From Singer, R. (ed.), 1999, *Encyclopedia of Paleontology*, Fitzroy Dearborn Publishers, Chicago.

PERISSODACTYLS

The perissodactyls are the order of herbivorous "odd-toed" hoofed mammals that includes the living horses, zebras, asses, tapirs, rhinoceroses, and their extinct relatives (Figure 1). They are recognized by a number of unique specializations, but their most distinctive feature is their feet. Most perissodactyls have either one or three toes on each foot, and the axis of symmetry of the foot runs through the middle digit. The woodchuck-like hyraxes, or conies, are apparently closely related to perissodactyls, although there is still some controversy about their relationships. The perissodactyls (other than hyraxes) are divided into three groups: the Hippomorpha (horses and their extinct relatives), the Titanotheriomorpha (the extinct brontotheres), and the Moropomorpha (tapirs, rhinoceroses, and their extinct relatives).

Origins

Perissodactyls once were thought to have evolved in Central America from the phenacodonts, an extinct group of archaic hoofed mammals placed in the invalid taxon (group; plural, taxa) "Condylarthra." Then, in 1989 a specimen was recovered from deposits in China approximately 57 million years old. Described and named *Radinskya,* this specimen shows that perissodactyls originated in Asia approximately 57 million years ago and were unrelated to North American phenacodonts. *Radinskya* is very similar to the earliest relatives of the tethytheres (the proboscideans, or elephants, plus manatees, and their kin). This agrees with other evidence that perissodactyls are more closely related to tethytheres than to any other group of mammals.

By 55 million years ago, the major groups of perissodactyls had differentiated and migrated from Asia 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 became extinct, horses and rhinoceroses were the most common perissodactyls, with a great diversity of species and body forms. About five million years ago, both groups were decimated during another mass extinction, and today only five species of rhinoceros, four species of tapir, and a few 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.

Horses

From their Asian origin, the hippomorphs spread all over the northern continents. In Europe, the horselike palaeotheres substituted for true horses. North America became the center of evolution of true horses, which occasionally migrated to other continents. *Protorohippus* (once called *Hyracotherium* or *Eohippus*) was a terrier-sized horse with four toes on the front feet. It lived 55 to 50 million years ago, and its descendants evolved into many different lineages living side-by-side. Fossils of the collie-sized three-

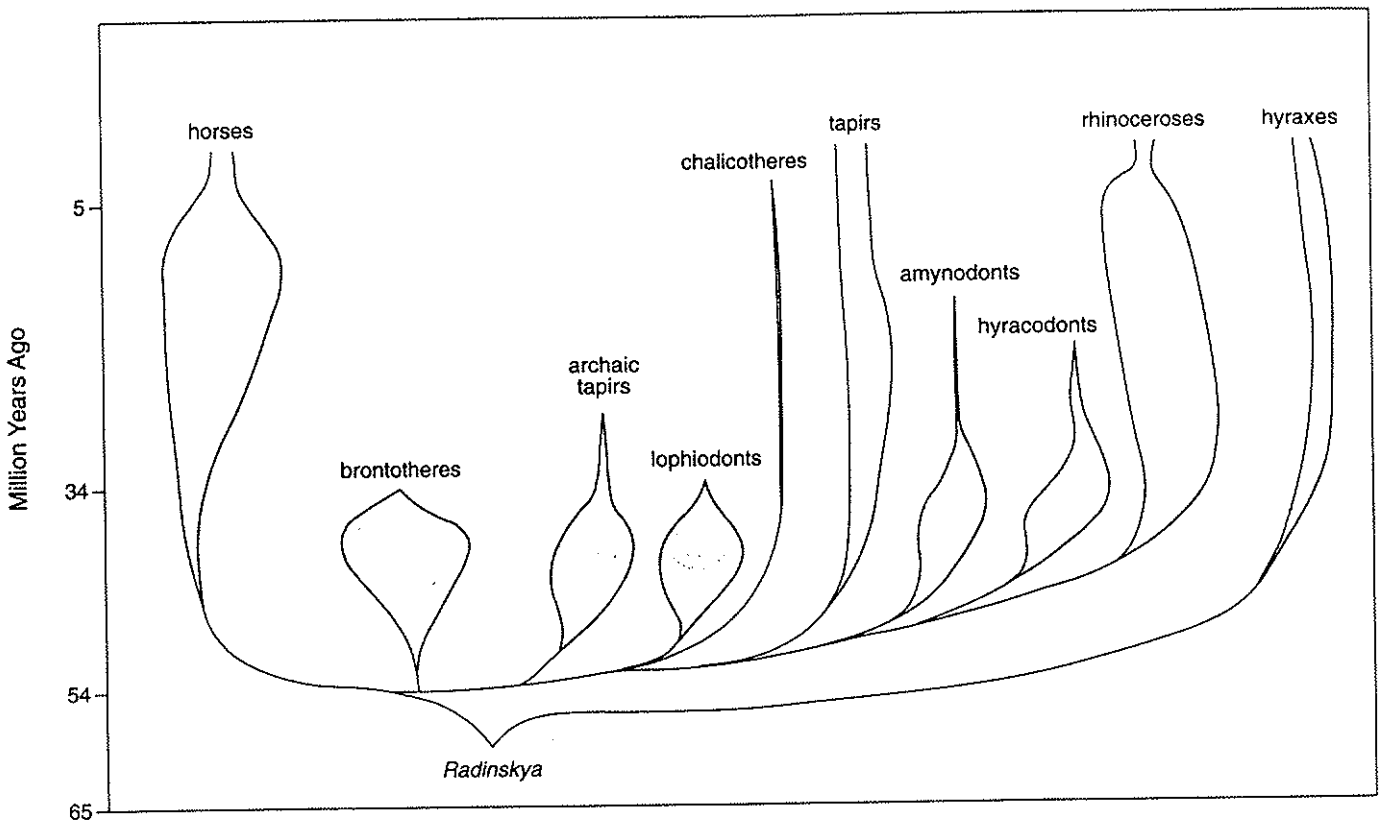

Figure 1. Family tree of the perissodactyls. Illustration by Catherine P. Sexton, after Prothero and Schoch, 1998.

toed horses *Mesohippus* and *Miohippus* (from rock strata, or layers, dated approximately 30 to 37 million years ago) once were believed to be sequential segments on the unbranched trunk of the horse evolutionary tree. However, these groups coexisted for millions of years, with five different species of the two genera (groups; singular, genus) living at the same time and place. From *Miohippus*-like ancestors, horses diversified into many different ecological niches. One major lineage, the anchitherines, retained low-crowned teeth, presumably for browsing soft leaves in the forests. Some anchitherines, such as *Megahippus*, were almost as large as the living horse. *Anchitherium* migrated from North America to Europe approximately 20 million years ago, the first true horse to reach Europe.

Approximately 15 million years ago, there were at least 12 different lineages of three-toed horses in North America, each with slightly different ecological specializations. This situation is analogous to the diversity of modern antelopes in East Africa. The ancestors of this great radiation (spread and diversity) of horses are a group of three-toed, pony-sized animals that long have been lumped into the "wastebasket" genus *Merychippus*. However, recent analyses have shown that the species of "*Merychippus*" are ancestral to many different lineages of horses. True *Merychippus* was a member of the hipparion lineage, a group of three-toed horses that developed highly specialized teeth and had a distinctively concave bone on the front of the face. Hipparions were a highly diverse and successful group of horses, with seven or eight different genera spread not only across North America but also migrating to Eurasia. Merychippines also were ancestral to lineages such as *Calippus* (a tiny dwarf horse), *Protohippus*, and *Astrohippus*.

On two different occasions (*Pliohippus* and *Dinohippus*), three-toed horses evolved into lineages with a single toe on each foot. Approximately 5 million years ago, most of these three-toed and one-toed horse lineages became extinct, leaving only *Dinohippus* to evolve into the modern horse *Equus*. The main lineage of horses, known as the equines, survived the extinctions 5 million years ago. The living genus *Equus* first appeared approximately 3 million years ago and was widespread throughout the northern hemisphere. When the Isthmus of Panama rose approximately 2.5 million years ago, horses also spread to South America. There they evolved into the hippidions, distinctive horses with a short proboscis. At the end of the last Ice Age (approximately 10,000 years ago), horses became extinct in the New World. They were reintroduced to their ancestral homeland by Columbus in 1493. Wild horses that have escaped from domesticated stock are known as mustangs.

Most extinct horses were browsers that ate soft, leafy vegetation, but all living horses are grazers, using their sharp incisors and mobile lips to crop low-growing grasses. The only common wild

horse, the plains zebra, lives in large herds (up to 100 individuals) and migrates over large areas of grasslands in search of food. Grevy's zebra, on the other hand, is a denizen of the African deserts, living in small herds, with a stallion guarding a small harem of mares. The mountain zebra is extremely scarce and is confined to the high elevations of southern Africa. The quagga, a partially striped zebra from southern Africa, became extinct in 1883.

The purpose of zebra stripes long has been a mystery. Plains zebras live on the open grasslands, not in the dense undergrowth where stripes might help camouflage the body (as do the stripes on a tiger). Zoologists now believe that when a herd of zebras stampede, their coloration creates a dizzying arrangement of moving stripes that makes it hard for a predator 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-colored horses and asses can be thought of as zebras that have lost their stripes.

In addition to the three living species of zebras, there also are 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 into their backgrounds. Their long legs and ears help them shed heat in the desert, and the long ears also aid in long-range hearing to warn them of danger. Their narrow hooves are excellent for moving across rocky terrain without slipping. The onager, a common Asiatic ass, lives in deserts from Mongolia to Iran to Syria to Turkey. Tibet's high plateaus are home to the kiang, or Tibetan wild ass, which is adapted to the cold, harsh conditions in the Himalayan steppes between 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 wild ass. Its incredible ruggedness and ability to carry large loads over long distances are inherited from its ancestry among the desert-dwelling asses of Africa and Asia.

All living domesticated horses are thought to have descended from wild species once found in the steppes of central Asia. The only living relic of these wild horses is Przewalski's horse, fossils of which date as far back as the Ice Age, over 200,000 years ago. These horses have reddish brown coats, a short stiff mane, a light ring around the eyes and a dark stripe along the back. Around 6,000 years ago, prehistoric populations of Ukrainian nomads first began to domesticate the horse. Today, they are apparently extinct in the wild, although a number of zoos have specimens. Even though it is extinct in the wild, Przewalski's horse has many thousands of descendants in stables and also running wild as mustangs.

Brontotheres (Titanotheres)

The brontotheres began as pig-sized, hornless animals approximately 53 million years ago, and quickly evolved into multiple lineages of cow-sized animals with long skulls and no horns. In the late Middle Eocene (between 40 and 47 million years ago), there were six different lineages of brontotheres. Some had long skulls, while others had short snouts and broad skulls. Still others had a pair of tiny blunt horns on the tip of their noses. Between 37 and 34 million years ago, their evolution culminated with huge, elephant-sized beasts bearing paired blunt horns on their noses. Throughout their history, brontotheres were the largest animals in North America. They also appeared in Asia in the Late Eocene, where beasts such as *Embolotherium*, with a huge single "battering-ram" horn, evolved.

Because of their large size and spectacular appearance, brontotheres frequently have been illustrated in popular books, but much of what is said about them is wrong or badly out of date. In 1929, Henry Fairfield Osborn published an imposing two-volume monograph on brontotheres. Unfortunately, most of what Osborn wrote is wrong, and paleontologists have just begun to correct his mistakes. For example, he divided the North American brontotheres into dozens of genera in 12 subfamilies, but currently only 18 genera in 2 subfamilies are recognized. Osborn was a believer in "straight-line" evolution and showed brontothere evolution as a simple linear sequence of genera. Modern research, on the other hand, shows that multiple genera lived at the same time and adopts no linear evolutionary trend. Most of the names that appear in popular books, such as *Brontotherium, Titanotherium, Titanops, Diploclonus,* or *Menodus,* are no longer valid. Only three genera (*Megacerops, Menops,* and *Brontops*) are recognized for the huge brontotheres of the Late Eocene, with a pair of horns near the snout. Numerous paleontologists have compared the "battering ram" horns of brontotheres to those of sheep and goats, suggesting that brontotheres rammed head-to-head after lowering their horns and charging. However, this cannot be so, because the bone in the snout beneath the horn is very delicate and spongy and could not have survived a strong impact without shattering the skull. Instead, brontothere horns served mainly for display, fighting off predators, and low-impact wrestling and butting with other brontotheres. One brontothere specimen shows a healed fracture high in the rib cage, a wound most likely inflicted by the horn of another brontothere.

Finally, Osborn thought that brontotheres became extinct because of some internal forces during their evolution, or "racial senescence." Recent research has shown that the extinction of brontotheres approximately 34 million years ago was owing to a global climatic change (triggered by the first Antarctic glaciers) that caused worldwide cooling and drying of climates. This change decimated the forests of the temperate regions and eliminated most of the soft, leafy vegetation on which brontotheres fed.

Moropomorphs

The earliest moropomorphs, such as *Homogalax*, occur in rock strata approximately 55 million years old. They are virtually indistinguishable from the earliest horses, such as *Protorohippus*. 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 they died out when their forest habitats shrank, approximately 34 million years ago. Only the modern tapir, with its distinctive long proboscis, still survives in the jungles of Central and South America (three species) and southeast Asia (one species). All are stocky, piglike beasts with short stout legs, oval

hooves, and a short tail. They have no natural defenses against large predators (such as jaguars or tigers), so they are expert at fleeing through dense brush and swimming to make their escape.

Another moropomorph group, the horselike clawed chalicotheres, are closely related to some of these archaic tapirs. When chalicotheres were first discovered, paleontologists refused to believe that the claws belonged to a hoofed mammal related to horses and rhinos. However, many specimens have clearly shown that chalicotheres are an example of a hoofed mammal that evolved to regain its claws. There has been much speculation about the uses of chalicothere claws. Traditionally, they were considered useful for digging up roots and tubers, except that the fossilized claws show no sign of the characteristic scratches due to digging. Instead, chalicotheres 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 hind limbs that it apparently knuckle-walked like a gorilla, with its claws curled inward. In North America and Eurasia, chalicotheres were always rare; however, the animal did survive in Africa until the Ice Ages.

Rhinoceroses

The third group of moropomorphs, the 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 hippolike forms, to the largest land mammal that ever lived, *Paraceratherium*. Unlike the horns of cattle, sheep, and goats, rhino horns are made of cemented hair fibers. Having no bony core, they rarely fossilize. In fossils, the presence and size of the horn must be inferred from a roughened area on the top of the skull where the horn once attached. Most rhinoceroses were hornless. Even in species without horns, rhino fossils are easy to recognize by a number of anatomical features in the skeleton, skull, and braincase. One of the easiest to spot is the crests on the crowns of the upper molars, which look like the Greek letter "pi" (π).

The earliest rhinos, known as *Hyrachyus*, were widespread over Eurasia and North America approximately 53 million years ago and are even found in the Canadian Arctic. They apparently crossed back and forth between Europe and North America using a land bridge across the North Atlantic (before that ocean opened to its present width). From *Hyrachyus* three different families of rhino diverged. One family, the amynodonts, were hippolike amphibious forms, with stumpy legs and a barrel chest for living in ponds and rivers. They occupied this niche long before the hippo evolved. In addition, amynodonts are usually found in river and lake deposits. The last of the amynodonts, which had a short trunk like an elephant's, died out in Asia approximately 15 million years ago.

The second family was known as the hyracodonts, or "running rhinos," because they had unusually long slender legs compared to other rhinos. They were particularly common in Asia and North America between 42 and 34 million years ago. The last of the North American forms was *Hyracodon*, which was about the size and proportions of a Great Dane and survived until approximately 29 million years ago. The second group of hyracodonts were the gigantic indricotheres, which were the largest mammals in Asia during the Late Eocene and Oligocene (approximately 40 to 30 million years ago). The biggest of all was *Paraceratherium* (once called *Baluchitherium* or *Indricotherium*), which was 6 meters tall at the shoulder and weighed 20,000 kilograms). It was so tall that it must have browsed leaves from the tops of trees, as giraffes do today. Despite its huge bulk, it did not have the massive limbs and short, compressed toes of most giant land animals, such as sauropod dinosaurs, brontotheres, or elephants. Instead, it reveals its heritage as a running rhino by retaining its long slender toes—even though it was much too large to run. Indricotheres were also the last of the hyracodonts, vanishing from Asia approximately 15 million years ago.

The third family is the true rhinoceroses, or family Rhinocerotidae. They first appeared in Asia and North America approximately 40 million years ago and lived side-by-side with the hyracodonts and amynodonts on both continents. Rhinocerotids can be distinguished from hyracodonts and amynodonts by their distinctive molars and by the development of a tusklike lower incisor which occluded against a chisel-like upper incisor. In the Late Eocene and Early Oligocene (approximately 37 to 28 million years ago), there were several different genera of rhinocerotids, including the primitive *Trigonias* and the common Badlands rhinocerotid, *Subhyracodon* (formerly called *Caenopus*). These cow-sized animals had low-crowned teeth for eating soft, leafy vegetation and probably lived in the more densely wooded parts of their habitat, unlike the running hyracodonts (which lived in open habitats) or the amphibious amyndonts (which occupied the rivers and lakes). When the brontotheres died out approximately 34 million years ago, rhinocerotids were the largest land mammals in North America, and they remained so until mastodonts arrived approximately 16 million years ago.

Until this point, all the rhinoceroses we have mentioned were hornless. Rhinos with horns first appeared approximately 28 million years ago; two different lineages independently evolved paired horns on the tip of the nose. Both of these groups became extinct approximately 18 million years ago, when two new subfamilies immigrated to North America from Asia: the browsing (leaf-eating) aceratherines, and hippolike grazing teleoceratines. Between 18 and 5 million years ago, browser-grazer pairs of rhinos were found all over the grasslands of Eurasia, Africa, and North America. The teleoceratine *Teleoceras* was remarkably similar to hippos, with its short limbs, massive barrel-shaped body, and high-crowned teeth for eating gritty grasses. We know these animals were aquatic because they are usually found in ancient lake or river sediments. Some extraordinary specimens buried in volcanic ash preserve the grass seeds of their last meal.

A mass extinction event that occurred approximately five million years ago wiped out North American rhinos and decimated most of the archaic rhino lineages (especially the teleoceratines and aceratherines) in the Old World. The surviving lineages diversified in Eurasia and Africa and even thrived during the Ice Ages. They included the gigantic, elephant-sized elasmotheres, which had a huge 2-meter-long horn in the center of their forehead. Elasmotheres were found from Spain to Siberia to China during the Ice Ages, as were the woolly rhinos and their relatives. Woolly rhinos are known from numerous mummified specimens

that give us detailed information about their hair, tissues, and even stomach contents. Their two horns grew one in front of the other along the snout and were shaped like flattened blades resembling sabers. Scratches on the front edge show that they were used to scrape away snow in the search for food. Despite the great success of woolly rhinos all over Eurasia during the Ice Ages, for some reason they never crossed the Bering land bridge back into North America (even though the woolly mammoths and bison did). The only surviving descendant of the woolly rhino lineage is the endangered Sumatran rhinoceros. Only a few hundred individuals still live in the mountainous jungles of Sumatra.

Four other species of rhino survive in Asia and Africa. The Javan rhinoceros is rarely seen in the dense jungles of Java and Vietnam; fewer than 50 individuals may still be living in the wild. The Indian rhinoceros and the two African rhinos (the browsing black rhinoceros and the grazing white rhinoceros) inhabit grasslands, although they prefer to hide in dense vegetation. Rhinos have very poor eyesight but excellent senses of smell and hearing, so they can detect danger long before being seen by predators. Most live in small family groups of females with their calves; bull rhinos tend to be solitary.

All of the living species of rhinoceros are on the brink of extinction owing to heavy poaching for their horns. Rhino horn is widely used in Chinese folk medicine for reducing fevers and is also popular for the handles of the traditional dagger worn in the Arab states. As a result, the poaching has been particularly intense, because rhino horn is more valuable per ounce than gold or cocaine. In the 1970s and 1980s, the slaughter was so severe that over 90 percent of the rhinos living in the wild (hundreds of thousands of animals) were killed, leaving only a few thousand in countries in Africa (such as South Africa and Zimbabwe) that have excellent game protection. Despite the international ban on the trade of rhino horn and protection as endangered species, rhinos are still being killed and their horn smuggled through the black market because the demand of Chinese apothecaries only increases as the horn becomes scarcer.

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