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Age estimation of the White rhinoceros (*Ceratotherium simum*)

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(With 4 plates and 5 figures in the text)

Age estimation criteria for the southern White rhinoceros (*Ceratotherium simum simum*) are presented both for free-ranging live animals and for cranial material. These are based on: (i) size appearance and horn development of live animals; (ii) stages of tooth eruption; (iii) tooth wear classes; (iv) attrition in height of the first molar tooth; (v) counts of cementum lines visible in tooth sections. Selected measurements are presented for live animals, skulls and horns.

For live animals, eight size classes are distinguished, seven of these covering immature animals up to ten years of age. Sixteen tooth wear classes are established, based on eruption and surface wear of maxillary dentition. Chronological ages were assigned from individually known animals followed in the field, and from skulls from animals for which exact records of age were available, or which could be assigned to an age category from appearance at death. Cementum line counts corresponded approximately with age in years, despite difficulties in interpreting lines. Some variability was observed, possibly related to nutritional conditions.

The maximum cementum line count obtained indicates a longevity of at least 40 years. Full body weight and socio-sexual maturity are attained by males between 10 and 15 years of age, while females first give birth between six and eight years of age. Sequences and times of tooth eruption are similar to those reported for the Black rhinoceros (*Diceros bicornis*).

Comparative cranial and body measurements are presented for the northern subspecies (*Ceratotherium simum cottoni*).

Contents

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Introduction

For studies on mammalian population dynamics and their application in wildlife management, criteria are needed for assigning animals to particular age classes. These criteria are particularly difficult to establish for large, long-lived mammals like rhinoceroses (Perissodactyla: Rhinocerotidae), due to the lack of discrete breeding seasons, and the fact that stages of immaturity are spread out over several years. Moreover, there are the practical problems of securing sufficient material from populations that are relatively sparse, and frequently specially protected because of their rarity. However, it is particularly for such rare species that this information is needed in order to assess population trends and hence conservation status.

In this paper, we present age estimation criteria for the White or Square-lipped rhinoceros, *Ceratotherium simum*. These cover (a) visual features that can be applied to free-ranging live animals; (b) cranial characteristics, especially aspects of dentition such as the time of tooth eruption, wear patterns and counts of cementum lines visible in sectioned teeth (Morris, 1972) that can be applied to found skulls. For the Black rhinoceros (*Diceros bicornis*), age estimation criteria have been reported in terms of field characteristics by Schenkel & Schenkel-Hulliger (1969) and Hitchins (1970), while dental features have been described in detail by Goddard (1970) for East African animals, and Hitchins (1978) for South African specimens. For White rhinos, the early pattern of tooth eruption in calves has been described by Bigalke *et al.* (1950) and Dittrich (1972). Apart from this, there have been no previous publications describing dentition and other age estimation criteria for White rhinos. All specimens described in this paper are from the southern race, *C. s. simum*.

Materials and methods

Field criteria

Age estimation criteria for live animals were developed as part of a field study carried out by N.O-S. in the Umfolozi Game Reserve in Natal between 1968 and 1971 (Owen-Smith, 1973). All adult White rhinos and many subadults could be identified individually from variations in horn sizes and shapes, and 35 animals were marked with identifying ear-tags. Initially, immature animals were assigned to size classes based on height relative to that of an accompanying adult female, and on the size of the horns estimated in terms of ear-lengths. During the course of the study, known individuals were photographed repeatedly in order to record their development over the 2·8-year period of observation. By matching the appearance of younger age classes at the termination of the study with photographs of older age classes taken at the start, it was possible to piece together a complete sequence of development in relation to age. Growth in height with age was assessed from repeated photographs of known individuals, whose ages were known to within ± 1 month for animals younger than 6 months, and ± 2 months for animals aged between 6 and 12 months, when first seen. Photographs were taken so that the calf was standing close in front of its mother in lateral perspective, with the camera approximately level with its back, so as to reduce perspective distortion. The point where the top of the pre-sacral crest (the highest point of the body) reached was marked on the side of the image of the adult female, and height was measured from the feet of the adult to this mark, relative to the pre-sacral height of the adult in the photograph.

Weight ranges are based on estimates made by Natal Parks Board personnel involved in capturing White rhinos for translocation. The prior estimates made at the time of capture agreed closely with the subsequently measured weights of 8 young rhinos transported to Zimbabwe (Condy & Davison, 1964). These estimates are supported by a few weights that were measured for animals found dead in the field, which could be assigned to size classes on the basis of other measurements made (P. M. Hitchins, pers. comm.).

Standard measurements were taken from live animals that had been immobilized for ear-tagging or placement of radio transmitters. Measurements include horn length (along the anterior curve), basal circumference of the anterior horn, head circumference (measured between the 2 horns in earlier specimens, but subsequently behind the posterior horn with the tape extending over the eye), spine length (occiput to base of tail), and heart girth (round the body behind the shoulder).

Cranial characteristics

All rhino skulls and mandibles found during the field study in Umfolozi Game Reserve were collected and photographed by N.O-S. to show dentition. Animals that were encountered freshly dead could be assigned visually to age classes, so that approximate ages were established for the subsequently collected skulls. The sample includes one juvenile for which the exact month of birth was known (Table I, Plate IIIa).

Found skulls from Umfolozi were supplemented with skulls from animals that had died in Pilanesberg Game Reserve, Bophuthatswana, including some animals shot as trophies. All skulls were examined by A.K.K.H-S. with the assistance of J.P.S. and J.L.A. to establish dental and cranial characteristics for age determination. Skulls were grouped into wear classes according to the stages of tooth eruption and attrition and measurements of the first permanent maxillary molar (M^1). They were related to the dental appearance of animals whose age at death was known, or estimated from size and appearance. These included photographs of 4 skulls from Umfolozi animals that had been encountered by N.O-S. shortly after death, and 5 skulls from animals kept in a 2·5 km² enclosure near Pretorius Kop Camp in the Kruger National Park, for which age records had been kept (supplied by A.J.H-M.) (Table I). For early stages of

TABLE I

Known-age skulls used in assigning chronological ages

Source locality	Material	Label	Sex	Age
Kruger Park enclosure	complete skull	K1	female	9 y 7 m
Kruger Park enclosure	complete skull	K2	male	4 y 0 m 3 d
Kruger Park enclosure	complete skull	K3	female	6 m 24 d
Kruger Park enclosure	complete skull	K4	female	6 m 21 d
Kruger Park enclosure	complete skull	K5	female	10 y 4 m
Umfolozi Reserve	photographs	N0	male	4 ± 1 y
Umfolozi Reserve	photographs	N8	female	5 ± 1 y
Umfolozi Reserve	photographs	N20	female	14 ± 1 m
Umfolozi Reserve	photographs	N27	female	3·5 ± 0·5 y

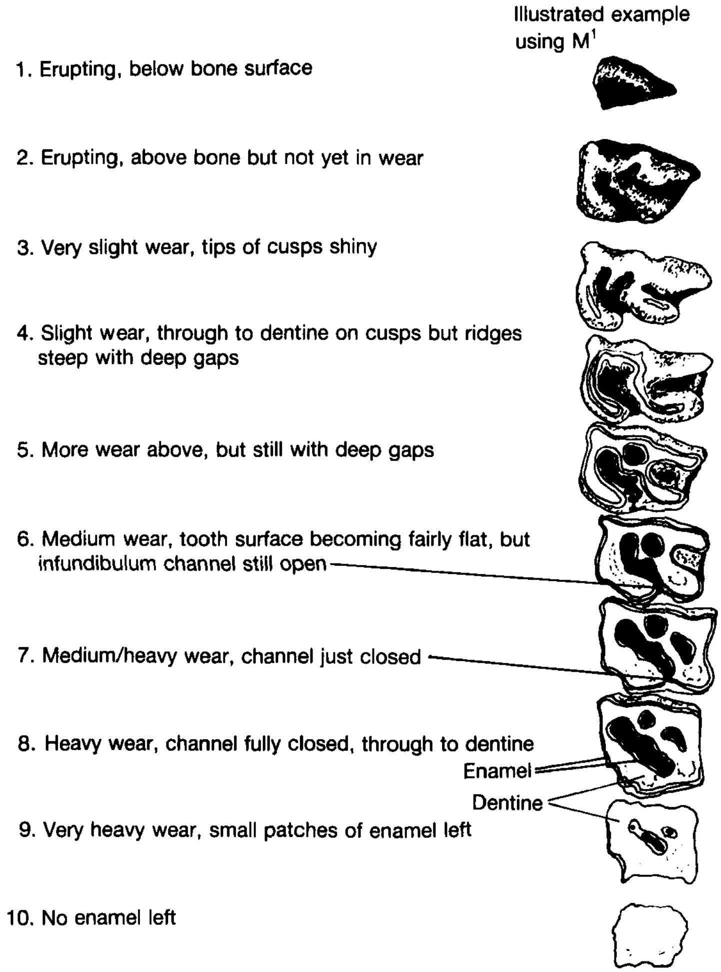


FIG. 1. Definitions of tooth eruption and wear stages.

tooth development, reference was made to the published reports of Bigalke *et al.* (1950) and Dittrich (1972) based on captive calves. Both the Kruger and Pilanesberg populations are derived from animals translocated from the Umfolozi Reserve. The total sample comprised 74 skulls.

A tooth was defined as erupting when the tip protruded above the bone of the maxilla or mandible, and as fully erupted when the tip began to show wear. Subsequent wear stages were based on the degree of attrition of the enamel cusps and channels visible on the surface. The wear stages differentiated are presented in Fig. 1. The patterns recorded for each tooth were combined to yield an overall dental description of the complete maxilla or mandible. Fairly obvious changes, such as the eruption of a new tooth, were used to separate overall wear classes. Classification was based on maxillae for which sample size was larger and eruption/wear stages more uniform than for mandibles. However, tooth eruption and wear patterns are also described for corresponding mandibles, since these are more easily transported and stored than the bulky skulls.

The maximum height above bone level and maximum width were measured for a maxillary first molar (M^1), or, in young animals where M^1 was not fully erupted, for the first deciduous premolar (pm^1). First molar teeth were removed from the skull, and crown height was measured on the buccal side from the lowest point between the buccal crests to the saddle between the roots, as described by Spinage (1971, 1972).

Cementum line counts. A maxillary M^1 from each skull was cut in half using a hacksaw. The angle of cut was maintained constant as far as possible: vertically, bucco-lingually through the tooth between the anterior and posterior roots and through the cementum pad. The cut surface was polished using 2 grades of carborundum paper (pl20 and p360) and metal polish, to give a smooth surface. The surface was examined through a binocular microscope using an oblique light source. The cementum shows alternate light and dark lines. Light lines only were counted. The lines frequently subdivided along their lengths, particularly in teeth from older animals. The number of lines was assessed by following lines along their lengths to eliminate those that were merely subdivisions, and by taking a mean value from counts at different points along the cementum pad. As a further check, counts were made on the same specimen by different observers, and the overall mean value used.

From a sample of 2 skulls for each age class, every tooth on one side of the maxilla was removed, cut and the cementum lines counted. This was done to determine the relative ages of eruption for each tooth.

External cranial measurements, as defined by Roberts (1951), were made for all skulls. Horns were also measured where available. The lengths of both the anterior and posterior horns were measured along the curve, while basal circumference was measured along the rim where the horn joined the skull.

Results

(*a*) *Field criteria for live animals*

Labels and definitions of the size classes established in the field study are presented in Table II, together with the estimated age range. Measurements of horns and body dimensions and estimated ranges in weight are presented in Table III. Five size classes represent juveniles, i.e.

TABLE II

Size classes used in field ageing of White rhinos in Umfolozi Game Reserve

Category	Label	Definition based on height relative to an adult female	Est. horn length (in ear-lengths*) anterior	posterior	Est. age range (months)
Infant	I1	Height below adult's shoulder fold	bump	none	0-2
Infant	I2	Slightly larger, still lacking posterior horn	lump	none	2-4
Juvenile	J1	Pre-sacral crest not more than half-way up side of adult	$\frac{1}{4}$	discernible	4-9
Juvenile	J2	Pre-sacral crest up to top of adult's flank fold	$\frac{1}{2}$	bump	9-18
Juvenile	J3	Pre-sacral crest up to top of adult's iliac projection	$\frac{3}{4}$-1	knob	18-30
Subadult	S1	Pre-sacral crest not above adult's sacrum	1-1$\frac{1}{2}$	knob	30-72
Subadult	S2	Discernibly smaller than an adult	1$\frac{1}{2}$-2	$\frac{1}{3}$-$\frac{1}{2}$	72-120
Adult	A	Fully grown	1$\frac{1}{2}$-4	$\frac{1}{4}$-1$\frac{1}{4}$	120-480

*One ear-length = 23 cm for class J3, 26 cm for adult

TABLE III

Measurements for immobilized White rhinos within each size class in Umfolozi Game Reserve

All lengths in cm, weights in kg. Upper figure = mean; lower figures = range. Also included are measurements for dead or captured animals corresponding to measured weights, supplied by P. M. Hitchins

		Sample size		Horn length			Head circum.				
Label	Sex	max.	min.	ant.	post.	Ant. horn basal circ.	between horns	post horns	Spine length	Heart girth	Est. weight range
I1		—	—	—	—	—	—	—	—	—	40-110
newborn											
infant[a]	♀	1	1	—	—	—	—	—	82	94	75*
small											
infant[b]	♀	1	1	—	—	—	—	—	99	119	115*
I2		—	—	—	—	—	—	—	—	—	110-180
J1		—	—	—	—	—	—	—	—	—	180-400
small											
juv.[c]		—	—	—	—	—	—	—	—	—	261*
J2		—	—	—	—	—	—	—	—	—	400-600
				25	7	45		104	202	208	
J3	♂	4	4	23-28	6·5-7·5	42-48	—	102-107	195-207	206-210	600-800
				27	9	46	—	93·5			
	♀	2	2	23-30							
injured[d]	♂	1	1	24	5	—	—	—	183	206	687*
				39	13	55	107	121	218	238	
S1	♂	5	1	34-47	9-16	45-60	102-109	119-122			800-1200
				35	11	50	100	116	226	240	
	♀	7	4	27-41	7-16	46-54	100-101	111-122	223-231	228-252	800-1100
dead[e]	♂	1	1	—	—	—	—	—	224	238	1090*
				53	16	69	121	137	262	288	1200-2000
S2	♂	6	3	41-57	15-21	67-72		133-144	256-270		
				46	16	60	119	129	246		1100-1500
	♀	3	1	43-52	15-17			127-132		—	
				60	26	75	125	144	269	284	2000-2400
A	♂	9	4	43-69	16-39	70-79	121-130		259-284	260-328	
				69	20	66		130	262	286	
	♀	6	5	52-82	16-26	65-68	—	126-137	248-273		1500-1700
killed[f]	♂	1	1	—	—	—	—	—	—	—	2130*

a—umbilical cord present but dry, est. age 2 d, but probable age *c.* 3 wks; b—est. age 3 wks, but probable age 2 m; c—est. age 5·5 m; d—gored by another rhino, destroyed; e—dead from horn wounds; f—killed and weighed in the field in sections; * measured weights.

animals that were generally still accompanying their mothers. Separation from the mother usually took place between two and three years of age at the time of birth of the subsequent offspring. Two classes of subadult were distinguished, with the division between them corresponding roughly to the age at sexual maturity. In Umfolozi, females generally gave birth to their first offspring at about 6–7 years of age (Owen-Smith, 1973). In zoos, the mean age at first parturition was 5 y 10 m for known-age animals ($n = 6$, range 5 y 1 m – 6 y 2 m), and *c.* 8 y for animals for which only the year of birth was known (Lindemann, 1982). Zoo records show that males can become sexually potent at six years of age, but in the wild males do not become sexually active until they acquire territory holding status at about 10–12 years of age (Owen-Smith, 1975).

Photographs of known-age individuals representing each size class are presented in Plates I and II. A curve for growth in height of known-age calves relative to the mother, based on measurements taken from photographs, is presented in Fig. 2. Kirby (1920) gives the shoulder

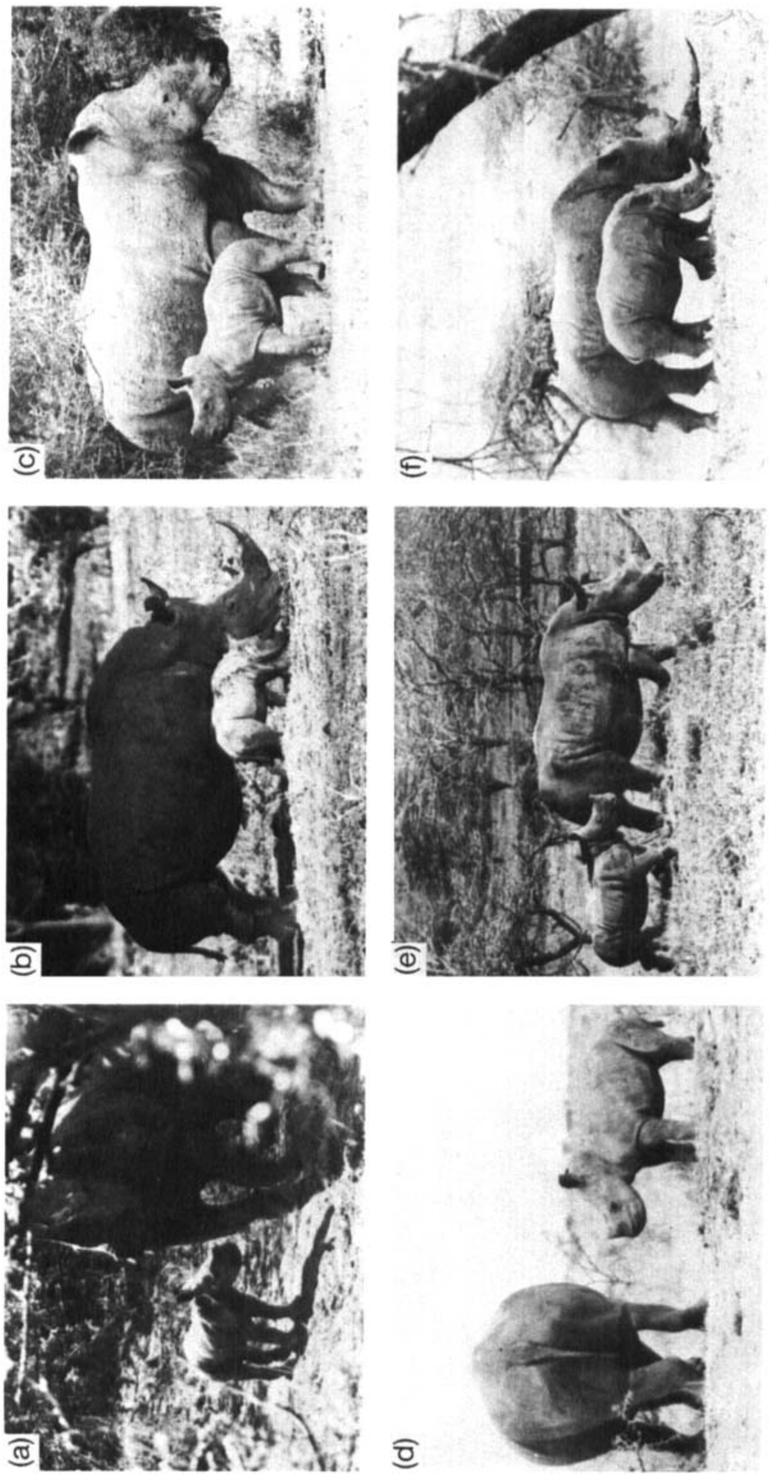


PLATE I. Photographs of known-age White rhinos in Umfolozi Game Reserve: infant and juvenile size classes. (a) newborn I1 male, age 3 d; (b) infant I1 male, age 22 d; (c) infant I1 male, age 7 wks; (d) infant I2 male, age 4 m; (e) juvenile J1 male, age 6·7 m; (f) juvenile J2 male, age 11·5 m.

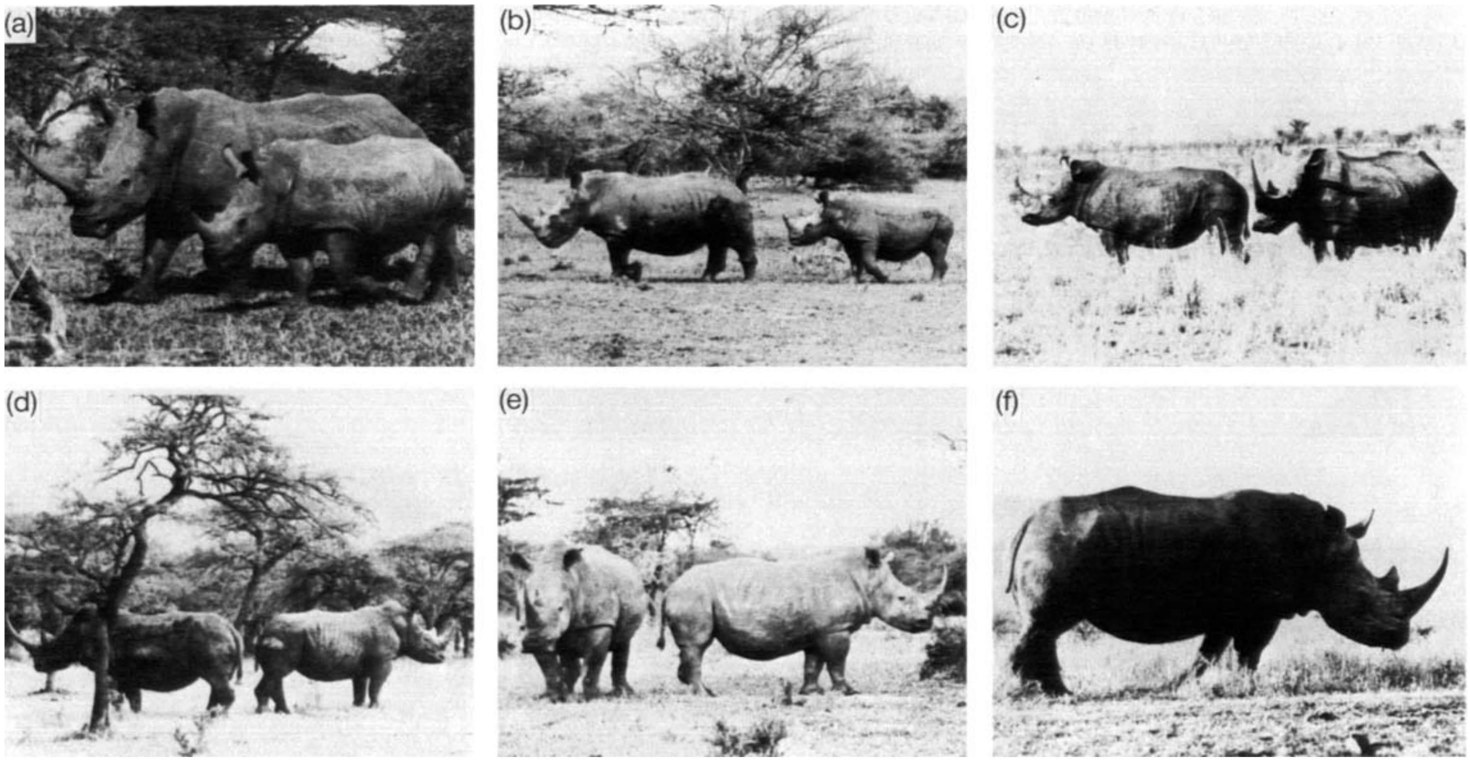


PLATE II. Photographs of known-age White rhinos in Umfolozi Game Reserve: juvenile and subadult size classes. (a) juvenile J3 male, age 18·5 m; (b) juvenile J3 male, age 22 m; (c) subadult S1 female, age 3·5 y; (d) subadult S1 male, age 5 y; (e) subadult S2 female, age 6 y; (f) subadult S2 male, age 8 y.

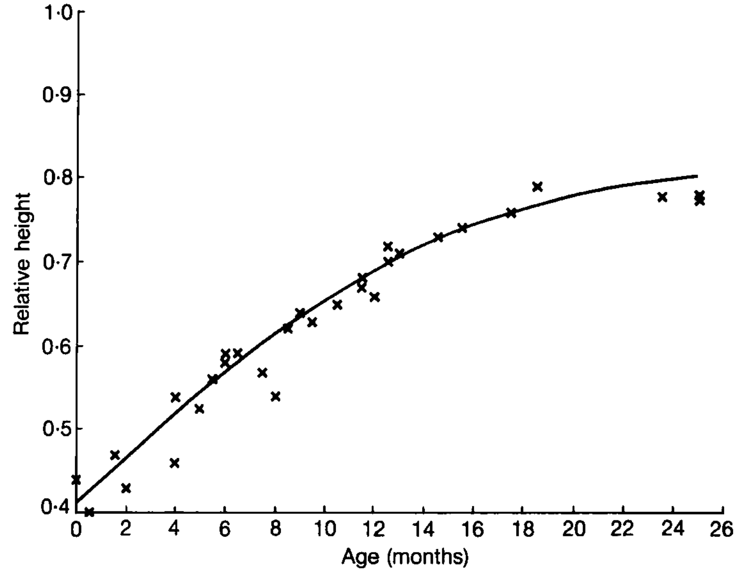


FIG. 2. Growth in height with age of White rhino calves, based on photographic measurements of height relative to that of an adult female.

heights of two adult specimens selected for their large size as: male—179 cm; female—177 cm. Foster (1960) lists the shoulder heights of four specimens (sex not stated) as 171–185 cm. The shoulder heights of two adult males measured while recumbent after immobilization were 178 cm and 174 cm, respectively (P. M. Hitchins, pers. comm.).

Measured weights are sparse. There is only one record of a measured weight for an adult. This is derived from a youngish adult male, with the last molar not fully erupted, that was sectioned and weighed in the field for the purpose of estimating the drug dosages required for immobilization. This animal weighed 2130 kg (J. Clark, pers. comm.). Maximum weights estimated for males are about 40% greater than those estimated for adult females; but, from the relatively small differences in linear measurements between the two sexes (Table III), the weight difference is probably exaggerated.

Two measurements clearly separate adult males and adult females into discrete groups: head circumference, and the basal circumference of the anterior horn. Male horns are stouter, but tend to be shorter, than those of females. Some females exhibited an anterior horn that projected strongly forwards rather than upwards, but this aberration was not observed in any male.

(*b*) *Cranial features*

Dental formula

The typical dental formula for White rhino is:

Deciduous: i 0/0, c 0/0, pm 4/4
Permanent: I 0/0, C 0/0, PM 3/3, M 3/3

The deciduous premolars 2, 3 and 4 are replaced by permanent premolars, while premolar 1 is not replaced. Individual aberrations recorded among skulls ($n = 74$) include the retention of a relict pm^1 in a maxilla in wear class XIV (22–23 y), and in a mandible of wear class X (8–11 y). A tooth developing posteriorly to M^3 was found in one maxilla from wear class XI (10–15 y). There were no signs of incisors or canines in any specimen in the sample.

Tooth eruption

Deciduous teeth. Bigalke *et al.* (1950) document the full sequence of eruption of the deciduous teeth for 'Zuluana', a calf acquired by the Pretoria Zoo in 1946 at the age of 6 days. However, the growth of this animal, fed on a mixture of cow's milk and maize-meal porridge, was evidently retarded compared with the measurements reported for a White rhino calf born in the Hanover Zoo allowed to nurse from its mother (Dittrich, 1972). For instance, the weight of 'Zuluana' increased from 48 kg on arrival to only 63 kg at 3 months of age. In comparison, the Hanover calf increased in weight from about 40 kg at birth to 100 kg at 51 days and 145 kg at 105 days. Tooth eruption in 'Zuluana' tended to be retarded by about 30 days compared with the Hanover calf (Dittrich, 1972).

The deciduous premolars pm^3 and pm^2 erupt in close synchrony in both jaws. In both the Hanover calf and 'Zuluana', the first tooth to appear was a mandibular pm^3, at an age of 42 days in the former animal, and 77 days in the latter. In another calf captured from the wild at an age of 22 days, the first premolar appeared at an age of 70 days (Wallach, 1969). In 'Zuluana', the lower pm^4 teeth appeared at an age of 83 days, and the upper ones at 140 days; while premolar pm^1 first appeared in the upper jaw at 358 days, and in the lower jaw at 389 days (Bigalke *et al.*, 1950).

Permanent teeth. From the sample of skulls, it is evident that the first permanent premolar, PM^2, begins to erupt between three and four years of age (Table IV). Premolars PM^3 and PM^4 erupt in sequence after PM^2, and only after about eight years of age are all permanent premolars in wear.

Molar M^1 begins erupting before the first permanent premolar at an age of about three years and comes into wear between three and four years. There were differences in the wear shown by the M^1 between two Umfolozi skulls and a Kruger Park skull of similar age. Skulls N8 and N27 from Umfolozi, with ages estimated to be 5 ± 1 y, and $3{\cdot}5 \pm 0{\cdot}5$ y, respectively, both have M^1 at wear stage 4. However, the Kruger Park skull K2, from an animal exactly 4 y 3 d old at death, shows M^1 only just starting to wear (wear classes 2 and 3 on opposite sides), as also does a third Umfolozi mandible with an estimated age of 4 ± 1 y (N0). Molar M^2 erupts between 4 and 7 years of age, and M^3 between 8 and 16 years.

Tooth wear classes

Sixteen tooth wear classes were distinguished (Table IV, Fig. 3), though these show some overlap in assigned ages. Photographs showing the dentition for known-age specimens representing particular age classes are presented in Plate III. Tooth eruption and wear generally take place concurrently in both upper and lower jaws, but more variation in wear was shown by mandibles from older age classes than by maxillae. Corresponding teeth from opposite sides of the same jaw may occasionally show differing wear stages.

Tooth measurements

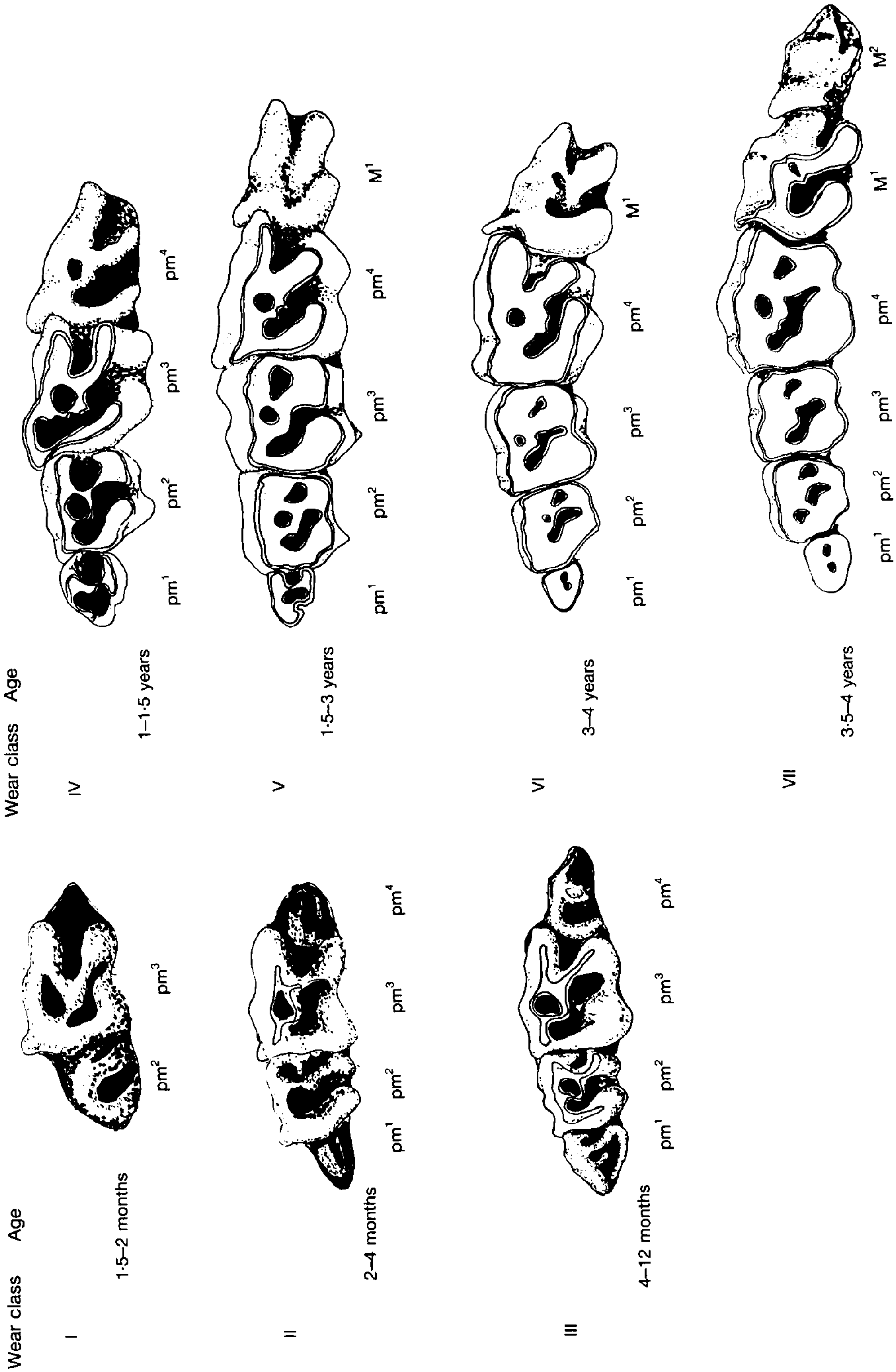
The crown height of maxillary M^1 teeth increases through wear classes V to VII (ages 1·5–4 y), indicating continuing growth (Table IV). The height of M^1 above the jaw bone, which is a

TABLE IV

Wear classes of the dentition for White rhino maxillae and mandibles, and cementum line counts

Numbers represent the tooth wear stages defined in Fig. 1. Where necessary, a range of stages is given, e.g. 3/4; 0 indicates this tooth is absent. Tooth measurements and cementum line counts are given as mean ± standard deviation

Age class	Assigned ages	Known-age material	n	Maxilla: Deciduous premolars pm¹	pm²	pm³	pm⁴	Maxilla: Permanent premolars PM²	PM³	PM⁴	Maxilla: Molars M¹	M²	M³	Mandible: Deciduous premolars pm¹	pm²	pm³	pm⁴	Mandible: Permanent premolars PM²	PM³	PM⁴	Mandible: Molars M¹	M²	M³	Maxillary M¹ measurements: Width (cm)	Crown height (cm)	Height above jaw (cm)	Cementum lines
0	0–1·5 m	Zuluana, Hanover	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	—	—	—	—
I	1·5–2 m	,, ,,	1	0	1/2	1/2	0	0	0	0	0	0	0	0	1/2	1/2	1/2	0	0	0	0	0	0	—	—	—	—
II	2–4 m	,, ,,	1	0/1	2/3	2/3	1/2	0	0	0	0	0	0	0/1	2/3	2/3	2/3	0	0	0	0	0	0	—	—	—	—
III	4–12 m	,, ,,	3	1/2	3/4	3/4	2/3	0	0	0	0	0	0	1/2	3/4	3/4	2/4	0	0	0	0	0	0	—	—	—	—
IV	12–18 m	K3 K4 Zuluana, N20	3	3/4	4/5	4/5	2/3	0	0	0	0/1	0	0	2/3	4/5	4/5	3/4	0	0	0	0	0	0	—	—	—	—
V	1·5–3 y		3	7/8	6/7	5/6	4/5	0	0	0	1/2	0	0	8	6	6	4/5	0	0	0	2	0	0	2·6 ±0·2	8·8	1·4 ±0·2	0
VI	3–4 y	K2,N0	7	8/9	7/8	6/7	5/6	0/2	0	0	2/3	0/1	0	8/10	8/9	7/8	6/9	0/1	0/1	0/1	2/3	1	0	2·7 ±0·2	9·3 ±0·6	3·3 ±0·5	0·3 ±0·2
VII	3·5–4 y	N27	6	0/9	8/9	7/8	6/7	2/3	0/1	0	4/5	1	0	9/0	8/9	8/0	7/8	1/3	1	0	4/5	0/1	0	3·2 ±0·6	9·7 ±0·6	4·5 ±0·2	0·3 ±0·3
VIII	4–7 y	N8	11	0/9	0/9	0/8	7/8	3/4	1/2	1	4/5	2/3	0	9/0	9/0	8/0	7/8	3/8	1/7	1/7	4/6	2/5	1/2	3·8 ±0·4	9·1 ±0·4	4·7 ±0·3	2·0 ±1·0
IX	7–9 y		4	0	0	0	0	5/6	4/6	1/2	5/6	3/4	1	9/0	9/0	9/0	9/0	4/7	5/7	3/7	5/7	3/7	1/3	4·0 ±0·2	7·9 ±1·0	4·6 ±0·5	5 ±1·0
X	8–11 y	K1	3	0	0	0	8/9	7/8	6/7	2/3	6	4/5	1	0	0	0	0	6/7	6/7	3/7	5/9	3/7	1/4	4·3 ±0·2	7·1 ±0·4	4·3 ±0·4	7 ±1·5
XI	10–15 y	K5	9	0	0	0	0/9	8	6/7	3/5	6/7	4/5	2	0	0	0	0	5/8	6/8	4/7	5/8	4/6	2/4	4·5 ±0·3	6·4 ±0·5	4·6 ±0·2	9 ±2·0
XII	14–20 y		9	0	0	0	0	8/9	7/8	6/7	7/8	5/6	2/3	0	0	0	0	6/8	7/8	5/7	6/8	5/6	1/4	4·5 ±0·3	5·3 ±0·4	4·2 ±0·3	14 ±2·6
XIII	20–28 y		8	0	0	0	0	0/8	8	8	7/8	6/7	4/6	0	0	0	0	7/10	7/9	7/8	6/10	5/8	4/5	5·2 ±0·6	3·6 ±0·8	3·3 ±0·5	22 ±4·0
XIV	25–32 y		8	0	0	0	0	0/9	8/9	8	8	7	6	0	0	0	0	7/10	8/9	7/8	7/10			6·0 ±0·5	3·1 ±0·8	2·5 ±0·5	24 ±7·0
XV	30–38 y		4	0	0	0	0	—	—	8/9	9	8	7/8	0	0	0	0	8/10	8/9	8/10	8/10	7/10	6/7	5·6 ±0·1	1·6 ±0·3	1·2 ±0·3	31 ±7·0
XVI	35–40 y		1	0	0	0	0	—	—	—	—	9/10	9	0	0	0	0	—	8	0/10	10	8/10	7/8	—	—	—	32


Wear class
Age
I
1·5–2 months
pm2 pm3
II
2–4 months
pm1 pm2 pm3 pm4
III
4–12 months
pm1 pm2 pm3 pm4
Wear class
Age
IV
1–1·5 years
pm1 pm2 pm3 pm4
V
1·5–3 years
pm1 pm2 pm3 pm4 M1
VI
3–4 years
pm1 pm2 pm3 pm4 M1
VII
3·5–4 years
pm1 pm2 pm3 pm4 M1 M2

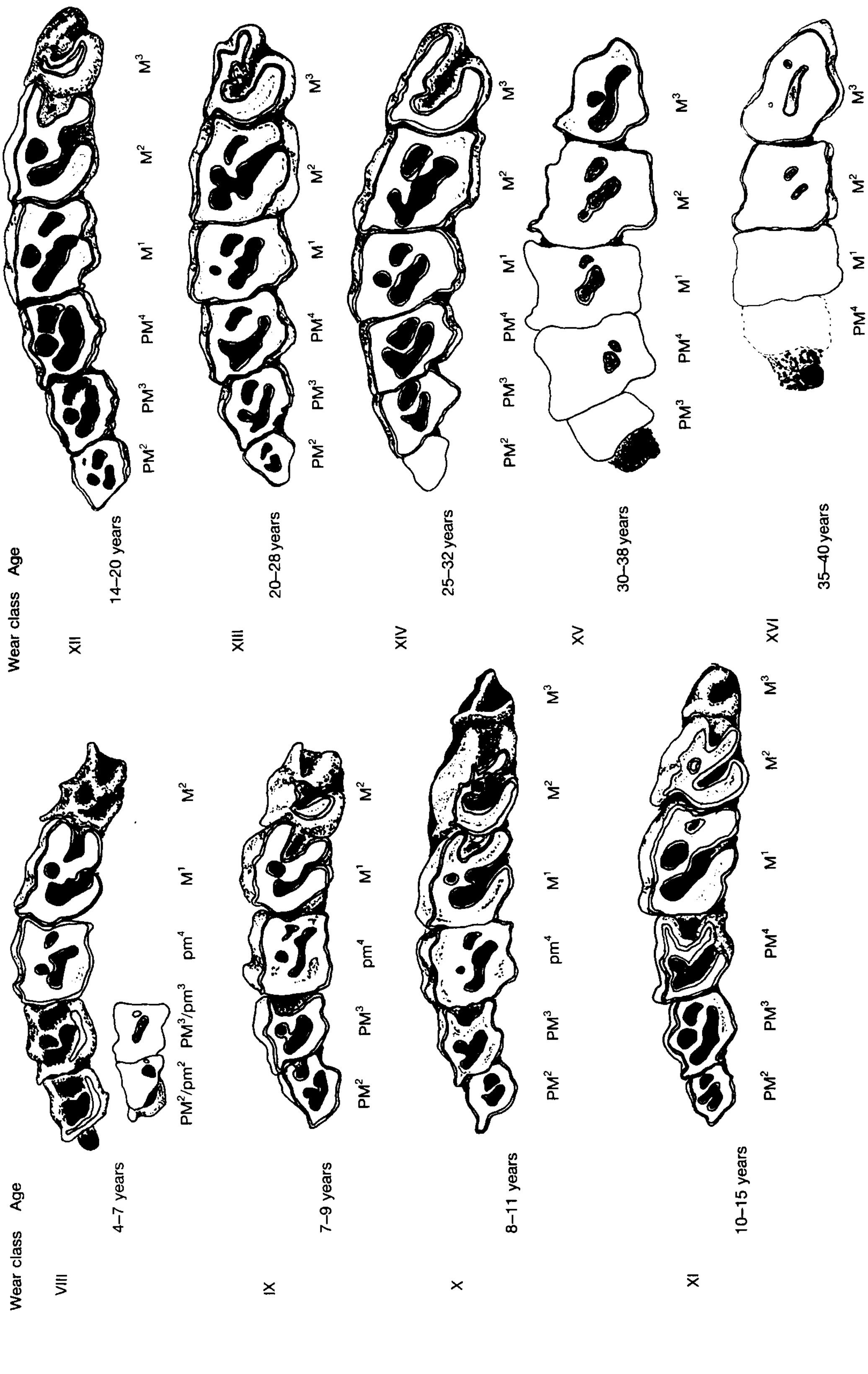
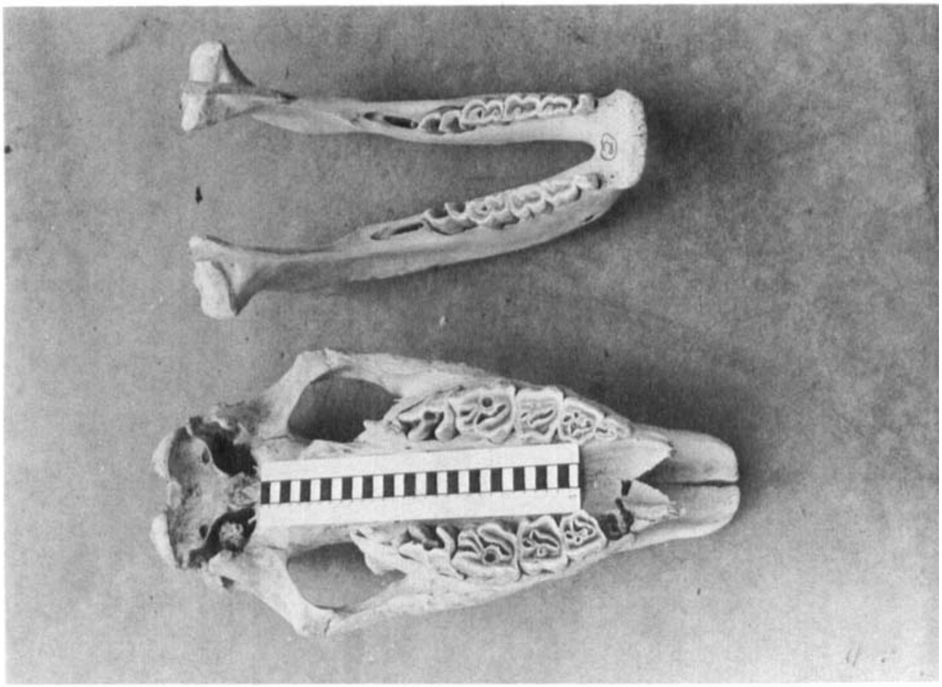
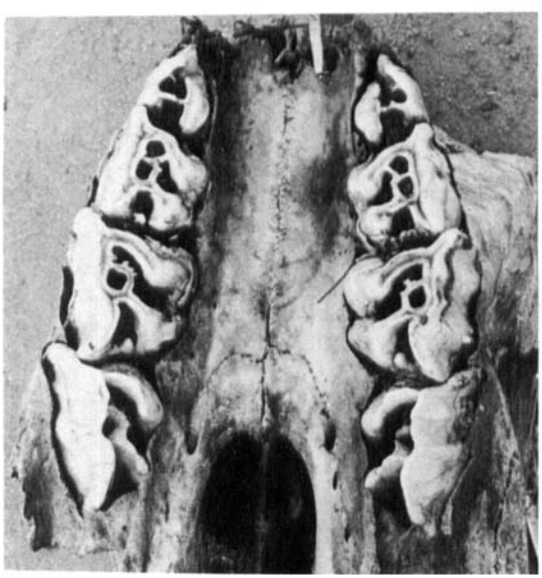


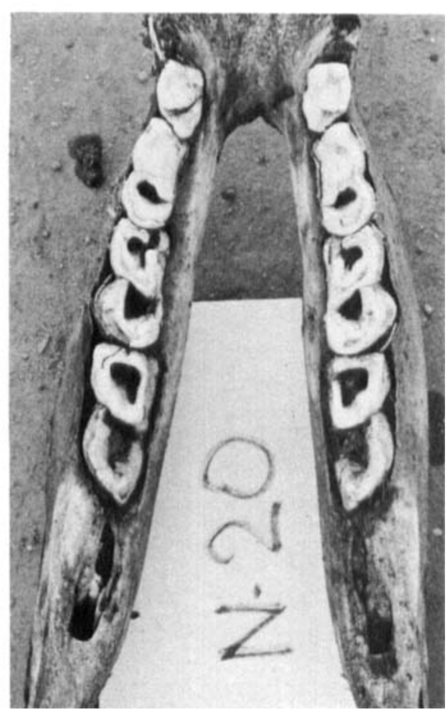
FIG. 3. Appearance of maxillary dentition in each of the tooth wear classes established.



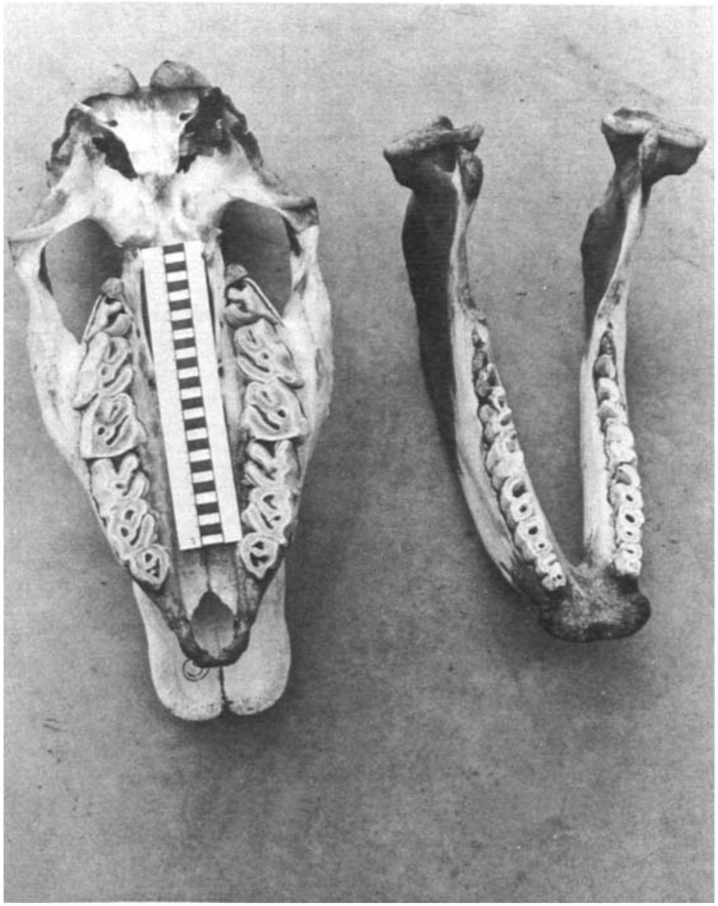
(b)



(a)



(c)



(d)

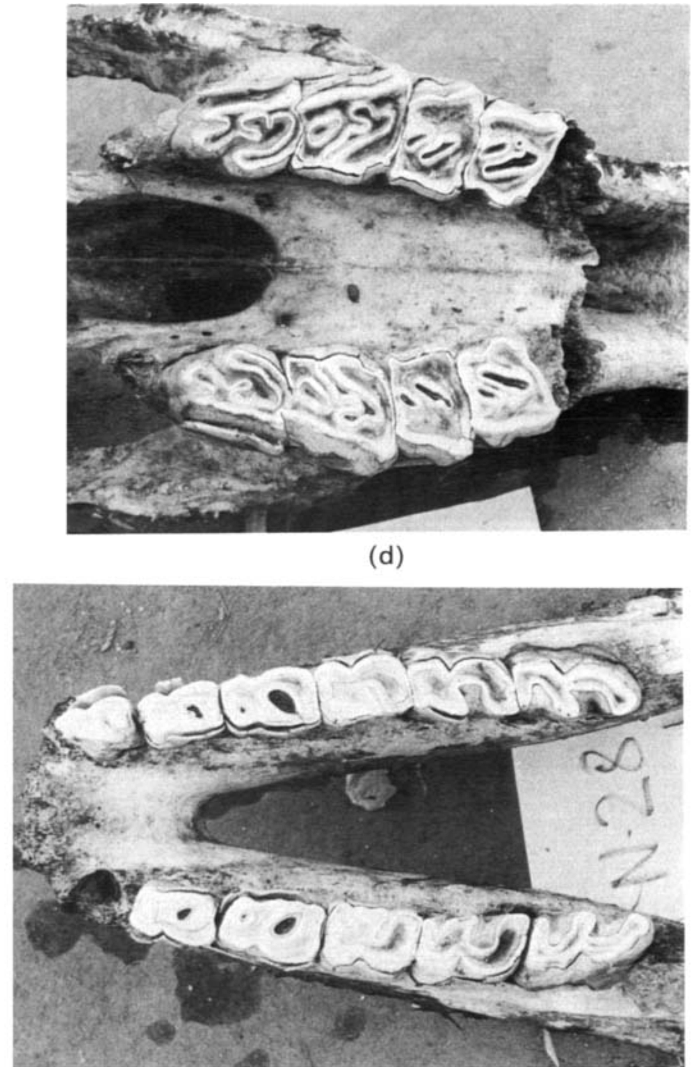


PLATE III. Photographs showing dentition of representative skulls. (a) juvenile female (N20) from Umfolozi, age 1 y 2 m, wear class IV; (b) subadult male (K2) from Kruger, age 4 y 0 m, wear class VI; (c) young adult female (K-5) from Kruger, age 10 y 4 m, wear class XI; (d) prime adult female (N28), 22 cementum lines counted in M^1, wear class XIII (note: pm^2 and m^3 are missing from the maxilla).

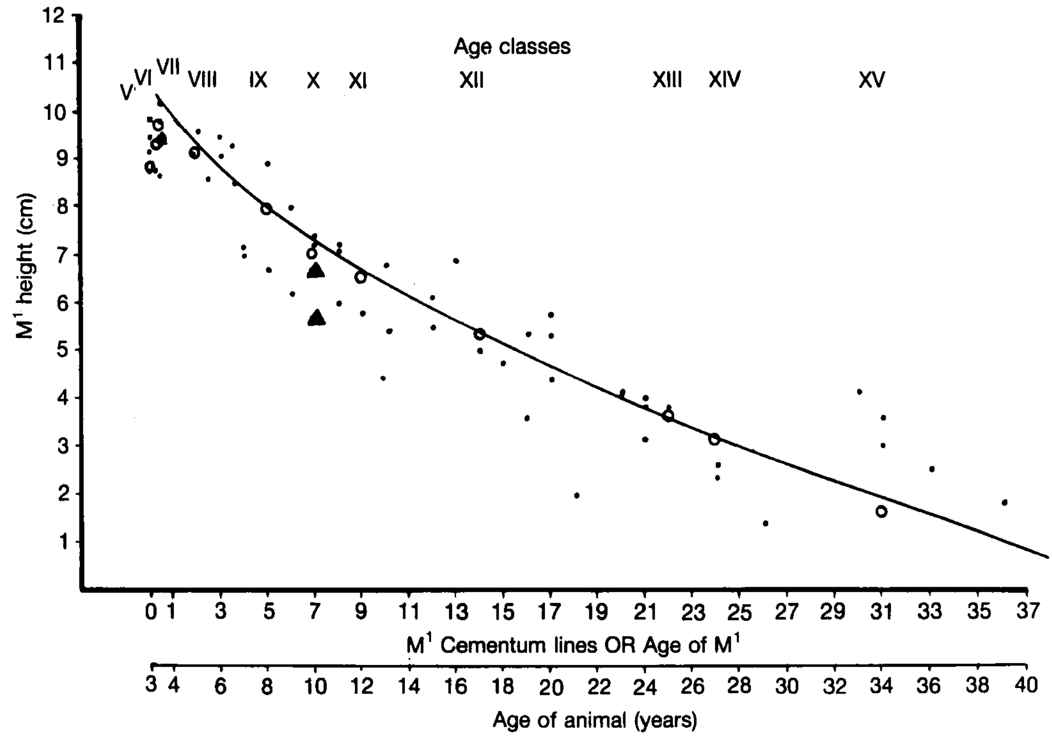


FIG. 4. Crown heights of maxillary M^1 teeth in relation to cementum line counts and assigned ages: dots (·) = individual skulls; open circles (o) = means for each tooth wear class; solid triangles (▲) = known-age skulls. The curve drawn is based on the formula $y = 11\,(1-(t/42)^{0\cdot 6})$.

less precise measurement, does not decrease significantly until after wear class XI (10–15 y), suggesting that the tooth continues to push up from the bone until this age. The width of M^1 continues to increase slowly until an age of about 30 y. The latter is an easy measure to take on skulls in the field; but crown height is preferable as a more precise measure where possible.

The crown height of the first molar is plotted against cementum line counts in Fig. 4. Ages can be assigned by assuming that each pair of light and dark cementum lines represents one year, and by adding three years for the age at which M^1 erupts. Crown height shows a steady decrease until an estimated age of about 25 years. Thereafter, the growth of the cementum pad partly offsets the tooth attrition, and differences between individual specimens become more marked.

Spinage (1971) suggests that attrition in the crown height of molar teeth may be approximated by an exponential curve. He proposes the formula:

$$y = y_0\,(1-(t/n)^k)$$

where y = tooth height at time t, y_0 = extrapolated maximum height of the tooth, t = age in years of tooth, n = age at which tooth height is zero. For attrition of M^1 teeth from White rhinos, the best fit equation was found to be:

$$y = 11\,(1-(t/42)^{0\cdot 6})$$

This curve is plotted in Fig. 4, and shows a good fit with the mean measurements for each tooth wear class in relation to cementum line counts. However, M^1 teeth from all three of the Kruger

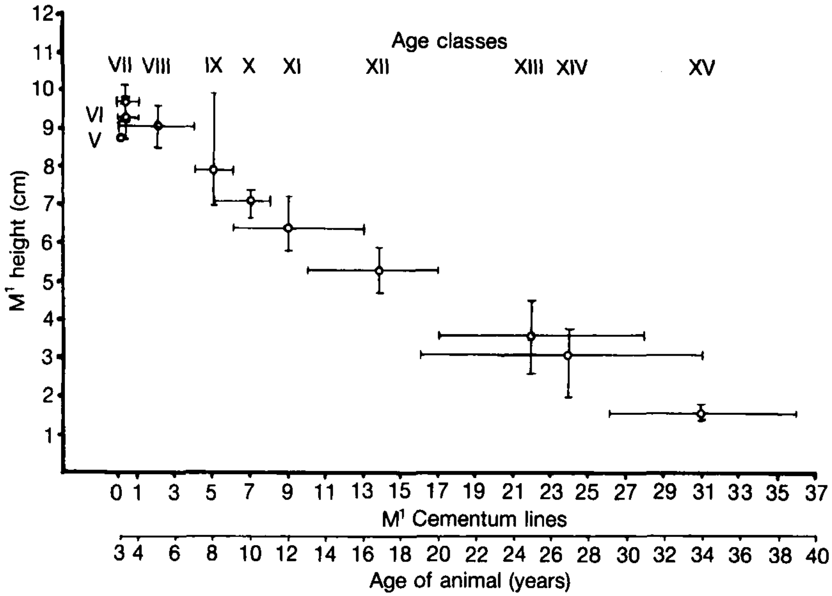


FIG. 5. Means and ranges of variation of M^1 crown height, cementum line counts and assigned ages for tooth wear classes VII to XV.

Park skulls from known-age animals showed less wear than expected for their ages, even though cementum line counts agreed closely with age.

As an aid to assigning age classes from cranial material, the means and ranges of variation that were found for M^1 height and cementum line counts within each wear class are plotted in Fig. 5.

Cementum line counts

Cementum line counts for complete sets of teeth from each wear class are presented in Table V. The rank order of counts from different teeth is consistent with their eruption sequence, but numerical differences do not correspond closely between specimens from different wear classes. The deciduous premolar pm^3 yielded cementum line counts that generally exceeded assigned ages in years, while those for pm^4 agreed closely with assigned ages. According to the records of tooth eruption for the captive calf 'Zuluana', pm^3 and pm^2 erupt in close sequence, pm^4 erupts two months later than pm^3, and pm^1 erupts about one year later. Counts for M^1 averaged about two lines less than those of pm^4, while this tooth erupts about 2·5 years later. M^2 averaged seven lines fewer than M^1 in teeth from younger age classes, and up to 14 lines fewer in older classes, though it erupts only 2-3 years later. This suggests that cementum lines tend to become obscured as M^2 ages. M^3 showed 5-7 lines fewer than M^2 in younger classes, but up to 15 lines fewer in older classes, confirming the same trend. Similarly, cementum line counts for the permanent premolars show no further increase beyond a certain stage. The teeth pm^4 and M^1 appear to be the most reliable for assigning chronological ages on the basis of cementum line counts.

Cranial measurements

External cranial measurements and horn lengths from skulls corresponding to the tooth wear classes are presented in Table VI. Means have been calculated separately for each sex for those

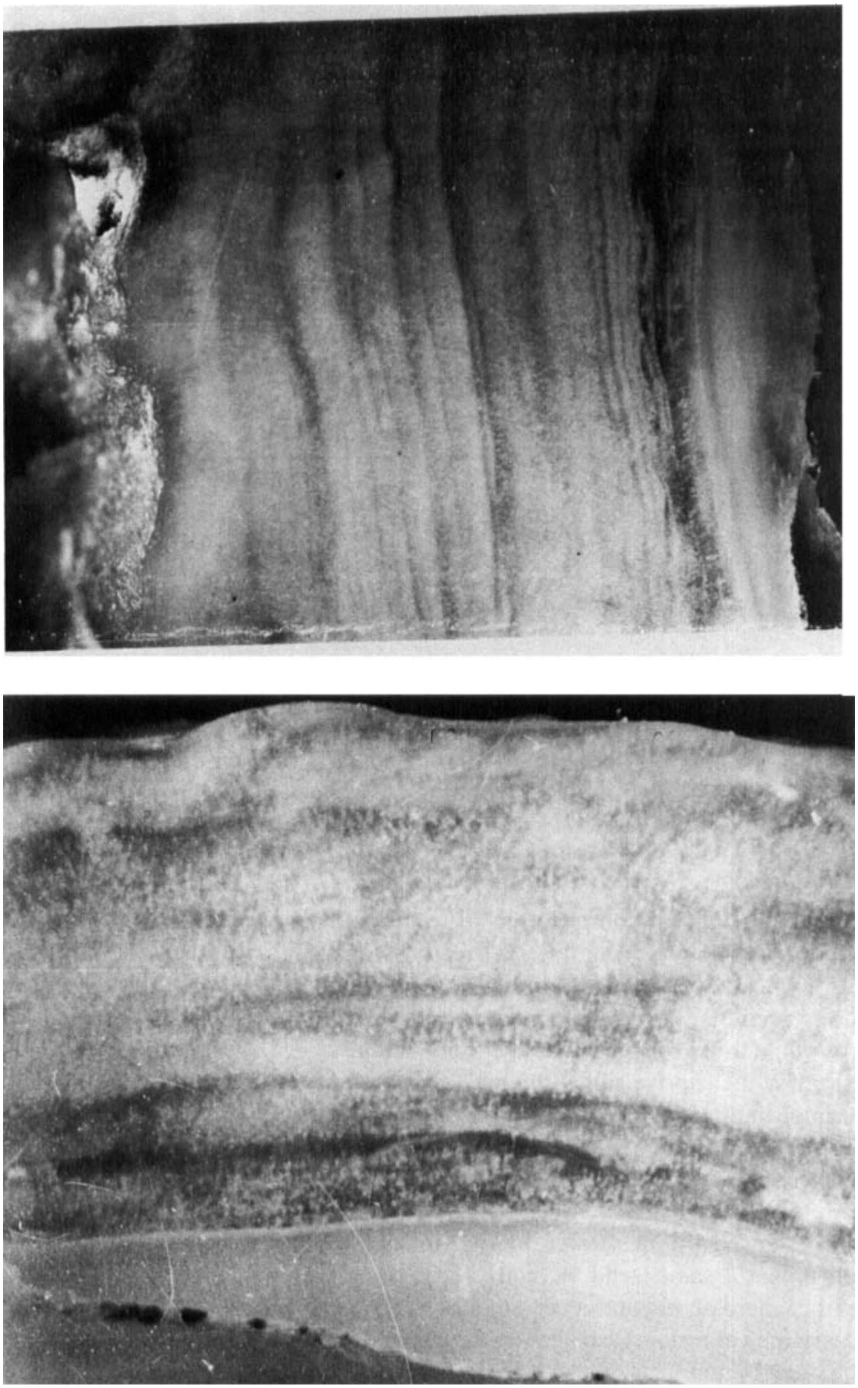


PLATE IV. Photographs showing cementum lines in M^1 teeth from White rhinos. (a) Specimen P27, wear class XII, showing approximately 20 cementum lines; (b) Specimen K1, age 9 y 7 m, wear class X, showing one part of a line of cementum in which approximately seven lines are visible.

TABLE V

Cementum line counts for complete sets of teeth (two skulls per class, maxillae only)

Wear class	Cementum lines (mean ± standard deviation)									
	pm^1	pm^2	pm^3	pm^4	PM^2	PM^3	PM^4	M^1	M^2	M^3
IV		1·0	1·5	0·5						
V	1·5	3·3±1·1	3·8±0·4	1·0±1·4						
VI	2·1±1·4	3·3±0·4	5·0±1·4	2·8±1·8						
VII	3·0	2·8±0·4	5·0	3·5±0·7				0·5	0	
VIII	4·0±1·4	3·0±0·7	4·8±0·4	5·3±1·1	0·5	0·5	0	2·6±1·2	0·5	
IX				5·5	0·5	0·5	0	4·0	0	
X				5·8±0·4	0·8±0·4	0·5	0·3	7·5±1·4	1·0	
XI					2·5	4·8±2·5	2·5	9·5±4·5	2·3±1·1	1·5±1·4
XII					4·0	4·0	3·3±3·9	16·5±1·4		1·0±0·7
XIII						22·0	17·5±5·4	24·0	14·5	7·0
XIV					12·0±1·4	15·7±2·5	11·0±3·0	22·7±7·6	10·0	5·2±2·6
XV							14·0	36·0	22·0	12·0
XVI									27·0	12·0

skulls for which sex was known, in addition to the combined means for all skulls. The skulls of adult males are consistently longer than those of females in the same wear classes. Although male horns tend to be slightly shorter, their basal circumference and weight are much greater than those of horns from similar-aged females.

Discussion

Rates of growth and development and tooth wear are not rigid features, but are subject to environmental modification. There is evidence that White rhinos are no different from other species in this response. The slow initial growth rate shown by the Pretoria Zoo calf, 'Zuluana', which was reared on an artificial diet, was associated with a retardation in the times of tooth eruption by about a month compared with another zoo calf that was able to nurse from its mother. Kruger Park animals that were confined to a 2·5 km^2 enclosure showed a delay in the eruption of the first molar by roughly a year compared with Umfolozi animals. Photographs of known-age calves from the Kruger Park show that the horn development of these animals was also slower than that of Umfolozi calves of similar age. Thus environmental factors introduce a degree of uncertainty in applying age ranges from body or horn size, or tooth eruption and wear, to animals from different areas.

The timing of tooth eruptions in White rhinos is closely similar to that reported for Black rhinos, for young calves by Dittrich (1972), and for older animals by Goddard (1970) and Hitchins (1978). In Black rhinos, rudimentary incisors are occasionally present, but this condition was not observed in any White rhino material. In White rhinos, the persistent pm^1 is lost between four and seven years of age, while in Black rhinos it invariably persists until 14 years of age or later in the maxilla, though in the mandible it is lost at about 12 years of age (Hitchins, 1978).

Cementum line counts provide a valid aid in assigning chronological ages to White rhinos, as has been found in other mammals (Morris, 1972). It appears that one pair of light and dark lines is formed per year, corresponding to the single rainy season typical of the study region. However, precision is limited by the difficulties experienced in interpreting lines, and by the diminishing

Table VI

External cranial and horn measurements for skulls corresponding to each wear class
(Figures are given as mean ± standard deviation)

Wear class	Sample size: Combined	Sample size: Female	Sample size: Male	Cranial measurements (mm): Greatest length	Dorsal concavity	Chondylo-basilar length	Chondyles-nasals	Foramen magnum-nasals	Inter-orbital constriction	Maxillary tooth row	Mandibular tooth row	Horn weight (kg): Ant.	Horn weight (kg): Post.	Horn measurements (mm): ant. Length	ant. Basal circ.	post. Length	post. Basal circ.	Known age
III		1		304	21	326	302	287	85	125	125							7 m
IV	1			—	—	—	—	—	97	160								
V	3			480		530	498±31	470±30	89±11	202±8	205							
VI	7			565±28	63±7	590	533±30	509±11	94±5	203±7	199±4	2·5		419	654			
		1		545	70	—	480	505	91									4 y 2 d
VII	5			637±15	62±9	630	593±58	565±46	90±10	197±12	202±18							
VIII	6			674±32	67	670±14	588±20	561±28	85±5	230±8	231±33							
IX	3			657±21	74±8	—	593±6	563±6	87±11	228±5	—							
X	8			695±36	83±6	663±26	611±25	578±28	91±7	245±7	250±28	4·0±1·4	1·3±0·4	496±144	554±61	164±21	523±26	
		1		705	78	661	605	577	94									9 y 7 m
XI	8			733±35	84±8	689±26	618±25	608±37	95±6	244±12	263±20	4·5±1·8	0·5±0·4	617±62	637±68	179±63	522±140	
			6	748±23	84±9	698±18	625±19	620±31	96±3			5·0±1·8		623±66	656±51	199±59	550±137	
		2		685±7	78±2	660±28	595±35	570±28	94±13			3·0		584	523	127	381	
		1		710	76	675	595	575	90									10 y 4 m
XII	7			740±49	83±9	695±24	621±22	599±31	95±4	274±11	272±21	4·5±1·3	0·8±0·4	686±76	686±76	202±77	670±185	
		2		700±57	84±5	685±21	615±21	585±21	96					616	743	216	692	
			5	756±42	82±10	624±24	624±24	604±35	94±4			4·5±1·3		743±62	734±39	224±14	753±98	
XIII	9			740±35	77±5	679±30	623±20	596±18	97±6	247±21	275±7			607±95	597±160	188	580±174	
		2		765±21	82±2	700±28	630	610±14	93			2·8	0·5	527±41	464±18	139	387	
			2	765±7	76±2	690	635±7	605±5	99					686±18	730±72	213±4	677±67	
XIV	7			756±15	78±11	716±15	647±15	623±18	96±8	270±8	268±11	6·0		679±81	609±114	218±111	517±224	
		2		755±21	69±1	705±21	630±28	610±28	100±6			4·0		730±81	511±23	175±166	367±243	
			3	765±7	90±7	720	645±7	625±7	93±8			8·0		627±52	707±11	261±45	667±40	
XV	4			767±40	79±4				89±9									
		1		720	76				95									
			2	790	81													
XVI			1	740	87				90			4·0	1·5	584	562	156	556	

distinctness of lines as teeth age. Cementum line patterns for Black rhinos described by Hitchins (1978) seem to be easier to count than those observed in White rhinos, though in Black rhinos clarity also decreases with chronological age. Possibly, seasonal fluctuations in food availability are more consistent for a browser like the Black rhino than they are for a grazer like the White rhino, for which grass growth is more directly dependent on the vagaries of rainfall.

For Indian rhinos (*Rhinoceros unicornis*), Laurie (1978) sectioned the tusk-like lower incisors to count cementum lines, which seemed to be fairly clearly defined. The maximum number of lines counted in his limited sample was 26. For Black rhinos, Hitchins (1978) counted a maximum of 34 cementum lines, which, allowing for the time of eruption of the M^1, suggests a chronological age of 37 years. This is in concordance with zoo records showing a potential longevity of 35–40 years (Goddard, 1970). For White rhinos, the maximum cementum line count was 36, suggesting an age of 39–40 years. Zoo records of potential longevity are unavailable for White rhinos, due to the limited period over which specimens have been kept. The oldest White rhino in a zoo is 'Zuluana', who is currently still alive in the Pretoria Zoo at an age approaching 38 years, though showing signs of senility.

For field age estimation, the defined size classes, aided by horn growth, allow White rhinos to be assigned to functional age classes as follows: (i) newborn infants—class I1 (0–2 m); (ii) unweaned infants (only small amounts of nibbling on grass)—classes I1 and I2 (0–4 m); (iii) calves likely to be still nursing—classes I1–J2 (0–18 m); (iv) calves generally still accompanying their mothers—classes I1–J3 (0–30 m); (v) adolescents independent of their mother, but not sexually potent for males and pre-parturient for females—class S1 (2·5–6 y); (vi) subadults, including males that are sexually potent but not yet full weight and thus not socially active in reproduction, and females that are late in producing their first calves—class S2 (6–10 y). Trophy size horns are attained at an age of 10–15 years, and no further increase in horn length or basal circumference was apparent.

Skulls of adult animals could potentially be sexed by relating either linear dimensions or circumference around the orbital region to tooth wear class. For adult horns, measurements of basal circumference would allow sex to be established fairly reliably.

In Table VII, the field size classes are related to the tooth wear classes. Patterns of tooth eruption, surface wear and attrition in height allow full-grown animals to be assigned to age ranges, which cannot be done reliably from visual observations of live animals. Dental patterns can potentially be examined, or impressions taken, in live animals that have been immobilized;

TABLE VII

Interrelation between field size classes, tooth wear classes and age

Size class	Wear class	Age range (months)
I1	0, I	0-2
I2	II	2-4
J1	III	4-9
J2	III, IV	9-18
J3	V	18-30
S1	VI, VII, VIII	30-72
S2	IX, X	72-120
A	XI–XVI	120-480

but in White rhinos this is difficult because of the limited extent of the gape. For younger age classes, ages could be assessed approximately from the sizes of either intact or isolated anterior horns.

The information presented in this paper provides a basis for estimating the ages of White rhinos either as living animals, as found skulls, or even as isolated horns. Immature animals up to six years of age can readily be assigned to age categories on the basis of relative size and horn development. Patterns of tooth eruption and wear may be used to assign ages to skulls from animals up to about 15 years of age, when the last molar erupts. Stages of tooth wear and measurements of M^1 height can be used to assign broad age ranges to skulls of older animals. Cementum line counts can provide supporting evidence for assigned ages; but because of problems of interpretation they provide little real gain in reliability in return for the effort required. Caution must be used in applying the age ranges given in this paper to White rhinos from other populations, because of potential variations in growth rates, timing of tooth eruption, rates of tooth wear and clarity of cementum lines, and the relative paucity of known-age material that was available to us.

We should like to thank the Bophuthatswana National Parks Department who supported and provided facilities for the cranial work in Pilanesberg Game Reserve, the Natal Parks Board who supported the field study and provided cranial material, and the National Parks Board of South Africa for known-age material and facilities in the Kruger National Park. Very many thanks to those involved in the skull measurements, particularly Blair Ludbrooke, Don Parry and Sydney D. Sekhadelo at Pilanesberg, Grant Holton and Ross English at Kruger; and also to Fraser Smith and Roger Collinson for support and facilities, to Peter Hitchins for kindly making available his measurements on White rhinos, to Carol Sam and Margaret Marshall for typing some tables, and to Phillip Prim for printing the photographs.

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Addendum

Notes on dentition, cranial and body measurements of the northern White rhinoceros (*Ceratotherium simum cottoni*)

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For comparative purposes, similar measurements are presented for the endangered subspecies of the northern White rhinoceros (*Ceratotherium simum cottoni*).

Methods

Cranial measurements and dentition were recorded as above from the skulls of 6 wild northern White rhinos found dead in the Shambe area of South Sudan and Garamba National Park in northern Zaire, during a survey of the subspecies in 1983 (Hillman & Smith, 1983). They were also taken from a dead captive female at Vychodeceska Zoo, who originated from Shambe (by kind courtesy of Dr J. Safarik).

Body measurements of 8 live captive northern White rhinos of approximately known age (one measured twice at different ages) were provided by Mr M. Svitalsky and Dr J. Safarik of the Vychodeceska Zoo in Czechoslovakia. Those comparable to the measurements taken on southern White rhinos are presented here. One animal originated from Uganda, the rest from Shambe, South Sudan.

Results and discussion

The dentition and sequences of eruption and wear appear to be the same as those of the southern White rhinos and the same wear classes can be defined. There is insufficient material from known-age animals to verify whether the same ages would correspond with the same wear classes. However, the dentition of the captive female, who was estimated to have been born in 1972 and who died on 4 January 1982, is clearly that of eruption/wear stage X, which is defined

TABLE VIII
Cranial measurements (mm)

Origin	Wear class	Identification	Greatest length	Dorsal concavity	Chondylo-basilar length	Chondyles —nasals	Foramen magnum —nasals	Maxillary tooth row	Mandibular tooth row	M^1 width	M^1 ht. in jaw
S. Sudan	IV	S5				480	450	180	155		
(Shambe)	XI	S1		38		690		270			
	XII	S2	720			690		270			
	XII	S3	810	35		725	690	225			
Zaire	XI	G1	800	65	705	620	590	225	206	41·4	45·5
(Garamba)	XII	G2	710			600	550	270		44·0	44·0
S. Sudan (Shambe)	X	Nuri*	730	35	650			230	175	45·0	50·0

*Captive female, age at death 9–10 years