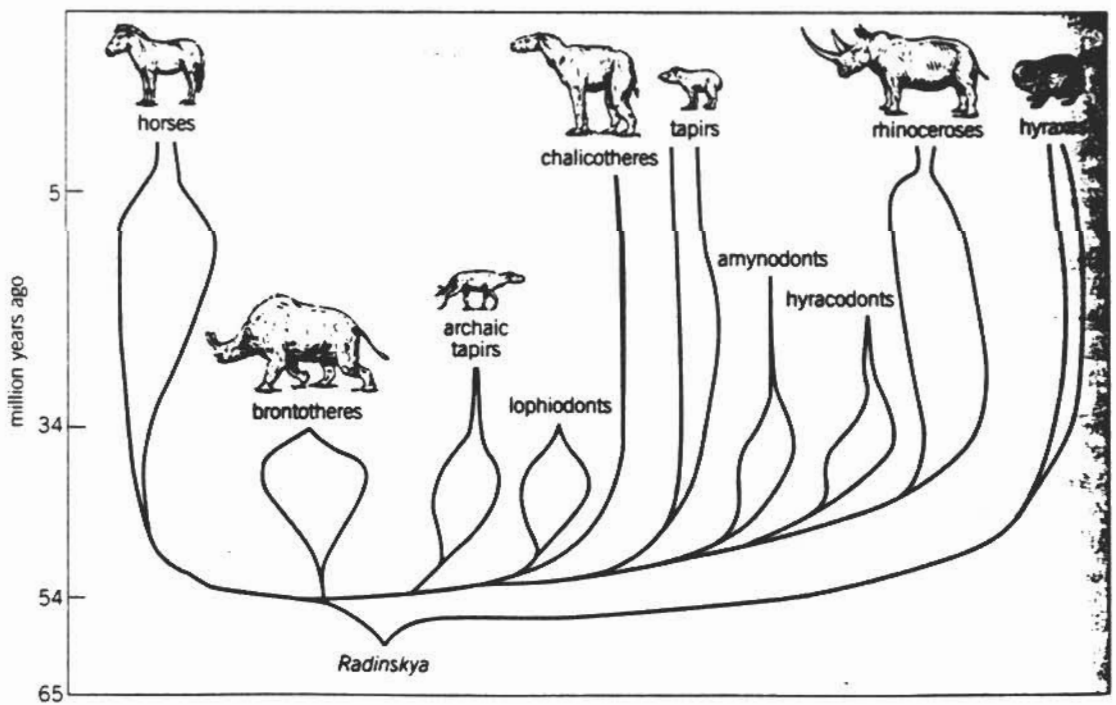
Perissodactyla

The perissodactyls, or odd-toed hoofed mammals, include the horses, rhinoceroses, tapirs, and their extinct relatives. Recent discoveries have radically changed the notions about perissodactyl evolution. New fossils from China show that perissodactyls arose in Asia about 55 million years ago (m.y.a.), along with their close relatives, the elephants and their kin. Anatomical evidence suggests that the living hyraxes, also called conies, long thought to be related to elephants, are probably related to perissodactyls. The remaining nonhyracoid perissodactyls are now divided into three groups: the Hippomorpha (horses and their extinct relatives), the Titanotheriomorpha (the brontotheres, extinct rhino-sized animals with paired blunt horns), and the Moropomorpha (tapirs, rhinoceroses, and their extinct relatives, including the clawed chalicotheres).

Before about 34 m.y.a., the brontotheres, archaic rhinos, and primitive tapirs were the dominant large mammals around the world. After these groups became extinct, horses and rhinoceroses were the most successful perissodactyls, although they have been ecologically replaced by even more successful cattle, antelopes, deer, and their relatives. Today, most nondomesticated perissodactyls are endangered in the wild. Rhinoceroses, for example, are being killed by poachers at an alarming rate.

Origins. Perissodactyls were once thought to have originated in Central America from the phenacodonts, an archaic hoofed mammal group. In 1989, a specimen from Chinese deposits about 55 m.y. old was described and named *Radinskya*. This specimen showed that perissodactyls must have originated in Eurasia some time before 55 m.y.a. (see illus.). The similarities to the most primitive relatives of the elephants suggested that elephants and perissodactyls have a close common ancestry in Eurasia about this time. This close relationship is also suggested by the hyraxes, a group of woodchucklike hoofed mammals found today in Africa and the Near East. Although they were long thought to be related to elephants, new anatomical evidence suggests that hyraxes are probably perissodactyls. Hyraxes and other perissodactyls have very striking similarities in their internal-ear anatomy, in the structure of their hooves, in the muscles of their limbs, and even in the irises of their eyes. If elephants, hyraxes, and other perissodactyls are all closely related, then they must have diverged in Eurasia-Africa about 60 m.y.a., shortly after the extinction of the dinosaurs.

Horses. Once perissodactyls spread from Asia to North America and Europe, they began to diverge into three main groups: the Hippomorpha (horses and their relatives), Titanotheriomorpha (brontotheres), and Moropomorpha (tapirs, rhinos, chalicotheres, and their relatives). Among the hippomorphs, the earliest horses occurred in North America about 53 m.y.a., and their close relatives, the palaeotheres, occurred in the European archipelago about the same time. (High sea levels isolated Europe into a number of small islands at this time.) The name of the earliest true horse in North America was long thought to be *Eohippus* or *Hyracotherium*, but the correct name is probably *Protorohippus*. From this four-toed, dog-sized ancestor, horses underwent a well-known evolutionary history, becoming larger and longer limbed with reduced side toes. By about 30 m.y.a., horses had become very common in North America.



The horses *Mesohippus* and *Miohippus*, long thought to be sequential segments of the main trunk of the horse family tree, are in fact bushy side branches that overlap by millions of years. From *Miohippus*-like ancestors, some horses became specialized for eating gritty grasses and developed high-crowned, ever-growing teeth. Others remained leaf-eating browsers with low-crowned teeth. By 15 m.y.a., horses were so diverse that as many as 12 species occurred in one locality; they were ecologically equivalent to the diversity of antelopes on the modern African savanna. About 5 m.y.a., most of this diversity of horses (particularly the primitive browsing types and the three-toed hipparions) had waned, leaving only the living genus *Equus*. Although the primary area of horse evolution was always North America (with occasional migrations to Eurasia), horses disappeared from this continent at the end of the last ice age, only to be reintroduced by Columbus in 1493.

Brontotheres (titanotheres). Brontotheres started out as small, pig-sized animals and evolved into larger, cowlike animals during the span of about from 50 to 40 m.y.a. At the end of their evolution, they reached elephantine proportions, with large paired blunt horns on the tip of the nose. Brontotheres were the largest land mammals in North America and Eurasia until about 34 m.y.a. when they became extinct. Their extinction, long a mystery, now appears to be related to massive climatic changes. These climatic changes, triggered by the first Antarctic glaciation, caused changes in the vegetation that led to extinction of many archaic browsing mammals, such as the brontotheres and the primitive tapirs.

Tapirs, rhinoceroses, and chalicotheres. The third major group of perissodactyls is the Moropomorpha, which includes the tapirs, rhinos, and their extinct relatives. They originated about 50 m.y.a. as dog-sized animals that were virtually indistinguishable from the earliest horses. Until about 34 m.y.a., archaic tapirs were very diverse in both Asia and North America. Although they already had leaf-cutting teeth like those of modern tapirs, they did not develop the tapir's trunk or proboscis until later in their evolution. Like the brontotheres, most archaic tapirs became extinct with the climatic changes 34 m.y.a. that nearly wiped out their forest habitat.

One descendant of the archaic tapirs, the lophiodonts, lived in the European archipelago 40–50 m.y.a. The lophiodonts independently developed a proboscis and huge leaf-cutting teeth, so that they looked very much like modern tapirs. Recent evidence has shown that the lophiodonts are closely related to another extinct group, the chalicotheres, whose relationship to other perissodactyls has long been a mystery. Chalicotheres looked like heavy-bodied horses, with claws on their feet instead of hooves. Some of them could knuckle-walk on their long gorillalike forelimbs. Their claws were used for hauling down branches for feeding. Chalicotheres were rare but persistent in the Northern Hemisphere until the beginning of the last ice age, when they disappeared from Asia and Africa.

The most diverse and successful group of perissodactyls was the rhinoceroses. From their origin in tapirlike forms about 50 m.y.a, rhinoceroses diverged into three groups: the amynodonts (aquatic hippolike and tapirlike forms), the hyracodonts (long-legged runners), and true rhinoceroses. Amynodonts and hyracodonts both suffered from the extinction event of about 34 m.y.a., although both managed to survive until about 20 m.y.a. One group of hyracodonts became gigantic. Of these, a hornless long-necked hyracodont called *Paraceratherium* (formerly known as *Baluchitherium* or *Indricotherium*) was the largest land mammal that ever lived. It reached 20 ft (6 m) at the shoulder and weighed over 44,000 lb (20,000 kg, or about three times the weight of the largest elephant). *Paraceratherium* probably browsed on the tops of trees in Asia about 35 m.y.a.

The oldest known true rhinoceros was described in 1989 from deposits in Oregon about 40 m.y. old. The earliest true rhinoceroses were hornless, and remained small in body size until the extinction of brontotheres about 34 m.y.a. From about 34 to 20 m.y.a., rhinoceroses were the largest herbivorous mammals in North America or Eurasia. Then mastodonts migrated out of their isolation in Africa and took over the megaherbivore niche. True rhinoceroses have occupied many different habitats. Some were generalized forest browsers, and others grazed tough grasses with their ever-growing teeth. One group was short-legged and fat like the hippopotamuses, and must have had an aquatic habitat much like that of modern hippos. Most extinct rhinoceroses were hornless, but some groups evolved a single horn on the nose or forehead, or tandem horns on both nose and forehead. Two groups of rhinos independently evolved paired horns on the tip of the nose. Rhinoceroses suffered severe extinctions during the major climatic changes about 5 m.y.a. They disappeared completely from North America, and only five living species managed to survive in Africa and Eurasia.

Conservation. Perissodactyls have been declining for the last 10 m.y., driven to near extinction by competition with cattle, antelope, deer, and other hoofed mammals with a more efficient, cud-chewing digestion. Perissodactyls suffered even more severe extinctions during the climatic crisis of 5 m.y.a., and during the great extinction of large mammals at the end of the last ice age. Most of the living species are very rare or endangered in the wild. Among the horse family, the domestic horse is very widespread, but its ancestor, Przewalski's horse, is nearly extinct in central Asia. Although the plains zebra is common, the Grevy's and mountain zebras are endangered, and the quagga became extinct in the nineteenth century. Wild asses and onagers are now extremely rare. Tapirs are endangered in the jungles of both South America and southeast Asia. All of the five living species of rhinoceros are now endangered in the wild, since rhinoceros horn is worth its weight in gold for use in folk medicines and Arab dagger handles. There are only a few thousand white rhinos, a few hundred Indian rhinos, and a few dozen Sumatran or Javan rhinos surviving. Once abundant, the black rhinoceros is now being decimated by poachers. Of 65,000 in 1970, only a few hundred remain today, and it may be extinct in the wild by the turn of the century. Despite over 50 m.y. of evolutionary success, the fate of wild perissodactyls is uncertain as long as human populations continue to expand and destroy wild habitat.

For background information SEE EXTINCTION (BIOLOGY); HYRACOIDEA; MAMMALIA; PERISSODACTYLA; RHINOCEROS; TAPIR in the McGraw-Hill Encyclopedia of Science & Technology.

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