

III.I The evolution of the rhinoceros

Introduction

Rhinos can be traced back over some 50 million years, with a complex series of evolutionary paths throughout a sequence of geologic or evolutionary epochs (the term scientists use for these periods of time). These epochs are all part of the Cenozoic Era, known as the Age of Mammals, and include:

Epoch	Began
Paleocene	- 65 millions years ago
Eocene	- 58 millions years ago
Oligocene	- 37 millions years ago
Miocene	- 23 millions years ago
Pliocene	- 5 millions years ago
pleistocene	- 2 millions years ago
Holocene or recent	- 100 thousand years ago

All rhinoceroses belong to the mammalian order, Perissodactyla (from the Greek *perissos*, meaning numbers odd, and *daktulos*, meaning a finger or toe). In other words, they are all odd-toed ungulates (ungulates meaning hoofed-animals), with the axis of symmetry of the foot passing through the central toe, a characteristic also known as mesaxonic. Other Perissodactyla include horses and tapirs, and their evolution began during the early Paleocene, or possibly even earlier in the late Cretaceous.

In contrast, Artiodactyla (bovids, cervids, suids etc.) are even-toed, or paraxonic, with the axis of symmetry of the foot passing between the third and the fourth digit. Both Perissodactyle and Artiodactyle are Unguligrades: they walk on the terminal enlarged phalange, which forms a hoof.

Rhinoceroses were a very diverse and abundant family of mammals and were the largest terrestrial mammals on all the northern continents from about 35 to about 20 million years ago. During this time they ranged over all ecosystems and exhibited a wide range of behaviour, with many different size and morphological adaptations.

Paleontological history

The earliest known rhinoceros-like mammal is the *Hyrachyus eximus*, dating from Early Eocene, and which was found in North America. This small animal resembled early tapirs and horses, and had no horn.

Horns only became a defining characteristic later in rhinos' evolutionary history, with the appearance of Rhinocerotidae family in the late Eocene.

In fact three families evolved in the late Eocene: the Hyracodontidae or running rhinos; the Arynodontidae or aquatic rhinos; and the Rhinocerotidae, the forefathers of today's five species of rhino.

The Hyracodontidae, running rhinos, were adapted for speed and ranged in size from small (like today's dogs) to horse and even mega-giraffe size (the Indricotheres, discussed below). The hyracodontids flourished from the mid-Eocene until the early Miocene. The second family, the Arynodontidae, was incredibly successful, with the maximum of diversification and dispersal – throughout America and Eurasia – in the late Eocene and early Oligocene. But during the Oligocene the Arynodontidae species declined, with just one hippo-like rhino species surviving until the middle Miocene.

The third family is the Rhinocerotidae, which first appeared in the late Eocene in Eurasia. The earliest species were small in size, with larger species only coming later, and Rhinocerotidae spread to North America. Some 26 different genera are known, but in the early Oligocene a large wave of extinction made all these early genera disappear. They displayed varying characteristics and were able to live in a wide range of habitats, one of the features that may account for their biological success.

For example, the *Menoceras* occurred in Europe until the early Miocene. It was a pig-sized rhinoceros, with males sporting two horns side-by-side, whereas females had no horns. They evolved locally in several lineages, e.g. *Teleoceras*, which had short legs, a barrel chest, and a single small nasal horn.

In Asia, Rhinocerotidae appeared during the Oligocene times. The most famous group is the Indricotheres, which included the *Paraceratherium*, believed to be the largest terrestrial mammal that ever existed. This hornless rhino is evaluated to be almost six metres high and nine metres long. Its weight would have been close to 20 tonnes. It ate leaves from trees with tusk-shaped upper teeth pointing down, while the lower teeth pointed forward.

Asia became the departure point for a big dispersal of all the large mammals from the Miocene to late Pleistocene periods. All the European rhinoceroses were connected to Asian forms. The woolly rhinoceros (*Coelodonta antiquitatis*), for example, appeared nearly one million years ago in China. It first arrived in Europe some 600,000 years ago (the oldest fossil record is found in Germany), and probably re-entered with a second migration wave around 200,000 years ago, together with the woolly mammoth, when it became common in Europe.

This rhino was a large genus, with morphological adaptations to live in steppic land (sub-hypsodont teeth) and a cold and dry climate, the most distinctive of which was the thick coat of long brown hair (like that of woolly mammoths), and a body septum separated the nasal bone in two parts, to warm the air easily). This two-horned rhino was hunted and drawn in caves by the early humans in the Ice Age. Like the woolly mammoth, the woolly rhino became extinct about 10,000 years ago, probably due to over-hunting by the early humans.

Another Asian species was the well-known *Elasmotherium*, the giant unicorn rhinoceros. It was two metres high and five metres long, and is estimated to have weighed nearly five tonnes. It had a single and enormous horn, hypsodont teeth with wrinkled enamel, and its long legs designed for running gave it a horse-like behaviour. Its habitat was similar to that of the woolly rhino. It seems this rhino became extinct around 10,000 years ago.

Rhinocerotidae only arrived in Africa from Asia in the early Miocene, with genera such as *Brachypotherium* and *Chilotheridium*. They evolved in Africa until the next exchange with Asia in the Late Miocene. The last species of *Brachypotherium* of Africa evolved at the beginning of Pliocene.

In Europe, the genus *Ronzotherium* is the first Rhinocerotidae known from the very end of Eocene and early Oligocene. Several species of it were found in western and eastern Europe, with *Protoceratherium* and *Menoceras* being the most important genera found in late Oligocene and early Miocene. In middle Pliocene, the genus *Stephanorhinus* ranged over all of Europe, coming in several migration waves from Asia. This genus, confused for a time with *Dicerorhinus*, experienced a large dispersal throughout Eurasia until it disappeared some 12,000 years ago. At the end of Middle Pleistocene and in Late Pleistocene some species of *Stephanorhinus* were found together with the woolly rhinoceros (*Coelodonta antiquitatis*).

The evolution of today's five species of rhino

Since the end of Miocene, Rhinocerotidae have been on the decline, probably triggered by changes in climatic conditions. Numerous species became extinct, and rhinos no longer survive in Europe (since about 12,000 years ago) or America (since about four million years ago).

The five species found today (white, black, greater one-horned, Sumatran and Javan) come from different lineages. The Sumatran rhino is thought to be the oldest and the most archaic form. As far as we can tell (fossil records with radioactive

dating disagree with molecular DNA clocks), the five modern species probably originated at these approximate times in the past

Sumatran	+ 15 millions years ago
Black	4-10 millions years ago
White	2-5 millions years ago
Greater one-horned	2-4 millions years ago
Javan	2-4 millions years ago

Morphological characters of the Rhinocerotidae

The rhinoceros has a massive body and a large head with one or two horns, depending upon the species, placed in the middle of the frontal or nasal bone of the skull. The horn has a dermal origin. It is composed of compressed fibrous keratin. Rhinoceroses have a very elongated skull, which is elevated in the occipital part. They have a small braincase, and the nasal bone is clearly projected forward, beyond the premaxillae bone. Its surface is rough where the insertion of the horn takes place.

All the Perissodactyla, especially rhinoceroses, have or had lophodont teeth, in other words the teeth are formed by two transverse lochs of enamel. The dental formula varies between species. I 0-3/0-3, C 0-1/0-1, P 3-4/3-4, M 3/3 x 2 = 24-44. They could be grazers (eg *Elasmotherium*), which means their premolars and molars are hypsodont (high crown), or sub-hypsodont (e.g. the woolly rhino, *Coelodonta antiquitatis*); but most of them are browsers with brachydont teeth (low crown). These characteristics are directly related to the species' environment. The hypsodont species could eat grass (a very rough food for the enamel), so lived in open habitat. On the contrary, the brachydont species could only eat soft vegetable (such as leaves); consequently, they live in a more forested environment.

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