The Rise and Fall of the American R

For 45 million years, North America was the land of the hyracodonts, amynodonts, and rhinocerotids

by Donald R. Prothero

One day in early December of 1850, a package was delivered to Joseph Leidy in his Philadelphia study. Its contents were to prove startling. A pioneering scientist in the study of American fossil mammals, Leidy had been receiving shipments of fossils since 1847 from collectors working in the wild Dakota territory. Some contained fossils of typically American mammals, such as dogs, cats, rabbits, peccaries, and deer, although these fossils were often such early types that they could barely be recognized for what they were. Others held remains of extinct animals with no living descendants. (Leidy's knowledge of anatomy often enabled him to describe what these strange beasts might have looked like.) Some parcels contained the bones of mammals with extant relatives on other continents but not previously known to have lived in North America. These included primitive horses and camels. On this particular day, Leidy's package of fossils was of the last group: it contained teeth and an upper jaw of what was unquestionably a North American rhinoceros.

Leidy exhibited the bones at the next meeting of the Philadelphia Academy of Natural Sciences. There he gave the rhino the scientific name *Rhinoceros occidentalis*, or "Western rhinoceros." Throughout the remaining twenty years of his scientific career, Leidy continued to receive rhinoceros fossils from the Dakotas, Oregon, California, Nebraska, Texas, and even Florida. (Florida is among the few states east of the Mississippi that have any terrestrial fossil deposits from the geological time of American rhinos.) Leidy and his contemporaries went on to give descriptions of many other rhinoceros fossils. By the turn of the century, the picture was becoming clear. Rhinoceroses had not only lived in North America, they were

Rhino

The plains of western Nebraska in the late Miocene hosted great congregations of mammals. In Charles Knight's depiction of a 10-million-year-old scene, forerunners of the American pronghorn (left) and of the modern horse (right) graze, while giraffe-camels stretch to browse the treetops. Center stage, a herd of the North American rhino Teleoceras *takes to the placid water. Knight painted this mural for the American Museum of Natural History in New York in 1930.*
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also the commonest large herbivores on this continent for most of the last 50 million years.

In the last two decades, the number of North American rhinoceros fossils has multiplied many times, and the quality of the sample has vastly improved. Some fossil quarries have produced thousands of rhino bones. Research is just now catching up. In the American Museum of Natural History alone, an entire storage floor is devoted to rhino bones. A typical Museum drawer may contain two hundred right kneecaps of one species from one quarry, all neatly arranged. The thighbones of a single population of another species might fill an entire cabinet.

Rhinos have one of the best fossil records of any North American mammal, fully as good as that of the horse. Unlike horses, however, rhinos exploited a wide variety of ecological niches and took many forms, from sheep-sized runners to hippo-like grazers. In North America, rhinos were the largest herbivores until 15 million years ago, when mastodons began to share that niche. (Nearly every continental ecosystem has a large mammalian herbivore that can eat the highest-growing, toughest vegetation and is relatively protected from predation by its size.) Indeed, the evolutionary history of rhinos is typical of many groups of North American mammals: early diversification and experimentation; then specialization into distinct lineages; finally, extinction, usually during a major climatic change.

When we think of rhinos today, the first thing that comes to mind is their horn. But because rhino horns are composed of agglutinated hair, rather than bone, they are not often preserved as fossils (horns, however, leave rough, bumpy areas where they were attached to the skull). Moreover, most extinct rhinos were hornless.

The size of a Great Dane, Hyracodon *raced across the grasslands of the Dakota Badlands some 30 million years ago. The hyracodonts, one of three main rhino lines to evolve, were long-legged, efficient runners.*
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Paleontologists recognize fossil rhinos chiefly by their distinctive teeth and by features of the skull. In most other respects, the very earliest rhinoceroses bear little resemblance to living rhinos.

Rhinos are members of the order Perissodactyla, or the "odd-toed" hoofed mammals. Their closest living relatives are horses and tapirs. Unlike the even-toed pigs, sheep, deer, camels, and cattle, rhinos, horses, and tapirs have feet with either one or three toes. Early rhinos were sheep-sized mammals that were widespread in Eurasia and North America in the middle Eocene, about 50 million years ago. At that time, the world was much warmer and more tropical than it is today. There were no polar icecaps. The Eocene climate was so mild that alligators and semitropical plants lived in Alaska. In temperate Eurasia and North America, the climate and vegetation were similar to those of tropical Mexico today. The inhabitants of this environment showed few of the specializations of modern rhinos, horses, or tapirs. Instead, they were primitive mammals with low-crowned teeth, for browsing leaves, and short limbs with a full complement of five toes. The best known of the early rhinos was *Hyrachyus*, which looked much like its close relatives among the early horses and tapirs. From this primitive, unspecialized ancestor, rhinos diverged into three major lines during the late Eocene. Two of these families flourished for about 10 million years and then became extinct. The third is the family of the living rhinoceroses.

The first branch to emerge from the basic rhino line was the amynodonts. In the late Eocene, amynodonts rapidly joined the ranks of the largest land mammals in North America and Eurasia. By the Oligocene, some 37 million years ago, they had become very specialized. In North America, they were represented by the stocky, hippolike river dweller *Metamynodon*. Remains of this animal are so characteristic of the river-channel sandstones of the Badlands of South Dakota that these beds are known as the *Metamynodon* channels. Amynodonts disappeared from North America about 30 million years ago but persisted in Eurasia until about 15 million years ago. One group of amynodonts, the cadurcodonts, developed a short trunk, or proboscis, much like that of a tapir or elephant. Presumably, they lived in the forest and browsed with their snouts, as tapirs do today. The last surviving amynodont, *Cadurcotherium*, vanished from Pakistan and Burma at about the time that mastodons emigrated from Africa, where they had been evolving in isolation for millions of years. Perhaps amynodonts were driven to extinction by competition from mastodons or from the more advanced rhinos that had appeared in Asia by this time.

While the squat, semiaquatic amynodonts wallowed and browsed in the riparian habitats of Oligocene North America and Asia, the second major branch of rhinos was evolving. These were running rhinos, or hyracodonts. Small and unspecialized through the late Eocene, they differed only slightly from their ancestor *Hyrachyus*. One key difference distin-

guished hyracodonts from all other rhinos: their limbs, and especially their feet, were elongated for more efficient running.

By the Oligocene, the environment of the rhinos had changed. Worldwide cooling in the early Oligocene was triggered by the beginning of glaciation in the Antarctic. Naturally, the vegetation in the temperate climates changed in response to this cooling. In what is now the Dakota Badlands, the fossil soils tell the story. As described by Greg Retallack of the University of Oregon, the early Oligocene soils were formed under thick forests, which by the late Oligocene, were broken up into mixed forest and open savanna.

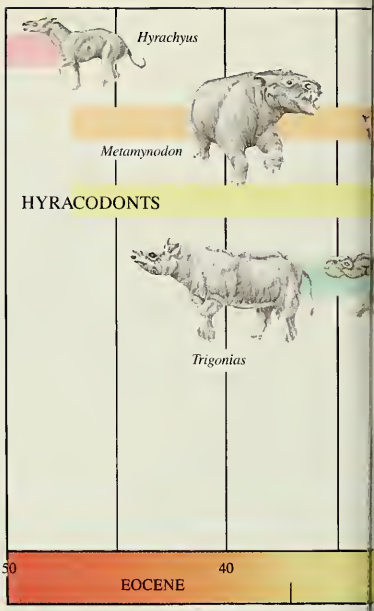
Most archaic animals did not survive this change. Some animals that were better adapted to this new habitat diversified. Rhinos succeeded by diverging into distinct ecological niches: the aquatic amynodonts could be found wallowing in the river channels; the running hyracodonts probably frequented the open savanna. *Hyracodon* was about the size of a Great Dane and slightly larger than *Mesohippus*, the horse of its time. *Hyracodon* vanished from North America about 28 million years ago, but in Eurasia, its relatives had specialized in a different way—they had become gigantic.

And gigantic they were! The largest rhino—and the largest land mammal ever to live—was *Paraceratherium* (also known as *Baluchitherium* or *Indricotherium*), which could browse, giraffelike, in the tops of trees twenty-five feet high and may have weighed twenty-five tons. The Museum found some of the best fossils of these giants on the famous central Asian expeditions to Mongolia in 1922. In one place, they found all four legs of this beast buried and fossilized upright, exactly where it had sunk into quicksand and died. Even as a weighty mammalian record holder, *Paraceratherium* retained the hallmarks of its running hyracodont ancestry. The limbs were long, and the three toes of each foot were still elongated, although such a beast clearly didn't need to run from predators. Most large animals, such as elephants and dinosaurs, have short, compressed toes designed to sustain their great weight. The long legs and toes of *Paraceratherium* are a good example of how vestiges of inherited anatomy can be retained even when no longer used for their original purpose.

While amynodonts and hyracodonts adapted to aquatic, running, or giraffelike life styles, the main rhino branch remained relatively unspecialized. What we call true rhinoceroses, the family Rhinocerotidae (the only surviving rhino family), also developed in the late Eocene; the first known rhinocerotid fossil on this continent was found in Oregon and dates to about 40 million years ago. Apparently they, like many species before and since, immigrated across the Bering Strait from Eurasia and continued to develop in both the Old and New World. The first North American rhinocerotid was not much larger than *Hyracodon*, but it already had the key features of a true rhinoceros.

In the Oligocene, the most common true rhino in North America was Leidy's first rhino, *Rhinoceros occidentalis*, now

Some rhinos emigrated to North America, others evolved here, but all were descendants of Hyrachyus *(see chart right). Rhino lines died out in North America, but the rhinocerotids survived in Eurasia and gave rise to the modern rhinos. In contrast to its contemporary, the swift, savanna-dwelling* Hyracodon, Metamynodon, *below right, was a stocky, semiaquatic inhabitant of Dakota streamsides, wallowing in Badlands rivers and browsing on succulent shoots of riparian vegetation.*



known as *Subhyracodon occidentalis* (a misnomer because this rhino was not a hyracodont at all). Nearly horse sized, hornless, and quite unspecialized, it apparently lived in the forested glades around the rivers of what is now South Dakota. By the late Oligocene (about 30 million years ago), *Subhyracodon* had evolved into the first horned rhino, *Diceratherium* ("two-horned beast"). With paired horns on the tip of its nose, *Diceratherium* represents one of two different groups of rhinos that independently evolved paired nasal horns. After the extinction of the amynodont and hyracodont families, it was the undisputed king of late Oligocene North America. The period from about 28 to 21 million years ago was the time of least diversity of rhinos in North America. The solitary reign of *Diceratherium* ended in the earliest Miocene when another rhino appeared on the scene. A recent immigrant from Europe, *Menoceras* was sheep sized. Although it also had paired horns on the tip of its nose, they were very different from those of *Diceratherium*. Instead of the long nasal ridges seen in true *Diceratherium*, rounded knobs on the tips of its nasal bones supported *Menoceras*'s horns. Additional anatomical evidence shows that *Diceratherium* and *Menoceras* were not very closely related. The paired horns on the nose are a good example of evolutionary parallelism. Nevertheless, confused by the similarity, most scientists erroneously called *Menoceras* "*Diceratherium*."

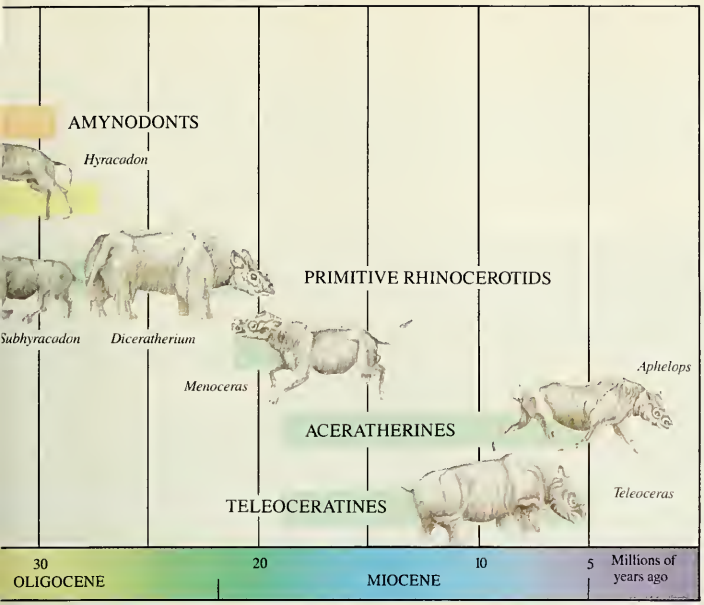
Menoceras is best known from the famous bone beds at Agate Springs National Monument in western Nebraska. In the early part of this century, thousands of fossils of this little rhino were collected by many museums. A typical Agate slab is a solid network of rhino bones. Bob Hunt of the University of Nebraska has analyzed the population structure of the Agate rhinos. The relative numbers of adults and juveniles show that the assemblage represents death at normal rates and under normal conditions and then concentration of the bones by river action.

A few million years after *Menoceras* arrived in North America, there was another wave of immigrations from Eurasia. It brought the two dominant groups of Miocene rhinos, the aceratherines and the teleoceratines, which drove *Diceratherium* to extinction through competition for the large herbivore niche. About 18 million years ago, these groups drove *Menoceras* to extinction, too. Like the horses and most Miocene mammals, both immigrant rhino groups soon developed exceptionally high-crowned teeth for grinding abrasive grasses, which rapidly wear teeth down. This was essential, since the Miocene environment had changed from the mixed forest-savanna of the Oligocene to a world of broad, grassy plains with little foliage to browse on.

Miocene rhinos had to evolve a different set of specializations for this new environment. Typically, rhinos occupy two ecological niches in the savanna. One niche is that of a browser, which selects small amounts of high-quality vegetation. It pulls down tender leaves and shoots, often with a prehensile lip. The African black rhino lives this way to this day. The other niche is that of a grass eater, or grazer. Rather than select high-quality leaves, it mows grass in large quantities to obtain its nutrition. Grazers often have square lips (like the African white rhino) and exceptionally high-crowned teeth.

From the early Miocene onward, two rhinos are usually found in most fossil localities in North America: a hippolike grazer (usually *Teleoceras*) and a prehensile-lipped browser, feeding on leaves and brushy vegetation (usually the aceratherine *Aphelops*). These browser-grazer pairs are a common pattern in rhinos wherever they are found in savanna environments, such as existed in North America throughout the entire Miocene. Miocene rhinos of Eurasia also show similar browser-grazer combinations, although different genera of rhinos are represented.

The aceratherines were nearly always hornless and tended to retain their primitive skeletal proportions, with relatively long legs. Their specialization is evident in their snout. The nasal notch on the skull became deeply incised, leaving room for the attachment of snout muscles that apparently controlled a prehensile lip or even a short trunk. The teleoceratines, on the

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other hand, became highly specialized for an aquatic life style much like that of a hippopotamus. *Teleoceras* had a stout, barrel-shaped body with shortened, stumpy limbs—a better hippo than the hippo itself. Except for a small horn on the tip of its nose, it looked more like a hippo than a rhino. Its bones are found by the thousands in ancient river deposits all over western North America.

The most amazing discovery of *Teleoceras* was made by Mike Voorhies of the University of Nebraska in 1977. Unlike the Agate Springs lode of fossils, Voorhies's find was the site of a catastrophic die-off. Eighteen complete *Teleoceras* skeletons were found in their death pose, buried in volcanic ash in eastern Nebraska—a true rhino Pompeii. *Teleoceras* appears to have been a social, herding beast, unlike the living rhinos, but like hippos. There were some mothers with calves at their sides, and others with unborn fetuses. Grass seeds were found in the throat cavities, evidence that *Teleoceras* was a grazer. This strengthens the analogy with the hippopotamus, since modern hippos spend their days sleeping in the river and nights roaming the banks, feeding on grass.

North American Miocene rhinos exploited other ecological niches as well. Although *Teleoceras* was the dominant hippolike grazer, other rhinos have tried this aquatic life style. Just as *Metamynodon* lived this way in the Oligocene, one species of the aceratherine genus *Peraceras* also developed a heavy-bodied, hippolike form in the middle Miocene. Apparently less successful, it lasted only a few million years and was restricted to northern regions with few *Teleoceras*, such as South Dakota and Montana.

Along the swampy shoreline of the Texas gulf coast lived dwarf species of *Teleoceras* and *Peraceras*. These dwarf rhinos are analogous to the pygmy hippopotamus, which lives today in forested areas in central Africa not inhabited by its full-sized relative. In addition to the pygmy hippo, the forest species of the African elephant and Cape buffalo are also small. Dwarfing appears to be a common evolutionary response of a large sa-

vanna grazer in adapting to the restricted, browsing diet in the denser forest.

After almost 50 million years of dominance, the rhinoceros dynasty came to an end in North America about 5 million years ago. An extinction at the end of the Miocene wiped out not only rhinos but also most of the deerlike animals, pronghorns, and most of the once-diverse camels and horses. Recent data from deep-sea-floor sediment cores have provided an answer to the mystery of the Miocene extinctions. A major expansion of the Antarctic ice sheet trapped vast amounts of seawater as ice; this caused cooling and lowered the sea level worldwide. Sea level dropped so severely that no water flowed through the Strait of Gibraltar, and the Mediterranean became a gigantic salt lake. When it had completely evaporated, a deep basin covered with more than a mile of salt and gypsum remained. These severe changes in temperature, sea level, and oceanic salinity had a devastating effect on most life on land. American rhinos were among the most notable victims.

Only in Africa and Eurasia did relatives of the present-day rhinos survive. They included *Coelodonta*, the woolly rhino depicted by Ice Age peoples, and the Siberian *Elasmotherium*, with a single enormous horn on its forehead. Although many cold-adapted Ice Age mammals, such as the mammoth and bison, successfully crossed the Bering land bridge to North America during the Pleistocene, from about one million to 10,000 years ago, rhinos did not. No one has yet developed a convincing explanation for this curious fact.

The five species of surviving rhinos—the white and black rhinos of Africa and the Indian, Sumatran, and Javan species—are magnificent creatures, but their numbers are a pitiful remnant of their once worldwide distribution. Sadly, these long-successful animals are now on the brink of oblivion as poachers push them inexorably toward extinction. Perhaps by the end of the century, a few horns ground down as supposed medicines in the Orient or carved up into dagger handles for status-conscious Yemenite men will be all that is left of this amazing family. □

One of the last of the North American rhinos, Teleoceras *frequented rivers and lakes, as had* Metamynodon *20 million years earlier. Squat, barrel-chested, and hippolike,* Teleoceras *was a grazer, mowing vast amounts of grass with its specially adapted high-crowned teeth. A site in eastern Nebraska has yielded complete fossil skeletons of* Teleoceras *that were killed and buried by volcanic ash. The remains of calves and unborn young found with the group of adults suggest that these rhinos were social beasts that lived in herds.*

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