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Ceratotherium simum.

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Ceratotherium Gray, 1868

Ceratotherium Gray, 1868:1027, based on two species. Type species *Rhinoceros simus* Burchell, 1817, by selection (Allen, 1939:555, who referred to Sclater, 1900:297, who regarded Gray's species *simum* and *oswellii* as subjective synonyms).

Serengeticeros Dietrich, 1945:56. Type species *S. efficax* Dietrich, *loc. cit.*

CONTEXT AND CONTENT. Order Perissodactyla, Suborder Ceratomorpha, Family Rhinocerotidae, Subfamily Dicerotinae. The genus *Ceratotherium* includes one species as treated below.

Ceratotherium simum (Burchell, 1817)
White or Square-lipped Rhinoceros

Rhinoceros simus Burchell, 1817:97. Type locality Chué Spring, about 26°15′ S and 23°10′ E, Makuba Range, Botswana, according to Cave (1947).

Rhinoceros camus Griffith, 1827:292. Type locality southern Africa.

Rhinoceros Burchellii Lesson, 1827:332. Type locality interior of Cape of Good Hope.

Rhinoceros Oswellii Gray, 1853:46. Type locality interior of South Africa.

†*Rhinoceros* (*Atelodus*) *mauritanicus* Pomel, 1895:13. Type locality Ternifine, Algeria.

†*Serengeticeros efficax* Dietrich, 1945:56. Type locality Laetolil, Tanzania, early Pleistocene.

†*Rhinoceros scotti* Hopwood, 1926:17. Type locality Kaiso Beds (early Pleistocene), Uganda.

CONTEXT AND CONTENT. Context noted in generic summary above. Two living and two extinct subspecies are recognized as follows:

C. s. simum (Burchell, 1817:97), see above (*camus* Griffith, *burchellii* Lesson, *oswellii* Gray, and *crossii* Gray are synonyms).

C. s. cottoni Lydekker, 1908:319. Type locality Lado Enclave, in what is now Sudan.

†*C. s. germanoafricanum* Hilzheimer, 1925:45. Type locality Olduvai, Tanzania (*efficax* Dietrich and *scotti* Hopwood are synonyms).

†*C. s. mauritanicum* Pomel, 1895:13, see above. Hooijer (1969: 73) did not regard this subspecies as well founded.

Of the two living subspecies, *C. s. simum* has longer maxillary tooth row, 270 to 305 mm (as opposed to 236 to 280 in *cottoni*); deeper dorsal concavity of skull, 55 to 75 mm (as opposed to 33 to 57); and body hair throughout life (lost in adults of *cottoni*); according to Heller (1913), Alexander and Player (1965), Hooijer (1969), and the author.

DIAGNOSIS. Skull is markedly dolichocranial, with backward-leaning occipital crest; no incisors or canines; jaws abbreviated in front; mandibular symphysis broad, spatulate; nasal bones broad, short, high; ascending ramus of mandible backward-leaning; no marked angulation at gonion. Cheek-teeth are hypsodont; protoloph and metaloph strongly curved back, showing early fusion with wear; much cement on crown. Thoracic vertebra 17 or 18 is anticlinal, forming a presacral eminence well-separated from sacral eminence. Nostrils are long, slitlike; eye situated behind back of frontal horn base; ears close together, rounded, but pointed at tip; a nuchal hump consisting largely of muscular and ligamentous tissue; copious subcutaneous fat; body-folds, including costal grooves, little developed. Penis has translucent preputial skin, both eccrine and apocrine glands. Horns have enlarged, squared base and thick, massive stem; nasal horn tapers, not markedly back-curved; frontal horn short, conical; horns not joined at base.

GENERAL CHARACTERS. The white rhinoceros may be distinguished externally from the sympatric black rhinoceros (*Diceros bicornis*) by larger size, presence of a nuchal hump (more obvious when head is held up), long head, square lip (Figure 1), enlarged horn-bases, and straight back with marked presacral, as well as sacral, eminence. The head is normally held low. The lips are squared and suitable for grazing. The lower lip bears a hardened pad (Van den Bergh, 1955). The color is generally pale gray. Skin-folds are little developed, probably due to the large amount of subcutaneous fat (Cave and Allbrook, 1959); these authors ascribed the lack of body-hair in the northern race to this fat, but Alexander and Player (1965) stated that in the southern race copious, if sparse, body-hair can easily be detected by running the hand along the animal's back and flanks.

Foster (1960) listed the measurements of four adults, sex not stated, as follows: head and body length 3.35 to 3.77 m; shoulder height 1.71 to 1.85 m; girth 2.84 to 2.94 m; weight, about 3200 to 3600 kg. Former claims of bulls reaching 6 ft 6 in and 6 ft 9 in were shown by Heller (1913) to be false; but some bulls may actually exceed 6 ft (1.83 m) in height (Guggisberg, 1966).

The nasal horn is considerably longer and thinner in the female; the record length of 65¼ in (1660 mm) reported by

FIGURE 1. Head of male *Ceratotherium simum* from Faradje, Congo (Lang-Chapin Expedition of The American Museum of Natural History) to show the broad upper lip.

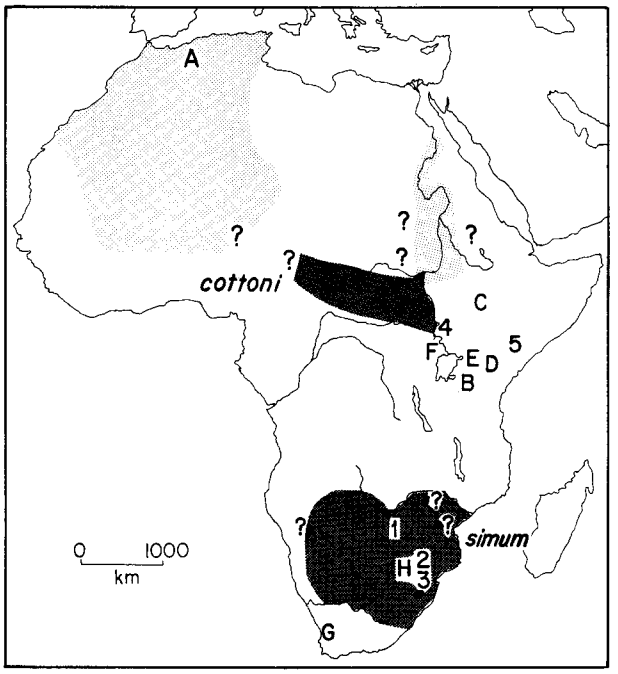

FIGURE 2. Range of *Ceratotherium simum* in Africa. Probable range about 2000 years ago shown in light stipple in northwest Africa and Nile Valley. Probable range about 1850 shown in dark tone. Remnants of natural range in South Africa are shown by black spots. Numbers indicate places where introductions have been made by man as follows: 1, Matopos National Park; 2, Kruger National Park; 3, Mlilwane Game Sanctuary; 4, Murchison Falls National Park; and 5, Meru National Park. Letters indicate fossil localities as follows: A, Ternifine; B, Olduvai and Laetolil; C, Omo; D, Naivasha; E, Kanam West and Chemeron; F, Kaiso; G, Hopefield; and H, Transvaal sites.

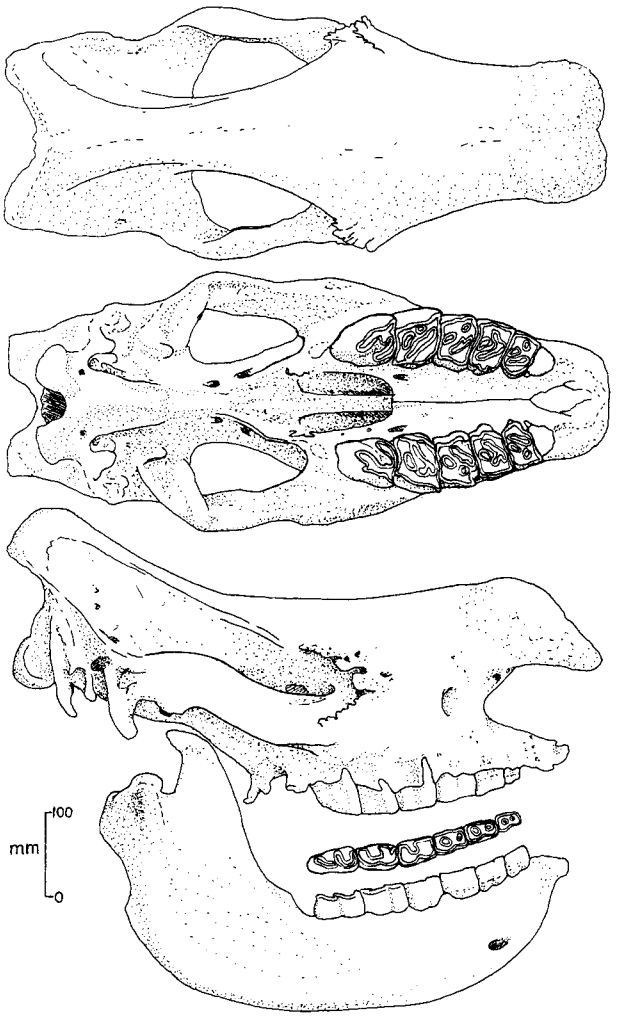

FIGURE 3. Skull of *Ceratotherium simum*, shown from top to bottom in dorsal, ventral, and lateral views, and lateral view of lower jaw with adjacent occlusal view of lower teeth (adapted from de Blainville, 1839).

Heller in 1913 has not since been exceeded. In males with unusually heavy horns, the horn may lean forward and scrape the ground when the animal grazes; rarely is it as curved or as backward-pointing as in many *Diceros*.

Although now frequently seen in captivity, the gross anatomy of this species, even the visceral anatomy, is virtually unknown. This is a major gap in our knowledge, since the other species of Rhinocerotidae (especially the Asiatic taxa) are well-known in this respect. The papers of Cave and Aumonier (1962 and later) have, however, supplied certain histological data.

DISTRIBUTION. Player and Feely (1960) mapped the former distribution of the species in southern Africa, Schomber (1966) mapped the northern part of the range (Figure 2). The southern race appears not to have been found in Recent times north of the Zambesi, except perhaps between the Mashi and Zambesi rivers in western Zambia (Ansell, 1967). Ansell also detailed its former occurrence in Southwest Africa and Angola, and recorded it marginally in the Orange Free State. Its gradual disappearance from Rhodesia has been traced by Roth (1967); although considered outside its previous range by Player and Feely (1960), the Kruger National Park appears to have harbored some, and they have now been reintroduced there. In 1874, Selous found the species plentiful south of Linyanti, on the Chobe River; by 1879 they had gone from that area. When the last few individuals in Mashonaland were shot in 1892 and 1893, the species was considered extinct; but the following year a few were discovered in Zululand, and these are the forebears of the population today. However, from time to time others have been reported: Lake Ngami in 1899 and 1903, in Mozambique between Gauveia and Marcorsa in 1935, and at the present time it is reported to occur in Southwest Africa between Otjikuvare and Otjovathandu, and in Rhodesia between the Chewore and Angwa rivers. The above data are derived from Sidney (1965) and Ansell (1967). The history of its extensive reintroduction is dealt with under "Conservation" in the section on ecology.

In the Sudan, the species exists in the tree-savannah of Equatoria and Bahr-el-Ghazal provinces, west of the Nile; probably also to the north, between the Bahr-el-Arab and Lol rivers (Schomber, 1963). In Uganda, the southern limit of distribution is the Ora River; in the Congo *Ceratotherium* occurs in the Garamba National Park, in the northeastern corner; in Chad, a few may survive in the south-central region near Lake Iro, and these rhinos once lived all along the Salamat River; in the Central African Republic, there are some 80 in the Goz Sassulko National Park, and a few occur along the upper Ubangui between 6° and 9° N on the upper Kotto and upper Chinko, and in Ndende and Birao districts (Simon, 1970).

FOSSIL RECORD. The genus probably separated from *Diceros* in the early Pliocene; *Diceros pachygnathus* (of Pikermi, Samos, and Maragha) shows some features tending toward those of *Ceratotherium* (see Thenius, 1956). Fossils are recorded (Figure 2) from: Makapansgat, Transvaal (Hooijer, 1959); Olduvai, where the less specialised *C. s. germanoafricanum*, with lower-crowned, less plagiolophodont molars, can be seen to have evolved into *C. s. simum* in upper Bed II; Laetolil, Chemeron, Omo, and Kanam West; at Naivasha, and the Omo upper series (Hooijer, 1969); and from the late Pleistocene at Hopefield (Hooijer and Singer, 1960). The range in the late Pleistocene and early Holocene can be delineated on the basis of rock-paintings—in the western Sahara (Mauny, 1956) and in Botswana, Southwest Africa, and Cape Province (Schaurte, 1960).

FORM. In a youthful specimen, the epidermis was 1 mm thick, the dermis 18 mm (45 mm over the nuchal hump), extremely dense, with densely felted collagen fibres at all angles to the surface; fat up to 25 mm thick on dorsum, 50 mm on abdomen; hairs undetectable (to the naked eye) beyond 2½

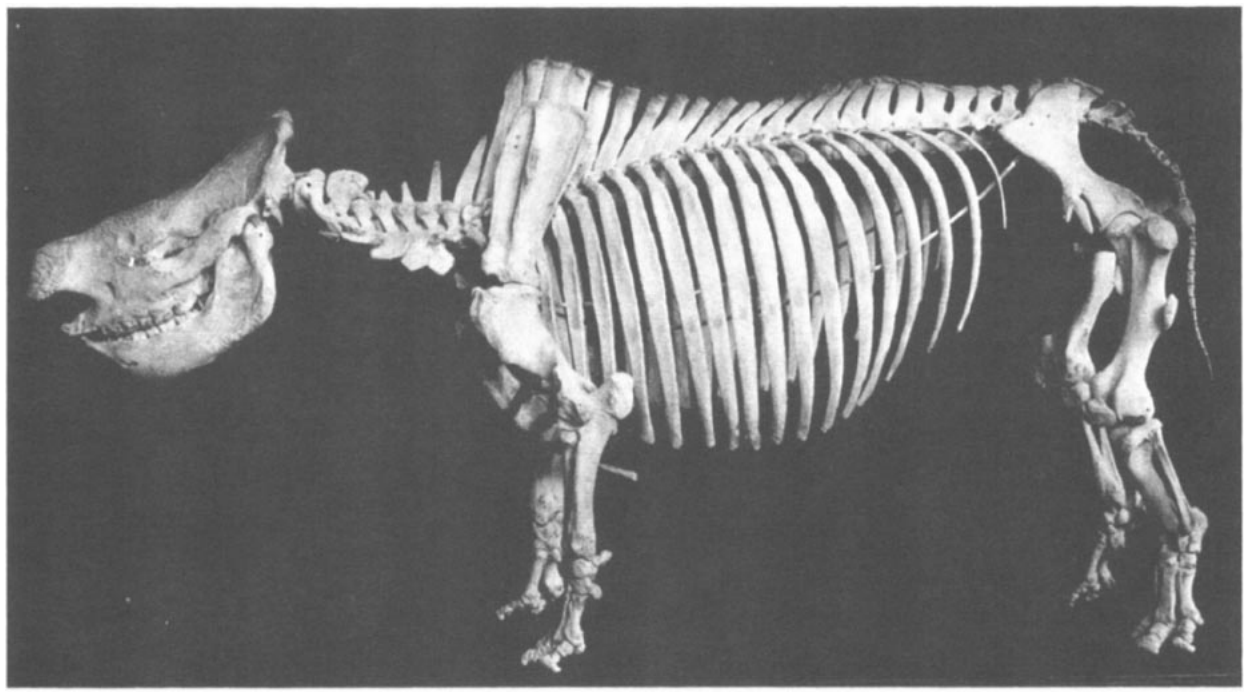

FIGURE 4. Skeleton of specimen from Faradje in the Congo (American Museum of Natural History no. 51867).

years of age, but follicles present, at least on hump (Cave and Allbrook, 1959; Cave, 1969). However, an adult specimen of *C. s. simum* had hair detectable by touch, as did several other specimens (Alexander and Player, 1965). A subspecific difference in this regard was suggested. The skin lacks normal sweat glands; possesses comparatively few, but large, apocrine sweat glands, well-provided with huge myoepithelial cells allowing the sudden discharge of copious sweat (Cave and Allbrook, 1959). Arrector pili muscles are absent. The hump of the young animal dissected by Cave and Allbrook extended from occiput to withers, over the spines of cervical vertebrae 2 to 6, and was said to consist of dermal thickening only; however Guggisberg (1966) suggested this was due to the youth of the specimen, whereas Alexander and Player (1965) suggested that the sample sent to Cave and Allbrook was defective, as an adult dissected by them had a skin callus 49 mm thick, beneath this a fatty pad 30 mm thick, and beneath this a muscular-ligamentous mass, more than twice as thick as the total of the skin, consisting of enlarged *M. semispinalis capitis*, *M. rectus capitis*, and nuchal ligament. This, they point out, explains both the reputed succulence of the hump and the fact that it is larger when the head is raised. The skin over the hump in the specimen studied by Alexander and Player was slightly more than three times as thick as that lateral to it, whereas the fatty pad was absent laterally and was replaced by connective tissue in a calf. They see the hump as an adaptation to the grazing mode of life, muscular hypertrophy being necessary to lift the long, heavy head.

Two cows, after 5 months and 18 months of lactation, respectively, had the following milk composition in percentages (Smith, 1968; Wallach, 1969); total solids 8.26 and 8.84, fat "trace" and 0.60, lactose 6.50 and 6.85, protein 1.18 and 1.54, ash 0.20 and 0.23. The milk pH was 6.4.

Skull elongated behind eyes, with long backwardly extended occipital crest (Figure 3); shortened in front of eyes, with nasals, premaxillae, and mandibular symphysis all abruptly ending shortly in front of level of cheekteeth. Symphysis broad; nasals broad and humped; mandible with convex lower border and no prominence in angular region. Antorbital process quadrangular in form; lacrimal bridge invariably ossified (Cave, 1965). Foramen ovale temporo-sphenoidal (Cave, 1962). Radius length 82% of humerus; tibia 73% of femur; humerus 93.2% of femur; tibia 95.2% of radius; total forelimb length 100.0% of total hindlimb; humerus 73.7% of basal skull length; metacarpal III 49.2% of radius. Vertebral formula: C 7, T 18 (or 19), L 4, S (3 to) 5, Cd 22 (5 skeletons). Spine of first thoracic long; length of spines decreasing anteriorly to C 5, posteriorly to T 6; spines of T 15 to 17 slightly raised; T 17 or 18 anticlinal. Ischial tuberosities thick, rounded; ribs strongly expanded (author's unpublished data). A complete skeleton is illustrated in Figure 4.

Premolar row occupies 43 to 47% of whole toothrow; dentition i 0/0, c 0/0, p 3/3, m 3/3; deciduous dentition di 0/0, dc 0/0, dp 4/4. Height of unworn third upper molar, 120 to 130 mm—strongly hypsodont. Protoloph and metaloph (these and following terms are illustrated in Figure 5) both curved and backwardly inclined, disturbing the usual π shape of the rhinocerotid upper cheektooth; protocone and hypocone show early fusion, especially in premolars, isolating a median valley. Crista present on upper premolars and first upper molar, united early with crochet to form a medifossette; postfossettes isolated early in wear; paracone bulge prominent, parastyle pointed and projecting. In lower cheekteeth, anterior and antero-external walls of metalophid form a right angle; metaflexid and entoflexid commonly become enclosed with wear (Cooke, 1950; author's unpublished data). The crowns of the permanent teeth are heavily coated with cement; those of deciduous teeth are not. Upper deciduous dentition: ectoloph undulate with raised parastyle and metastyle and three weak ridges between (paracone style, mesostyle, and metacone style), less marked in dm 2 than in dm 3 and 4; in dm 1, parastyle projecting. Cingulum weak, descending lingually, and never continuous lingually; crista strong, often duplicated; often joins crochet to enclose a medifossette; inner part of protoloph curved backward, especially on dm 4; postfossette as deep as median valley (Hooijer, 1959). Hardness of dentine 47.2 kg/mm^2, cement 24.4, enamel 256.0 (Schaurte, 1966).

Lymph nodes all of haemolymph type, with no differentiation between cortex and medulla (Cave and Aumonier, 1962, 1964).

Kidney tubules of a young adult female contained much albuminous material (Aumonier and Cave, 1959).

Penis has dorsal skin of prepuce semitranslucent, with skin apocrine glands visible as "goose pimples." Eccrine glands are present in confluent clusters or short rows on both prepuce and glans and are pale, low, and each has a flat raised ostium. They are associated with dense surrounding lymphoid tissue and perhaps function as scent glands (Cave and Aumonier, 1965; Cave, 1966). Medial surface of *processus glandis* attached to glans as in *Diceros*, but shorter, lacking angulation in the free border, and curved upward but not encroaching on dorsum of glans (Cave, 1964).

Parathyroid parenchyma arranged as solid branching cell-cords; highly vascularized. A single gland was observed in a 10 or 11 year old female (Cave and Aumonier, 1966).

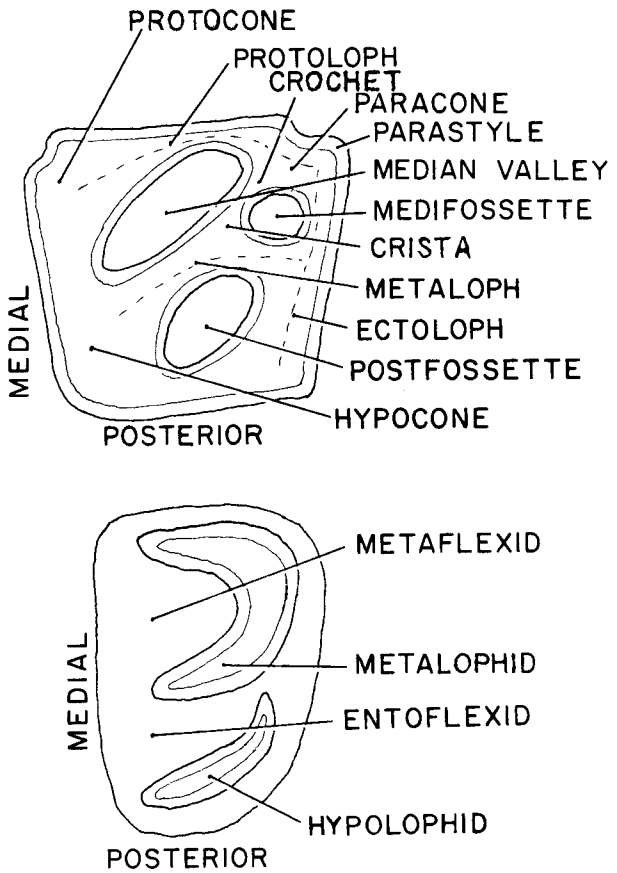

FIGURE 5. Molar teeth (first upper left molar above and last lower right molar below) to show the parts mentioned in text.

FUNCTION. The white rhinoceros sweats freely when persistently disturbed in hot sunshine, and can release copious sweat very suddenly (Cave and Allbrook, 1959).

Body temperature is 29.4 to 35.0°C; heart rate in a young specimen 64 to 70 per minute; respiration 12 to 16 per minute (Wallach, 1969). A nycthemeral variation in deep body temperature of more than 3° is normal (Allbrook *et al.*, 1958).

By scent, these animals can detect a man downwind at 800 yards (730 m; Player and Feely, 1960). Hearing is acute; the ears move constantly and independently. A pair in Antwerp zoo could recognize their keeper by sight at 20 m; Lang considers they can probably see better at 50 m than at 15 m (Van den Bergh, 1955). Calves probably have somewhat better eyesight than adults (Player and Feely, 1960).

Much albuminous material is probably excreted in urine, which is milky, slightly reddish, and highly odoriferous, especially in the male (Van den Bergh, 1955).

ONTOGENY AND REPRODUCTION. Gestation period estimated at 530 to 550 days by Dekeyser (Simon, 1970), 547 days (Player and Feely, 1960), and 540 to 550 days (W. E. Foster, 1960). This is considered too long by Schenkel and Lang (1969); Heppes (1958) suggested 17 months (510 days).

Births have been recorded for the southern race in June (Smith, 1968) and July (Bigalke *et al.*, 1950). A birth weight of 107 lb (= 48.5 kg) has been recorded; this was doubled in 6 months (Smith, 1968). The same specimen was 0.59 m high at one month. At 28 months, a male was 1.20 m high; at 52 months, 1.54 m; a female had comparable measurements (Van den Bergh, 1955).

Growth during 18 months was described by Bigalke *et al.* (1950): costal folds were apparent in the first few months, but disappeared with development of body fat by 12 months. At 6 weeks the stratum corneum began to flake off, revealing a whitish skin below. This process was virtually complete by 4 months, and was repeated when 10 months old. Sparse black body hair was visible all over at 3½ months, and was still apparent at 15 months. The hump first appeared as three separate callosities, one behind the other, which ultimately fused. A black membrane covering the developing horn fell off at 6 weeks. Thick black hoofs were present at birth; these gradually wore off and were replaced from their bases by lighter, clearly demarcated gray hoofs, which then gradually turned black. Milk teeth began to erupt with the upper dm 2 and 3 at 3 months. However in another specimen (Wallach, 1969), the upper dm 1 was the first to erupt, at 2½ months.

The basal skull length, in young skulls with the full deciduous complement, is 47 to 49% of adult size; by the time the first upper molar is beginning to erupt, this has increased to 72 to 75%. Full size is reached while the third upper molar is still erupting, except that the zygomatic arch continues to expand in males, and so does nasal breadth in both sexes (author's data).

Females may mature in 3 years (Heppes, 1958); a recognized cow in Umfolosi was still producing calves at 36 years, though showing signs of age (Player and Feely, 1960). The young suckle for "at least a year" (Player and Feely, 1960) or "about two years" (Van den Bergh, 1955). The calf stays close to its mother, even remaining by her body for several days after her death (W. E. Foster, 1960).

Mating occurs throughout the year, but is commonest from July to September in Zululand, and from February to May in Uganda. Males fight fiercely and bloodily for the females, charging head-on; deaths are caused in this way (Pitman, 1955; J. B. Foster, 1967). Several males follow a female in estrus, and one finally succeeds in driving away the others and copulates several times with the female (Backhaus, 1964; Player and Feely, 1960). Mating is preceded by sparring between the male and female, as in the black rhinoceros; the female occasionally repulses the male altogether, or even kills him (Backhaus, 1964; Guggisberg, 1966; Schenkel and Lang, 1969). A female with a calf is always aggressive towards a male; a male will often at this time try to kill an unprotected calf (J. B. Foster, 1967). In copulation, the male places both feet on the female's back; the couple stay mated for an hour or more, and may mate several times in succession (Backhaus, 1964). In Zululand, estrus females form consort pairs with territorial males, which may last for 2 to 3 weeks (Owen-Smith, 1971).

ECOLOGY. No known predators except man. Symbiotic associates are *Buphagus africanus* (in Garamba National Park, Congo; Micha, 1958) and *Bubulcus ibis* and *Lamprocolius nitens* (in South Africa; Player and Feely, 1960). The rhinoceros responds to the birds' warning calls, the birds feed on the insects that settle on its hide or are disturbed by its feet. In Hluhluwe Game Reserve, white rhinos occasionally associate with black rhinos in a common grazing group (Steele, 1960).

Parasites include six species of ticks (Guggisberg, 1966), which are eaten by the birds, and by terrapins when the rhinos visit wallows (Player and Feely, 1960). They are bitten by flies, especially *Lypeosia*. Bot-fly larvae have been found in the stomach, hatched from eggs laid in the skin of the head and shoulders.

Population structure: In South Africa, white rhinos associate in groups of 10 to 14; in East Africa, groups of more than four are rare (Guggisberg, 1966; Micha, 1958). In Uganda, the most common grouping (38% of all encounters) is of a cow with a calf; one or more males with a female—perhaps accompanied by a calf—and groups of two females with their calves, are also common groupings. Males are usually solitary. The sex ratio is 1:1 (J. B. Foster, 1967). The large associations sometimes reported, at least in the Congo, are undoubtedly *ad hoc* grazing or resting groups, which are brought together by localized facilities, and which later separate again into their component parts (Backhaus, 1964). Populations have been estimated to increase by 12% per annum (Simon, 1970). The following estimates of population density per square kilometer have been made (Schomber, 1966): Umfolosi 0.81, Hluhluwe 0.17, Garamba 0.12 to 0.20, western Uganda 0.03 to 0.05, Nimule 0.35, Yei district (Sudan) 0.03.

Habitat: Player and Feely (1960) pointed out that in South Africa the former distribution of the species corresponded mostly with the Bushveldt zone. In the Nile region, white rhinos inhabit open *Combretum* forest and the nearby plains (Guggisberg, 1966). Steeply undulating country is traversed, but not permanently inhabited. In Uganda, the rhinos go into swampy country in the dry season; when the rains come, they go 10 km inland from the Nile, especially to Biliba ridge (J. B. Foster, 1967).

Territoriality: These animals are very sedentary; Backhaus (1964) observed a bull marking high grass-tufts with urine every 100 m or so. An approaching bull, accompanied by a cow, turned tail on scenting these marks, and the female

followed without scenting. The territory of one or a pair of animals measured 5 to 6 square km in Garamba; Player and Feely reported that the area occupied by one or more rhinos is 20 to 30 acres (8 to 12 hectares) in the wet season, but they wander more in the dry season. Owen-Smith (1971) reported male territories of 2 square km in Zululand, some of which are shared by subordinate males; these territories are defended by ritualized boundary confrontations, and marked by feces and urine. Females have widely overlapping home ranges of 12 to 15 square km and wander through 7 or 8 male territories.

Disease: Young (1965) recorded lesions near the eye, probably due to infection of an injury, accompanied by blockage of the noso-lacrimal canals. They were successfully treated under local anaesthetic by a mixture of chloromycetin, corticoid, and methyl cellulose. Rinderpest does not affect the species, but anthrax is endemic (Heppes, 1958).

Diet: Entirely graminivorous. In Sudan, said to feed largely on tall *Pennisetum* grass; in Zululand, eats such grasses as *Pannicum*, *Urochloa*, and *Digitaria*, which occur in shady areas in *Themada triandra* grasslands, but the climax species is rarely eaten except during rains when it is regenerating after burning (Player and Feely, 1960; Sidney, 1965). Will often eat grass more than 0.3 m high.

Conservation: Player (1967) and Sidney (1965) recorded the history of conservation of the species in Zululand as follows: only four were reported there in 1899, six in 1903, 15 in 1912 and 25 in 1920. However Maqubu Ntombela, a game guard since 1918, noted (according to W. E. Foster, 1960) that there were at least as many white rhinos in Umfolosi then as now, and that their protector, Vaughan-Kirby, deliberately exaggerated their rarity in order to press home the need for a reserve. It is agreed, however, that a drought in 1932 reduced the population to about 180, since when they have built up again to more than 600, creating considerable management problems. These have been relieved by reintroducing the species over wide areas of its former range: to Matopos National Park and Kyle Dam Game Reserve, Rhodesia, in 1962 (Condy and Davison, 1964); to Murchison Falls National Park in 1961 and 1964 (Anon., 1970a); to Kruger National Park, Pretorius Game Reserve, and other localities (Player, 1967); to Mlilwane Game Sanctuary, Swaziland (Anon., 1965); and to Meru National Park, Kenya (J. B. Foster, 1967). Most, but not all, of these reintroductions have been from Umfolosi.

In the Congo, political disorders (notably the invasion of the Garamba National Park by dissident troops) reduced the numbers from more than 1200 in 1963 to a maximum of 50 in 1970; while in Uganda the numbers have been reduced from Cave's (1963) estimate of about 80, to some 20 to 25 (Anon., 1970a). In Chad and Central African Republic, there are a few still, and in the Sudan an unknown number (Simon, 1970).

The species was first exhibited in captivity in 1946; it does well there (Reynolds, 1960). The first specimen born in a zoo (in Pretoria) was evidently conceived prior to capture of the female (Smith, 1968). The second was sired and born in the same zoo (Anon., 1970b).

White rhinos have been captured using the immobilizing dart technique, with a mixture of 3 gm diethylthiambutene, 100 mg hyoscine hydrobromide and 14 cc chlorpromazine hydrochloride ("Largactil") (Condy and Davison, 1964); a similar tranquillizer was used by Player (1967).

BEHAVIOR. Backhaus (1964) gave the hours of daily activity as 0500 to 0900 and 1500 to 1830. Other hours are spent resting or wallowing, although wallows are rarely visited in the morning. On warm, windless days this rhythm is broken, and the animals may feed continuously all day (Player and Feely, 1960). During the rest period in the heat of the day, the animals lie in the shade of a *Kigelia* tree (in Garamba), or near a termite hill, although often the shade these offer is minimal (Backhaus, 1964); Heppes (1958) noted that in Uganda an animal generally stands under a tree for about half an hour before lying down, and in the afternoon will rise and stand awhile before moving off.

Communication and vocalization: The bull is noisier than the cow. A bull grunts and snorts while following a cow in estrus, utters a loud bass bellow when fighting another bull, and if repulsed by the cow gives a sound like an elephant's trumpet. The young squeal if separated from their mothers (Player and Feely, 1960).

Locomotion and posture: The white rhino trots at 18 mph (24 kph) and can gallop over short distances at 25 mph (40 kph; Player and Feely, 1960). It runs with the head down, with the hindfeet rapidly striking the ground and the forefeet "following the direction of gyration" (Van den Bergh, 1955). The animal sleeps on its belly with the legs tucked under it.

Learning: Little investigation has been done on this subject. The calf generally, but not always, runs ahead of its mother and is "steered" with her horn (Guggisberg, 1966). The Antwerp pair became tame and learned to recognize their keeper (Van den Bergh, 1955).

Ingestion: Grazing takes place in morning and late afternoon; the animal walks slowly forward, pulling grass with its lips. Drinking often takes place just before wallowing, in the same place—hence, often in very muddy water (Heppes, 1958; Backhaus, 1964). The animal drinks with its lips immersed (Bigalke, *et al.*, 1950). In Antwerp, white rhinos drink 60 liters of water per day in winter, 80 liters in summer (Van den Bergh, 1955).

Display: The "Complex bull ceremony" occurs as in the Black rhino (Schenkel and Lang, 1969), and is of territorial significance (Owen-Smith, 1971).

Washing and dusting: The species often wallows in mud, but rarely actually bathes (Guggisberg, 1966). Wallows are used by several individuals; no wallowing takes place in the morning. The animal usually wallows for an hour or more, and never less than 5 minutes; it lies quietly, occasionally snorts, and rolls only rarely (Backhaus, 1964). In winter, in South Africa, a sandbath tends to replace the mud wallow (Player and Feely, 1960).

Defensive behavior: They react immediately to the alarm note of *Buphagus*, their ears twisting and turning in opposite directions; if lying down, the animals immediately stand up and face in opposite directions (Player and Feely, 1960). Flight is short, in a group, and not panicky (Guggisberg, 1966); when in flight, they often utter a chirping sound (J. B. Foster, 1967), and hold the tail upright or curled forward with the tip resting by the base (Schenkel and Lang, 1969). When handled, the young animal tosses its head (Bigalke *et al.*, 1950).

Eliminative behavior: The female urinates and defecates with the hindlimbs straddled, hindquarters depressed, and the tail curved up in a circle (Bigalke *et al.*, 1950); the male emits a pungent stream of urine, in about three backwardly directed squirts (Micha, 1958; Van den Bergh, 1955; Player and Feely, 1960) that serve to mark the area of a territory (Owen-Smith, 1971). Defecation occurs three times a day; after defecating, the animal scrapes the pile with its hindfeet (Bigalke, *et al.*, 1950; Van den Bergh, 1955), but never horns its dung as the black rhinoceros does (Backhaus, 1964; Van den Bergh, 1955; Heppes, 1958). Dungheaps are found mainly on regular paths, where these cross hills or dense bush, or on the way to wallows or streams; they attain much greater sizes than do those of the black rhino; several animals may contribute, each one backing up to the pile and scraping with the hindfeet afterward (Player and Feely, 1960; Heppes, 1958; Backhaus, 1964; Guggisberg, 1966).

GENETICS. There are 82 diploid chromosomes (Heinichen, 1969), only the X chromosome is metacentric, the Y and all autosomes are acrocentric, in which feature they differ strongly from those of *Diceros*. The karyotype differs from that of *Rhinoceros unicornis*, not in number of chromosomes, but in having more with terminal centromeres and fewer with subterminal centromeres (Wurster and Benirschke, 1968).

REMARKS. According to Gowers (1950) the species is the one that was known to the Romans; it existed as far north as Aswan in the Nile Valley.

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