EVOLUTION OF THE VERTEBRATES

A History of the Backboned Animals Through Time

Fourth Edition

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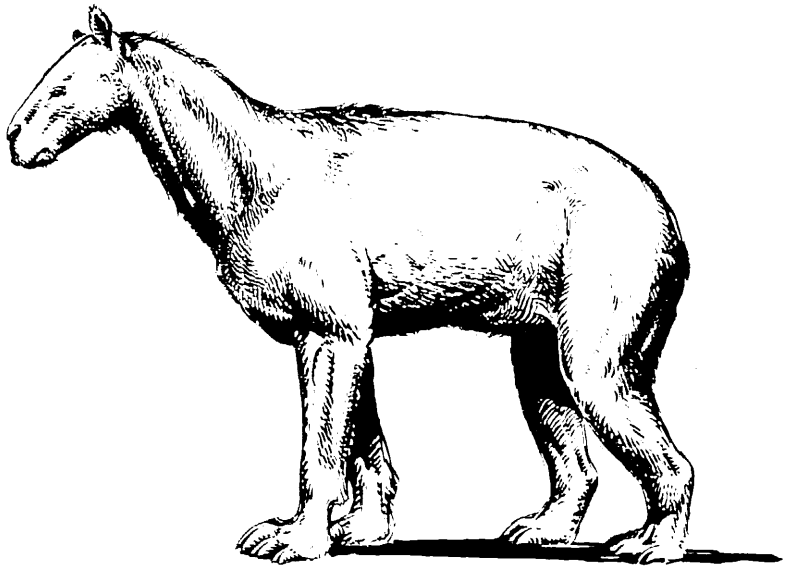


Figure 28-11. A Miocene chalicothere, a perissodactyl as large as a modern horse, with large claws on its feet. Prepared by Lois M. Darling.

the harder grasses that were spreading during the middle reaches of the Cenozoic era. Their food supply was changing, and they seem to have been unable to adapt themselves to this change. This factor, together with a comparatively primitive brain, probably had much to do with bringing an end to the titanotheres.

THE CHALICOTHERES

The chalicotheres, perhaps related to the titanotheres, yet sufficiently distinct to be placed in a separate suborder, were successful perissodactyls in that their phylogenetic life extended from Eocene times into the Pleistocene epoch. They seemingly were never very numerous animals. They were unique among the perissodactyls, in that the advanced genera had large claws on the feet, rather than hoofs, and it is possible that these beasts lived in small groups along streams, where they could dig up roots on which to feed, instead of browsing or grazing across the plains in large herds.

The first chalicotheres, typified by the upper Eocene genera, *Eomoropus* of North America and *Grangeria* of Asia, were generally similar to other primitive members of this order of ungulates. From these ancestors the chalicotheres evolved rapidly through the Oligocene epoch, reaching the full stature of their phylogenetic development by early Miocene times. From the Miocene into the Pleistocene epoch the chalicotheres continued without much evolutionary advancement.

The chalicotheres followed the general perissodactyl trend of size increase, so that the Miocene and later chalicotheres, like *Moropus* in North America and *Macrotherium* in Eurasia, were as large as large horses. In some respects the later chalicotheres had a horselike appearance, for the skull had a long, deep face, the body was compact, and the limbs were elongated. But here the similarity ends. The teeth were essentially similar to those of the titanotheres, with low crowns, large molars, and small premolars. As in the titanotheres, the teeth in front of the premolars were variously reduced or completely suppressed. In the advanced chalicotheres the front legs were longer than the hind limbs, so that there was a slope back from the shoulders to the hips, somewhat as in modern giraffes. The feet were short, with three functional toes in each foot and, as already mentioned, there were claws on all the toes, these claws being larger in the front feet than in the hind feet. Of the claws on the front feet, the inner one was the largest.

Some large Miocene chalicotheres of North America, belonging to the genus *Tylocephalonyx*, are remarkable in the presence of a large, hollow, bony dome on the top of the skull above the braincase. The function of this structure is puzzling; perhaps it was used in low-impact butting, as seen in modern giraffes, and perhaps it was for visual display.

The chalicotheres managed very well with their strange way of life until sometime during the Pleistocene epoch, and then they became extinct. However, their disappearance probably cannot be blamed upon any inadequacies in their adaptations; their continuation during most of Cenozoic times shows that they were well suited for a very particular mode of life. They finally vanished during the wide extinction of large mammals that took place in late Pleistocene times, when many of the spectacular animals that had graced the Ice Age landscapes of the world disappeared.

EVOLUTION OF THE RHINOCEROSES

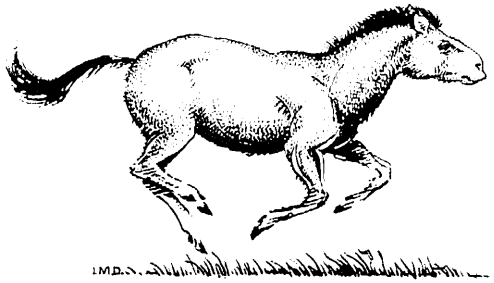
Having reviewed the perissodactyls that can be grouped in the suborders Hippomorpha, namely the horses and titanotheres, and Ancylopoda or chalicotheres, we now come to the other suborder of perissodactyls, the Ceratomorpha, which contains the rhinoceroses and the tapirs.

At the present time, rhinoceroses are a very restricted group of ungulates, represented by two species in Africa and three in Asia—the latter being among the rarest of modern mammals. It can safely be said that the rhinoceroses are well on their way toward extinction, and it is possible that one or two species of rhinoceroses, thanks in large part to the activities of modern man, will become extinct within the next few decades. In Tertiary times, however, the rhinoceroses were numerous and varied, belonging to several lines that were evolving parallel to each other. This parallelism makes the past history of the rhinoceroses difficult to interpret.

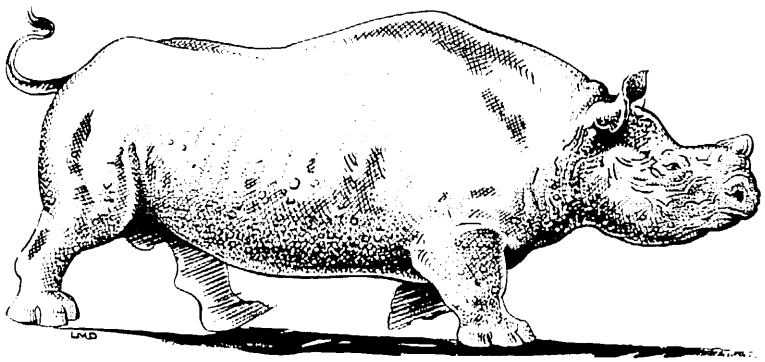
The first known rhinoceroses appear in sediments of Eocene age, and like many other very early odd-toed ungulates they show the primitive characters of the stem perissodactyls that have already been described. It is likely that the earliest rhinoceroses were closely related to the primitive tapirs; indeed, the perissodactyls known as hyrachyids (long considered as very primitive rhinoceroses) are now placed among the Helaletidae, a family of early tapirs.

With this assignment of the hyrachyids to the tapirs, the rhinoceroses assume a threefold division represented by three families: the Hyracodontidae, the Amynodontidae, and the Rhinocerotidae. Among them, the hyracodonts, or running rhinoceroses, were the most generalized.

These rhinoceroses appeared in middle and late Eocene times and reached the culmination of their evolutionary development during the Oligocene epoch. *Hyracodon*, from the Oligocene sediments of North America, was a characteristic hyracodont. This rhinoceros was rather small, lightly built, with slender limbs and long feet that were adapted for rapid running, and although the feet were function-



Hipparion



Teleoceras

Figure 28–12. Two Pliocene perissodactyls of North America. *Hipparion* was a three-toed horse, *Teleoceras* a very heavy, short-limbed rhinoceros. Prepared by Lois M. Darling.

ally tridactyl, there were four toes on the front feet. The skull was rather low, the eye was centrally located, and the orbit was confluent with the temporal opening. All of the incisor teeth were present, and immediately behind them were small canines, in effect, forming a part of this series of teeth. These teeth were separated from the cheek teeth on each side by a diastema or gap. The last premolars were molariform in structure; the molars were crested in the manner that was to be characteristic for rhinoceroses throughout their evolutionary history; in brief, each upper molar had a strong outer crest or ectoloph, to which at slightly oblique angles were two cross-crests or lophs, while the lower molars were strongly cross-crested. These tooth patterns indicate an early specialization for browsing. The hyracodonts, which enjoyed the height of their evolutionary development during Oligocene history, barely survived into Miocene times, and then became extinct.

The second branch of rhinoceros evolution, the amynodonts, arose during late Eocene times, when the hyracodonts were still in the early phases of their evolutionary history. The amynodont rhinoceroses are characteristically represented in the upper Eocene by *Amynodon*, in the Oligocene by *Metamynodon*. From the first the amynodonts were large, heavy rhinoceroses, with strong limbs and short, broad feet. They are frequently found in stream channel deposits, and it seems logical to think that they may have been water-lovers with hippopotamuslike habits. The skull was heavy, the incisor teeth and the anterior premolars were greatly reduced, and the canines and the molars were greatly enlarged, the former as large daggers, possibly for fighting, and the latter as long, cutting teeth. For a time the amynodonts were successful, spreading from North America, which would seem to have been the center of origin, into Asia and Europe. They became extinct soon after the close of the Oligocene epoch.

We now come to the central stock of rhinoceros evolution. *Caenopus*, an Oligocene member of the evolutionary line, probably arose from some of the running rhinoceroses. *Caenopus* was a large rhinoceros, standing some four or five feet in height at the shoulders, and it illustrates the early growth to large size that was so typical of most lines of rhinoceros evolution. It was a fairly heavy rhinoceros, seemingly hornless, and it showed some molarization of the premolars. From this point on, the later rhinoceroses evolved in several different directions. Their adaptive radiation included a general increase in size (although the members of a few lines remained comparatively small), the development of broad, three-toed feet for supporting the weight of the strong limbs and the heavy body, the molarization of the premolars, the lengthening of the crowns in the cheek teeth and the continuation of the pattern of strong crests established in the primitive rhinoceroses, and finally the development of horns on the skull.

The horns of rhinoceroses, known mainly from the modern forms, are unique among mammals in that they are formed completely of coalesced hair and have no bony cores. As might be expected, horns such as these were rarely fossilized, but their presence is clearly indicated by roughened areas on the skull, where the bases of the horns were attached.

The baluchitheres were the largest of the rhinoceroses, and the largest of all land mammals, past or present. *Baluchiterium*, which lived in Asia during Oligocene and early Miocene times, was an animal that stood sixteen or eighteen feet in height at the shoulders, and in life it must have weighed many tons. This giant rhinoceros was hornless. It probably browsed upon the leaves of trees.

The Miocene diceratheres were small rhinoceroses with a pair of horns, side by side, on the nose.

The Miocene and Pliocene teleocerines, as typified by *Teleoceras*, were heavy rhinoceroses with remarkably short limbs and feet. They carried a single horn on the nose.

The single-horned rhinocerines appeared in late Miocene times and have continued to the present day as the one-horned rhinoceroses, *Rhinoceros* of India and Java.

Various two-horned rhinoceroses, with one horn in front of the other, appeared during late Cenozoic times. One of these survives as the modern two- horned Sumatran rhinoceros. The well-known wooly rhinoceros of the Ice Age, depicted in many European caves by Stone Age men, was probably related to this modern two-horned type. On a somewhat separate branch are the modern two-horned rhinoceroses of Africa, *Diceros*, the black rhinoceros, and *Ceratotherium*, the white rhinoceros.

The elasmotheres were giant rhinoceroses that lived in Eurasia during Pleistocene times. They had a single large horn on the forehead, not on the nose as in modern one-horned rhinoceroses, and were characterized by tall cheek teeth with very complicated enamel patterns.

From the above it can be seen that the rhinoceroses were numerous in most continental regions during late Cenozoic times. Many evolutionary lines coexisted side by side, but as the Cenozoic era came to a close most of these lines disappeared, one by one. Rhinoceroses became extinct in North America during the Pliocene epoch. At the same time various lines of rhinoceroses died out in Eurasia, but other Old World lines continued

into the Pleistocene. Finally, at the close of Pleistocene times some of these disappeared, to leave the five species of rhinoceroses known to us as living animals. And as said above, they represent a vanishing group of ungulates. The heyday of rhinoceroses is long since past.

THE TAPIRS

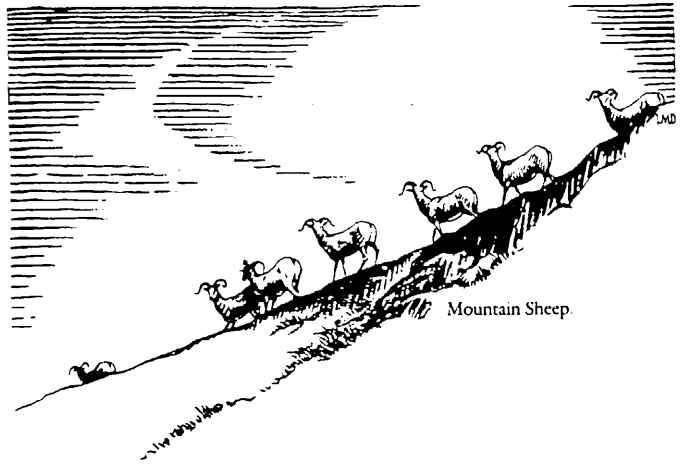
The modern tapirs of South America and Malaya are in some respects the most primitive of living perissodactyls. They retain the four toes on the front feet and the three toes on the hind feet, seen in various early Eocene members of the order. The body is heavy, the back is curved, and the limbs and feet are stocky and short. On the other hand, the tapir skull is specialized, in that the nasal bones are retracted. These mammals have a very flexible nose, a short proboscis that they can wrap around stems of plants or other objects. All the incisor teeth are present, and the canines are sharp and separated by a gap from the low-crowned cheek teeth. There is strong molarization of the last three premolars, and all the cheek teeth have crested crowns that are obviously related to the crested cheek teeth of the rhinoceroses. In the tapirs, however, the cheek teeth are perhaps more strongly cross-crested than in any other perissodactyls. The modern tapirs have a curious distribution, but it is obvious from the fossil history that they are remnants of a group that was once widely distributed over much of the earth.

Primitive tapirs appear in Eocene sediments. It is evident that during the Eocene epoch the tapirs were evolving rather complexly, along several parallel lines. These are indicated by the several families of Eocene tapirs that have been recognized—the isectolophids, helaletids, lophialetids, deperetellids, and lophiodonts. In general, however, these early tapirs may be compared with other primitive perissodactyls, already described. They were for the most part small, and were characterized by the usual primitive perissodactyl features, including a lack of molarization in the premolars. However, the teeth were strongly cross-crested. *Heptodon*, a lophiodont, was an Eocene genus that may be considered as approximately ancestral to the later tapirs.

In Oligocene times *Protapirus* appeared as a probable descendant of *Heptodon*. This tapir showed most of the characters that have been outlined above in the discussion of modern tapirs, except that there was less retraction of the nasal bones and, therefore, probably not so much of a flexible nose or proboscis as is seen in living tapirs. From here on, the evolution of the tapirs was comparatively simple, and involved mainly a certain degree of size increase. *Miotapirus* of the Miocene had strongly retracted nasals, as in modern tapirs, of which it was without much doubt the direct ancestor. *Tapirus* appeared in the Pliocene epoch and has continued to the present day. In Pleistocene times there was a giant tapir living in China that has been recognized as a separate genus, *Megatapirus*, but except for size this tapir was little different from the surviving tapirs.

Tapirs roamed widely during Pleistocene times, and were prominent in the Ice Age faunas of North America and Eurasia. But as the Pleistocene epoch came to a close the tapirs disappeared in northern continental regions, and have continued only in the East Indies, and in South America, a region they invaded after the isthmian link between the two Americas had emerged above the sea.

In looking at modern tapirs we get in some ways a glimpse of the primitive perissodactyls of early Tertiary times. We are carried back in our minds to a time when the perissodactyls were beginning the long and varied evolutionary history that carried them through the Cenozoic era. It is a history that has passed its culminating point. Several million years ago the decline of the perissodactyls began, as these hoofed mammals gave way to the dominant ungulates of modern times, the artiodactyls.



Mountain Sheep.

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Artiodactyls