Superorder **PARAXONIA**

Order **PERISSODACTYLA**

SUBEDITOR: *J. T. du Toit*

XXXVII. Family **RHINOCEROTIDAE** Gray, 1821

Rhinoceroses

FOUR GENERA OF fossil rhinoceros are known from the early Miocene some 23–19 Mya, namely *Brachypotherium*, *Aceratherium*, *Dicerorhinus* and *Chilotherium*. Their ancestors are unknown but must have lived during the preceding Oligocene.

There are five extant species of rhinoceros: the white (or square-lipped) rhinoceros (*Ceratotherium simum*); the black (or hook-lipped) rhinoceros (*Diceros bicornis*); the Sumatran (or Asian two-horned) rhinoceros (*Dicerorhinus sumatrensis*); the Indian (or greater one-horned) rhinoceros (*Rhinoceros unicornis*); and the Javan (or lesser one-horned) rhinoceros (*R. sondaicus*).

The two species occurring in the subregion, *C. simum* and *D. bicornis*, arose from a common ancestor, and fossil remains recorded from Plio-Pleistocene beds some four 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 7 Mya. It has four incisors, which are lacking in the extant *C. simum*.

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

With the increase in the European settlement of southern Africa from the seventeenth century, both species were gradually eliminated from parts of their range. By the end of the nineteenth century the southern white rhinoceros was reduced to only one population of about 10–20 individuals in the southern part of the area that now forms the Hluhluwe-Imfolozi Park in KwaZulu-Natal. As a result the Hluhluwe and Imfolozi game reserves were established in 1895, which along with St Lucia makes them the oldest game reserves in Africa. The black rhino did not fare much better, being reduced to only about 100–150 in the Hluhluwe and Mkhuze game reserves. The species was extinct in the former Cape Province by 1880 and the last black rhino in the former Transvaal was seen in the Kruger National Park in 1936. Fortunately, the proclamation and protection of the KwaZulu-Natal reserves, coupled with the development of rhino capture techniques and translocation programmes, led to both species being saved from extinction in South Africa.

Rhino horn is highly valued in south-east Asia for its supposed medicinal properties and for ornamentation. In Yemen rhino horn is used to manufacture the handles of daggers. Its medicinal properties have long been disparaged in the West, although there is evidence to suggest that, when taken at very high dosages, it has a possible antipyretic effect (But *et al.*, 1990). The sustained erroneous belief that rhino horn has aphrodisiac properties continues to hinder efforts to stop the illegal trade in rhino products.

Key to the genera (after Ansell, 1974a)

1. 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　　　　… *Ceratotherium*

Upper lip pointed and prehensile – a finger-like projection that 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　　　　… *Diceros*

Genus *Ceratotherium* Gray, 1868

This is a monotypic genus.

No. 273

Ceratotherium simum (Burchell, 1817)

White rhinoceros

Plate 30, Print Plate 1

Colloquial name

The name white rhinoceros has been in use for more than 200 years (Barrow, 1801, 1804; Harris, 1852; Selous, 1908). The most popular explanation for the derivation of the colloquial name is that it probably derives from the uninformed interpretation of the Cape Dutch word *weit* meaning wide, referring to the species' wide mouth (Pitman, 1931a; Owen, 1956; Maberly, 1963; Penny, 1987; Cumming *et al.*, 1990; Booth, 1992; Toon & Toon, 2002). Rookmaaker (2003), however, examined Dutch and Afrikaans spoken during the nineteenth century and indicated that this explanation is highly unlikely as there is no evidence that the words *weit* or *wyd* were ever used in combination with rhinos. Rookmaaker (2003) suggests that the more likely explanations are that the term may have originated as the opposite of black rhinoceros (*Diceros bicornis*), or that 'white' may be a translation or derivation from an indigenous African language. Owen-Smith (1973), however, suggested that the term might have originated from the paler white colour obtained by the species wallowing and rolling in calcareous soil. Unfortunately there is insufficient evidence for a definite explanation of the origin of the name 'white rhinoceros'.

Despite the names black and white rhinoceros, both *C. simum* and *D. bicornis* have grey skin. However, they are inclined to assume the colour of the soil on which they live, through mud-wallowing and dusting.

One of the most obvious characters that differentiate the two species is the square lips of *C. simum* (Fig. 273.1) and the hooked, prehensile upper lip of *D. bicornis* (Fig. 274.1), these being adaptations to their feeding habits of grazing or browsing respectively. Because of its lips, the white rhino is also referred to as the square-lipped rhino.

Taxonomic notes

Burchell (1817) originally described this species from a specimen from 'the interior of South Africa', the type locality later being established by Shortridge (1934) as near Kuruman, Northern Cape. Two subspecies are recognised: *C. s. simum* from the southern part of their distributional range and Kenya, and *C. s. cottoni* (Lydekker, 1908) from the Democratic Republic of Congo, which is somewhat longer in the legs, shorter in the body (Cave, 1962) and has a skull that is less concave.

FIG. 273.1 Anterior view of head of white rhinoceros (*Ceratotherium simum*), showing the square-shaped lips of the species and the hump on the neck that shows clearly when the head is raised

Description

With a shoulder height of up to 1.8 m for males and 1.77 m for females (Kirby, 1920), and an adult mass of 2 000−2 400 kg for males and 1 600 kg for females, the white rhino ranks as Africa's second largest land mammal. It has a barrel-shaped body and short, thickset limbs. Body length increases with age, approaching an asymptote at about 14 years, but chest girth only attains an asymptote at about 20 years (Rachlow, 1997). Characteristic features include the long head with long anterior and shorter posterior continually growing horns; pointed ears fringed with hair; wide squared-off lips; and a distinct hump on the neck (Figs 273.1 and 274.2B). The thick skin is 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 hairless, but upon close inspection is seen to have a sparse coating of bristly hairs. The skin may reach a thickness of about 20 mm on the shoulders and 50 mm behind the horns on the forehead, the thick dermis being covered with a thin layer of epidermis barely 1 mm thick. In places, such as in the neck fold and behind the ears, the skin is very thin, making the attachment of radio collars problematic because abrasive or tight collars may result in skin lesions. This, coupled with the fact that a rhinoceros's neck is bigger than its head, has led to transmitters being implanted in the anterior horn (Pienaar & Hall-Martin, 1991; Shrader & Beauchamp, 2001). Underlying the skin there is a thick layer of fat on the abdomen, which may reach a thickness of 50 mm.

The horns, which are composed of a mass of keratin filaments (Ryder, 1962), are outgrowths of the skin and are not attached to the bone of the skull. The front horn is almost invariably longer than the hind, 1 581 mm being the record length of a front horn, its accompanying rear horn 566 mm (Ward, 1998). In the white rhino (*C. s. simum*) the front horn has a straighter transverse edge in front when compared to the black rhino. Male horns have a greater anterior basal circumference than female horns (730.4±65.0 mm; $n = 65$; compared with 610.0±34.4 mm; $n = 39$). The female's horn is more slender but not necessarily longer than the male's (583.4± 141.9 mm; $n = 72$; compared with 589.4±98.0 mm; $n = 107$). There is no difference between the adult sexes in intrinsic anterior horn growth (mean rate of 50.5±3.52 mm/year; range = 25−66).

Intrinsic horn growth rate is most rapid in young animals, being about 150 mm in the first year of life. The calf is born hornless. In one animal the anterior horn pierced the skin at five weeks and grew to 39 mm at three months and 100 mm at seven months. Growth of anterior horns decreases with age from 59.8 mm/year in young adults to 36.5 mm/year for old animals. Adult males have heavier horns than females (anterior: 6.1±1.8 kg; $n = 91$; compared with 4.0±1.5 kg; $n = 33$; posterior: 2.2±1.1 kg; $n = 69$; compared with 1.2±0.7 kg; $n = 19$). The mean mass of adult horns is 5.16±2.0 kg ($n = 163$) for the anterior horn and 1.86±1.0 kg ($n = 153$) for the posterior horn (Pienaar *et al.*, 1991; Pienaar, 1993).

The lower lip has a hard ridge or callosity on the surface; the upper is fleshy and soft, which allows the individual to detect and then crop grass. 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, armed with broad, stout nails that mark clearly in the print. The front feet are slightly larger than the hind feet. However, the difference is less marked than in the black rhino. The cushioned pads on the soles of the feet have a hard surface with a mosaic of irregular cracks and, characteristically, a distinct indentation on their rear edges that marks in the print and distinguishes the prints from those of the black rhino, in which the indentation is absent (Print Plate 1).

Skull

The skull (Fig. 273.2) is more elongated in this species than in the black rhino, 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 raise 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. The posterior edges of the lower edge broaden out to give an extra wide area of attachment for 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.

FIG. 273.2 Lateral view of skull and lower jaw of white rhinoceros (*Ceratotherium simum*); total length of skull 760 mm

The deciduous dentition is:

$$i_0^0 \; c_0^0 \; p_4^4 = 16$$

In the deciduous dentition, the anterior premolar is the last to erupt and, in adolescence, is lost at 4−7 years and not replaced. Some, however, may persist into early adulthood. There is no sign of the incisors or canines in the deciduous dentition that are sometimes present in the black rhino.

The second upper premolar is the first permanent premolar to erupt at 3−4 years of age. The third and fourth upper premolars follow, and by eight years all permanent premolars are in wear. The first upper molar erupts before the first permanent premolar at the age of roughly three years, subsequently coming into wear at 3−4

years; the upper second and third molars erupt at 4−7 and 8−16 years respectively (Hillman-Smith *et al.*, 1986).

The permanent dentition, therefore, 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 cheek-teeth. All cheek-teeth are broad-faced, have convoluted enamel layers on their biting surfaces, and are adapted to grinding up food.

Distribution

From evidence of skeletal remains and their depiction in rock art, white rhinos once occurred from the coastal areas of Morocco, Algeria and Tunisia, through the Sahara and East Africa to South Africa. During the Pleistocene their distribution was continuous from Morocco through the Sahara to parts of the Western Cape.

The last record of a white rhino in Zimbabwe was of one shot at Mpanda's Kraal in the north-east of the country in 1895. Selous (1908) stated that he shot one in Botswana at Thamma Setsi (Tamuseche Pan) on the Zimbabwe border in 1874, but they persisted beyond this date in the area as he recorded their prints in 1877. In Mozambique one was shot at Marcorsa by Sir Hugh Beadle in 1935.

By the end of the nineteenth century the southern white rhinoceros had been reduced to a single relict population in what is now the Imfolozi Game Reserve in KwaZulu-Natal, South Africa. Renshaw (1904) reported that at this time there were only about 10 rhinos remaining, while in 1916 Vaughan-Kirby, the first Game Conservator in Zululand, estimated that only 20 individuals survived. The first official estimate in 1930 revealed that there were 120 in Imfolozi and 30 in adjacent areas and by 1960 an aerial count gave a total of just over 700, although this is likely to be a significant underestimate (P. M. Brooks, pers. comm.).

In 1961 the Natal Parks Board launched 'Operation Rhino', a programme that up to 1997 had seen the removal of about 4 000 surplus rhinos from reserves (initially Imfolozi) under its control, and their re-establishment in state-run reserves and on private land throughout their former range and beyond. By 1999 there were an estimated 10 377 southern white rhinoceroses in 47 key and important populations in Africa, distributed between eight countries (Emslie, 2000). The major range states are: South Africa (9 754 animals), Zimbabwe (208 animals), Kenya (164 animals) and Namibia (163 animals). Approximately 22% of the rhinos are either privately owned or in custodianship for the state on private land (Emslie, 2000), while around 80% of the rhinos in Kenya occur on private land (R. F. du Toit, pers. comm.). There were also approximately 650 southern white rhinoceroses recorded in captivity in the world in 1997 (P. M. Brooks, pers. comm.).

The northern subspecies, *C. s. cottoni*, is critically endangered, with a drastic reduction in numbers and a shrinkage in distribution. In the wild they are now only definitely found in the Garamba National Park in the northern Democratic Republic of Congo, where some 28 animals are all that are left (Emslie, 2000). However, the population is in critical danger of extinction largely as a result of recurrent civil wars and general unrest in the area. Although there are an additional nine northern white rhinoceroses in the San Diego Zoo, USA, and the Dvur Kralove Zoo, Czech Republic, none are breeding and this has become an issue of some concern and dispute regarding the way in which these captive animals are being managed (P. M. Brooks, pers. comm.). It is believed that, as is the case with southern white rhinos, the captive northern whites would be more likely to breed if they were kept in groups instead of in pairs (R. F. du Toit, pers. comm.).

Africa, north of the southern African subregion

The northern white rhinoceros (*C. s. cottoni*) now only occurs in the Democratic Republic of Congo. The southern white rhinoceros (*C. s. simum*) occurs in Kenya, and in small out-of-range populations in Ivory Coast (4) and Zambia (6), all originating from KwaZulu-Natal in South Africa.

Southern African subregion

Sizeable populations exist in South Africa, Namibia, Zimbabwe, and Swaziland (50), but Botswana (31) has lost most of the southern white rhinoceroses that had been re-established over the course of the past 30 years.

In South Africa the largest populations are in the Kruger National Park (about 3 600) and the Hluhluwe-Imfolozi Park (about 1 600). Other South African populations rated as important to the survival of the subspecies occur in Mkhuze, Ithala, Pilanesberg, Madikwe and Manyaleti and on two private properties.
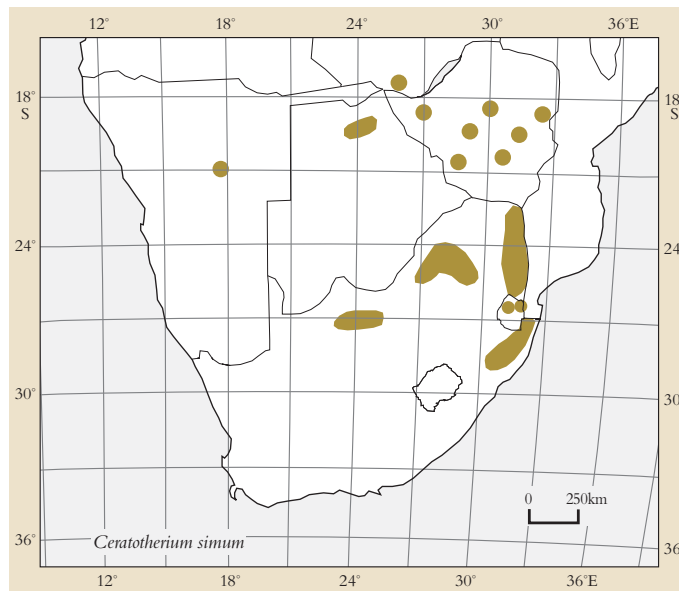

FIG. 273.3 White rhinoceros

Habitat

Player & Feely (1960) listed four basic habitat requirements: (1) areas of short grass, for which they have a marked preference, but including stands of medium-tall *Panicum maximum* found under trees (Shrader, 2003) and *Themeda triandra* (Owen-Smith, 1988); (2) the availability of water for drinking and in which to wallow; (3) adequate bush cover; and (4) relatively flat terrain. These requirements are met in the wooded grasslands that are common in many parts of the subregion where they formerly occurred. This woodland carries the palatable grasses that form their principal food. Reintroduced to areas where these conditions prevail, the species is flourishing. Steep slopes within habitats are avoided, although white rhinos will traverse them to move between feeding grounds or to water.

Owen-Smith (1988) recorded that the white rhinos in the Hluhluwe-Imfolozi Park utilise four broad grassland types throughout the year: during the summer wet season they favour short-grass grasslands; as the dry season progresses they increase their use of woodland grasslands; as the availability of green grass declined in the woodlands, they utilise accessible *Themeda* grasslands; and at the end of the dry season, when the availability of food in the accessible *Themeda* grasslands has declined, they utilise the less accessible *Themeda* grassland on hill slopes.

Habits

White rhinos are essentially solitary. However, they express an incipient sociality, manifested through associations involving subadults of both sexes and adult females without small calves. These associations can last from days to years (Shrader & Owen-Smith, 2002). Group size usually ranges between two and five individuals. However, larger groups of up to 15 have been reported (Owen-Smith, 1973; P. M. Brooks, pers. comm.). Territorial bulls occupy clearly defined territories, which they defend against other trespassing bulls from neighbouring territories. In the Imfolozi Game Reserve, KwaZulu-Natal, these territories vary in size from

0.75 km² to 2.60 km² (Owen-Smith, 1973); in the Ndumu Game Reserve, KwaZulu-Natal, from 2.5 km² to 13.9 km² ($\bar{x}$ = 7.9; n = 6) (Conway & Goodman, 1989); in the south-western Kruger National Park, Mpumalanga, from 6.2 km² to 13.8 km² ($\bar{x}$ = 9.86; n = 4) (Pienaar, 1993; Pienaar et al., 1993b); and in the Kyle National Park, Zimbabwe, from 5 km² to 11 km² (Condy, 1973). The territories of neighbouring bulls do not overlap. The boundaries of these territories often coincide with topographic features such as watercourses, crests of watershed ridges, or roads. 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.

Territorial bulls mark their territories by spray-urinating or scattering dung on middens along the boundaries. Urine-spraying is directed backwards between the hind legs. Having defecated, dung is scattered by kicking with the back feet. Sometimes the urine emerges as a stream and the dung is deposited without scattering. These actions may also take place anywhere within the territory. Defeated territorial bulls cease this practice, and when the territorial bull has to leave his territory to drink, he urinates in a stream in the manner of subordinates (Owen-Smith, 1973).

Several subordinate bulls may live in a territory of a single territorial bull. A territorial bull may tolerate subordinate bulls, providing they remain submissive. Subordinates spend much of their time within the territory, although they make occasional explorations outside it. 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 (Owen-Smith, 1973).

Where water is not available seasonally within their territories, territorial bulls will leave their territories every two to three days to drink. Territorial bulls trespassing into the territory of an adjacent bull normally take avoidance action and thus serious fights are usually averted. Encounters may take the form of short charges or, at closer quarters, horn-clashing accompanied by vocalisations. However, when a territorial bull is with an oestrous female, encounters between the bulls may become more aggressive. Wounding may be caused by the horn or by heavy shoulder battering that can lead to internal injury.

Although the population was small, Rachlow et al. (1998) found that in the Matobo National Park, Zimbabwe, territorial males tended to be older and the mean age for territorial males was 16.0 ± 4.7 years (range = 9–25; n = 3). Upon the death of the oldest male (25 years), who was killed in a fight, and the establishment of a new territorial male, this mean subsequently declined to 11.7 ± 1.5 (range = 9–13; n = 3). By comparison the mean age of non-territorial males was 8.8 ± 0.7 years (range = 6–12; n = 8). Territorial males also had significantly larger neck ($1\,796 \pm 40$ mm; n = 5) and chest ($2\,980 \pm 118$ mm; n = 5) girths than non-territorial males ($1\,593 \pm 24$ mm; n = 3, and $2\,540 \pm 36$ mm; n = 4, respectively). Testosterone levels also differed significantly between territorial and non-territorial animals but were not related to age.

Cows have home ranges that overlap with those of other cows and may overlap the territories of as many as six or seven territorial bulls (Owen-Smith, 1973; Pienaar et al., 1993b). In Imfolozi home ranges were 6.1–20.5 km² (Owen-Smith, 1973); in Ndumu 4.7–22.9 km² ($\bar{x}$ = 11.3; n = 9) (Conway & Goodman, 1989); in Kruger 7.23–45.23 km² ($\bar{x}$ = 22.83) (Pienaar, 1993; Pienaar et al., 1993b); and in Kyle 3–20 km² (Condy, 1973). Females in south-western Kruger had a larger wet-season range (21.44 ± 11.98 km²) than dry season range (11.64 ± 6.2 km²) (Pienaar, 1993; Pienaar et al., 1993b). As with territorial bulls, the individual ranges of females are much smaller in Imfolozi, which has a higher white rhino density (3.0–5.7 animals/km²) than south-western Kruger (0.5–1.4 animals/km²), Kyle (0.7 animals/km²) or Ndumu (0.6–1.8 animals/km²).

Population size is regulated through the dispersal of individuals (primarily subadults of both sexes and a few adult males) from areas of high density to areas of low density (Owen-Smith, 1988). In the Hluhluwe-Imfolozi Park, Shrader & Owen-Smith (2002) recorded that subadults made exploratory excursions into novel areas outside their established home ranges. These excursions were made with a companion (either an adult female lacking a young calf or another subadult), who guided the subadult into an area with which the companion was familiar. Shrader & Owen-Smith (2002) suggested that this 'buddy system' might be important in reducing the high costs potentially associated with dispersal.

Communication within the species depends heavily on olfactory signals (urine and dung constituents), which individual rhinos detect through their sensitive sense of smell as they cross the paths of other members of their community and encounter their dung middens. Vocalisations 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 may occasionally snort when another moves nearby. While courting a female, a territorial bull may squeal when trying to block a female in oestrus from leaving his territory. Other members of the group may snort or snarl, which is a sign for others to keep their distance; pant, when maintaining contact or as a sign to join up; shriek, as an attack-inhibiting signal; squeal to elicit protection or as a distress signal in calves; or puff when suddenly alarmed.

Displays may involve charges; pulling the ears back as a sign to others to keep off; advancing steps, often accompanied by a snarl, as a threat; and 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. Head flinging in the young is an invitation to play. Although white rhinos have preputial glands in the region of the penis or vulva, olfactory communication appears to be limited to the odours of 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 white rhinos encountered.

White rhinos 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 print. 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 rhinos pay little attention to other mammalian species, even at close range. They are, however, susceptible to attack by elephants in certain situations, and a number of white rhinos have been killed in this manner in the Pilanesberg National Park, the Kruger National Park, and the Hluhluwe-Imfolozi Park (Slotow & Van Dyk, 2001; Slotow et al., 2001). Lions (Panthera leo) and spotted hyenas (Crocuta crocuta) may occasionally kill calves.

Red-billed and yellow-billed oxpeckers (Buphagus erythrorhynchus and B. africanus) are frequently seen on white rhinos. These birds feed on ticks embedded in the soft portions of the rhinoceros's hide (i.e. in and around the nasal cavity, ears and anus). Terrapins may also remove ticks while rhinos wallow in pans. White rhinos have poor eyesight but acute senses of smell and hearing. They respond more readily to moving objects, discerned at ranges of up to 40 m, than to those at rest. They are frequently alerted to approaching danger by their accompanying oxpeckers. Owen-Smith (1973) recorded that when they are 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. White rhinos are generally temperamentally quieter and less prone to provocation than black rhinos.

During the summer months they indulge in mud-wallowing or lie in muddy pools as a means of thermoregulation, but more especially

to coat the body with a layer of mud as a means of ridding themselves of ectoparasites. Following mud-wallowing they rub themselves on the trunks of trees or boulders that eventually, through continued use as rubbing posts, become debarked and polished. Mud-wallowing is infrequent during winter (Owen-Smith, 1973).

Food

The white rhino is the world's largest purely graminivorous animal and is capable of cropping grass to within 25–60 mm of the ground (Owen-Smith, 1988). Lacking incisors, they extend the movable and extremely sensitive upper lip over a grass clump, pressing the grass against the hard lower lip and cropping it with an upward move-ment of the lips and head. When they feed, the head is held low and the wide nostrils maintain contact with the grass. An adult female's bite width is about 200 mm (Owen-Smith, 1973; Shrader, 2003). Owen-Smith estimated that about 50% of daylight hours are taken up in feeding. The feeding rate averages 58 bites per minute with a maximum rate of 83 bites per minute (Shrader, 2003). When feeding they chew the food for a moment or two but do not ruminate.

In KwaZulu-Natal Shrader (2003) found that the following seven grass species constituted 73% of the food intake: *Panicum maximum, Themeda triandra* (an important dry-season food resource), *Digitaria argyrograpta, P. coloratum, Heteropogon contortus, Enteropogon monostachyus* and *Sporobolus nitens*. About 35 other species are eaten to a lesser extent. Some species, such as the resinous turpentine grass (*Cymbopogon plurinodis*), *Bothriochloa insculpta* and *Aristida* spp., are avoided. Forbs made up only 1% of the food ingested. In a study of wet-season feeding behaviour of grazers in west Imfolozi in 1984, R. H. Emslie (pers. comm.) found that 42% of the grass biomass in white rhino feeding patches was made up of *Urochloa mosambicensis* and *Panicum maximum*. These two species contributed 51% to the diet. *Themeda triandra*, *Sporobolus smutsii* and *Panicum coloratum* contributed a further 33%. Owen-Smith (1973) recorded geophagia, especially around termitaria. In the sour, tall grassveld areas of the Kruger National Park white rhinos feed extensively on *U. mosambicensis* growing on termitaria (D. J. Pienaar, pers. comm.). They drink water regularly and are dependent on its availability. Owen-Smith (1973) found that most drinking is done between 17h00 and 21h00 and that less drinking takes place during the day. A drinking frequency of every 2–3 days was most usual during the dry season.

Reproduction

White rhinos breed at any time of the year, but in KwaZulu-Natal there are peaks of calving in March and July. Females may breed from the age of four years (Owen-Smith, 1988). Bulls appear to become sexually mature from around six years but only start holding territ-ories at 10–12 years of age (Condy, 1973; Owen-Smith, 1988). Bulls can detect when cows are in pro-oestrus for they form a close attach-ment with a cow for a considerable time before mating. During this period a bull takes active steps to prevent the cow from leaving his territory: he chases her, squeals, and sometimes horn-clashes with a cow in pro-oestrus until she remains. While in pro-oestrus she will drive him off with snarling and snorting. Interested subordinate males are actively driven off during this period by the territorial bull (Owen-Smith, 1973).

The length of the oestrous cycle of captive *C. s. cottoni* – based on faecal hormonal analysis – is approximately 35 days ($n = 10$) (Patton *et al.*, 1999), which is longer than the inter-oestrous interval of around 30 days reported for a single *C. s. simum* female in the wild (Owen-Smith, 1973). One calf is born after a gestation period of about 16 months and birth weight is about 40 kg.

The female usually moves away from other rhinos to give birth. At birth the calf's wrinkled skin is pale grey with a pink tinge. For the first three days following parturition the calf is unsteady on its feet, and thereafter it keeps close to its protective mother. Bigalke *et al.* (1950) recorded that the outer horny layer of the skin is moulted at about 1.5–4.0 months, revealing a new paler skin. A further moult takes place at about 10 months.

Females have a pair of inguinal mammae. The calf is weaned at about a year and separates from its mother at about two or three years. After separation the calf (now subadult) moves alone until it forms an association with another subadult or an adult female lacking a young calf (Owen-Smith, 1973). The mean calving interval for nine multi-parous females in the Matobo National Park, Zimbabwe, was 2.3–3.3 years (Rachlow & Berger, 1998). When the cow and calf move, the calf usually precedes its mother, whereas in the black rhino the calf usually runs behind her. Jones (1993) gives a longevity record for *C. s. simum* in captivity of 40 years, 8 months.

No. 274

Diceros bicornis (Linnaeus, 1758)

Black rhinoceros

Plate 30, Print Plate 1

Colloquial name

Also referred to as the hook-lipped rhinoceros. See the discussion of colloquial names under white rhinoceros (*Ceratotherium simum*).

Taxonomic notes

Groves (1987) described seven subspecies based largely on minor cranial and pelage differences, but Du Toit (1987) did not support this degree of taxonomic splitting and the IUCN's African Elephant and Rhino Specialist Group now recognises four conservation units on the continent (Du Toit *et al.*, 1987). These are a north-western group in Cameroon (tentatively designated as *D. b. longipes*); an eastern group in Kenya and northern Tanzania (designated as *D. b. michaeli*); a desert group in Namibia and in the Namib-Karoo biome of South Africa (*D. b. bicornis*); and a relatively large bushveld group extending from KwaZulu-Natal in South Africa through southern and Central Africa into southern Tanzania (*D. b. minor*).

Swart & Ferguson (1997) have demonstrated that a large degree of genetic variation exists in southern African black rhino populations, with no genetic bottleneck or inbreeding taking place on a general scale in recent years. Small isolated populations have experienced inbreeding, but this is not serious enough to reduce the overall genetic diversity at the species level (R. F. du Toit, pers. comm.). The population in Etosha (*D. b. bicornis*) does not differ in a discrete way (apart from larger body size) from populations of the subspecies *D. b. minor*. Swart & Ferguson (1997) found evidence for an east-west cline of genetic variation that should, ideally, be maintained by avoiding unnecessary mixing of animals from either end of the cline. An analysis of variation in mitochondrial DNA (Brown & Houlden, 2000) supported the subspecies differentiation between *D. b. minor* and *D. b. michaeli*. As with *D. b. minor* grading into the larger-bodied 'desert rhinoceros' group of *D. b. bicornis,* this varia-tion between *D. b. minor* and *D. b. michaeli* may well have been clinal, with intermediate populations along the genetic continuum now extirpated.

An out-of-range population of *D. b. michaeli* was successfully estab-lished in Addo National Park (South Africa) in the early 1960s, with animals imported from Kenya, but animals from this group have either been repatriated to East Africa or have been sold to the private sector in order to make this habitat available for *D. b. bicornis*. The latter have been reintroduced from Namibia in small numbers to reserves within their former range in the Karoo region of South Africa.

Description

Adult black rhinos stand about 1.6 m at the shoulder and have a mass of around 1 000 kg. The mean mass of live individuals from the Hluhluwe Game Reserve, KwaZulu-Natal, was: males 852 kg ($n = 8$); females 884 kg ($n = 6$) (Hitchins, 1968b). The heaviest black rhino weighed in the Kruger National Park was an adult female of 1 400 kg (D. J. Pienaar, pers. comm.).

Some characteristic features that serve to distinguish them from their near relative, the white rhino, include their prehensile upper lip (Fig. 274.1), which is used for grasping the twigs of the woody plants on which they feed, the shorter head, the longer neck, and the smaller, rounded ears. The outline of the back (Fig. 274.2A) is also different in the two species, the black rhino lacking the nuchal hump that is a well-developed and obvious feature of the white rhino.
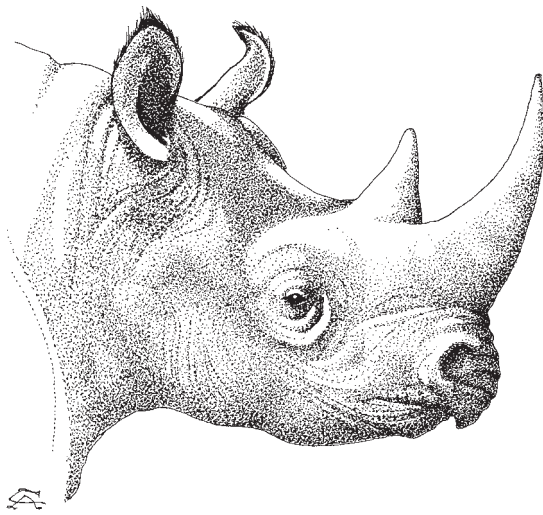

FIG. 274.1 Lateral view of head of black rhinoceros (*Diceros bicornis*), showing the hooked upper lip of the species
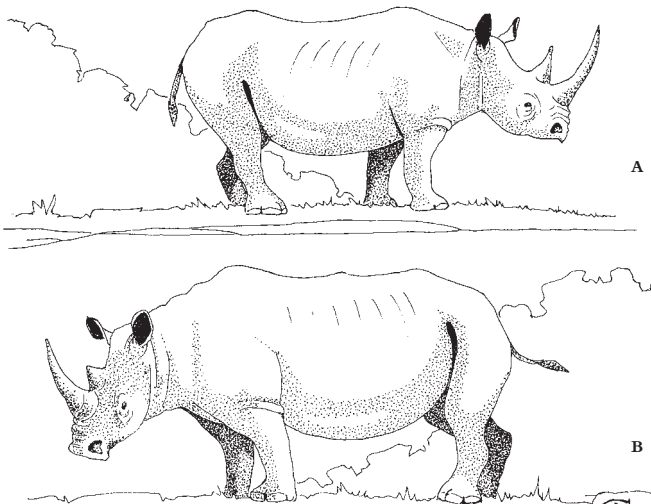

FIG. 274.2 Outline of lateral view of the body of (A) black rhinoceros (*Diceros bicornis*) and (B) white rhinoceros (*Ceratotherium simum*)

Their overall colour is dark grey. Like the African savanna elephant (*Loxodonta africana*) and the white rhino they tend to take on the colour of the soil 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, but is thinner and more delicate behind the ears and in the neck fold. They have eyelashes and hairy fringes on 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 glands that exude droplets of sweat with a red tinge 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 KwaZulu-Natal the front horn in the black rhino is invariably longer than the back. In Hluhluwe-Imfolozi in 1973 only 2.5% of males had the anterior horn of the same length as the posterior, and none shorter ($n = 120$). For females the figures

are 14.2% and 5.7% ($n = 106$). The figures in 1985 were 0% and 0% ($n = 58$) for males and 29.0% and 4.3% ($n = 69$) for females (Hitchins, 1989). The maximum front horn length recorded for a specimen from northern KwaZulu-Natal is 1.05 m, with a rear horn of 0.52 m, which is surpassed by several from East Africa, where the maximum front horn length is 1 359 mm from Kenya (Ward, 1998). Horn length and basal circumference are greater in adult males than in adult females (length: 446.1 ± 101.2 mm; $n = 63$; compared with 417.6 ± 107.9 mm; $n = 49$; and circumference: 492.7 ± 69.5 mm; $n = 58$; compared with 453.5 ± 44.2 mm; $n = 38$) (Pienaar *et al.*, 1991). Age and horn size are related, there being a stronger correlation in females than in males (Berger & Cunningham, 1995, 1998b). In a sample of anterior horns from the Kruger National Park and KwaZulu-Natal, the mean mass of anterior horns was 1.7 ± 0.7 kg (range = 0.2–3.8; $n = 75$) and for posterior horns it was 0.9 ± 0.5 kg (range = 0.02–2.4; $n = 74$), amounting to some 2.65 kg of horn per animal (Pienaar *et al.*, 1991; Pienaar, 1993). Intrinsic anterior horn growth is similar to that in the white rhino (Pienaar *et al.*, 1991; Rachlow & Berger, 1997) and Berger *et al.* (1993) have determined regrowth rates for dehorned black rhinos at 60 mm and 27 mm per year for anterior and posterior horns respectively. Regrowth was more rapid in juveniles, at 89 mm and 44 mm per year respectively.

The limbs have three digits each, with broad, stout nails that mark clearly in the print (Print Plate 1). 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. Individuals may be identified by the wrinkle patterns left behind in the print (R. A. Brett, pers. comm.). The pads are rounded at the back and lack the indentation characteristic of the white rhino. This aids in distinguishing the prints of the two species, as does the size of the nails, which are larger in the white rhino.

Black rhinos suffer from skin lesions caused by a filaria parasite. At their fullest development these lesions take the form of black, blood-encrusted areas that ulcerate and haemorrhage. Usually these are situated on the skin behind the shoulders, but also occur on the chest, neck and forelegs. All adult KwaZulu-Natal black rhinos have these lesions, but they are absent in rhinos from Central Africa (N. Leader-Williams, pers. comm.) and are not found on desert rhinos in Namibia, no doubt owing to the absence of flies that serve as specific vectors for the parasite (R. F. 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 4.5–5.0 years. These lesions are not related to their state of health and appear on perfectly healthy individuals (J. M. Feely, pers. comm.). Oxpeckers (*Buphagus* spp.), which frequent the backs of rhinos 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 rhinos with these birds has mutual benefits, for by their loud chattering and calling they alert the rhinos to danger, even when the animal is resting or sleeping.

Skull

The skull of this species is less elongated, the supra-occipital crest not extending upward and backward to the extent seen in the white rhino (Fig. 274.3). The occipital crest lacks the broad rugose area on top seen in the white rhino 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 rhinoceros forms possessed cutting incisors and, in some, canines, these are absent in the black rhino.

The deciduous dental formula is:

$$\text{i}\frac{0}{1-2} \ \text{c}\frac{0}{0} \ \text{p}\frac{4}{4} = 18-20$$

The permanent dentition is:

$$\text{I}\frac{0}{0} \ \text{C}\frac{0}{0} \ \text{P}\frac{4}{3-4} \ \text{M}\frac{3}{3} = 26-28$$

Rarely, there may be only three premolars in the upper jaw and three in the lower jaw. The persistent anterior premolar is lost at around 12–14 years of age in the maxilla (Hitchins, 1978). The premolars are molariform, all the cheek-teeth being broad-faced and adapted to grinding up the food. Goddard (1970a) describes tooth eruption and tooth-wear patterns, and age estimation is discussed by Hitchins (1978).
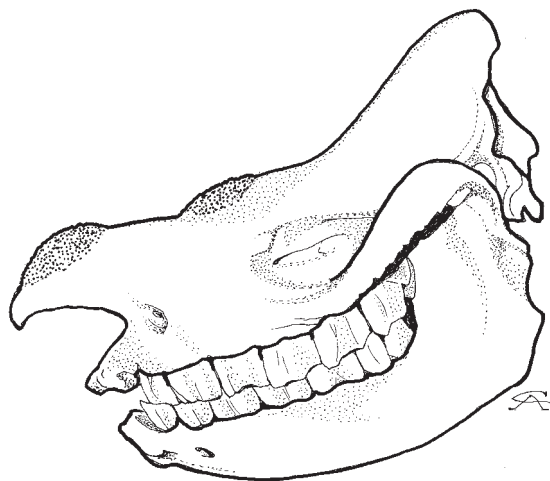

FIG. 274.3 Lateral view of skull and lower jaw of black rhinoceros (*Diceros bicornis*); total length of skull 550 mm

Distribution

It is a sad reflection that a species that formerly had such a wide distribution in the subregion should have suffered such a drastic reduction in historical times. World population estimates clearly indicate this decline: 1960 – 100 000; 1970 – 65 000; 1980 – 14 800; 1987 – 3 780; 1992 – 2 475; 1997 – 2 600 (Brooks, IUCN AfRSG records).

Jan van Riebeeck's journal of 1652 recorded rhinoceroses occurring on the slopes of Table Mountain and being common on the Cape Flats. At that time no European was aware that two species occurred in Africa, and names differentiating the two species (discussed by Rookmaker, 2003) must have come into use only towards the end of the eighteenth century, when hunters and pioneers entered the area north of the Orange River and first saw white rhinos. From this date onwards the distribution of both species declined as a result of human pressure. The last record of a black rhino being shot in the Eastern Cape was 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 Free State is dated 1842. In the former Transvaal the last record of a naturally occurring black rhino was of a solitary female seen in the Kruger National Park in 1936 (Penzhorn, 1971). In KwaZulu-Natal the establishment of the Hluhluwe and Imfolozi game reserves in 1895 and the Mkhuze Game Reserve in 1912 came just in time to save the black rhino from extinction in South Africa. In Zimbabwe populations survived mainly in semi-arid areas (especially the Zambezi Valley), where low rainfall and trypanosomiasis constrained farming activities (R. F. du Toit, pers. comm.). Throughout much of the twentieth century other populations persisted in Mozambique, Botswana, Namibia and Angola, as well as in many countries in Central and East Africa. However, widespread poaching in the 1970s, 1980s and early 1990s – made possible through political instability, the ready availability of firearms, and faltering post-colonial economies – led to the decimation or extinction of many of these populations.

Translocation operations have been crucial in redistributing the increasingly threatened species within its former range. In South Africa alone a total of 263 *D. b. minor* were translocated between 1962 and 1995, mainly from the founder populations of Hluhluwe-

Imfolozi Park and Mkhuze, to form new populations elsewhere in the country on state and private land. By 1997 the number of *D. b. minor* populations had risen to 19 (six of which were privately owned). In 1998, 28 black rhinos were relocated to Malilangwe, a private property in the Zimbabwe lowveld, representing the second black rhino group from South Africa to be re-established in another African country, after Swaziland. Similarly, the translocation of 16 *D. b. bicornis* between 1985 and 1990, originally from donor populations in Namibia, resulted in the creation of four new populations in South Africa (P. M. Brooks, pers. comm.). Namibia began establishing new black rhino populations in the country in 1989 (K. P. Erb, pers. comm.).

An interesting translocation was that of seven *D. b. michaeli* in 1961/1962 from the Kenya Game Department to the Addo Elephant National Park (Penzhorn, 1971; Hall-Martin & Penzhorn, 1977), four of which survived. This out-of-range population expanded to over 30 before being deliberately removed, through repatriations to Tanzania and sales to private owners, in order to make space for the indigenous subspecies.

According to the last IUCN continental survey, which took place in 2001, the southern African countries of South Africa (1 179), Namibia (893) and Zimbabwe (524) conserve 84% of Africa's black rhinos. Of the remaining six range states, only Kenya (430 *D. b. michaeli*), where the population has stabilised over the past 10 years or so, and Tanzania (60 *D. b. michaeli*; 16 *D. b. minor*), where rhino conservation is now receiving greater attention, have sizeable populations (P. M. Brooks, pers. comm.). *Diceros b. longipes* is confirmed surviving in northern Cameroon, with fewer than 10 animals scattered over an area of some 30 000 km². However, prospects for survival are poor unless drastic conservation measures are taken. A single survivor of *D. b. michaeli* was recently confirmed in the Akagera National Park, Rwanda. A small population (fewer than 10) of *D. b. minor* has been re-established in Malawi, through translocations from South Africa. Other recent reintroductions from South Africa to former range states are to the North Luangwa National Park in Zambia, and to the Moremi Game Reserve in Botswana. These have involved fewer than 20 animals so far but there are plans to supplement the new populations, possibly from Zimbabwe as well as South Africa.

It is very unlikely that there are any survivors in the Central African Republic, Chad, Sudan, Somalia, Uganda, or Angola, largely as a result of continued poaching fuelled by the high demand for rhino horn as a component of traditional medicines in south-east Asia and, to a lesser extent, as a raw material in the manufacture of Yemeni dagger handles. There may still be a very small number of survivors in Mozambique and Ethiopia. Rhino poaching for horn continues despite major efforts by international conservation agencies to eradicate the illegal trade, although the rate of loss is now considerably less than in the 1980s and early 1990s. This can be attributed more to the fact that most of the remaining populations are well managed and protected than to the influence of trade bans (P. M. Brooks, pers. comm.).

Africa, north of the southern African subregion
They occur in Cameroon (*D. b. longipes*), Kenya (*D. b. michaeli*), Tanzania (*D. b. michaeli* and *D. b. minor*), Rwanda (*D. b. michaeli*), Malawi (*D. b. minor*), and Mozambique north of the Zambezi River (*D. b. minor* – see below).

Southern African subregion
Between 1970 and 1972 in northern Namibia, 43 black rhinos were removed from Kaokoland and Damaraland to the Etosha National Park as a conservation measure (Hofmeyr *et al.*, 1975). The remaining rhino population outside the park was reduced by poachers to some 60 animals in the early 1980s, but has since 1982 increased to some 120 animals living in a very arid environment. Etosha National Park is home to the largest black rhino population in Africa, with 650–800 animals distributed fairly evenly over the park, excluding the saline pans and some areas without permanent

water. A number of smaller populations have been established since 1989 in conservation areas and on commercial farmland under the custodianship programme. A small number was reintroduced from Namibia into the Augrabies Falls National Park and the Vaalbos National Park in the Northern Cape (Raath & Hall-Martin, 1989), from where they are being used to restock other semi-arid reserves. One small population was also established on a private property in South Africa.

In Zimbabwe they were previously confined (after the colonial hunting era) to the Zambezi valley and adjacent parts of the escarpment from the western end of Lake Kariba to the Mozambique border, but have now been translocated to the Hwange National Park, the Matobo National Park and the Chipinge Safari Area. In addition, between 1986 and 1992 over 160 were established on private ranches as part of a programme to establish at least four major breeding groups under free-range conditions (R. F. du Toit, pers. comm.). This was most successfully achieved in conservancies in the south-eastern lowveld of Zimbabwe, where the number of introduced black rhinos has more than doubled to a present total of about 250 (including a new breeding group that was established in this region through translocations from KwaZulu-Natal in mid-1998) (R. F. du Toit, pers. comm.). However, populations on private land are now under threat owing to invasions by subsistence farmers and 'bushmeat' poachers, while commercial rhino poaching flared up again during 2003 in the Hwange National Park. In Mozambique south of the Zambezi River they no longer occur in the Gorongosa National Park and the only recent reliable reports from the country are from Niassa province north of the Zambezi River. (R. F. du Toit, pers. comm.).
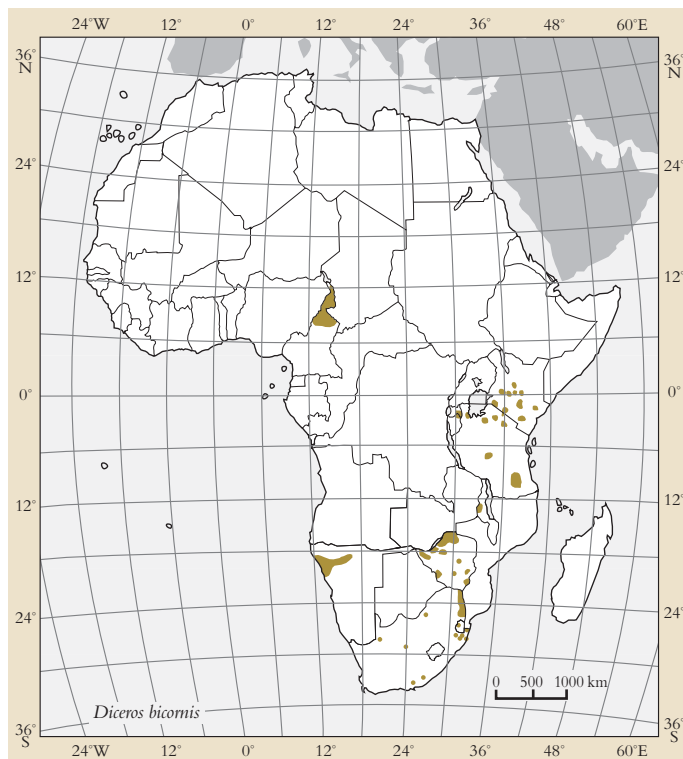

FIG. 274.4 Black rhinoceros

South African populations considered critically important for taxon survival are those in the Hluhluwe-Imfolozi Park (320), the Mkhuze Game Reserve (90) and the Ithala Game Reserve (43) in KwaZulu-Natal, and the Kruger National Park (about 300), while a number of other protected areas such as the Addo Elephant National Park, the Ndumu Game Reserve, the Pilanesberg National Park, the Tembe Elephant Park and the Great Fish River Reserve are also very important (P. M. Brooks, pers. comm.). Black rhino conservation activities in South Africa are run according to the guidelines set out by Brooks & Adcock (1997), which espouse the management of populations

below ecological carrying capacity so as to maximise population growth rates. The Hluhluwe-Imfolozi Park remains the most important donor population, having provided surplus rhinos for the creation of at least 15 new populations to date (P. M. Brooks, pers. comm.). In addition, about 31 *D. b. minor* have been sent to the USA as part of a captive breeding programme (Emslie & Adcock, 1990a).

Diceros b. minor have been reintroduced in small numbers to Swaziland, Zambia, Botswana and Malawi.

Habitat

Black rhinos require a habitat that provides adequate shrubs and young trees up to a height of about 4 m, 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 in which to bathe and mud-wallow, is also important.

While not usually associated with open plains country, the black rhino occurs in a wide variety of habitats ranging from forest to savanna woodland and scrub, from sea level to an altitude of at least 1 500 m in the subregion and up to 2 700 m in East Africa (Kingdon, 1979). In the subregion they live at higher densities in semi-arid eutrophic bushveld habitats (lowveld areas) than in higher-rainfall dystrophic habitats (sourveld), which are often dominated by 'miombo' plant communities.

They are dependent on water and, in the subregion, are seldom found more than 10−15 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 of river beds, excavating with their forelegs.

The early stages of bush encroachment favour this species, especially if this is coupled with heavy grazing (R. H. Emslie, pers. comm.). However, later successional trends − from closed *Acacia nilotica* woodland to lowland forest dominated by *Euclea schimperi*, *Berchemia zeyheri* and *Rhus pentheri* − have reduced habitat quality in the Hluhluwe Game Reserve and are likely to have contributed to the decline in the Hluhluwe population over the last 25 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 areas. In contrast, favourable food plants have grown up in cleared sites in drier areas of the complex. In addition, R. H. Emslie (pers. comm.) has found grass interference to be very important. Black rhinos 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 the Hluhluwe-Imfolozi Park young tamboti (*Spirostachys africana*) thickets are key habitats, with *S. africana* being the dominant item in the black rhino summer diet, accounting for 20−25% of woody browse eaten. Emslie & Adcock (1990b) also found that size structure changes in the vegetation were important to the rhino even if the species composition remained very similar (e.g. mature *S. africana* and *Acacia grandicornuta* woodland was rejected). Riverine bush, tamboti thickets and lowland forest margin vegetation were among the most preferred habitats in Hluhluwe. In Imfolozi one of the most preferred habitats was heavily grazed short-grass country with a few small acacias.

Habits

Black rhinos tend to be solitary, the only stable bond being between the female and her calf, but even this is of a temporary nature, persisting into the female's next pregnancy and generally ceasing with the birth of her next calf. Sometimes, after a cow has chased off a subadult to give birth to a new calf, she allows the subadult to rejoin her once she has become relaxed with her new calf (R. F. du Toit, pers. comm.). Other associations, such as that of an adult male with a female, or with a number of individuals of all age classes, are transitory. Subadults sometimes associate together in pairs for months or even years after being separated from their mothers (R. F. du Toit, pers. comm.). Aggregations of up to 16 individuals have been observed concentrating at and around waterholes (Cunningham & Berger, 1997).

Black rhinos 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 that may overlap with the home ranges of other members of the population. The size of the home range 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 km² in Imfolozi (Emslie & Adcock, 1990a). In Hluhluwe Hitchins (1969) found home ranges to be smaller at 0.5−0.75 km², while in the Ndumu Game Reserve home ranges varied from 4.3 km² for a mixed group of animals to 13.8 km² for an adult female and calf to 14.3 km² for an adult male (Conway & Goodman, 1989). Rowe-Rowe (1994) mentions that home ranges in KwaZulu-Natal's protected areas generally range from 0.2 km² in dense thickets to 0.5 km² in open areas. 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 Damaraland. In East Africa, on the Serengeti Plains, home ranges were 43−133 km² (Frame, 1980).

The size of a bull rhinoceros's home range and its location (relative to water points, female home ranges and other features of importance to the species) are 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 (R. F. du Toit, pers. comm.). Young bulls especially may be killed during these fights to establish dominance (K. P. Erb, pers. comm.). Although adult bulls are inclined to be aggressive towards other bulls when they meet, 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. In meetings between bulls there may be some testing behaviour, which sometimes involves one individual rushing forward with lowered head and screaming, and at other times he may simply lift his head and stare. A bull will approach a cow with a stiff-legged gait, head swinging from side to side, or may jerk his horns in the air. If the cow shows signs of aggression the bull usually retires. When individuals fight, the front horn is used to buffet each other, the action taking place with tail raised, ears flattened and much screaming and squealing.

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). 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 will also lie in dusty hollows, sometimes in the full sun, or at waterholes or mud wallows. Sometimes they sleep lying on their sides, a position not as often adopted by the white rhino (J. M. 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 apparently asleep their ears move restlessly, rotating in all directions or flicking quickly from back to front.

Black rhinos deposit their dung in latrines (middens) but will also defecate on paths or 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 that leave scrape marks on the ground that may reach a depth of 0.3 m in soft ground (J. M. Feely, *in litt.*). The adherence of portions of the dung to the hind feet may mark the presence of the individual in its prints. In northern KwaZulu-Natal many latrines are used by both species of rhino (J. M. Feely, *in litt.*). Smell is very important to rhinos and they have been observed changing direction by 90° to investigate the presence of strange rhinos (R. H. Emslie, pers. comm.).

Urination may produce a fine stream or the urine may be ejected backward by the bulls in a spray, in short bursts, onto a bush or other object. Cows, likewise, may squirt small quantities of urine when moving. The spraying of urine may have the effect of advertising the individual's presence in an area.

Lions (*Panthera leo*) and spotted hyaenas (*Crocuta crocuta*) have been reported attacking adults, with the outcome usually in favour of the rhino. Berger & Cunningham (1995) reported on 193 encounters between rhinos and hyaenas and lions and demonstrated that rhinos are rather aggressive, females more so than males. In most areas predation on calves is a rare occurrence as cows will vigorously defend their young. Predation on calves by lions has occasionally been reported (Joubert & Eloff, 1970; Elliot, 1987), while in the Hluhluwe-Imfolozi Park spotted hyaenas are believed to take a toll on young (Deane, 1962b; Hitchins, 1969; Hitchins & Anderson, 1983), but this is not a significant factor affecting population growth rate (P. M. Brooks, pers. comm.). Goddard (1966) estimated that there was a 16% loss of calves less than two years old to predation by lions and hyaenas. Brain *et al*. (1999) have reported on the killing of three subadult black rhinos by a coalition of three male lions in the Etosha National Park within the space of a few months. The three rhinos killed were of very similar size (1.27−1.31 m at the shoulder) and age (3−4 years) and Brain *et al*. (1999) suggested that subadult rhinos that have just left their mothers and are still relatively small may be particularly susceptible to lion predation. In the Kruger National Park more black rhinos have ears or pieces of tail missing than do white rhinos. This may indicate that they are attacked more often by predators, perhaps as a result of the calf running alongside or behind the mother (D. J. Pienaar, pers. comm.).

Black rhinos normally give way to African elephants, but aggressive encounters during drought conditions at waterholes with these and with African buffalo (*Syncerus caffer*) have been recorded. In 159 encounters between African elephants and black rhinos observed by Berger & Cunningham (1998a) in Etosha, female African elephants dominated both sexes of black rhino while male black rhinos, but not females, were capable of displacing African elephant bulls.

Black rhinos vocalise in a number of ways, the most commonly heard being a 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 50−70 m away. A charging black rhino may swing away from a rifle shot or, at closer quarters, 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 take 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 occurs (Clemens & Maloiy, 1982). They browse, manoeuvring food into their mouths with the aid of the prehensile upper lip, biting off shoots with the premolars and grinding the food with the massive molars. 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 that 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 Imfolozi *Acacia* spp. or their close relatives comprised at least half of the 10 most preferred species, and as the plants 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. In Ithala Nature Reserve *A. nilotica*, *A. karroo* and *D. cinerea* contributed most to the diet (Table 274.1), although *Cassine transvaalensis*, *Rhus guenzii* and *A. gerrardii* were most preferred. Some 86% of browse was taken from plants less than 2.5 m in height (Kotze & Zacharias, 1993).

Table 274.1

Percentage contribution of the preferred woody species in the diet of the black rhinoceros (*Diceros bicornis*) in the Hluhluwe and Imfolozi reserves (Emslie & Adcock, 1990b) and in Ithala Nature Reserve (Kotze & Zacharias, 1993)

Food items	% occurrence by location		
	Hluhluwe	**Imfolozi**	**Ithala**
Spirostachys africana	22.5	24.1	–
Acalypha glabrata	13.9	–	–
Dichrostachys cinerea	10.8	10.5	11.2
Acacia karroo	8.2	10.3	10.5
Berchemia zeyheri	6.1	–	4.6
Acacia borleae	5.4	–	–
Acacia caffra	5.2	–	2.7
Ehretia rigida	4.3	–	7.6
Acacia tortilis	4.3	–	–
Acacia nilotica	3.8	4.7	18.4
Acacia gerrardii	3.6	5.1	5.9
Hibiscus spp.	3.4	–	–
Maytenus nemorosa	3.2	3.1	7.0
Schotia capitata	2.9	–	–
Coddia rudis	–	–	7.3
Scolopia zeyheri	–	–	4.9
Rhus guenzii	–	–	2.5
Cassine transvaalensis	–	1.5	–
Dalbergia armata	–	–	1.1

Through browsing, black rhinos 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 that characterises elephant feeding. However, black rhinos may cause significant breakage of bushes and trees by pushing them over or sweeping their horns through the foliage in order to make the browse more accessible (R. F. du Toit, pers. comm.).

In Damaraland, Namibia, of the 103 plant species encountered, rhinos utilise 74 (Loutit *et al.*, 1987). Apart from expected species, such as *Acacia albida*, *Euphorbia virosa* was also eaten and this plant and *Merremia* spp. had the highest water content. The high tannin content and other defence mechanisms such as the formidable spines on *E. virosa* did not deter black rhinos from eating them, nor did the very high crude fibre content of *Commiphora virgata*, *Sterculia africana* and *Euphorbia damarana*. However, in deserts the selection of food may be influenced by factors other than nutritional value. For example, in parts of East Africa *Euphorbia tirucalli* forms 70% of their diet during the dry season (Goddard, 1968), the rhinos obtaining their moisture requirements in this way. This was also the case with *D. b. michaeli* in the Addo Elephant National Park, where they selected succulent plants such as *Portulacaria afra* with a high moisture content in the dry season (Hall-Martin *et al.*, 1982). Maddock *et al.* (1995) found that captive black rhinos ate an average of 37.8 ± 9.0 kg (wet mass) of thorny, woody plants per day.

From studies in the subregion, one can conclude that black rhinos feed on an unusually wide variety of plant species, and that they are flexible, shifting their preferences according to availability of species and also utilising plants with formidable chemical and morphological defences that make them unavailable to many other browsers.

In the Zambezi River valley in Zimbabwe in the 1982/1983 and 1983/1984 wet seasons, rainfall was only about half the mean over 17 years. This resulted in reduced vegetation growth and at least 38 rhinos 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 which were 31−40 years old (Dunham, 1985). This indicates the importance of not exceeding carrying capacity with species such as rhinos that cannot be translocated rapidly from one area to another.

They drink nightly in the well-watered Hluhluwe Game Reserve, but in the cooler months they drink every second night (Owen-Smith, 1988). Waterhole counts in Etosha have revealed that they drink at least every second or third night (K. P. Erb, pers. comm.).

Reproduction

Black rhinos may breed at any time of the year in the subregion. In the Hluhluwe-Imfolozi Park 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 old. There is a confirmed case of a rhino giving birth at six years of age in Zimbabwe (R. F. du Toit, pers. comm.), while cows in Etosha have been recorded giving birth at 6−7 years (K. P. Erb, pers. comm.). The youngest age of first calving – four years and nine months – was recorded in the Great Fish River Reserve in the Eastern Cape.

In KwaZulu-Natal Hitchins & Anderson (1983) found that pro-oestrus lasts 6−7 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. Complex encounters between a bull and a cow occur during pro-oestrus, the cow squirting small amounts of urine onto 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 (SD = 7.7; n = 10), although captive animals cycled approximately every 25 days (n = 7), based on inter-oestrous intervals and urinary hormone profiles (Hindle *et al.*, 1992). Observations confined to daytime showed that copulation occurred two to seven times (n = 47), the duration of each copulation being 12−43 minutes and the number of ejaculations ranging from twice in 12 minutes to 9 in 43 minutes.

Following a gestation period of 15 months a single calf of about 40 kg is born. Between 1986 and 1989 the average inter-calving intervals in South Africa varied from 2.1 years (Augrabies Falls National Park) to 3.4 years (Imfolozi). In Zimbabwe the intervals are generally under 30 months (they have been as low as 23 months) (R. F. du Toit, pers. comm.).

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. Cows may hide their calves in thickets when they have to move some distance to find water (Joubert & Eloff, 1971).

At a few weeks of age the calf starts to browse, but continues to suckle for over a year. The cow calls the calf by emitting a high-pitched mew, while the calf, if it has strayed, calls the cow with a bellowing squeal or a series of soft squeaks. 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 2−4 years of age, either during the cow's next pregnancy or at the 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 subadult continues to grow until 7−8 years old. It may join another calf, a bull or another female, the females being usually more tolerant of their presence. Hitchins & Anderson (1983) report that spermatogenesis commences in males after eight years of age and they did not observe any males under the age of nine holding a territory or mating, although R. F. du Toit (pers. comm.) has records of several bulls in Zimbabwe mating successfully with cows when only 6.5−7 years old (although this was in the absence of older bulls, which would have monopolised mating).

In the first two years of their lives mortality is high. Goddard (1966) estimated that there was about a 16% loss, resulting from predation by lions and spotted hyaenas or lowered resistance to disease caused by lack of food or water (see also **Habits**). Jones (1993) gives longevity for *D. b. michaeli* in captivity as 45 years, 10 months.

XXXVIII. Family **EQUIDAE** Gray, 1821
Zebras

Churcher & Richardson (1978) regarded the African fossil equids as descendants of immigrants that crossed into north-eastern Africa during the Late to Middle Miocene some 15−5 Mya. The earliest known of these immigrants was the small equid *Hipparion primigenium*, 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, perhaps being unable to compete with antelopes. A much larger species, *Equus mauritanicus*, from North Africa was the ancestor of the modern Burchell's zebra (*E. burchellii*). The most common zebra in the African Pleistocene was *E. capensis*, arguably nothing more than a large version of Grevy's zebra (*E. grevyi*) (Churcher & Richardson, 1978), which would then have extended to the south-western tip of Africa.

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 and some of the material is of doubtful validity because it was collected at a time when there was no clear distinction between species and the name quagga applied to all zebras. Based on the variability of the striping on the body, Rau (1974, 1978, 1983, 1986) suggested that the southern plains zebra (*E. burchellii*) (*sensu stricto*) is only subspecifically distinct from *E. quagga*. His conclusions are supported by evidence based on mitochondrial DNA (Higuchi *et al.*, 1984; George & Ryder, 1986; Harley, 1988) and protein analysis (Lowenstein & Ryder, 1985), but too few authenticated skins were used in these studies. Furthermore, Eisenmann (1980), using a morphometric analysis of 13 adult quagga skulls, concluded that the quagga was similar to the plains zebra, although Thackeray (1988) indicated that Eisenmann's (1980) sample may well have come from the plains zebra. Based on multivariate analysis of skeletal features, Bennett (1980) concluded that each is worthy of specific rank.

Azzaroli & Stanyon (1991) drew attention to the similarity between the hooves of the quagga and those of the mountain zebra. In addition, Klein & Cruz-Uribe (1996b) found evidence to support a relationship between the quagga and the mountain zebra based largely on craniometric evidence (see also Skinner, 1996a). The fact that both species had habitats in the arid zone lends support to this theory. Thackeray (1997) conducted a multivariate analysis of 48 measurements from mandibular dentition and concluded that *E. zebra* and the plains zebra are more closely related to each other than either is to the quagga. More recently, Klein & Cruz-Uribe (1999), using multivariate analysis of cranial measurements of four authentic quagga skulls, re-affirmed that the quagga differed from the plains zebra in as much as the plains zebra differs from the mountain zebra, and they concluded that the quagga may also have been specifically distinct. For further details on quaggas see Skinner & Smithers (1990).

It is clear then that the validity, taxonomy and phylogeny of the quagga are in dispute and still much debated. Grubb (1993d) retained *E. zebra*, *E. burchellii* and *E. quagga* as separate species, *E. quagga* (which occurred in the south-western parts of the subregion) having become extinct towards the end of the nineteenth century (*c.*1883). The treatment here follows that of Bronner *et al.* 2003, in which the family is represented by four extant species of zebra: *E. grevyi* Oustalet, 1882 from East Africa; *E. zebra* (Linnaeus, 1758) from the subregion and south-west Angola; *E. burchellii* from Central and north-east Africa, and *E. quagga* Boddaert, 1785 (including the extinct quagga) from the north-eastern parts of the subregion west to Angola. Ansell (1974a) gave the chromosome numbers of three of the species as: *E. grevyi* $2n = 46$; *E. zebra* $2n = 32$; and *E. burchellii* $2n = 44$.

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 that of all extant equids. The deciduous dentition is:

$$i_3^3 \, c_1^1 \, p_4^4 = 32$$

The dental formula of the permanent dentition in adults is:

$$I_3^3 \, C_{0-1}^{0-1} \, P_3^3 \, M_3^3 = \tfrac{36}{40}$$

In females the canines are rudimentary or absent, but they are present in the males. In juveniles, the deciduous canines are present but never pierce the gums.

The deciduous first premolars are rudimentary and are soon shed, not to be replaced. The deciduous incisors have narrow necks and the permanent incisors are columnar with broad cutting faces. The incisors have an enamel-lined hollow or depression (the infundibulum) running down the centre for a variable distance. As the incisors wear down to flat surfaces the shape of the infundibulum can be used as a criterion for age class determination. This has been discussed for the Cape mountain zebra (*E. z. zebra*) (Penzhorn, 1982b, 1987; Penzhorn & Grimbeek, 1987), Hartmann's mountain zebra (*E. z. hartmannae*) (Joubert, 1971b, 1972b) and Burchell's zebra (*E. burchellii*) (Klingel & Klingel, 1966a; Smuts, 1972, 1974c). The cheek-teeth have high crowns, with folds of enamel on their occlusal surfaces.

Key to the species (after Meester *et al.*, 1964)

1. The dark stripe running down the middle of the upper parts of the body forms a distinct 'gridiron' pattern on the croup; a dewlap present; ears large, their mean length over 200 mm ... *Equus zebra*

    The dark stripe does not form a 'gridiron' pattern on the croup; no dewlap; ears smaller, their mean length under 200 mm ... *E. quagga*

Genus *Equus* Linnaeus, 1758

Over the last 20 years there has been considerable debate over the status of the extant plains zebra (*Equus burchellii*) and of the extinct quagga (*E. quagga*) (Bronner *et al.*, 2003). While some workers, largely on morphometric grounds, maintain that the two are distinct (e.g. Bennett, 1980; Thackeray, 1988, 1997; Klein & Cruz-Uribe, 1996b, 1999), others − using cranial morphology, body stripes and molecular data − consider the quagga as a subspecies of the highly variable plains zebra.

Nevertheless, most authors have retained *E. burchellii* and *E. quagga* as separate species despite increasing morphological and molecular evidence considering both taxa as conspecific (see Bronner *et al.*,

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The Mammals of the Southern African Subregion

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FRONTISPIECE: *Loxodonta africana* African savanna elephant