

UNGULATES, ARCHAIC

The ungulates, or hoofed animals, include most of the extinct and living large-bodied herbivorous mammals (Figure 1). They make up over one-third of the known genera (groups, singular genus) and families of mammals, outnumbering even the rodents. Ungulates include the even-toed artiodactyls (pigs, hippos, peccaries, camels, deer, cattle, antelope, sheep, giraffes, and their extinct relatives), the odd-toed perissodactyls (horses, rhinos, tapirs, hyraxes, and their extinct relatives), the tethytheres (the proboscideans, or elephants, plus manatees, and their extinct relatives), and surprisingly, the cetaceans (whales) and their extinct relatives, the mesonychids. The largest known animal (the blue whale), the largest known land mammal (the extinct rhinoceros *Paraceratherium*), and the largest living land mammal (the African elephant) are all ungulates.

Ungulates dominate the large herbivore niche in most ecosystems, but they were much more ecologically diverse. Some groups were probably bearlike omnivores, while the whales and their relatives feed on fish, squid, or plankton. Although ungulates are partially defined as having hooves on their toes, several groups (including the whales and manatees) have evolved further to become aquatic and have not only lost their hooves but even their hind limbs; their arms have become flippers. Some ungulates (such as elephants and several extinct groups) became huge, with thick, stocky limbs, while others became adapted for running (especially horses, antelopes, and many extinct ungulates). One group is even adapted for climbing trees.

The earliest ungulates were only the size of rats and showed no obvious signs of evolving into horses, elephants, cows, or whales. Discovered in Late Cretaceous (85-million-year-old) rocks in Uzbekistan in central Asia, these earliest ungulates (called the "zhlestids") already showed the characteristic ungulate teeth, with low rounded cusps for grinding vegetation. By the end of the age of dinosaurs, 65 million years ago, ungulates were represented by a rat-sized animal known as *Protungulatum* ("first ungulate"), which had not only plant-eating molar teeth but also a highly distinctive foot and ankle structure that distinguished ungulates from primates, insectivores (such as moles and shrews), and other mammals that lived in a world dominated by *Tyrannosaurus* and *Triceratops*.

After the extinction of the dinosaurs, hoofed mammals evolved rapidly to fill the niche of large-bodied herbivores and have dominated that role ever since. Almost 70 percent of the mammals that arose during the Early Paleocene (the time immediately after the extinction of the dinosaurs) are ungulates. The earliest group to evolve from *Protungulatum* were the arctocyonids. Although these animals had low-crowned, blunt molar teeth for eating an omnivorous diet and hooves on their fingers and toes, they were similar in size and ecology to raccoons. The largest members of this group, such as *Claenodon* and *Arctocyon*, date from the Late Paleocene (60 to 56 million years ago) in Europe and North America. These animals were the size of small bears, and given their large canine teeth and low-crowned molars for eating a wide variety of foods, they probably also lived and fed much like bears.

One of the earliest groups to branch off from this ancestral ungulate stock were the even-toed hoofed mammals, or artiodactyls. The next major group of archaic ungulates include the periptychids and the hyopsodonts. Periptychids were particularly common in the Early Paleocene, some 60 to 65 million years ago. The periptychid *Ectoconus* was a large (2 meters long), clumsy, unspecialized animal, with broad five-toed feet and a long tail. Periptychids have few specializations except for their teeth, which have a peculiarly wrinkled enamel surface that is immediately recognizable. They were extinct by the end of the Paleocene, about 55 million years ago.

Although closely related to periptychids, hyopsodonts were much smaller animals having the size and proportions of a dachshund. These animals were particularly common in the Late Paleocene and Early Eocene, between 58 and 50 million years ago. Hyopsodont molars have high crowns with numerous cusps, sometimes forming half-moon-shaped crests that vaguely resemble the teeth of artiodactyls, but apparently this is the result of evolutionary convergence (they evolved independently). Although hyopsodonts became increasingly rare after the Early Eocene, they straggled on until the late Middle Eocene, about 45 million years ago. They were the last of the archaic ungulate groups to become extinct.

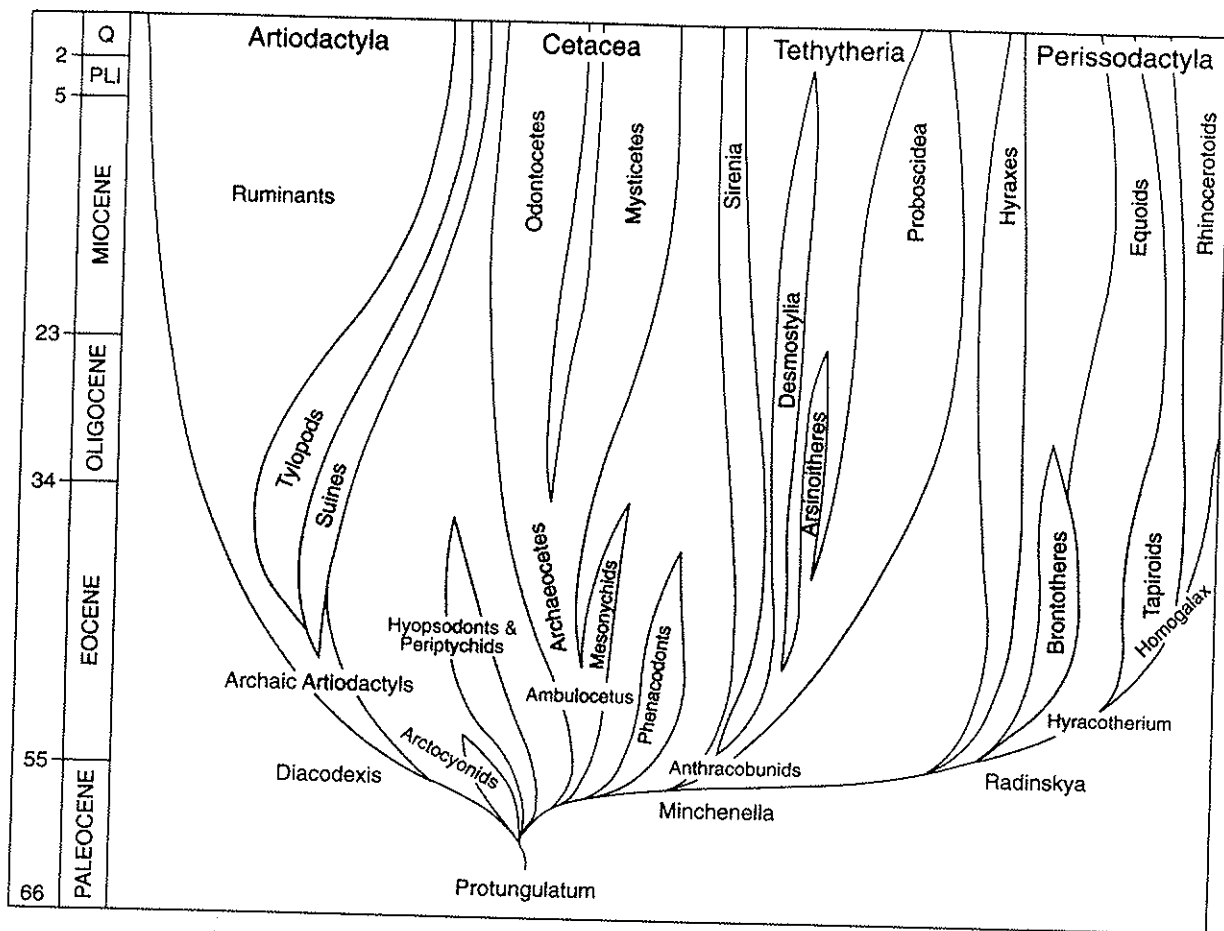


Figure 1. Family tree of the ungulates, or hoofed mammals; the various archaic lineages at the base of the radiation (such as the arctocyonids, periptychids plus hyopsodonts, phenacodonts, and mesonychids) were once placed in a "wastebasket" order "Condylarthra." Illustration by Catherine P. Sexton, after Prothero and Schoch (1998).

After the early divergence of artiodactyls, and the hyopsodont-periptychid group from the archaic arctocyonids, the next major group to branch off was the whales and their extinct relatives, called the mesonychids. Finally, the higher ungulates (perissodactyls, tethytheres, and their extinct relatives) diverged from the common ungulate stock. The most primitive group in the perissodactyl-tethythere lineage is known as "phenacodonts." They were common animals of the Late Paleocene and Early Eocene, but their abundance and diversity decreased rapidly during the Middle Eocene until their final extinction about 47 million years ago. The sheep-sized *Phenacodus* had relatively long toes and limbs and a long tail. Its ankles were specialized for front-to-back running and had restricted ability to move side-to-side. The molar teeth were highly squared off and flattened for eating vegetation, and the canines were relatively reduced.

For many years, paleontologists thought that the phenacodonts were ancestors of the perissodactyls, since the resemblance between Late Paleocene phenacodonts such as *Tetraclaenodon* and the earliest perissodactyls is quite close. However, that notion has been discredited by the discovery of fossils much closer to perisso-

dactyls, such as *Radinskya*, dating from the Late Paleocene of China. Another group from the Late Paleocene and Early Eocene, the meniscotheres, developed molars with half-moon-shaped crests on their crowns very early, but these are apparently convergent on the molars of artiodactyls and hyopsodonts. Meniscotheres are now considered a subgroup of the phenacodonts.

For over a century, some archaic hoofed mammals (arctocyonids, periptychids, hyopsodonts, phenacodonts, meniscotheres, and mesonychids) were not clearly related to the living perissodactyls, artiodactyls, tethytheres, or whales. These "orphan" groups were placed in a taxonomic "wastebasket," the order "Condylarthra." The name "condylarth" is completely meaningless, except as a convenient term for hoofed mammals that were not clearly members of living groups. Since 1988, however, the phylogenetic relationships of the ungulates have become much clearer, so the term "condylarth" is obsolete and has no further use. It is disappearing from paleontology, since it obscures evolutionary relationships.

See also Artiodactyls; Hyraxes; Mesonychids; Perissodactyls; Proboscideans; Sirenians; Whales

Further Reading

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