

Taxonomic notes on the White Rhinoceros *Ceratotherium simum* (Burchell, 1817)

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With 2 Figures

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Ceratotherium is perhaps the most remarkably specialised genus of the living Rhinocerotidae. DIETRICH (1945) assigned it to a special subfamily, Ceratotheriinae, but CAVE (1962), THENIUS (1956) and others have stressed its close relationship to *Diceros*, while HOOIJER & PATTERSON (1972) have demonstrated its derivation from species classified as *Diceros* in the Late Miocene, at around 8 million years B.P. HEISSIG (1973) proposes to classify all living rhinos in a single tribe, Rhinocerotini. In the present paper the attitude taken is that the differences between the Asiatic and African series of living rhinos is great enough for subfamilial distinction in the manner of POCCOCK (1945). The fossil evidence is in accord with this assessment, since the specialisations of the Dicerotinae (the African subfamily, including *Diceros* and *Ceratotherium*) can be traced back as far as the Middle Miocene in *Paralicerops* from Fort Ternan. As HEISSIG indeed points out, the latter genus still shows many characters of rhinos referred to *Diceros* rhinos, which belongs to the other subfamily, Rhinocerotinae; this is of course only to be expected at such a period, and is not a basis for uniting the two subfamilies.

HOOIJER & PATTERSON (1972) point out that the Dicerotinae are a typically African lineage, confined to the continent in which they evolved except for a brief appearance in southeastern Europe in the Upper Miocene.

Characters of *Ceratotherium*

The distinctiveness of this genus has been stressed by CAVE (1962), who lists many characters separating it from *Diceros*. The following features are among the most distinctive (CAVE 1962, GROVES 1972): 1. Elongated skull with flattened dorsal outline and backwardly extended occipital crest. — 2. Mandible with broad symphysis, backwardly inclined ascending ramus, and no gonial angulation. — 3. Hypsodont cheekteeth with incement on crown; protoloph and metaloph strongly curved back, tending to fuse with wear. — 4. A presacral eminence, formed by antinatal status of 17th or 18th thoracic vertebra. — 5. Ears pointed at tips; broad square mouth. — 6. A muscular nuchal hump. — 7. Copious subcutaneous fat causing atrophy of body folds and costal grooves. — 8. Penis with translucent perpuce and eccrine as well as apocrine glands. — 9. Body hair at least in young, though very reduced. — 10. Horn base enlarged, square.

HOOIJER & PATTERSON (1972) find that the cranial characters of the Pliocene species *Ceratotherium praecox* represent an incipient stage of specialisation; while the dental features are not fully evolved even in the Plio-Pleistocene *C. simum germano-africanum* (HOOIJER 1969).

Finally, it was found in the course of the present study that *Ceratotherium* is characterised by its larger premolars compared to *Diceros*. The premolar row (excluding the vestigial P1) forms over 40% of the toothrow length in the former, under 40% in the latter. This is unexpected in view of the findings of GENTRY (1964) that in gazelles, species which eat more grass have smaller premolars — for the White rhinoceros is a strict grazer, while on the contrary the Black rhino is predominantly a browser. In this case it is evidently the latter species which is specialised, as the Asiatic species have a long pre-molar row like the White rhino. From HOOIJER & PATTERSON'S figures, *C. praecox*

evidently has large premolars like *C. simum*, although in *Diceros pachygnathus* they are around 40% of the length of the toothrow and so intermediate.

Ecology and Distribution

The White rhinoceros is so strictly a grazing animal that its distribution is discontinuous, it having disappeared from areas where grasslands have vanished. PLAYER & FEELY (1960) found that its former distribution in southern Africa was more or less coterminous with the Bushveldt zone, a zone offering tall grasses in abundance as well as vital shade in the grasslands of the Sudan region; the species favours open *Combretum* forest, showing again the importance of shade availability.

In historic times the White rhino existed in southern Africa from the Orange River and Zululand north to the Zambezi, and from the Indian Ocean coast west to some part of southern Angola, although not as far as the Atlantic shore. It may have crossed the upper Zambezi in western Zambia as far as the Mashi river (ANSELL 1967), but was nowhere else found north of the Zambezi. In the northern part of its range the species was found from the Nile — which it nowhere crossed — about to Lake Chad, going north to the Lol river and south to the Ora river in Uganda, and the Garamba district (now Parc National du Garamba) in Zaïre.

It is of interest to examine the relations of the White rhino with the Black rhino (*Diceros bicornis*). In southern Africa the two species coexisted throughout the range of the former, but with different habitat preferences. The Black rhino alone ranged south of the Orange river, but it may be significant that here a special subspecies, *D. b. bicornis*, occurred which converged in its large size with the White rhino. In the northern area, the White rhino occurs alone: to the east of the Nile it is replaced by *Diceros bicornis ladogensis*, in the region south of Lake Chad (though precisely where is not known) by *D. b. longipes*; while north of the Lol river it was found (BENZON 1947) that once again the Black rhino replaces it, probably *D. b. brycei* (GROVES 1967 b). As population densities are much higher for the White rhino in Umfolosi (SCHOMBER 1966) than anywhere in the northern range, it may be suggested that the latter is less prime habitat for the species than the former; comparable densities are not known for the Black rhino, but it seems likely that in second-class habitat the two species might compete more than in better areas so that one species would completely exclude the other from whichever side of a given river barrier offered its own preferred habitat in greater measure.

In late Pliocene and Pleistocene sites in east and south Africa, the White rhinoceros far outnumbered the Black in early deposits — if the latter occurs at all, which it does not for example in the earlier levels at Olduvai — but the position gradually changes until it is completely reversed in the higher levels (HOOIJER 1969). This is a very eloquent demonstration of the gradual diminution of true grasslands in Africa. Other grassland types, such as the hominid genus *Paranthropus* and the giant monkeys (*Theropithecus*, subgenus *Simopithecus*) disappeared altogether.

Age and sex differences in the skull

The specimens of White rhinoceros studied for the present paper were as follows: British Museum (Natural History): southern 8, northern 13. — Leiden Rijksmuseum van Natuurlijke Historie: southern 2, northern 3. — Tervuren Koninklijk Museum voor Midden-Afrika: northern 7. — U. S. National Museum: northern 18. — Powell-Cotton Museum, Birmingham, Kent: northern 13.

In addition, certain measurements were taken from HEIJER (1913). The number of northern specimens was large enough to be arranged into dental eruption groups, by sex where sex was known, for study of skull growth. In some cases, the sex of a given skull was not known but could be reasonably assigned on the basis of certain measurements. Fig. 1 shows that the breadth of the nasal boss (which reflects the size of the horn) seem to sort specimens very clearly. Thus for Stage 6, the nasal breadths of + ♂ skulls are above 185 mm., those of 10 ♀♀ are below 170 mm. Other specimens

whose values fall decisively above or below these limits, respectively, can be fairly certainly allocated to one or other group. Study of some other measurements (especially Occipital breadth) leads to the same conclusions, but the gap between ♂♂ and ♀♀ is less wide. When this is done only three Stage 6 skulls remain unassigned: B. M. 1963.8.13.2 (nasal breadth 188), 67.8.31.3 (nasal breadth 170) and Leiden 13119 (nasal breadth 175). These three, either between the two extreme values or only just beyond them, are for safety's sake left out of the analysis.

Dental eruption stages as used in this paper follow those employed for Asiatic rhinos in a previous study (GROVES 1967 a): Stage 1. First permanent molar not visible. — Stage 2. First permanent molar in process of eruption. — Stage 3. Second permanent molar erupting; second and third premolars in process of replacement. — Stage 4. Second molar in wear; fourth premolar in process of replacement. — Stage 5. Third molar in process of eruption. — Stage 6. Third molar fully erupted, beginning to wear. In addition there were two specimens available in which the milk teeth were in process of eruption; these were assigned to a "Stage 0". There were also two foetal skulls; in one, evidently near term, the milk teeth are visible in their crypts, in the other, omitted from the analysis for total want of age data, no teeth at all are visible.

GODDARD (1970), using plentiful material of *Diceros* in the Tavvo National Park, was able to divide his material into 20 age stages, of which Stage 6 of the present study is divided among 9 different stages; he is thus able to show growth patterns much more accurately than can be done with the much smaller sample of *Ceratotherium*, and among other findings is the somewhat unexpected one of age changes within adult life itself. This needs to be further investigated; but the present small samples permit of no further splitting than is performed here.

Table 1a shows the results. Sexual differentiation begins to appear at Stage 3 or Stage 4, according to measurement. Some measurements increase right up to Stage 6, others reach their full growth before then. ♀♀ stop growing, in most skull features, before ♂♂. There are one or two anomalies, where a measurement appears to decrease from one stage to the next; in the most blatant case, where the ♂♂'s basal length declines from 705.3 mm in Stage 5 to 688.6 mm in Stage 6, Student's *t*-test gives a probability of 0.20 that the two measurements are in fact the same, i.e. the scale of the difference and the sizes of the variances mean that such a result would be arrived at by chance if the values are really the same, 20% of times. So that no significance can be assigned to such an apparent decrease.

Table 1b shows the sex differences. The measurements are arranged into five groups which show approximately similar types of growth relations. Basal length and occipital height begin to show sexual dimorphism at about Stage 4 (although the data are ambiguous), with the ♀ growing more and more slowly than the ♂ and ending up 93 to 94% of his size. Occipitonasal length and Occipital breadth show sexual dimorphism earlier; by Stage 4 it is already marked; in the adult there is very big difference. In that the expansion of the occipital crest enters into both these measurements, and that Occipital breadth (which depends entirely on this) shows greater sexual dimorphism than Occipitonasal length (which has other components), it is fairly plausible that we have here a measure of the ♂♂'s generally heavier head and horns (though the horns are not necessarily longer than the ♀♀'s), supported by bulkier nuchal musculature, such as *Musculus rectus capitis* which constitutes perhaps the main component of the nuchal hump, more prominent in the ♂ than in the ♀.

Zygomatic breadth shows a pattern of increment different from other measurements. In stage 3 the ♂ pulls markedly ahead of the ♀ and seems to remain at about the same level all through, perhaps showing a final jump ahead at Stage 6.

Postorbital breadth is a measurement which, evidently, does not show sexual dimorphism at all, until maturity is reached — and then the size difference is very weak.

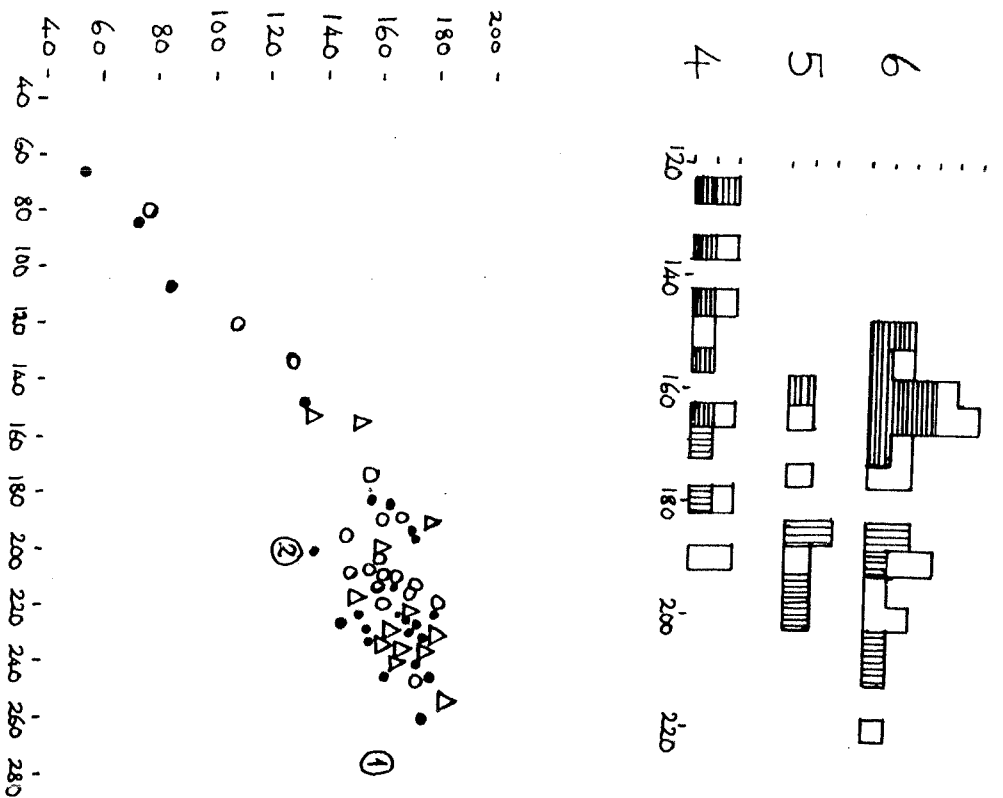


Fig. 1 (above): Sexual dimorphism in nasal breadth. Abscissa: breadth of nasal bone, in mm. Ordinate: number of specimens. 6, 5, 4: growth stages. Vertical shading: males. Horizontal shading: females. Unshaded: sex unknown.

Fig. 2 (below): Growth changes in shape of Occiput. Abscissa: occipital breadth. Ordinate: occipital height (opisthion to inion). The breadth of the occipital crest continues to increase, more markedly in ♂♂ than in ♀♀, after general growth is complete. Triangles: ♂♂. Open circles: ♀♀. Dots: unsexed specimens. (1) = Heree skull (FOOLJER), (2) = *manirhinense* skull (ARKAMBURG), may however be distorted.

Finally Nasal breadth and Lacrimal breadth, like the "group 2" measurements, show very strong sexual size differentiation which increases gradually through the stages of growth; whereas the "group 2" measurements are ones whose dimorphism is established early on and does not greatly increase thereafter.

Table 1a: Skull measurements in *Ceratolherium simum cottoni*, arranged by tooth eruption stages

Stage:	6	5	4	3	2	1	0	foetus (1)
Occipito-nasal L.	M 827.9 (8)	829.8 (6)	770.6 (5)	713.3 (4)	509.5 (6)	352.0 (1)	285.0 (2)	237
	F 765.3 (10)	770.5 (2)	750.6 (8)	662.0 (5)	502.3 (4)	352.0 (1)	288.2 (2)	217
Basal L.	M 688.6 (8)	705.3 (6)	647.0 (7)	539.4 (5)	332.5 (2)	260.6 (6)	195.0 (1)	140
	F 665.3 (10)	662.0 (2)	647.0 (7)	539.4 (5)	332.5 (2)	260.6 (6)	195.0 (1)	140
Zygomatic breadth	M 346.6 (8)	335.8 (6)	339.4 (5)	318.5 (2)	229.7 (6)	157.1 (3)	134.8 (6)	66
	F 350.9 (10)	315.0 (2)	321.1 (8)	318.5 (2)	229.7 (6)	157.1 (3)	134.8 (6)	66
Occipital breadth	M 234.6 (7)	229.7 (6)	212.3 (4)	195.0 (2)	159.8 (9)	139.5 (2)	127.0 (1)	47
	F 204.9 (10)	207.0 (2)	195.0 (2)	191.3 (3)	159.8 (9)	139.5 (2)	127.0 (1)	47
Occipital height	M 172.8 (8)	164.8 (6)	157.4 (5)	155.0 (2)	132.2 (3)	86.0 (1)	70.0 (2)	60
	F 159.8 (9)	159.5 (2)	165.4 (5)	155.0 (2)	132.2 (3)	86.0 (1)	70.0 (2)	60
Nasal br.	M 195.3 (8)	188.3 (6)	171.2 (5)	156.5 (2)	102.0 (6)	68.0 (1)	78.5 (2)	74
	F 163.9 (10)	156.0 (2)	147.5 (4)	134.5 (2)	102.0 (6)	68.0 (1)	78.5 (2)	74
Postorbital br.	M 111.6 (5)	115.0 (6)	111.3 (3)	114.0 (2)	100.3 (4)	—	88.0 (1)	—
	F 110.2 (6)	114.0 (2)	114.0 (2)	114.0 (2)	100.3 (4)	—	88.0 (1)	—
Lacrimal breadth	M 296.6 (5)	277.0 (5)	271.7 (3)	267.5 (2)	244.8 (4)	178.5 (4)	124.0 (1)	102
	F 275.8 (6)	256.5 (2)	267.5 (2)	267.5 (2)	244.8 (4)	178.5 (4)	124.0 (1)	102

Table 1b: Female as a percentage of male size

Stage:	foetus, 0, 1, 2, 3	4	5	6
(1) Basal length	100	100 (92)	99 (103)	94 (97)
(2) Occipital height	100	100 (92)	99 (103)	94 (97)
Occipitonasal L.	100	100	95	93
Occipital breadth	100	100	92	88
(3) Zygomatic breadth	100	96	95	98
(4) Postorb. br. 100	100	100	99	95
(5) Nasal br. 100	98	86 (83)	84 (85)	84 (83)
Lacrimal br. 100	100	98	93	95

Table 1c: Percent of adult value for different eruption stages

	foetus	0	1	2	3	4	5
(1) Basal L.	M 31	41	48	72	(95-)	94	100
	F 33	43	50	75	(100-)	97	100
Occip. br.	M 27	41	50	77	91	92	96
	F 29	44	51	83	97	103	100
Occip. L.	M 29	34	43	62	86	93	98
	F 31	37	46	67	93	95	100
Occip. br.	M 23	35	46	57	81	92	98
	F 32	45	52	66	93	95	100
Zyg. br.	M 40	49	56	75	92	97	97
	F 42	51	60	80	97	98	100
Post. br.	M 66	78	—	89	96	98	100
	F 67	79	—	90	97	103	100
Nas. br.	M 31	41	35	52	72	88	96
	F 37	48	42	62	82	90	95
Lacr. br.	M 34	42	45	60	82	92	95
	F 37	45	—	64	88	97	(93)

Table 1c shows the rate of growth for these same features. The "group 1" measurements reach nearly their adult value by Stage 4, and are full-sized by the time dental eruption is

completed; in the foetus near term these measurements are about one-third the size of their adult values. "Group 2" are not full-sized in ♂♂ by Stage 5, but are in ♀♀; at any given eruption stage they are a smaller proportion of their final size than "group 1". Zygomatic breadth ("group 3") is in the foetus already 40% of its adult value but thereafter grows relatively slowly and, after stage 4, keeps pace with "group 1". Postorbital breadth ("group 4") is in the foetus two-thirds of its adult size. "Group 5" are the most strongly sexually dimorphic ones, and the ones which go on augmenting right up to maturity.

In working out means and standard deviations for adult samples, for taxonomic purposes, it seems therefore that to Group 6 can be validly added, as "full-sized", the following: Basal length: Stage 5, both sexes. — Occipital height: Stages 4 and 5, ♀ only. — Occipitonasal length: Stage 5, ♀ only. — Occipital breadth: Stage 5, ♀ only. — Zygomatic breadth: Stage 5, ♀ only. — Postorbital breadth: Stage 5, both sexes; Stage 4, ♀ only. — Nasal breadth: none. — Lacrimal breadth: none. Two other measurements were employed in the present study: Toothrow length (maxillary, P3-M3), and "Depth of dorsal cavity", the measurement which HELLER (1913) found to be the best discriminator between the two subspecies of *C. simum*. The latter is hardly a measurement of the skull, and its changes with age seem somewhat haphazard and are probably not significant (samples being mostly too small to apply a *t*-test).

Some chronological ages can be provisionally put to these eruption stages. HELLER (1913) mentions that the specimens collected for the Smithsonian include 12 "full-sized" (some, as we have seen, are not in fact full-sized), 1 nursing calf and 1 foetus. The foetus, a smaller foetus than the Powell-Cotton Museum one, is not used for this study. The nursing calf, no. 164588, is a Stage 2 animal of occipitonasal length 419 (and so one of the smallest of the series); a still smaller specimen, no. 164585, is curiously not mentioned by HELLER although, being in numbered series, was presumably available at the time.

BIGALKE et al. (1950) describe the milk teeth as erupting at 3 months; this therefore marks a stage between "Stage 0" and Stage 1. The young suckle for "at least a year" (PLAYER & FEELY 1960), so the smaller Stage 2 animals could be over a year old. According to HEPPELS (1958) ♀♀ may begin breeding at 2 years; the Powell-Cotton "Stage 0" skull, no. C. 17, is stated to be the young of C. 18 which is a Stage 4 specimen, therefore, allowing a gestation period of about 18 months (though there is dispute about this; see GROVES, 1972, p. 4, "Ontogeny and Reproduction"); this Stage 4 ♀ should be at least 4½ years old. Finally SCHAURTE (1966) describes the skull of a bull known to have been 14 years old at death, in which the third molars had not yet come into full wear.

These data contrast somewhat with those for the Black Rhino, which is better known in this regard. GODDARD (1970) gives Stage 1 at about 6 months, Stage 2 beginning at about 1½ years, Stage 3 at some 4 years, Stage 4 at 5 years, Stage 5 at 6 years, and Stage 6 at 8 or 9 years. While the earlier ages are compatible with the evidence given above for the White Rhino, M3 eruption in the latter species would seem to be extremely delayed, at least in the ♂. If this is indeed true, it might go some way towards explaining the species' long premolar row: these are, after all, molarised teeth, and would have to bear the brunt of mastication for a long period until at last M3 erupts and begins to share the burden.

The following age criteria are therefore suggested: Stage 1: begins 3–6 months. — Stage 2: still suckling; a year to 18 months old. — Stage 3: ? 4 years. — Stage 4: at least 4½, more probably over 5 years old. — Stage 5: ? 6 years. — Stage 6: in ♀♀ perhaps 8 or 9 years; in ♂♂ 15 years. This proposed schema will be able to be tested as soon as longitudinal studies are made on captive-born specimens. Meantime it will only be observed that the apparent long gap between the beginnings of Stages 2 and 3 is compatible with the great size variability of Stage 2 skulls (Occipitonasal lengths 419 to 602 mm.).

HELLER (1913) was the first to elucidate the differences between northern and southern subspecies of *Ceratotherium simum*. They are disarmingly slight: the northern subspecies PLAYER (1965) suggests that there might be an external difference as well: they were able to feel hairs along the flanks of even adult specimens of the southern subspecies by no hairs, only follicles, in the skin of a northern animal. This putative difference needs to be investigated further. Comparing photographs and captive individuals, it has seemed to the author that the southern subspecies is longer in the body, while the northern is higher-legged; but this difference too needs to be further investigated, and there are as yet insufficient postcranial skeletons in collections to do so.

The purpose of the present investigation was to see whether HELLER'S conclusions, made over 60 years ago, could be confirmed on a larger range of specimens: whether further differences between northern and southern types could be found; whether there were any differences within each type; and how the fossil material related to the modern subspecies.

The number of specimens in museum collections is unfortunately not large enough to permit divisions to be made within the two broad groups. In the case of the southern subspecies this situation can never be rectified, for by the time the appalling slaughter of Zululand. As far as can be ascertained, the only skull in collections not known to be from Zululand or else labelled just "South Africa" is a British Museum skull from Mashona-land. One wonders what happened to the thousands upon thousands that fell to the gun in the days of Queen Victoria. There is a striking irony here: against all odds the Southern White Rhino has survived while it is Queen Victoria's African Empire that has met the finality of extinction.

As for the northern subspecies, there are specimens available from three areas: the West Nile district of Uganda, the Lado area of the southern Sudan, and the Garamba region of northeastern Zaire. The first two areas are separated only by a political boundary, and it is hardly worth looking for differences between their White Rhinos; the third is a little further away and may be separated from the others by unsuitable high ground. Once again, however, the numbers of specimens from each area were not sufficient to permit separation of various series each with its own mean and standard deviation statistics. It could only be noted that, as far as skull measurements go, they do not seem to differ: so the skull measurements from all areas were pooled to make an overall "northern sample". This of course assumes identical means and variances for all measurements; between the Zaire and Sudan-Uganda populations, and so is not strictly a valid procedure: it can be justified only by the assessment that any differences between the two are not very great, and that they are in any case likely to be less than those between northern and southern subspecies. In this way two statistical entities, the northern and southern subspecies, are "inverted" and given means which are not the means of any one constituent population, and variances which are larger than would be found for any of their constituent populations.

In the case of individual tooth measurements, however, a difference between Zaire and Sudan specimens did indeed leap to the eye. The samples are larger because there does not appear to be any (noticeable) sexual size difference; and smaller because of want of time and, on occasion, of suitable measuring devices calibrated in tenths of a millimeter. So in Table 2 a, skull measurements of full-grown examples of both ♂♂ and ♀♀ White rhinos are given, separated into the northern (*cottoni*) and southern (*simum*) subspecies; and in

Table 2b. Dental measurements are given separated not by sex but by locality only, into *simum*, *cottoni* (Sudan-Uganda) and *cottoni* (Garamba).

Table 2a: Skull measurements of full-grown specimens of *Ceratotherium simum*

	<i>C. s. simum</i>		<i>C. s. cottoni</i>		<i>C. s. cottoni</i>		<i>C. s. cottoni</i>	
	Mean	s. d.	Mean	s. d.	Mean	s. d.	Mean	s. d.
Basal length	689.3	3.79	688.6	25.17	693.5	33.23	664.9	22.96
Ocupipomastal l.	830.2	23.34	827.9	11.21	827.8	21.45	766.2	22.57
Zygomatic breadth	349.8	19.53	346.6	18.52	316.3	35.29	338.3	13.52
Ocupipal breadth	238.0	10.23	234.6	10.42	216.7	7.77	320.3	14.49
Ocupipal height	176.8	7.27	170.8	9.16	165.5	4.95	159.7	9.77
Nasal breadth	192.3	11.15	195.3	16.28	162.0	4.24	163.9	10.48
Lateral breadth	326.0	—	296.6	18.04	282.0	2.83	275.8	10.09

	<i>C. s. cottoni</i>		<i>C. s. simum</i>	
	Mean	s. d.	Mean	s. d.
Toothrow length, P ₁ -M ₃	281.4	9.63	262.9	12.64
Depth dorsal concavity	86.4	7.14	44.1	6.61
Postorbital breadth	117.0	1.73	112.3	5.14

Table 2b: Dental measurements of *Ceratotherium simum*

	<i>simum</i>		<i>cottoni</i> : Sudan		<i>cottoni</i> : Zaire	
	Mean	s. d.	Mean	s. d.	Mean	s. d.
Mandibular: widths (anterior)						
P2	34.5	—	36.9	2.91	36.0	3.57
P3	49.5	—	50.8	5.09	52.7	3.06
P4	56.5	—	52.8	4.62	62.0	4.42
M1	62.0	—	56.3	7.68	67.0	4.42
M2	64.5	—	54.0	6.06	70.8	4.21
M3	63.0	—	53.3	5.54	57.8	3.56
Mandibular: lengths						
P2	34.5	3.24	36.5	2.35	36	—
P3	40.4	2.70	41.8	1.94	46	—
P4	46.9	4.62	44.6	2.88	5	—
M1	48.9	5.98	50.4	5.29	8	—
M2	56.0	3.74	53.1	3.80	8	—
M3	64.3	7.23	53.8	1.71	4	—

The data in Table 2a certainly confirm HELLER'S (1913) division of the species into two subspecies, and confirm that the differences were more or less as he described. They also confirm the view of HOOFFER (1969) that, on skull characters, the two are not very well differentiated: certainly not as strongly as one might expect seeing that the two are totally isolated with no gene-flow between them. The two subspecies are approximately the same size, and even the 30 mm difference in basal length in the ♀♀ is not enough, given the large standard deviations, to be taxonomically valuable. The only large differences are the two that HELLER nominated as geographically distinctive:

1) Toothrow length. The two sexes do not appear to differ in toothrow length, so their data have been pooled. *C. s. simum* has a much longer toothrow than *cottoni*, but the size of the standard deviations is such that the Coefficient of difference is only 0.83, meaning that there would be a joint non-overlap of 80% — but 90% is necessary for a taxonomic separation on a given character.

2) Depth of dorsal concavity. *C. s. simum* has a much deeper concavity along the top of the skull than *cottoni*: the occipital crest is raised higher (this can be seen, much less well expressed, in the difference in the Occipital height). In this case, the Coefficient of Difference is 1.67: a 95% joint non-overlap, easily above the standard for subspecific difference. It is interesting that this difference reflects a higher phylogenetic level for *C. s. cot-*

form: in the phylogenetic advance from *Diceros* via *C. praecox* to *C. simum* the dorsal outline of the skull becomes flatter, indicating that the occipital crest is becoming lower and angled more backwards, so that the axis of the skull slants more downwards towards the ground. As the northern race has this character more evolved than the southern, it implies a further specialisation for it.

Wherever a relatively unworn cheektooth was found, its crown height was measured. Unfortunately very few of these were available, and no third molars (the tooth which is generally taken as standard, e.g. DIETRICH 1945). But a specimen of *C. s. simum* was found with an unworn M₂ crown of 68 mm high, and a little-worn M₁ crown 72 mm high; therefore, although much more material needs to be studied, that in this character the southern subspecies is more evolved than the northern (as it appears to be in development of hairlessness).

Table 2 b records the measurements of cheekteeth in White rhinos. Here, as explained above, the measurements of *cottoni* from the Sudan (with a few from Uganda) and from Zaire (Parc National de la Garamba) have been kept apart. The breadths of the upper cheekteeth of the Zaire specimens are greater than those from Sudan, the difference increasing up to M₂ and being smaller again for M₁. (Breadths are used as length is a very difficult measurement to take, with considerable subjectivity associated with it). In some cases the differences are above the 90% joint non-overlap level; but subspecific differentiation is not warranted on the small number of specimens currently available. The values for *C. s. simum* fall between those of the two *cottoni* samples, except that M₂ - in the single measured specimen! - is larger than in any specimen of the latter. In the mandible (no mandibular teeth from Zaire were measured) M₃ is also much bigger in *simum*, this time the difference being based on three specimens.

Fossil White rhinoceros

HOOIJER & PATTERSON (1972) find that the earliest specimen referable to *Ceratotherium* is a molar tooth, M₂, from Lothagam I, over 5 million years old. The specimen is tentatively referred to *C. praecox*, a species now well known from Kanopoi, Ekeru and early Chemeron (Baringo), all around 4 ma, and also from the Pliocene Langebanweg site in South Africa (HOOIJER & PATTERSON 1972, HOOIJER 1972).

Ceratotherium simum is first definitely recorded from Shungura B at Omo, dated to around 3.7 ma. It is now known as a fossil from many succeeding levels at Omo (Uno and Shungura Formations), from Herer (East Rudolf; at a level now dated by BROCK & ISAAC 1974 at around 1.6 to 1.8 ma), Laetoli, Olduvai, and Ravi, Kavirondo; all these are Lower to early Middle Pleistocene, and outside the species' modern range. In the Upper Pleistocene it occurs in the Kibish Formation at Omo (date controversial; here placed tentatively at $\pm 100,000$ B.P.) and in undated, probably Upper Pleistocene deposits at Naivasha. These, too, are outside the modern range. Remains of the species are continuous throughout the Pleistocene in North Africa (ARAMBOURG 1970) and rock paintings and engravings depict the species in the western Sahara (probably early Holocene) (MAUNY 1956). This was also the species known to the Romans (GOWERS 1955); it occurred at that time as far north as Aswan. Thus, the present discontinuity of range, at least with the boundaries of the Zambesi and the Nile, is a fairly recent event.

From the Olduvai material HOOIJER places the transition from the archaic subspecies *C. simum gemmatricatum* to a form resembling the modern White rhino - labelled by him *C. s. simum* - at somewhat over 1 million years B.P.; intermediate remains occur in Upper Bed II, which spans this general period.

Measurements of skulls and teeth from the literature are presented in Table 3, together with measurements of two skulls in the British Museum not apparently described to date. Measurements are as given except that Basal length is used instead of Condylbasal (being

Table 3a: Skull measurements of fossil *Ceratotherium simum*

	2.0 ma Baringo J. M. 91	1.6-1.8 ma Herer K.N.M.-ER.1288D II	>1 ma Olduvai M.I.14803	75 ma? Olduvai Bed IV	? Ravi, Kavirondo L. M. Pleist.	ca. 0.1 ma Omo, Kibish AP 671-1	"Villa- franchian" <i>mauritanicum</i>
Basal L.	-	ca. 745	-	ca. 755	710	ca. 675	ca. 725
Occip. l.	-	-	-	ca. 925	-	-	ca. 785
Zygomatic br. ca. 38C	-	375	-	-	ca. 430?	-	380
Occip. br.	-	275	ca. 235?	-	292	-	ca. 267?
Occip. ht.	-	160	170	-	-	ca. 180	150(+)
Nasal br.	-	180	-	-	-	-	160
Lacrimal br.	-	285	-	-	-	-	350
Toothrow l.	-	ca. 285	-	ca. 335	ca. 275+	ca. 315	290
Toothrow conc.	-	55	-	-	-	-	60
Postorb. br.	-	120	127	-	-	-	ca. 170?

Table 3b: Dental measurements of fossil *Ceratotherium simum*

	3.7 ma Omo, Shungura B	2.9 ma Omo, Shungura G	2.5 ma Laetoli, Olduvai & Shungura D	1.75 ma Olduvai C; Bed II	ca. 1 ma? Olduvai Beds III & IV	75 ma? Olduvai Kibish; Naivasha	ca. 0.1 ma Omo, Kibish; Naivasha	"Villa- franchian" <i>mauritanicum</i>
Maxillary: widths (anterior)			23 (sic!)	40.0 (4)	54.0 (2)	54.0 (2)	51	57
P ₂			61	59.3 (4)	54.0 (2)	54.0 (2)	61	68
P ₃			66				61	61
P ₄				85	71.5 (2)		53	53
M ₁								
M ₂								
M ₃								
Mandibular: lengths								
P ₂		43			38	37	48	
P ₃								
P ₄								
M ₁	43		44.0 (2)		54	54	51	
M ₂			57.0 (2)					
M ₃			64.5 (2)			65.0 (2)	66	58

Sources: Baringo, Olduvai, Laetoli, Omo Kibish and some Omo Shungura & Uno - HOOIJER (1969); Rudolf (Herer), remainder of Omo Shungura & Uno - HOOIJER (1973); *mauritanicum* - ARAMBOURG (1970); Olduvai Bed II skull, and Ravi - authors' measurements of BM M. 14803 and M. 26538.

estimated from HOOIJER's figures for the latter by subtraction of 25 mm); and a full toothrow length has been estimated from HOOIJER's P₂-M₂ figures with the addition of 75 mm. (the mean of 4 M₂ quoted by HOOIJER for Lower Pleistocene remains) and subtraction of 10 mm for contact attrition: the resulting figures having a standard error of 3.5 mm.

1) *C. s. mauritanicum*. The skull, of Villafranchian date, whose measurements are given by ARAMBOURG (1970), is similar in general size (Basal length) to modern male skulls, but in Occipitonasal length and Nasal breadth with modern ♀♀. The figures for Zygomatic breadth and Lacrimal breadth are at the top end of the ♂ range. This all suggests a ♀ skull, of a large and broad-skulled subspecies. The toothrow is long and the dorsal concavity deep, as in *C. s. simum*: the latter feature being, as we have seen, a conservative character. It would be useful to have material from later North African deposits to trace possible evolutionary changes. Of the dental measurements little can be said except that they are within the modern range, and M₂ is small as in *cottoni*.

2) Omo (Kibish) and Naivasha. All measurements of the skull from the Kibish Formation fit into the modern range, although the teeth are very large. The basal length is lower than average (except *cottoni* ♀♀), while Occipital height is great, suggesting a ♂, and/or a deep dorsal concavity. The teeth however are huge: bigger than in any modern specimen.

3) Ravi, Kavirondo. This skull, undated but said to be "Lower Middle Pleistocene", is slightly bigger than the average modern skull, but within the range of variation; the teeth

are as big as *simum* or bigger; the occiput is proportionally broader than in any modern skull (Fig. 2).

4) Olduvai Beds III and IV. The Bed IV skull is extremely big, and not disproportionate (Basal to Occipitonasal lengths) like *mauritanicum*. The teeth are also very large – slightly bigger even than the Omo (Kibish) teeth. While the crown height and molar/premolar shapes may be quite modern (HOOIJER 1969) the late Olduvai White rhino cannot be referred to either of the modern subspecies. At present, however, it is better to refer to the form as *C. simum* subsp.; a name and formal diagnosis should await more material both because of the ignorance of the sex of the available skull, and because of the uncertainty as to its relationship to the Kibish and North African specimens. It should be remarked also that, if the stratigraphic assessment of the Rawi skull has any validity, then the likelihood of the two skulls being representatives of the same population (the Olduvai skull presumably therefore ♂, the Rawi one ♀) must be borne in mind.

5) Olduvai Bed II. In the middle of Bed II at Olduvai there is a faunal break; below it are deposits not much later in age than – and directly following on – Bed I, while above it a rather later, more drawn-out time-span must be envisaged. Teeth whose measurements are given by HOOIJER (1969) come from the Upper section of Bed II, and may be given a notional date of ± 1 million years B.P.; these are the teeth which he assigns to the transitional phase between *C. s. gemmatrochicum* and *simum*. The upper teeth are considerably bigger than those of modern specimens; lowers, however, are comparable in size – an apparent anomaly which may be resolved by supposing that either the breadth, relative to length, is what differed, or (since the Bed IV form had a long upper tooththrow) some unrepresented elements of the lower tooththrow were of compensatingly large size.

The teeth are also bigger on average than the Beds III and IV teeth, although one specimen of P3 is 54 mm broad like the average of two from the two higher beds. The British Museum skull, M.14803, is unfortunately labelled only "Bed II"; it could therefore be as young as the above-mentioned teeth, or much older. Its measurements fit with those of modern skulls although it is so fragmentary that little weight can be put on this; but the postorbital breadth is much greater than any modern specimen, suggesting that the general size of the skull could have been greater than most modern individuals.

6) Olduvai Bed I. A single M1 from this level is quite gigantic, by far the largest known for a White rhino.

7) Heret, East Rudolf. This skull – possibly contemporary with the Olduvai Bed II skull – is the most satisfactory fossil skull of the species, being nearly complete and apparently undistorted. It is referred by HOOIJER (1973) to *C. s. gemmatrochicum*. It is large, nearly as big as the Olduvai Bed IV skull, but with smaller teeth. The occiput is lower than in modern skulls, but equivalent in breadth (Fig. 2). The concavity depth is between the two modern races. Like the Olduvai Bed II skull its postorbital breadth is greater than in any modern skull. Direct comparison with the still more complete, and perhaps contemporary, *mauritanicum* skull is precluded by the latter's distortion.

8) Baringo. A very fragmentary skull; its broad zygomatica fit well with the Heret measurements.

9) Omo (Shungura and Usno). The loose teeth from these sites are rather nondescript; the unexceptional nature of P₃, M₁ and M₂ from all three levels is belied by the rather large M₂, P₃ and P₄ of the later levels, and the astonishingly small P₂. These pieces have to be left in suspense account until more material is discovered.

In conclusion, then, it seems that *C. s. gemmatrochicum* was a White rhino with the archaic characteristics delineated by HOOIJER (1969); with a skull of large size and low occiput (in view of which the dorsal concavity must be regarded as rather deeply indented); with fairly large cheekteeth, especially the upper cheekteeth being very broad. Its successor and descendant in the East African Middle Pleistocene was similar in size with

again rather broad upper cheekteeth, a long upper tooththrow and at least some of the lower cheekteeth quite small as in modern forms. The skull would, on the whole, appear to have changed little; the teeth, quite a bit. Finally in the upper Pleistocene we have a small-sized animal, no bigger in skull dimensions than the modern subspecies, but still with large teeth (at any rate upper teeth). It must be remembered that this lineage is in a region where White rhinos are no longer found, so that no direct comparisons can be made with living subspecies on ancestor/descendant assumptions. As a whole the East African lineage was a large-toothed one, with a dorsal concavity perhaps similar to the living southern subspecies (to judge from HOOIJER's 1969 plate of the Olduvai Bed IV skull, and assessing measurements as above).

Outside East Africa there are very few fossil White rhinoceros finds. In South Africa, milk teeth are known from the australopithecine site of Makapansgat (HOOIJER, 1968); these are said to be slightly larger than their modern homologues. From the late Middle Pleistocene come dental remains from Hopfield, South Africa (HOOIJER & SINGER 1960); the lower teeth here are comparable in size to their modern (or indeed their contemporary East African) equivalents, while an upper M3 is larger.

The North African race needs to be investigated further. The early (Villafranchian) representative was, it would seem, very large and broad-skulled with, perhaps, a short occipital crest not as backwardly inclined as in modern or contemporary East African rhinos (cf relationship between basal and occipitonasal lengths). How this form developed through the Pleistocene is not yet apparent. It should be borne in mind that the type material of POMEL's *mauritanicus* was from Ternifine, of Middle Pleistocene age; so that if changes occurred comparable to those in East Africa, a new name will have to be found for the earlier North African subspecies.

Conclusions and Summary

The White Rhinoceros is divided into two subspecies, *Coradoborn simum simum* and *C. s. coroni*. Although the ranges of the two are entirely separate and discontinuous, the differences between them in skulls and teeth are very slight, though there may be further differences in the postcranial skeleton and in the degree of hairiness. The northern subspecies, *coroni*, is more progressive in having a flatter dorsal outline to the skull. There seem to be size differences in the teeth between Zairens and Saldanian populations of *coroni*.

The Pliocene/Lower Pleistocene *C. s. gemmatrochicum* had primitive dental characteristics, but the skull was fully modern in form, although large, and with very large teeth. In the Middle Pleistocene in East Africa it was succeeded by a form, (unnamed) differing in its more modern cheekteeth and longer tooththrow, but similar in overall size. The Upper Pleistocene form was smaller – like modern subspecies – but still with very large teeth. Then, the species died out in East Africa presumably as a consequence of the disappearance of grassland habitats. In North Africa in the Villafranchian the subspecies *C. s. mauritanicum* (or a related form) would appear to have been very large; like its East African contemporaries, but without such a backwardly inclined occipital crest.

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