

---

Walker's

# Mammals of the World

Sixth Edition

6601

Volume II

Ronald M. Nowak



The Johns Hopkins University Press  
Baltimore and London 1999

rainy season and give birth early in the rainy season of the following year. The gestation period in *T. terrestris* is usually 385–412 days (and probably is about the same in the other two South American species), the number of offspring is one or rarely two, and weight at birth is about 4–7 kg. The young initially remains in a sheltered spot, begins to follow its mother after a week, and remains with her for 10–11 months (Eisenberg, Groves, and MacKinnon in Grzimek 1990). Young tapirs of all species are dark reddish brown with yellow and white stripes and spots. They usually lose this juvenile pattern at 5–8 months. They probably require 3–4 years to attain sexual maturity and full growth (Carter 1984). Female *T. terrestris* have conceived at as early as 23 months and have given birth when as old as 28 years (Padilla and Dowler 1994). A captive *T. terrestris* lived 35 years (Jones 1982).

In some areas tapirs are hunted extensively for food and sport (for religious reasons, however, certain Indian tribes do not kill tapirs). In addition, all species have declined in recent years mainly because of the clearing of forests by humans for agricultural purposes and cattle grazing. Populations have almost or completely disappeared in several countries of Central and South America (Thornback and Jenkins 1982). *T. pinchaque* has been eliminated from western Venezuela and northern Colombia. Its main stronghold is in Ecuador and southern Colombia, but more than half of the forests in that region were destroyed between 1980 and 1989, and the process is continuing, even in national parks. *T. pinchaque* now is estimated to number only 1,000–2,500 individuals and could be extinct by the year 2000; this would not only be a wildlife tragedy but could be disastrous to the entire environment, as this tapir is a key disperser of plant seeds (Downer 1995, 1996). The IUCN classifies *T. pinchaque* as endangered, *T. bairdii* and *T. indicus* as vulnerable, and *T. terrestris* as near threatened. *T. pinchaque*, *T. bairdii*, and *T. indicus* are on appendix 1 of the CITES, and *T. terrestris* is on appendix 2. The USDI lists all four species as endangered.

The discontinuous distribution of modern tapirs suggests that they represent the remnants of a once widespread family. The fossil record shows that tapirs originated in the Northern Hemisphere and at various times occupied the land masses between where the present-day Asiatic and South American forms exist. The fact that tapirs are now living in both the American and Asiatic tropics supports the many pieces of evidence that the two continents were connected rather recently as measured by geological time and that during the period when the two were joined the climate was mild to warm in the northern portion of these continents, making conditions favorable for animals to move from one continent to the other. Subsequently the continents were separated at the Bering Strait or any other land bridge that may have existed, and the climate changed, so the animals were prevented from moving between the two continents by the strait and by colder climatic conditions.

According to Schoch (1989), animals related to the Tapiridae were most common and underwent a prolific radiation in the Eocene. However, the geological range of the family Tapiridae itself is Oligocene to Recent in North America, Oligocene to Pleistocene in Europe, Pliocene to Recent in South America, and Miocene to Recent in Asia. The geological range of the genus *Tapirus* is early Miocene to Recent. Eight other tapirid genera have been described, but all of them disappeared prior to the Pliocene except for *Megatapirus*, which has been found in Pleistocene deposits of Sichuan Province in China. It was much larger than any Recent tapir and had a shorter and deeper skull.

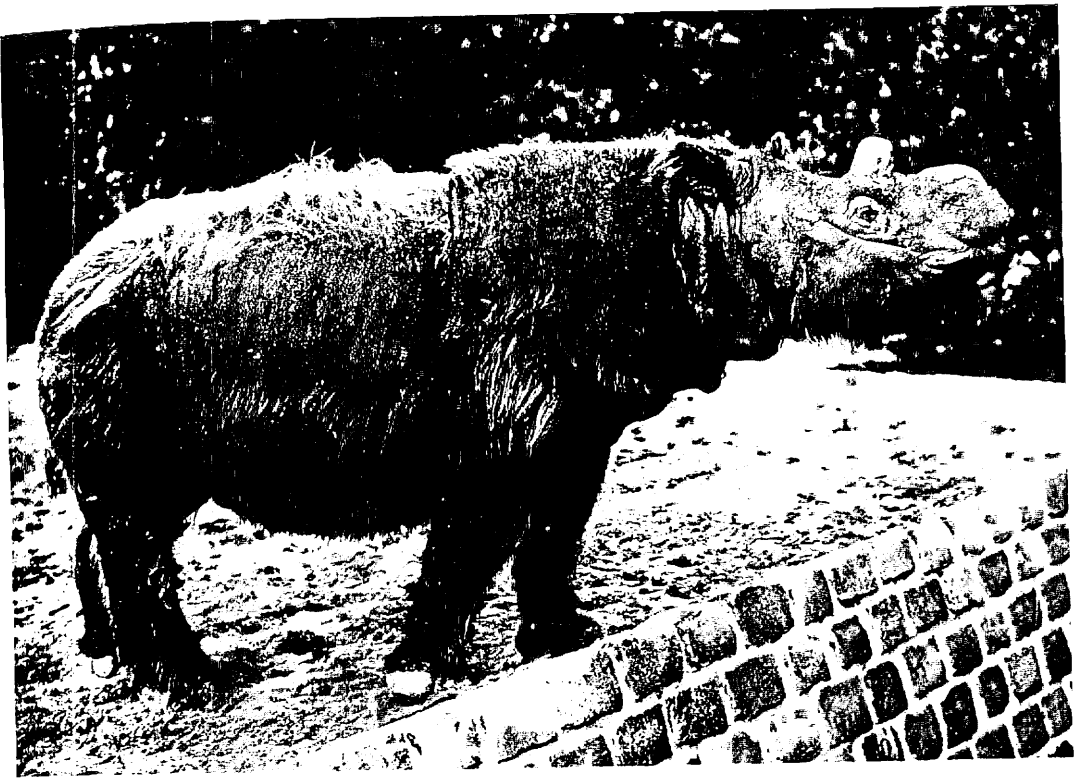
## Rhinoceroses

This family of four Recent genera and five species occurred in historical time in most of Africa south of the Sahara, perhaps in parts of North Africa, and in south-central and southeastern Asia. Two or three subfamilies have been recognized by various authorities: the Dicerorhininae, for *Dicerorhinus*; the Rhinocerotinae, for *Rhinoceros* (and sometimes also for *Dicerorhinus*); and the Dicerotinae, for *Diceros* and *Ceratotherium* (Groves 1967c, 1975a; Owen-Smith 1984). More recently it has been recognized that the living genera should be placed in the same subfamily, the Rhinocerotinae (Groves 1983), or even the same tribe, the Rhinocerotini (Prothero, Manning, and Hanson 1986; Prothero and Schoch 1989a). Of the four, *Dicerorhinus* is thought to be the most primitive and to have affinity to *Rhinoceros*, and *Diceros* and *Ceratotherium* are considered to be closely related to each other. There are additional subfamilies and families of fossil rhinoceroses.

Head and body length is 200–420 cm, tail length is 60–75 cm, shoulder height is 100–200 cm, and adult weight is around 1,000–3,500 kg. Females are smaller than males. The coloration is grayish to brownish, but the true color is often concealed by a coating of mud. The thick skin, which is scantily haired and wrinkled, is furrowed or pleated, having the appearance of riveted armor plate in some species. The tail bears stiff bristles.

Rhinoceroses have a massive body, a large head, one or two horns, a short neck, a broad chest, and short, stumpy legs. The radius and ulna, and the tibia and fibula, are only slightly movable but well developed and separate. The forefoot has three digits (four in some fossil forms), and the hind foot also has three; the hooves are distinct and separate for each digit. The upper lip is prehensile in *Rhinoceros* and *Diceros*. The small eyes are located on the side of the head, midway between the nostrils and the ears. The ears are fairly short but prominent and erect. The dental formula in the family is: (i 0–2/0–1, c 0/0–1, pm 3–4/3–4, m 3/3) × 2 = 24–34. The incisors and canines are vestigial. Except for the small first premolar, the premolars resemble the molars. The cheek teeth, which are high-crowned in *Ceratotherium* (the only species of Recent rhino that grazes rather than browses) and fairly low-crowned in the other Recent genera, are marked with transverse ridges of enamel. The skull, which is elongate and elevated posteriorly, has a small braincase. The nasal bones project freely beyond the skull. One or two median conical horns are present in rhinos, though they may be short or obscure in some forms (they were not present in many extinct species). If there is only one horn, it is borne on the nasal bones; if there are two horns, the posterior one is over the frontal bones of the skull. These horns are dermal in origin; although solid, they are composed of compressed keratin of a fibrous nature.

Rhinos generally inhabit savannahs, shrubby regions, and dense forests in tropical and subtropical regions. The African species usually live in more open areas than do the Asiatic forms. Rhinos generally are restricted to areas where a daily trip to water is possible. Their paths between the watering and feeding places often pass through tunnels in the brush. They penetrate dense thorn thickets by sheer force. Rhinos are active mainly during the evening, through the night, and in the early morning, resting during the day in heavy cover that may be several kilometers from the water holes. They sleep in both standing and recumbent positions and are fond of wallowing in muddy



Top, Sumatran rhinoceros (*Dicerorhinus sumatrensis*). Bottom, Indian rhinoceros (*Rhinoceros unicornis*). Photos by Lothar Schlawe.

pools and sandy riverbeds. They run with a cumbersome motion, reaching their top speed at a canter, that is, at a gait resembling a gallop but with moderate and easy bounds or leaps. *Diceros* can attain speeds of up to 45 km/hr for short

distances. Vision is poor, but smell and hearing apparently are acute. Rhinos eat a variety of vegetation, but succulent plants make up the bulk of the diet.

Rhinos often are accompanied by tick birds and egrets,



African black rhinoceros (*Diceros bicornis*), photos by P. F. Wright of skull in U.S. National Museum of Natural History.

which act as sentinels and feed on external parasites that often infest these mammals. Rhinos are usually timid but can be ferocious at bay. They sometimes charge an enemy, though their attack often is poorly directed. They may grunt or squeal when excited. Rhinos drop their dung in well-defined piles and often furrow the area around the piles with their horns; these piles may be scattered afterward. They are believed to act as "sign posts" or territory markers (urination spots and rubbing sticks also seem to serve this purpose).

During the breeding season a pair of rhinos sometimes remains together for 4 months; females may give birth every 2 years. The gestation period in most species is about 420–570 days. The single offspring is active soon after birth and remains with the mother until the next youngster is born. The mother sometimes guides the baby with her horn. Rhinos have a potential life span of almost 50 years. The large cats prey on young rhinos, but the adults apparently have no enemies other than humans.

The geological range of the Rhinocerotidae is middle Eocene to early Pleistocene (Blancan) in North America, late Eocene to Recent in Asia, early Miocene to Recent in Africa, and early Oligocene to Pliocene in Europe (Madden and Dalquest 1990; Prothero, Guérin, and Manning 1989). However, this family is only part of a superfamily, the Rhinocerotoida, which also contains two fossil families of rhinos and more than 80 known genera (Prothero, Manning, and Hanson 1986; Prothero and Schoch 1989a). The extinct members of this group showed remarkable diversity in size and proportions; most lacked horns. The newly described *Fouchia elyensis*, from the early part of the middle Eocene of Nevada, may represent the origin of the Rhinocerotoida but also is perhaps the smallest known perissodactyl (Emry 1989). Most lineages died out in the

late Miocene in association with severe climatic changes. However, two genera that survived in the Eurasian Pleistocene were *Coelodonta*, the widespread woolly rhinoceros (a close relative of the modern hairy rhinoceros *Diceroshinus*), and *Elasmotherium*, a huge animal (the size of modern male *Elephas*) with a single giant frontal horn.

*Indricotherium* (which includes *Baluchitherium* as a synonym and which itself sometimes is considered a synonym of *Paraceratherium*), a hornless rhinoceros of the late Oligocene and early Miocene of Asia, may have been the largest land mammal ever to exist. Willoughby (1974) estimated that it measured 4–5 meters at the shoulder and weighed about 11,000 kg. Other estimates have ranged up to 30,000 kg, but detailed recent calculations by Fortelius and Kappelman (1993) also indicate a mean weight of 11,000 kg and a maximum of 15,000–20,000 kg, about the same as that estimated for the largest known individuals of *Mammuthus* and more than twice that of the largest modern *Loxodonta*.

Although modern rhinos are far more restricted in distribution and diversity than was the group in the geological past, it would be wrong to think that they are inevitably doomed to a natural extinction. Even in the nineteenth century they occurred in large numbers over much of Africa and Asia. The subsequent population crashes have been entirely the fault of relentless killing and habitat usurpation by people. Nearly all parts of rhinoceroses are used in folk medicine, but by far the greatest demand is for the horn, which in powdered form is reputed to cure numerous physical problems and which whole is used for artistic carving. Only about 12,500 rhinos survive throughout the world. Few other animals that occur over such large stretches of wilderness have been so well mapped and counted. There is much international interest in saving those that remain, though there is some debate whether efforts should be concentrated on protecting existing populations in their natural habitat (Leader-Williams 1993) or devoted substantially to captive breeding, genetic manipulation, and reintroduction (Foose 1993; Stanley Price 1993).

PERISSODACTYLA; RHINOCEROTIDAE; Genus  
**DICERORHINUS**  
*Gloger, 1841*

## Sumatran Rhinoceros, or Hairy Rhinoceros

The single species, *D. sumatrensis*, originally occurred from Assam and southeastern Bangladesh to the Malay Peninsula and possibly Viet Nam and in Sumatra and Borneo (Groves and Kurt 1972; Lekagul and McNeely 1977; Rookmaaker 1977, 1980; Van Strien 1975). Except as noted, the information for the remainder of this account was taken from Groves and Kurt (1972).

The smallest living rhinoceros, *D. sumatrensis* is relatively short-bodied. Head and body length is 236–318 cm, shoulder height is 112–45 cm, and two estimated weights were 800 kg and 2,000 kg; however, Van Strien (1986) stated that weight is up to about 1,000 kg. The skin is leathery, up to 16 mm thick, and dark gray-brown in color. The facial skin is characteristically wrinkled around the eye, but the muzzle is rounded and unwrinkled due to heavy keratinization. The body folds of the skin are less pronounced than in *Rhinoceros*; but more so than in *Diceros* and *Ceratotherium*. There is more hair than in other rhinos. The pelage is fairly long and dense in calves, is still copious and



Sumatran rhinoceros (*Dicerorhinus sumatrensis*), photo by Erna Mohr.

is reddish brown in young adults, and becomes sparse, bristly, and almost black in older animals. There are two horns; but the one over the frontal bones often is inconspicuous. The nasal horn generally is short, the record well-authenticated specimen measuring 381 mm, but two horns that probably are referable to this species are 690 mm and 800 mm long. The dental formula is: (i 1/0, c 0/1, pm 3/3, m 3/3)  $\times 2 = 28$ .

The Sumatran rhinoceros occurs mainly in hilly country near water. It inhabits both tropical rainforest and mountain moss forest but may be attracted to forest margin and secondary growth. Van Strien (1975) concluded that this species can live in a wide variety of habitats, from swamps at sea level to high in the mountains. It may make seasonal movements, keeping to the hills when the lowlands are flooded during the rains, descending when the weather becomes cool near the end of the rains, and returning to high ground by March, possibly to escape the attacks of horse flies, which abound at low elevations in the dry season. It can move up and down steep slopes with great agility, can swim well, and has been known to swim in the sea. It feeds before dawn and after sunset and moves mostly by night. Much of the day is spent in rainwater ponds or other wallows that are dug out or deepened by the animals themselves, usually located on a mountaintop or in a catchment area of a small stream. The surrounding area is cleared of vegetation for 10–35 meters and used as a resting place. Wallowing is thought to be a mechanism for cooling or to provide protection against insects. *Dicerorhinus* reportedly is regular in its movements, making well-defined trails to wallows and feeding sites, changing the latter every 10–15 days. Young saplings, which form a major food source, are bitten off, stepped on, or broken off with the horns. The diet includes fruit, leaves, twigs, and bark. Favored foods are wild mangoes, figs, bamboo, and all kinds of plants found in secondary growth. Cultivated crops sometimes are eaten. Average daily consumption may be more than 50 kg (Van Strien 1986).

*Dicerorhinus* evidently depends on salt licks; during a

study in Gunung Leuser National Park, in northern Sumatra, Van Strien (1986) found this factor to have considerable behavioral influence. Females with calves tended to remain at lower elevations and to visit the licks frequently. Average time between visits was 23 days for such pairs, 44 days for other adult females, 59 days for subadults, and 55 days for adult males. Population density in the study area was 13–14/sq km, probably considerably higher than in localities with fewer salt licks. Each individual rhino had a permanent, well-defined home range that included a salt lick. The home ranges of adult males averaged 30 sq km and overlapped extensively, but there appeared to be small, exclusive core areas. Female ranges were smaller but generally were separate from one another except in the vicinity of salt licks. Females were thought to be territorial and to avoid one another. When not involved in breeding, adult females tended to stay at higher elevations in an area of about 10 sq km or less. When accompanied by a calf, the females moved to a lower area of about 10–15 sq km close to a salt lick. Following separation, the young rhinos remained for 2–3 years in their natal range. Adults of both sexes regularly marked their ranges with scrapes, bent or twisted saplings, feces, and sprayed urine.

Females commonly are found together with their offspring. Males usually are solitary but seem to visit the territories of females and possibly fight over the latter after the young are weaned. In his study area Van Strien (1986) found males to sometimes frequent salt licks with the evident objective of meeting a female. Most births there (northern Sumatra) took place from October to May, the period of heaviest rainfall. A gestation period of 8 months has been reported but seems unlikely considering the 15–18 months recorded for other rhinos. One newborn was 914 mm long and weighed 23 kg. The coat is short, crisp, and black in the neonate; later it becomes long, shaggy, and almost fleecy. The calf separates from its mother at 16–17 months and possibly then associates with other young, but it later becomes solitary and probably does not begin to breed until at least 7–8 years; the interbirth interval seems

to be at least 3–4 years (Van Strien 1986). A captive specimen lived 32 years and 8 months (Jones 1982).

The Sumatran rhino is classified as critically endangered by the IUCN, is listed as endangered by the USDI, and is on appendix 1 of the CITES. It has disappeared from much of its original range, principally because of habitat destruction and overhunting for supposedly aphrodisiac and medicinal products made from the horn and other parts of its body by some peoples of Asia. Flynn and Abdullah (1984), reporting that extinction appeared imminent in peninsular Malaysia, noted that logging and clearance for agriculture not only reduces habitat and fragments populations but also facilitates access by poachers. Van Strien (1986) stated that the species is very sensitive to all forms of disturbance and is driven away from an area by logging operations, but he also suggested that numbers were not so small as once feared and that concerted conservation efforts might yet save the species. Khan (1989) reported that the total number of individuals remaining in the wild was 536–962, mostly on Sumatra, and that there were another 16 in captivity. An update by Khan et al. (1996) indicated fewer than 400 in the wild and 21 in captivity. Those known to be in the wild are at restricted sites, some of which are parks or reserves but others of which are totally unprotected. The subspecies *D. s. lasiotus*, formerly found in India, Bangladesh, and Burma, is designated extinct by the IUCN, though it still may be represented by 6–7 animals in Burma. There appear to be only about 60 survivors of *D. s. harisoni*, the subspecies of Borneo. All the remaining animals belong to *D. s. sumatrensis*, there being about 85–126 in peninsular Malaysia, perhaps 10 in Thailand, and 233–341 on Sumatra. A conservation program being coordinated by the IUCN includes monitoring and improved protection of wild populations and the transfer of animals from high-risk areas in the wild to breeding facilities in captivity.

PERISSODACTYLA; RHINOCEROTIDAE; Genus  
RHINOCEROS  
*Linnaeus, 1758*

## Asian One-horned Rhinoceroses

There are two species (Ellerman and Morrison-Scott 1966; Groves 1983; Khan 1989; Rookmaaker 1980):

- R. sondaicus* (Javan rhinoceros), originally found from Sikkim and eastern India to Viet Nam and apparently southern China, and on the Malay Peninsula, Sumatra, and Java;
- R. unicornis* (greater Indian rhinoceros), originally found in northern Pakistan, much of northern India, Nepal, northern Bangladesh, and Assam.

These rhinos are large, awkward-looking creatures with a large head, short, tubular legs, small eyes, and wide nostrils. The single horn on the nose is composed of agglutinated hairs and has no firm attachment to the bones of the skull. The dental formula is: (i 1/1, c 0/1, pm 3/3, m 3/3)  $\times$  2 = 30. These rhinos also may be distinguished from their African relatives by their skin, which has a number of loose folds, giving the animal the appearance of wearing armor; the African rhinos lack such folds. *R. unicornis* has a fold of skin that does not continue across the back of the neck; *R. sondaicus*, on the other hand, has a fold that continues across the midline of the back. The skin is practically naked except for a fringe of stiff hairs around the ears and the tip of the tail. The skin of *R. unicornis* has large convex tuber-

cles, whereas that of *R. sondaicus* is covered with small, polygonal, scalelike disks. Additional information for each species is provided separately.

### *Rhinoceros sondaicus* (Javan rhinoceros)

Except as noted, the information for the account of this species was taken from Lekagul and McNeely (1977). Head and body length is 300–320 cm, tail length is about 70 cm, shoulder height is 160–75 cm, and weight is 1,500–2,000 kg. Analysis of cranial measurements by Groves (1982b) indicates that females are larger than males. This species is nearly as tall as *R. unicornis* and has the same dusky gray color but is less massive, has a much smaller head, and has less developed folds of skin on the neck. It has three folds of skin across the back, one in front of the shoulder, the second behind the shoulder, and the third over the rump. The single horn is short, record length being only 250 mm, the average length for males is closer to 150 mm, and females often lack a horn or have only a small bump. The upper lip is pointed and prehensile, being used for drawing browse toward the mouth.

The Javan rhinoceros inhabits dense rainforests with a good supply of water and plentiful mud wallows. It generally prefers low-lying areas, though some animals have been found above 1,000 meters. Individuals tend to have loosely defined centers of activity where they may spend several days at a time and to which they periodically return. Some animals may travel 15–20 km within 24 hours. In the course of feeding, branches up to 15–20 mm thick are torn off, stems at different heights above the ground are broken, and trees up to 150 mm in diameter are uprooted. The diet consists of shoots, twigs, young foliage, and fallen fruit.

This species is generally solitary except for mating pairs and mothers with young. Data cited by Laurie (1982) indicate that home ranges are small, population densities originally were greater than 0.30/sq km, there are a variety of vocalizations comparable to those of *R. unicornis*, there also is olfactory communication like that of *R. unicornis*, and courtship involves fighting between the sexes. Females probably are polyestrous and come into heat every 46–48 days. A single calf is born after a gestation period of about 16 months. It is suckled for at least 1 year and perhaps as long as 2. Females reach sexual maturity at about 3–4 years, and males at about 6 years. Mature females probably do not breed more often than every fourth or fifth year. Record longevity in captivity is 21 years, though only 9 individuals are known ever to have been in captivity.

According to Khan (1989), the Javan rhinoceros is the rarest large mammal in the world. It once was widespread, and about 150 years ago the three recognized subspecies were distributed as follows: *R. s. inermis*, eastern India, Bangladesh, Assam, Burma; *R. s. annamiticus*, Viet Nam, Laos, Cambodia, eastern Thailand; *R. s. sondaicus*, Tenasserim, Malay Peninsula, Sumatra, western Java. Still earlier, perhaps until the sixteenth century, other populations ranged as far north as the Chinese provinces of Sichuan and Hunan (Rookmaaker 1980). Like other rhinoceroses, *R. sondaicus* declined because of habitat loss and persistent killing to obtain parts, especially the horn, for alleged medicinal purposes. Today the only substantial and relatively secure population consists of 54–60 individuals of *R. s. sondaicus* in Ujung Kulon National Park, at the extreme western tip of Java (Khan et al. 1996). Even that group is highly vulnerable to poaching, epidemics, and other problems. No animals currently are in captivity.

The subspecies *inermis* is almost certainly extinct, and *annamiticus* is restricted to a few scattered groups in southern Laos, southern Viet Nam, and Cambodia. There

long was doubt whether rhinos even survived in Indochina, and if so, whether they represented *R. sondaicus* or *Dicerorhinus sumatrensis*. Based on reports, Rookmaaker (1988) concluded that only *R. sondaicus* was present. Subsequently, Schaller et al. (1990) learned that a specimen of *R. sondaicus* had been taken illegally in November 1988 about 130 km northeast of Saigon, and they found evidence that perhaps 10–15 individuals still were present in this area. Groves (1995) reported that examination of a specimen taken in 1978 confirmed that the involved population represents *R. sondaicus annamiticus*. Santiapillai, Giao, and Dung (1993) estimated that 8–12 animals survived in a 350-sq-km area of Viet Nam, indicated that this group is the only Javan rhino population other than that in Ujung Kulon Park, and reported that it is jeopardized by poaching and slash-and-burn agriculture; however, they also noted that the area was legally protected from further encroachment. *R. sondaicus* is classified as critically endangered by the IUCN, is listed as endangered by the USDI, and is on appendix 1 of the CITES.

#### *Rhinoceros unicornis* (greater Indian rhinoceros)

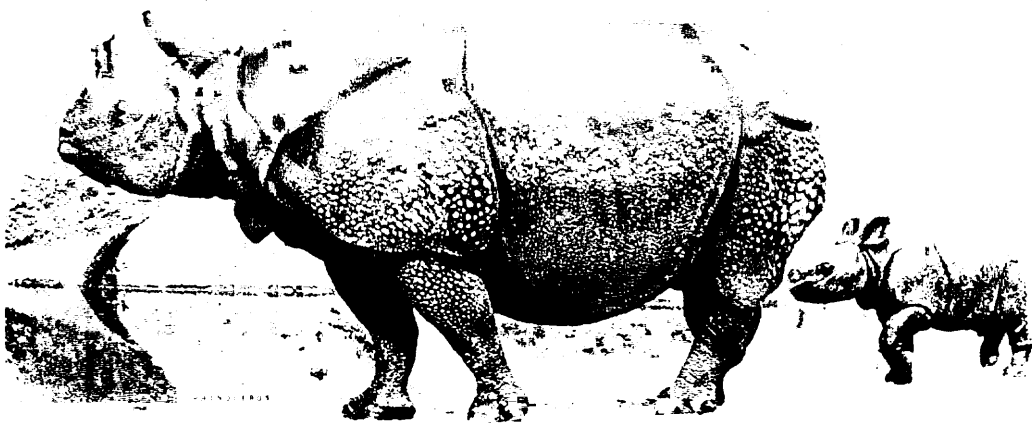
Except as noted, the information for the account of this species was taken from Laurie, Lang, and Groves (1983). Head and body length is 368–80 cm in males and 310–40 cm in females, tail length is 70–80 cm, shoulder height is 170–86 cm in males and 148–73 cm in females, and weight is about 2,200 kg in males and 1,600 kg in females (Owen-Smith 1984). A black nasal horn, reaching a maximum length of 529 mm, is present in both sexes. The hide is generally gray brown, becomes pinkish in the skin folds, and is covered with rivetlike knobs. Males show enormous development of the neck folds. Body hair may occasionally be apparent; eyelashes, ear fringes, and a tail brush are always present.

The greater Indian rhinoceros originally occurred mainly in alluvial plain grasslands, where the grass grew up to 8 meters tall. It also was found in adjacent swamps and forests. Its range now has been so restricted by human activity that it often must use cultivated areas, pastures, and modified woodlands. Activity takes place mostly at night, in the early morning, and in the late afternoon. The middle of the day commonly is spent resting in the shade or in mud wallows. The animal wallows and bathes in lakes, rivers, and pools; this behavior is especially frequent dur-

ing hot seasons and seems to be important for thermoregulation and for escaping flies. The diet consists mainly of grass and also includes fruit, leaves, branches of trees and shrubs, and cultivated crops. When feeding on tall grasses, *R. unicornis* curls its prehensile upper lip around the grass stems, bends the stems over, and bites off and chews the tops, drawing the tips into the mouth from the side. Drinking takes place on a daily basis, and mineral licks are visited regularly.

Population densities of 0.4–2.0/sq km have been found in some areas; Laurie (1982) reported densities of up to 4.85/sq km in favored high-diversity habitat of the Chitwan Valley of Nepal; and Dinerstein and Price (1991) found densities of 1.7–3.2/sq km in grasslands and a maximum of 13.3/sq km in riverine forest. Apart from cow-calf pairs, groups are rare. Temporary associations of a few subadults or adult males sometimes form at wallows or on grazing grounds. Only the strongest bulls participate in breeding, and these animals have home ranges of at least 2 sq km to more than 8 sq km. There is some degree of range exclusivity but no true territoriality; the ranges of dominant bulls overlap with one another and with the ranges of non-breeding males. Individuals usually take sudden flight from a disturbance rather than attack, but on some occasions, especially when a cow with a young calf is disturbed at close quarters, they may charge with the head down. Rhinos, mainly cows, reportedly kill several people each year in India and Nepal. Encounters between two rhinos may result in agonistic displays, charges, chases, horn clashes, and lunges with the sharp-pointed lower tusks at the neck, flanks, and rump of the opponent. There are 10 distinct vocalizations, including a snort for initial contact and a honk, bleat, and roar heard during agonistic interaction. Olfactory communication is important and is carried out through urination, defecation, and pedal scent glands. Animals of all ages and both sexes defecate at a communal dung heap. Deposition of scent apparently aids males in determining the availability of receptive females.

Breeding occurs throughout the year. A male accompanies an estrous female intermittently for several days. Courtship often involves a lengthy chase of the female and severe fighting. Females are polyestrous, estrus takes place every 21–42 days, gestation lasts 462–91 days, and there normally is a single young. At birth head and body length is 96–122 cm, shoulder height is 56–67 cm, and weight is



Greater Indian rhinoceroses (*Rhinoceros unicornis*), photo by Dorothy Y. Mackenzie.

40–81 kg. The calf suckles frequently until 12 months and only rarely after 18 months. It is driven away at least one week before the birth of the next calf. In the wild, females are full grown at 6.5 years, and males at about 10 years. Recent studies in Nepal by Dinerstein and Price (1991) suggest that the birth interval is commonly 3–5 years and that the average age of females at sexual maturity is 7.0–7.5 years. The record longevity in captivity is 47 years.

The rhinoceros remained common in northwestern India and Pakistan until about 1600 (Rookmaaker 1984). It disappeared from those regions shortly thereafter and declined sharply in the remainder of its range over the next 300 years. The main reason was the loss of alluvial plain grasslands to agricultural development, which destroyed the prime habitat of *R. unicornis*, led to conflicts with human interests, and made the rhino more accessible to hunters. Sport hunting of the species by both Europeans and Asians became very popular in the late nineteenth and early twentieth centuries. One maharajah killed 207 rhinos from 1871 to 1907 (Khan 1989). Surprisingly, even more were systematically slaughtered during this period for a government bounty established to protect tea plantations from the ravages of rhinos (Martin 1983; Martin, Martin, and Vigne 1987). By the first decade of the twentieth century the species was very near extinction; in India there were only a few scattered survivors, the main group comprising 12 individuals along the Brahmaputra River in the Kaziranga area of Assam, and in Nepal there were perhaps another 50. At that point there was a complete change in human treatment of the species: the bounty and sport hunting were halted, general legal protection was established, and Kaziranga was made a reserve (and eventually a national park).

Although there has been an encouraging overall recovery in the twentieth century, *R. unicornis* is jeopardized by loss of habitat to the expanding human population and illegal killing, especially in response to the astonishing rise in the value of the horn. The wholesale value of Asian rhino horn increased from U.S. \$35 per kg in 1972 to \$18,000 per kg in 1991. The retail price, after the horn has been shaved or powdered for sale, has at times and in certain East Asian markets exceeded \$50,000 per kg (Martin 1983; Martin and Martin 1991; Martin, Martin, and Vigne 1987; Martin and Vigne 1987; Vigne and Martin 1991). By contrast, in November 1996 pure gold was worth about \$12,000 per kg. The processed horn is used extensively in Oriental medicinal and pharmaceutical preparations as a pain reliever and fever suppressant and as a supposed cure for other problems. In India it is used as an aphrodisiac. The hide, internal organs, blood, and even the urine and dung of the rhino are also valuable. Strenuous efforts have been made by the governments of India and Nepal to control poaching and illicit trade in rhino products. The Chitwan National Park, which has Nepal's largest rhino population, now is protected by nearly 1,000 armed troops and rangers (Martin 1985a; Martin and Vigne 1995b). Although some poaching continues there, the number of rhinos has more than quadrupled since a period of unrest in the 1960s. Kaziranga National Park, with the largest population in India, is not as well protected and experienced intense poaching during the 1980s and early 1990s but still saw a modest increase in rhino numbers. Projects are under way both in India and Nepal to reintroduce breeding populations in areas where they formerly occurred (Mishra and Dinerstein 1987; Sale and Singh 1987). The sources of the animals for these projects are Chitwan in Nepal, now with about 460 rhinos, and Kaziranga in India, with 1,200 (Khan et al. 1996). Despite the severe numerical reduction in the past, genetic diversity in the Chitwan population remains high

(Dinerstein and McCracken 1990; McCracken and Brennan 1993). *R. unicornis* now numbers about 2,000 in the wild and 134 in captivity (Foose 1993; Khan 1989; Khan et al. 1996). The species is classified as endangered by the IUCN and the USDI and is on appendix 1 of the CITES.

PERISSODACTYLA; RHINOCEROTIDAE; Genus  
**DICEROS**  
Gray, 1821

## Black Rhinoceros

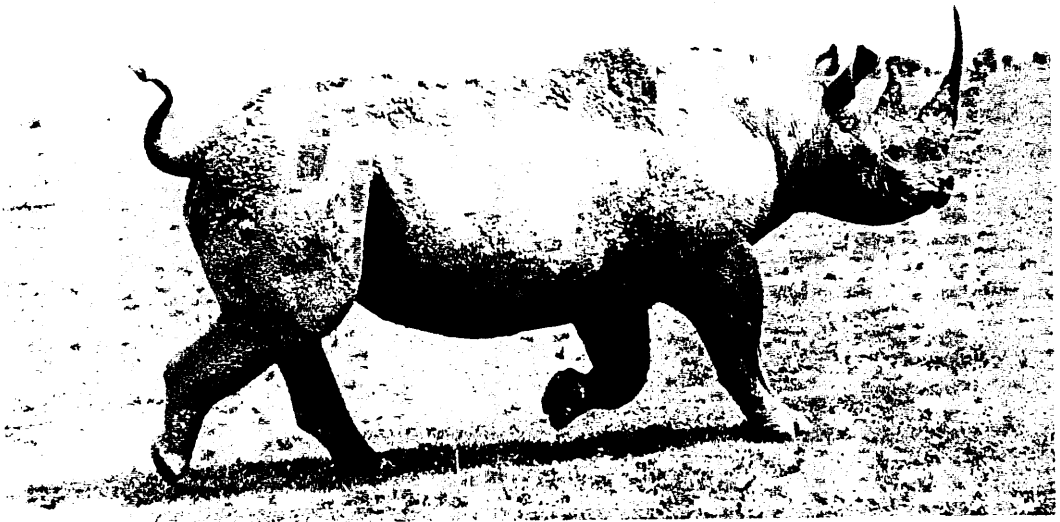
The single species, *D. bicornis*, originally occurred throughout eastern and southern Africa and in the north ranged as far as northeastern Sudan and at least as far west as northeastern Nigeria (Ansell in Meester and Setzer 1977). The extent of the former range in western Africa is not precisely known, though maps by Kingdon (1979) and Western and Vigne (1985) suggest that prior to 1900 *Diceros* was found in the savannah zone as far west as Guinea.

Head and body length is 300–375 cm, tail length is about 70 cm, shoulder height is 140–80 cm, and weight is 800–1,400 kg. The anterior horn is larger than the posterior one, averaging about 50 cm in length; sometimes the beginning of a third posterior horn is present. Data cited by Hillman-Smith and Groves (1994) indicate that there is little sexual dimorphism in overall size but that females generally have longer horns, the record length being 135.9 cm. Both this rhino and the white rhino (*Ceratotherium*) are dark in color, but the black rhino is somewhat darker. Its coloration is dark yellow brown to dark brown or dark gray. An external feature more clearly distinguishing these genera is the upper lip: in *Diceros* it protrudes slightly in the middle and its tip is prehensile, whereas in *Ceratotherium* it is squared and nonprehensile. The dental formula of both genera is: (i 0/0, c 0/0, pm 3/3, m 3/3) × 2 = 24.

The black rhinoceros is found mainly in the transitional zone between grassland and forest, generally in thick thornbush or acacia scrub but also in more open country (Schenkel and Schenkel-Hullinger 1969). It is not primarily a grassland animal but favors the edges of thickets and extensive areas of short woody growth and also is restricted to habitat within about 25 km of permanent water (Kingdon 1979). In Etosha National Park, Namibia, Joubert and Eloff (1971) reported the factor most influencing distribution to be the presence of many natural, permanent water holes. According to Kingdon (1979), the black rhino frequents mud or water wallows to counteract heat and flies and commonly rests and sleeps therein. Well-worn paths lead to such areas. Normal movement is at the rate of around 3–4 km/hr, but in a charge the animal can reach a rate of 50 km/hr. Sleeping usually occurs at midday, and the most intensive feeding takes place during the early morning and evening. *Diceros* is a browser, its main foods being the thin regenerating twigs of woody growth and legumes. A great variety of plant species are utilized, though acacias seem to be a favorite. Twigs are gathered with the prehensile upper lip, drawn into the mouth, and snapped off with the premolars. Drinking occurs every day if water can be reached, and mineral licks are visited regularly.

Data cited by Kingdon (1979) suggest that in areas of favorable habitat the black rhinoceros can become remarkably plentiful and have a dominant ecological influence. As many as 23 individuals, including all ages and both sexes, have been known to reside in an area of less than 3 sq km in the Ngorongoro Crater, 17 of them permanently. Other





Black rhinoceroses (*Diceros bicornis*): Top, photo by Bernhard Grzimek; Bottom, photo from Zoological Society of London.

reported natural densities have been around 0.1–1.0/sq km. In the Ngorongoro Crater the home range of adults of both sexes averaged 15.5 sq km (2.6–44.0 sq km). In the more barren Olduvai Gorge the range averaged 25.0 sq km (3.6–90.0 sq km). Smithers (1983) noted that ranges overlap, there being no territoriality. However, in one South African reserve with an unusually dense population the

breeding males do occupy mutually exclusive home ranges of about 4 sq km each (Owen-Smith 1984).

*Diceros* has a social system somewhat like that of *Ceratotherium*. Kingdon (1979) wrote that there seem to be clans of animals that are known to one another. Temporary aggregations of as many as 13 such individuals have been observed at a wallow. Females usually are found together

with a calf and sometimes an older daughter; those without young join a neighboring female. The young of both sexes also attach themselves to other animals. Only fully adult males become solitary, and even they may form temporary groups that move and feed together. Animals are usually tolerant of others that they know in adjacent ranges. Most conflicts involve strangers that move into the area used by a clan. Although at times several bulls may court a female simultaneously without apparent antagonism, Smithers (1983) noted that serious fights and frequent deaths result from conflicts over estrous females. There are a variety of vocalizations, including snorts for alarm, threat, and making contact. Olfactory communication also is important; males spray urine to mark the areas they utilize, and all animals utilize communal dung heaps, sometimes scraping their feet therein and thence leaving scent as they travel about. Such mechanisms may help individuals identify one another and facilitate contact between potential mates.

Breeding apparently occurs throughout the year, though Kingdon (1979) indicated that there may be mating peaks in Kenya during September–November and March–April, and Hitchins and Anderson (1983) indicated peaks in Zululand during October–November and April–July. These and other reports suggest that births tend to take place in the rainy season. A pre-mating bond develops between the bull and the cow, and the pair remain together during resting and feeding; they even sleep in contact with each other. There evidently is no serious fighting such as found in *Rhinoceros*. Females usually give birth every 2–5 years, the estrous cycle is 17–60 days, estrus lasts 6–7 days, the gestation period is 419–78 days, and there is a single calf weighing about 40 kg at birth. Some solid food may be taken within a few weeks of birth, weaning is completed after about 2 years, independence is achieved at 2.5–3.5 years, and reproductive maturity is reached at 4–6 years in females and 7–9 years in males (Grzimek 1975; Hayssen, Van Tienhoven, and Van Tienhoven 1993; Hitchins and Anderson 1983; Jarvis 1967; Kingdon 1979). One black rhino lived 45 years and 10 months in captivity (Jones 1993).

Although its pugnacity has been greatly exaggerated, the black rhino is unpredictable and can be a dangerous animal, sometimes charging a disturbing sound or smell. It has tossed people in the air with the front horn and regularly charges vehicles and campfires. Catching the scent of humans, it usually crashes off through the brush and runs upwind, sometimes for several kilometers before stopping. Apparently the sense of smell is the primary method of detecting danger. Schenkel and Schenkel-Hullinger (1969) found that human scent alone causes great alarm among black rhinos. On the other hand, if they detect no scent, rhinos will show no interest in a motionless person or car unless it is closer than 20–30 meters.

The black rhinoceros has been hunted by people since ancient times, but exploitation accelerated during the nineteenth and twentieth centuries. It was killed for sport because it was considered dangerous, to obtain its durable hide, and to secure its horn, which was carved into various ornamental objects or shaved or ground into powder for use as an alleged medicine or aphrodisiac. The largest subspecies, *D. bicornis bicornis*, of central and southern Namibia and most of South Africa, became extinct when the last known individual was shot in 1853 (Rookmaaker and Groves 1978; Smithers 1983). By about 1900 the black rhinoceros also had been eliminated in West Africa, though it still was distributed continuously from Cameroon to Ethiopia and south through East Africa to eastern South Africa (Cumming 1987). Numbers and distribution declined substantially in East Africa in the first half

of the twentieth century, partly because of government-sponsored killing carried out on the grounds that the presence of the rhino was incompatible with human settlement (Kingdon 1979). Persecution and habitat destruction had led to the disappearance of *Diceros* in most of Ethiopia and Somalia by the 1960s (Yalden, Largent, and Kock 1986). Nonetheless, in 1970 at least 65,000 black rhinos were still estimated to exist, with populations present in most countries of the original range. Over the next decade, however, it was increasingly recognized that disaster was befalling the species as the value of its horn and consequent poaching increased. The black rhino was placed on appendix 1 of the CITES in 1975 and was listed as endangered by the USDI in 1980. It also was classified first as vulnerable, then as endangered, and finally as critically endangered by the IUCN.

The continued collapse of populations of *Diceros* represents perhaps the greatest single mammalian conservation failure of the late twentieth century. Total numbers in the wild fell to about 15,000 in 1980, to fewer than 9,000 in 1984, and to only 3,800 in 1986 (Cumming 1987; Western and Vigne 1985). The most recent estimates put the number in the wild at closer to 2,400 (Khan et al. 1996), and there are approximately 182 in captivity (Foose 1993). Rhino populations of entire countries, such as that of the Central African Republic, which had about 3,000 rhinos in 1980, have been totally wiped out by poachers. A supposedly well-protected population of 1,700 present in Zimbabwe as late as 1987 has since been reduced to only 300. There also now are about 1,000 black rhinos in South Africa, 600 in Namibia, 400 in Kenya, and smaller numbers in Cameroon, Tanzania, Zambia, Malawi, and Swaziland. This situation has been brought about entirely by an irrational demand for the horn and to a large extent through a strictly ornamental utilization by a single class of persons in one small country. If such a narrow and needless desire has led to the near extinction of one of the world's most spectacular and popular animals at a time when wildlife conservation is receiving immense international interest and support, how can we ever hope to save the multitude of other creatures and ecosystems that are jeopardized by much more trenchant problems of human population growth and development or by far broader and more substantive commercial pressures?

The factor that triggered the recent collapse of rhino populations was a great increase in the demand for horn in the carving of ornamental handles for the traditional daggers (jambias) worn by many men in Yemen (Martin 1979, 1985b; Martin and Martin 1987; Martin and Vigne 1987; Varisco 1989; Vigne and Martin 1987). Although this tradition dates back to the Middle Ages, many citizens of Yemen recently went to work in nearby oil-producing regions, thus bringing an influx of wealth, with far more people being able to afford jambias made from rhino horn rather than from cheaper materials. From the early 1970s to 1984 about half of the entire supply of rhino horn on the world market went to Yemen. Annual importation peaked in 1976, when more than 8,300 kg entered the country. In 1982 the government banned importation. That measure had little initial effect; ironically, the source of most of the horn that continued to come in was Sudan, a member of the CITES. By 1987 intensified enforcement efforts, as well as the scarcity of rhinos, had reduced the trade. Illegal importation continued, however, with several hundred kilograms entering Yemen annually through the early 1990s. Moreover, there is an established investment value for rhino horn jambias, and market potential remains high. High-level religious and administrative decrees issued in Yemen in 1992 and the apparent success of agate-handled jambias

introduced in 1994 may be helping to mitigate the crisis (Martin and Vigne 1995a; Vigne and Martin 1993).

The most substantial ongoing problem for the black rhino is the demand for horn for use in traditional Oriental medicines (E. B. Martin 1989; Martin and Vigne 1987). The horn typically is sold in a pharmacy, shavings being made in front of the customer; they then are taken home, boiled, and given to the patient (Martin 1979). The horn may also be ground into powder and then fabricated into pills or mixed in potions and tonics. It has a wide variety of uses, including fever suppression. It evidently is not used as an aphrodisiac in Oriental countries, but it is in parts of India. China, the main producer of Oriental medicines, apparently obtains most of its supply of raw horn from Hong Kong and other nearby countries. Hong Kong itself prohibited horn imports in 1979, but much illegal activity continues. Singapore was the largest importer until 1986, when it also implemented a ban, and now little horn goes there. Since the late 1980s the biggest importer has been Taiwan (Martin and Martin 1991; Vigne and Martin 1989). Importation was legally banned in 1985, and stringent restrictions on domestic trade were enacted in 1989. However, enforcement is lax, with much horn continuing to enter Taiwan, often by way of South Africa, and local commerce proceeding (Loh and Loh 1994). In response to this situation, in 1994 the United States imposed trade sanctions against Taiwan in accordance with the Pelly Amendment to the Fishermen's Protective Act (Heck 1994).

It has been estimated that 90 percent of all adult rhino deaths are caused by poaching to obtain the horn. About 200,000 kg of horn entered trade from 1970 to 1987; the average weight of a black rhino horn is 2.88 kg (Western 1989a). In the late 1960s the price of rhino horn was only about U.S. \$20 per kg. It now fluctuates according to both time and place, but in the early 1990s in East Asian markets the retail value of black rhino horn was around U.S. \$4,000–\$10,000 per kg (Heck 1994; Martin and Martin 1991). So great was the demand for horn for medicinal purposes that antique carvings were being ground up and sold.

Several organizations are working to help the black rhino, and a number of individuals have made outstanding contributions, notably Esmond Bradley Martin, whose extensive travels and studies in Asia and Africa have yielded remarkably detailed accounts of the trade in rhino products. The IUCN, assisted by the World Wildlife Fund and other agencies, has developed a conservation plan for the black rhino (Cumming, Du Toit, and Stuart 1990). Strategy centers on a concentrated effort to save the most significant remaining wild populations while simultaneously working to halt the trade and utilization of rhino horn.

One radical and controversial technique, not in the IUCN plan, is the deliberate removal of horns from living (tranquilized) individuals in order to discourage poaching (Berger 1994; Berger et al. 1993; Milner-Gulland, Leader-Williams, and Beddington 1993; Ricciuti 1993). It is being done in Namibia, Zimbabwe, and Swaziland and is being considered in other countries. This process is expensive, costing about U.S. \$1,000 per capture, and also may be stressful to the animals, especially because the horns must be repeatedly cut off. The anterior and posterior horns grow back at annual rates of 6 cm and 3 cm, respectively, therefore attaining a market value in the thousands of dollars just a year after dehorning. Observations in some areas suggest that this effort has substantially reduced but not completely stopped poaching. Moreover, there are concerns about the potential danger of the removal of a structure that may have critical social and protective roles, particularly in the mother's defense of her young from hyenas and other predators. Lindeque and Erb (1995) challenged

such concerns, arguing that horn size has little to do with calf protection. Unfortunately, when Berger and Cunningham (1994a, 1994b) reported investigations in Namibia indicating poor calf survivorship in areas where adults had been dehorned and suggested that a better approach would be to concentrate rhinos in guarded sanctuaries, they were forced to leave the country (MacIlwain 1994).

There also is concern regarding the genetic viability of many of the small, fragmented populations that remain, and there are questions whether attempts to consolidate such groups might upset natural systematic units (Du Toit 1989; Foose 1987a). Groves (1967a) recognized seven subspecies of *D. bicornis*, and Western and Vigne (1985) reported that all still survived but that several were approaching extinction (they mistakenly referred existing South African populations to the extinct *D. b. bicornis*). It now appears that *D. b. brucei*, of Sudan, Ethiopia, and Somalia, and *D. b. chobiensis*, of southeastern Angola, have indeed disappeared and that *D. b. longipes*, of Central Africa, is represented only by a few dozen individuals in Cameroon and possibly Chad. *D. b. michaeli*, a small subspecies of East Africa, survives only in a few fragmented groups containing a total of 50–100 animals (Prins 1990). Some recent studies, including analysis of mitochondrial DNA, suggest that taxonomic distinctions are less meaningful than once thought and thus that more flexibility in transfer and captive breeding programs may not be objectionable (Ashley, Melnick, and Western 1990; Du Toit 1987; O'Ryan, Flamand, and Harley 1994). However, Rookmaaker (1995) argued for continued recognition of Groves's (1967a) seven subspecies.

PERISSODACTYLA; RHINOCEROTIDAE; Genus  
**CERATOTHERIUM**  
 Gray, 1868

## White Rhinoceros, or Square-lipped Rhinoceros

In the nineteenth century the single species, *C. simum*, inhabited two widely separated regions of Africa (Ansell in Meester and Setzer 1977; Groves 1972a; Kingdon 1979). The subspecies *C. s. cottoni* occurred in southern Chad, the Central African Republic, southwestern Sudan, northeastern Zaire, and northwestern Uganda. The subspecies *C. s. simum* occurred in southeastern Angola, possibly southwestern Zambia, central and southern Mozambique, Zimbabwe, Botswana, eastern Namibia, and northern and eastern South Africa. About 2,000 years ago the range of *Ceratotherium* extended up the Nile Valley into southern Egypt and probably covered much of northwestern Africa. Rock paintings and skeletal remains show that rhinos once occurred as far to the northwest as coastal Morocco and Algeria, but there are questions about species identity and time of latest survival. Based on the relative length of the horn shown in some of the rock pictures, Kádár (1991) suggested that *Ceratotherium* was present in Morocco and Libya about 3,500 years ago.

Except for *Elephas*, *Loxodonta*, and perhaps *Hippopotamus*, *Ceratotherium* is the largest living genus of land mammals. Head and body length is 335–420 cm, tail length is 50–70 cm, shoulder height is 150–85 cm, and weight is about 1,400–1,700 kg in females and 2,000–3,600 kg in males. Coloration is yellowish brown to slaty gray. This mammal is almost naked except for the ear fringes and tail bristles; there is copious but sparse body hair in *C. s. simum*



White rhinoceroses, or square-lipped rhinoceroses (*Ceratotherium simum*): Top, photo from Société Royale de Zoologie d'Anvers through Walter Van den Bergh; Bottom, photo by K. Rudloff through East Berlin Zoo.

(Groves 1972a). Additional hairs are present in the skin but do not protrude. The front horn averages about 60 cm in length but can reach more than 150 cm. From *Diceros*, *Ceratotherium* can be distinguished externally by its usually lighter coloration, squared upper lip with no trace of a proboscis, elongated and pointed ear conchae with a few bristly

hairs at the tips (compared with rounded conchae with hairy edges in the black rhino), more sloping and less sharply defined forehead, shoulder hump, and less conspicuous skin folds on the body. The dental formula of both genera is: (i 0/0, c 0/0, pm 3/3, m 3/3)  $\times 2 = 24$ .

In South Africa the primary habitat of *Ceratotherium* is

woodland interspersed with grassy openings. Its four main requirements seem to be relatively flat terrain, thick bush cover, short grass for eating, and water for drinking and wallowing (Smithers 1983). In East Africa this genus lives in open forest and nearby plains; it traverses but does not permanently inhabit steeply undulating country, and it may utilize swampy country along the Nile in the dry season and then move to higher ground 10 km away when the rains come (Groves 1972a). Daily movements of 4–15 km have been reported (Van Gysegem 1984). Activity generally is in the early morning, late afternoon, and evening. The rhino wallows or rests in the shade during the middle of the day. Wallowing in the mud is especially important during hot weather for purposes of thermoregulation and for ridding the body of ectoparasites. As in other rhinos, vision is relatively poor, but the senses of hearing and smell are acute. There is a graceful trot at about 24 km/hr and a gallop for short spurts at 40 km/hr. *Ceratotherium* differs from other rhinos in that it is entirely a grazer. It feeds largely on short grasses, using only the broad, flexible lips for cropping the stems (Groves 1972a; Kingdon 1979; Owen-Smith 1975).

Reported overall population densities vary from 0.03/sq km to 0.81/sq km (Groves 1972a), though local densities in favorable habitat may exceed 5.0/sq km (Owen-Smith 1981, 1984). Data obtained by investigations in eastern South Africa (Kingdon 1979; Owen-Smith 1974; Pienaar, Bothma, and Theron 1993; Smithers 1983) indicate that some adult males occupy territories of 0.75–13.80 sq km. They spend almost their entire life in these areas, unless water is unavailable, in which case they follow a narrow corridor to a drinking site every 3–4 days. Male territories are bordered by topographical features such as watercourses and ridges and overlap one another by only about 50–100 meters. Adult females in South Africa have home ranges of 6–8 sq km in good habitat and as large as 45 sq km in less favorable areas. These ranges overlap one another extensively and are not defended; each may overlap as many as seven male territories.

In a study of a small introduced population in Murchison Falls National Park, Uganda, Van Gysegem (1984) found a somewhat different situation. The population, consisting of 15 individuals, occupied a total range of 130 sq km, of which 66 sq km was used in the rainy season and 74 sq km in the dry season. The single adult male was territorial, using 6 sq km during the rainy season and 24 sq km in the dry season. The other animals had overlapping home ranges of 30–97 sq km each.

*Ceratotherium* appears to have the most complex social structure among the rhinoceroses (Kingdon 1979; Owen-Smith 1974, 1984; Smithers 1983; Van Gysegem 1984). Temporary associations of as many as 14 individuals have been observed, and there are smaller, cohesive units. Territorial bulls are usually solitary; they mark and patrol the boundaries of their areas and challenge any intruding adult male. Sometimes there are ritualized engagements involving repeated apposition of horns, but serious fighting is rare at such times, and usually one or both of the opponents retreats. More intensive conflicts, with head-on charges and the infliction of injuries by horning or ramming, may occur when males compete for estrous females. A dominant bull usually tolerates the presence of several subordinate males within his territory and also allows females and subadults to wander freely through the area. He attempts to prevent estrous females from leaving. Several females and their calves commonly form an association. Subadults, which are driven off by their mothers before the birth of the next calves, pair with one another; sometimes as many as six young animals will join an adult female.

The white rhino has about 10 vocalizations, including a panting contact call, grunts and snorts associated with courtship, squeals of distress, and deep bellows or growls for threats. Dominant males spray urine to demarcate the boundaries of their territories; subordinate males and other animals do not spray urine. There are communal dung heaps, which facilitate olfactory identification among animals in an area. Territorial males have the habit of scattering their dung after defecation.

The following data on reproduction were taken from Groves (1972a), Kingdon (1979), Owen-Smith (1974, 1984), and Smithers (1983). A pair bond may last 5–20 days and involve some chasing and horn clashing. Breeding occurs throughout the year, but mating peaks have been observed in South Africa from October to December and in East Africa from February to June. The gestation period has been estimated to last as long as 18 months, though now it is thought to be closer to 16 months. The single calf weighs about 40–65 kg at birth and remains unsteady for 2–3 days. When alarmed, it runs ahead of the cow, whereas the calf of *Diceros* tends to follow its mother. Weaning commences at 2 months, but nursing may continue for well over a year. Females commonly give birth every 2–3 years and drive off their previous calf just before parturition. Sexual maturity may come at 4–5 years, but females do not have their first calf until they are 6.5–7.0 years old, and males probably are 10–12 years old before they can claim a territory and mate. A wild, 36-year-old female was still reproductively active. Potential longevity is probably 40–50 years.

In contrast to *Diceros*, the white rhino is mild-tempered and interspecifically nonaggressive. It becomes tame and tractable in captivity and reportedly can be approached safely by people in the wild (Kingdon 1979; Owen-Smith 1984). Unfortunately, these traits have contributed to its downfall, as it has been relentlessly hunted for the same reasons as those described above in the account of the black rhino. The subspecies *C. s. simum* was largely eliminated in the course of the settlement of southern Africa during the eighteenth and nineteenth centuries. It was considered to be totally extinct by 1893, but in the following year a small population was discovered in the Umfolozi area of Zululand in eastern South Africa. Some accounts indicate that fewer than 10 individuals survived at that time, but there probably were more than that, and the true low point may have come in the 1930s, when a drought reduced the population to fewer than 100. Subsequent careful protection led to a growing population at Umfolozi and adjoining reserves that appeared to be excessive for the available habitat. Numbers had reached about 1,000 individuals by 1970 and 2,000 by 1980; a subsequent management program involved the live capture of many animals, which then were used in massive reintroduction programs in other parts of South Africa as well as in other countries (Groves 1972a; Owen-Smith 1981; Smithers 1983). Cumming and Du Toit (1989) reported that numbers had increased to 4,404, and Khan et al. (1996) listed a total of 7,533 southern white rhinos, including 7,095 in South Africa, 41 in Swaziland, 20 in Botswana, 138 in Zimbabwe, 107 in Namibia, 5 in Zambia, and 122 in Kenya (outside of the natural range). A small group introduced to Mozambique apparently has been eliminated by poachers. *C. s. simum* is designated as conservation dependent by the IUCN and is on appendix 1 of the CITES (except that South African specimens under certain conditions are on appendix 2).

The northern subspecies of the white rhino (*C. s. cottoni*) was not discovered by science until 1903, at which time it was still fairly numerous in the range given at the start of this account. Subsequently populations have fluctuated in

response to the alternating prevalence of human exploitation and protection, but the overall trend has been disastrously downward (Hillman-Smith, Oyisenzo, and Smith 1986; Kingdon 1979; Western and Vigne 1985). Numbers in Uganda fell to about 133 in 1928, increased to 500 in 1950, and then declined to 71 in 1963. In an effort to protect some of the last survivors from poachers, 15 individuals were captured and moved to Murchison Falls National Park. Their numbers grew to about 80, but all were killed in 1980. When Garamba National Park was established in Zaire in 1938 there were only about 100 white rhinos in the area. Numbers then grew to about 1,200 in 1963, fell

sharply during a period of political turmoil in the 1970s, bounded to about 500 after government control was restored in the 1970s, and finally collapsed as poaching intensified in the early 1980s. Populations in the Central African Republic also disappeared during this period. Groves (1972a) stated that a few individuals might survive in Chad, but they evidently had been killed by 1980. By the latest count, there now are only 31 northern white rhinos in the wild, all at Garamba (Khan et al. 1985). Another 13 are in captivity. *C. s. cottoni* is classified as critically endangered by the IUCN, is listed as endangered by the USDI, and is on appendix 1 of the CITES.