

MAMMALS OF AFRICA

VOLUME V

CARNIVORES, PANGOLINS, EQUIDS AND RHINOCEROSES

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B L O O M S B U R Y

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Family RHINOCEROTIDAE

RHINOCEROSES

Rhinocerotidae Owen, 1845. Odontography: 587. [Previously spelled Rhynocerotidae by J.E. Gray, 1821. London Medical Repository 15: 306.]

<i>Ceratotherium</i> (1 species)	White Rhinoceros	p. 445
<i>Diceros</i> (1 species)	Black Rhinoceros	p. 455

Rhinoceroses were, until recently, among the largest land mammals inhabiting African landscapes. True rhinoceroses, of the family Rhinocerotidae, together with the extinct Amynodontidae and Hyracodontidae, constitute the superfamily Rhinoceroidea, the largest and ecologically most diverse group of Perissodactyla (Prothero *et al.* 1989). The rhinocerotoids were distributed widely across Eurasia, North America and Africa, and by far outnumber all other perissodactyl groups in terms of valid fossil genera (>50) and species (several hundreds). While the amynodonts and hyracodonts were reduced to a few genera by the early Oligocene, the Rhinocerotidae began to diversify and to dominate the fauna of the northern hemisphere and Africa during the Miocene. The rhinos of North America were extinct by the end of the Miocene, while those of Europe and the northern parts of Asia survived to the end of the Pleistocene. As remnants of this diverse group, the genera *Rhinoceros* (represented by two species) and *Dicerorhinus* (one species) are precariously still extant in Asia, and the monotypic genera *Ceratotherium* and *Diceros* currently survive in Africa.

All recent species have been allocated to the subfamily Rhinocerotinae, and the African species form the tribe Dicerotini and the Asian species the tribe Rhinocerotini. However, there are a number of different views on the phylogenetic relationships of the extant rhinos; for instance, in a classification proposed by Antoine (2002) all five extant species have been combined in tribe Rhinocerotini and subtribe Rhinocerotina, while Prothero *et al.* (1986) and Cerdano (1995) separated the two recent African genera into the subtribe Dicerotina.

According to Tougaard *et al.* (2001), the origin and evolution of African rhinos occurred in the middle Eocene, with the *Diceros/Ceratotherium* split dated to 17.1 ± 2.5 mya (middle Miocene). It has been suggested by Geraads (2005) that the Pliocene *Ceratotherium neumayri* was a likely ancestor for both living African species, because it was morphologically and ecologically intermediate between them. The two lineages leading to the recent species split soon after the Miocene–Pliocene boundary leading from an ancestral mixed feeder (*C. neumayri*) to a lineage of grazers (*Ceratotherium* species) and one of browsers (*Diceros*). *Ceratotherium* adapted to open grasslands and savannas, while the *Diceros* ecological niche consisted of more closed habitats (Geraads 2005).

The genera *Diceros* and *Ceratotherium* are morphologically defined by synapomorphies that include the loss of both upper and lower incisors, an astragalus facet that is more or less flattened, an occipital crest angle above 100° , an inclined orbital floor, strong supraorbital processes, and short rounded nasals (Groves 1983, Cerdano 1995, Tougaard *et al.* 2001, D. Geraads pers. comm.). *Diceros* has three molars and 3–4 premolars (total 24–28 teeth), while *Ceratotherium* always has three molars and three premolars (total 24).

Rhinoceroses are large-bodied, pachydermatous animals, endowed with one or two nasal horns consisting of aggregations of keratin fibres (Cave 1969). The skin consists of a heavily keratinized and pigmented

epidermis (about 1 mm thick) and a dense dermis (about 18–20 mm thick) composed of pure collagen fibres (Cave & Allbrook 1959). A covering of very sparse hairs is found in some individuals, especially when young (Neuville 1927). The White Rhinoceros *Ceratotherium simum* exceeds all other extant rhino species in size, with a body length reaching 4.2 m, a shoulder-height up to 1.9 m and weight of 3600 kg in adult ♂♂, compared with 3.75 m, 1.8 m and 1500 kg, respectively, in the Black Rhinoceros *Diceros bicornis* (Zecchini 1998). African rhinos do not show conspicuous folds in the skin characteristic of *Rhinoceros* species.

The cytogenetics of the family have been investigated by several authors. The modal diploid chromosome number for all species is $2n = 82$ (the ancestral condition), with the exception of *Diceros* ($2n = 84$) and the Javan Rhino *Rhinoceros sondaicus*, where the karyotype is unknown; the X chromosome in *Ceratotherium* and *Diceros* is identical (Houck *et al.* 1995).

Rhinoceroses always have one young, after a gestation period of about 480 days in all species (Rookmaaker 1998a). Placentas are large and consist of a thin membrane of allantochorion with rather diffusely scattered villi (Benirschke & Lowenstine 1995). In the wild, rhinos were originally found in a large variety of habitats, probably only avoiding very dense forests. They are generally solitary, but *Ceratotherium* sometimes congregated in groups, aggregations that were much rarer in *Diceros*. They are sedentary and territorial, and consume a wide variety of available plant species shifting preferences according to circumstances. They have few natural enemies, and there are few instances in which predators attack young rhinos.

Rhinoceroses were shown a dozen times in the arenas and menageries of the Roman empire, and some of these must have been caught in Africa (Störk 1977). In Renaissance Europe, most descriptions of the animal in the bestiaries of the period were based on the image of a single-horned animal, probably from India, seen in Lisbon in 1515 (and notably copied in a woodcut by Albrecht Dürer) (Clarke 1986). African rhinoceroses were first observed by European adventurers from about 1650 when the interior of the Cape of Good Hope began to be explored. For at least a century, however, reports were equivocal about the number of horns, and Linnaeus (1758) still called it an obscure species (Rookmaaker 1998b). Rookmaaker (2005a) has pointed out that the distinctions between rhinos from Asia and those of Africa only became formalized at the end of the eighteenth century.

In the course of the nineteenth century adventurers and hunters travelling inland from the South African coast described a proliferating number of rhinoceros species, mainly because they thought that the sizes and shapes of horns were significant characteristics. Two kinds of Black Rhino and two kinds of White Rhino came to be recognized in the southern part of Africa, but when still more types were added the picture became so confused that a prolonged nomenclatural silence followed while a revision was awaited (Rookmaaker 2005b). The first captive Black Rhino arrived in Europe in 1868, while the White Rhino was first seen in a zoological garden as late as 1946 (Rookmaaker 1998a). The studbooks of African rhinos in captivity are kept by the

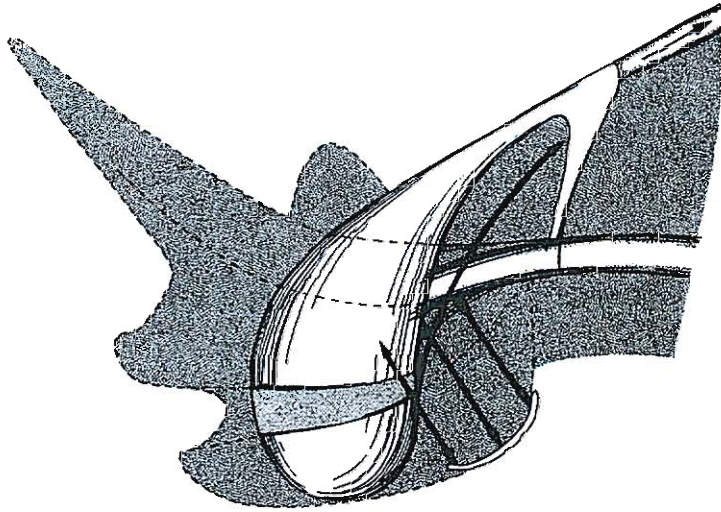
Zoological Gardens in Berlin and contain data on all specimens around the world (Ochs & Mercado 2005a, b, Rookmaaker 2005c).

The rhinoceros has limited value in traditional African societies. In a few cases, the hide was used to prepare shields or the meat was eaten (Lagercrantz 1960). The major threat to rhinos in recent years stems from the immense value of the horns to the Chinese as an essential ingredient in traditional fever-reducing medicine (Martin & Martin 1982, Chapman 1999, Ellis 2005) and to Yemeni to produce handles of the

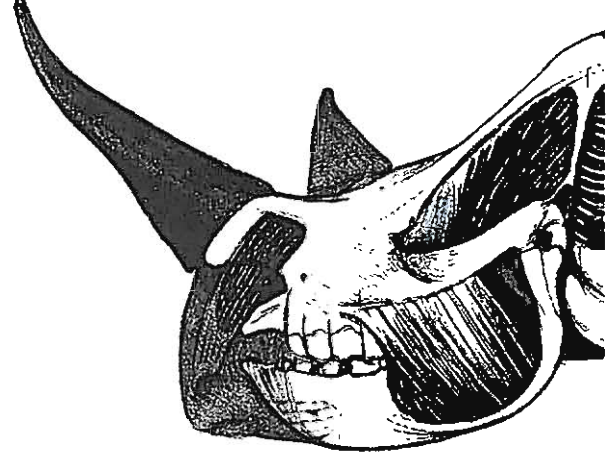
daggers worn by the men (Leader-Williams 1992, Martin & Vigne 1993). The conservation of the species is discussed in further detail elsewhere.

References to an extensive literature about all aspects of rhinoceros biology and conservation have been listed and discussed by Rookmaaker (1983), Wildi (1989), Miller (1992), Du Toit *et al.* (1994) and Van der Westhuizen (1994).

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Ceratotherium, principal mass of skull in relation to mastication, horns, vertebral column and suspension.



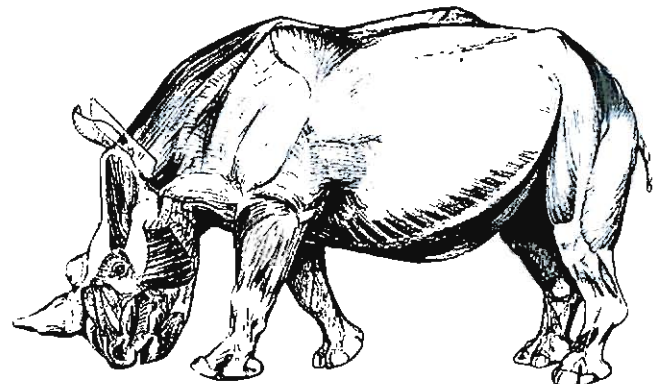
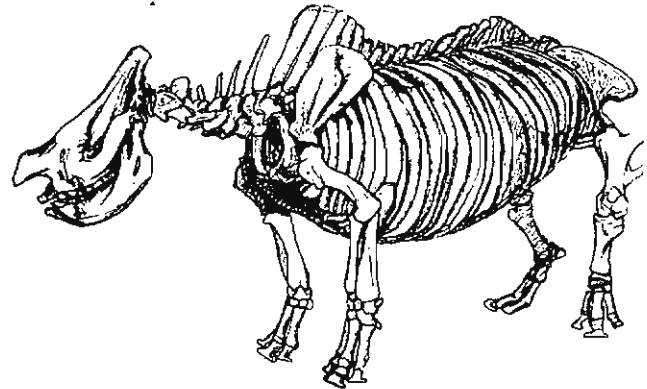
GENUS *Ceratotherium*

White Rhinoceros

Ceratotherium J. E. Gray, 1868. Proc. Zool. Soc. Lond. 1867: 1006, 1027.

Ceratotherium is a monotypic genus (but see Groves *et al.* 2010), represented by a single extant species, the White Rhinoceros *Ceratotherium simum*. This species once was found in Africa south of the Zambezi R. and further north in central Africa in parts of Uganda, DR Congo, Sudan, Central African Republic and Chad (Heller 1913, Groves 1972, 1975). The unbridged gap between the two populations merits further investigation. The White Rhino was exterminated in Zimbabwe in 1893, at which time only a small population of a minimum of 20, but most likely about 200, individuals remained in the south-eastern part of South Africa (Player 1972, Rookmaaker 2002, 2003b).

The earliest African representative of *Ceratotherium* in the Pliocene is known from Langebaanweg in South Africa and has recently been identified as *Ceratotherium mauritanicum* (Geraads 2005). In North Africa, *C. mauritanicum* survived into the late Pleistocene; *Ceratotherium simum* was first found in the early Pleistocene. Specimens found in East Africa have been described as *Ceratotherium simum germanoaffricanum* (see Groves 1975). Evidence of skeletal material suggests that the transition from *C. mauritanicum* to *C. simum* took place in East Africa (Geraads 2005). Fossil and extant members of the genus are typical grazers, which shows in the elongation of the occiput and the development of the nuchal hump to accommodate the muscles needed to lift the head from the grazing posture (Alexander & Player 1965).



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White Rhinoceros *Ceratotherium simum*: skeleton (top) and myology (bottom).