# THE MAMMALS OF THE SOUTHERN AFRICAN SUBREGION

BY

## JOHN D. SKINNER

M.Sc. Ph.D. F.I.Biol. F.Z.S. F.R.S.(SA)

Director Mammal Research Institute University of Pretoria

AND

### THE LATE REAY H.N. SMITHERS

D.Sc. M.I.Biol.

Senior Research Officer Mammal Research Institute University of Pretoria

WITH COLOUR PLATES BY
DICK FINDLAY

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University of Pretoria, Pretoria Republic of South Africa

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# Order PERISSODACTYLA

# XLI. Family RHINOCEROTIDAE

#### Rhinoceros

Four genera of fossil rhinoceros are known from the early Miocene Epoch of some 23 million to 19 million years ago, whose ancestors, at present unknown, must have lived during the Oligocene Epoch which preceded it. These four genera are Brachypotherium, Aceratherium, Dicerorhinus and Chilotherium.

The two rhinoceros, the white rhinoceros, Ceratotherium simum, and the black rhinoceros, Diceros bicornis, arose from a common ancestor and fossil remains recorded from Plio-Pleistocene beds of some four million to three million years old show that they occurred throughout Africa during this period. A fossil species, Ceratotherium praecox Hooijer & Patterson, 1972, whose remains have been recovered from fossil beds at Langebaanweg, was among the commoner of the large mammals in the assemblage, dating back some seven million years ago.

Both species of rhinoceros formerly occurred widely in the southern parts of Africa. The white rhinoceros, however, never occurred very far south of the Orange River and generally was absent from the Orange Free State and parts of the southern Transvaal, although in the east it occurred throughout most of Natal, except in the extreme south. The black rhinoceros, on the other hand, had a wider distribution and occurred throughout most of southern Africa, except in parts of the Orange Free State and southern parts of the Transvaal (du Plessis, 1969).

With the increase in European settlement of southern Africa from the 17th century both species were exterminated gradually throughout their range. By the end of the 19th century the southern white rhinoceros was reduced to only one population of about 50 to 100 in the southern part of the area which now forms the Hluhluwe-Unfolozi Game Reserve in Natal. It appears the population estimate of 20 for this time was a deliberate under-estimate to convince the politicians of the urgency of the situation (Emslie, pers. comm.). As a result the Hluhluwe and Umfolozi Game Reserves were proclaimed in 1897, which along with St Lucia makes them the oldest game reserves in Africa. The black rhinoceros did not fare much better, being reduced by 1930 to only about 85 to 135 black rhinoceros in northern Hluhluwe-Umfolozi Game Reserve, with a further 15 in the Mkuzi Game Reserve in Natal. The species was extinct in the Cape by 1880 and the last black rhinoceros in the Transvaal was seen in the Kruger National Park in 1936. Happily, the proclamation and protection of these Natal reserves, coupled with the development of rhino capture techniques, led to both species being saved from extinction in South Africa. To date a staggering 3 440 white and 185 black rhinoceros have been translocated from Natal reserves to form new populations both in the Subregion and abroad (Meiklejohn & Strauss, pers. comm.). Similar action with the black rhinoceros has been taken by other National Parks organisations in the Subre-

Key to the genera after Ansell (1974a)

 Lips square and broad to pluck grass; pronounced nuchal hump visible when the head is raised; skull longer and narrower, with occipital part produced backwards beyond the condyles; high crowned molars and premolars adapted for grazing

... genus Ceratotherium

Upper lip pointed and prehensile—a finger-like projection which aids browsing; no nuchal hump; the back has much more of a hollow/saddle appearance when viewed from the side; ears are more rounded and "trumpet-like"; skull shorter and broader, with occipital part not produced backwards beyond the condyles; molar teeth are lower crowned with high cusps to support browsing

... genus Diceros

Genus Ceratotherium Grav. 1868

No. 295

Ceratotherium simum (Burchell, 1817)

White rhinoceros Witrenoster

Plate 28

#### Colloquial Name

The colloquial name white rhinoceros is entrenched and originates from the name given to them by the early Dutch hunters, witte renoster, or in Afrikaans witrenoster, which was used to distinguish them from the black rhinoceros, Diceros bicornis. Barrow (1801/4), Harris (1852) and Selous (1908) used the name wit or white, so it has been in use for nearly 200 years. In spite of this, both C. simum and D. bicornis are grey, and they are inclined to assume the colour of the soil on which they live through mudwallowing and dusting. One of the most obvious characters that differentiates them is the square lips of C. simum (Fig. 295.1) and the hooked, prehensile upper lip of D. bicornis (Fig. 296.1), which are adaptations to and in their feeding habits, and they may also be referred to in this way.

#### **Taxonomic Notes**

Burchell (1817) originally described this species from a specimen from "the interior of South Africa", the type locality later being fixed by Shortridge (1934) as near Kuruman, Cape Province. Two subspecies are recognised, C. s. simum from the southern part of their distributional range and C. s. cottoni (Lydekker, 1908) from central Africa which are somewhat higher in the legs and less long in the body (Cave, 1962).

#### Description

With a shoulder height of up to 1,8 m for males and 1,77 m for females (Kirby, 1920), with a mass of some 2 000-2 300 kg for males and females 1 600 kg, the white rhinoceros ranks as Africa's third largest land mammal. They have a barrel-shaped body and short, thick-set limbs. Characteristic features include the long head with long, continually growing horns, one in front and a shorter one behind; pointed ears fringed with hair; wide squared-off lips; a distinct hump on the neck and a hump on the back, just in front of the thighs (Fig. 296.2). The thick skin is

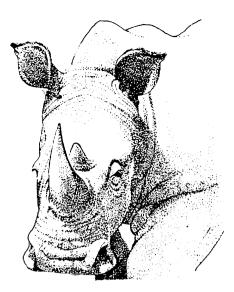


Fig. 295.1. Head: white rhinoceros, C. simum, to show the square-shaped lips of the species and the hump on the neck which shows clearly when the head is raised.

prominently folded on the front of the shoulders, on the upper part of the hind limbs and at the junction of the forelimbs and the body.

The colour of the skin is grey, but like that of the elephant, is often obscured by a coating of soil or mud. The skin on the body appears naked, but at close quarters is seen to have a sparse coating of bristly hairs. The skin may reach a thickness of about 20 mm on the shoulders, the thick dermis covered with a thin layer of epidermis barely 1 mm thick. Scattered over the surface of the skin are sweat glands which, when the individual is under stress, exude droplets of sweat. Underlying the skin there is a thick layer of fat which, on the abdomen, may reach a thickness of 50 mm.

The horns, which are composed of a mass of tubular filaments similar in substance to hair, are outgrowths of the skin and are not attached to the bone of the skull. The front is almost invariably longer than the hind, 1,58 m being the record length of a front horn from the Subregion (Best & Best, 1977), its accompanying rear horn 0,566 m. In the white rhinoceros, C. s. simum, the front horn has a straighter transverse edge in front. The lower lip has a hard surface; the upper is sensitive and soft which allows the individual to detect and then crop grass to within 10 mm of the ground. The tail is relatively short, in adults up to about 1,0 m, and has a sparse fringe of bristly hair.

The limbs have three digits, each armed with broad, stout nails, which mark clearly in the spoor. The front feet are slightly larger than the hind. However, there is a less marked difference between them than in the black rhinoceros. The cushioned pads on the soles of the feet have a hard surface with a mosaic of irregular cracks and, characteristically, have a distinct indentation on their rear edges, which marks in the spoor, and distinguishes the spoor from that of the black rhinoceros in which the indentation is absent (Plate I).

#### Skull (Fig. 295.2)

A

The skull is more elongated in this species than in the black rhinoceros, the occipital crest rising high at the back of the skull. The crest has a broad rugose area on top to provide a firm attachment for the huge muscles that actuate the raising and lowering of the heavy head. The high crest also provides for a broad area at the back of the skull for the attachment of the other neck muscles. The zygomatic arches are heavily built to give a firm attachment for the masseter muscles that actuate the lower jaw, which, at their posterior edges, broaden out to give these an extra wide area of attachment for the lower end of these muscles. The lower jaw is massive, particularly so at the level of the posterior angle, the condyles very broad and fitting into deep sockets.

The earliest known fossil form of the species, Ceratotherium praecox Hooijer & Patterson, 1972, has been recorded from Langebaanweg, Cape Province. In other parts of Africa

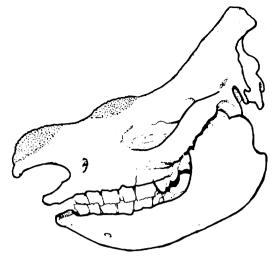


Fig. 295.2. Skull: white rhinoceros, C. simum. TL Skull 0,76 m.

this species is known from fossil beds laid down some seven million years ago. It has four incisor teeth which are lacking in the extant white rhinoceros. The dental formula of the white rhinoceros, C. simum, is:

 $I_0^0 C_0^0 P_3^3 M_3^3 = 24$ 

The upper and lower second molars are the largest of the cheekteeth. All cheekteeth are broad-faced and have convoluted enamel layers on their biting surfaces and are adapted to grinding up the food.

In the deciduous dentition they have four premolars on either side in the upper and lower jaws, the anterior premolar being the last to erupt and which, in adolescence, is lost and not replaced. Some, however, may persist into early adulthood. There is no sign of the incisors or canines in the deciduous dentition, which are sometimes present in the black rhinoceros, D. bicornis.

#### Distribution

The white rhinoceros, from the evidence of skeletal remains and their depiction in rock art, at one time occurred from the coastal areas of Morocco, Algeria and Tunisia, through the Sahara and East Africa to the Republic of South Africa.

In the wild the northern white rhinoceros is now only found in the Garamba National Park in Zaire, while the southern white rhinoceros is now spread throughout much of the Southern African Subregion. There is no doubt that at one time, during the Pleistocene Epoch, their distribution was continuous from Morocco through the Sahara to parts of the Cape Province, the break caused by climatic changes which rendered the intervening terrain unsuitable for them.

Renshaw (1904) recorded that at the turn of century there were only about 10 alive in Zululand and in 1916 Vaughan-Kirby, the first Game Conservator in Zululand, estimated that only 20 individuals survived in the reserves. However, the first official estimate in 1930 revealed that there were 120 in the Umfolozi Reserve and 30 on adjacent ground and by 1960 an aerial count gave a total of just over 700. Since then numbers in the Zululand reserves have more than doubled and up to October 1989 a total of 1 240 have been relocated out of South Africa and 2 199 within South Africa (total 3 439) (Strauss, pers. comm.). White rhinoceros have been moved to the following countries (figures correct to 31/12/1983—Meiklejohn, pers. comm., 1990): Subregion -Cape 80, Natal 487, Orange Free State 23, Transvaal 931, Bophuthatswana 330, Ciskei 6, Transkei 15, Venda 6, Botswana 97, Namibia 88, Swaziland 96, Zimbabwe 152; Africa, excluding Subregion-Angola 10, Kenya 23, Mozambique 85 (although Emslie (pers. comm.) believes Mozambique now holds the dubious distinction of the species going extinct twice), Zambia 4; Elsewhere -Argentina 6, Belgium 19, Burma 4, Canada 6, Cuba 2, Czechoslovakia 7, Denmark 2, East Germany 5, Great Britain 64, Holland 62, India 5, Israel 8, Italy 6, Japan 37, Java 2, Portugal 2, Saudi Arabia 1, Spain 33, Sweden 2, Switzerland 4, Taiwan 7, USA 257, West Germany 96. The majority were relocated inside South Africa. They have not done so well in the sourveld areas of Natal (eg. Chelmsford) or in the drier parts of the northern Transvaal (Emslie, pers. comm.). Once again this represents a remarkable effort by conservationists in the Subregion in removing a subspecies from the endangered category.

The northern subspecies, C. s. cottoni, is endangered, with a drastic reduction in numbers and shrinkage in their distribution (Kingdon, 1979).

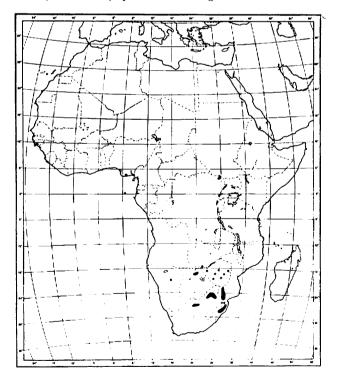
South of the Sahara, excluding the Southern African Subregion

The northern white rhinoceros now only survives (a group of 25–30) in Garamba National Park, northeastern Zaire. A further 13 are in zoological gardens, of which only one female is breeding (Hodges, pers. comm.). Following introductions from Natal, there are about 40 southern white rhinoceros in Kenya.

#### Southern African Subregion

At the end of the 19th century they were restricted to what is now the Umfolozi Game Reserve, but spread during the 1930's and 1940's to the Hluhluwe Game Reserve. At first confined to the Umfolozi-Corridor-Hluhluwe Game Reserve Complex, subsequently they have been reintroduced to the Mkuzi, Itala and Ndumu Game Reserves in Natal and many other reserves including the Kruger National Park and Pilanesberg National Park.

The last record of individuals in the three neighbouring countries was of one which was shot in Zimbabwe at Mpanda's Kraal in the northeast of the country in 1895. In Botswana, Selous (1908) stated that he shot one at Thamma Setsi (Tamuseche Pan) on the Zimbabwe border in 1874, but they persisted beyond this date in this area as he recorded their spoor in 1877. In Mozambique one was shot at Marcorsa (SE 1733 D4) by the late Sir Hugh Beadle in 1935.



#### Habitat

Player & Feely (1960) listed four basic habitat requirements: areas of short grass, for which they have a marked preference; stands of medium tall Panicum maximum which they find under trees (Emslie, pers. comm.); the availability of water for drinking and in which to wallow; adequate bush cover, and relatively flat terrain.

These requirements are met in the wooded grasslands, common in many parts of the Subregion, where they formerly occurred. This woodland carries the palatable grasses

which form their principal food. Reintroduced to areas where these conditions prevail, the species is flourishing. The type of woodland is a secondary consideration, for its function is to provide shade from the sun during the hotter parts of the day. Steep slopes within the habitat are avoided, although they will traverse them freely to feeding grounds or to water.

Melton (1987) found that white rhinoceros showed a reduction in broad scale habitat selectivity during winter, changing from favouring the Acacia nigrescens open woodland in west Umfolozi in summer to using habitats at random during winter.

#### Habits

White rhinoceros occur in small groups consisting of a single dominant or territorial bull, subordinate bulls, cows and their offspring. Territorial bulls occupy clearly defined territories, which they defend against the trespass of other bulls from neighbouring territories. In the Umfolozi Game Reserve in Natal, these territories vary in size from 0,75  $km^2$  to 2,60  $km^2$  (Owen-Smith, 1973); somewhat smaller than those of the black rhinoceros, D. bicornis. The boundaries of these territories often coincide with topographic features such as watercourses, crests of watershed ridges, or roads. The boundaries have narrow, common zones 50-100 m wide, visited by neighbouring territorial bulls. Territorial bulls mark their territories by spray urination or defecating on latrines along the boundaries. Owen-Smith (1973) recorded that, only on five occasions during his study in Umfolozi, territorial bulls moved more than 100 m beyond their own territorial boundary where this had an available water supply. Where water is not available seasonally within their territories, the territorial bull will leave it every three or four days to drink.

Territorial bulls trespassing into the territory of an adjacent bull normally take avoidance action and serious fights are usually averted. Encounters may take the form of short charges with much dust raising or, at closer quarters, horn clashing. Where a territorial bull is accompanied by a female in oestrus, however, serious fighting may ensue. Wounding may be caused by the horn or by heavy shoulder battering and may lead to internal injury. A deposed territorial bull may be allowed to remain in the territory providing he clearly demonstrates his submissiveness. Subordinate bulls respond to territorial bulls with snorting, snarling or shrieking, but seldom actually engage in fighting, although they have been killed in such encounters.

Where a territory does not include a water supply, a narrower corridor is used leading to it. Within the territory the dominant bull usually has a number of favourite resting places in which he lies up in the shade during the heat of the day, either standing or reclining on his belly or side. The territorial bull alone sprays urine which is directed backwards between the hind legs. Having defecated, he scatters his dung by kicking with the back feet. Sometimes the urine emerges as a stream and the dung is deposited without scattering. These actions are common near territorial boundaries, but may take place anywhere within the territory. However, when the territorial bull has to leave his territory to drink, he urinates in a stream in the manner of subordinates (Owen-Smith, 1973).

Subordinate bulls are tolerated by a territorial bull, providing they remain submissive, and they spend most of their lives within his territory, although they make occasional explorations outside it. Several subordinate bulls may live in a territory of a single territorial bull.

Cows on the other hand have home ranges that overlap with those of other cows and may overlap the territories of as many as seven territorial bulls (Owen-Smith, 1973). In areas with good grazing and water the home range of individual cows may be as small as 6–8 km². With deteriorating food supplies this may increase to 10–15 km² and, if there is no water available, be increased to 20 km².

Communication within the species depends heavily on olfactory signals (urine and dung constituents), which individual rhinoceros detect through their sensitive sense of smell as they cross the paths of other members of their community and encounter their dung middens. Vocalisa-

tions and subtle displays are used for direct communication; Owen-Smith (1973) recognised 10 of the former and 15 of the latter. Territorial bulls are normally silent, even in encounters, but occasionally may snort when another moves nearby. During courtship of a female, they may squeal when trying to block a female in oestrus from leaving their territory. Other members of the group may snort or snarl, which is a sign for others to keep their distance; they pant, when maintaining contact or as a sign to join up; shriek, as an attack inhibiting signal; squeal for eliciting protection or as a distress signal in calves; or puff when suddenly alarmed.

Subtle displays may involve pulling the ears back as a sign to the others to keep off; advancing steps often accompanied by a snarl are used as a threat; charges; prodding with the horn or staring at each other, horn against horn, as intimidatory gestures. Horn against horn clashing is a more intense ritual attack, which may develop into horn-wrestling and finally jabbing with the horn. Side-rubbing may be a means of more closely cementing the bonds within a group and head-flinging in the young is an invitation to play. Although white rhinoceros have preputial glands in the region of the penis or vulva, olfactory communication appears to be limited to the odours of the urine and dung. Frequently territorial bulls will ascertain whether cows within their territories are in oestrus, but cows take little notice of each other. Calves are inquisitive and will investigate other members of the group, sometimes even cars and road signs!

White rhinoceros walk slowly, their heads held close to the ground, their nostrils in close contact with it to the extent that, in sandy soil, the broad mouth may mark clearly in the spoor. When in a hurry they move with a graceful trot, timed from a vehicle as up to 28 km/h, and under stress canter and gallop at up to 40 km/h. They tend to use established routes to water or to preferred grazing areas. In cool cloudy weather with high winds they tend to shelter in thickets. Cows and subadults do not seem so prone to use established sheltering places as do territorial bulls.

White rhinoceros pay little attention to other mammalian species, even at close range. Pienaar (1970a) recorded an unusual incident of an elephant killing one at a water hole. Predation on them, except by man, is minimal, although rarely they may be killed by lions.

Fork-tailed drongos, Dicrurus adsimilis, often hawk insects by flying along the sides of resting rhinoceros and frequently they are accompanied by red-billed oxpeckers, Buphagus erythrorhynchus, which remove ticks from their hides. Terrapins may also remove ticks while rhinoceros are wallowing in a pan. The birds serve the useful purpose of warning them of approaching danger.

White rhinoceros have poor sight but acute senses of smell and hearing. They respond more readily to moving objects, which are only discerned at ranges of 10–25 m, than to those at rest. Owen-Smith (1973) recorded that, when downwind, they respond with alertness to human scent at about 0,8 km, and continually investigate odours when moving. The ears which can be rotated independently, orientate quickly to face any strange sound and move continually, even when the individual is apparently asleep. They are generally temperamentally quieter and less prone to provocation than black rhinoceros.

During the summer months, white rhinoceros indulge in mud-wallowing or lying in muddy pools as a means of thermoregulation, but more especially for the purpose of coating the body with a layer of mud as a means of ridding themselves of ecto-parasites. Following mud-wallowing they will rub themselves on the trunks of trees or boulders which eventually, through continued use as rubbing posts, become debarked and polished. Mud-wallowing is infrequent during the winter months (Owen-Smith, 1973).

#### Food

White rhinoceros are grazers with a preference for feeding on short grass, which they are capable of cropping to within 25–60 mm of the ground (Owen-Smith, 1988). Lacking incisor teeth, the movable and extremely sensitive upper lip is extended over a grass clump, pressing the grass against the hard lower lip to be cropped with an upward movement of

both lips. Sometimes the process is assisted by a slight movement of the head. As the individual feeds the head is held low, the wide nostrils maintaining contact with the grass. They are selective feeders. Owen-Smith (1973) gave the bite width of an adult female as about 200 mm and estimated that about 48% of daylight hours are taken up in feeding. Feeding rate on short grass averaged 78 bites per minute. In doing so they stand in one place, moving the head in an arc, then take a step forward to repeat the process. In wetter years when the grass is taller they do not crop the grass as short, and their bite rate is greatly reduced (Emslie, pers. comm.) They may chew the food for a moment or two, but do not ruminate.

Owen-Smith (1973) showed that, in Natal, four species of grasses constituted 74% of the food intake, these being: red grass, Themeda triandra (an important dry season food resource); buffalo grass, Panicum maximum; small buffalo grass, P. coloratum, and common signal grass, Urochloa mosambicensis, the first-named being by far the most heavily utilised, sprouting green grass being preferred. In a study of wet season feeding behaviour of grazers in west Umfolozi in 1984, Emslie (pers. comm.) found that 42% of the grass biomass in white rhinoceros feeding patches was made up of Urochloa mosambicensis and Panicum maximum. Both these species favour lower-lying, more alluvial soils. P. maximum is also a species often found in shady sites under trees. These two species contributed 51% to the diet. Themeda triandra, Sporobolus smutsii and Panicum coloratum contributed a further 33% to the diet. White rhinoceros were found to preferentially graze the shorter, more erect central tillers of P. coloratum than the longer, more prostrate side stoloniferous tillers (Emslie, 1985; Diamond, 1986). Some 30 other species are eaten to a lesser extent. Other species such as the resinous turpentine grass, Cymbopogon plurinodis, are rigorously avoided. Owen-Smith (1973) recorded geophagia, especially around termitaria.

White rhinoceros drink water regularly and are dependent on its availability. Owen-Smith (1973) found that most drinking is done between 17h00 and 21h00 and continues after sundown, less drinking taking place during the day. A drinking frequency of every 2-3 days was most usual during the dry season.

#### Reproduction

White rhinoceros breed at any time of the year, but in Natal there are peaks of calving in March & July.

Bulls start holding territories at an age of 12,5 years (Condy, 1973) and can detect when cows are in pro-oestrus for they form a close attachment with a cow for a considerable time before mating. During this period bulls will take active steps to prevent cows from leaving their territory, chasing cows, squealing and sometimes horn-clashing with a pro-oestrous cow until she remains. While in pro-oestrus she will drive him off with snarling and snorting. Interested subordinate males are driven off actively by the territorial bull during this period (Owen-Smith, 1973).

Females breed from an age of four years (Owen-Smith, 1988). The oestrous cycle length is approximately 28 days (n=5) based on the inter-oestrus intervals and hormonal profiles of captive C. s. cottoni (Hodges, pers. comm.). One calf was born after a gestation period of about 16 months and had a birth weight of about 40 kg.

The female usually moves away from the group to give birth. At birth the wrinkled skin is pale grey with a pink tinge. For the first three days following parturition the calf is unsteady on its feet, thereafter it keeps close to its protective mother. Bigalke, Steyn, de Vos & de Waard (1950) recorded that the outer horny layer of the skin is moulted at about one and a half to four months, revealing a new paler skin. A further moult takes place at about 10 months.

The calf is weaned at about a year old and separates from its mother at about two or three years of age. If the female loses her next calf, the bond between them may be reestablished. During the association of the cow and her calf, the calf usually precedes its mother when moving, being guided by gentle prods of her horn. This is in contrast to the

black rhinoceros, *D. bicornis*, where the calf usually runs by her side or behind her.

Females have a pair of inguinal mammae.

Genus Diceros Gray, 1821

No. 296

Diceros bicornis (Linnaeus, 1758)

#### Black rhinoceros Swartrenoster

Plate 28

#### Colloquial Name

Alternative name: Hook-lipped rhinoceros.

#### **Taxonomic Notes**

While seven subspecies have been described (Groves, 1967), more recent research (du Toit, 1987) has not supported this degree of taxonomic splitting, and the African Elephant and Rhino Specialist Group (of the International Union for the Conservation of Nature) now recognizes four conservation units within the continent (du Toit, Foose & Cumming, 1987). These are a northwestern group in Cameroun and the Central African Republic (it is no longer certain if any of these survive), an eastern group in Kenya and northern Tanzania (designated as D. b. michaeli), a desert group in Namibia (D. b. bicornis), and the relatively large bushveld group extending from Natal through Zimbabwe and Zambia into southern Tanzania (D. b. minor). In addition to D. b. minor and D. b. bicornis (which has recently been reintroduced to the Cape Province), the Subregion also has a small population of D. b. michaeli, originating from Kenya, in the Addo Elephant National Park.

#### Description

Adult black rhinoceros stand about 1,6 m at the shoulder and have a mass of up to about 1 000 kg. The mean mass of live individuals from the Hluhluwe Game Reserve, Natal is males 852 kg (n=8), females 884 kg (n=6) (Hitchins, 1968b).

Some characteristic features which serve to distinguish them from their near relative, the white rhinoceros, Ceratotherium simum, include their possession of a prehensile upper lip (Fig. 296.1), which is used in grasping the twigs of the woody plants on which they feed, the shorter head, longer neck and smaller, rounded ears. The outline of the back is also different in the two species, the black rhinoceros lacking the nuchal hump, which is a well developed and obvious feature of the white rhinoceros (Fig. 296.2). The black rhinoceros carries its shorter head higher than the white rhinoceros.

In overall colour they are dark grey. Like the elephant and the white rhinoceros, they tend to take on the colour of the ground on which they live, through their habit of wallowing in mud and dusting themselves after bathing. The skin is thick, with a sparse scattering of hairs. They have eyelashes and hairy fringes to the ears and the end of the tail. The folding of the skin is confined to an area above the knees, on the front limbs, across the nape behind the ears and on the flanks. Scattered throughout the skin are sweat glands which exude droplets of sweat when the individual is under stress.

The horns are composed of a mass of tubular filaments, similar in substance to hair. They grow from the skin and are not attached to the underlying bone, but the bony surface of the skull is rugose under the bases of the horns to allow a firm attachment of the skin to the skull in these areas. In Zululand the front horn in black rhinoceros is invariably longer than the back. In Hluhluwe-Umfolozi in 1973 only 2,5% of males had anterior horns = posterior, and none shorter (n=120). For females the figures are 14,2% and 5,7% (n=106). For 1985 the figures are for males 0% and 0%

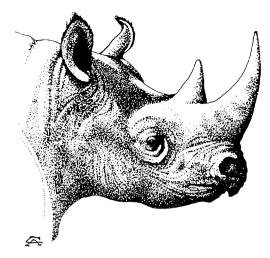


Fig. 296.1. Black rhinoceros, D. bicornis, to show the hooked lip of the species.

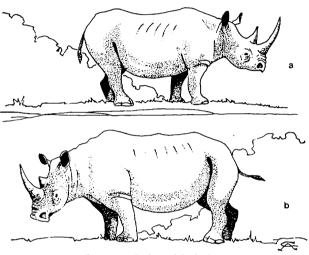


Fig. 296.2. Outline of the body: (a) black rhinoceros, D. bicornis. (b) white rhinoceros, C. simum.

(n=58) and females 29,0% and 4,3% (n=69) (Hitchins, 1989). The shape of the horns also depends upon the habitat. Horns in Kaokoveld for example are much straighter than those in Zululand, presumably as a result of different wear patterns. The maximum front horn length recorded by Best & Best (1977) for a specimen from northern Natal is 1,05 m, with a rear horn of 0,52 m, which is surpassed by several from East Africa where the maximum is 1,20 m and 0,445 m respectively.

The limbs have three digits each, with broad, stout nails which mark clearly in the spoor (Plate I). The front feet are larger than the hind as they have to carry the great mass of the huge shoulders, neck and head. The cushioned pads on the soles of the feet have a hard surface with a mosaic of irregular cracks. In Kenya, Rob Brett has been able to identify individuals based on photographs of the wrinkle patterns left behind in the spoor. The pads are rounded at the back and lack the indentation characteristic of the white rhinoceros. This aids in distinguishing the spoor of the two species, as does the size of the nails which are larger in the white rhinoceros.

Black rhinoceros suffer from skin lesions caused by a filaria parasite. At their fullest development these lesions take the form of black, blood-encrusted areas which ulcerate and haemorrhage. Usually these are situated on the skin behind the shoulders, but also occur on the chest, neck and forelegs. All adult Natal black rhinoceros have these lesions, but they are absent in rhinos from central Africa (Leader-Williams, pers. comm.) and are not found on desert rhinoceros in Namibia, no doubt due to the absence of flies that

serve as specific vectors for the parasite (du Toit, pers. comm.). The calves are free of these until they are about six months old, when the lesions begin to appear as bare pink patches on their chests. By the age of three years they are found on the chest and sides, but only appear behind the shoulders of the individual at the age of four and a half to five years. These lesions are not related to their state of health and appear on perfectly healthy individuals (Feely, pers. comm.). Oxpeckers, Buphagus spp, which frequent the backs of rhinoceros in search of ticks, flies and the blood issuing from these lesions, tend to keep the lesions open by their activities. The association of the rhinoceros with these birds has mutual benefits, for, by their loud chattering and calling, they alert the rhinoceros to danger, even when the animal is resting or sleeping.

#### Skull (Fig. 296.3)

The skull of this species is less elongated, the supraoccipital crest not extending upwards and backwards to the extent seen in the white rhinoceros. The occipital crest lacks the broad rugose area on top seen in the white rhinoceros and is narrower. The zygomatic arches are heavily built to give a firm attachment for the masseter muscles that activate the massive lower jaw. While ancestral forms of rhinoceros possessed cutting incisor teeth and, in some, canines, these are absent in the black rhinoceros whose dental formula is:  $I_0^{\rm n}$   $C_0^{\rm n}$   $P_3^{\rm n}$   $M_3^{\rm n}$  = 24

The premolar teeth are molariform, all the cheekteeth being broad-faced and adapted to grinding up the food.

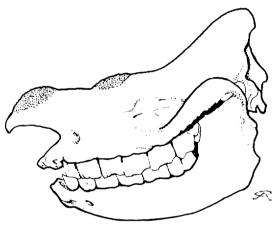


Fig. 296.3. Skull: black rhinoceros, D. bicornis. TL Skull 0,55 m.

#### Distribution

It is a sad reflection that a species which formerly had such a wide range in the Subregion, should have suffered such a drastic reduction in its distributional range within historical times. World population estimates were: 1960–100 000; 1970–63 000; 1980–14 800; 1990–3 000 (Emslie & Adcock, 1990a)

Van Riebeeck's Diary of 1652 recorded rhinoceros as occurring on the slopes of Table Mountain and as being common on the Cape Flats. At that time no European was aware that two species occurred in Africa and this species did not have a distinguishing name. Names differentiating the two species must have come into use towards the end of the 18th century, when the hunters and pioneers entered the area north of the Orange River and first saw the white rhinoceros. From this date onwards the distribution of both species of rhinoceros shrunk in the face of human pressures. The last black rhinoceros was shot in the Cape Province at Graaff Reinet in 1880. The horns of this individual are now in the collection of the Reinet House Museum, Graaff Reinet. It was shot in the parsonage garden by James Murray on the instructions of his brother, the Rev. Charles Murray, as it was eating his vegetables. The last record from the Orange Free State is dated 1842. In the Transvaal, the last record of a naturally occurring black rhinoceros was of a solitary female seen in the Kruger National Park in 1936 (Penzhorn, 1971). In Natal, the proclamation of the Hluhluwe and Umfolozi Game Reserves in 1897 and the Mkuzi Game Reserve in 1912 came just in time to save them from extinction in this province. In Zimbabwe populations survived mainly in Lowveld areas where low rainfall and trypanosomiasis constrained farming activities (du Toit, pers. comm.)

Since these days, with a growing appreciation of wildlife as a natural resource with economic, recreational and aesthetic values, as a further measure to ensure the future of the species, surplus black rhinoceros have been translocated to a number of areas in the Subregion where they formerly occurred. Since 1962 a total of 131 Hluhluwe-Umfolozi and Mkuzi D. b. minor animals have been moved to re-establish seven new populations: Ndumu Game Reserve (which now has also become a donor reserve, with 19 animals translocated from Ndumu to date); Kruger National Park (12 also brought in from Zimbabwe), Itala Game Reserve, Pilanesberg National Park, Weenen Nature Reserve, Eastern Shores and Andries Vosloo Kudu Reserve in the Cape (Emslie & Adcock) 1990a). Their limits of distribution are still rapidly altering, for example within recent years in Zimbabwe, the remnants of two isolated populations in the Chipinga and Mtoko districts, threatened by land development, were translocated to the Gonarezhou National Park.

The distribution, as depicted, shows a scattered and discontinuous occurrence and, except where they are afforded protection in National Parks and reserves, the continued existence of some of the smaller island populations is doubtful. In Kaokoland and Damaraland in northern Namibia, 43 were removed in 1970–72 as a conservation measure to the Etosha National Park (Hofmeyr et al., 1975). The remaining rhinoceros were almost wiped out by poachers, only a relict population of some 60 rhinos remaining by the early 1980's. Following extensive protection measures records for 1987–88 show there are about 100 rhinoceros now occurring in the area (Britz & Loutit, 1989).

Outside South Africa, Namibia and Zimbabwe, the species is close to extinction owing to continued poaching, which is fuelled by the high demand for rhinoceros horn as a component of traditional medicines in Asia and, to a lesser extent, as a raw material for the manufacture of Yemeni dagger handles. Markets for horn remain despite major efforts by international conservation agencies to stop the trade (du Toit, pers. comm.).

There are currently at least 600 black rhinoceros in South Africa, 400 in Namibia and 1 500 in Zimbabwe. Two small populations of D. b. bicornis have been reintroduced recently from Namibia to the Vaalbos and Augrabies National Parks in the Cape. An unknown but very small number still survive in northern Botswana. Six D. b. minor have been reintroduced recently into Swaziland. In Mozambique, a few scattered survivors are still present in remote areas of dense bush (du Toit, pers. comm.). Only in Mozambique can it be regarded as endangered. Elsewhere in the Subregion populations have been increasing under sound scientific management. Contrast this with the decline, due to poaching, in the rest of Africa, from an estimated 63 000 in 1970 to 4 000 (including those in the Subregion) in 1986 (du Toit et al., 1987) and one can appreciate the great effort put into conservation by authorities within the Subregion.

An interesting translocation was that of seven black rhinoceros in 1961/62 from the Kenya Game Department to the Addo Elephant National Park (Penzhorn, 1971; Hall-Martin & Penzhorn, 1977). These represent the subspecies D. b. michaeli and, with the species now endangered in Kenya, effective steps have been taken to ensure the short-term genetic conservation of the Addo rhinoceros which in 1989 numbered 20. The National Parks Board is presently negotiating with zoological gardens to import animals for a breeding programme for the subspecies' conservation in the Park (Hall-Martin, pers. comm.). Details of their biology can be found in the cited publications.

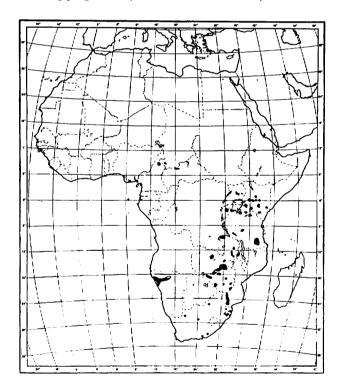
South of the Sahara, excluding the Southern African Subregion

While a small number (under 50) of black rhinoceros have been reported in Cameroun and the Central African Republic, the survival of these animals has not been confirmed. There is also no recent confirmation of a remnant population in the Akagera National Park, Rwanda. The only other remaining wild populations are in Kenya (300–400), Tanzania (probably under 200), Zambia (under 50) and a very small number in Malawi (du Toit, pers. comm.).

#### Southern African Subregion

They still exist in Kaokoland and Damaraland in northwestern Namibia, and in the eastern parts of the Etosha National Park. The largest concentration (some 100 animals) is in the Otjovasandu area in the southwest of the park (Cilliers, 1989). There are other widely scattered records south to 21°30'S and east to about 17°E. A small number have been reintroduced from Namibia into the Augrabies Falls and Vaalbos National Parks in the Cape Province (Raath & Hall-Martin, 1989).

In Zimbabwe, previously confined to the Zambezi Valley and adjacent parts of the escarpment from the western end of Lake Kariba to the Mozambique border, they have been translocated to the Hwange National Park and Matobo National Park. During the period 1986-1989, 160 were established on private ranches, as part of an ongoing programme to develop four major breeding groups under free-range conditions (du Toit, pers. comm.). In Mozambique, south of the Zambezi River, they may still occur in the Gorongoza National Park. In Natal they occur in the Hluhluwe-Corridor-Umfolozi Game Reserve Complex. A few survive in the area north of the Mkuzi Game Reserve and east of the Pongola River, and a small number have been reintroduced to Ndumu (16), Itala (34), Eastern Shores (15) and Weenen (5) Game Reserves. In the Transvaal there have been reintroductions from Natal to the Kruger National Park (81) and Pilanesberg National Park (30). In addition, seven D. b. minor have been sent to the USA to take part in a captive breeding programme (Emslie & Adcock, 1990a).



#### Habitat

The black rhinoceros requires a habitat providing adequate shrubs and young trees up to about 4 m high, including well developed woodland or thickets in which to shelter during the heat of the day or in inclement weather. A water supply, not only for drinking but also in which to bathe and mud-wallow, is also important.

While not usually associated with open plains country, the black rhinoceros occurs in a wide range of habitats ranging from forest to savanna woodland and scrub, from sea level to at least 1 500 m in the Subregion and up to 2 700 m in East Africa (Kingdon, 1979).

They are dependent on water and, in the Subregion, are seldom found more than 10 or 15 km from it. Kingdon (1979) stated that in East Africa the maximum dry season distance from water was found to be about 25 km. Where it is not available, they will dig for it in the sand in river beds, excavating with their forelegs.

The early stages of bush encroachment favour this species, especially if this is coupled with heavy grazing (Emslie, pers. comm.). However, later successional trends from closed Acacia nilotica woodland to lowland forest dominated by Euclea schimperi, Berchemia zevheri and Rhus pentheri have reduced habitat quality in the Hluhluwe Game Reserve, and is likely to have contributed to the decline in the Hluhluwe population which has taken place over the last 20 years. Interestingly many of the most rejected species (e.g. Euclea crispa, Lippia javanica) in Hluhluwe have grown up on bush-cleared sites in wetter, low-lying sites. By way of contrast favourable food plants have grown up in cleared sites in drier areas of the complex. In addition, Emslie has found grass interference to be very important. Black rhinoceros prefer the smaller sizes of Acacias but when these are hidden they are forced to eat the larger and less preferred plants. They avoid feeding in the tall grass areas of northern Hluhluwe, except along paths. In both Hluhluwe and Umfolozi young tamboti, Spirostachys africana, thickets were key habitats, with S. africana being the dominant item in the black rhinoceros summer diet, accounting for between 20-25% of woody browse eaten. Emslie & Adcock (1990b) also found that size structure > changes in the vegetation were important to the rhinoceros even if the species composition remained very similar (e.g. mature S. africana and Acacia grandicornuta woodland was rejected). Riverine bush, tamboti thickets, ridges and lowland forest margin habitat were amongst the most preferred habitats in Hluhluwe. In Umfolozi one of the most preferred habitats was heavily grazed short grass country with a few small Acacias.

#### Habits

Black rhinoceros tend to be solitary, the only stable bond being between the female and her calf, but even this is only of a temporary nature, persisting into the female's next pregnancy and ceasing altogether with the birth of her next calf. Other associations, such as that of an adult male with a female, or with a number of individuals of all age classes, are transitory.

Black rhinoceros are not strictly territorial in the sense of defending delimited areas against others of their species, but each adult does tend to remain within a specific home range which may overlap with the home ranges of other members of the population. The size of a bull rhinoceros' home range and its location (relative to waterpoints, female home ranges and other features of importance to the species), is determined by the dominance status of the individual, the establishment of which may involve some fighting when the animals are living at medium to high densities in typical bushveld situations (du Toit, pers. comm.).

The size of their home ranges differs according to sex, age and the type of habitat, immature animals usually occupying larger areas than adults. In the Hluhluwe Game Reserve, Hitchins (1969) found that the size of the home range varied according to the nature of the habitat. Where there is a high proportion of thicket and dense stands of woody plants, a young female had a home range of some 3 000 ha in Umfolozi (Emslie & Adcock, 1990a). In Hluhluwe, Hitchins found home ranges to be smaller at 500 to 750 ha. Hitchins (1969) found that they do not occupy territories in the sense of areas exclusively held and defended against other black rhinoceros. Joubert (1969) believed that in Namibia the size of the home range varies with the density of the population as well as the availability of food and cover. Where their feeding areas are far from water, they are nomadic in habit and will share tracks, feeding and resting sites and water supplies with others. Loutit (1984) estimated the home range size as about 500 km² in Kaokoland.

Although adult bulls are inclined to be aggressive towards other bulls, they deliberately tend to avoid contact. Serious fighting, however, does take place, especially between bulls over a female in oestrus, between bulls and cows, but rarely between cows. There is a higher mortality in males (11 cases) than females (five cases) (Hitchins & Anderson, 1983). In meetings between bulls there may be some testing behaviour, which takes the form of one rushing forward with lowered head and screaming, to simply lifting the head and staring. A bull will approach a cow with a stiff-legged gait, head swinging from side to side, or may jerk the horn in the air. If the cow shows signs of aggression, the bull usually retires. In fighting, the front horn is used to buffet the other, the action taking place with tail raised, ears flattened and with much screaming and squealing.

During the heat of day they retire to the shade of thickets or woodland to sleep, either standing motionless or lying with their legs curled under them. They tend to rest on the tops of ridges but they will also lie in dusty hollows, sometimes in the full sun, or by water holes or mud wallows. Sometimes they sleep lying flat on their sides, a position never adopted by the white rhinoceros (Feely, in litt.). As they are unable to roll right over, they wallow in mud or dust on one side, then rise, and wallow on the other side. While asleep the ears move restlessly, rotating in all directions, or

flick quickly from back to front.

Black rhinoceros deposit their dung in latrines but will also defecate on paths or fortuitously anywhere in their home range. The latrines may be used by a number of individuals. Usually a small bush marks the centre of the latrine. After deposition the dung is vigorously scraped by the bulls with alternate kicks of the hind feet which leave scrape marks on the ground which, in soft ground, may reach a depth of 0,3 m (Feely, in litt.). Possibly the adherence of portions of the dung to the hind feet may mark the presence of the individual on tracks. In northern Natal, many latrines are used by both species of rhinoceros (Feely, in litt.). Smell is very important to rhinoceros and they have been observed to change direction by 90 degrees to investigate the presence of strange rhinoceros (Emslie, pers. comm.).

Urination may take place in a fine stream or the urine may be ejected by the bulls in a spray in short bursts, backwards on to a bush or other object. Cows likewise, when moving, may squirt small quantities of urine. Spraying of urine may have the effect of advertising the individual's presence in an area.

Both lions and spotted hyaenas have been reported as attacking adults, with the outcome usually in favour of the rhinoceros. Adults exhibit no fear of the larger predators and generally disregard even the near presence of other mammals. They normally give way to elephants, but aggressive encounters during drought conditions at waterholes with these and with buffaloes have been recorded. In parts of their distributional range predation on calves is a rare occurrence, but has been reported in the Hluhluwe Game Reserve in Natal (Deane, 1962), where Hitchins (1969) believed spotted hyaenas, Crocuta crocuta, take a toll of the young, and Hitchins & Anderson (1983) provided circumstantial evidence to support this. Goddard (in Moss, 1976) witnessed five incidents in which spotted hyaenas tried unsuccessfully to pull down calves.

In Hluhluwe females and males were active most of the night, but only for a third to half of the day respectively (Owen-Smith, 1988).

Black rhinoceros vocalise in a number of ways, the most commonly heard being the repeated loud snort given when the individual gets a fright or is angry. They grunt and growl when fighting and may squeal or scream loudly.

They appear heavy-footed when walking, but are extraordinarily agile when provoked. At a gallop they can cover the ground at speed and can spin around within their own length. Their sight is poor, but their senses of hearing and smell are acute.

While they have a reputation for being irascible and bad-tempered, this depends on circumstances and the individual. Normally human scent will make them move off, but their reactions depend on whether they have been hunted or

harried, or left in peace, and they do sometimes charge from 50 to 70 m away. A charging black rhinoceros may swing away from a rifle shot or, at closer quarters, to a loud shout, and they seldom return to press home an attack. They are unlikely to charge uphill and like to retreat into cover. When seriously annoyed or when wounded they may work out their anger on inanimate objects such as bushes or termite mounds, attacking them with lowered horns, and demolishing them.

#### Food

They have a simple stomach, and digestion of herbage takes place mainly in the voluminous sacculated caecum where most fermentation takes place (Clemens & Maloiy, 1982). They browse, manoeuvering food into their mouths with the aid of the prehensile upper lip, biting shoots off with the premolar teeth and grinding the food in the massive molar teeth. They will push over higher growth to obtain edible parts. Sticks and thorns are included in the diet, different parts of different plants being utilised. In some cases only the outer tips of the shoots are taken, in others the twigs as well. Small forbs which grow low on the ground are also eaten and small quantities of grass are taken at certain times of the year, usually during the wet season (Moss, 1976). They are selective feeders and generally reject dry plant material (Goddard, 1968).

In both Hluhluwe and Umfolozi Acacia spp or their close relatives comprised at least half of the 10 most preferred species, and as they grew in size they became less and less preferred (Emslie & Adcock, 1990b). The most preferred species were A. gerrardii, A. senegal and A. borleae. The more common A. karroo and Dichrostachys cinerea were less preferred, but more important in the diet, accounting for about a fifth of woody browse eaten in summer.

Despite the different species composition of the Umfolozi and Hluhluwe study areas, the striking feature of the black rhinoceros feeding was the very similar contribution to the diet by a number of important species that occurred in both areas (\*) (Table 296.1).

**Table 296.1** 

Percentage contribution of the top 10 woody species in the woody diet of black rhinoceros, *D. bicornis*, in the Hluhluwe and Umfolozi Game Reserves (Emslie & Adcock, 1990b)

	Hluhluwe	Umfoloz
*Spirostachys africana	22,5	24,1
Acalypha glabrata	13,9	
*Dichrostachys cinerea	1,0,8	10,5
*Acacia karroo	8,2	10,3
Berchemia zeyheri	6,1	
Acacia caffra	5,2	
*Acacia nilotica	3,8	4,7
*Acacia gerrardii	3.6	5,1
Hibiscus spp	3,4	
*Maytenus nemorosa	3,2	3,1
Acacia borleae	5,4	
Ehretia rigida	4,3	
Acacia tortilis	4,3	
Schotia capitata	2,9	

Through browsing, rhinoceros prune the bushes on which they feed, so that they become rounded on the sides and top. The bushes show little sign of the breaking or tearing which characterises elephant feeding.

In Kaokoland, Namibia, of the 103 plant species encountered, rhinoceros utilise 74 (Loutit, Louw & Seely, 1987). Apart from expected species such as Acacia albida, Euphorbia virosa was also fed upon and this plant and Merremia spp had the highest water content. The high tannin content and other defence mechanisms such as formidable spines on E. virosa did not deter the rhinoceros from eating them, nor did the very high crude fibre content of Commiphora virgata, Sterculia africana and Euphorbia damarana. However, in deserts, food selection may be influenced by other factors than nutritional value. For example, in parts of East Africa. Euphorbia tirucalli forms 70% of their diet during the dry season (Goddard, 1968), the rhinoceros obtaining their moisture requirements in this way. This was also the case with D. b. michaeli in the Addo National Park where they

selected succulent plants with a high moisture content in the dry season (Hall-Martin, Erasmus & Botha, 1982).

From studies undertaken in the Subregion, one can conclude that black rhinoceros feed on an unusually wide variety of species, and they are flexible, shifting their preferences according to availability of species. They can also utilise plants unavailable to other herbivores because of their formidable chemical and morphological defences.

In the Zambezi Valley, Zimbabwe in the 1982/83 and 1983/84 wet seasons, rainfall was only about half the mean over 17 years. This resulted in reduced vegetative growth and at least 38 rhinoceros died of malnutrition in the subsequent dry seasons. Most (22) of these animals were under 10 years of age, with the next biggest category (18) being those 31–40 years of age (Dunham, 1985). This indicates how important it is not to exceed carrying capacity with species such as rhinoceros which cannot be translocated rapidly from one area to another.

In the well-watered Hluhluwe Game Reserve, they drink nightly, as they do in the hot, dry months in the Etosha National Park, but in the cooler months they drink every second night (Owen-Smith, 1988).

#### Reproduction

Black rhinoceros may breed at any time of the year in the Subregion. In the Hluhluwe/Umfolozi Game Reserve there are minor peaks in births in January and again from June to August. Hitchins & Anderson (1983) found that females may produce calves when only 6,5 years of age, but this is exceptional and they usually only conceive after seven years of age.

In Natal, Anderson (1983) found that pro-oestrus lasts six to seven days and is characterised by frequent tail-erecting by the female. During this time the male was in attendance and oestrus lasted only one day. During pro-oestrus complex encounters between a bull and a cow occur, the cow squirting small amounts of urine on to the ground, the bull then sniffing this and performing "flehmen" (Moss, 1976). Initially events are largely governed by the cow. The bull approaches her circumspectly in a stiff-legged gait, his hind legs dragging on the ground, and, face to face, they spar with their front horns or nudge one another with the sides of their heads. The bull horns the cow between the hind legs and under the stomach. She may attack him from time to time,

but during courtship no serious or vicious fighting takes place (Goddard, 1966; Schenkel & Schenkel-Hullinger, 1969). The length of the oestrous cycle was 35 days (S.D. = 7,7; n=10), although captive animals cycled approximately every 25 days (n=7), based on inter-oestrous intervals and urinary hormone profiles (Hodges, pers. comm.). Observations confined to daytime showed that copulation occurred two to seven times (n=47); duration of copulation varied from 12 to 43 minutes and the number of ejaculations ranged from twice in 12 minutes to nine times in 43 minutes. Following a gestation period of 15 months, a single calf of about 40 kg is born. Calving intervals in Hluhluwe were 44 months and in Umfolozi 30 months.

Calves walk and suckle within three hours of birth. At this stage the females are extremely intolerant of disturbance. At birth calves are lighter in colour than adults and are sparsely haired. They are alert and playful and appear to have keener eyesight than their mothers. Suckling at first takes place standing up, but as they grow older, the calves have to lie down on their bellies to reach the teats, a pair being situated in the cow's inguinal region. During the early life of the calf the cow tends to keep to thick bush, the calf always in close proximity, walking at her side or behind her. At a few weeks of age the calf starts to browse, but continues to suckle for about a year. The cow calls the calf by emitting a highpitched mew, while the calf, if it has strayed, calls the cow with a bellowing squeal. The cow will defend her young vigorously. Goddard (1966) witnessed a cow killing a lion in these circumstances.

The calf is rejected by the cow at two to four years of age, either during the cow's next pregnancy or at birth of the new calf. If rejection of the calf takes place after the new calf is born, the rejection by the female may be active and vicious (Moss, 1976). The calf continues to grow until seven to eight years old. It may join another calf, a bull or another female, the females being usually more tolerant of their presence. Spermatogenesis commences in males after eight years of age, but no male was observed holding a territory or mating which was under nine years of age (Hitchins & Anderson, 1983).

In the first two years of their lives mortality is high. Goddard (1966) estimated that there was about a 16% loss, caused by predation by lions and spotted hyaenas or lowered resistance to disease caused by lack of food or water.

# XLII. Family EQUIDAE Zebra

Churcher & Richardson (1978) regarded the African fossil equids as being descendants of immigrants that crossed into northeastern Africa during the late to middle Miocene Epoch some 15 to five million years ago. The earliest known of these immigrants was a small equid, Hipparion primigenium, which is known from the late middle to early late Miocene beds of East Africa. It was a forest dwelling species that became extinct by the end of the Pleistocene Epoch, perhaps being unable to compete with the antelopes. A much larger species, Equus burchelli mauritianus, from North Africa was the ancestor of the later, modern E. burchelli subspecies. The origins of the mountain zebra, E. zebra, and the extinct quagga, E. quagga, are obscure. The latter is poorly represented in the fossil record, some of the material being of doubtful validity. Churcher (1970) described a distorted palate with seven teeth from the early Pleistocene which he ascribed to E. quagga. Churcher & Richardson (1978) thought that E. quagga might well represent the ancestral condition seen in E. b. mauritianus as represented by fossil remains from the middle Pleistocene.

Today the Family is represented by three living species of zebras: Equus grevyi Oustalet, 1882 of East Africa; E. zebra Linnaeus, 1758 of the Subregion and southwest Angola, and E. burchelli which has a wide distribution from the northeastern parts of the Subregion west to Angola and north to East Africa. Ansell (1974a) gave the chromosome numbers of the three species: E. grevyi 2n=46; E. zebra 2n=32; and E. burchelli 2n=44. The quagga, E. quagga, which occurred in the southwestern parts of the Subregion, became extinct towards the end of the 19th century.

In the equids the mid-toe on the foot is fully developed and ends in a hoof, only the vestiges of digits two and four (the splint bones) being present.

The dental formula of the zebra is similar to all extant equids; the deciduous dentition is:

 $i\frac{3}{3}c\frac{1}{1}p\frac{4}{4} = 32$ 

and the dental formula of the permanent dentition in adults is:

 $I_{\frac{3}{4}}^{3}C_{0-1}^{0-1}P_{\frac{3}{4}}^{3}M_{\frac{3}{4}}^{3}=36 \text{ or } 40$