and more slender than those of extant *C. simum* (Table 9.17).

The dimensions and comparative proportions of the fourth metacarpal are comparable to those of Mc III (Table 9.18). This bone is longer than that of the largest measured specimen of extant *C. simum* but the other dimensions approach the mean for the latter species or are even a little smaller. One known fourth metacarpal of a fossil *C. simum* is much more massive though of shorter length. The proximal articulation is very broad posteriorly and thus triangular in shape; the posterior edge is nearly straight. On the medial surface of the proximal epiphysis the posterior facet is subrectangular (taller than broad). The anterior facet is long and low (its height being less than a third of that of the posterior facet) with an oblique proximal edge. The diaphysis is triangular in transverse section. The morphological characters of Mc IV are very close to those of extant *C. simum* but the latter has a diaphysis that is elliptical in section (Guérin 1980*a*).

The astragalus is larger than the mean for extant *C. simum* (Table 9.19) but is smaller than fossil *C. simum*. In comparison with three *C. praecox* astragali from Hadar, the Laetoli material is a little narrower and less tall. The articular trochlea is wide and deep. On the medial surface there is a strong distal tubercle sited well above the distal border and midway between the front and the rear. The articulation on the inferior surface has a nearly straight anterior border without a notch at the contact of the navicular and cuboid facets. These two facets are similarly elongated and are not offset. The morphological characters of extant *C. simum* are very similar (Guérin 1980*a*). Hooijer (1972, p. 179) noted that 26 of the 67 Langebaanweg astragali are larger in all dimensions than in extant *C. simum* but his sample of the latter was not very large.

The calcaneum is longer than the mean for extant *C. simum* (Table 9.20) but is close to the latter in all other dimensions. It is smaller than all known fossil *C. simum* for all dimensions but only slightly smaller than

six *C. praecox* calcanei from Hadar. On the lateral surface one may note a clear difference in height between the proximal point of the bone and the front of the anterior tuberosity but both extend forward for the same distance. The upper part of the posterior border is very strongly convex and faintly curved in its distal portion. The anteroposterior development of the distal edge is weak when compared to the anteroposterior development of the head. On the posterior surface the sustentaculum axis makes a right angle with the axis of the body of the calcaneum. The extension of the sustentaculum is strong and its extremity is thick and rounded. With the exception of size and proportions the characters of the calcaneum are close to that of extant *C. simum,* whereas *C. praecox* calcanea from Langebaanweg are longer than those of extant *C. simum* (Hooijer 1972, p. 181).

The dimensions of the navicular (Table 9.21) are smaller than those of fossil *C. simum* but close to the average for extant *C. simum* except that the Laetoli specimens are taller. On the lateral surface a low proximal facet occupies nearly the entire length of the surface but does not reach the posterior edge; towards the rear is a discontinuous articular surface which extends towards the distal border. The proximal surface has a very rounded, obtuse medial angle and a salient antero-external projection. The articulation is wider than long. The posteromedial tuberosity is faintly developed and there is a weak posterior notch. The morphological characters differ little from those of extant *C. simum* except in the proportions of the proximal articular surface and in the arrangement of the facets on the lateral surface; in the latter there is usually a small anterosuperior facet and two superimposed posterior facets.

The second metatarsal is longer than that of the extant *C. simum* (Table 9.22) but, as in the latter, the proximal epiphysis is narrow and elongate and the diaphysis and distal epiphysis have similar dimensions. One Mt II of *C. praecox* from Hadar is a little smaller than that from Laetoli but the proportions are identical. The proximal articulation is elongate and narrow and is D-shaped with a straight medial edge. The anterior tuberosity is very reduced, the anteriormost point of the articulation surface being very close to the anteriormost point of the epiphysis. The lateral surface of the proximal epiphysis is poorly preserved in its anterior portion where there is a tall and narrow facet whose superior edge is scarcely taller than the upper edge of the posterior facet. The posterior facet is well separated from the anterior, has a rounded shape, is not subdivided, and is almost as tall as and a little wider than the anterior facet. In section the diaphysis has a trapezoidal shape with rounded angles and is widest on the posterior border. The Laetoli material differs from extant *C. simum* in the shape of the diaphysis and in the general proportions of the bone but the proximal epiphyses of the two are very similar.

The third metatarsal is represented at Laetoli only by six proximal epiphyses which are similar in size and appearance to those of extant *C. simum* (Table 9.23).

Discussion

The abundance of *C. praecox* material from Laetoli permits a number of interesting observations to be made. The cranial and dental characters evidently confirm the suggestion by Hooijer and Patterson (1972) that *C. praecox* was the ancestor of the extant *C. simum.*

The Laetoli material differs dentally from *C. praecox* material recovered from Lothagam, Kanapoi, Ekora, and Langebaanweg in the greater complexity of the upper molars (generally having closed medifossettes in all molars), by the presence in some lower premolars of closed valleys, and by its generally larger size but is comparable to *C. praecox* specimens from Hadar. The latter have an absolute age similar to that of the Laetoli fauna and perhaps somewhat younger than the other sites mentioned. It is therefore necessary to establish if these morphological characters typify the more recent specimens of *C. praecox.*

The size and proportions of the limb bones, and particularly the metapodials, are very different in *C. praecox* than in *C. simum.* In *C. praecox* the metapodials are much longer and more gracile suggesting a more cursorial form whereas by the end of the Pleistocene *C. simum* had become more graviportal. I put forward this idea in 1977 (Guérin 1979, 1985) after studying the Hadar material and in contrast to the interpretation of Hooijer (1972) who had good material of *C. praecox* but only a small sample of *C. simum.* Perhaps for the same reason Hooijer (1972, p. 188) stated that the Mc II of *C. simum germanoafricanum* could not be distinguished from that of extant *C. simum* whereas such a distinction is relatively easy.

Laetoli is the eleventh locality from Africa in which *C. praecox* has been discovered, the others being in Kenya (Kanapoi, Lothagam, Ekora, Aterir, Mpesida, Chemeron), Ethiopia (Mursi Formation of Omo and Sidi Hakoma Member of the Hadar Formation), and South Africa (Langebaanweg and Swartlinjes Farm). *C. praecox* is thus confirmed as a characteristic species of the Pliocene and earliest Pleistocene.

C. praecox shows sufficient similarity to *C. simum* to infer that they had very similar ecological preferences. Both had very hypsodont teeth and carried their head

low to graze but each clearly differed postcranially and in locomotory habit.

Diceros bicornis (Linn.)

Remains of the 'black rhinoceros' have been recovered from numerous localities of Late Pliocene and Pleistocene age in Africa but not in sufficient quantity to determine any taxonomic difference from the extant species (Hooijer 1969; Harris 1976; Guérin 1979, 1980*a*, 1980*b*, 1985). *Diceros* was not recorded from Laetoli until 1976 (Leakey *et al.* 1976) and I attributed the Laetoli material to the extant species in 1979 (Guérin 1979).

Description

The cranium (LAET 75 3065; Pl. 9.5, A and B) is crushed and deformed and only three measurements may be obtained (Table 9.24). These are smaller or much smaller than comparable measurements for extant *D. bicornis*, confirming my earlier interpretation that the remains of *D. bicornis* from the African Plio-Pleistocene did not show any major metric differences from extant specimens (Guérin 1979, p. 286). The Laetoli cranium has the anterior border of the orbit located above the front of M^2 (Pl. 9.5A); in extant crania the orbit is variously located between above M^1 and above the front of M^2.

I attribute with some reservation a fragment of one mandibular ramus with very worn teeth to *D. bicornis* (Table 9.4). Its dimensions are a little larger than the mean for extant *D. bicornis*.

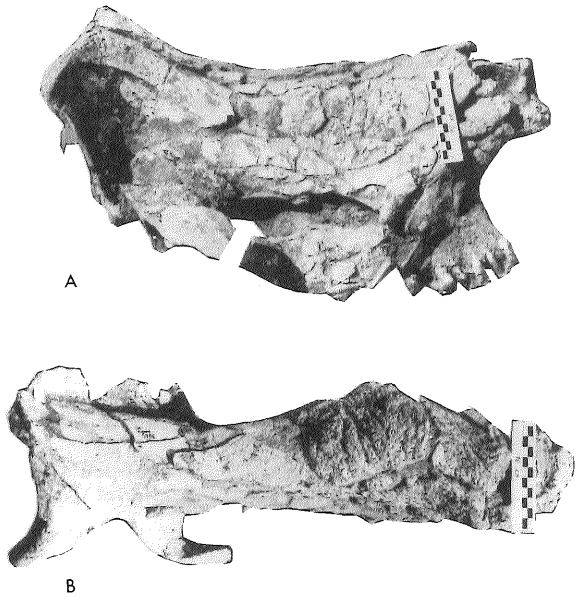

PLATE 9.5. *Diceros bicornis* cranium (LAET 3065) from Laetoli. A: Lateral view; B: Dorsal view. (Photographs by John Reader)

Extant *D. bicornis* dentitions have P^3 and P^4 with a paracone fold that is always present but variously developed. The ectoloph becomes flat behind this fold. The crista is often absent from P^3 but usually present on P^4. The crochet is nearly always present and often double or bifid. There is a well marked internal cingulum and often a closed medifossette. M^1 and M^2 have a moderately strong paracone fold and a weak depression at the level of the metacone. The crista is often absent on M^1 and generally absent on M^2. The crochet is nearly always present. The internal cingulum is usually present but discontinuous on M^1 and discontinuous or absent on M^2. The protocone is frequently constricted on the molars (Guérin 1980*a*).

On the Laetoli cranium the right tooth-row is not very broken and P^3–M^2 can be studied although very worn. The characters, in particular the profile of the ectolophs, are those typical of *Diceros*. There is a continuous internal cingulum on the premolars and there is a crochet on P^4, M^1, and M^2. The dimensions are within the limits of variation of extant *D. bicornis*, P^4 being a little smaller than the average of the latter while M^1 and M^2 are a little wider.

Extant *D. bicornis* is characterized by relatively brachyodont lower cheek-teeth that have V-shaped valleys of clearly different height and a wide and shallow labial shelf. In the Laetoli material the P_4 and M_1 are smaller than the mean for extant *D. bicornis* but the M_2 and M_3 are larger. The available teeth are too worn for detailed study of the morphological characters.

Two examples of the scaphoid are known (Table 9.10) and are much smaller than those of *C. praecox* from the same locality. Their dimensions are within the range of variation but a little larger than the mean of other fossil *D. bicornis*. One fossil specimen from Olduvai is shorter, narrower but a little taller. The anterior surface has a medial edge that is strongly convex and spherical, and with a more regular convexity than in *C. praecox*. The lateral edge is shorter than that of *C. praecox*, is nearly straight and nearly vertical, and the curvature of the proximal edge is a little more symmetrical. The medial and lateral heights are almost identical. In extant *D. bicornis* the scaphoid characters are similar but the lateral height is always a little taller than the medial, and the curvature of the proximal edge of the anterior surface is more asymmetrical (Guérin 1980*a*).

The cuneiform has a width and length close to that of the mean of extant *D. bicornis* (Table 9.12) and to that of a fossil *D. bicornis* from Olduvai. Its height is a

little low but within the limits of extant specimens. Morphologically it is identical to the cuneiforms from the extant species (Guérin 1980*a*).

I am attributing two incomplete unciforms to *D. bicornis* (Table 9.16); their width and height is close to the means for living and fossil *D. bicornis* and are smaller than for *C. praecox*. The anterior surface is a little taller on its lateral edge than on its medial. The distal edge is a little straighter and the inferolateral angle is rounded but less convex than in *C. praecox*. In contrast to the latter species, the superolateral angle is depressed and this depression corresponds, in superior view, to an absence of contact between the cuneiform and Mc V facets. In the extant representatives of *D. bicornis* the distal edge of the anterior surface is more rounded but the other morphological characters are identical (Guérin 1980*a*).

The cuboid is a little larger than the mean for extant *D. bicornis* (Table 9.25). The anterior face has a trapezoidal outline. The lateral edge, which is nearly straight, is much more elevated than the medial edge. The proximal edge is strongly oblique, the distal edge is subhorizontal. The morphological characters of the Laetoli material are identical to those of extant *D. bicornis* with the same arrangement of the articular facets on the medial surface, the same contour of the anterior surface, and the same aspect and proportions of the proximal articulation (Guérin 1980*a*).

There are two external cuneiforms, both incomplete (Table 9.26). In size they are a little larger than the mean for extant *D. bicornis*.

Discussion

The occurrence of *D. bicornis* at Laetoli brings the number of sites of Plio-Pleistocene age in Africa at which this species has been recorded to more than fifteen (Guérin 1979, 1980*b*, 1985). It is, however, necessary to await the recovery of more abundant material before attempting to define the precise taxonomic status of the fossil black rhinoceros. I have previously stated that the anatomical differences between extant and fossil forms are minor, that the dimensions of the teeth and postcranials are essentially similar, and that it is unlikely that the fossil forms warrant more than subspecific status (Guérin 1979). The material from Laetoli confirms this hypothesis.

CONCLUSIONS

The Laetoli fauna contains two species of rhinoceros with *Ceratotherium praecox* being represented by more than 28 individuals and *Diceros bicornis* by more than seven. There are a large number of specimens that cannot be identified to species or genus but identifiable remains are most common at Localities 2, 10, 8, 6, 5, and 21 (in order of decreasing abundance). It is interesting to compare this information with a list prepared by M. D. Leakey of the proportion of rhino remains at the different localities:

Locality	Percentage of rhinos
1	3.3
2	14.3
3	3.7
4	2.5
5	4.3
6	9.2
7	2.8
8	5.4
9N + 9S	8.9
10 + 10E + 10W	19.6
11	1.1
12	4.8
13	1.7
15	0
16	1.7
17	1.1
18	0.2
19	0
20	0.9
21	10.4
22	4.3

C. praecox is present at all localities except 15 and 19. *D. bicornis* occurs only at Localities 2, 3, 5, 6, 8, 10, and 21 and is always associated with *C. praecox*.

C. praecox has until now been best known from its cranium and dentition. The Laetoli material furnishes additional information about the postcranial skeleton, in particular the elongation of its metapodials, and provides some insight about evolutionary changes, particularly in the teeth. In individuals from the latest Pliocene and earliest Pleistocene the upper premolars generally have a continuous internal cingulum but only one crochet while the upper molars generally lack an internal cingulum but have cristae and closed medifossettes. The lower premolars often have closed posterior valleys. In general such specimens are large. The evolution of *C. praecox* towards *C. simum* appears to be confirmed and distinction can now be made between the postcranials of *C. praecox*, *C. simum germanoafricanum* and extant *C. simum*.

The association of *C. praecox* and *D. bicornis* was previously known only from the Omo Mursi formation and from the Sidi Hakoma Member of the Hadar

Formation. In contrast, the association of *D. bicornis* and *C. simum* in the middle and upper Pleistocene has been more widely documented in East and South Africa (Hooijer 1969, 1973; Harris 1976; Guérin 1979, 1980*b*). This association is of interest for two reasons:

C. praecox from Laetoli appears more advanced than at the Pliocene localities of Kanapoi, Ekora, Lothagam, and Langebaanweg, which may be as old as 5 Ma, and much closer to the Hadar specimens. Other than at Laetoli, the most ancient *D. bicornis* specimens are from Mursi (perhaps 4 Ma?) and the Sidi Hakoma Member at Hadar (3+ Ma). The association of advanced *C. praecox* and *D. bicornis* is thus seen to be a late Pliocene or earliest Pleistocene phenomenon, which tends to confirm the radiometric dating for the Laetoli fossiliferous levels. Rhinos represent between 0.2% and 19.6% of the fauna from any one Laetoli locality. *C. praecox*, which predominates, is a savanna form while *D. bicornis* prefers a bush environment. The association of the two species denotes a dry thorn bush savanna, which is also suggested by other elements of the fauna. It should be noted also that both of the species known from skeletal material are also represented by footprints and this would appear to be the first occurrence together at one locality of both skeletal remains and ichnofossils of rhinocerotids.

(During the final (1981) field season at Laetoli, when the stratigraphic position of Locality 14 was being investigated, a complete rhinocerotid cranium (LAET 81/74) was found in the Upper Ndolanya channel. Photographs of the specimen were sent to Drs Guérin and Hooijer who both identified it as *Ceratotherium simum*. It thus falls perfectly into place in the Ndolanya Beds fauna of Locality 14. M.D.L., ed.)

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TABLE 9.3. Measurements of *C. praecox* crania from Laetoli. Location of comparative material of *C. praecox:* Afar (Addis Ababa), Chemeron formation (Nairobi); *C. simum germanoafricanum*: Koobi Fora, (Nairobi)

	LAET 4979	LAET 323	*C. praecox* n	x̄	S	min–max	*C. simum germanoafricanum* n	x̄	S	min–max	extant *C. simum* n	x̄	S	min–max
Length nasal to nuchal crest		742					2	864		805–923	23	796.87	37.9165	667–836
Minimum width cranial vault	154	132	3	126.50	11.7579	115–138.5	4	117.75	10.5633	103–128	26	111.65	6.2092	94–121
Length post-orbital process to nuchal crest	414		1	411			2	448.50		422–475				
Length suborbital process to nuchal crest	414		1	411			2	473.50		445–502	24	427.96	13.6492	406–454
Length preorbital process to nuchal crest	476		1	473			3	500.33	27.4651	478–531	25	486.44	23.2541	395–515
Length orbit to external nares	179		3	177.67	6.6583	172–185	4	185.13	19.5112	160–206	26	182.42	10.0286	160–198
Length between M_3 and occipital condyle	345		3	368.17	31.5528	333–394	3	394.67	30.6159	376–430	24	374.17	27.9310	315–430
Maximum width nuchal crest	304		2	272.50		265–280	3	253.17	42.6389	204–280	26	224.31	16.0698	181.5–249
Width at mastoid processes	258		2	250		235–265	3	246	24.5153	222–271	26	257.02	18.0994	212–291
Maximum width occiput	299		2	292		268–316	1	264			26	268.35	18.8847	230.5–307
Width postorbital processes	305		3	265.83	17.8978	250–285								
Width suborbital processes	305		3	265.33	17.8978	250–285	2	224.50		193–256	23	276.61	16.6309	237–313
Width zygomatic arch	369		3	369	33.6005	337–404	1	372			26	339.35	16.1423	300–373
Width external nares	180	181	3	174.33	8.6216	165–182	2	173.50		168.5–178.5	25	163.70	8.2726	149–178
Height occiput	169		2	176		176–176	4	169.75	18.2460	149–187	26	169.35	11.5557	149–185
Height above P^4–M^1	204		1	223			2	251		221–281	23	242.96	20.3419	211–302
Height above M^3	187		2	222.75		218–227.5	2	241		215–267	25	247.80	19.4673	211–302
Width palate at P^2	54						2	64.50		60–69	24	69.79	7.7360	55.5–81
Width palate between P^4–M^1	76		4	92.75	12.5465	77.5–107 0	2	79.50		75–84	24	100.08	11.4708	80–127
Width palate between M^3	94		3	102.50	3.2787	99.5–106	1	82			23	105.72	7.0932	95–126
Transverse width foramen magnum	69.5		3	61	6.0	55–67	4	57.75	4.5734	52–63	25	58.56	3.8657	50–65.5
Width between occipital condyles	164		3	154.33	12.4230	140–162	4	161.25	11.3247	151–175	25	154.74	8.7382	133–172.5

TABLE 9.4. Mandible measurements of *C. praecox* and *D. bicornis* from Laetoli. Location of comparative material of *C. praecox*: Afar (Addis Ababa); location of *C. simum* fossils: Koobi Fora (Nairobi); Omo, Afar (Addis Ababa)

	LAET	*C. praecox*				fossil *C. simum*				extant *C. simum*			
	5395	n	$\bar{x}$	S	min–max	n	$\bar{x}$	S	min–max	n	$\bar{x}$	S	min–max
Depth horizontal ramus at level of													
P_4–M_1	95.5	4	108	10.7393	92–115	5	114.50	13.3182	101.5–131.5	25	123.86	6.6387	113–138
ditto M_1–M_2	102	5	110	5.8736	102–117	6	122.33	10.7222	107–135	25	125.82	6.7698	114–140
ditto M_2–M_3	109.	9	111.94	6.2572	106–122	7	114.57	12.8951	93–133	25	120.84	6.6531	113–138
ditto behind M_3	109	9	116.56	6.5975	108–128	5	115.40	8.4734	108–130	22	127.70	6.5930	116–140.3
Width horizontal ramus at the level of													
P_4–M_1	55.5	5	63.40	2.3291	60–65.5	6	63	5.5136	57–70.5	25	59.88	3.6236	54.5–68
ditto M_3	62.5	9	62.11	3.5158	59–69	7	63.71	7.7344	47–70.5	25	61.90	3.9843	52–67

	LAET	extant *D. bicornis*			
	188	n	$\bar{x}$	S	min–max
Depth horizontal ramus at level of					
M_1–M_2	105	40	89.35	7.2405	79–112
ditto M_2–M_3	101	40	91.05	7.7920	80–116
ditto behind M_3	100.5	35	94.56	7.1019	83–110
Width horizontal ramus at level of M_3	57	43	54.37	4.2469	46–67

TABLE 9.5. Measurements of upper dentition of *C. praecox* and *D. bicornis* from Laetoli. Location of comparative material of *C. praecox*: Langebaanweg (South African Museum), Hadar (Addis Ababa); location of fossil *C. simum*: Koobi Fora and Olduvai (Nairobi); Location of fossil *D. bicornis*: Koobi Fora (Nairobi)

	LAET	*C. praecox*				fossil *Ceratotherium*				extant *C. simum*			
	4979	n	$\bar{x}$	S	min–max	n	$\bar{x}$	S	min–max	n	$\bar{x}$	S	min–max
M^1 tr	71	8	69.88	2.4604	66–73	3	69.67	8.7368	60–77	16	61.16	5.8387	50.5–72
M^2 ap	75	6	68.67	3.1251	63–72	3	71.33	5.5075	65–75	12	64.13	4.8294	58–73.5
tr	65	7	73.07	3.3220	69–77.5	3	65.67	14.5028	51–80	17	62.35	7.9210	50.5–74
M^3 max ap	77	5	74.60	6.8044	63–80	3	67.33	9.2915	57–75	14	69.18	10.0567	53–83.5
ap anat.	58	4	67.63	2.0564	65–69.5	1	67 00			13	62.46	8.9941	45–78
tr	62	6	64.58	4.4092	58–70	2	69		66–72	11	55.09	7.8797	43–67.5
Length P^3–P^4	99.5	8	96.94	2.1453	93–100.5	2	100.75		100.5–101	23	88.67	8.9931	62–106
Length M^1–M^3	182.5	7	182.07	9.8675	170–202	3	177	11.7898	164–187	21	166.76	10.6308	148.5–186

	Diceros bicornis					
	LAET	extant				
	3065	Fossil	n	$\bar{x}$	S	min–max
P^3 ap	37	49.5	32	42.39	3.0046	37–51.5
P^4 ap	40	55.5	33	47.76	3.9193	39–56.5
tr	56	65.0	40	59.56	4.1481	53–69.5
M^1 ap	50.5	65.0	32	54.48	4.7527	41–65
tr	63.5	63.0	41	59.65	3.9453	52.5–68
M^2 ap	54	65.5	33	58.92	4.5639	48.71
tr	66	62.0	41	60.57	3.6955	53.5–71
Length P^3–P^4	78	95.5	54	84.13	6.5316	67.5–103
Length M^1–M^3	160	157	51	148.45	7.8557	137–174

TABLE 9.6. Measurements of isolated upper teeth of *C. praecox* from Laetoli

		LAET 4714						
D^2	ap	38						
	tr	36.5						
		LAET 543						
M^1	ap	60						
	tr	64.5						
		LAET 4640	LAET 1378					
M^3	ap (max)	100	(70)					
	ap	75	69					
	tr	68.5	73					
		LAET 1275	LAET 2617					
P^1	ap	27.5	29					
	tr	23.5	23					
		LAET 2115	LAET 1992	LAET 3582	LAET 2648	LAET 2544	LAET 3649	LAET 5009
P^2	ap	41	(39.5)	(34)	(36)	36	36	35
	tr	43	39	39	39	38	39.5	36
		LAET 3647	LAET 985	LAET 1385	LAET 1194	LAET 3091		
P^3	ap	50		49	50	45		
	tr	61	56	58	58	53		

TABLE 9.7. Measurements of the lower dentitions of *C. praecox* and *D. bicornis* from Laetoli
Location of fossil *C. simum*: Koobi Fora (Nairobi); Omo and Hadar (Addis Ababa)

	LAET	*C. praecox*				fossil *C. simum*				extant *C. simum*			
	5395	n	$\bar{x}$	S	min–max	n	$\bar{x}$	S	min–max	n	$\bar{x}$	S	min–max
P_4 ap	41.5	3	45.67	3.5118	42–49	5	47.40	2.9664	44–52	11	44.64	3.0748	40.5–49
tr	35	3	31.50	2.7838	28.5–34	5	33	2.8939	28.5–36.5	17	29.15	3.0860	25–38
M_1 ap	46.5	2	52.75		52.5–53	5	49.90	4.6421	45–56	9	49.22	4.6577	43.5–58
tr	34.5	2	32.50		32–33	5	32.90	4.0681	28–39	19	30.76	2.6319	27–36
M_2 ap	50	4	57.25	2.8722	53–59	5	51.20	2.3874	47–53	13	55.46	4.2350	48–62.5
tr	38	3	33.50	4.9244	29.5–39	5	34.80	2.7748	32.5–39.5	18	30.75	3.2095	27–37
M_3 ap	53	4	57.25	5.2519	50–62	4	60.38	0.9464	59–61	16	57.75	3.8944	51.5–66.5
tr	34.5	3	30.83	3.8837	26.5–34	4	32	3.0822	28–35.5	11	30.14	3.3770	25.5–35.5
Length M_1–M_3	148.5	3	163.67	1.5275	162–165	5	158.80	9.0180	145–168	23	153.13	8.3763	138–175

	LAET	extant *D. bicornis*			
	138	n	$\bar{x}$	S	min–max
P_4 ap	39	23	42.96	3.1941	39–52.5
ap	41	21	46.95	2.0549	43.5–50
M_1 tr	28.5	38	33.36	2.3764	28.5–39
M_2 ap	53	26	50.63	2.2385	46–54.5
tr	33	38	33.32	2.6417	30–39
M_3 ap	57	23	52.43	4.0879	47.5–65
tr	31	32	30.50	2.2824	26.5–35
Length P_3–P_4	75.5	43	77.09	6.1945	55.5–95
Length M_1–M_3	152.5	42	145.36	9.4797	123.5–178

TABLE 9.8. Measurements of isolated lower teeth of *C. praecox* from Laetoli

	LAET 1369			LAET 3847	LAET 4883	
D_1 ap	24		M_2 ap	53	47	
tr	13		tr	32.5	34	
	LAET 1782			LAET 598	LAET 2238	LAET 4646
D_2 ap	31		P_1 ap	20.5	24.5	20
tr	17.5		tr	10.5	11.5	10.5
	LAET 214	LAET 3531		LAET 413	LAET 5248	
D_3 ap	42	39	P_2 ap	32	29.	
tr	23.5	21.5	tr	18	20	
	LAET 2209			LAET 649		
D_4 ap	44		P_4 ap	37.5		
tr	24.5		tr	25		

TABLE 9.9. Measurements of radius of *C. praecox* from Laetoli

	LAET 2136	LAET 293	n	extant *C. simum* $\bar{x}$	S	min–max
Length	420		11	386.5	15.7146	358–406
prox tr	133	125	11	119.09	7.2932	106.5–130
prox ap	85.5	83	8	72.69	2.5345	70–76.5
diaphysis tr	74		11	61.52	4.4783	54–68
diaphysis ap	51		11	48.18	4.1489	41–53
dist tr	120		11	115.77	6.7021	106–127
dist ap	81		11	77.41	5.0339	72–88.5
dist artic tr	107.5		7	98.75	3.9237	94–105
dist artic ap	56		6	52.75	2.2967	48.5–55

TABLE 9.10. Measurements of scaphoid of *C. praecox* and *D. bicornis* from Laetoli. Location of *C. simum* fossils: Olduvai; location of *D. bicornis* fossils: Olduvai

	Laetoli *C. praecox*					*C. simum*						
						fossil			extant			
	LAET 3528	LAET 1424	LAET 581	LAET 2230	LAET 3652	n	$\bar{x}$	min–max	n	$\bar{x}$	S	min–max
Length	81	78	86	81.5	85	2	96.75	89.5–104	11	75.45	1.7095	73–79.5
Width	58.5	61.5			63	2	71.50	68–75	11	60.0	2.6832	55.5–65
Height	70	62	70	70	63	2	74	70.5–77.5	11	64.14	4.9804	55–75
Length sup. artic.	58	55	64		63.5	2	67	66–68	11	58.14	3.1071	51.5–61
Width sup. artic.	56.5	58		56	55	2	64.5	63–66	11	57.41	2.5181	52.5–61.5
Length inf. artic.	72	69.5	76	74	71	2	84.25	83.5–85	10	70.35	3.0189	65–75
Width inf. artic.	32	34	38	37	38.5	2	45	44–46	10	36.40	1.6465	32.5–38

	Laetoli *D. bicornis*		*D. bicornis*				
			fossil	extant			
	LAET 1316B	LAET 1652		n	$\bar{x}$	S	min–max
Length	76	71.5	66	26	68.21	4.8993	61–82
Width	54		50	26	50.52	4.5639	45–63
Height	59.5	59	62.5	24	59.27	4.2348	52.5–68.5
Length sup. artic.	50	53		25	48.72	4.0673	40.5–57
Width sup. artic.	49			25	48.44	3.9536	41–60
Length inf. artic.	68.5	63.5	66	21	65.26	4.1491	59–73.5
Width inf. artic.	33.5	35.5	28	21	30.71	2.8397	24.5–35

TABLE 9.11. Measurements of semilunar of *C. praecox* from Laetoli. Location of *C. simum* fossil: Olduvai

	Laetoli *C. praecox*							*C. simum* fossil	*C. simum* extant			
	LAET 1316	LAET 1156	LAET 3413	LAET 2124	LAET 3190	LAET 1109	LAET 3427		n	$\bar{x}$	S	min–max
Length	78	78	75					86.5	11	76.05	3.3200	71–84
Width	54	59	55.5	54	56	53.5	54.5	71	11	56.45	2.7879	53–63
Height	51		52					55	10	55.95	4.2390	51–65.5
Height ant. face	57.7	58	58	64.5	57	55	56	62	10	60	2.6034	55–65

TABLE 9.12. Measurements of cuneiform of *C. praecox* and *D. bicornis* from Laetoli. Location of *D. bicornis* fossil: Olduvai

	Laetoli *Ceratotherium praecox*								*C. simum* extant			
	LAET 582	LAET 3140	LAET 1154	LAET 163	LAET 2282	LAET 3210	LAET 2946	LAET 650	n	$\bar{x}$	S	min–max
Length	48		53.5	57.5	52	50	48	49.5	11	47.36	3.8864	42–54
Width	62	69	58.5	67	64	57	59	58	11	64.59	3.4700	58.5–71.5
Height	56	69	56	67	58	57	54.5	56.5	11	55.41	2.8356	51.5–61

	Laetoli *D. bicornis*	fossil	*D. bicornis* extant			
	3426		n	$\bar{x}$	S	min–max
Length	43.5	42	24	41.98	2.8646	37.5–49
Width	56	57	24	55.56	3.6335	46.5–61
Height	47.5	53	24	51.08	4.4322	41–60

TABLE 9.13. Measurements of pisiform of *C. praecox* from Laetoli

	Laetoli *C. praecox*		*C. simum* extant			
	LAET 254	LAET 67	n	$\bar{x}$	S	min–max
Length	67.5	76	6	62.83	3.4448	59–69
Width	47		6	38.75	2.7156	35–42.5
Height	39	41	6	34.50	2.9664	31.5–40

TABLE 9.14. Measurements of trapezoids of *C. praecox* from Laetoli

	Laetoli *C. praecox*			extant *C. simum*			
	LAET 2359	LAET 640	LAET 1613	n	$\bar{x}$	S	min–max
Length	45	48	49	9	44·33	4·0155	35–49
Width	32	36	36	9	34·44	2·3109	30–37·5
Height	32	40	38	9	34	2·3979	29·5–37·5

TABLE 9.15. Measurements of magnum of *C. praecox* from Laetoli

	Laetoli *C. praecox*							extant *C. simum*			
	LAET 639 A	LAET 2635	LAET 1153	LAET 3414	LAET 2945	LAET 2099	LAET 2195	n	$\bar{x}$	S	min–max
Length	95·5							10	88.40	8.7774	77·5–108
Width	59·5	57	54	53	54	55	53	10	57·35	2.3810	53–62.5
Height	70							10	62.40	3.1340	57·5–69
Height artic	68.5	70	60	63.5	63	64·5	64·5	10	59·50	2.8577	56–65

TABLE 9.16. Measurements of unciforms of *C. praecox* and *D. bicornis* from Laetoli. Location of *C. simum* and *D. bicornis* fossils: Olduvai

	Laetoli *C. praecox*					*C. simum*							
						fossil				extant			
	LAET 3048	LAET 3653	LAET 71	LAET 2890	LAET 1657	n	$\bar{x}$	S	min–max	n	$\bar{x}$	S	min–max
Max length	99.5	102.5				3	121.83	11.2731	111–133.5	11	95.73	4.9008	90–107
Length anat.	76	78				3	95.33	3.2145	93–99	11	72.91	2.9139	66.5–76
Width	72	77	75	71.5	78.5	3	90.50	9.9874	82–101.5	11	71.73	4.0948	66–81
Height	54	56	58.5	54	59	3	73.17	5.0579	70–79	11	52.0	2.4186	48–56

	Laetoli *D. bicornis*		*D. bicornis*						
			fossil			extant			
	LAET 1153	LAET 3284	n	$\bar{x}$	min–max	n	$\bar{x}$	S	min–max
Max length						25	86.70	6.4662	76–106
Length anat.						25	65.22	5.5716	51–75
Width	65	66	2	68.75	65.5–72	25	66.28	4.0209	60–77.5
Height	54	55	2	55.50	55–56	23	52.07	3.0049	46–59

TABLE 9.17. Measurements of third metacarpals of *C. praecox* from Laetoli. Comparative fossil material from Olduvai and Omo

	Laetoli *C. praecox*				*C. simum*							
					fossil				extant			
	LAET Loc. 8	LAET 1246	LAET 819	LAET 1729	n	$\bar{x}$	S	min–max	n	$\bar{x}$	S	min–max
Length	203				5	216.30	9.1760	206–228	12	184.67	7.2121	174–197.5
prox tr	70.5	64	76	67	5	80.40	4.2485	73.5–84	12	68.54	3.5894	64–76
prox ap		55	60	59	4	65.38	0.9464	64–66	12	52.75	2.8163	49.5–59.5
diaphysis tr	51				5	65.90	5.8137	57–73	12	55.42	2.8985	49.5–60
diaphysis ap	26				5	33.90	1.2449	33–36	11	26.32	1.8340	22–29
dist max tr	63				4	82.75	2.6299	80–85	12	70.60	3.9506	66–80
dist tr artic	59				4	69.63	5.3443	65–77	12	57.92	2.7620	55–65
dist ap	47				4	56.75	2.2173	54–59	11	48.09	2.6722	44–52.5

TABLE 9.18. Measurements of fourth metacarpa of *C. praecox* from Laetoli. *C. simum* fossil from Olduvai Bed I

	Laetoli *C. praecox*		*C. simum*			
		fossil	extant			
	LAET 3888		n	$\bar{x}$	S	min–max
Length	176.5	177	12	150.25	6.4296	140–163
prox tr	54	67.5	12	54.38	4.3281	48.5–65
prox ap	43	50.5	12	43.17	3.1066	37–48
diaphysis tr	36	48	12	39.13	2.9086	34–43
diaphysis ap	26	28.5	12	23.67	1.6966	21.5–28
dist max tr	48	58	12	52.08	4.7330	45–61.5
dist tr artic	42	52.5	12	45.67	4.0075	41.5–55.5
dist ap	41	51	12	42.38	2.7561	38–47.5

TABLE 9.19. Measurements of astragalus of *C. praecox* from Laetoli. Comparative material of *C. praecox*. from Hadar (Addis Ababa); comparative material of *C. simum* from Koobi Fora. Olduvai (Nairobi), and Omo (Addis Ababa

	Laetoli *C. praecox*						Hadar *C. praecox*				fossil *C. simum*			
	LAET 1455	LAET 1896	LAET 2168	LAET 393	LAET 1895	LAET 753	n	$\bar{x}$	S	min–max	n	$\bar{x}$	S	min–max
Transverse diameter	94.5		95	112.5	103	101	3	95.33	3.3291	92.5–99	10	108.70	5.2238	102–116
Height	88	92	90		90	91.5	3	98.50	6.5383	91–103	10	100.15	8.9133	84–112
Anteroposterior diameter	59	58.5	62	65	65	61.5	3	64.33	3.7859	60–67	9	67.56	4.2163	60.5–74.5
Dist artic tr	81.5		78	92	70	77	3	79.50	3.1224	76–82	10	90.30	7.4580	77–102.5
Dist artic ap				60		51	3	51.50	3.2787	48.5–55	6	56	5.6833	50.5–66
Dist tr	86.5		83.5	101	83.5	89.5	3	88	2.6457	86–91	10	96.85	5.3802	89–106
Trochlea width	71.5	68	69		74	67.5	3	71	4.8218	67.5–76.5	10	74.90	6.5565	62–84

	extant *C. simum*			
	n	$\bar{x}$	S	min–max
Transverse diameter	12	95.08	6.3347	88–111
Height	12	84.46	3.8756	80–92
Anteroposterior diameter	12	58.50	3.5611	53.5–65
Dist artic tr	11	79.95	4.5959	74–86
Dist artic ap	11	48	2.6645	44–52
Dist tr	12	86.54	3.8244	81–93
Trochlea width	11	64.86	3.2178	60–71

TABLE 9.20. Measurements of calcaneum of *C. praecox* from Laetoli. Comparative material of *C. praecox* from Hadar (Addis Ababa); comparative material of *C. simum* fossils from Koobi Fora and Olduvai (Nairobi), and Hadar (Addis Ababa)

	Laetoli *C. praecox*										*C. praecox*			
	LAET 1565	LAET 1130	LAET 1129	LAET 1157	LAET 2497	LAET 3150	LAET 2170	LAET 2111	LAET 1116	LAET 1131	n	$\bar{x}$	S	min–max
Height	136.5	141	140							132.5	6	145.25	4.3214	139–151
Hd tr	51	56	52	58						53	6	58.75	2.1851	56–61
Head ap	81										5	91.20	5.5968	85–99
Sustentaculum tr	78	77.5		82	78	83		74	77		5	83.70	4.1170	80–89
Beak ap	73	81.5	72	84	76	79	76	67.5	77	73	5	79.90	0.8215	79–81
Width at middle of posterior edge	47	45	46							43	6	41.42	4.9134	36–49.5

	C. simum							
	fossil				extant			
	n	$\bar{x}$	S	min–max	n	$\bar{x}$	S	min–max
Height	3	153.33	9.2915	143–161	13	126.69	6.0433	120–142
Head tr	3	61.17	3.7527	59–65.5	13	54.04	2.4787	50.5–60.5
Head ap	2	92		88–96	13	75.94	5.3464	66–82.5
Sustentaculum tr	3	89.33	2.3094	88–92	13	76.75	3.8514	71–83.5
Beak ap	3	86.67	6.6583	79–91	13	76.65	5.3672	62–81
Width at middle of posterior edge	2	49.50		49.5–49.5	2	46.50		44–49

TABLE 9.21. Measurements of navicular of *C. praecox* from Laetoli. *C. simum* fossil material from Koobi Fora (Nairobi)

	Laetoli *C. praecox*			*C. simum*				
				fossil	extant			
	LAET 19	LAET 21	LAET 2100		n	$\bar{x}$	S	min–max
Length	65.5	77	72	82	11	66.86	4.1054	58–72
Width	51	55.5	56.5	69	11	53.56	3.3097	50–61.5
Height	38	38	38.5	48	9	33.56	1.8446	31.5–36.5

TABLE 9.22. Measurements of second metatarsal of *C. praecox* from Laetoli

	LAET 3445	*C. simum*			
		n	$\bar{x}$	S	min–max
Length	178	12	149.38	8.1551	138–164
prox tr	32.5	12	34.46	2.0389	31–38
prox ap	49.5	12	46.17	2.0037	42–49
diaphysis tr	32	12	28.29	2.0052	24–31.5
diaphysis ap	26.5	12	24.29	1.8148	21.5–28
dist max tr	40	12	40.54	3.3060	37–49.5
dist tr artic	36	12	36.13	1.4943	33.5–39
dist ap	42	12	40.63	2.9781	37.5–47

TABLE 9.23. Measurements of third metatarsal of *C. praecox* from Laetoli

	Laetoli *C. praecox*						extant *C. simum*			
	LAET 583	LAET 1227	LAET 1339	LAET 3454	LAET 3207	LAET 2171	n	$\bar{x}$	S	min–max
prox tr	57.5	53.5	54	53	58	51	12	55.83	3.5760	51.5–64.5
prox ap	46	48.5	50		50	48.5	11	49.36	2.1919	46–53
diaphysis tr			45.5				12	47.25	2.8643	43–52.5
diaphysis ap			26				11	25.18	1.5374	23–28.5

TABLE 9.24. Measurements of cranium of *D. bicornis* from Laetoli. Comparative material of fossil *D. bicornis* from Koobi Fora (Nairobi)

	Laetoli	fossil *D. bicornis*			extant *D. bicornis*			
	LAET 3065	n	$\bar{x}$	min–max	n	$\bar{x}$	S	min–max
Length nasal-nuchal crest	580	1	537		46	567.41	36.9057	480–655
Length external nares	111				22	122.50	7.3969	110–138
Length nasal-orbit	226				22	251.93	16.9025	223–296.5

TABLE 9.25. Measurements of cuboid of *D. bicornis* from Laetoli

	Laetoli	*D. bicornis*			
	LAET 1223	n	$\bar{x}$	S	min–max
Length	65	24	62.40	4.0162	54.5–71.5
Width	47.5	24	40.85	3.6548	36.5–52
Height	63.5	23	58.17	4.2921	48–68
Anterior height	45	24	40.17	2.9696	36–47
prox artic tr	39	20	42.95	2.9907	38–48
prox artic ap	44.5	19	42.16	3.5514	37–50

TABLE 9.26. Measurements of greater cuneiform of *D. bicornis* from Laetoli

	Laetoli		extant *D. bicornis*			
	LAET 1714	LAET 3211	n	$\bar{x}$	S	min–max
Length	52		22	50.98	4.1071	43–60
Width		46	22	43.73	2.6935	39–48.5
Height	25	27	22	24.95	2.3396	22–28.5

TABLE 9.27. *Ceratotherium praecox* material

Field Number (LAET)	Specimen	Locality	Field Number (LAET)	Specimen	Locality
4979	nearly complete cranium	3	3433	upper tooth frag.	21
323	cranium frag.	7	4657	upper tooth frag.	3
5395	Lt mandible frag.		4699	upper tooth frag.	7
4714	Lt DP^2	6	4774	upper tooth frag.	11
138	Rt M^1	8	4938	upper tooth frag.	5
543	Lt M^1	10	4964	upper tooth frag.	2
1378	Rt M^3	8	5151	upper tooth frag.	9
2208	M^3	10E	5420	upper tooth frag.	10
3042	M^3	17	1369	DP_1	12
4640	Lt M^3	3	1782	Rt DP_2	10W
1275	Lt P^1	8	214	Lt DP_3	5
2617	Lt P^1	10W	3531	Lt DP_3	8
1992	Lt P^2	10E	2209	Lt DP_4	10E
2115	Lt P^2	2	3847	M_2	11
2544	Lt P^2	2	4669	Lt M_2	7
2649	Rt P^2	5	4883	Rt M_2	17
3582	Lt P^2	9S	5141	Lt M_3	4
3469	Lt P^2	22	598	Lt P_1	5
5009	Lt P^2	2	2238	Lt P_1	10E
985	Lt P^3	11	4648	Rt P_1	3
1194	Lt P^3	6	413	P_2	14
1385	Lt P^3	7	5248	Rt P_2	2
3091	Lt P^3	12	649	P_3	1
3647	P^3	22	1378	11 worn lower teeth	8
250	$\underline{P}$	3	4742	lower tooth frag.	11
441	upper tooth frag.	9S	4964	lower tooth frag.	2
492	upper tooth frag.	11	5420	lower tooth frag.	10
507	upper tooth frag.	8	2136	Rt radius	7
1119	upper tooth frag.	6	293	Rt proximal radius	5
1306	upper tooth frag.	8	581	Lt scaphoid	5
2040	upper tooth frag.	10NE	1424	Rt scaphoid	9S
2149	upper tooth frag.	10E	2230	Lt scaphoid	10E
2150	upper tooth frag.	10E	3528	Lt scaphoid	8
3371	upper tooth frag.	21	3652	Lt scaphoid	22

TABLE 9.27 *(continued)*

Field Number (LAET)	Specimen	Locality
71	unciform	1
1657	unciform	14
2890	unciform	4
3048	unciform	17
3653	unciform	22
639	magnum	1
153	magnum frag.	6
2099	magnum frag.	2
2195	magnum frag.	2
2535	magnum frag.	5
2945	magnum frag.	16
3414	magnum frag.	21
163	cuneiform	4
582	cuneiform	5
650	cuneiform	1
1154	cuneiform	6
2282	cuneiform	10E
2946	cuneiform	16
3140	cuneiform	12
3210	cuneiform	21
1109	semilunar	6
1156	semilunar	6
1316	semilunar	8
2124	semilunar	2
3190	semilunar	20
3413	semilunar	21
3427	semilunar	21
67	pisiform	1
254	pisiform	3
640	trapezoid	1
1613	trapezoid	13
2359	trapezoid	10
(LAET 79 Tuff 7)	Rt Mc III	8
819	Mc III frag.	7
1246	Mc III frag.	8
1729	Mc III frag.	2
3888	Mc IV	22
393	Rt astragalus	1
753	Lt astragalus	1
1455	Rt astragalus	9S
1895	Rt astragalus	2
1896	Lt astragalus	2
2168	Lt astragalus	2
1116	calcaneum	6
1117	calcaneum	6
1129	Rt calcaneum	6
1130	Rt calcaneum	6
1131	calcaneum	6
1565	Rt calcaneum	9S
2170	Rt calcaneum	2
2497	Rt calcaneum	2
3111	calcaneum	12
3150	calcaneum	12
19	navicular	2
21	navicular	2
2100	navicular	2
3445	Mt II	21
583	proximal Mt III	5
1227	proximal Mt III	6
1339	proximal Mt III	8
2171	proximal Mt III	2
3207	proximal Mt III	21
3434	proximal Mt III	21

TABLE 9.28. *Diceros bicornis* material

Field Number (LAET)	Specimen	Locality
3065	crushed cranium	10W
188	Lt mandible frag.	5
5406	Lt M^1	?
456	lower molar frag.	3
316	Rt scaphoid	8
652	Rt scaphoid	14
3426	cuneiform	21
1653	unciform	14
3284	unciform	10
223	cuboid	6
1714	greater cuneiform	2
3211	greater cuneiform	21

TABLE 9.29. Unidentifiable rhinocerotid material

Field Number (LAET)	Specimen	Locality	Field Number (LAET)	Specimen	Locality
2836	Lt mand. frag. (edentulous)	2	1359	immature trapezoid	10
2851	Lt mand. frag. (worn M_{2-3})	2	1110	proximal Mc II frag.	6
38	upper tooth frag.	2	1112	proximal Mc II frag.	?
215	upper tooth frag.	5	1716	proximal Mc II frag.	2?
472	upper tooth frag.	10	2148	proximal Mc II frag.	7
618	upper tooth frag.	5	3110	proximal Mc II frag.	12
630	upper tooth frag.	22	3655	proximal Mc II frag.	22
757	upper tooth frag.	1	1803	proximal Mc III frag.	10W
1134	upper tooth frag.	6	1175	proximal Mc IV frag.	6
1182	upper tooth frag.	6	1198	proximal Mc IV frag.	6
1307	upper tooth frag.	8	1247	proximal Mc IV frag.	8
1615	upper tooth frag.	13	1340	proximal Mc IV frag.	8
1872	upper tooth frag.	10E	1936	proximal Mc IV frag.	2
2193	upper tooth frag.	2	2097	proximal Mc IV frag.	2
3100	upper tooth frag.	12	2102	proximal Mc IV frag.	2
3118	upper tooth frag.	12	2353	proximal Mc IV frag.	10
3434	upper tooth frag.	21	3562	proximal Mc IV frag.	7
3450	upper tooth frag.	?	3564	proximal Mc IV frag.	7
3648	upper tooth frag.	22	3656	proximal Mc IV frag.	22
100	lower tooth frag.	1	754	astragalus frag.	1
101	lower tooth frag.	1	1231	astragalus frag.	6
145	lower tooth frag.	3	2010	astragalus frag.	10
153	lower tooth frag.	2	2169	calcaneum frag.	2
215	lower tooth frag.	5	1279	proximal Mt II frag.	?
524	lower tooth frag.	?	1506	proximal Mt II frag.	9N
987	lower tooth frag.	11	1606	proximal Mt II frag.	13
1855	Lt DP_3 frag.	10E	3529	proximal Mt II frag.	8
2760	lower tooth frag.	3	1157	proximal Mt III frag.	6
2851	lower tooth frag.	2	1945	proximal Mt III frag.	2
3182	lower tooth frag.	20	2825	proximal Mt III frag.	6
3353	Lt DP_2	21	9	proximal Mt IV frag.	2
3530	lower tooth frag.	8	814	proximal Mt IV frag.	7
3747	DP_4 frag.	10W	1174	proximal Mt IV frag.	6
4755	lower tooth frag.	?	2002	proximal Mt IV frag.	10E
4884	lower tooth frag.	?	3658	proximal Mt IV frag.	22
4964	lower tooth frag.	?	1165	Mt IV frag.?	6
4986	lower tooth frag.	?	1341	Mc III frag.?	8
5137	lower tooth frag.	?	1887	Mt III frag.?	?
5328	lower tooth frag.	?	1888	Mc IV frag.?	10
5335	lower tooth frag.	?	2147	metapodial frag.	7
?	humerus frags	7	2245	Mt IV frag.	10E
24	ulna frag.	2	2962	metapodial frag.	16
2123	ulna frag.	2	584	medial intermediate phalanx	5
1440	patella frag.	9S?	1359	lateral intermediate phalanx	10
162	scaphoid frag.	4	1507	lateral intermediate phalanx	9N
2244	scaphoid frag.	10E	2094	medial terminal phalanx	2
3113	scaphoid frag.	12	2098	lateral intermediate phalanx	2
2358	immature unciform frag.	10	2232	lateral terminal phalanx	10E
4183	immature magnum frag.	12	3402	medial intermediate phalanx	21
2453	magnum frag.	10			