FOSSIL RHINOCEROSES FROM THE LIMEWORKS CAVE, MAKAPANSGAT

By D. A. Hooijer*

ABSTRACT

The rhinoceros remains from Makapansgat consist almost exclusively of milk molars. An investigation of the milk teeth of the two living African rhinoceroses *Ceratotherium sinum* and *Diceros bicornis* discloses adequate distinguishing characters on a basis of which both species are recognised to occur in the fossil collection. The white rhinoceros is the more abundant and the teeth appear rather larger than in the living races of *C. sinum*. The significance of the occurrence only of juvenile individuals is discussed.

In the spring of 1958, while visiting South Africa under the auspices of the Netherlands Organization for Pure Research (Z.W.O.), I was privileged to see the fossil collections in the Bernard Price Institute for Palaeontological Research of the University of the Witwatersrand in Johannesburg. The present paper deals with the rhinoceros material from the Limeworks Cave, Makapansgat. This is the most prolific of the Australopithecine sites in the Transvaal as far as the non-hominid fauna is concerned; a faunal list will be found in Wells and Cooke (1957, pp. 50-51). In this list, the rhinoceroses are cited as "*Ceratotherium sp.*" and "*Diceros* cf. *bicornis*". I am greatly indebted to the Institute for the opportunity to work on this interesting material.

The rhinoceros remains from Makapansgat consist almost exclusively of milk molars, most of them in the unworn state or in early stages of wear. In the recent fauna of Africa there are two sub-species of the white rhinoceros, *Ceratotherium simum* (Burchell) (Heller, 1913), and about five of the black rhinoceros, *Diceros bicornis* (L.) (Hopwood, 1939). Racial differences are slight, and are not manifest in the milk teeth. Very young skulls of *Diceros* are available in the Leiden Museum, and a very young skull of *Ceratotherium* is in the British Museum (Natural History); my thanks are due to Miss Judith E. King for sending me this specimen (B.M., reg. no. 1851. 12.23.2) on loan.

Before passing on to the description of the fossil material it is best to discuss the distinguishing characters of the milk teeth of *Ceratotherium* and *Diceros*.

The distinguishing characters of the upper milk molars are most clearly shown in DM^{3-4}, less so in DM^2, and least in DM^1. Thus, there is progressive divergence in molar pattern between *Ceratotherium* and *Diceros* as we pass backward along the series. The main characters for distinction between the milk molars of the two genera pertain to the shape of the ectoloph, the development of the cingulum, the height of the crown, the development of the crista, the shape of the protoloph, and the depth of the postsinus. They will be dealt with in this order below.

* Rijksmuseum van Natuurlijke Historie, Leiden.

In DM^{3-4} of *Ceratotherium* the ectoloph is undulate: the anterior and posterior margins (parastyle and metastyle) are raised, and between them there are three weak vertical ridges, the paracone style above the anterior outer root, the mesostyle, and the metacone style, which latter is above the posterior root. The mesostyle flattens out toward the base, which is depressed between the roots. In *Diceros* the ectoloph of DM^{3-4} has but one prominent vertical ridge, the paracone style, marked off in front by the parastyle fold, which does not continue down to the base of the crown. The mesostyle is slight, forming a bulge in the apical part of the ectoloph, and there is no metacone style. The posterior moiety of the ectoloph is flattened or slightly concave anteroposteriorly due to the metastyle being a little raised.

In DM^2 of *Ceratotherium* the undulations seen in the more posterior milk molars are hardly evident. The parastyle is prominent to the front, and the ectoloph is flattened or convex anteroposteriorly, with or without a depression at the base between the roots; a mesostyle may sometimes be distinguished. In DM^2 of *Diceros* the marked paracone style seen in the more posterior elements is absent; the ectoloph is gently convex from before backward, as in *Ceratotherium,* although the parastyle is less prominent anteriorly and the unworn height is less than in its homologue in *Ceratotherium.* Occasionally there is a mesostyle in DM^2 of *Diceros.*

In DM^1 of *Ceratotherium* as well as of *Diceros* the ectoloph is convex without any styles showing except for the paracone style, forming a bulge near the tip of the paracone. The parastyle projects forward to a much greater extent in *Ceratotherium* than in *Diceros,* making the ectoloph longer anteroposteriorly and thereby relatively lower than that in *Diceros.*

The development of the cingulum differs markedly in the two genera. In DM^{2-4} of *Ceratotherium* the anterior cingulum is a weak ledge descending inward from the depression for the metastyle of the molar in front, but not extending beyond the inner angle of the front surface of the crown. In *Diceros* the anterior cingulum is much stronger and more nearly horizontal; it does continue along the inner surface of the crown, forming a ledge along the base of the protocone, sometimes extending along that of the hypocone as well. In these cases it is continuous with the posterior cingulum, which is more marked off than that in *Ceratotherium,* too. The inner cingulum becomes progressively stronger in the more anterior milk molars; in DM^2 it may bear a kind of cusp just behind the protocone obstructing the entrance to the medisinus. In *Ceratotherium* there is never a continuous inner cingulum, but there often is a tubercle at the entrance to the medisinus. In the posterior milk molars it is small, if present at all, but in DM^2 it may be of considerable size, and merged in part with the protocone, or the hypocone, or with both, transforming the entrance to the medisinus into a pass which is on a higher level than the anterior and posterior cingula. Without this tubercle the entrance to the medisinus is on a lower level than the cingula.

In DM^1 anterior and posterior cingular development does not offer a means of distinction between *Ceratotherium* and *Diceros.* In *Diceros* there may or may not be a cingular ledge at the narrow entrance to the medisinus. However, in *Cerato-*

therium the tubercle blocking the entrance to the medisinus may be of such dimensions that the entrance forms a high pass, or even that protocone and hypocone appear to be fully united.

The premolars and molars of *Ceratotherium* are higher crowned than those of *Diceros,* but the difference is not very marked in the milk molars. Several unworn or nearly unworn upper milk molar crowns, recent as well as fossil, show that those of *Ceratotherium* are higher than their homologues of *Diceros,* but wider anteroposteriorly as well, and in the relation between anteroposterior length and height of the ectoloph there is no great difference. The basal widths of DM^2 and DM^3 are about equal to the unworn ectoloph height in *Diceros,* whereas in *Ceratotherium* the basal width is less than the height. DM^1, however, is higher crowned relative to the basal width in *Diceros* than in *Ceratotherium.*

The crista, although present in both genera, is stronger in *Ceratotherium* than in *Diceros,* and often duplicated. It invariably joins the crochet so as to cut off a medifossette; in *Diceros* a medifossette is not always formed.

The inner portion of the protoloph is more distinctly curved backward in *Ceratotherium* than in *Diceros;* this distinction holds good for the permanent molars and the posterior milk molar, but is less conspicuous in DM^3 and no longer obtains in DM^2.

In all upper milk molars of *Ceratotherium* the postsinus is about as deep as the medisinus, whereas in *Diceros* it is decidedly shallower than the medisinus.

The heavy cement coating characteristic of the permanent teeth of *Ceratotherium* in contrast to those of *Diceros* does not appear to develop on the milk teeth.

Ceratotherium simum (Burchell) subsp.

The best specimen in the collection is M 164, a set of three milk molars, DM^{2-4}, in situ in a maxillary fragment. The whole of the parastyle of DM^2 and the apical part of the metastyle of DM^3 have broken off. As the crowns are unworn they had not cut the gums yet (fig. 1A).

Comparison with recent unworn crowns of *Ceratotherium simum* does not reveal any difference in structure: the undulations of the ectoloph are as in the recent form; the anterior cingulum of DM^3 terminates turned up hook-shaped at the anterointernal angle; there is no inner cingulum; DM^2 has a tubercle merged with the protocone that does not block the entrance to the medisinus; the crista is strong but single, and joins the crochet; the protoloph becomes progressively recurved backward internally in the more posterior milk molars; the postsinus is as deep as the medisinus. The base of the ectoloph of DM^{2-3} is not exposed, that of DM^4 incomplete, and hence the basal widths cannot be taken. The greatest length of the ectoloph of DM^3 is ca.54 mm. (53 mm. in the recent specimen), that of DM^4, 68 mm.

There are two isolated specimens of DM^1, both from the left side and unworn (M 179 and M 2103). They resemble the recent DM^1 of *Ceratotherium simum* in the marked anterior projection of the parastyle (differing in this respect from DM^1 of *Diceros*), but exceed the recent specimen in size: the anteroposterior diameter of the ectoloph in the two fossil specimens is ca.31 mm., and 30 mm.,

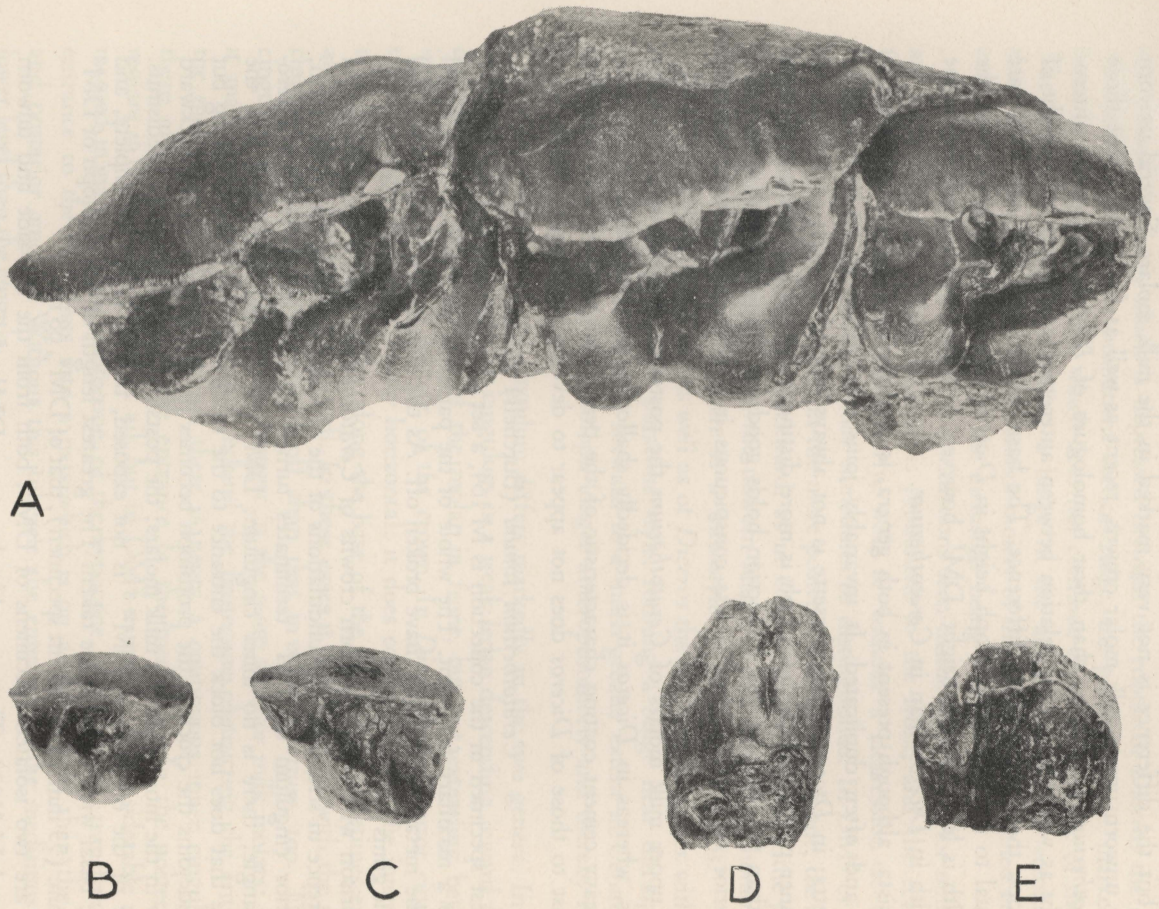

Figure 1

A, C, and E, *Ceratotherium simum* (Burchell) subsp.; A, M 164, DM^{2-4} dext., crown view; C and E, M 179, DM^{1} sin; C, crown view; E, lingual view.

B and D, *Diceros bicornis* (L.) subsp., M 180, DM^{1} sin.; B, crown view; D, lingual view.

All figures natural size.

respectively, against 26 mm. in the recent. The base of the ectoloph of the fossil specimens is broken; the width at the level of the posterior cingulum is ca.25 mm. and 23 mm. respectively, against 20 mm. in the recent specimen. In M 2103 protocone and hypocone are partially fused, but still distinguishable individually, whereas in M 179 the two cusps are fully united (figs. 1 C and E).

DM^2 is the best represented milk molar in the Makapansgat collection. Of eighteen isolated specimens, nine are from the right, and nine from the left side. Most of these are unworn or nearly so, but the base of the ectoloph is complete only in one-half of the total number of specimens. The variability in size is not great

Table 1

Measurements of DM^2 of fossil *Ceratotherium* (in mm)

No. of specimen	greatest length ectoloph	anterior width	posterior width
M 172	43	39	—
M 178	—	—	—
M 641	44	—	—
M 2089	45	40	43
M 2090	51	41	43
M 2091	44	40	40
M 2093	47	—	—
M 2101	44	41	—
M 2102	42	—	—
M 166	44	40	39
M 168	45	—	39
M 174	44	—	—
M 2088	46	40	40
M 2092	ca.46	—	—
M 2094	44	40	40
M 2095	—	—	—
M 2097	44	—	—
M 2099	—	41	41

(table 1), and all the fossil specimens are larger than the (single) recent DM^2 of *Ceratotherium simum* available for comparison, the dimensions of which are: greatest length ectoloph 41 mm., anterior width 36 mm., and posterior width 35 mm.

In one-half the number of specimens there is no tubercle at the entrance to the medisinus; the others have a sizable cusp at the lingual entrance to the valley, which is either attached to the base of the protocone (M 178, 641, 2088-2090, 2092), or to that of the hypocone (M 2095), or to both (M 168, 2094). Without a cusp at its entrance the medisinus opens internally at a level lower than that of the anterior and posterior cingula; the condition in the recent specimen available is like that in

M 168 and M 2094, with the entrance forming a high pass, but in the recent specimen figured by Heller (1913, pl. 30 fig. 2) the lingual entrance to the medisinus of DM^2 does not appear to be blocked at all. Hence, the lingual tubercle is either present or absent both in the recent and in the fossil DM^2 of *Ceratotherium,* and may be safely considered an individual variation. An almost unworn left DM^2 without the tubercle (M 166) is shown in crown view in fig. 2A; a lingual view of another specimen (M 2099), with an incipient tubercle at the bottom of the medisinus, is in fig. 2B. Crown and lingual views of two specimens, one (M 2088) with a large tubercle attached to the protocone but with its apex projecting freely upward, and another (M 168) with a tubercle connecting protocone and hypocone up to a level above that of the cingula, are shown in figs. 2 C-F.

Table 2

Measurements of fossil DM^3 and DM^4 of *Ceratotherium* (in mm)

No. of specimen		greatest length ectoloph	anterior width	posterior width
M 640	DM^3 sin.	54	—	46
M 2098	DM^3 sin.	—	48	—
M 167	DM^3 dext.	56	ca.48	—
M 171	DM^3 dext.	57	—	—
M 2104	DM^3 dext.	61	—	—
Recent DM^3 (B.M.)		53	46	44
M 639	DM^4 sin.	—	55	—
M 2110	DM^4 sin.	—	ca.54	—
M 2111	DM^4 sin.	66	—	60

The crista is strong and makes a contact with the crochet in all of the specimens; occasionally it is duplicated; in one of the specimens figured (M 2088) there are seen to be two tiny projections from the ectoloph flanking the crista, the apex of which latter extends even beyond the crochet and cuts off the labial part of the medisinus in front of the medifossette. The same condition obtains in the recent specimen available to me.

DM^3 and DM^4 are again much less well represented in the Makapansgat collection than is DM^2; six specimens of DM^3 and only four of DM^4 beside the series DM^{2-4} already recorded above. Only one of each series (a partial DM^3 sin. with part of DM^2 attached to it: M 2105, and an incomplete DM^4 dext.: M 2112) is worn; the others are unworn or very nearly so. A DM^3 sin. in situ in a maxillary

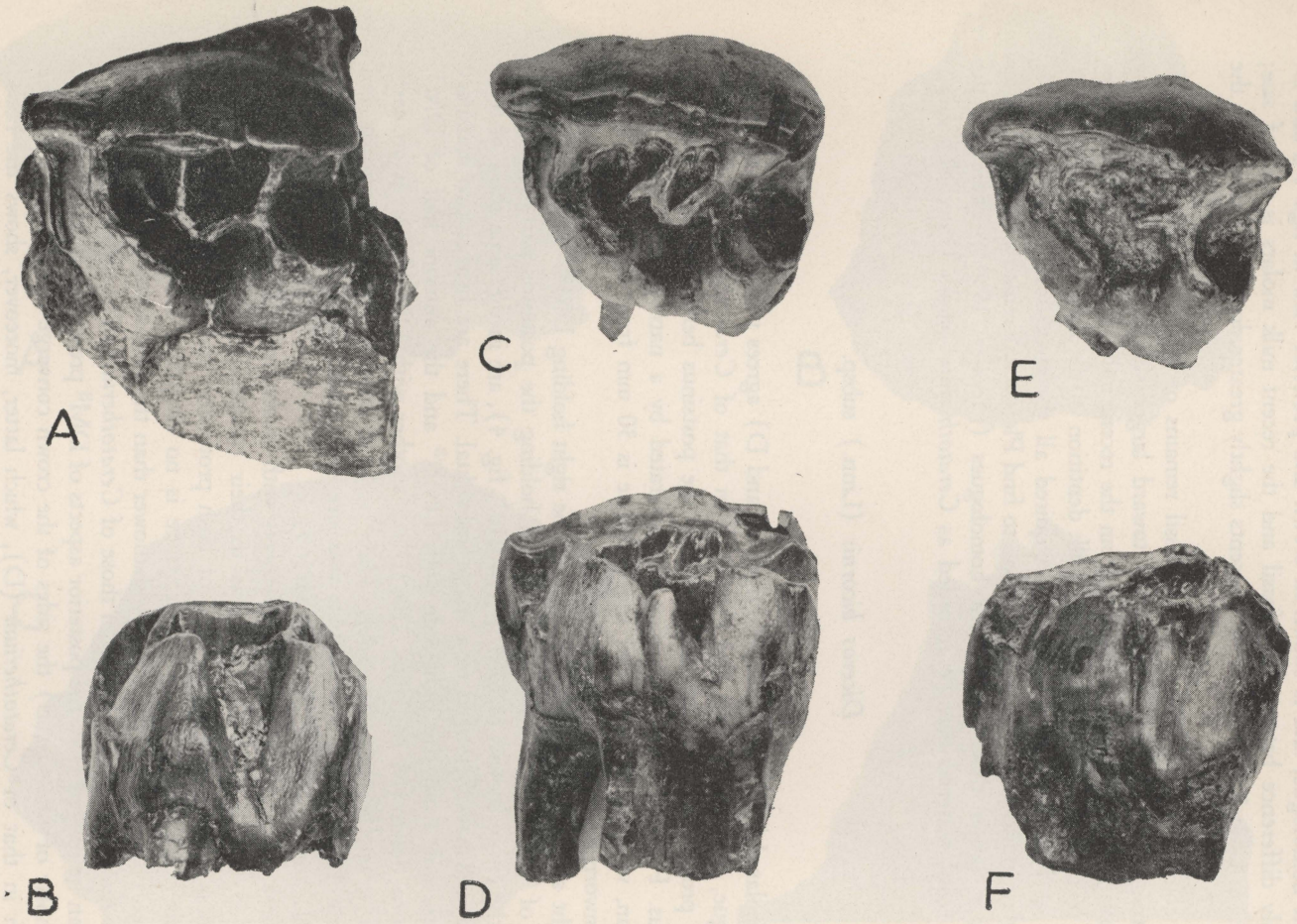

Figure 2

Ceratotherium simum (Burchell) subsp., DM^2 sin.; A, M 166, crown view; B, M 2099. lingual view; C-D, M 2088; C, crown view; D, lingual view; E, F, M 168; E, crown view; F, lingual view.

Natural size.

fragment (M 640) is the most complete specimen. It has all the characters of its recent homologue, and is shown in crown and posterior view in figs. 3C and D. The only difference between the fossil and the recent milk molars is one of size; as shown in table 2 the fossil DM^3 presents slightly greater dimensions than does the recent.

This completes the account of the fossil remains of *Ceratotherium* recovered at Makapansgat. Apart from a tendency toward larger size there is nothing in the fossil milk molars to distinguish them from the recent milk molars of *Ceratotherium simum*. It is evident that at least the milk dentition of the Early Pleistocene *Ceraotherium* of Makapansgat had already acquired all the structural characters of the living white rhinoceros. It is very common to find Pleistocene remains of living species to average larger than their recent homologues (Hooijer, 1950). Therefore, the present fossil material may be recorded as *Ceratotherium simum* (Burchell) subsp.

Diceros bicornis (Linn.) subsp.

One isolated DM^1 sin., M 180 (figs. 1B and D) agrees perfectly with its recent homologue, also as to size, and differs from that of *Ceratotherium* in the lesser anterior projection of the parastyle and in the postsinus being less deep than the medisinus. Protocone and hypocone are separated by a narrow cleft; their height is 15 mm, whereas the height of the paracone is 30 mm from the gingival border to its unworn tip.

A right and a left maxillary fragment, the right holding DM^{2-3} and an anterior portion of DM^4 (M 2108), and the left holding the posterior part of DM^2 as well as the entire crowns of DM^{3-4} (M 2107, fig. 4), are in the same stage of wear and may well have belonged to a single individual. There are further two maxillary fragments, one from the right side with DM^{2-3} and the anterior half of DM^4, much worn down (M 642 plus 2106), and another with DM^{2-3} sin. in an early stage of wear (M 165, fig. 3A). Three isolated crowns, perfectly unworn and incomplete basally, represent DM^3; two are from the right side (M 2096 and M 2100), and one from the left (M 169).

All these specimens agree in all respects with recent milk dentitions of *Diceros bicornis* so that there is no doubt as to their conspecificity. In DM^2 the inner cingulum is present along the bases of both protocone and hypocone; in DM^{3-4}, with their prominent paracone styles, there is no cingulum along the base of the hypocone. The postsinus is decidedly shallower than the medisinus, another character in which *Diceros* molars differ from those of *Ceratotherium*. The difference in crown height can be judged from the posterior aspects of DM^3 presented in figs. 3B and D; in the molar of *Diceros* (B) the sides of the crown converge more markedly to the top than in that of *Ceratotherium* (D), which latter, moreover, shows the raised metastyle not developed to such an extent in the black rhinoceros.

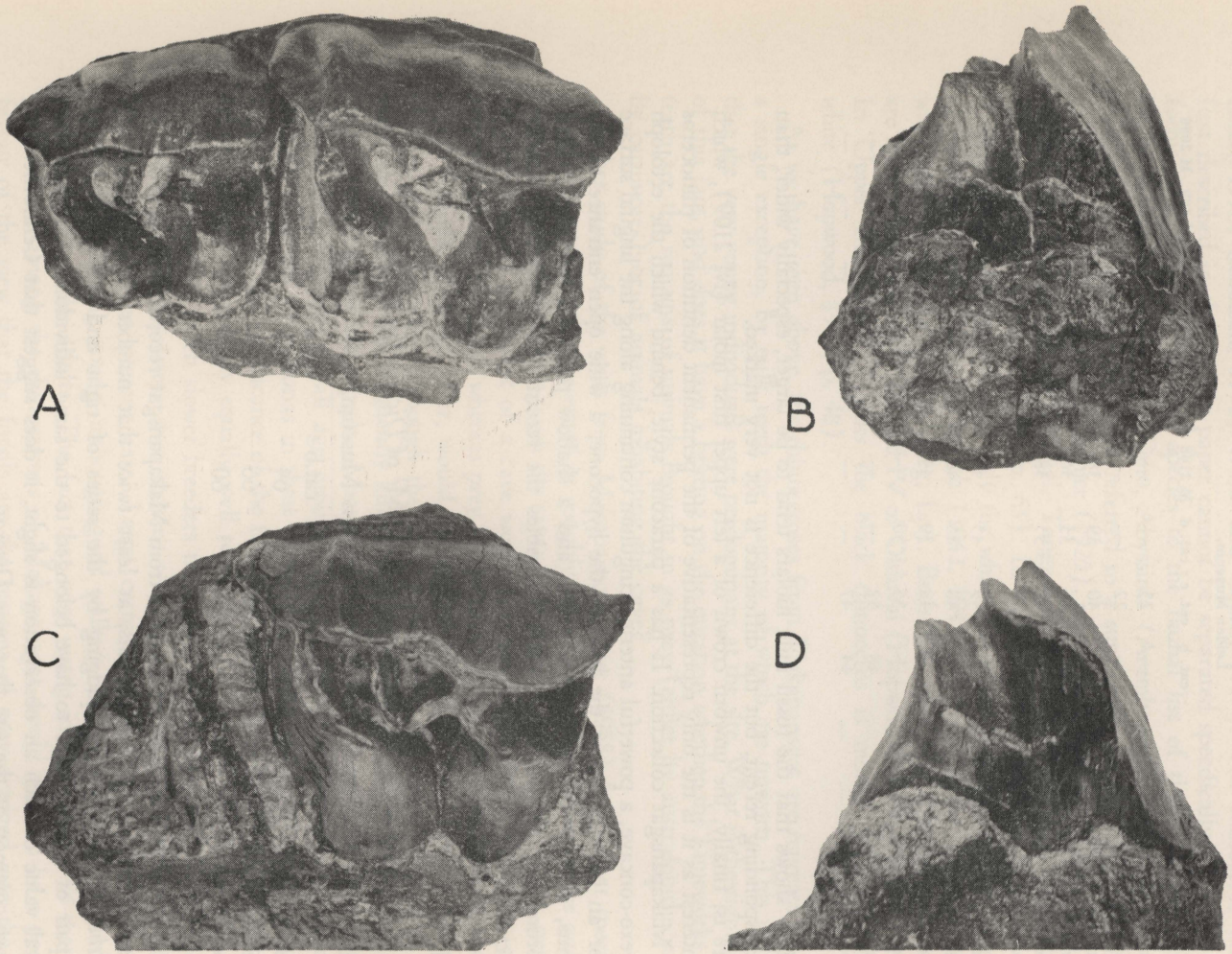

Figure 3

A, B, *Diceros bicornis* (L.) subsp., M. 165, DM^{2-3} sin.; A, crown view; B, posterior view of DM^3.

C, D, *Ceratotherium simum* (Burchell) subsp., M 640, DM^3 sin.; C, crown view; D, posterior view.

Natural size.

Table 3.

Measurements of recent and fossil upper milk molars of *Diceros* (in mm)

	Leiden Museum,					M 642			
	cat. b	cat. c	cat. d	M 2108	M 180	M 2106	M 165	M 169	M 2096
DM^1, greatest length ectoloph	—	25	—	—	25	—	—	—	—
posterior width	—	22	—	—	21	—	—	—	—
DM^2, greatest length ectoloph	—	40	39	38	—	—	41	—	—
anterior width	—	—	33	36	—	36	39	—	—
posterior width	—	40	35	38	—	39	40	—	—
					M 2107				
DM^3, greatest length ectoloph	—	49	45	48	47	—	51	50	52
anterior width	—	48	45	46	46	—	50	—	—
posterior width	—	42	39	43	43	45	47	—	—
DM^4, greatest length ectoloph	—	55	50	—	55	—	—	—	—
anterior width	48	52	—	—	53	52	—	—	—
posterior width	44	47	—	—	51	—	—	—	—

Table 3 shows that the fossil milk molars tend to be larger, especially wider, than the corresponding recent, but the difference is not very marked.

There is, finally, the unworn crown of a left upper first molar (M 2109), which is of interest as it is the only representative of the permanent dentition of rhinoceros in the Makapansgat collection. It has a paracone style, behind which the ectoloph is convexo-concave, a powerful anterior cingulum continuing along the lingual surface save for an interruption at the base of the hypocone, a wide open entrance to the medisinus, a large crochet but no crista, and a shallow postsinus bounded behind by a prominent cingulum. It closely resembles the recent M^1 of *Diceros bicornis* in structure as well as in size (table 4).

Table 4.

Measurements of recent and fossil M^1 of *Diceros* (in mm)

	Leiden Museum,			M 2109
	cat.a	cat.b	cat.e	
Greatest length ectoloph	64	64	63	61
Anterior width	68	66	66	69
Posterior width	63	60	62	63

While the dental remains of *Diceros* from Makapansgat recorded above probably represent seven or eight individuals, at least twice that number of individuals of *Ceratotherium* was present, judging by the series of right and left DM^3 not a single pair of which seems to have belonged to the same individual. Although the statistical value of such an observation is slight, it does suggest that *Ceratotherium* was more common at the site than was *Diceros*.

The fauna of the Transvaal Australopithecine deposits is now pretty generally agreed upon as (Upper) Villafranchian, i.e., Early Pleistocene (Oakley, 1954; Ewer, 1956; Robinson, 1956; Wells and Cooke, 1957). The rhinoceros material first described in the present paper cannot be separated specifically from the living forms, and adds two modern species to the faunal list of these deposits. In the Early Pleistocene fauna from Omo, Abyssinia (Arambourg, 1948) only the white rhinoceros is present; it has been referred to a supposedly extinct race, *"Rhinoceros simus germano-africanus"* Hilzheimer (1925), which is based on a partial skull from the Middle Pleistocene of Olduvai, Tanganyika, not more primitive than that of the recent form (Zeuner, 1934, p. 63). In the (?) Early Pleistocene of Laetolil, Serengeti, Tanganyika, likewise only the white rhinoceros has been found; described as *"Serengeticeros efficax"* Dietrich (1942, 1945), it is very close to, or identical with, the recent form (Arambourg, l.c.). Both the white and the black rhinoceros are known from Beds II, III, and IV of Olduvai (Hopwood, in Leakey, 1951, p.21). In Upper Pleistocene deposits the black rhinoceros is more common than the white (Hopwood, 1954, p. 48).

As we have seen above, the rhinoceroses from Makapansgat are represented, with a single exception, by milk teeth the majority of which are unworn. This indicates that the very young individuals were predominant at the site. What is the significance of this fact, and does it have a bearing on the question whether the Limeworks Cave teeth are the remains of animals brought in as prey (either by australopithecines or by carnivores) or of animals inhabiting the cave?

In her study of the suids from Makapansgat Ewer (1958) found that specimens of all age groups are represented in roughly equal numbers. Discussing the question raised in the preceding paragraph she says: "On *a priori* grounds one might, perhaps, suppose that an inhabitant of a cave would be represented mainly by bones of the very young and the aged, whereas prey might show a more uniform age composition. Aged animals, although rarer, would be more easily killed than those in the prime of life; and the young, although the most numerous class might, because of their small size, be either less frequently killed by a large predator, or be killed and eaten on the spot, so that the sample of bones in the predator's lair might show approximately equal numbers of all age groups" (l.c., p. 369/70). In the absence of an analysis of recent cave faunas in these terms, Mrs. Ewer is careful in avoiding any conclusion as to the significance of the fact that among the suids from Makapansgat all age groups are roughly equally well represented.

Rhinoceroses are much slower breeders than pigs, and (as far as I know) do not use caves as living quarters; two reasons why the remarks quoted do not seem to be applicable in the present case. Large carnivores (and man) are their main enemies, and nursing young, although good walkers, might fall a prey to predators more easily than the adults. The fact that very young individuals are so markedly predominant among the rhinoceroses of Makapansgat would seem to be a point in favour of the view that the fossils are the remains of prey dragged into the cave.

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Figure 4
Diceros bicornis (L.) subsp., M 2107, DM^{2-4} sin., crown view.
Natural size.

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