

Perissodactyla

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The mammalian order Perissodactyla, or 'odd-toed' ungulates, includes the living horses, rhinoceroses and tapirs, and two extinct groups, the brontotheres and chalicotheres. Over their 55 million years, they evolved into an amazing variety of forms, and about 40 million years ago, they were the dominant hoofed mammals on the planet. Since then, they have been largely replaced by the even-toed artiodactyls, and today most wild perissodactyl species are on the brink of extinction.

Basic Design

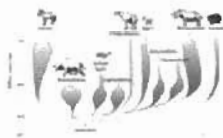
The perissodactyls are hoofed mammals with a number of unique shared specializations ([Figure 1](#)). The most obvious is their 'odd-toed' foot, which typically has one or three toes, although a few taxa have four toes on the front foot. A better definition is that the axis of symmetry and weight bearing runs through the middle digit (digit III) of each foot. The perissodactyl ankle bone has a distinctive saddle-shaped facet on the lower end. In addition, there are a number of distinctive specializations in the skull and teeth, including upper molar teeth which tend to develop an outer crest from the two outer cusps, and cross-crests connecting the outer crest to two inner cusps. Beyond these shared specializations, the body forms of perissodactyls were highly variable. They ranged from tiny, leaf-eating forms with multiple toes (like the earliest horses and tapiroids), to long-legged horses and running rhinoceroses, to the clawed chalicotheres, to a variety of rhinoceros with hippopotamus like bodies, to the huge brontotheres and indricotheres. The latter included the hornless hyracodontid rhinoceros *Paraceratherium*, which reached 6 m at the shoulder and weighed 20 tonnes, the largest land mammal that ever lived.

Figure 1

Specializations that define the perissodactyls. (a) Left hind feet of typical perissodactyls, with a line drawn through the axis of symmetry in the third toe. They include (from left) the tapir *Tapirus*, the primitive three-toed horse *Protorohippus*, the modern one-toed horse *Equus*, the brontothere *Brontops*, and the clawed chalicothere *Moropus*. Between these last two feet is the ankle bone, or astragalus, of a typical perissodactyl, with its flat, saddle-shaped lower facet. (Modified from Colbert and Morales, 1991.) (b) Crown view of right upper first, second and third molars of typical perissodactyls, showing the characteristic connection of cusps by crests in different groups. The cheek is towards the top, the tongue towards the bottom, and the front of the mouth towards the right in each example. Top row, left: the primitive horse *Protorohippus*, with four distinct cusps and only weak crests connecting them. Top row, right: the primitive tapir *Homogalax*, with strong cross-crests connecting the cusps. Second row, left: the rhinoceros *Subhyracodon*, with crests connected so that they resemble the Greek letter π ('pi'). Second row, right: the brontothere *Palaeosyops*, with the typical 'W'-shaped outer crest, and large blunt inner cusps. Bottom row: the chalicothere *Moropus*, with the 'W'-shaped outer crest partially connected to the inner cusps with crests. (Modified from Romer, 1966.)

Diversity

The Perissodactyla consists of five well-established superfamilies (**Figure 2**): the horses plus palaeotheres (Equoidea), with about 45 genera known from the early Eocene to Recent; the brontotheres or titanotheres (Brontotherioidea), with about 41 genera known entirely from the Eocene; the chalicotheres (17 genera, known from the middle Eocene to the Pleistocene); the rhinoceroses (Rhinocerotoida), with about 96 genera ranging from the middle Eocene to Recent; and the paraphyletic 'tapiroids' (Tapiroidea), with 36 genera ranging from the early Eocene to Recent. Some authors have argued that the hyraxes (Hyracoidea) are also members of the order, as Richard Owen thought when he created the Perissodactyla in 1848, but this proposal has been controversial. These five superfamilies are clustered into three suborders: the Hippomorpha (horses and their extinct relatives); the Titanotheriomorpha (the extinct brontotheres); and the Moropomorpha (tapirs, rhinoceroses, chalicotheres and their extinct relatives).

**Figure 2**

Family tree of the perissodactyls.

Of this original diversity of over 200 genera, only one genus of equine (*Equus*), one genus of tapir (*Tapirus*), and four genera of rhinoceros (*Rhinoceros*, *Dicerorhinus*, *Ceratotherium*, and *Diceros*) survive today. The genus *Equus* today contains only seven living species. The horses (subgenus *Equus*) include the domesticated horse (*E. caballus*) and its ancestor, the Przewalski's horse (*E. przewalskii*), which once lived in the Siberian-Mongolian steppes but is now extinct in the wild. The asses (subgenus *Asinus*) include the African ass (*E. africanus*) of northeastern Africa, and the Asian ass (*E. hemionus*) of the steppes and deserts from the Middle East to Tibet. The third group of equines are the zebras, including the common plains zebra (*E. burchelli*), the rare mountain zebra (*E. zebra*) and Grevy's zebra

(*E. grevyi*).

The species diversity of living rhinoceroses and tapirs is even lower. The genus *Tapirus* includes the black-and-white banded Malayan tapir of southeast Asia (*T. indicus*), and three species in Central and South America: the Brazilian tapir (*T. terrestris*), the mountain tapir (*T. pinchaque*), and Baird's tapir (*T. bairdii*). Five species survive among the four genera of living rhinoceroses. They include the Indian rhino (*Rhinoceros unicornis*) of northern India and Nepal, and the extremely rare Javan rhino (*R. sondaicus*), of which less than 100 individuals may still survive in Java and Vietnam; the Sumatran rhino (*Dicerorhinus sumatrensis*), a slightly hairy form now restricted to a few hundred individuals in Sumatra; and the two African rhinos, the prehensile-lipped browsing black rhino (*Diceros bicornis*) and the broad-lipped grazing white rhino (*Ceratotherium simum*). The names 'black' and 'white' are misnomers, because both of these rhinos are grey. The 'white' rhino may be a mistranslation of the Afrikaner word 'weit,' meaning 'wide', in reference to its broad upper lip. Both African species are known from fewer than 10 000 individuals in protected reserves in southern and eastern Africa.

Habitats and Abundance

Most perissodactyls are large-bodied (greater than 200 kg, with some over 1000 kg), hoofed mammals, so they occupy a wide range of terrestrial habitats wherever there is enough vegetation to support them. Unlike ruminant artiodactyls, which have special digestive chambers in their foregut, perissodactyls have the primitive mammalian hindgut (intestines and caecum) digestion system, so they are not as efficient in extracting nutrition from vegetation as ruminants. Consequently, they survive by eating larger quantities of low-quality vegetation, while ruminants can be highly specialized browsers since their digestion is more efficient and food intake is less. Many perissodactyls (such as the zebras and white rhinoceros) are very efficient grazers, while others (such as the tapirs and other rhinos) are leaf-eating browsers. In open grasslands, equids such as zebras and wild horses can be very numerous. More often, however, perissodactyls such as rhinos and tapirs tend to be solitary or live in small mother–daughter groups, because they live in densely forested habitat unsuitable for large herds. Because they are extremely hardy and can digest even poor-quality vegetation, some perissodactyls (such as wild asses and onagers) live even in harsh desert climates and mountainous steppe habitats. However, extensive poaching and human encroachment on their habitats have severely threatened most living species of perissodactyl. Of the wild species, only the plains zebra is still numerous, while nearly every other species of living equid, rhino and tapir is endangered in the wild. Of course, domesticated horses and donkeys are very numerous all over the world, thanks to human introduction.

Habits and Lifestyles

Today, the three surviving groups of perissodactyls occupy three well-defined niches. The equids (horses, zebras, and asses) are specialized for grazing and running in open habitats, typically grasslands or deserts. They have two basic forms of social organization. In rich grassland habitats, wild horses and plains zebras live in large, highly social, permanent herds, with a dominant stallion and his harem of mares. These huge herds can consist of hundreds of individuals, and often migrate seasonally with the water and food supply over a range as large as 600 km². On the other hand, equids that live in sparsely vegetated habitats, such as the Grevy's zebra and the wild asses and onagers, form small, ephemeral social groups, where the stallion is normally solitary, and defends a large territory. In these equids, mares form small family groups which range through each territory, and are joined by the stallions only during the mating season.

The purpose of zebra stripes has long been a mystery, because plains zebras live out on the open

grasslands, not in the dense undergrowth where stripes might help camouflage the body (as the stripes on a tiger do). Zoologists now believe that when a herd of zebras stampede, they create a dizzying arrangement of moving stripes that makes it hard for a lion to single out its prey. However, the striped pattern is deeply engrained in the genes of all horses, and occasionally horses and asses are born with zebra stripes. Solid-coloured horses and asses can be thought of as zebras that have lost their stripes.

In addition to the three living species of zebras, there are also three living species of wild asses, divided into a number of subspecies. They live in the rocky regions and deserts of southern Asia and northern Africa, and have light tan coats to reflect the heat and blend in to their backgrounds. Their long legs and ears help them shed heat in the desert, and the long ears are also excellent for long-range hearing to warn them of danger. Their narrow hooves are excellent for moving across rocky terrain without slipping. The common Asiatic ass is known as the onager, and it lives in deserts from Mongolia to Iran to Syria to Turkey. The high plateaus of Tibet are home to the kiang or Tibetan wild ass, which is adapted to the cold harsh conditions in the Himalayan steppes between 4000 and 5300 m (13 000 and 16 000 feet). The African wild ass is found in the rocky deserts of Sudan, Ethiopia and Somalia. The donkey or burro is a domesticated descendant of the African wild ass. Its exceptional ruggedness and ability to carry large loads over long distances are inherited from its ancestry among the desert-dwelling asses of Africa.

The rhinoceroses live in the grasslands and forests of Africa and Asia, where they are among the largest herbivores eating both grass and leaves. They are basically solitary, or form small female-calf groups, but never occur in herds. Each individual or small group wanders over a large (3 km^2 in forests, but up to 90 km^2 in arid grasslands) home range, and bulls mark their territory with dung piles and urine spraying. When another bull enters the territory of a dominant male, there is usually a protracted confrontation. The subordinate males (or females as well) utter a series of loud roars or shrieks to warn off males that approach too near. However, if the intruder does not back off, the confrontation escalates into a fight, where the rhinos push against one another with their horns, and rub their noses and horns on the ground repeatedly until the weaker male yields. Contrary to popular belief, rhinos do not charge at each other; that behaviour is reserved for scaring off intruders and predators other than rhinos. Because they have poor vision (they cannot detect a motionless person at distances of greater than 30 m), they depend upon their hearing and smell to detect threats. Consequently, they can be easily startled, and often react to a threat by charging, or by fleeing.

The short-legged, barrel-bodied tapirs live exclusively in the dense jungles of Central and South America and southeast Asia, where they browse on leaves with their flexible proboscis. Tapirs are solitary, ranging over a wide area of jungle, swimming rivers with ease, and even climbing mountainsides. They swim to feed, cool themselves off, and rid themselves of skin parasites, as well as seek refuge in water, where they can stay submerged for several minutes. They follow well-established routes in the jungle and even make tunnel-like trails through the vegetation, which they mark with urine during their daily routine. They browse leaves or green shoots, as well as soft twigs, fruits, grasses and aquatic vegetation. They follow a zigzag course while feeding, moving continuously and taking only a few leaves from each plant.

Life Histories

Life histories are best known for the equids, which have been studied extensively in the wild. Mares usually bear only one foal after a gestation of about a year. They come into heat within 7–10 days after bearing a foal, so their mating and birth seasons both occur during the periods of best foraging. The foals are precocious, able to run within a few hours of birth, since there are so many predators around and they must run to keep with the herd and survive.

Foals are weaned after about 8–13 months, but remain with their mothers for some time afterward. Female colts do not leave until they are sexually mature at about 2 years of age, at which point they may join a neighbouring harem, or bachelor males will attempt to steal them. Male colts remain until they are about 4 years old, after which they roam in bachelor herds until they are mature enough to displace dominant males and defend their own territory and establish a harem.

Rhinoceroses are very long-lived (30–45 years), and females do not bear their first calves until 5–8 years of age. They bear a single calf after a 15-month gestation, and will not breed again for 2–4 years. The babies are relatively small at birth (about 65 kg in the white rhino, and 40 kg in the black rhino), weighing only about 4% of the mother's weight. After about 3 days, they leave their hiding place and are capable of following their mother around, while she feeds and defends them from predators. Although female calves may remain with their mothers for many years, male calves leave at about 5–8 years of age, when they become sexually mature. However, they may not breed until they are 10 years old or older, when they are strong and mature enough to claim a breeding territory from another bull.

In tapirs, breeding occurs throughout the year in the nonseasonal tropics, with females going into heat every 2 months or so. Mating is preceded by a noisy courtship, with the tapirs giving high-pitched squeals as they stand head-to-tail, sniffing their partner's sexual parts and circling at increasing speed. They nip at each other's feet, ears and flanks (as do horses and zebras), and prod their partner's belly with their proboscis. After a gestation of about 390–400 days, the female finds a secluded lair where she bears a single calf. Newborn tapirs have a brown coat with white spots and stripes that serves as camouflage. This coat is eventually replaced by the normal solid brown coat (in American tapirs) or black and white coat (in the Malayan tapir) as they mature. Calves stay with their mothers until they are fully grown at around 6–8 months, but they are not sexually mature for another 2–3 years.

Oddities Within the Phylum

The living horses, rhinos and tapirs are familiar to many people, but they are not representative of the tremendous diversity of shapes and anatomies that perissodactyls have evolved. For example, among the rhinos there were several taxa that developed a tapir-like or elephant-like proboscis, and several lineages that developed hippo-like bodies for an aquatic lifestyle. In addition, there were rhinos with slender horse-like bodies and long limbs for running, and the gigantic indricotheres were adapted for browsing leaves off the tops of trees. The extinct brontotheres began as tapir-like forms, but developed into huge rhino-like beasts toward the end of their evolution. The chalicotheres were the most aberrant of all perissodactyls. Their hooves were modified into large claws, and apparently they used their long, powerful clawed forelimbs to haul down branches for browsing.

Fossil History

Perissodactyls were once thought to have evolved in Central America from the phenacodontids, an extinct group of archaic hoofed mammals placed in the invalid taxon 'Condylarthra'. However, in 1989, a specimen recovered from deposits in China about 57 million years old was described and named *Radinskya*. This specimen shows that perissodactyls originated in Asia sometime before 57 million years ago, and were unrelated to North American phenacodonts. *Radinskya* is very similar to the earliest relatives of the tethytheres (elephants, manatees, and their kin). This agrees with other evidence that perissodactyls are more closely related to tethytheres than they are to any other group of mammals.

From their Asian origin, the hippomorphs spread all over the northern continents. North America became the centre of evolution of true horses, which occasionally migrated to other continents. In Europe, the horse-like palaeotheres substituted for true horses. From *Protorohippus* (once called *Hyracotherium* or *Eohippus*), a dog-sized ancestor with four toes on the front feet that lived 55–50 million years ago, horses evolved into many different lineages living side by side. The three-toed horses *Mesohippus* and *Miohippus* (from beds dated about 30–37 million years ago) were once believed to be sequential segments on the unbranched trunk of the horse evolutionary tree. However, they coexisted for millions of years, with five different species of the two genera living at the same time and place. From *Miohippus*-like ancestors, horses diversified into many different ecological niches, with some species adapted for eating soft, leafy vegetation, and others with high-crowned teeth for eating tough, gritty grasses. About 15 million years ago, there were as many as 12 different lineages of three-toed horses in North America, each with slightly different ecological specializations, and they were analogous to the diversity of modern antelopes in East Africa. On two different occasions (*Pliohippus* and *Dinohippus*) three-toed horses evolved into lineages with a single toe on each foot. About five million years ago, most of these three-toed and one-toed horse lineages became extinct, leaving only *Dinohippus* to evolve into modern *Equus*.

On various occasions in the last 20 million years, different genera of horses migrated back from North America to Eurasia, most recently about 3 million years ago, when *Equus* reached Europe. They also migrated to Africa (evolving into zebras and wild asses) and South America. At the end of the last Ice Age (about 10 000 years ago), horses became extinct in the New World. However, they were reintroduced to their ancestral homeland by Columbus in 1493. Wild horses that have escaped from domesticated stock are known as mustangs.

Brontotheres began as pig-sized, hornless animals about 53 million years ago, and quickly evolved into multiple lineages of cow-sized animals with long skulls and no horns. Between 37 and 34 million years ago, their evolution culminated with huge, elephant-sized beasts bearing paired blunt horns on their noses. The extinction of brontotheres about 34 million years ago was due to a global climatic change (triggered by the first Antarctic glaciers) that eliminated most of the soft, leafy vegetation on which they fed.

The earliest moropomorphs, such as *Homogalax*, from strata about 55 million years old, are virtually indistinguishable from the earliest horses. From this unspecialized ancestry, a variety of archaic tapir-like animals diverged. Most retained the simple leaf-cutting teeth characteristic of tapirs, and like brontotheres, died out about 34 million years ago when their forest habitats shrank. Only the modern tapirs, with their distinctive long proboscis, still survive.

The horse-like clawed chalicotheres are closely related to some of these archaic tapirs. They apparently used their claws to haul down limbs and branches to eat leaves (much as ground sloths did), rather than for digging. *Chalicotherium* had such long forelimbs and short hindlimbs that it apparently knuckle-walked like a gorilla, with its claws curled inward.

Rhinoceroses have been highly diverse and successful throughout the past 50 million years. They have occupied nearly every niche available to a large herbivore, from dog-sized running animals, to several hippopotamus-like forms, to the largest land mammal that ever lived, *Paraceratherium* (once called *Baluchitherium* or *Indricotherium*). Most rhinoceroses were hornless. Rhinos with horns first appeared about 28 million years ago; two different lineages independently evolved paired horns on the tip of the nose. Other groups evolved a single nasal horn, or a huge horn on the forehead, or a pair of horns in tandem on nose and forehead. Unlike the horns of cattle, sheep and goats, rhino horns are made of

cemented hair fibres, and have no bony core.

Between 5 and 20 million years ago, rhinos diversified into several browsing (leaf-eating) lineages, and hippopotamus-like grazing lineages, and browser–grazer pairs of rhinos were found all over the grasslands of Eurasia, Africa and North America. The mass extinction event that occurred about 5 million years ago exterminated North American rhinos, and decimated most of the archaic rhino lineages in the Old World. During the Ice Ages, woolly rhinos and their relatives were common all over Eurasia, their only surviving descendant being the endangered Sumatran rhinoceros.

Phylogeny

Prothero and Schoch summarized the most recent comprehensive phylogenetic analysis of the group in 1989. As outlined above, the sister taxa of the perissodactyls include the hyraxes and the tethytheres (elephants, sirenians and their extinct relatives). The Hippomorpha are divided into two clades, the Palaeotheriidae and the Equidae. The latter family has had an extremely diverse, bushy phylogenetic history, with many subgroups, including the browsing Anchitheriinae, the three-toed Hipparionini, and the living tribe Equini. The Titanotheriomorpha have been allied to the Hippomorpha by some authors, and to the chalicotheres by others, but there are no strong derived characters supporting either hypothesis of relationship. The Moropomorpha have a complex pectinate phylogeny, with the isctolophids branching off first, followed by the lophiodont-chalicotheres clade, several other extinct groups of ‘tapiroids’, and finally the tapirids and rhinocerotoids as the crown group of the cladogram.

Synopsis

Although they are nearly extinct in the wild today, the order Perissodactyla has been one of the most diverse, ecologically dominant, and successful groups of hoofed mammals throughout the last 55 million years. Originating from the late Palaeocene *Radinskya* of China, by the early Eocene the major groups of perissodactyls had differentiated, and migrated to Europe and North America. Before 34 million years ago, the brontotheres and the archaic tapirs were the largest and most abundant hoofed mammals in Eurasia and North America. After these groups died out, horses and rhinoceroses were the most common perissodactyls, with a great diversity of species and body forms. Both groups were decimated during another mass extinction about five million years ago, and today only five species of rhinoceros, four species of tapir, and seven species of horses, zebras, and asses cling to survival in the wild. The niches of large-hoofed herbivores have been taken over by the ruminant artiodactyls, such as cattle, antelopes, deer and their relatives.

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