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FIFTY MILLION YEARS OF RHINOCEROS EVOLUTION

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ABSTRACT

Rhinocerotoids were the most ecologically diverse and successful group of large herbivores around the world during the last fifty million years. From their origin on the northern continents during the early Eocene, they diverged into three main families: the Amynodontidae, the Hyracodontidae, and the Rhinocerotidae. The Amynodontidae were primarily aquatic grazers, some of which were amazingly hippo-like or tapir-like. The Hyracodontidae were long-legged, mostly small running forms, although *Paraceratherium* reached 6 m at the shoulder, and may have weighed 20,000 kg. The Family Rhinocerotidae includes the five living species, as well as a great diversity of extinct forms. Most Eocene and Oligocene rhinocerotids were small, hornless browsers, although *Diceratherium* and *Menoceras* independently developed paired horns in the late Oligocene. In Miocene savannas of North America, Africa, and Eurasia, rhinocerotids became specialized into browsers and grazers, with the grazer often a rotund hippo-like beast. After great success in North America, rhinos died out there about 4 million years ago as a result of climatic changes that caused extinctions in most large mammals.

Eurasia and Africa remained the home of a great diversity of rhinos through the Ice Ages, including woolly rhinoceros, with a saber-like horn for scraping away snow. The Sumatran rhino, *Dicerorhinus*, is the last remnant of the woolly rhino family, which first appeared about 20 million years ago. The genus *Rhinoceros* can be traced to *Gaiotherium* from the middle Miocene, which occurs about 15 million years ago in Portugal. African rhinos (Tribe Dicerotini) can be traced back to at least 20 million years ago, although the oldest known fossils than can be clearly assigned to either black or white rhino lineages are about 8 million years old. The data from the fossil record suggest much more ancient divergence times than do molecular clock data.

INTRODUCTION

Although only five species of rhinoceros cling to survival today, rhinos have a long and distinguished history. Since their origin about 50 million years ago, they have been an extremely diverse group. At least 60 genera and hundreds of species of rhinocerotoids have occupied nearly every niche available to large mammalian herbivores, from small running forms, to hippo-like grazers, to proboscis-bearing tapir-like forms, to gigantic animals which could browse treetops like giraffes. Rhinos were the largest land mammals on all the northern continents from 34 million years ago until mastodons escaped from Africa about 18 million years ago.

Yet despite the excellent fossil record of this distinguished history, there has been relatively little study of rhino evolution. Until recently, the last general reviews of rhino evolution were those of Wood (1927) and Matthew (1931). In Simpson's (1945, p. 257) classification of the mammals, he characterized the situation this way:

"The human factor in classification is nowhere more evident than in dealing with this superfamily [Rhinocerotidae]. It is, as mammalian superfamilies go, well known, but what is 'known' about it is so inconsistent in places that much of it must be wrong. Some authorities still recognize 'genera' (e.g. *Orthocynodon*, an amynodont) that are, beyond much doubt, based on slight individual variation, while others lump together in one genus a whole tribal lineage that must almost

certainly include a whole cluster of genera, even if generic lines be drawn as broadly as could be desired (e.g. the supposed European *Dicerorhinus* line). Some of the most competent students (e.g. Matthew) follow very broad lines, emphasize skull and foot characters, and tend to neglect dental mutations; others (e.g. Wood) split the groups into many short, narrow sequences emphasizing minor dental characters and tending to neglect skeletal structure. Much of the published work (aside from that of Matthew, Wood, and some others) is simply incompetent and has not been revised by a properly instructed and judicious student."

As a consequence, most popular publications on rhinoceroses reprint vague or badly out-of-date information. Even authoritative textbooks, such as Romer (1966), Savage and Long (1986), Carroll (1988), and Colbert and Morales (1991) continue to publish errors, and nearly every fossil rhino illustration is identified by names that have been out of date for over fifty years. For example, the abundant rhino fossils from the famous Agate Springs Quarry in Nebraska is *Menoceras*, not *Diceratherium* (first clarified in 1921); the common Oligocene rhino is *Subhyracodon*, not *Caenopus* (this has been true since 1878, and reaffirmed in 1941); and the treetop-browsing giant is *Paraceratherium*, not *Indricotherium* or *Baluchitherium* (Lucas and Sobus, 1989). In the popular mind, the defining feature of the rhino is its horn, yet most fossil rhinos were hornless. Clearly, there are many misconceptions about rhinos in both public and professional circles.

The latest research into rhino evolution has been summarized by Prothero, Manning, and Hanson (1986), Prothero (1987), and Prothero, Guérin, and Manning (1989). Although much work remains to be done on the detailed systematics of individual species, the broad outlines of rhino evolution have become clear. In many ways, the present picture is very different from the popular misconceptions found in most textbooks and trade books. In a book devoted to rhinoceros biology, such misconceptions should be corrected.

EARLY RHINOCEROS EVOLUTION

Among living mammals, rhinos and tapirs are the most closely related to each other. This is further affirmed by study of the fossil records of these two groups (Prothero and Schoch, 1989). In the earliest Eocene, there were small (beagle-sized) animals such as *Homogalax* which were probably ancestral to both rhinos and tapirs, and indeed were barely distinguishable from the earliest horses (formerly called "*Hyracotherium*" or "*Eohippus*," but now probably *Protorohippus*). By the late early Eocene (about 50 million years ago), there was a great diversification of these "tapiroid" groups (Radinsky, 1963, 1965; Schoch, 1989). Some lineages (such as the isctolophids, deperetellids, and lophialetids) became extinct, and some led to other groups of perissodactyls, such as lophiodonts, chalicotheres, and modern tapirs. One lineage became the rhinocerotoids.

The earliest known member of the Superfamily Rhinoceroidea was *Hyrachyus*. It was the size of a German shepherd, but with longer limbs and well-developed hooves for running. Like its "tapiroid" relatives, its teeth had well-developed cross-crests for chopping leafy vegetation. The middle Eocene world in which *Hyrachyus* lived was very different than today. The world was in a global "greenhouse climate," with tropical vegetation and animals extending from the equator to above the Arctic Circle. Semi-tropical plants and animals (including alligators) have been found in several places in the Canadian Arctic, yet these localities must have experienced Arctic darkness during the Eocene winters. North America was still connected to Europe across Greenland, and to Asia via the Bering Strait, and many mammals took advantage of these connections to spread across all the northern continents. *Hyrachyus*, for example, was common in Wyoming, Europe, Ellesmere Island in the Canadian Arctic, and possibly Asia. By the later Eocene, however, most of these intercontinental connections were severed, and each continent developed its own endemic faunas. In addition, world climate began to deteriorate, with cooling and drying affecting most of the continents (Prothero, 1989; Berggren and Prothero, 1992). This climatic change

broke up the Eocene tropical forests, and drove many of the unspecialized forest browsers to extinction.

As a consequence of this climatic change, geographic separation and isolation, rhinocerotoids also began to diversify into several new groups. The first of these was the Family Amarynodontidae, reviewed by Wall (1989). Some amynodonts were very hippo-like (*Metamynodon* from the late Eocene and Oligocene of North America), and some had a proboscis like a tapir or elephant (*Cadurcodon* from the late Eocene-early Oligocene of Asia). They were dominant in Asia during the late Eocene, but became rare by the early Oligocene, and were nearly extinct by the late Oligocene. One lingering survivor, *Cadurcotherium*, managed to invade Europe about 32 million years ago, and persisted in Pakistan until the middle Miocene (about 15 million years ago).

The second major family of rhinocerotoids were the Hyracodontidae (Radinsky, 1967). Their most striking feature was their long limbs and toes, adapted for rapid running. The most familiar hyracodont is *Hyracodon* itself, which was a swift runner about the size of a Great Dane. Small, running hyracodonts were common in the middle and late Eocene of both Asia and North America, but by the Oligocene, only *Hyracodon* remained.

The other major subfamily of hyracodonts were the gigantic treetop-feeding indricotheres. Beginning with the cow-sized *Forstercooperia* in the middle Eocene of both Asia and North America, they soon reached gigantic proportions in Asia (Lucas and Sobus, 1989). The most spectacular of these was the largest land mammal that ever lived, *Paraceratherium* (once known as *Indricotherium* or *Baluchitherium*). It was 6 meters at the shoulder, with a skull over 2 meters long, and weighed about 20,000 kg (about as much as four bull elephants)! Its gigantic size, long neck, and tapir-like teeth suggest that it was a rhino "giraffe," browsing on the tops of trees. The feet of *Paraceratherium* are a good example of how inherited features can persist despite their lack of utility. Most other land giants, such as elephants and dinosaurs, have short, compressed toe bones to accommodate their great weight. *Paraceratherium* retained the long toes of its running ancestry, even though an animal this size was clearly too big to run. Indricotheres were the last of the hyracodonts, persisting in Pakistan until about 15 million years ago (along with the last of the amynodonts).

The only family to survive to the present are the Rhinocerotidae. Like amynodonts and hyracodonts, early rhinocerotids lacked horns. They can be distinguished primarily by their chisel-like upper incisors and tusk-like lower incisors, and by distinct features of the rest of the teeth and skeleton (Prothero et al., 1986, 1989). The earliest known rhinocerotid is the recently described *Teletaceras*, from the late Eocene of Oregon (Hanson, 1989), which was very similar in size and most features to the hyracodonts of the late Eocene. Through the late Eocene and Oligocene, cow-sized hornless rhinocerotids were common in North America (e.g., *Trigonias* and *Subhyracodon* [= "*Caenopus*"]), the early Oligocene of Europe (e.g. *Ronzotherium*) and Asia (e.g. *Guixia*). In North America, the *Subhyracodon* lineage developed into *Diceratherium*, the first rhinoceros with horns. Unlike later rhinos, however, its horns were two broad flanges along the side of its nose. *Diceratherium* reigned unchallenged in North America from about 31 to 21 million years ago. It was not only the sole remaining rhinocerotoid in North America (since hyracodonts and amynodonts were extinct here), but the largest land mammal as well. Mastodonts did not arrive in North America to challenge rhinos until about 16 million years ago.

Diceratherium is frequently confused with another paired-horn rhino, *Menoceras*. Although they both have paired horns on their noses, the similarities end there. While true *Diceratherium* was a North American endemic that retains mostly primitive features, *Menoceras* was an earliest Miocene immigrant from Europe, with highly advanced features in its skull and skeleton. Its closest relative is *Pleuroceros* from the early Miocene of Europe. When abundant specimens of *Menoceras* were found at the famous Agate Springs Fossil Beds in western Nebraska, they were routinely mislabeled as "*Diceratherium*" in museum displays and textbooks, and this error persists today. Ironically, Troxell realized the two

rhinos were different in 1921, and Tanner (1969) cleared up the confusion once and for all. The two are easy to distinguish. Even the "paired horns" are different. Unlike the paired nasal flanges on true *Diceratherium*, *Menoceras* has rounded bosses on the tips of its nasal bones. These features are found only in males, and females are hornless. The female skulls, in fact, are so distinct that they would never had been mistaken for each other; only the superficial similarity of the paired horns in males led to a century of confusion.

MIOCENE RHINO SAVANNAS

By the early Miocene, most of the northern continents were covered with an open savanna-grassland very similar to that found in modern East Africa. This led to a great diversification of hoofed mammals. Many developed high-crowned teeth for eating gritty grasses, and long limbs and toes for running and escaping ambush predators. This trend has been well documented in horses, but it also occurred in camels, deer, antilocaprids, antelopes, as well as in a number of extinct groups. Rhinos, too, developed high-crowned teeth, but because of their role as megaherbivores, they did not depend on high-speed running to escape predators. Instead, like modern elephants and rhinos, they were largely protected by their size and ability to defend themselves.

Since they lived in the absence of competition from other megaherbivores through much of the Miocene, they quickly became specialized into ecological niches that they no longer occupy. As we see in the East African savanna today, there are two main niches for megaherbivores: browsing leaves and grazing grasses. Browsers retain low-crowned, unspecialized teeth for their soft vegetation, but may develop a specialized lip or proboscis to grasp and manipulate leaves and twigs. This is true not only of the living black rhino, but also of living tapirs, and, as we have seen, of the proboscis-bearing amynodonts and many of the browsing hyracodonts. In the Miocene, several extinct groups of rhinocerotids became browsing specialists. The best known are the aceratherines, a group which developed a long proboscis or prehensile lip (as indicated by the retraction of the nasal notch in their skulls). *Aceratherium* first appeared in the early Oligocene of Eurasia, where most of their diversification (*Mesaceratherium*, *Alicornops*, *Hoploaceratherium*, *Chilotherium*, and *Dromoaceratherium*) took place. Aceratherines migrated to North America in the early Miocene, where two genera (*Aphelops* and *Peraceras*) performed the role of browsing megaherbivore throughout the Miocene.

The other main rhino niche on the savanna takes advantage of the great abundance of grasses. Although grasses are easy to obtain, they require dietary specializations to digest large amounts of their high-fiber, low-quality nutrition, and to resist the gritty siliceous phytoliths contained in their tissues. Such specializations usually include high-crowned, ever-growing teeth which continue to wear through the life of the animal, and a broad snout for efficient lawnmowing. Both of these features are seen in the living white rhino, a true grazer, and in many extinct Miocene rhinos. The main group to exploit the grazing niche in the Miocene were the teleoceratines. They not only had high-crowned teeth, but most had fat, short-limbed bodies like a hippopotamus. The living hippopotamus is also a grazer, hiding in bodies of water during the day, and coming out to graze at night. Teleoceratines were such good ecological vicars for hippos that they match them in many anatomical features, and even in population structure! *Teleoceras*, the best known North American teleoceratine, is found in river channels or pond deposits, and in one famous "rhino Pompeii," a herd was covered with volcanic ash and preserved as they died in the pond, with grass seeds still imbedded in their throats (Voorhies, 1981; Voorhies and Thomasson, 1979).

Teleoceratines first arose in the late Oligocene in Europe with *Diaceratherium* (not to be confused with *Diceratherium*!), and diversified into a number of genera during the Miocene (e.g. *Brachypotherium*, *Prosantorhinus*). *Brachypotherium* was also found in Africa and Asia during the Miocene, and immigrated to North America in the early Miocene, where it evolved into *Teleoceras*. In addition to the teleoceratines, several other groups of rhinos

convergently developed into hippo-like forms with high-crowned grazing teeth. They include the aceratherines *Chilotherium* in Asia, and one species of *Peraceras* in North America.

After dominating the Miocene savannas of North America, Eurasia, and Africa through the entire late Oligocene and Miocene (from about 30 to 5 million years ago), both the teleoceratines and aceratherines were decimated by an extinction event at the end of the Miocene. This crisis affected not only rhinos, but many other savanna specialists, such as camels, horses, protoceratids, dromomerycids, and antilocaprids in North America, and many species of ruminant in Eurasia. This crisis marked the end of savanna habitat in most continents except Africa. It was probably caused by major climatic changes at the end of the Miocene, including cooling and drying triggered by the onset of the present Arctic and Antarctic glaciation and the Ice Ages.

The most severe event, however, was the drying up of the Mediterranean when the Straits of Gibraltar closed. The Mediterranean became a gigantic Dead Sea, collecting acres of salt and gypsum, and changing the salinity of the world's oceans (Hsü, 1983). When the Straits were again breached, the cataract must have dwarfed Niagara Falls, with water shooting into the dry basin. This "Messinian event," more than anything, capped the late Miocene crisis and triggered wholesale extinctions. In North America, both teleoceratines and aceratherines died out, and this continent never again had native rhinos. The disappearance of teleoceratines and aceratherines from Eurasia severely diminished their rhino diversity. Only the teleoceratine *Brachypotherium lewisi* survived into the Pliocene of Africa, but it too was gone by about 3 million years ago.

THE ORIGIN OF MODERN RHINOS

In addition to the aceratherine and teleoceratine lineages, there were other rhinos evolving in Europe during the Oligocene and Miocene. The oldest such lineage is the primitive group that led to the living Sumatran rhino, *Dicerorhinus sumatrensis*. The dicerorhinines may have originated with "*Ceratorhinus*" *tagicus* from the early Miocene (about 22 million years ago) in Europe, although the first unquestioned taxon is *Dicerorhinus sansanienensis* from the late early Miocene (about 15-20 million years ago). Unfortunately, the genus *Dicerorhinus* has become a "wastebasket" for nearly every primitive member of the lineage, and it may be incorrect to refer early Miocene fossils to the living genus. Nevertheless, the dicerorhinines have been distinct from all other rhinos for at least 15-20 million years.

Dicerorhinines were a very persistent and widespread group, even if they retain many primitive features as forest browsers. They originally lived all over the Old World (especially Europe and Asia, but also Africa), but they are now restricted to the Sumatran rhino populations in southeast Asia. Their most specialized member was the woolly rhinoceros, *Coelodonta*. It was found all over Eurasia during the peaks of the Ice Ages, and is even known from freeze-dried mummies and specimens pickled in peat bogs. Its horn was flattened laterally into a saber-like shape, and the scratches along the anterior edge indicate that it brushed aside snow with broad sweeps of its horn to feed on the grasses beneath (Fortelius, 1983). Despite its great success in the Old World, it never managed to cross the Bering Strait to North America. Why it did not do so is a mystery, when similarly adapted woolly mammoths and bison did.

One of the most spectacular of the Ice Age rhinos was the elephant-sized *Elasmotherium*. Unlike other rhinos, which had a single or paired horn on the nose, or tandem horns (as in the African rhinos), elasmotheres had a gigantic horn located on a huge boss on their foreheads. Elasmotheres were also bizarre in that their molar teeth were extremely high crowned, with complexly folded enamel that resemble intricate curlicues in crown view. The earliest elasmothere was *Sinotherium* from the late Miocene (7-9 million years ago) of China. *Elasmotherium* itself was restricted to Siberia and eastern Europe, and died out at the end of the last Ice Age, about 10,000 years ago.

The other major group of Asian rhinos, the rhinocerotinines, are known from the extinct genus *Gaioatherium*. First described from the middle Miocene of the Siwalik Hills of Pakistan (in beds about 10 million years old), it has since been recognized from the early Miocene (about 15-20 million years) of Portugal. The genus *Rhinoceros* is recognized from the Pliocene (about 4 million years ago), and specimens referable to the Javan rhino, *R. sondaicus*, have been identified from the early Pleistocene (about 2 million years old). Unlike the dicerorhinines, the rhinocerotinines were restricted to southeast Asia through most of their history.

The African rhinos, or dicerotines, first occur in the fossil record during the middle Miocene (about 18 million years ago) with *Paradiceros mukirii* from Kenya and Morocco. Hooijer (1968, 1978) did not consider it ancestral to the living African rhinos, but clearly the group was present at this time. By the upper Miocene (about 10 million years ago), the black rhino *Diceros* was present in Africa, Spain, Italy, Greece, and the Near East. The white rhino, *Ceratotherium*, however, is not known until the late Miocene (about 7 million years ago), and apparently was restricted to Africa.

All four major lineages can be traced back at least 10 million years. Their relationships have been analyzed by several people. Guérin (1982) placed the rhinocerotines and dicerotines as closest relatives, with the dicerorhinines as their sister group. Based on a much more extensive character analysis, Groves (1983) considered the Asian rhinos to be closest relatives, with the African rhinos as their sister group (Figure 2). This arrangement was followed by Prothero et al. (1986).

Molecular analyses are just beginning to be conducted on rhinoceroses. In the program to this conference, Benveniste, George, and Ryder presented results of a DNA-DNA hybridization study which placed the Asian rhinos as closest sister taxa, and the African rhinos as their sister group. This is in good agreement with Groves (1984) and Prothero et al. (1986). However, the timescale of this molecular clock is in serious disagreement with the fossil record. It postulates a divergence of African rhinos at less than 2 million years ago. In the conference report, Harley reported a divergence estimate of 3.4 ± 0.8 million years. Clearly, this is conflict with the fossil record of African rhinos, which has both genera represented by fossils at least 7-10 million years old.

Likewise, the Benveniste et al. molecular clock puts the Indian/Sumatran divergence at about 4 million years, while the fossil evidence pushes both lineages past 15 million years. The African/Asian divergence is estimated at less than 6 million years, but the evidence is clear that both groups were distinct 18-20 million years ago. Clearly, the calibration of the rate of this molecular clock needs to be checked carefully. Since the details were not published, I cannot comment on how the rates were calculated, but they seem too fast by about a factor of 2-3.

This is even more apparent when other perissodactyls are considered. Benveniste et al. place the divergence of rhinos and tapirs at about 12 million years, but as we have seen, the evidence is clear that they have been distinct for at least 45-50 million years (Figure 2). Likewise, the equid/ceratormorph split is placed at about 17 million years by molecular methods, but the fossil record is clear that both groups diverged in the early Eocene, about 52-55 million years ago. Until the full details of the calibration methods are published, it is unwise to comment further, but these data are clearly in conflict with the fossil record.

CONCLUSION

Rhinoceroses have a long and distinguished history as one of the most ecologically diverse and widespread of megaherbivores. In the last 50 million years, they have occupied almost every imaginable ecological niche, from "giraffes" to "hippos" to "tapirs" to "ponies." Although they were once extremely diverse, they were wiped out of North America about 4 million years ago, and have been in decline in much of the Old World since. The lineages of

all four living genera have long histories going back 10-15 million years, contrary to molecular clock estimates that place their origin much sooner.

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Figure 1. Stampede of extinct rhinoceroses. In the lower right is the ancestral form *Hyrachyus*. The hippo-like amynodont *Metamamocodon* is shown on the left center. The running *Hyracodon*, and the giant *Indricotheres chosroia* and *Paraceratherium* (= *Indricotherium*) are all hyracodontids. *Mammuthium* is a primitive rhinocerotid, and *Mammoceras* (mislabelled here as *Diceratherium*) is an early rhinoceros with paired horns. The hippo-like *Teleoceras* is shown in the left foreground. The Etruscan rhinoceros, *Dicerorhinus etruscus*, and the woolly rhino, *Coeloceros*, are both related to the living Sumatran rhino. The gigantic *Elasmotherium*, with its single frontal horn, lived in Siberia during the Ice Ages. Copyright Wildlife Education, Ltd., ZOOBOOKS

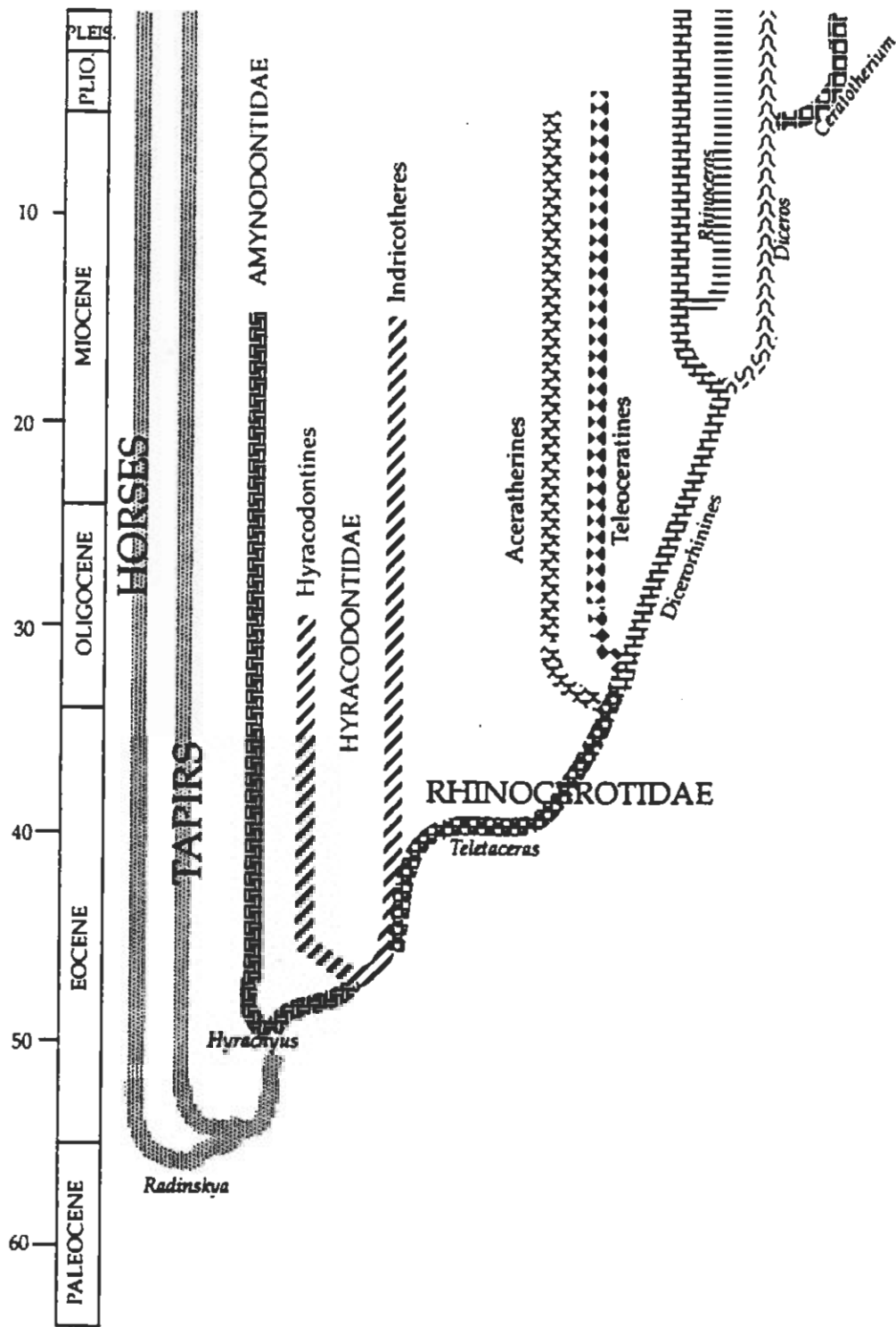


Figure 2. Family tree of the major groups of rhinocerotoids and related perissodactyls, showing their phylogenetic relationships and divergence and extinction times. Geological time scale on left (in millions of years); abbreviations: P.LIO. = Pliocene; PLEIS. = Pleistocene (the Ice Ages).