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Order Perissodactyla

Odd-toed Ungulates (Hoofed Mammals)

This order of 3 Recent families, 6 genera, and 17 species is native to eastern Europe, central and southern Asia, parts of the East Indies, Africa, and the region from southern Mexico to Argentina. Introduction by human agency has led to establishment of wild-living populations of two species (*Equus caballus* and *E. asinus*) in certain areas where the order does not naturally occur. Simpson (1945) divided the living Perissodactyla into two suborders: Hippomorpha, for the family Equidae (horses, asses, and zebras); and Ceratomorpha, for the families Tapiridae (tapirs) and Rhinocerotidae (rhinoceroses). A third suborder, the extinct Ancylopodia, contained the family Chalicotheriidae, which developed clawed feet and which survived until the Pleistocene.

These are medium-sized to large animals adapted to running (especially members of the family Equidae). All the Recent families are quite distinct, with tapirs and rhinos resembling one another more than either family resembles the horses. The main feature common to all is that the weight of the body is borne on the central digits, with the main axis of the foot passing through the third digit, which is the longest on all four feet. In the horses, only the third digit of each foot is functional; in tapirs, four digits are developed on the fore-foot and three on the hind foot; in rhinos, three digits are present on all four feet. The first digit is not present in any Recent forms; it was vestigial in certain fossil species. The terminal digit bones are flattened and triangular, with evenly rounded free edges, and are encased by hooves (some members of the extinct family Chalicotheriidae had clawed digits). Perissodactyls progress on their hooves or on their digits, never on the sole of the foot with the heel touching the ground. The ulna and the fibula are reduced, so the movement of these bones is reduced or lacking. The ankle bone, or astragalus, has only a single, deeply grooved, pulleylike surface for the tibia, and its lower end is nearly flat; the calcaneum, or heel bone, which has a widened lower end, does not articulate with the fibula.

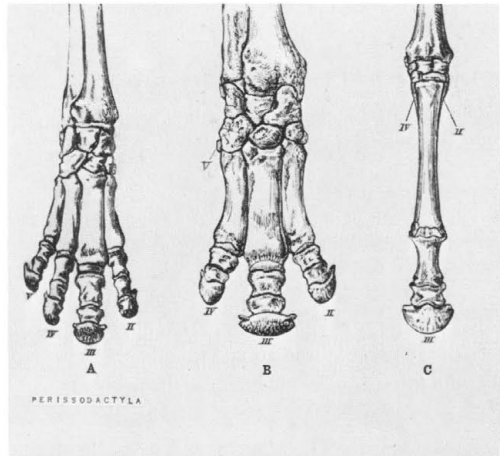
The skin usually is thickened, and sparsely to densely haired. The mammae are located in the region of the groin, and the males do not possess a baculum.

The dental formula for the order is as follows: (i 0-3/0-3, c 0-1/0-1, pm 2-4/2-4, m 3/3) $\times 2 = 20-44$; for the Recent species it is: (i 0-3/0-3, c 0-1/0-1, pm 3-4/3-4, m 3/3) $\times 2 = 22-44$. The canines, when present, are never tusklike in the Recent species. The cheek teeth are arranged in a continuous series; the premolars (at least the rear members of the series) are molarlike in the Recent species; the first cheek tooth is a persistent milk premolar. The grinding teeth

are usually complex in structure, massive, and low-crowned to high-crowned; prominent transverse ridges are present in the cheek teeth of tapirs and rhinos, whereas the cheek teeth of horses, which are grazers rather than browsers, develop high crowns with four main columns and various infoldings. Some fossil species in this order had tubercles on the crowns of the grinding teeth. The skull is usually elongate with an abrupt slope in the back. The nasal bones are expanded posteriorly. Characteristic of the order is the arrangement of openings in the skull by which nerves and blood vessels enter and leave the braincase. The Recent species lack horns with true bony cores, though roughened cushions on the nasal bones of the skull bear horns in rhinos.

The development of the foot, in its highest form in the horses, is a specialization that enables the animals to be swift and strong runners. The foot is not developed to such an extent in the rhinos and tapirs. However, rhinos can run rapidly for short distances, and tapirs also can run well, though they usually inhabit a type of terrain that permits them to plunge into dense cover or water to escape their enemies.

Rhinos and horses usually live on grassy plains or in open scrub country, while tapirs are found in humid tropical forests. Members of this order are strict herbivores and can be classified as either browsers or grazers depending on how they feed. The structure of their lips and teeth facilitates the obtaining and chewing of coarse vegetable food. Adulthood in



Bones of the forefeet: A. Tapir (*Tapirus indicus*); B. Rhinoceros (*Dicerorhinus sumatrensis*); C. Horse (*Equus caballus*). Photos from *Mammalia*, F. E. Beddard.

these animals is attained in four to six years, and individuals may live five to seven times that long.

Perissodactyls flourished in early and middle Tertiary times. Carter (1984) listed 11 extinct families, gave the geological range of the order as early Eocene to Recent, and noted that it almost certainly had originated in the late Paleocene. Except for domestic horses and asses, however, perissodactyls are not now very numerous either in species or in individual animals. The living genera are mere remnants of a major evolutionary sequence that at one time was extremely diversified and widely distributed over the world. Even these genera each have one or more species that are in danger of extinction.

PERISSODACTYLA; Family EQUIDAE; Genus EQUUS
Linnaeus, 1758

Horses, Zebras, and Asses

The single Recent genus, *Equus*, contains six subgenera and eight species (Ansell, in Meester and Setzer 1977; Corbet 1978; Elleman and Morrison-Scott 1966; Groves 1986b; Groves and Willoughby 1981):

subgenus *Asinus* Gray, 1822

E. asinus (African wild ass, donkey, or burro), probably once found in the wild from Morocco to Somalia and from Mesopotamia to Oman, now occurs in domestication throughout the world and feral populations established in some areas;

subgenus *Hemionus* Stehlin and Graziosi, 1935

E. hemionus (kulan and onager), originally found in the desert and dry steppe zone from the Ukraine and Palestine to Manchuria and western India;
E. kiang (kiang), Tibet and adjacent highland regions;

subgenus *Equus* Linnaeus, 1758

E. caballus (horse), probably once found in the wild throughout the steppe zone from Poland and Hungary to Mongolia, now occurs in domestication throughout the world and feral populations established in many areas;

subgenus *Dolichohippus* Heller, 1912

E. grevyi (Grevy's zebra), southern and eastern Ethiopia, Somalia, northern Kenya;

subgenus *Hippotigris* H. Smith, 1841

E. zebra (mountain zebra), southwestern Angola, Namibia, western and southern South Africa;

subgenus *Quagga* Shortridge, 1934

E. burchelli (Burchell's zebra), open country from southern Ethiopia to central Angola and eastern South Africa;
E. quagga (quagga), formerly found in South Africa.

Bennett (1980) concluded that there are only two subgenera: *Asinus* for the ass, kulan, and kiang; and *Equus* for the horse, quagga, and zebras. Dalquest (1988) recognized the two as full genera, based on his view that they had evolved sep-

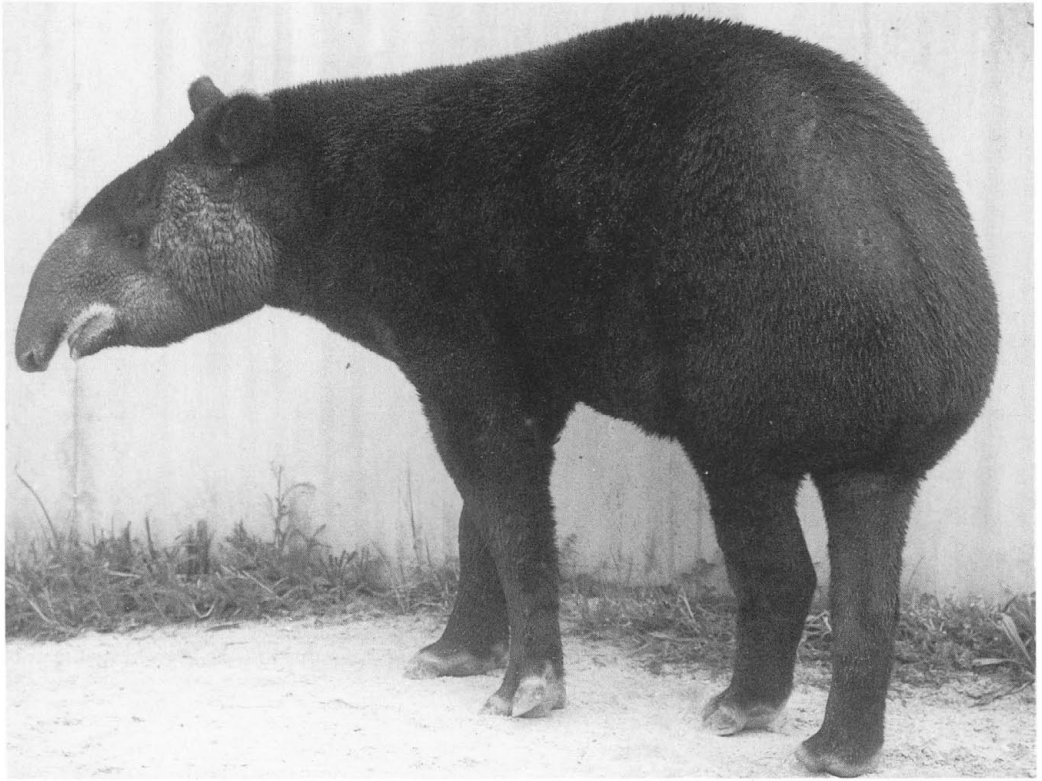
arately in the Pliocene, *Asinus* from the fossil genus *Astrohippus* and *Equus* from *Dinohippus*. Bennett also treated *E. onager* as a species distinct from *E. hemionus*, thereby restricting the range of the latter to regions east of Soviet Central Asia, and in this regard she was followed by Corbet and Hill (1986b) and Honacki, Kinman, and Koepl (1982). The names *E. caballus* and *E. asinus* are based on domestic animals, and some authorities, such as Corbet (1978) and Groves (1986b), prefer to use the names *E. ferus* for the wild horse and *E. africanus* for the wild African ass. The diploid chromosome number is 64 in the domestic horse but 66 in the true wild horse, and some authorities thus treat the latter as a distinct species, *E. przewalskii*. Moreover, Ryder (1988) reported that analysis of mitochondrial DNA suggests that the ancestors of *E. caballus* and *E. przewalskii* diverged about 250,000 years ago. This methodology still is unproven, however, and Honacki, Kinman, and Koepl (1982) regarded *caballus* and *prezewalskii* as conspecific, noting that their fundamental chromosome numbers are the same and that matings between the two produce fertile offspring. Grubb (1981), R. E. Rau (1978), and Kingdon (1979) suggested that *E. quagga* and *E. burchelli* may be conspecific, but Meester et al. (1986) retained each as a species.

The general body form of *Equus* ranges from thick-headed, short-legged, and stocky to slender-headed and graceful. The size is variable, especially among the domesticated forms. The wild species measure 100–160 cm high at the shoulders. The tail is moderately long, with the hairs reaching at least to the middle of the leg when the tail is hanging down. Equids are heavily haired, but the length of the hair is variable. Most species have a mane on the neck and a lock of hair on the forehead of the head known as the forelock. The two mammae of the female are located in the groin region.

Coloration in most species is generally grayish or brownish above and white below, occasionally with stripes on the shoulders and legs. Striping is carried to an extreme in the zebras. Kingdon (1979, 1984) rejected the hypotheses that stripes serve as camouflage for zebras, that they visually confuse predators and pests, and that they assist in regulating body temperature through heat absorption; instead, he suggested that stripes facilitate group cohesion and socialization. It may be that stripes developed originally as foci for grooming behavior and that the animals then came to associate this attractive tactile stimulus with a visual pattern. There is evidence that zebras, even unrelated individuals, are drawn closely to one another by such a pattern, whereas other equids maintain greater distances. This behavior is important in tropical savannah habitat, where animals seasonally congregate at high densities to exploit resources. In colder regions equids do not assemble in such large and compact groups. In addition, a crisp pattern of stripes can not be maintained in a shaggy winter coat. It is likely that stripes are a primitive characteristic and that they initially appeared in the narrow form seen in *E. grevyi*. That species may be near the ancestral line leading to other zebras and the horse. The latter species, spreading into temperate, desert habitat, lost the need for an intense pattern of stripes. Likewise, such a pattern was greatly reduced in the most southerly of zebras, *E. quagga*, which was restricted to a temperate part of Africa.

The Recent species of equids have only one functional digit, the third. The terminal digit bone on each foot is widened and evenly rounded or spade-shaped; equids walk on the tips of their toes. The radius and ulna are united, although the ulna is greatly reduced in size, so all the weight is borne on the radius. In the hind leg, the enlarged tibia supports the weight, and the fibula is reduced and fused to the tibia.

The dental formula in the Recent forms is: (i 3/3, c 1/1, pm 3–4/3, m 3/3) × 2 = 40–42. The incisors are shaped like



Mountain tapir (*Tapirus pinchaque*), photo by Lothar Schlawe.

The geological range of the Tapiridae is early Eocene to Recent in North America, early Oligocene to Pleistocene in Europe, Pleistocene to Recent in South America, and Miocene to Recent in Asia. The geological range of the genus *Tapirus* is late Miocene to Recent. *Megatapirus* is the only extinct tapir that has been found in Pleistocene deposits of the Old World; it is known from Sichuan Province of China. It was much larger than any Recent tapir and had a shorter and deeper skull.

PERISSODACTYLA; Family RHINOCEROTIDAE

Rhinoceroses

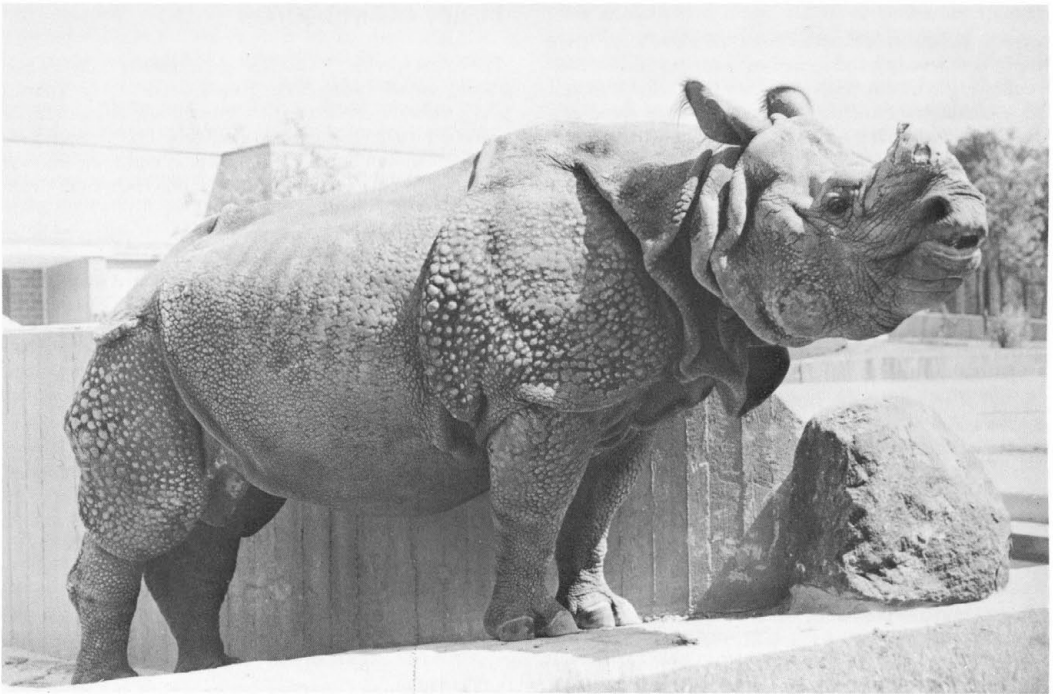
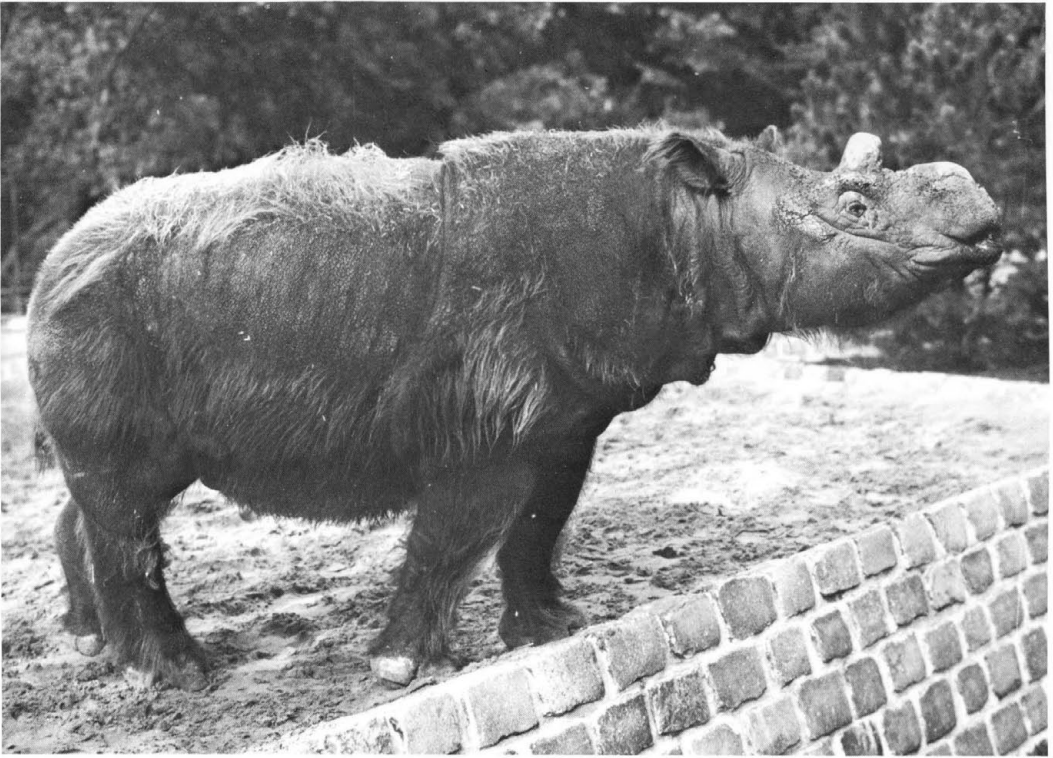
This family of four Recent genera and five species occurred in historical time in most of Africa south of the Sahara, perhaps in parts of North Africa, and in south-central and south-eastern Asia. Two or three subfamilies have been recognized by various authorities: Dicerorhinae, for *Dicerorhinus*; Rhinocerotinae, for *Rhinoceros* (and sometimes also for *Dicerorhinus*); and Dicerotinae, for *Diceros* and *Ceratotherium* (Groves 1967b, 1975b; Owen-Smith 1984). More recently, there has been recognition 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). Of the four, *Dicerorhinus* is thought to be the most primitive and to have affinity to *Rhinoceros*, while the other two genera are considered to be closely related to one another. There are additional subfamilies and families of fossil rhinoceroses.

Head and body length is 200–420 cm, tail length is 60–75

cm, height at the shoulder 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 two genera (*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.

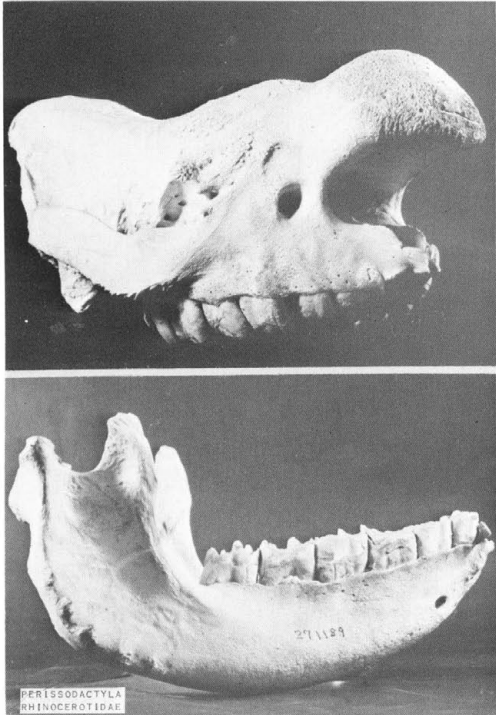
Rhinos generally inhabit savannahs, shrubby regions, and



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

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



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

that may be several kilometers from the waterholes. They sleep in both standing and recumbent positions and are fond of wallowing in muddy pools and sandy river beds. 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, 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 lifespan 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 Pleistocene in Europe, late Eocene to Recent in Asia, Miocene to Recent in Africa, and middle Eocene to Pliocene in North America (Carter 1984). However, this family is only part of a superfamily, the Rhinocerotoidae, which also contains two fossil families of rhinos and a total of over 50 known genera (Prothero, Manning, and Hanson 1986). The

extinct members of this group showed remarkable diversity in size and proportions; most lacked horns. Two genera of the Eurasian Pleistocene were *Coelodonta*, the woolly rhinoceros, and *Elasmotherium*, a huge animal with a single giant frontal horn. *Indricotherium* (= *Baluchitherium*), a hornless rhinoceros of the late Oligocene and early Miocene of Asia, was the largest known land mammal. It is estimated to have been 4–5 meters tall at the shoulder and to have weighed about 11,000 kg (Willoughby 1974).

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 10,000 rhinos survive throughout the world. There is much international interest in saving those that remain. Few other animals that occur over such large stretches of wilderness have been so well mapped and counted.

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 on 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, height at the shoulder 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 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) × 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



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

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 mountain top or a catchment area of a small stream. The surrounding area is cleared of vegetation for 10–35 meters and is used as a resting place. Wallowing is thought to be a cooling mechanism 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 over 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 individuals per 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; interbirth interval seems to be at least 3–4 years (Van Strien 1986). A captive specimen lived for 32 years and 8 months (Jones 1982).

The Sumatran rhino is classified as endangered by the IUCN and 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 num-

ber of individuals remaining in the wild was 536–962 and that there were another 16 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, now may be represented only by 6–7 animals in Burma. There appear to be only 30–50 survivors of *D. s. harrisoni*, the subspecies of Borneo. All the remaining animals belong to *D. s. sumatrensis*, there being about 100 in peninsular Malaysia and 400–700 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. They have a single horn on the nose, which 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

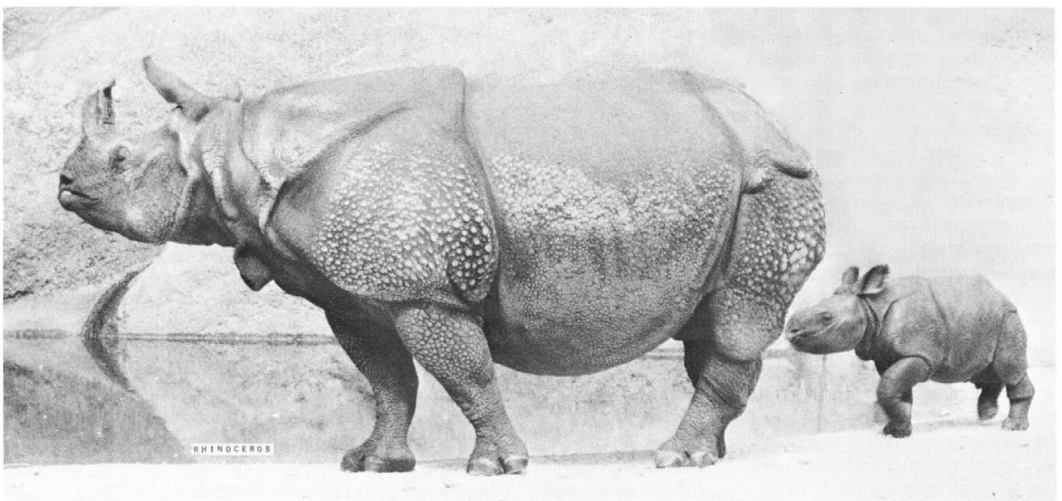
midline of the back. The skin is practically naked except for a fringe of stiff hairs around the ears and the tip of the tail. The skin of *R. unicornis* has large convex tubercles, whereas that of *R. sondaicus* is covered with small, polygonal, scalelike disks. Additional information for each species 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, height at the shoulder 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. 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 and perhaps as long as 2 years. Females reach sexual maturity at about 3–4 years, and males



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

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 50–54 individuals of *R. s. sondaicus* in Ujung Kulon National Park, at the extreme western tip of Java. 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. *R. sondaicus* is classified as endangered by the IUCN and 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, height at the shoulder 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. Wallowing and bathing occur in lakes, rivers, and pools; this behavior is especially frequent during hot seasons and seems to be important for thermoregulation and to escape 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 individuals per sq km have been found in some areas, and densities of up to 4.85 per sq km have been reached in favored high-diversity habitat of the

Chitawan Valley of Nepal (Laurie 1982). 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 to more than 8 sq km. There is some degree of range exclusivity but no true territoriality; the ranges of dominant bulls overlap with each other and with the ranges of nonbreeding males. Individuals usually take to sudden flight away 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, height at the shoulder is 56–67 cm, and weight is 40–81 kg. The calf suckles frequently up to 12 months of age and only rarely after 18 months. It is driven away at least one week before birth of the next calf, the interbirth interval being about 3 years. In the wild, females are full-grown at 6.5 years, and males at about 10 years. Females attain sexual maturity at 5–7 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 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 \$9,000 per kg in the mid-1980s. The retail price, after the horn has been shaved or powdered for sale, has at times and in certain East Asian markets reached \$20,000–\$30,000 per kg (Martin 1983; Martin, Martin, and Vigne 1987; Martin and Vigne 1987).

By contrast, in May 1990 pure gold was worth about \$13,000 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 Chitawan National Park, which has Nepal's largest rhino population, now is protected by 700 armed troops and rangers (Martin 1985a). Projects are under way both in India and Nepal to reintroduce breeding populations in areas of former occurrence (Mishra and Dinerstein 1987; Sale and Singh 1987). The sources of the animals for these projects are Chitawan in Nepal, now with about 375 rhinos, and Kaziranga National Park in India, with 1,080. *R. unicornis* now numbers 1,724 in the wild and about 75 in captivity (Khan 1989). 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, height at the shoulder 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. 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) $\times 2 = 24$.

The black rhinoceros is found mainly in the transitional zone between grassland and forest, generally in thick thorn bush 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 most important factor influencing distribution to be the presence of many natural, permanent water holes. According to Kingdon (1979), the black rhino frequents mud or water walls to counteract heat and flies and commonly rests and sleeps therein. Well-worn paths lead to such areas. Normal movement is around 3–4 km/hr, but a charge can reach 50 km/hr. Sleeping usually occurs at midday, while 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

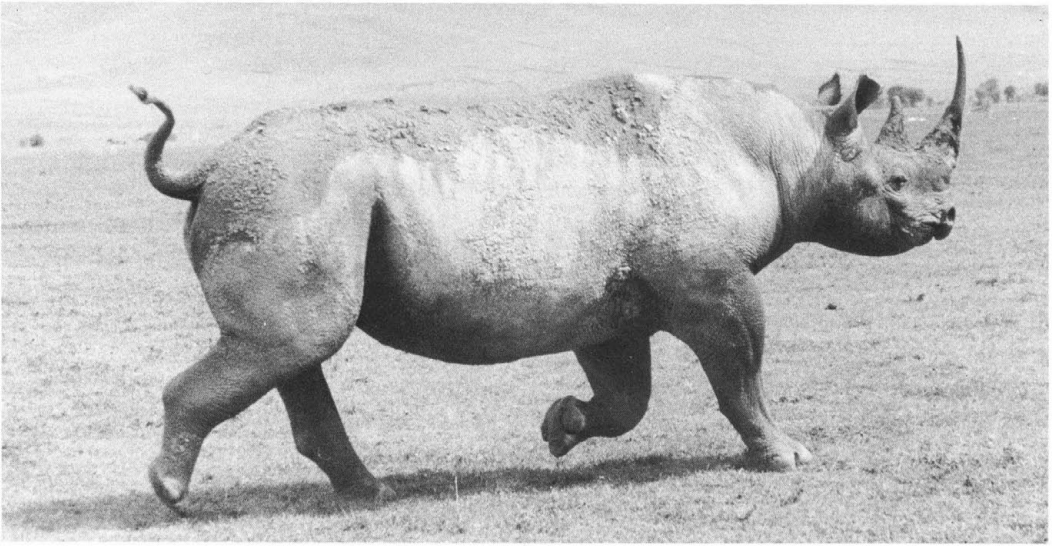
a favorite. Twigs are gathered with the prehensile upper lip, drawn into the mouth, and snapped off with the premolars. Drinking occurs every day if water can be reached, and mineral licks are visited regularly.

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. Up to 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 reported natural densities have been around 0.1–1.0 per 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 up to 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 the same for 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, the gestation period is 419–78 days, and there is a single calf weighing about 40 kg at birth. Weaning occurs after about 2 years, independence at 2.5–3.5 years, and reproductive maturity at 4–6 years in females and 7–9 years in males (Grzimek 1975; Hitchins and Anderson 1983; Jarvis 1967; Kingdon 1979). One black rhino still was living after 45 years in captivity (Jones 1982).

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



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

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 led to the disappearance of *Diceros* in most of Ethiopia and Somalia by the 1960s (Yalden, Largent, and Kock 1986). Nonetheless, in 1970 there were estimated still to be at least 65,000 black rhinos, with populations present in most countries of the original range. Over the next decade, however, there was increasing recognition 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 and then as endangered by the IUCN.

The subsequent 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 3,000, and there are approximately 200 in captivity. 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. There now are about 1,700 black rhinos in Zimbabwe, a few hundred each in Kenya, Namibia, South Africa, Tanzania, and Zambia, and a few dozen each in Cameroon, Malawi, and Rwanda. 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 North 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 North 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 North Yemen. Annual importation peaked in 1976 when over 8,300 kg entered the country. In 1982 the government banned importation. That measure had little initial effect, and, 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 continues, however, with several hundred kilograms entering North Yemen each year. Moreover, there is an established investment value for rhino horn jambias, and market potential remains high.

The most substantial ongoing problem for the black rhino is the demand for horn for use in traditional oriental medicines (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 and then fabricated into pills or mixed in potions and tonics. It has a wide variety of uses, including fever suppression. While it evidently is not used as an aphrodisiac in oriental countries, 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. The biggest importer for the last three years, and hence now the single greatest threat to the black rhino, is Taiwan (Vigne and Martin 1989). Although there has been a legal import ban since 1985, it is not enforced, and much horn enters, often by way of South Africa.

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 1989c). 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 1987–88 in East Asian markets the retail value of black rhino horn was around U.S. \$15,000–\$20,000 per kg, more than the price of gold (Vigne and Martin 1989). So great is the demand for horn for medicinal purposes that antique carvings are 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, is developing a conservation plan for the black rhino. Strategy centers on a concentration of effort to save the most significant remaining wild populations while simultaneously working to halt the trade and utilization of rhino horn. There 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; Foote 1987b). Groves (1967c) 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. brucii*, 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. Recent studies 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 (Du Toit 1987).

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 1972b; Kingdon 1979). The subspecies *C. s. cottoni* occurred in southern Chad, the



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.

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 proba-

bly covered much of northwestern Africa. Rock paintings and skeletal remains show that rhinos once occurred as far as coastal Morocco and Algeria, but there are questions as to species identity and time of latest survival.

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* (Groves 1972b). 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 1972b). 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 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 1972b; Kingdon 1979; Owen-Smith 1975).

Reported overall population densities vary from 0.03/sq km to 0.81/sq km (Groves 1972b), though local densities in favorable habitat may exceed 5.0/sq km (Owen-Smith 1981, 1984). Data obtained by investigations in Zululand (Kingdon 1979; Owen-Smith 1974; Smithers 1983) indicate that some adult males occupy territories of 0.75–2.60 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 up to 20 sq km in less favorable areas. These ranges overlap one another extensively and are not defended; each may overlap up to 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 up to 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 up to 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 between animals in an area. Territorial males have the habit of scattering their dung after defecation.

The following data on reproduction were taken from Groves (1972b), 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 shaky 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 of age, 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 under 100. Subsequent careful protection led to a growing population at Umfolozi, and adjoining reserves, that appeared to be in excess of available habitat. Numbers 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 1972b; Owen-Smith 1981; Smithers 1983). A recent count showed the existence of 4,404 southern white rhinos, including 4,062 in South Africa, 208 in Zimbabwe, 63 in Namibia, and 6 in

Zambia (Cumming and Du Toit 1989). Small groups introduced to Mozambique and Kenya (outside of the natural range) may have been eliminated by poachers. *C. s. simum* is on appendix 1 of the CITES.

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 1960s, rebounded to about 500 after government control was restored in the 1970s, and finally collapsed as poaching for horn intensified in the early 1980s. Populations in Sudan and the Central African Republic also disappeared during this period. Groves (1972b) had stated that a few individuals might survive in Chad, but they evidently were lost by 1980. By the latest count, there now are known to be only 18 northern white rhinos in the wild, all at Garamba (Cumming and Du Toit 1989). There are another 13 in captivity. *C. s. cottoni* is classified as endangered by the IUCN and the USDI and is on appendix 1 of the CITES.