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The extinct Cape Rhinoceros, *Diceros bicornis bicornis* (Linnaeus, 1758)

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With 1 Figure

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Introduction

Little work had been done on the infrageneric taxonomy of the Black Rhinoceros, *Diceros bicornis* (Linnaeus, 1758), other than the occasional description of new races, until the revision by HOPWOOD (1939). Working on skulls in the British Museum (Natural History), he divided up his material into a number of geographic segments and recognised each as a distinct subspecies: southern Africa, south of the Zambesi (*bicornis*), East Africa (*holmwoodi*), the Horn of Africa (*somaliensis*), Angola (unnamed) and Nigeria (unnamed). In truth, it was HOPWOOD's method of procedure that led him to his conclusions: each "population" differed in its mean values for certain measurements, and no attention was paid to matters like degree of overlap, or the allocation of specimens to one subspecies rather than another. If more groups had been used in the study, more subspecies would have resulted; if fewer, then again just that number of subspecies would have been recognised.

A much more ambitious piece of work was that of ZUKOWSKY (1964). Some of the same criticisms can be levelled at this study: namely that no indication was given as to what a subspecies ought to be, so that it is sometimes a little mysterious what basis he had for allocating a given specimen to one form rather than another. But the painstaking descriptions, and in particular the elaborate documentation, make ZUKOWSKY's monograph a landmark in the study of the species. In southern Africa, ZUKOWSKY accepted six subspecies and a "variety": *bicornis* (southernmost Africa, now extinct), *keitloa* (western Transvaal), *keitloa* var. *minor* (Natal), *niger* (southern Namibia), *occidentalis* (northern Namibia), *angolensis* (Angola) and *chobiensis* (Chobe valley); the last two being described for the first time.

Because of the extreme "splitting" in ZUKOWSKY's work, a new revision was made by GROVES (1967). (Such a revision had, as a matter of fact, been commenced as early as 1963, but was discontinued on learning of ZUKOWSKY's study, then nearing completion; it was resumed after publication of the latter, because GROVES had already seen material not studied by ZUKOWSKY; because of certain errors – traceable to HOPWOOD – over the aging of British Museum material; and because the old-fashioned taxonomy of ZUKOWSKY's work seemed likely to lead to it's being ignored, unjustly, by the scientific community). GROVES retained *bicornis* and *chobiensis* – sinking *keitloa* and *niger* into the former – and made *minor* into a full subspecies which would include *occidentalis* and *angolensis* as well as sundry East African forms. This was partly confirmed by JOUBERT (1970) who compared skulls from the Kaokoveld with some from Natal: although the former proved to be somewhat broader and longer than the latter, they could not be distinguished statistically.

Further studies based on large skull samples, or other characteristics, are still highly desirable and these may lead to modifications of the classification proposed by GROVES. One essential population, that of the Cape region (the nominate race according to THOMAS, 1911), became extinct around the middle of the last century. This subspecies was extensively discussed by ZUKOWSKY (1964: 8–37) but new material, and a re-study of that previously known, shows that some of his conclusions must be modified. We shall therefore attempt to redescribe *Diceros bicornis bicornis* in what follows.

Description of museum specimens

At present two skeletons and seven skulls of the Cape rhinoceros are known in museums; an additional one is now known only from engravings. They will be only briefly mentioned here since ZUKOWSKY described them extensively in his monograph.

1. Leiden cat. a. Mounted skeleton, adult but with third molars not worn. Received in Leiden museum on 3rd June 1826, sent from the Cape by H. BOIE and H. C. MACKLOT (VROLIK, 1837). ZUKOWSKY nominated this as "holotype", but it is in fact the neotype (MERTENS, 1966). JENTINK (1892: 197) is in error in describing this as "très jeune".

2. Stockholm 1572. Skull of a juvenile male rhinoceros (third molars not yet erupted) shot by SPARRMAN near Quammadacka (Kommadagga on the Klein Visrivier) on December 19th 1775 (SPARRMAN, 1778, 1787).

3. Paris A. 7. 969. Mounted skeleton of an adult, collected at the Cape by DELALANDE and arrived in the museum in 1821 (DESMAREST, 1822). It is the type of *Rhinoceros africanus* Desmarest, 1822).

4. Paris A. 2. 270. Juvenile skull (first molars in process of erupting) from the Cape, probably received in the late 18th or early 19th century. It was mentioned and figured by CUVIER (1812: 15, fig. 7) and by FAUJAS-ST-FOND (1809, pl. 10).

5. Frankfurt 699. Young adult skull (third molars not quite in place) without nasalia, received from the Cape of Good Hope by RÜPPELL in 1840.

6. Capetown 21383. Adult skull, with no provenance or date of accession; we follow ZUKOWSKY (1965: 28–29) in simply assuming that it belongs to this subspecies, because of its large size. (Measurements of this specimen have been kindly provided by Dr. Q. B. HENDEY).

7. London, BM (NH), 1962. 2. 16. 1. An adult skull picked up along the Hottentots River near Beaufort West. It is in a bad condition and only a few measurements can be taken.

8. London, BM (NH), 1838. 6. 9. 101. Skull of an aged rhinoceros, collected by ANDREW SMITH "about 180 miles N. E. of Lattakoo" (this would make it in the vicinity of Mafeking), and in the museum since 1838 (HOPWOOD, 1939: 454). It is the type of *Rhinoceros keitloa* A. SMITH, 1836; it was included with some misgivings in this subspecies by GROVES (1967) but, as will be shown below, there is no longer any reason for not allocating it firmly.

9. London, BM (NH), 1948. 1. 28. 4. Skull of a subadult (third molars in process of eruption) from the Rothschild collection; labelled "S. Africa; pseudo-simus form". It does not show any tangible similarities to "simus" – i.e., *Ceratotherium simum*, the White rhinoceros – beyond sheer size, and its measurements fit very well into the present race.

Certainly more rhinoceros material from the Cape was at one time in European collections. MERCK (1786: 4, pls. 1–2) had, for instance, a complete skull of which he figured the upper and lower jaws. Much better known are the head and skull of a rhinoceros sent by JOACHIM BARON VAN PLETTENBERG, from the Cape to Petrus CAMPER in 1771. CAMPER discussed and illustrated these in his well-known publications of 1777 and 1782 (with later translations into German and French). The skull was lodged in the Groningen museum where it was destroyed by fire in 1913. The head was sent to the Paris museum after Camper's death (CUVIER, 1812: 3), but is at present unrecognised.

Skull measurements

Rhinoceros systematics below the species level have been based almost solely upon skull measurements as a practically objective and generally used character. The measurements of the skulls listed above are given in Table 1.

It will be noticed that the measurements given by ZUKOWSKY (1964), derived in fact from the literature or from data to him by his correspondants, differ rather considerably from those taken (on all skulls except those of Stockholm and Cape-Town) by one of us (C. P. G.). It seems probable that the greatest discrepancy, that in Toothrow length, is due to the inclusion of the diminutive P¹ by ZUKOWSKY's sources: this is so frequently absent in *D. bicornis* adult skulls that it was thought better by C. P. G. to exclude it. This being done, it can be seen that the toothrow length of the type of *R. keitloa*, instead of falling well below the others – HOPWOOD evidently took the measurement without P¹ unlike other workers – now fits well within the general range; as its "small teeth" formed the only reason for GROVES (1967) suggesting it

Table 1: Skull measurements of available specimens of *Diceros bicornis bicornis*

Museum no.	Age	Occipito-nasal length		Basal length		Zygomatic breadth		Occipital breadth		Occipital height		Toothrow length	
		a	b	a	b	a	b	a	b	a	b	a	b
1) Groningen	YA?	—	732	—	650	—	392	—	245	—	198	—	340
2) BM 1838. 6. 9. 101	Aged	638	645	562?	—	355	357	192	195	—	—	274	265
BM 1962. 2. 16. 1	Adult?	—	—	—	—	373	—	198	—	—	—	255	—
3) Paris A. 7. 969	Adult	653	650	600	595?	352	350?	235	250?	152	150?	281	300
Capetown 21383	Adult	645	646	618	—	(394)	383	(220)	—	177	—	282	—
4) Leiden cat. a	YA/Adult	629	640	595	590	366	370	212	—	152	—	294	—
Frankfurt 699	YA	(580)	—	574	590	367	368	204	197	154	154	287	306
BM 1948. 1. 28. 4	J. II/YA	593	—	542	—	334	—	204	—	—	—	(272)	—
Stockholm 1572	J. II	—	562	—	542?	—	336	—	188	—	158	—	240?
Paris A. 2. 270	Inf./J. I	446	—	420?	—	283	—	149	—	—	—	—	—
<i>D. b. bicornis</i>	Mean	641.3	(4)	604.3	(4)	368.0	(5)	211.4	(5)	160.3	(3)	277.9	(7)
(adults)	s. d.	10.21	(4)	12.10	(3)	16.81	(5)	17.23	(5)	14.43	(3)	12.54	(7)
<i>D. b. chobiensis</i>	Mean	615.0	(4)	560.0	(4)	352.0	(4)	197.5	(4)	150.0	(4)	282.3	(4)
(adults)	s. d.	15.6	(4)	8.4	(4)	9.9	(4)	6.3	(4)	4.3	(4)	7.4	(4)

a: As measured by one of the present authors (C. P. G.); the Capetown skulls was measured by Dr. Q. B. HENDEY. The means and standard deviations are based on these measurements. b: As reported by ZUKOWSKY (1964); measured by various people. 1) Holotype of *Rhinoceros camperi* Schinz and of *Rhinoceros bicornis capensis* Gray, 2) Holotype of *Rhinoceros keitloa* A. Smith (and of *Rhinoceros ketloa* A. Smith?), 3) Holotype of *Rhinoceros africanus* Desmarest, 4) Neotype of *Rhinoceros bicornis* Linnaeus.

represented an intergrade population with *D. b. minor*, it suffices to place *keitloa* as an absolute synonym of the nominate subspecies.

The next greatest discrepancy, that in Occipitonasal length, can probably be explained as follows. In the African rhinoceroses, with their backwardly inclined occipital crest, the lateral wings of the crest extend caudal to the midline rim: the larger the skull, in general, the greater the discrepancy between midline and lateral measurements. This is not noticeable in smaller subspecies of *D. bicornis*, but certainly is in skulls measured in both ways by C. P. G. But ZUKOWSKY's correspondent JACQUES NOUVEL seems to have measured Paris A. 7. 969 along the midline, so that C. P. G.'s measurement of this nearly corresponds.

We have also included in Table 1 the measurements of the Groningen skull as converted to metric equivalents by ZUKOWSKY. Somewhat naively these were accepted at face value by GROVES (1967), but we do not feel so inclined here. The problem is that a scale of two feet—in Rhineland feet—is given on one of CAMPER's illustrations; so that obtaining measurements for the skull involves measuring the illustration itself. We find that ZUKOWSKY measured a little too large, although even so it would be a very large skull. Another problem now arises: the two-foot scale is on the figure not of the skull, but of the head! So it must be further assumed that the two are drawn to the same scale. Careful comparison of the two figures suggests that the skull is a little more enlarged than the head. The final question is the accuracy of the drawings themselves. One way to approach this is to compare the two figures, on the same plate, of the skull: one labelled, the other not. They are not identical, although as nearly so as could be expected of a superb draftsman in the pre-photographic era. Another way is to measure, against the two-foot scale, the figure of the head, of which CAMPER did give measurements in the text (if only he had quoted measurements for the skull). He gives the snout-ear distance, in the text, as 680 mm (converted), whereas taken from the figure it would be around 700; and the posterior horn length is given by CAMPER as 327 mm, but from the illustration it would be 350. (CAMPER's other measurements are too subjective, or else cannot be measurements of the Groningen skull). They were probably not quite as enormous as supposed by ZUKOWSKY and GROVES, though it still seems likely that the skull was the largest of the series.

The skull of GORDON's rhino (never sent to Europe) was said (CAVE & ROOKMAAKER 1977) to be 23½ inches (616 mm) long and 14 ins. (367 mm) broad. The first of these measure-

ments is on the small side for the Cape rhino, although the skull seems unquestionably adult; the second is well within the range.

Comparisons are necessary only with the largest living subspecies of black rhino, *D. b. chobiensis* (also a southern African race). *D. b. bicornis* is considerably larger (Table 1); it is relatively narrower, with a low occipital surface, and relatively small teeth: the toothrow length, in fact, is not much greater even than in the smallest subspecies (GROVES 1967), this feature being evidently one which cannot vary much and still be compatible with efficiency.

Dentition, and other skull features

As well as measurements, some non-metrical data on the teeth and skull are of interest. Of the five complete adult skulls of the Cape race (i.e. excluding the incomplete Beaufort West skull), only one retains the mandibular first premolar (P_1): and this, the Groningen skull, may simply not have been mature enough to have shed it. Of the other subspecies, the East African ones (*minor*, *michaeli*, *ladoensis*) generally lack it like the Cape race; while the two other extreme races, the Somali-Ethiopian *brucii* and the West African *longipes*, usually retain it. Interestingly, 60% retain it in the southernmost population of *D. b. minor*, that of Hluhluwe (ANDERSON 1966).

The crochet on each of the molariform maxillary premolars ($P^{2/3}$) is bifid in the Paris and Frankfurt skulls, in B. M. 1838. 6. 9. 101, and slightly so in the Leiden specimen; but only on P^3 in B. M. 1948. 1. 28. 4. This again is fairly like the East African races where it is often – but not invariably – bifid; and contrasts with *brucii* and *longipes* where it is simple.

Paris A. 7. 969 has a large crista on each of its molariform cheekteeth; the Leiden and Frankfurt skulls have a large one on each of the premolars, a small one on each of the molars; the two London skulls have a crista on P^3 and P^4 only. In this case, the similarities with other subspecies are reversed: *brucii* and *longipes* commonly have a crista on the premolars, occasionally on the molars also, while the East African races lack a crista altogether, or have an extremely minute one. Interestingly, although not very detailed, the drawings of the GORDON rhinoceros (CAVE & ROOKMAAKER, 1977, pl. 4) clearly show a crista on M^1 of at least the left side.

Examination of skulls reveals some interesting non-metrical characteristics which distinguish the nominate race. All the smaller subspecies have the posterior edge of the nasal notch above the distal half of P^2 , or above the $P^{2/3}$ space. In the Cape race, this point is further back along the toothrow: only B. M. 1838. 6. 9. 101 has the position above the distal part of P^2 , and the Stockholm skull (from photo, ZUKOWSKY, 1964: 22) has it above the $P^{2/3}$ space; all the others – Leiden, Paris, Frankfurt, Cape Town (ZUKOWSKY, 1964: 30), the Groningen skull and the other London skull – have it above the mesial half of P^3 , as does the illustration of the GORDON rhinoceros.

The position of the anterior edge of the orbit, relative to the toothrow, is also further back in the Cape race: between halfway along M^1 (Stockholm) and a quarter along M^2 (B. M. 1838. 6. 9. 101), compared to a position between a quarter and halfway along M^1 in the other races (very rarely as much as three-quarters along M^1 , in *brucii*). The GORDON rhino again shows a typical, even extreme, "Cape" position, about halfway along M^2 .

The infraorbital foramen is placed vertically above a point a quarter to halfway along P^3 in *brucii* and *longipes*; half to three-quarters along P^3 in East African races; and above the $P^{3/4}$ space in the Cape race, except in the Groningen skull where it seems to have been halfway along P^3 . In addition, this foramen is divided into two by a thin bony partition in all Cape skulls except Frankfurt, Cape-Town and Groningen; this is rather rare, although it does occur, in other subspecies. In the GORDON rhino, it is shown as being above the $P^{3/4}$ space, although not apparently bifid.

Postcranial skeleton

Paris A. 7. 969 and Leiden cat. a are complete, mounted skeletons, not skulls only. As shown in Table 2, there are differences from all other subspecies. The individual long bones are bigger

than in other races, but not as large as might have been predicted from the skull size: compared to the basal skull length, the humerus is shorter than in *minor* and *ladoensis* but longer than in *michaeli*, and falls within the (rather wide) range of *brucii*. The radius is still shorter: compared to all other subspecies, the radius: humerus ratio being under 80 % whereas in all others it is above 80 %. Although the metacarpal is relatively long this would not compensate, and the Cape rhinoceros must have been a comparatively stocky, short-legged animal in life.

The total foreleg length (Humerus + Radius + Metacarpal) is in the Cape rhino slightly shorter than the total hindleg; it is the same as in *ladoensis* and the reverse of the usual relationship in the species.

The Leiden skeleton has 21 thoracic vertebrae, a number equalled only by a Bonn skeleton of *D. b. michaeli*; the Paris skeleton has 20, a common number in the species, as did the GORDON rhino (CAVE & ROOKMAAKER, 1977: 147). What is unusual, however, is that the combined number of Thoracolumbar vertebrae is 24: a number equalled only by one other specimen, a "pickup" skeleton in the possession of Mrs. J. F. M. HORNE (Karen, Nairobi), of *D. b. michaeli*. The Cape race can thus justifiably be called long-bodied, both absolutely and in relation to its short limbs.

Note that DESMAREST (1822) gave the height of the Paris skeleton as 7 feet (224 cm); but measurement by one of us (C. P. G.) gave a height of only 170 cm.

Table 2: *Diceros bicornis*, postcranial skeleton

	Humerus length	Radius Humerus	Tibia Radius	Foreleg Hindleg	Humerus Basal	M-carpal Humerus	M-carpal Radius
<i>bicornis</i>							
Paris	493	78.9	98.7	99.1	82.2	40.4	51.2
Leiden	480	78.3	98.4	98.7	80.7	39.2	50.0
<i>minor</i> (3-6)	454- 479	83.9- 85.0	87.7- 97.2	100.1- 104.9	84.3- 85.5	35.5- 41.0	42.3- 48.7
<i>ladoensis</i> (1-3)	480	85.6- 89.0	90.9- 94.9	98.3- 99.0	83.2	41.5- 42.9	45.6- 46.6
<i>michaeli</i> (2)	394- 413	85.5- 90.1	89.9- 90.3	100.8- 101.0	75.9- 79.3	41.4- 42.9	47.6- 48.4
<i>brucii</i> (4-5)	413- 440	80.9- 85.7	88.0- 93.8	100.3- 106.5	79.3- 83.8	36.4- 41.7	42.7- 51.5

		Vertebral formulae: Th L Th+L S			
<i>bicornis</i> :	Paris	20	4	24	4
	Leiden	21	3	24	5
<i>minor</i> :	USNM 198398 (Natal)	-	-	-	4
<i>ladoensis</i> :	Nairobi 9 (Nyeri)	19	3	22	5
	Nairobi 5 (Nyeri)	19	4	23	5
	Nairobi 4 (Nairobi)	20	3	23	5
<i>michaeli</i> :	Nairobi 6 (Kiboko)	19	4	23	4
	Nairobi 11 (Nguruman)	-	-	-	-
	coll. J. Horne (Nguruman)	19	5	24	4
	Bonn no. no. (Kahe)	21	2	23	5
<i>brucii</i> :	BM 76. 12. 15. 5 (Abyssinia)	20	3	23	5
	BM 71. 11. 29. 4 (Bogos)	20	3	23	5
	BM 69. 2. 2. 14 (Anseba R.)	20	3	23	5
	BM 76. 9. 26. 6 (Atbara)	20	3	23	5
	Virchow (1910)	20	3	23	4

Soft parts anatomy

In 1775 SPARRMAN dissected a male Cape rhinoceros and his notes (de BOUVEIGNES 1953) are the only published data about this race. The remarks and drawings of R. J. GORDON's dissection of another male Cape rhino provide another source and they are compared with material of living subspecies in CAVE & ROOKMAAKER (1977). It is rather extraordinary that published comparative data are very scarce for any of the living races, but what little information is available on one organ system or another can be used, and the comparison is interesting.

From the data published by de BOUVEIGNES, the heart in SPARRMAN's rhino (from Kommadagga) was 46 cm. long and the same breadth; GORDON's specimen measured 34×34 cm. This is larger than the heart in a female *D. b. minor* from Zambia which measured 30,5×28 cm (WILSON & EDWARDS 1965).

The stomach in the SPARRMAN specimen measured 120×61 cm.; in WILSON & EDWARD's Zambian female, 78.5×60.9 cm. The small intestine was small, 8.03 m. in the Cape animal cf. 11.6 m. in the Zambian; the colon 2.44 m., the caecum 1.05 m., cf. the two together 4.5 m. in the Zambian animal. The whole was 7 times the head and body length in the Zambian animal; in the Cape animal, if SPARRMAN's figure of 354 cm. is a straight length (which is doubtful) then the alimentary canal would be about 4.2 times the head and body length. If we estimate a more likely head and body length of 300 cm., then the alimentary tract is 5 times. Either way the difference is striking and hard to explain; it seems rather doubtful whether study of further specimens would completely close the gap even in this admittedly rather variable feature.

The liver in SPARRMAN's rhino measured 105×75 cm.; in GORDON's 73×60 cm.; and in WILSON & EDWARD's 75×50 cm. The Cape rhino's liver had three large lobes – and in SPARRMAN's specimen an additional small one only 30 cm long –, the Zambian one had five lobes.

The kidneys were 45 cm. in diameter in SPARRMAN's specimen, 23×18 cm. in the Zambian, while MEINERTZ (1972) found 32×18 cm. for the left kidney and 28×20 cm. for the right one in a male black rhinoceros that died in the Copenhagen zoo in 1969 (studbook no. 10–CPH 1, origin unknown).

CAVE (1977: 277, fig. 1h) compared GORDON's drawings of the tongue with material of another race and found them morphologically well in agreement. The spleen in SPARRMAN's rhino measured 120×45 cm. and in GORDON's 118×21 cm., but comparative data have not been published.

External appearance

According to GROVES (1967: 270–1) three general habitus-types, corresponding to geographical groupings, can be possibly distinguished for *Diceros bicornis*. In view of the fact that the Cape subspecies became extinct before the age of scientific photography, no really reliable depiction of it exists: at least none which can help us to give it as particular "habitus". But because most of the illustrations of it are practically unknown, they are discussed here.

1. JAN WANDELAAR made the first reasonably naturalistic engraving of a Cape Black Rhinoceros, after a sketch received from the Cape of Good Hope (ROOKMAAKER 1976). It was published by KOLB (1727).

2. ANDERS SPARRMAN shot two male rhinoceroses near Kommadagga on December 19th 1775. The smaller of these is the one dissected by him (see above), and the one whose skull is now in Stockholm. His publications include a plate of the penis, and another with a rather poor lateral view of the animal, and its skull below it (SPARRMAN 1778, 1779, 1787).

3. HENDRIK CLOETE, companion of HENDRIK SWELLENGREBEL, shot a rhinoceros on 1 November 1776 near the Kleine Visrivier. The artist JOHANNES SCHUMACHER, who was also present, made one drawing of the hunt and two depicting rhinoceroses from the side (HALLEMA 1951). These fine figures remain unpublished.

4. ROBERT JACOB GORDON killed a male black rhinoceros near the source of the Gamka river on 2 November 1778. He described, measured and dissected the animal and made several drawings that show anatomical details, and two very good side views (CAVE & ROOK-MAAKER 1977). The lateral view was badly copied by ALLAMAND (1782, pl. 6) and formed the ultimate source of LESSON's *Rhinoceros gordonii*.

5. BURCHELL (1824: 46, 79) published two drawings of rhinoceros heads taken from animals shot in the region of Britstown. On 19 October 1812 he killed a female near Chue Spring (Heuning Vlei), Bechuanaland (northern Cape Province). He made four drawings including a side-view of the rhinoceros when still alive, and another after having been shot; the latter shows several measurements (CAVE 1947, pl. 5, text-fig. 1).

6. ANDREW SMITH (1838, Mammalia pl. 2) illustrated his account with a mother and young. Although it is not stated, this figure probably depicts South African specimens.

7. HARRIS (1840, pl. 16) depicted a (probably) South African rhinoceros. His plate was (somewhat over-) praised by ZUKOWSKY (1964: 36-7).

Interpretation is difficult and must be done very carefully considering the difficult circumstances under which most of the illustrations were made. On the whole they seem to confirm the conclusions from the postcranial skeletons, of short – also perhaps slender – legs, and a long, but compact body; the skin seems smooth, and not deeply folded.

Size

Only two body measurements have been given in the literature with any frequency: body length and shoulder height (Table 3). Two methods of measuring the body have been applied: following the curvature of the back, and in a straight line. Most authors have evidently used the first method, the figures given being of the same order as those by GORDON and BURCHELL who took both, and compared them. The statements by HOP, THUNBERG, HARRIS and perhaps SPARRMAN must have been estimates, and not the measurements of one particular animal. Taking all this into account, we can say that the Cape rhinoceros probably had a body length of 280–290 cm. (in a straight line) or 340–365 (?) cm. (following curves), and a shoulder height of 160–180 cm.

Further measurements are available on BURCHELL's drawing (CAVE 1947, fig. 1) and in GORDON's notes (CAVE & ROOKMAAKER 1977; cp. ALLAMAND 1782, 1785).

Table 3: Body length and shoulderheight of the Cape rhinoceros in original sources. The measurements are usually given in feet and inches; an approximate conversion into cm is provided.

Source	body length in a straight line	body length following the curvature of the back	shoulderheight	notes
Hop 1778: 37	–	12' = 365 cm.*	6'-7' = 180–210 cm.*	
Sparrman 1778, 1787	–	11'6" = 354 cm.*	6'6"-7' = 195–210 cm.*	"estimated"
Gordon (1778)	9'3" = 290 cm.	11'0"3" = 346 cm.	5'3" = 165 cm.	Cave & Rook- maaker 1977
Thunberg 1811: 320	–	12' = 365 cm.*	7' = 210 cm.*	
Burchell 1824	9'3" = 282 cm.	11'2" = 340 cm.	–	
Burchell drawing	9'4" = 285 cm.	–	5'4" = 163 cm.	Cave 1947, fig. 1.
Smith 1838	–	10'11" = 363 cm.*	4'10" = 147 cm.	
Harris 1840: 371	–	about 13' = 400 cm.*	often 6' = 180 cm.	
Leiden, cat. a	–	–	170 cm.	
Paris, A. 7. 969	–	–	170 cm.	
Paris, see to Desmarest	–	11'6"6" (367,9 cm.)	7 ft (224 cm.)	

* In these cases it is not indicated how the measurements were taken.

Discussion

The map (Fig. 1) shows the localities from which the Cape rhinoceros has been recorded: localities supported by specimens are ringed. Also indicated is the approximate location of "Caffraria" – more or less equivalent to the modern Transkei – whence *Diceros bicornis minor* is known. The nearest *D. b. bicornis* locality (Kommadagga) approaches this quite closely, yet there is no indication of intermediacy. On the whole it seems improbable that there was reproductive isolation; rather, it is likely that there was a narrow zone of secondary intergradation. Under such circumstances the recognition of subspecies is a justifiable – and helpful – procedure.

The closest living subspecies to *D. b. bicornis* is not *minor* but *chobiensis*, a race restricted to the Chobe valley on the Angola-Zambia-Botswana border, where the Caprivi Strip of Namibia juts into this politically complex region. This at once suggests that large rhinos occur in well-watered areas, small ones in more arid regions. The range of *D. b. minor* more or less corresponds to the Southern Savannah zone (DAVIS, 1962), exclusive of the Highveldt, while *D. b. bicornis* extended from the Highveldt of the western Transvaal to the high-rainfall South-West Cape zone: in analogy to the *chobiensis* enclave in another wet enclave further north. Such geographical partitioning of subspecies in South Africa has many striking analogies (MAZÁK 1975: 9).

Included on Fig. 1, however, are the type locality of *Rhinoceros niger* Schinz (no specimen known), and Kolmanskuppe, the locality of the specimen in the Lüderitz museum – a damaged mandible – assigned by ZUKOWSKY to his subspecies *niger*. As ZUKOWSKY demonstrates

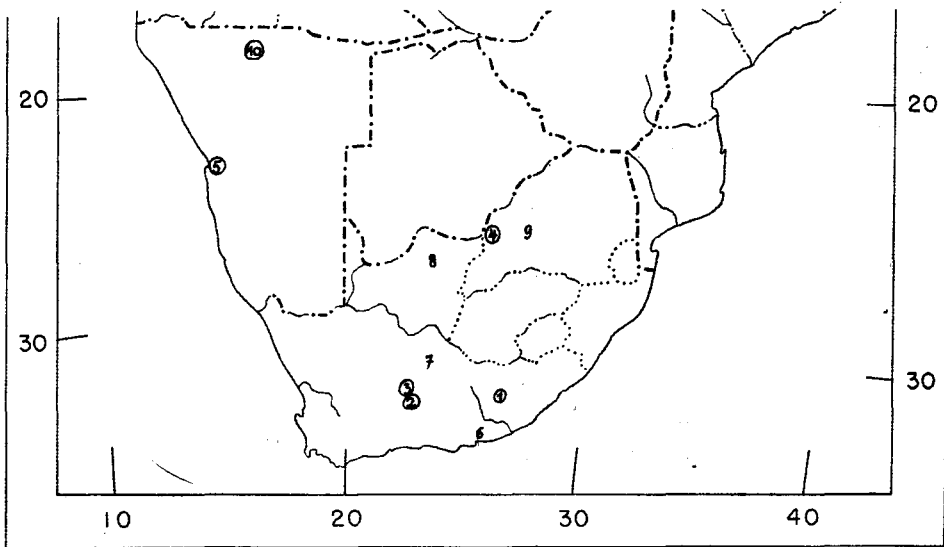


Fig. 1: Locality records for *Diceros bicornis bicornis*. Localities supported by a specimen are ringed. 1 Quammadacka (Kommadagga), Klein Visrivier, near Somerset (33.10 S, 25.55 E). SPARRMAN, 1778, 1779, 1787; de BOUVEIGNES, 1953. Stockholm, 1572. – 2 Hottentots River, near Beaufort West (32.21 S, 22.35 E). B. M. 1962.2.16.1. – 3 Source of Gamka River (about 10 miles north of Beaufort West). – CAVE & ROOKMAAKER, 1977. *Rhinoceros gordonii* Lesson, 1827 (specimen no longer in existence). – 4180 miles N. E. of Lattakoo (= Kuruman), Marico district; upper Kuruman River (would be near Mafeking; 23.53 S, 25.39 E). SMITH, 1838. B. M. 1838.6.9.101; type of *Rhinoceros keitloa* A. Smith, 1836. – 5 Kolmanskuppe, inland from Lüderitz (26.40 S, 15.12 E). ZUKOWSKY, 1964. – 6 Coega River, close to Port Elizabeth (33.46 S, 25.40 E). ZUKOWSKY, 1964. – 7 Britstown (30.36 S, 23.30 E). BURCHELL, 1824. – 8 Chue Spring, Heuning Vlei (26.18 S, 23.09 E). BURCHELL, 1824. – 9 Kurrichaine, 30 k. East of Mafeking (25.55 S, 26.00 E). SMITH, 1838. – Probably a generalised area for *Rhinoceros keitloa*, within which locality (4) falls. – 10 Chuntop River, near Mt Mitchell (= Tsondap River, Nuibeb Mts., 16.40 E, 23.50 S, *vide* ZUKOWSKY, 1964), Type locality of *Rhinoceros niger* Schinz, 1845 (specimen no longer in existence).

(1964: 52–54) the mandible in question is of this genus – not *Ceratotherium* – and has certain unusual features, notably its very large size. Such a size is, however, not impossible for *D. b. bicornis*. For example, ZUKOWSKY gives corpus height at M₃ (including M₃ itself) as 160 mm., which is only slightly greater than the same measurement for Leiden cat. a. (154 mm.) or the type of *keitloa* (149 mm.). Other specimens of *bicornis* vary from 130 to 143 mm., and other subspecies range up to about 130 mm. The length of the lower toothrow, 292 mm. according to ZUKOWSKY, falls in the upper half of the range of *D. b. bicornis* (from 267.5 in the Frankfurt skull, to 302 in the Leiden specimen), and is too large for any other subspecies (250–268).

The limited evidence, therefore, is compatible with the Kolmanskuppe jaw being a specimen of the present race. Whether the type of *niger* also belonged here, there is no means of telling; but the type locality is nearer to Kolmanskuppe than to the Kaokoveld localities where *D. b. minor* (or *occidentalis*, which may be a valid race) is found. Hypothetically, the two southern Namibia records represent the most northwesterly outposts of the southern race, which in that area would have been gradually fragmented into local isolates by the encroachment of the desert.

If *D. b. chobiensis* is truly related to *D. b. bicornis*, then the two could represent the remains of a former continuum, showing a south-north cline of size reduction, which has been interrupted by the spread of smaller races along with increasing aridity. But the general skull features of *chobiensis* seem to recall *minor* rather than *bicornis* (i.e. positions of infraorbital foramen, anterior orbital border, and nasal notch), and it is more likely that the only similarity – large size, much less in evidence in *chobiensis* – is an independent adaptation to somewhat similar environments.

In summary, then, the extinct Cape rhinoceros was not quite as large as supposed by ZUKOWSKY (1964) and GROVES (1967), but nonetheless still much the largest subspecies; apparently restricted to the Southwest Cape zone and the highveldt. It must have become extinct around 1850.

Synonymy

Diceros bicornis bicornis (Linnaeus, 1758). Cape rhinoceros

1758 *Rhinoceros bicornis* Linnaeus. "India": Cape of Good Hope (Thomas, 1911). Neotype, Leiden cat. a (complete skeleton), from the Cape, coll. BOEIE & MACKLOT.

1803 *Rhinoceros africanus* Blumenbach. Cape of Good Hope.

1822 *Rhinoceros africanus* Desmarest. Cape of Good Hope. Holotype, Paris Museum A. 7. 969 (complete skeleton), from the Cape, coll. DELALANDE.

1836 *Rhinoceros keitloa* A. Smith. Country north and south of Kurrichaine (now Marico). Holotype B. M. 1838. 6. 9. 101, skull only, from near Mafeking, coll. A. SMITH.

1837 *Rhinoceros ketloa* A. Smith. "180 miles N. E. of Lattakoo" (= Kurrichaine, = Marico). Lapsus for *keitloa*.

1842 *Rhinoceros gordonii* Lesson. Based on BLAINVILLE's and DESMAREST's "Rhinocéros de Gordon", and so on ALLAMAND's (1782) description of the rhinoceros shot by GORDON near sources of the Gamka River.

1845 *Rhinoceros niger* Schinz. "Chuntop, near Mt. Mitchell" (= Tsondap, Nuuibeb Mts., acc. to ZUKOWSKY 1964).

1845 *Rhinoceros camperi* Schinz. Cape of Good Hope. Holotype, the specimen described by CAMPER, formerly in the Groningen Museum, now no longer in existence.

1867 *Rhinoceros bicornis capensis* Gray. A formalisation of CAMPER's dog-Latin "*Rhinoceros bicornis capensis*", and so based on the same specimen as the previous name.

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