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Rhinoceros unicornis.

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Rhinoceros Linnaeus, 1758

Rhinoceros Linnaeus, 1758. Type species *Rhinoceros unicornis* Linnaeus 1758.

Naricornis Frisch, 1775. Type species *Rhinoceros unicornis* Linnaeus, 1758. Not available (Bull. Zool. Nomencl. 1950, 4: 547).

Monoceros Rafinesque, 1815. Type species *Rhinoceros unicornis* Linnaeus, 1758. Not of Meusch, 1787 (Mollusca).

Unicornus Rafinesque, 1815. Type species *Rhinoceros unicornis* Linnaeus, 1758; not of Montfort, 1810 (Mollusca).

Eurhinoceros Gray, 1867. Type species *Rhinoceros javanicus* Geoffroy-St. Hilaire and Cuvier, 1824 (= *R. sondaicus* Desmarest, 1822).

Monocerorhinus Wüst, 1922. Type species *Rhinoceros sondaicus* Desmarest, 1822.

CONTEXT AND CONTENT. Order Perissodactyla, Suborder Ceratomorpha, Family Rhinocerotidae, Subfamily Rhinocerotinae. The genus includes two species, the present one and *R. sondaicus* Desmarest, 1822.

Rhinoceros unicornis Linnaeus, 1758

Indian Rhinoceros

Rhinoceros unicornis Linnaeus, 1758:56. Type locality Bengal.

Rhinoceros indicus G. Cuvier, 1817: 239. Type locality India.

Rhinoceros asiaticus Blumenbach, 1830:107. No locality given.

Rhinoceros sivalensis Falconer and Cautley, 1847: pl. 73, fig. 2, 3; pl. 74, fig. 5, 6; pl. 75, fig. 5, 6. Type locality Upper Siwaliks; fossil.

Rhinoceros palaeindicus Falconer and Cautley, 1847: pl. 73, fig. 1; pl. 74, fig. 1–4; pl. 75, fig. 1–4. Type locality Upper Siwaliks; fossil.

Rhinoceros stenocephalus Gray, 1867:1018. Type locality "Asia."

Rhinoceros namadicus Lydekker, 1876:32. Type locality Narbada Beds; not of Falconer, 1868; fossil.

Rhinoceros jamrachii Sclater, 1877*a*:650. Type locality Munipore district (Manipur).

Rhinoceros kendengindicus Dubois, 1908:1259. Type locality Kedon Duren, Java (Trinil beds, Lower or Middle Pleistocene); fossil.

Rhinoceros kagavena Deraniyagala, 1958:122. Type locality Kuruvita Gem Pit, 20′, at Hiriliyadda, Talavitiya; fossil.

Rhinoceros barinagalensis Srivastava and Verma, 1972:77. Type locality Pinjor beds (Lower Pleistocene), near Chandigarh, India; fossil.

CONTEXT AND CONTENT. Context as above. The living species is monotypic, but certain Pleistocene representatives are distinguishable at the subspecific level. The type of *R. jamrachii* was originally referred by Sclater (1877*a*) to *R. sondaicus*, but in a later publication (Sclater, 1877*b*) he re-identified it, on the basis of personal examination, with the present species. The Indian rhinoceros is the type species of the genus *Rhinoceros* (Pocock, 1944*a*).

DIAGNOSIS. *Rhinoceros* differs from other genera in having: single, nasal horn; incisors and lower canines present, large; dental formula i 1/1, c 0/1, p 3/3, m 3/3, total 30; deciduous dentition having dp1; cheekteeth subhypsodont; protoloph on upper premolars fully formed (Guérin, 1980); medisinus of upper molars of approximately equal depth to postsinus (for figures illustrating these terms, see Groves and Kurt, 1972, fig. 3); crochet of upper molars springing from apex of metaloph; M3 triangular, without metacone bulge; skull short, with occipital plane inclined forward making dorsal profile strongly concave; orbitoaural length greater than orbitonasal; infraorbital foramen above P2, posterior edge of nasal notch over P1 position, anterior border of orbit over P4; auditory meatus closed inferiorly by fusion of postglenoid and posttympanic processes; vomer longitudinally ridged (Guérin, 1980; Pocock, 1945*a*; C.P.G., pers. observ.). Lacrimal bridge is usually ligamentous and antorbital process ovate (Cave, 1965). Skeletal forelimb length (humerus + radius + metacarpal III) is less than hindlimb (femur + tibia + metatarsal III): like *Dicerorhinus* but unlike African rhinoceroses. Bicipital groove of humerus is wide and shallow, bounded laterally by enlarged, medially hooked *tuberculum majus*. Femur has enlarged, laterally-pointed greater trochanter and broad, quadrangular third trochanter. Fibular head is confined beneath a shelf of the tibia, not articulating with femur (unlike African rhinoceroses). Trochlear surface of talus (astragalus) is low and long (Guérin, 1980; C.P.G., pers. observ.). Skin-folds are marked, including scapular, pelvic, humeral, femoral, and subcaudal folds; hairy covering reduced but often visible even in adult. *Processus glandis* of penis is located on either side of dorsum of glans, with relatively long sessile antero-posterior attachment to glans, and with long narrow projection laterally (Cave, 1964). Large free villi are present in small intestine (Garrod, 1878). Pedal scent glands are present (Cave, 1962).

The species *Rhinoceros unicornis* is diagnosed as follows: skull heavy, basal length above 600 mm; toothrow length above 241 mm; nasals rugose, their breadth rarely below 110 mm; occiput high, above 190 mm; premaxillae broad, united to maxillae from maturity; vomer thick, firmly united to sides of pterygoid processes; cheekteeth hypsodont, crown height of unworn M1–2 58 to 72 mm (Colbert and Hooijer, 1952); index of hypsodonty (=height as percent of length) of unworn P3–4 is 121.5 to 139.0 (Guérin, 1980); parastyle buttress not pronounced; ectoloph flat; crista generally well developed, uniting early with crochet; protocone fold present; cingulum absent; skin-folds heavy; subcaudal fold almost meets pelvic; posterior cervical fold nearly always maintains a horizontal course, failing to meet scapular fold; epidermal polygons well separated, raised, rivet-like; intestinal villi long, cylindrical, narrow; caecum and colon broad, elongate (Owen, 1862).

GENERAL CHARACTERS. *Rhinoceros unicornis* is a heavily built species; weights of two adult females were 1,599 and 1,608 kg, and three adult males weighed 2,070 to 2,132 kg (E.M.L., records from Basel Zoo; Owen, 1862). Average measurements are: head and body length, 4,120 mm; girth, 3,960; height of females, 1,625.0 (range 1,470 to 1,730, n = 11); height of males, 1,754 (range 1,630 to 1,930, n = 9; Anon., 1909; Owen, 1862; Sclater, 1872; authors' data). Nasal horn slightly back-curved; maximum length in British Museum material was 529 mm (straight), but W.A.L. measured a "trophy" horn in Assam which was 572 mm; Neuville (1927) mentioned one measuring 800 mm along the curve, but the specimen appears to C.P.G. to be a *Ceratotherium simum* horn sewn into a skin of *R. unicornis*. Base of horn is approximately

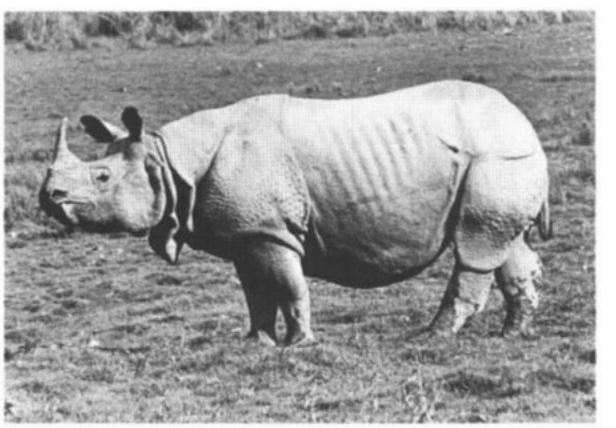

FIGURE 1. Adult male of *Rhinoceros unicornis* in Kaziranga National Park, India (photo by W.A.L.).

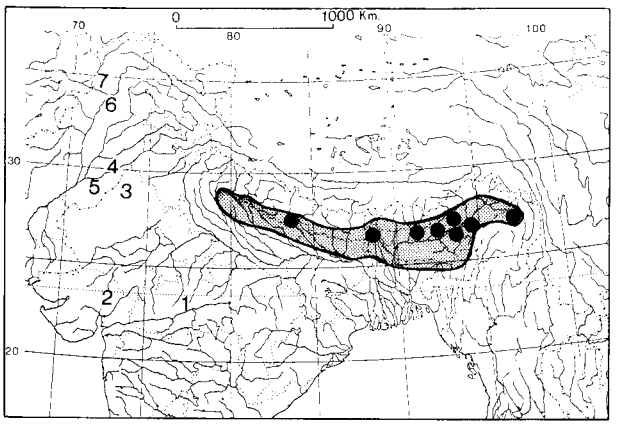

FIGURE 2. Map of known past and present distribution of *Rhinoceros unicornis* (Pleistocene records from Java and Sri Lanka excluded). Stippled: distribution as recorded in 19th century (Laurie, 1978). Black dots: known present occurrence (see text). 1, Bhimbetka (Mathpal, 1978); 2, Lothal, Ahmedabad district (Banerjee and Chakraborty, 1973); 3, Kalibangan, Ganganagar district (Banerjee and Chakraborty, 1973); 4, Banda district (Mukherjee, 1966); 5, Harappa (Mukherjee, 1966); 6, Hashnagar (Banerjee and Chakraborty, 1973); and 7, Peshawar (Rao, 1947) (see text).

185 by 120 mm, rapidly narrowing until smooth, even stem part (90 by 80 mm) begins approximately 55 mm above base of horn. Breadth of stem is 55 to 75% of breadth of base; base is roughened, irregularly grooved, but with a well-marked deep groove running up the front. In captive animals, the horn is worn down to a thick knob, or into an abnormal shape: Sclater (1877*a*) recorded one in London Zoo in which the horn grew forward, 46 cm in front of the nose.

Color of hide is grey-brown, becoming pinkish in skin-folds; horn is black (under natural conditions). Epidermal knobs are prominent on body, especially near folds. The posterior cervical fold sometimes crosses the shoulder as in *R. sondaicus* (W.A.L., observations in Chitawan and Kaziranga). Male shows enormous development of neck-folds ("bib" of Laurie, 1978). Presence of visible body hair has been denied (Cave, 1969), but occasionally may be apparent (Groves, 1967); eyelashes, ear-fringes, and tail-brush are always present.

Captive individuals do not always represent the true appearance of the wild animal. Good photographs taken under natural conditions, in color and in black-and-white, such as those in Ullrich and Ullrich (1964), should be sought for a true impression (also see Fig. 1).

DISTRIBUTION. Nowadays *R. unicornis* is confined to Nepal (Chitawan Valley) and India (states of Assam and West Bengal), with a few stragglers in northernmost Burma (Fig. 2). Banerjee and Chakraborty (1973) listed remains from metal-age deposits in Gujarat and Rajasthan. A rockpainting of a rhinoceros occurs in an apparently Mesolithic (about 8,000 to 3,000 B.P.) context at Bhimbetka, near Bhopal, Madhya Pradesh (Mathpal, 1978). Mukherjee (1966) mentioned subfossil remains from Banda District, Pakistan, and that its remains occurred at Harappa (4,500 to 1,500 B.C.); the age of remains from the Madras region is uncertain. In the early Moghul period, the species still extended as far west as the Punjab foothills, Peshawar, Sind, and the lower Indus (Rao, 1947); in modern times it has been known mainly from the Terai. Manners-Smith (1909) detailed its former distribution in Nepal; Rookmaaker (1980) detailed the former distribution in Eastern India and Bangladesh, and discussed records from China and Indo-China. A presumed specimen was shot in Namlang district, Putao subdivision, Burma, in 1956 (U Tun Yin, 1956), and in February 1962 about six to eight individuals were discovered on the lower slopes of Bumpha Bum, Sumprabum subdivision, Myitkyina district (U Tun Yin, 1967).

Laurie (1978) gave a summary of the status of this species in the mid-1970s as follows: (1) ASSAM. Kaziranga, 600; Laokhowa Reserve, "less than 50"; Orang, 25–30; Manas, 40; Sonai Rupai, 15; elsewhere, about 25. (2) WEST BENGAL. Jaldapara, 30–40; Goru mara, 5. (3) NEPAL. Chitawan, 270–310. The figures for Kaziranga and Chitawan in 1982 have increased since this census was made.

FIGURE 3. Skull of *Rhinoceros unicornis*, old male (B.M.61.5.10.1), from London Zoo. The abnormal form of the horn is a common consequence of wear seen in zoo specimens (photo by C.P.G.).

FOSSIL RECORD. Most known fossil remains of *R. unicornis* appear to be of Pleistocene date, probably Middle Pleistocene. The direct precursor of the living Indian rhinoceros was *R. u. fossilis* Baker and Durand (synonyms *sivalensis* and *palaeindicus* Falconer and Cautley), from the upper Siwalik beds, within the known historic range of the species. *R. namadicus* Lydekker from the Narbada or Narmada beds is probably synonymous with *R. u. fossilis*. Hooijer (1946) showed that *R. kendengindicus* Dubois from Java was closely related to the present species and should probably be regarded as a subspecies of it; *R. u. kendengindicus* occurred in the Djetis and Trinil beds alongside *R. sondaicus*, but has not been found in the Upper Pleistocene Ngandong deposits where the latter is the only rhinoceros. The unexpectedly wide Pleistocene range of the species has been confirmed by the discovery of *R. kagavena* in the Ratnapura fauna of Sri Lanka, which is undated but probably Middle Pleistocene (Deraniyagala, 1958). This form shows few characters to differentiate it from *R. unicornis*, and like the Javanese fossil occurs alongside a race of *R. sondaicus*. Holocene remains of *R. unicornis* from Rajasthan, Gujarat, and Pakistan (dating 2500 to 1200 B.C.) are mostly larger than their modern, more easterly counterparts (Banerjee and Chakraborty, 1973).

The various fossils of this genus from China can be referred to two species: the Pleistocene *R. sinensis* Owen, which though in many respects is intermediate between the two living species, shows progressive characters linking it to *R. unicornis* (Colbert and Hooijer, 1952); and the Upper Pliocene species *R. oweni* Ringstrom, which was placed in a separate genus *Sinorhinus* by Kretzoi (1942). Colbert (1942) traced the lineages of the living species.

FORM AND FUNCTION. The integument is insufficiently studied, and its histological structure is unknown; Cave (1969) denied the presence of body hair, and found no follicles on the metatarsal region, but see Groves (1967). Skin is covered with rivet-like knobs. The horn is developed from an area of hyperkeratinization on the snout; other such areas, which are presumably potential horns, may occur on the face (Neuville, 1927), and even a rudimentary frontal horn has been recorded and figured (Hill, 1958). Forefeet and hindfeet have scent glands. Each gland has a distensible orifice 5.5 to 7.5 mm above the sole pad, hidden in a transverse fold opposite the metapodial-autopodial articulation; 38 to 48 by 23 to 26 mm broad with a wall 8 mm thick, which is highly vascularized (Cave, 1962; Owen, 1862). There are two inguinal mammae (as in all rhinoceroses).

Premaxillae are short and stout and tend to fuse early across midline and with maxillae (Pocock, 1944*b*). Nasal septum never shows tendency to ossification (Pocock, 1945*a*). Skull (Fig. 3) is larger and heavier than that of *R. sondaicus*; nasal boss is more expanded, rounded, and rugose especially in male; occiput high, narrow, making dorsal outline of skull very concave; seen from behind, sides of occiput suddenly steepen, so crest is flat-topped; posterior margin of palate is concave or with a small median projection; basilar bones are narrow, pterygoids compressed; vomer is thick and united to pterygoids; mesopterygoid fossa is relatively narrow and deep (Colbert, 1942; Pocock, 1945*b*). Lacrimal bridge

is ligamentous in 93% of skulls (Cave, 1965). Ascending ramus is high. Teeth are hypsodont; height of unworn P3 exceeds breadth; ectoloph is relatively flat, with little parastyle buttress; crista is present, but may be small on M2, unites early with crochet to enclose a medifossette; postfossettes tend to form early in wear; postsinus as deep as medisinus; a protocone fold is present; paracone and protocone are separated by a fossa in unworn teeth; protocone is inclined backward; there is no tubercle, or cingulum remnant, at entrance to valleys. Lower canines huge, tusklike; lower incisors small, peglike. The following values are based on four specimens: length of radius is 80.5(77 to 85)% of that of humerus, tibia 73.5(72 to 75)% of femur, humerus 87.3(84 to 92)% of femur, tibia 104.0(102 to 107)% of radius, total forelimb 93.3(93 to 94)% of total hindlimb, humerus 76.8(71 to 81)% of basal skull length, metacarpal III 51.8(50 to 55)% of radius. Numbers of vertebrae are: T 19 (to 20), L 3 (to 4), S 6, C 17 to 22. Spines of T 1 to 4 raised evenly, suddenly decreasing anteriorly to C 7, gradually decreasing posteriorly to T 10; there is a very slight rise in lumbar spines; there is no anticlinal vertebra, although L 3 somewhat approaches this condition. Ischial tuberosities are expanded and angular.

The heart weighed 12.7 kg in an old male (Owen, 1862). W.A.L. weighed the heart of an adult female in Chitawan at 10 kg. Lymph nodes are of hemolymph type; submandibular node is highly vascularized, completely lacking cortico-medullary differentiation (Cave and Aumonier, 1964).

The brain was described by Owen (1862), and briefly compared to that of *Dicerorhinus sumatrensis* by Garrod (1878). Convolutions of cerebral hemispheres are less complicated than in the latter species.

The alimentary canal is seven to eight times head and body length. Stomach of an old male was 122 cm long, straight, 56 cm in diameter; the lesser curvature was 53.5 cm long. Bile duct enters duodenum 15 cm from pylorus; villi begin to appear thereafter; villi are long, narrow, cylindrical; Peyer's glands are present. Caecum was 91.5 cm long, broader than long. Colon was arranged in two folds, 5.8 to 7.6 m long. Liver weighed 9.5 kg in a young female, 20 kg in an old male (Owen, 1862).

Owen's (1862) description of the seminal vesicles was disputed by Beddard and Treves (1887), who considered it probable that their anatomy is as in *R. sondaicus*—tubular and slightly bulbous. Penis in an old male was 114.3 cm long; it had a lobular *processus glandis* and a long medial attachment to the glans penis and free lateral border; uterine horns in a young female were 43.2 cm long, corpus 4 to 5 cm (Cave, 1964; Owen, 1862).

Full-term placenta is bicornuate, one horn being longer and wider than the other. Villi are distributed over entire chorion except for certain strips along the larger vessels of the allantochorion. Two types of villi occur: foliate, similar to those of the Equidae, and plicate, which resemble the areolae of Bovidae (Dolinar et al., 1965). Foliate villi possess diplokaryons on the epithelium, with many mitochondria and well-developed ergastoplasm. In epithelial plate area there are many pinocytotic vessels (Ludwig and Villiger, 1965). The placenta weighs 5 kg (E.M.L., pers. observ.).

Only the parathyroids have been described (Cave and Aumonier, 1966) for the endocrine system. Parenchyma of parathyroid glands are in rounded cell-clusters. An 18-year-old male had four glands, one dextral (embedded superficially in corresponding thyroid lobe) and three sinistral in cranio-caudal sequence.

Jones (1979) gave a long list of blood values. All figures compare well with those for African rhinoceroses, but the red cell count is above that for *Diceros bicornis* and the mean cell volume and chloride concentration are lower, both being comparable to the values for *Ceratotherium simum*. Hemoglobin concentration, blood urea, and protein level are lower than those of *Ceratotherium simum*, but are comparable to those of *Diceros bicornis*; vitamin A and platelet levels are lower than those for African species.

ONTOGENY AND REPRODUCTION. A female in Mysore Zoo came into estrus every 21 to 33 days ($\bar{X}$ = 24; Gowda, 1969); in the wild, estrus occurs every 27 to 42 days (Laurie, 1978). Permanent anestrus in a captive female appeared to be connected with presence of leiomyomas in the uterine and vaginal walls (Jones, 1979). Gestation varied from 462 to 491 days; mean of 31 records, 479 days (E.M.L. collected records). Twin calves "about three years old" have been reported (Gee, 1956); this must be regarded as suspect, because subadults often join up with cow-calf pairs. Sex ratio at birth is 1.19 males to 1 female (Lang et al., 1977).

Birth is rapid, usually occurring about 30 minutes after the first signs of labor. Females may either lie or stand during parturition. Calves arrive either head or hindfeet first. After the birth, the mother turns round very swiftly to make nasal contact with the calf, tearing the umbilical cord. The neonate is not licked. The placenta is usually eaten.

The calf rises to its feet within about 30 min, and at once tries to suckle. Calves are suckled frequently up to the age of one year and only rarely after the age of 18 months. They are separated from their mothers at least a week before the birth of the next calf; sometimes the cow drives away her calf violently. Male calves leave their mothers at a mean age of 39 months compared with 34 months for female calves (Laurie, 1978).

At birth calves weigh 40 to 81 kg (mean of 20, 71.3 kg, E.M.L., pers. observ.). At birth head and body length ranges from 96.5 to 122 cm, shoulder height is 56 to 67 cm (Chowdhury, 1966; Gee 1953; Gowda, 1969; Hagenbeck, 1966, 1969). Birth weight is 4.4% of maternal; height at birth is 37% of adult female's. Initial rate of growth in captivity is 2 to 3 kg/day. The calf doubles its birth weight in one month; at one year of age it reaches ten times birth weight. (All these data refer to captive specimens.)

Young skulls, with their full complement of milk teeth, are 60 to 65% of the basal length of adult skulls, and when first molars begin to emerge, 78 to 82%. Relation between occipitonasal and basal lengths remains approximately constant at 90 and 92% throughout growth period, but relative zygomatic breadth decreases from 63 to 54% (at time of eruption of first molars), increasing again to 58 to 60% in adult. Nasal breadth in females reaches 99% of adult value by the time the first molars emerge, but in males reaches only 77% of adult value by this time—a reflection of the different horn sizes of the two sexes. Anterior premolars are shed early in adult life (dp1, lower) or during early juvenile stage (dP1, upper).

Growth in the wild is noticeably slower than under the best captive conditions. A 4-month-old calf found dead in Chitawan weighed 158 kg, only half the weight of a Basel Zoo calf at a similar age. In the wild, calves under 1 year old are less than 1 m high; under 2 years, up to 1.2 m; under 3 years, up to 1.35 m; under 5 years, up to 1.45 m, but in the Basel Zoo a 21-month-old female was already 1.36 m high, and a 33-month-old male was 1.57 m.

Females are fully grown at 4 years in captivity, but not for about 6.5 years in the wild, and males at 8 years in captivity, but about 10 years in the wild. Full growth is thus achieved much earlier than in African rhinoceroses, *Diceros* and *Ceratotherium*.

Sexual maturity is not, or not much, accelerated by captive conditions (Dittrich, 1976). Females begin estrous cycles at about 4 years (Jones, 1979) but do not usually conceive until at least a year later; in Chitawan, females have their first calves at 6 to 8 years ($\bar{X}$ = 7.1). Physical maturity therefore coincides with the initiation of estrous cycles in captivity, but with the onset of fertility in the wild.

Record longevity in captivity is 47 years; three others have lived over 40 years in captivity (Reynolds, 1960).

ECOLOGY. Indian rhinos are found throughout their present range in alluvial plain habitats: riverine grasslands with grass up to 8 m tall and swampy areas with *Arundo, Phragmites, Themeda, Saccharum* and *Narenga*, bordered by riverine woodlands (*Trewia, Bombax, Syzygium, Acacia* and *Dalbergia* communities) or, in parts of Nepal and Assam, by drier sal (*Shorea robusta*) or *Terminalia* forest. The great reduction in the range of the Indian rhino over the last 300 years was caused primarily by the disappearance of most of the alluvial plain grasslands of the northern Indian subcontinent. By the middle of this century rhinos were largely restricted to reserves and their survival depended upon efficient legal protection. The small sizes of the present reserves mean that rhinos are within easy reach of and regularly feed in cultivated land and in woodland areas transformed by human activity and by domestic stock into short grassland with scattered trees and scrubby undergrowth. The alluvial plain habitats are characterized by rapid and very marked seasonal changes in weather and vegetation. Fires, the annual monsoon floods, and frequent changes in river courses maintain a high diversity of early successional vegetation stages on the valley floors, and human activity and stock-grazing increase the habitat diversity where the protected areas border on arable or grazing land.

Diet and ranges.—In Chitawan (Nepal) rhinos fed from 183 species of plants belonging to 57 families, but grasses (mainly *Saccharum, Narenga* and *Cynodon*, but 53 species in all) made up between 70 and 89% of the diet according to season (Laurie, 1978). Other foods included fruits, leaves and branches of shrubs and trees (e.g., *Trewia, Callicarpa, Litsaea*), sedges and ferns (e.g., *Cyperus, Scleria, Pteris*), submerged and floating aquatic plants (e.g., *Hydrilla, Vallisneria, Commelina*), and agricultural crops (e.g., *Oryza, Zea*). Considerable seasonal variations in food avail-

ability result in movements of rhinos between vegetation types. Ranges were smallest in the regions of greatest vegetational diversity, with areas varying from 2 to over 10 km² (Laurie, 1982).

Interspecific relationships.—Tigers (*Panthera tigris*) prey on young calves up to the age of 6 months or possibly more (Laurie, 1982); W.A.L. also has one record of an unsuccessful attack on an adult by two tigers. Otherwise the only predation is by humans. Indian rhino have been hunted both for sport (Cooch Behar, 1908; Pollok and Thom, 1900) and for the horn and certain other parts of the body, which are reputed to have powerful magical or medicinal properties in many countries of south, southeast, and eastern Asia. In 1979 the retail price of Indian rhino horn in Taiwan and Hong Kong rose to US$18,000/kg (Martin, 1980).

Mynahs (*Acridotheres tristis*) and egrets (*Bubulcus ibis*) feed on invertebrates on the rhino's skin or around its feet. Rhinos are bitten by bloodsucking *Tabanus* flies.

Population structure.—Apart from cow-calf pairs, Indian rhinos rarely form groups; there were only 15% of sightings in Chitawan (Laurie, 1982) in other types of group. Only seven groups consisted of more than three individuals and the most common type of group was two or three subadults, especially subadult males, which had recently left their mothers. The largest group recorded in Chitawan was of six subadults. Adult males are usually solitary, but they sometimes occur in temporary associations of up to nine rhinos of various sex and age classes. These groups form at wallows and grazing grounds where animals often feed or rest together but move independently of each other. The population composition in Chitawan was reported as 32% adult females, 20% adult males, 21% subadults, and 27% calves, so the overall adult sex ratio was 61 males to 100 females (Laurie, 1982). The adult sex ratio varied locally in Chitawan and Assam from 52 to 92 males per 100 females (Laurie, 1978); sex ratio at birth, however, was 119 males to 100 females (see above, under Ontogeny and Reproduction). Both the Kaziranga and Chitawan populations are increasing, possibly by as much as 5% per year. Crude population densities vary from 0.4 to 1.8/km² in Nepal, but reach more than 2.0/km² in Kaziranga, Assam.

Disease.—Parasites include leeches, ticks (*Dermacentor auratus*), and gut nematodes (*Decrusia*) (W.A.L., pers. observ.).

Anthrax and hemorrhagic septicemia both occur; the latter was responsible for the deaths of 15 rhinos in Kaziranga in 1974. As the populations of both Kaziranga and Chitawan are increasing and there are no alternative refuges for the rhinos, there are dangers in the future of facilitated epidemics. In captivity, rectal prolapse and intestinal torsion have been recorded; excessive feeding on kale causes hemoglobinuria (Jones, 1979).

Conservation.—The already depleted populations of rhinos were hunted relentlessly in India during the nineteenth and early twentieth centuries. Butler (1847) considered that every military officer in Assam became "a keen and skilful sportsman," and some men shot more than 200 rhinos during their careers. Just after the turn of the century the government became concerned at the rapid decline in numbers of rhino and prohibited all rhino hunting in India in 1910. A number of reserves were created but illegal poaching still continued as the price of rhino horns increased. The rhino survived because of the efforts of West Bengal and Assam Forest officers; the population in Kaziranga has increased from an estimated 12 individuals in 1908 to 600 in 1975 and more than 750 in 1980. The Nepalese populations were well protected prior to 1950 in hunting reserves where the ruling family organized lavish hunts and dealt severe penalties for poaching. In the 1950s, however, a resettlement program destroyed large areas of rhino habitat, and poaching was rife for a while. The rhino was almost wiped out in Nepal at this time, but stricter protection of both habitat and the animals was enforced during the 1960s and led to the establishment of the Royal Chitawan National Park in 1973.

Rhinos are still threatened by poaching and human encroachment on their habitat, but there are now additional threats which stem from the concentration of the few remaining rhinos into a small number of tiny reserves and national parks. More than 1,200 of the estimated 1,500 surviving rhinos live in two parks with a total of 500 km² of suitable habitat. Any catastrophe, such as an epidemic disease, severe flooding, or a breakdown in law and order could drastically deplete the total rhino population. Furthermore, in these small patches of alluvial plains there is a danger that changes in the courses of the rivers could result in vegetational succession proceeding to a climax condition unsuitable for early successional species such as the rhino. There are plans, therefore, to reintroduce rhinos to protected areas within the former range of the species in India and Pakistan.

Captivity.—There are several reports of Indian rhinos being tamed, and even trained for work. Schenkel and Lang (1969) quoted early accounts of rhinos being used to pull ploughs in Assam and there are also reports that rhinos were used in war by the ancient kings of India (Guggisberg, 1966). Butler (1847) wrote that tamed rhinos were often grazed with domestic cattle in Assam during the early nineteenth century. Pollok and Thom (1900) reported that a washerman in Gauhati had a tame rhino that carried the laundry on his delivery rounds. Recent experiences in zoos (Lang, 1961) and circuses (Reynolds, 1960) confirm that Indian rhinos can be tamed and trained, but they can also be dangerous and unpredictable.

The first recorded captive birth was in Kathmandu in 1826 (Hodgson, 1834) and the next was in Calcutta in 1925 (Gee, 1953). Successful breeding was not achieved in Europe until 1956 (Lang, 1961), but there have been nearly 40 births in zoos since then and much has been learned about the reproductive and maternal behavior of the Indian rhino in captivity (Buechner and Mackler, 1975; Buechner et al., 1975; Lang, 1961, 1967; Mackler, 1975). Indian rhinos have been captured in the wild with pit-traps, lassos, and immobilizing darts with the drug etorphine hydrochloride (M99).

BEHAVIOR. Indian rhinos are active mainly at night, in early morning, and in the late afternoon. The middle of the day is mainly spent resting, either in the shade or in wallows (Laurie, 1978). During the monsoon this pattern changes slightly; there are cool, wet days when rhinos feed at mid-day. Crop-raiding takes place exclusively at night—much later during moonlit nights than moonless or cloudy nights. Less time is spent feeding during the monsoon (36%) than during the spring (65%) and winter (57%) (Laurie, 1978). There is often a rest period during the night, between midnight and 0300 h.

Territoriality.—There is some degree of range exclusivity among breeding bulls but no true territoriality. Only certain "strong" males mate with females, but their ranges overlap with those of both "weak" males, which do not display (see below), and with known, neighboring "strong" males. The rapidly changing distribution of food sources and hence of females possibly precludes year-round defense of a small territory as in *Ceratotherium simum* (Owen-Smith, 1975). Ranges of breeding males in Chitawan varied from at least 2 to more than 8 km².

Communication and vocalization.—Indian rhinos use 10 distinct vocalizations. The main ones are the Snort, used as an initial contact call; the Honk, Bleat, and Roar, used during prolonged agonistic interactions; the Squeak-pant, uttered most frequently by males during prolonged chases after females or other males; and the Moo-grunt, used by calves as a contact call with their mothers (Laurie, 1978). Olfactory communication is important. Scents are carried in the urine, the dung, and the pedal scent glands (Cave, 1962). All age and sex classes defecate on communal dung piles and commonly sniff them before defecation. Adult males display by squirting urine in jets behind them and dragging their hind toes at the same time, creating long parallel furrows in the earth (Laurie, 1982). There are frequent reactions to scents on the ground. Flehmen is performed by all age and sex classes, predominantly by adult males in response to the tracks or urine of female rhinos, but also by subadults in response to the tracks or urine of adult males (Laurie, 1982). The emphasis in visual displays appears to be on the head-on view of the neck folds and bib and the large tusks in the lower jaw.

Ingestion.—When feeding on tall grasses Indian rhinos use the prehensile upper lip to curl around the grass stems, then bend the stems over, bite the tops off and chew them, drawing the tips into the mouth from the side. In very tall grass rhinos often walk forward with the stems, or canes, between their legs, pushing the stems down and grazing from the tips before walking on. The same method is used when browsing on saplings, and often brings foliage within the reach of an accompanying calf. Short grasses and herbs are grazed close to the ground using the lips; the tip of the prehensile upper lip is curled back into the mouth and opposed against the lower lip. Plants are often uprooted, the foliage bitten off and the roots dropped again. Aquatic plants are taken by ducking the head beneath the water, sometimes to the level of the feet and a meter or more below the water surface (Laurie, 1978).

Rhinos drink daily from streams, rivers, lakes, puddles, or wallows. Drinking normally lasts a minute or two; the lips are immersed but the animals pause at intervals with head lifted. Rhinos often drink very dirty water heavily contaminated with rhino urine. They lick or eat soil or rock material at various sites at Chitawan (Laurie, 1982); the most frequently visited site, a cliff of micaceous sandstone, contained sodium, potassium, calcium and magnesium in particularly high concentrations.

Wallowing.—Rhinos wallow in lakes, rivers, and temporary pools. In Chitawan they wallowed most frequently between June and

October (51% of observations) and least frequently between December and March (4% of observations; Laurie, 1978). Heat regulation is probably a major function of wallowing, but escape from *Tabanus* flies, especially in tall grasslands during the monsoon, may also be important.

Defensive behavior.—When alarmed rhinos normally take to sudden flight, running swiftly away from the source of disturbance, sometimes snorting or honking as they go. On some occasions, particularly when cows with young calves are disturbed at close quarters, the rhino charges head down towards an intruder, usually veering off to one side at the last moment, or stopping, turning round, and running off. Occasionally, however, charges are carried through; several human deaths are reported annually from Nepal and India as a result of attacks by (mainly cow) rhinos.

Interactions between individuals.—Two rhinos, normally members of the same group, often lie together with their flanks touching, or rest their heads on each others' flanks. Prolonged licking of skin of a companion, mostly by subadults and calves, typically occurs in wallows. In Chitawan, cows spend 11% of their time in physical contact with their calves; subadults and adult males spent 8% and 1% of their time, respectively, in physical contact with other rhinos (Laurie, 1978).

Play and peaceful interactions between subadults and between cows and calves include nuzzling, spells of running and gamboling around a companion, head bobbing and waving, and playful horn-to-horn sparring contests (Laurie, 1978). When rhinos of different groups meet there are frequently brief agonistic interactions. These normally result in the flight of one or more of the rhinos after initial displays, which include curling back the lips to show the lower tusks, advancing slowly towards the antagonist, or charging with head down. In Chitawan (Laurie, 1982), 37% of agonistic interactions escalated to some kind of horn-to-horn confrontation, resulting, in extreme cases, in horn clashes and lunges with the lower tusks to the neck, flanks, and rump of the opponent. If the opponent turns to flee a prolonged chase can develop. Adult males sometimes chase other adult males or adult females over several kilometers. These chases, which are accompanied by loud vocalizations, can result in severe injuries being inflicted.

Reproductive behavior.—Mating takes place throughout the year. An adult male locates an estrous female by following her tracks, sniffing the ground intently from time to time and performing flehmen. He accompanies her intermittently for several days, she usually repelling his advances by simply turning and snorting. Horn-to-horn confrontations eventually develop and often result in severe fights or prolonged chases (Laurie, 1982) with loud vocalizations by the female. Severe tusk wounds are often inflicted on the female.

The mating ceremony itself begins with a chase lasting about 1 h (aggressive phase), followed by the two quietly standing together, or sometimes even by symbolic suckling (cow at bull) of from 1 to 3 h (peaceful phase). Both constantly squirt-urinate, accompanied by rhythmic squeak-panting. Mounting is usually achieved only after several attempts, the bull initially resting his head on the rump of the cow. Copulation lasts up to 1 h or more. Females grow aggressive shortly after parturition and choose secluded areas to give birth.

Up to the age of 6 months calves are left alone for periods as long as 90 min while their mothers feed up to 800 m away.

GENETICS. The diploid chromosome number is 82; there are 80 major autosomal arms. The karyotype differs from that of *Ceratotherium simum*, which has the same diploid number, in having more subtelocentric and fewer telocentric chromosomes (Wurster and Benirschke, 1968).

There is a clear-cut polymorphism in the occurrence, in a very few individuals, of a posterior cervical skin-fold resembling that of *R. sondaicus*, that is, running over the withers from side to side. One individual with this morph was a calf whose mother had the normal condition.

The descent of the present healthy, 750-strong Kaziranga population from a dozen or so (in 1908) appears to have had no adverse genetic effects.

REMARKS. This species of rhinoceros was the first to be exhibited alive in Europe during post-Roman times: in 1515, the specimen from which Albrecht Durer made his well-known woodcut (Rookmaaker, 1973).

Other vernacular names for the species are great Indian rhinoceros, greater one-horned rhinoceros, Panzernashorn, and gainda.

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