NORTH DAKOTA SAVANNA



Habitat reconstruction of a late Eocene/Oligocene mammal community.



Chadron, Brule, & Arikaree Formations



Photo by John Hoganson

Left: Map showing Chadron, Brule, and Arikaree Formation outcrop areas in North Dakota. Above: Outcrops of the Oligocene Brule Formation, Little Badlands, Stark County.

By the Oligocene, about thirty million years ago, the subtropical, swampy forests had given way to a mostly treeless plain, similar to a savanna, in North Dakota. This open plain was a scrubland consisting of shrubs, herbaceous plants, and possibly some grasses. True savanna habitats, dominated by grasslands similar to parts of Africa today, did not become established in the state until the Miocene. The Oligocene climate was seasonal and temperate, with an annual rainfall similar to that in the state today. Ponds and lakes punctuated the open plain, and gallery woodlands grew along the margins of streams and rivers. Rivers flowed across the plain, depositing sand and gravel in their channels. There were seasonal droughts and floods, with the latter spreading silt and mud over vast floodplain areas. Layers of volcanic ash in the rocks indicate that volcanoes were active in the western part of the continent. Sediments deposited in these ways, now lithified, are the Chadron (Eocene), Brule (Oligocene), and Arikaree (Miocene) Formations.72 These rocks have mostly eroded away in North Dakota, but remnants of them cap many buttes in the western part of the state; one spot where they are exposed is the Little Badlands

of Stark County.

The most spectacular mammals that lived during the late Eocene in North Dakota were the brontotheres. The size of elephants, about eight feet (2.5 m) tall at the shoulder, they were some of the largest mammals ever to live in North Dakota. They are also call titanotheres, or "thunder beasts," because of their immense size. Brontotheres resembled rhinoceroses and browsed on the soft forest vegetation in the dry woodlands of that period.73 The large, bony knobs on their snouts, which were probably covered with skin as in modern-day giraffes, were used for display or as weapons during fights among males to establish dominance. Fossils of these animals are found in the Chadron Formation.74 Brontotheres lived during the transition from warm swampland to cooler open-plain conditions, and apparently they did not survive this change because their fossils are not found in the younger Oligocene Brule Formation. Other plants and animals also became extinct at this time.

Fossils recovered from the Brule Formation show that the number of mammal species, mostly adapted for grazing, and the abundance of mammals dramatically increased in



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Brontops, a member of the group of large rhinoceros-like mammals called brontotheres, browsed on soft forest vegetation and was one of the largest mammals ever to live in North Dakota.

Below: *Brontops* lower jaws, Chadron Formation, Eocene, Bowman County, length 410 mm. UND D-232

the warm-temperate, dry, open-plain Oligocene habitats in North Dakota following the Eocene extinctions. Most of these mammals migrated to North America from Asia as a result of a drop in sea level caused by climate cooling and glacier development.⁷⁵ These immigrants were ancestral members of families that still exist today, including dogs, cats, camels, deer, squirrels, beavers, horses, rabbits, rhinoceroses, and mice.⁷⁶ Fish, turtles, lizards, amphibians, birds, insects, gastropods, and bivalves also lived in North Dakota during this time. Many of these animals preferred to occupy specific habitats within the open plain and associated woodlands.

Although there were no dense forests (and thus few treedwelling mammals like primates), sparse gallery woodlands grew along the waterways and other water bodies. We know little about the flora of these riparian forests because few plant fossils have been found. Calcified seeds of



Rhinoceros skull, *Subhyracodon occidentalis*, Brule Formation, Oligocene, Stark County, length 520 cm. The Manitoba Museum.

hackberry trees (*Celtis*) are present, indicating that this tree grew here during the Oligocene. The sparse forests appear to have been the favored habitat of several mammals, although surely these creatures would have roamed the open plains, too. The largest of these were the the giant pig-like *Archaeotherium*, the hippo-like *Metamynodon*, and *Subhyracodon*, one of the early rhinoceroses. Tapir-like in



Excavation of a *Subhyracodon* skeleton, Brule Formation, Stark County, with the ribs of the *Subhyracodon* exposed.

appearance, *Subhyracodon* had short, stout limbs, four-toed front feet, and three-toed hind feet. It had a large, hornless head and grew to lengths of about eight feet (2.5 m). *Subhyracodon* was a plant-eater that lived in herds.

Archaeotherium belonged to the group of pig-like mammals called entelodonts. It was similar in appearance to the living warthog and grew to about four feet (1.2 m) long. It had an elongated skull, with unusual protrusions of bone beneath the eyes. These bony knobs probably provided attachment points for the powerful jaw muscles. *Archaeotherium* mostly ate roots and tubers, but with its powerful jaws and teeth it could have eaten most anything, even carrion; in this sense it was like modern-day pigs. These animals had strong shoulder and neck muscles, as indicated by their bone structure. They may have spent much of their time rooting and grubbing in the ground. Large olfactory lobes suggest that they had a keen sense of smell.

Another pig-like mammal, *Merycoidodon*, and the diminutive horse *Mesohippus* were among the most common animals that lived in North Dakota during the Oligocene. They frequented the forests along the streams and also roamed the open plains. *Merycoidodon* was a member of the now-extinct family Merycoidodontidae, and are also sometimes referred to as oreodonts. These animals had some features that are typical of pigs and others that are typical of camels. They possessed advanced teeth, with long-lasting grinding surfaces adapted for effective side-to-side chewing of vegetation. *Merycoidodon* was sheep-sized, about four feet (1.2 m) long, but probably looked more like a pig or peccary. It was heavily built, with short legs and four-toed feet, and was not an efficient runner. Fossils of

The bony knobs below the eyes of *Archaeotherium* probably provided attachment areas for the powerful jaw muscles. The strong shoulder and neck muscles suggest that these animals spent much of their time rooting and grubbing in the ground for food.

Top: Skull and lower jaws of Archaeotherium, Brule Formation, Stark County, length 435 mm. MM V-1766



Merycoidodon was about four feet (1.2 m) long and probably looked somewhat like a pig. It roamed in large herds.

Left: Skull and lower jaws of *Merycoidodon culbertsoni*, Brule Formation, Oligocene, Stark County, length 198 mm. ND 303.1



Mesohippus, one of the early species of horses, was about the size of a greyhound dog. It had slender limbs adapted for trotting and running.

Below: Lower jaws of *Mesohippus*, Brule Formation, Oligocene, Stark County, length 135 mm. The Manitoba Museum.

Bottom: Skeleton (cast) of *Mesohippus bairdi* on exhibit at the North Dakota Cowboy Hall of Fame Museum in Medora, Brule Formation, height 465 mm.

Merycoidodon are common, indicating that these browsing animals lived in large herds.

Mesohippus was one of the early species of horses. It superficially resembled the modern horse, except that it was much smaller—only around two feet (60 cm) tall at the shoulder, and up to four feet (1.2 m) long. It was about the size of a greyhound dog. *Mesohippus* had slender limbs adapted for trotting and running. It had three toes on each foot, in contrast to the modern horse, which has one. Another difference between *Mesohippus* and today's horse is that *Mesohippus* teeth were low-crowned and therefore suited for browsing leaves from bushes and

trees, whereas teeth of a modern horse are high-crowned and suited for grazing primarily on grasses.

Other mammals that inhabited the wooded areas during the Oligocene were the squirrel-like rodent *Ischyromys*, the rabbit *Palaeolagus*, and the beaver *Agnotocastor*. *Ischyromys* is one of the earliest of the true rodents. Similar in appearance to today's rodents, it had a characteristic pair of upper incisors, as well as other rodent head features. Its strong hind limbs, with five clawed toes on each of its hind feet, were also like those of modern rodents. *Ischyromys* grew to lengths of two feet (60 cm). It is believed to have been an efficient tree climber, like today's squirrels.

> *Ischyromys* is one of the earliest of the true rodents. Right: Lower jaw of *Ischyromys*, Brule Formation, Stark County, length 20 mm. ND 248

Palaeolagus is in the Lagomorpha family, which includes pikas, rabbits, and hares. Because of their small size and continually growing incisors (gnawing teeth), lagomorphs are much like rodents, except that they have two pairs of incisors—one immediately behind the other—in the upper jaws compared to a single pair in rodents. The chewing action is also different in the two groups. In lagomorphs the jaws work sideways, in rodents backwards and forwards. *Palaeolagus* was similar in appearance to the modern rabbit except that its hind legs were proportionally shorter, which suggests that it was better adapted for scampering than for hopping. *Palaeolagus* grew to lengths of about ten inches (25 cm).

Large tortoises (Stylemys) and other turtles such as the soft-shelled Trionyx and Testudo lived in and around streams, ponds, and lakes during this time. Stylemys is in the family of dryland tortoises, the last major group of turtles to appear in the fossil record. It was similar to the modern Galapagos turtle. Stylemys grew to lengths of four feet (1.2 m) and had a high, domed shell and large legs. It was a herbivore. Its frequent presence in the Brule Formation indicates dry conditions were prevalent during the Oligocene. Trionyx, which inhabited ponds and quiet stream-marginal areas, was similar to the soft-shelled turtles that live today. Unlike most other turtles, Trionyx did not have a horny covering; instead the underlying bony plates were covered with a layer of soft, leathery skin. It probably fed on plants, insects, mollusks, and even small fish.

Palaeolagus grew to lengths of about ten inches (25 cm) and was similar in appearance to the modern rabbit.



Tortoise shell, *Stylemys nebrascensis*, Brule Formation, Stark County, length 226 mm. MM V-1931 *Trionyx* turtle skull, Brule Formation, Stark County, length 65 mm. ND 97-116.2

Trionyx turtle shell, Brule Formation, Stark County, length 230 mm. ND 97-116.3

Skull and lower jaws of *Palaeolagus* Brule Formation, Stark County, length 51 mm. ND 146.1





Terrestrial gastropods, Skinnerelix leidyi, Brule Formation, Stark County, width of largest 27 mm. ND 314.1, 314.2

Plioplarcus fish skeleton, Eocene, Chadron Formation, Golden Valley County, length 80 mm. ND 421.1



Skull of the rodent *Eumys*, Brule Formation, Stark County, width 51 mm. ND 271.3

Fish were common in the aquatic habitats, too. Spectacular fossil skeletons of the perch *Plioplarcus* have been found in the Chadron Formation. Remains of land snails, including pupillids and the large-shelled *Skinnerelix* (which could be called "Oligocene escargot"), pupal cells of burrowing beetles (*Pallichus*), and larval cells of sweat bees (*Celliforma*) have been discovered, indicating that they also lived in the streamside woodlands.

While herds of larger mammals like *Merycoidodon* and *Mesohippus* also frequented the open plain, smaller mammals seem to have been more abundant in that habitat. Rodents, like *Eumys*, were particularly common, and the fossils of several species of rodents have been found. *Eumys* was an early representative of the highly successful rat and mouse group of rodents, which today includes hamsters and voles. In recent times this has become the most widespread and abundant group of rodents, indeed of all mammals.

The small, gazelle-like camel *Poebrotherium* and tiny deer *Leptomeryx* were also common dwellers of the plains. Camels first evolved in North America, and modern camels are the remnants of a formerly much more widespread and diverse group. *Poebrotherium* was one of these early camels. Lightly built and goat-sized, it was about three feet (90 cm) long. Its head, with a distinctive narrow snout, and long neck made it look similar to the modern-day llama. The slender hind legs of *Poebrotherium* were Beetle pupal cells *Pallichus dakotensis* Brule Formation, Stark County, width of largest 20 mm. ND 363.1, 363.2, 363.3

longer than its forelegs, and it had hoofed toes. It was an efficient runner. This animal had long jaws, and its forwardextending front teeth (a feature it shared with living camels) enabled it to snip off vegetation.

Courtesy of Kingfisher Publishing

Painting of early camel Poebrotherium.



Leptomeryx was a small, antler-less, cloven-hoofed deer about two feet (60 cm) long. Graceful and dainty, with long, slender limbs, it was no larger than a jackrabbit. Leptomeryx resembled the chevrotain or "mouse-deer" living in Asia today.

Herbivores greatly outnumbered carnivores on the North Dakota Oligocene plain, as is the case today on the African savannas. Nevertheless, fossils of several groups of carnivores and insectivores have been found in the Brule

Dinictis was one of the early saber-toothed cats. Its sleek, threeto four-foot-long (1.2 m) body, much smaller than the Ice Age Smilodon, resembled that of the present-day lynx. Dinictis was an extremely efficient predator. Right: Dinictis skull, Brule Formation, Stark County. Length 180 mm. ND 05-67.1.



Formation. *Dinictis* was one of the early saber-toothed cats. Technically these were not true cats, belonging instead to a group of catlike carnivores known as mimravids. Their sleek, three- to four-foot long (1.2 m) bodies resembled that





of the present-day lynx. They were much smaller than the huge saber-toothed cat *Smilodon* that lived during the Ice Age, only a few thousand years ago. *Dinictis* was an extremely efficient predator. Its upper canine teeth, like those of saber-toothed cats, were elongate, serrated, and curved. These were used to stab into the throat and lower neck of prey, as well to slice into the muscle after a kill had been made. The modified lower jaws of *Dinictis* could open to a wide gape. The animal also possessed very strong neck muscles.

Hesperocyon was one of the earliest members of the Canidae, or dog, family. Its appearance, however, was more like that of a meerkat, a living mongoose. Small, active, and weasel-like, it had a slender body about two feet (60 cm) in length, short, weak legs, five-toed feet, and a long tail. It was a carnivore, with meat-cutting teeth similar to a modern dog's.

Daphoenus was another predator and a member of the primitive carnivorous group called beardogs. It was a lightly built animal about three feet (90 cm) long—akin to a greyhound dog. It had a long tail, long limbs, and a badger-like skull with crushing molar teeth and well-developed



Skull of the doglike mammal Daphoenus, Brule Formation, Oligocene, Stark County, length 120 mm. ND 282.7



Hesperocyon, an early member of the Canidae (dog) family, looked more like a meerkat, a living mongoose. About two feet (60 cm) long, it was a carnivore, with meatcutting teeth similar to a modern dog's. Skull and lower jaw of *Hesperocyon*, Brule Formation, Oligocene, Stark County, length 85 mm. MM V-1770, V-1771

Courtesy of Marshall Editions Ltd.

carnassial (cheek) teeth. *Daphoenus* was one of the main hunters of the abundant game present in North Dakota during the Oligocene. It has been suggested that *Daphoenus* may be an ancestor of the present-day wolf.

Hyaenodon was a member of the primitive and extinct group of flesh-eating mammals called creodonts. Creodonts had huge heads compared to the size of their bodies. Their posterior carnassial teeth were modified to form specialized shearing surfaces for eating flesh. The four-foot (1.2 m) long Hyaenodon had long legs, suggesting that it could

Courtesy of Marshall Editions Ltd.

Hyaenodon was probably an active hunter and also a scavenger, like the living hyena. Hyaenodon skull, Brule Formation, Stark County, length 310 mm. ND 02-28.3



Leptictis skull, Brule Formation, Stark County, length 60 mm. NDSU

run, but probably not fast because of its spreading toes. Its strong canines, large premolars, and shearing carnassial teeth indicate that the animal was probably an active hunter and also a scavenger, like the living hyena.

Insectivores were common on the North Dakota Oligocene plain. Well-preserved skulls of *Leptictis*, an insecteating mammal distantly related to modern shrews, have also been found in the Brule Formation. Its cheek teeth had high, pointed cusps ideally suited for eating insects and other small animals. Like most insectivores, *Leptictis* was a small creature, about a foot (30 cm) in length. It had a long snout similar to that of the hairy hedgehog which lives in Southeast Asia today.

By the late Oligocene and early Miocene (about twentyfive million years ago) the climate had cooled still further, and North Dakota and other areas of the High Plains had become more arid. This climate cooling caused extensive glaciation in Antarctica.⁷⁷ Open grasslands with riparian forests, similar to African savannas today, were established in the state by the Miocene. Average annual rainfall was only around fourteen to eighteen inches (35-45 cm), about what it is in western North Dakota today.⁷⁸ Little is known about life in North Dakota during this cool, dry period because most of the rocks that would have been deposited



Skull of the oreodont *Merychyus*, Arikaree Formation, Dunn County, length 120 mm. ND 93-93

then, along with the fossils entombed therein, have been removed by erosion. Also, land mammal diversity in the mid-continent was then at an all-time low.⁷⁹ Remains of a few grassland mammals, including the oreodont *Merychyus*, the horse *Miohippus*, and the unusual burrowing beaver *Palaeocastor*, have been found in the remnant Miocene-age rocks.⁸⁰ *Palaeocastor* is one of the earliest known beavers. Unlike today's aquatic beaver, *Palaeocastor* was terrestrial. It was about a foot (30 cm) long—the size of a muskrat. It excavated and lived in two-foot-long (60 cm) corkscrew-



Skull of the beaver *Palaeocastor*, Arikaree Formation, Stark County, width 50 mm. UND

Cross-section of *Daemonelix*, burrow made by *Palaeocastor*, after L.D. Martin and D.K. Bennett, "The Burrows of the Miocene Beaver *Palaeocastor*, Western Nebraska, USA," *Palaeogeography, Palaeoclimatology, Palaeoecology* (1977) during the Late Miocene. Right: Tooth, Amebelodon, Miocene, Emmons County, width 112 mm. SHSND 15032

shaped burrows. Scratch marks on the walls of these burrows indicate that the beavers dug them by scraping with their teeth. The helical-shaped burrows are preserved as trace fossils and are called 'Devil's corkscrews'; their scientific name is *Daemonelis*.

There is almost no record of prehistoric life in North Dakota from about twenty million years ago (most of the Miocene and all of the Pliocene) until about fifty thousand years ago, during the Pleistocene. Rocks deposited during that time, and the fossils that would have been found inside them, have also been removed by millennia of erosion. This was a time of global climatic flux, from warm conditions in the early Miocene to cooling in the middle part of that epoch, when glaciation again occurred in Antarctica and the modern East Antarctic ice sheet began to form.⁸¹ Isolated fossils which are occasionally found in North Dakota provide tantalizing hints of what life was like during this mysterious time. One of these finds is the tooth of the "shovel-tusked" gomphothere Amebelodon. Gomphotheres were elephantlike animals that migrated to North America from Eurasia across the Bering land bridge during the Miocene, about 16.5 million years ago. Amebelodon was about ten feet (3 m) tall at the shoulder and resembled a modern elephant. The skull and tusks of Amebelodon, however, were quite different from those of the living elephant. Three-foot-long (90 cm)

flattened, spade-like tusks projected from its lower jaws. These flattened tusks would have been used like shovels to dig up rooted water plants in rivers and ponds. *Amebelodon* was the largest herbivore that roamed the North Dakota plains during the Late Miocene.



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