

16. THE HISTORY OF THE RHINOCEROTOIDEA

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The largest and most ecologically diverse group of perissodactyls is the Superfamily Rhinoceroidea. This group includes the amynodonts (some of which were hippo-like or tapir-like aquatic forms), the hyracodonts (which included dog-sized cursorial forms, and gigantic forms which browsed treetops), and the true rhinoceroses of the Family Rhinocerotidae. All three groups diverged in the later Eocene from a form like *Hyrachyus*, and spread over the northern hemisphere. Both the amynodonts and hyracodonts were reduced to a few surviving genera by the early Oligocene, but the rhinocerotids began to diversify. Most early rhinos were hornless, but the first horned rhinos had paired horns on the tip of their noses, a feature that evolved independently in two different groups, the Diceratheriinae and Menoceratinae. By the late Oligocene, rhinos began to diverge into the major subfamilies and tribes that dominated the northern hemisphere and Africa during the Miocene: the hippo-like grazing single-horned Teleoceratinae, the prehensile-lipped browsing hornless Aceratheriinae, and the Rhinocerotinae, which includes all the five living species. These first two groups were almost completely wiped out by the extinctions at the end of the Miocene, leaving North America without rhinos, and only certain rhinocerotines surviving in Eurasia and Africa. During the Pliocene-Pleistocene in Eurasia, the dominant rhinos were several species of large derived *Dicerorhinus*, and the wide-ranging woolly rhino. *Iranotheres* and giant frontal-horned elasmotheres were also present, but all of these groups were extinct at the end of the Pleistocene. Today, only two genera of dicerotine rhinos survive in Africa, and three species of rhinos of the genera *Rhinoceros* and *Dicerorhinus* barely survive in Asia. All five of

these species are heavily poached and on the brink of extinction, a sad remnant of one of the most diverse and successful groups of mammals in the entire Cenozoic.

Introduction

One of the most taxonomically and ecologically diverse, widespread, and successful perissodactyl groups is the Rhinoceroidea. Rhinocerotoids have adapted to many herbivorous modes of life, from sheep-sized runners (*Hyracodon*), to ecological vicars of hippos (*Teleoceras*, *Brachypotherium*, *Metamynodon*), to tapir-like animals with a proboscis (*Cadurcodon*, *Aceratherium*), to the largest land mammal that ever lived (*Paraceratherium*, formerly known as *Indricotherium* or *Baluchitherium*). Rhinocerotoids far outnumber horses, hyraxes, tapirs, chalicotheres, or titanotheres in terms of valid fossil genera or species. In Eurasia, Africa, and North America, rhinos occurred in great numbers in the past; in a few localities they outnumbered all other mammals. This is true despite the fact that rhinos are often one of the largest herbivorous mammals in most Tertiary faunas. One would think that such a diverse and dominant group of large mammals would be well studied and understood.

Yet the opposite is the case. Of all the perissodactyls, rhinos have been among the least studied in the last few decades. There was some early phylogenetic work on the group (e.g., Cope, 1880; Gaudry, 1888;

Pavlowa, 1892; Scott and Osborn, 1898), but the last general reviews or phylogenies of rhinos prior to the work of Prothero, Manning, and Hanson (1986) were those of Wood (1927), Matthew (1931), Viret (1958), and Heissig (1973). Due to the complexity of the group, misconceptions or erroneous ideas about rhinos are common among both scientists and the public. In the popular image, the diagnostic character of the rhino is its horn. Yet many rhinos were hornless, and the first horn combination was not a single horn, but paired horns at the tip of the nose, which was evolved twice independently. Similarly, nearly every rhino illustrated in the popular books or the textbooks, such as Romer (1966), is identified by the wrong generic name, such as "*Caenop.*" (= *Subhyracodon*), "*Baluchitherium*" (= *Paraceratherium*) or "*Diceratherium*" (= *Menoceras*, if it is the small Agate Springs Quarry rhino).

Much of the information that has been published in the last thirty years has not been synthesized, compelling the paleontologist to undertake extra bibliographic work. The great complexity of the superfamily also confuses those who have not worked with the group in detail. Many paleontologists have tried to identify the rhino material in their faunas. Some have succeeded, but most have failed due to the difficult literature and the complexity of the task. Yet even fragmentary rhino material can now be correctly identified to species in many cases, yielding much interesting faunal information. In this chapter, we present our view of the general pattern of rhino evolution.

Phylogeny and classification

To unscramble the morass of misconceptions about rhinos, their systematics and phylogeny must be brought up to date. Several phylogenetic hypotheses have been presented in recent years for certain members of the Rhinocerotidae (e.g., Heissig, 1981; Guérin, 1982; Groves, 1983) and for the

whole Rhinocerotidae by Prothero, Manning, and Hanson (1986). As a consequence, rhino classifications can differ greatly: what Heissig (1973, this volume, Chapter 21) considers tribes are considered subfamilies by Guérin (1980b, 1982). Heissig (1973) synonymized the Tribes Elasmotheriini and Iranotheriini, while Antunes *et al.* (1972) considered them independent subfamilies. One of the commonest problems in earlier rhino phylogenies, such as those of Wood (1927), was that the crests of premolars undergoing molarization are highly variable. This can be shown by examining a number of quarry samples of rhinos such as *Trigonias* or *Subhyracodon*. Because of premolar variations, Gregory and Cook (1928) named seven species and two genera for a single, uniform-sized quarry sample of *Trigonias osborni*. This variability is also seen in a number of quarry samples of *Subhyracodon* (Prothero, in prep.). In some cases, the premolars differ on either side of the same skull. As a result, primitive rhinos are tremendously oversplit, and older phylogenies are often based on variable differences in premolars. Once premolars have become fully molarized, they are no more or less reliable than any other anatomical feature. In taxa such as *Hyrachyus*, *Triplopus*, *Trigonias*, *Subhyracodon*, and *Hyracodon*, however, they must be used with caution.

The evolution of the rhinocerotoids

The last general discussion of the history of rhinos was by Viret (1958), but much has happened in the last 30 years. The following discussion is summarized in the diagrams of the summary chapter of this volume (Prothero and Schoch, this volume, Fig. 28.2), which show the distribution of the major rhinocerotoid genera in time and space. In this chapter, we have incorporated the new argon-argon dates (see Chapter 28) that place the Eocene-Oligocene boundary at about 33.7 Ma, and place the Chadronian in the late Eocene.

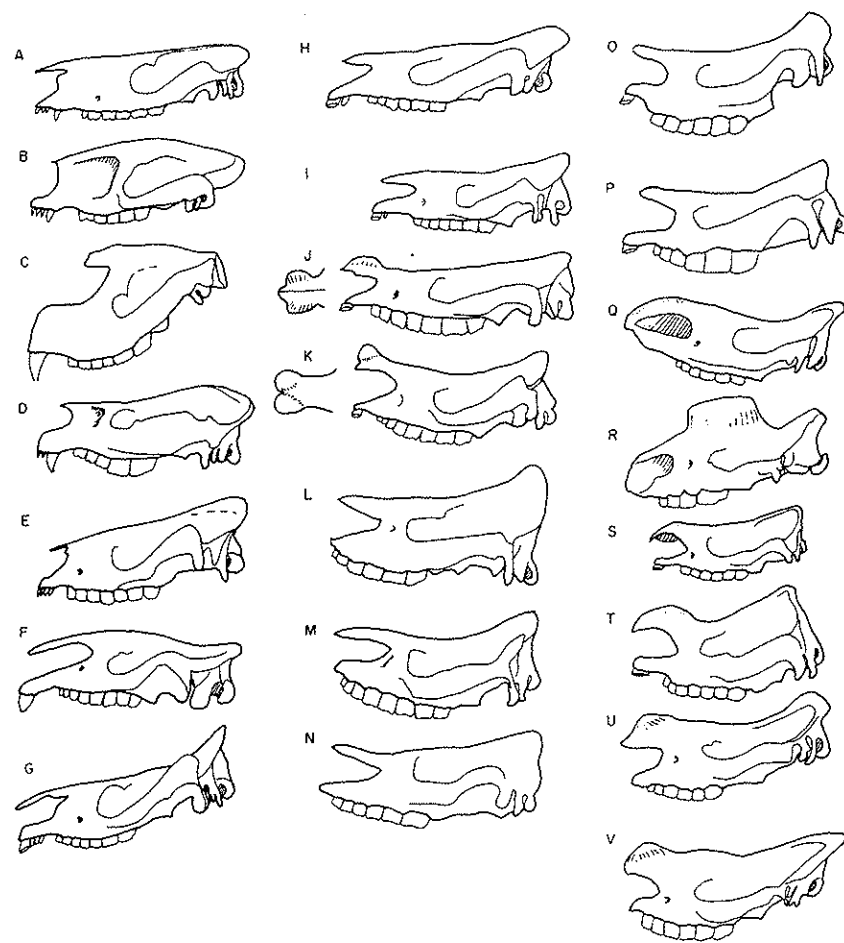


Fig. 16.1. Left lateral views of rhinocerotoid skulls (not to scale). A, *Hyrachyus*. B, *Sharamynodon*. C, *Cadurcodon*. D, *Metamynodon*. E, *Hyracodon*. F, *Paraceratherium* (= *Indricotherium*). G, *Trigonias*. H, *Amphicaenopus*. I, *Subhyracodon*. J, *Diceratherium* (showing dorsal view of paired nasal ridges). K, *Menoceras* (showing dorsal view of paired nasal knobs). L, *Aceratherium*. M, *Aphelops*. N, *Chilotherium*. O, *Brachypotherium*. P, *Teleoceras*. Q, *Coelodonta*. R, *Elasmotherium*. S, *Dicerorhinus*. T, *Rhinoceros*. U, *Diceros*. V, *Ceratotherium*. From Prothero *et al.* (1986, Fig. 5).

However, Fig. 28.2 was drafted before these revised concepts became available, so they may not always match the following discussion. From these diagrams, it is apparent that there have been a great variety of genera and family-level taxa of rhinos diversifying and diminishing throughout the Tertiary.

The oldest known rhinocerotoid is *Hyrachyus* (Fig. 16.1A) from the late Wasatchian and Bridgerian of North America. Radinsky (1966, 1967) placed *Hyrachyus* in the tapiroids based on shared primitive characters, but Prothero *et al.* (1986) gave evidence to show that it was a very primitive rhinocerotoid. It was a very cosmopolitan animal, occurring not only in the United States, but also on Ellesmere Island (West *et al.*, 1977), Europe, and possibly Asia (Radinsky, 1967). *Hyrachyus* was probably the only rhinocerotoid to cross the European-American land bridge over the North Atlantic, which was severed by the middle Eocene (McKenna, 1975). Once this route was disconnected, there was still periodic migration between Asia (east of the Turgai Straits) and North America across Beringia, but Europe became isolated from the rest of the world in the late Eocene. Instead of rhinocerotoids, European Eocene faunas were dominated by a number of endemic perissodactyls, such as palaeotheres and lophiodonts. In the early Oligocene, this endemic fauna was wiped out by a new wave of immigrants at the "Grande Coupure." Among the immigrants were the rhinocerotoids.

Meanwhile, the three major rhinocerotoid families began to diversify in Asia and North America in the late Eocene. Each of these three groups can be most easily recognized by the condition of the M^3 . Primitively, M^3 has a strong parastyle and metaloph, with a subquadrate shape, as seen in *Hyrachyus* (Fig. 16.2C). Amynodonts elongated the tooth anteroposteriorly, resulting

in a quadrangular tooth with a strong metastyle (Fig. 16.2A). In hyracodonts and rhinocerotids, the metastyle is shortened and inflected lingually (Fig. 16.2B). In some hyracodonts and all rhinocerotids, the metastyle is lost completely, producing a triangular tooth. In some populations of the last European rhino, *Coelodonta antiquitatis*, the M^3 reverted to the classical quadrangular shape.

Amynodonts and hyracodonts

The first of these three families, the Amynodontidae, are known from the early Uintan (middle Eocene) of North America, although the most primitive form (*Caenolophus*) is known from the late Eocene of Asia. During the late Eocene and early Oligocene, amynodonts reached their maximum diversity, particularly in Asia (Wall, 1982, this volume, Chapter 17). Two Duchesnean North American amynodonts (*Amynodontopsis* from the Sespe of California, *Procadurcodon* from the Clarno of Oregon) were short-ranging immigrants from Asia. *Metamynodon*, a very hippo-like form, ranged through almost ten million years in North America and three distinct species are currently recognized. *Metamynodon* occurs not only on the High Plains, but also from the late early Oligocene of Mississippi (Manning *et al.*, 1985). It may have been a coastal browser as well as a river dweller in the Oligocene. By the early Oligocene, amynodonts had declined considerably, and were extinct in North America by the Whitneyan. One lingering form, *Cadurcotherium*, managed to persist until the middle Miocene (Dera Bugti beds) of Pakistan, almost 15 million years after the rest of its family was extinct. *Cadurcotherium* was not only long-lived, but very mobile, since it also occurred in the early Oligocene of Europe. Wall (this volume, Chapter 17) reviews the phylogeny, paleobiology, and paleogeography of amynodonts in much greater detail.

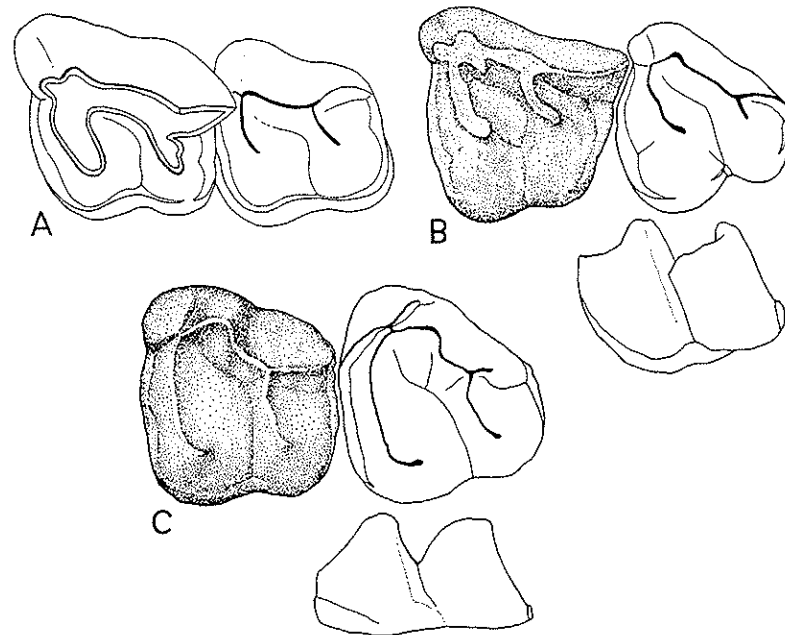


Fig. 16.2. Second and third left upper molars of: A, *Amynodon*. B, *Hyracodon*. C, *Hyrachyus*. From Radinsky (1966).

Like the amynodonts, the hyracodonts first appeared in the middle Eocene and flourished until the late Oligocene. All hyracodonts have long, laterally compressed metapodials, despite their enormous range in body size. More advanced hyracodonts also have distinctive conical incisors not found in any other rhino group. *Triplopus* (Radinsky, 1967) and *Forstercooperia* (Lucas *et al.*, 1981) are the oldest known taxa, occurring in the middle Eocene of both Asia and North America. In Europe, hyracodonts were represented during the entire Oligocene by the genus *Eggysodon*.

The Hyracodontidae are composed of two subfamilies: the small, cursorial Hyracodontinae and the large to gigantic indricotheres, the Indricotheriinae. The latter subfamily is discussed in detail by Lucas and Sobus (this volume, Chapter 19). From the primitive *Forstercooperia*, they grew to enormous proportions in Asia in the

Oligocene, producing *Paraceratherium* (= *Indricotherium*, *Baluchitherium*), the largest land mammal that ever lived. By the middle Miocene, indricotheres had vanished from Asia. Despite their gigantic proportions, their limbs did not become graviportal. Instead, their metapodials are still very long, an indication of their cursorial ancestry. Heissig (this volume, Chapter 21) suggests that the indricotheres were actually rhinocerotids, since the most primitive *Forstercooperia* has a four-digit manus. However, this is merely a primitive feature, retained in all the primitive members of the rhinocerotoid families, and sometimes secondarily regained in advanced forms. The long metapodials, however, are diagnostic of hyracodonts, and establish that indricotheres belong in this family. In addition, the enlarged upper and lower incisors of indricotheres do not resemble the

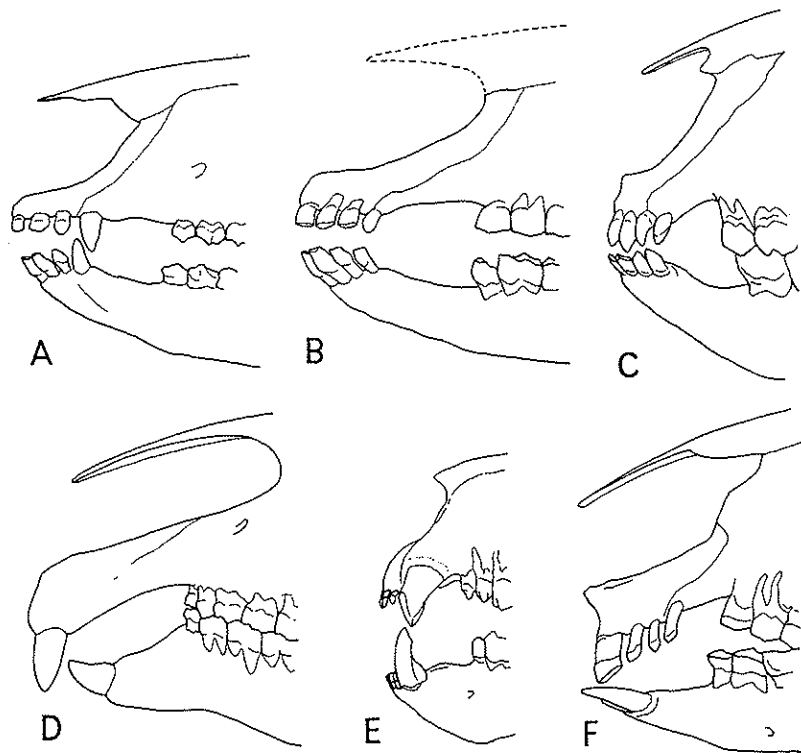


Fig. 16.3. Anterior dentitions of rhinocerotoids. A, *Hyrachyus*. B, *Ardynia*. C, *Hyracodon*. D, *Paraceratherium* (= *Indricotherium*). E, *Metamynodon*. F, *Trigonias*. From Radinsky (1966).

chisel/tusk combination of rhinocerotids (compare Fig. 16.3D with 16.3F).

The small, cursorial Hyracodontinae includes a number of lesser known forms from the late Eocene and early Oligocene of Asia and North America. Only one genus, *Hyracodon*, survived into the later Oligocene of North America. It persisted remarkably unchanged except for differences in size and in the molarization of the premolars. Since molarizing premolars are highly variable, there has been excessive oversplitting of the genus. After all other characters are taken into account, Prothero (in prep.) recognized only five valid species. The ear-

liest species, *H. primus* and *H. petersoni* of the Duchesnean and early Chadronian, are followed by the slightly larger Chadronian form, *H. priscidens*, which changed little in four million years. In the latest Chadronian, the type species, *H. nebraskensis*, appears and persists unchanged through the Orellan, Whitneyan, and possibly earliest Arikareean. Most of the invalid species of *Hyracodon* have been synonymized with *H. nebraskensis*. In the late Whitneyan, a larger, more advanced species, *H. leidymanus*, appeared and persisted sympatrically with *H. nebraskensis*. They last co-occur in the lower Sharps Formation of

South Dakota, which conventionally was considered earliest Arikareean. However, Tedford *et al.* (1985) has shown that the lowest part of the Sharps may be Whitneyan. When *Hyracodon* disappeared, it was the last of its subfamily. It lasted almost ten million years after the rest of the Hyracodontinae were extinct.

Late Eocene and Oligocene Rhinocerotidae

While the Arynodontidae and Hyracodontidae were successful in the late Eocene and Oligocene and then became extinct, the third family, the Rhinocerotidae, have become increasingly diverse and successful since the Oligocene. Like the hyracodonts and arynodonts, they appear to have arisen in the late Eocene of Eurasia. The oldest well-known rhinocerotid is the newly described form from the Clarno Formation (Duchesnean) of Oregon (Hanson, this volume, Chapter 20). Although it resembles a primitive hyracodont in size and most features, it has already begun to develop the diagnostic features of the Rhinocerotidae. Not only is the M^3 metacone nearly lost, but the I^1 and I_2 have begun to develop into the characteristic chisel/tusk combination (Fig. 16.3F).

In Europe, rhinocerotids first appear in the early Oligocene (upper Sannoisian) with *Ronzootherium*, a small-sized form which is the most common and best-known European Oligocene rhino (Heissig, 1969; Brunet, 1979). Three successive species are known: *R. velaunum* from the Upper Sannoisian, *R. filholi* from the Lower Stampian, and *R. romani* from the Upper Stampian. *R. breviostre* also occurs in the Oligocene of Mongolia. Another small European Oligocene form is *Protaceratherium albigena* from the Middle and Upper Stampian (Hugueney and Guérin, 1981). It occurs with "*Aceratherium*" (or *Protaceratherium?*) *minutum*, a small aceratheriine (de Bonis, 1973) whose generic affinities are controversial (Antunes and Ginsburg, 1983).

Other European rhinos from the Lower Oligocene are poorly known, like *Epiaceratherium bolcense* found in one single locality in Italy, and *Meninatherium* Abel, 1910 (type specimen probably destroyed during the Second World War--Kollman, pers. commun.), which is probably synonymous with *Prohyracodon* (Heissig, 1973).

Medium- and large-sized rhinos appeared in Europe during the Upper Oligocene, mainly with *Aceratherium* (*Mesaceratherium*) *paulhiacense* and *Diaceratherium lemanense*, predecessors respectively of the Miocene true *Aceratherium* lineage (with a four-digitated manus) and the large, semi-aquatic semi-hypsodont brachypotheres of the *D. aginense*-*D. aurelianensis* lineage (Antunes and Ginsburg, 1983). Rhinocerotids are not known from the Oligocene of Africa (Cooke, 1968; Hamilton, 1973).

In the latest Eocene (Chadronian) of North America, rhinocerotids became larger and more diversified. *Trigonias* is abundant in several Chadronian quarries, and was the last rhinocerotid to retain $I^3/3$ or canines (Figs. 16.1G, 16.3F). More advanced rhinos lost nearly all the anterior teeth except their $I^1/2$ chisel/tusk combination. The *Subhyracodon*-*Diceratherium* lineage first appeared in the Duchesnean, and became the dominant American Oligocene large mammal after the extinction of the titanotheres in the early Orellan (Fig. 16.1I,J). In the late Whitneyan, this lineage showed considerable sexual dimorphism in the skull as well as the tusks. Males of *Diceratherium* show paired subterminal nasal rugosities that become well-developed flanges or ridges in the Arikareean taxa. This is the first evidence of rhinos with horns. For almost the entire Whitneyan and Arikareean (from 21 to 31 Ma, almost ten million years), *Diceratherium* reigned unchallenged as the only rhinocerotoid, and the only large

mammal, in North America. Throughout in their history, this was the all-time low in rhinocerotoid generic diversity, although there were a number of species of *Diceratherium*, differing chiefly in size. In one quarry, 77 Hill, near Lusk, Wyoming, there is a large sample of both sexes of the large type species, *D. armatum*, and a smaller species, *D. annectens*. In the latest Arikarean (Agate Springs Quarry), the last species of the genus, *D. niobrarense*, came into competition with an immigrant from Europe, *Menoceras*. A few rare specimens of *Diceratherium* are known from the Hemingfordian, and possibly from the Barstovian of Railroad Canyon, Idaho, but the group apparently succumbed to competition from early Miocene immigrant rhinos.

Perhaps the greatest misunderstanding about North American rhinoceroses concerns the "paired horned" rhinos, *Diceratherium* and *Menoceras*. True *Diceratherium* is the end of the endemic North American *Subhyracodon* lineage, and has a long, primitive skull with paired, subterminal nasal ridges (Fig. 16.1f). This differs from *Menoceras*, which has a short, very derived skull with terminal nasal bosses (Fig. 16.1k). A number of derived features show clearly *Menoceras* is more closely related to higher rhinos than it is to *Diceratherium*. These include a shortened basicranium relative to the tooth row, reduced sagittal crests, reduced premaxillae, nasal incision retracted over the posterior part of P², I² lost, upper molar cingula weak or absent, strong crochets on the molars, and a shallow anteroventral notch on the atlas. The only similarity between the two genera is the paired nasal horns, and these are not homologous in detail. Instead, they are one of the truly clear examples of evolutionary convergence. If only the hornless female skulls had been known, there would have been no hesitation in putting them in separate genera.

Nevertheless, *Diceratherium* and

Menoceras have nearly always been confused because of their paired nasal horns. The genus *Menoceras* was separated by Troxell from *Diceratherium* as early as 1921, but virtually all later workers blurred this distinction until Tanner (1969) clarified the differences. *Menoceras* happens to be very abundant in one of the most famous quarries of all, Agate Springs Quarry in Nebraska, and so the misnomer "*Diceratherium cooki*" (actually *Menoceras arikareense*) has been associated with virtually every Agate rhino specimen for over eighty years. Most museum labels and popular and technical books which mention the Agate rhino still have it mislabeled.

The anatomical differences between the two genera are corroborated by their occurrence. *Menoceras* appears abruptly at the very end of the Arikarean (Agate), where it almost completely overwhelms the few *Diceratherium niobrarense* from that locality. *Menoceras* is very similar to the type specimen of *Pleuroceros pleuroceros* Duvernoy, 1853, from the Aquitanian of Europe. It seems clear, then, that *Menoceras* was an immigrant from Europe in the latest Arikarean. In the early Hemingfordian, a slightly larger species, *Menoceras barbouri*, is found in Nebraska, Florida, Texas, Wyoming, and New Mexico. (This name is the senior synonym of *M. marslandensis* and *M. falckenbachi*, and *Moschoedestes delahoensis* Stevens, 1969, from the Castolon l.f., early Hemingfordian of Texas.) By the late Hemingfordian, *Menoceras* was extinct.

Miocene rhinocerotids of North America

While North America was experiencing a low diversity of endemic rhinos during the Oligocene, the modern groups of rhinocerotids were developing in Europe, as described earlier. In the Burdigalian, migration reached a peak. A number of endemic groups reached Africa from Europe, and North America received a great many European immigrants as well during the

middle Hemingfordian. Prior to this time, North America had only *Diceratherium* and *Menoceras*, and Asia still sheltered archaic indricotheres and *Cadurcotherium*, the last of the hyracodonts and amynodonts. The great Burdigalian-Hemingfordian interchange completely altered the cast of characters. North America was invaded by two major groups, the aceratheriines and teleoceratines. The primitive aceratheriine *Floridaceras whitei*, the primitive teleoceratine *Brachypotherium americanum*, and an undescribed new genus of primitive aceratheriine occur in one or more of the early and middle Hemingfordian faunas, such as Thomas Farm in Florida, Warm Springs in Oregon, Martin Canyon in Colorado, J. L. Ray Ranch, and Box Butte in Nebraska. By the latest Hemingfordian Sheep Creek Fauna of Nebraska, the long-lived aceratheriines *Peraceras profectum* and *Aphelops megalodus* had appeared, although they are both so primitive that they are hard to distinguish.

From the late Hemingfordian until the late Hemphillian (18-4.5 Ma), the North American rhino fauna consisted of the aceratheriines *Aphelops* and *Peraceras* (until the early Clarendonian), and the teleoceratine *Teleoceras*. Aceratheriines are easy to recognize from a number of derived features, including a lower tusk with a reduced medial flange, a long diastema, a highly retracted nasal incision (to the level of P⁴), and especially by their loss of the chisel-like upper incisor and reduced premaxilla in most genera (Fig. 16.1L-N). They generally retain the skeletal proportions of the more primitive rhinocerotids, so they were relatively long-legged and adapted for browsing, like the living black rhino.

Along with the relatively primitive aceratheriines came the very derived teleoceratines (Fig. 16.1O-P). From the very beginning, they showed a number of unique features which make nearly every

skeletal element distinctive. All teleoceratines had brachycephalic skulls with broad zygomatic arches and flaring lambdoid crests, a nasal incision retracted to anterior P³, nasals shaped like an inverted U in cross-section, hypsodont grazing teeth, strong antecrochets on the molars, and an elongated calcaneal tuber. Their most distinctive feature, however, was their extraordinarily hippo-like skeleton, with a barrel-shaped chest, and short, stumpy legs. Their limb bones were so extremely shortened and compressed that every single element of the tarsus and carpus is immediately recognizable by its flattening. There is a suggestion of an early stage of fusion of carpal elements in later *Teleoceras* (Harrison and Manning, 1983).

The skeleton of *Teleoceras* is so hippo-like that it demands comparison with a living analogue. Despite its low-crowned teeth, *Hippopotamus amphibius* is a grazer that lives in the river by day, but comes out on the plains to graze at night. D. Wright (pers. commun.) has studied the population structure of *Teleoceras* from the late Clarendonian Love Bone Bed, Florida, and found that it matched *Hippopotamus* much better than any browsing rhino. *Teleoceras* is nearly always most abundant in river channel deposits, and the extraordinary Poison Ivy Quarry ash fall assemblage (Clarendonian of Nebraska) appears to have trapped a whole herd of *Teleoceras* in a lake (Voorhies, 1981). Some of these Poison Ivy Quarry rhinos even have grass seeds preserved in their throat regions (Voorhies and Thomasson, 1979).

It is typical for North American Miocene faunas to contain two genera of rhinos, one a browser, the other a grazer. Generally, the grazer can be distinguished from the browser by its hypsodont teeth and other features which permit a diet of abrasive grasses. The browser, on the other hand, often has a prehensile lip, or retracted nasals to support the muscles for a short proboscis for snapping off leaves and

twigs. In North America, the browser was often *Aphelops* or some other aceratherine. The grazer was usually *Teleoceras*, although *Peraceras superciliosum* seemed to mimic *Teleoceras* in many skull and tooth features and was probably also a grazer. This browser-grazer combination was typical throughout the history of rhinos, especially when they occurred in savannah/woodland environments. Significantly, the only such rhino pair still living (the browser *Diceros bicornis* and the grazer *Ceratotherium simum*) are found in East and South Africa, one of the few remaining savannah habitats left on earth.

The long Miocene history of rhinos in North America is fully documented elsewhere (Prothero, in prep.), but its salient features are now becoming clear. *Aphelops* has only three valid species which get progressively larger, more hypsodont, and have more retracted nasals through time. *Peraceras* was less common, and became extinct by the late Clarendonian. There are only three valid species: the primitive, medium-sized *P. profectum*, the large *P. superciliosum*, and the dwarf *P. hessei* (Prothero and Manning, 1987).

The teleoceratine story is more complex. Beginning with the Hemingfordian *Brachypotherium americanum*, *Teleoceras* gets progressively larger until the main lineage reached maximum size with *T. fossiger* in the early Hemphillian. Like many other early Hemphillian forms (*Aepyacamelus*, *Yumaceras*, *Tapirus*, *Calippus*, *Nimravides*, *Pliohippus*, *Neohipparion*, *Epicyon*, *Leptarctus*, *Macrogenis*, *Illingoceras*, *Barbourofelis*, *Indarctos*, and *Prosthennops*), the early Hemphillian *T. fossiger* is larger than the late Hemphillian species, *T. hicksi*. An even smaller species, *T. proterum*, is known from the early Hemphillian of Florida (Mixson's Bone Bed), and an unnamed species of *Teleoceras* is known from the latest Hemphillian of Oklahoma (Guymon l.f.). Another dwarf species, *T. meridi-*

anum, occurred in the late Barstovian of the Texas Gulf Coastal Plain along with the dwarf *Peraceras* (Prothero and Sereno, 1982; Prothero and Manning, 1987). Contrary to Matthew (1932), *Teleoceras* does survive into the very late Hemphillian. It is present but very rare in the Upper Bone Valley Formation of Florida, the Eden l.f. of California, the Sawrock l.f. of Kansas, and the Bidahochi Formation of Arizona. It was thought to be extinct because the typical late Hemphillian quarries, such as Coffee Ranch in Texas, and Edson in Kansas, are dominated by *Aphelops mutillus*. A single specimen of *T. hicksi*, however, is present in both quarries.

In addition to the dwarfing and ecological parallelism shown by several rhino species, North American rhino biogeography was very complex and interesting. Dwarf rhinos are particularly diverse in the Texas Gulf Coastal Plain Barstovian, which contains four sympatric species, an all-time high for North America. Prothero and Sereno (1982) suggested that the dwarfs inhabited a more coastal, forested environment, and were comparable to modern dwarf species of hippos, elephants, and Cape buffalo, which prefer browsing in forested habitats. The *Teleoceras* from the Barstovian and Clarendonian Santa Fe Group of New Mexico have peculiarly short nasals without horns and robust premaxillae, and may be an endemic new species. The abundant High Plains quarries of Nebraska, Kansas, Oklahoma, and Texas are typically dominated by the main line species of *Aphelops* and *Teleoceras*, but the northern localities (particularly Montana, South Dakota, and northern Nebraska) sometimes contained *Peraceras superciliosum*, another brachycephalic hippo-like form.

The Miocene record east of the Mississippi is generally poor, except for Florida. The Florida rhino fauna is generally similar to the High Plains fluvial assemblage, except that the early Hemphillian *Teleoceras proterum* from Mixson's Bone Bed is

much smaller than High Plains *T. fossiger*. There is a surprising scarcity of rhinos from the western states. Although there are many rich Miocene fossil mammal localities from California, Nevada, Oregon, Arizona, and elsewhere, rhinoceroses are extremely rare compared to their abundance in the High Plains. Horses and camels occur in great numbers in some of these localities, but only a few scraps of rhino are known.

By the latest Hemphillian (earliest Pliocene), rhinoceroses were very scarce in North America. Until recently, there were no rhinos reported from the Blancan, and North American rhinos were assumed to have gone extinct as a result of the Messinian climatic event at the Mio-Pliocene boundary. However, C. Madden and W. Dalquest (pers. commun.) are describing an isolated rhino tooth fragment from the mid-Blancan Beck Ranch locality in Scurry County, Texas. If this specimen is not transported from older deposits (as it appears), then rhinos survived in very small numbers until the mid-Blancan in North America.

Miocene rhinocerotids of Europe

While North America was dominated by only three genera of rhinos during the most of the Miocene, Eurasia saw far greater diversity. By the middle Miocene (Vindobonian), the menoceratines were extinct, and the fauna was dominated by *Brachypotherium*, primitive aceratheriines, and primitive rhinocerotines. Aceratheriines included *Aceratherium (sensu lato)* with related genera or subgenera *Mesaceratherium*, *Alicornops*, *Chilotherium*, and *Dromoaceratherium*. True *Aceratherium* was a medium-sized rhino with a functional fifth metacarpal. Its limbs were long, with proportions like those of the living tapir (Eisenmann and Guérin, 1984). It had brachyodont cheek teeth, and possibly a short proboscis (Hunermann, 1982). It was a browser, and

the anatomical similarities with tapirs suggest a similar way of life. The first known species was the Upper Oligocene (Upper Stampian) *Aceratherium (Mesaceratherium) paulhiacense*, leading to the European lineage composed of the Orelanian/Astaracian *A. platyodon*, the Astaracian *A. lumiarense*, the Astaracian/Early Vallesian *A. tetradactylum*, and the Vallesian/Turolian *A. incisivum* (Guérin, 1980b; Antunes and Ginsburg, 1983). The related genus *Dromoaceratherium* includes *D. mirallesi* of Orelanian/Astaracian age in Spain, and *D. fahlbuschi* from the Astaracian of southern Germany (Heissig, 1972a; Santafé-Llopis, 1978). Another related lineage begins with the little short-legged, three-toed rhino *Alicornops*, first found in the Middle Miocene from Wintershoff West (MN5 zone) and reaching its peak with *A. simorreense* from the Astaracian and Vallesian. *A. simorreense* ranged as far as India (Ginsburg and Guérin, 1979; Guérin, 1979).

A separate lineage of aceratheriines is the genus *Chilotherium*, which mimics the teleoceratines in acquiring hippopotamus-like body proportions and hypsodont cheek teeth. Possibly originating in the Middle Miocene of the Siwaliks, *Chilotherium* immigrated to China, the Middle East (Maragheh, Iran) and Europe. It is found in Samos in Greece, Italy (Guérin, 1980b), and *Chilotherium ibericum* migrated to the Iberian Peninsula (Antunes and Ginsburg, 1983). Many species have been described from this huge geographical range, but only four of the Eastern European species (*C. zernowii* from Odessa, Soviet Union, and *C. samium*, *C. schlosseri*, and *C. kowalewskii* from Samos) are considered valid (Heissig, 1975). The derived African genus *Chilotheridium* is endemic to the Miocene of Africa (Hooijer, 1971). These medium-sized grazers may have competed with *Brachypotherium*, although the latter genus had an even larger geographic range.

The teleoceratines first appear in Eu-

rope with the Upper Oligocene *Diaceratherium* (not to be confused with the American *Diceratherium*!). The first species was the Stampian form *D. lemanense*, which was followed by the Aquitanian *D. aginense* and *D. tomerdingense*. The lineage culminated with the Burdigalian *D. aurelianense*. True brachypotheres of the genus *Brachypotherium* replace *Diaceratherium* during the Middle Miocene with the Astaracian *B. stehlini* and *B. brachypus*. The last European species was the rare *B. goldfussi* from the lower Vallesian. The very large East Asian *B. permense* and African *B. lewisi* were more long-lived; the latter species is even found in the Pliocene. *Diaceratherium* and *Brachypotherium* were large to very large rhinos with hypsodont teeth and hippo-like proportions. The reduction in their limbs never reached the extent of American *Teleoceras*, however. Nevertheless, they must have been like *Teleoceras* in their hippo-like aquatic grazing lifestyle.

Prosantorhinus was a small teleoceratine with short legs and brachyodont cheek teeth. It is known from *Prosantorhinus* sp. from the Middle Burdigalian, *P. douvillei* from the Upper Burdigalian and Orleanian, *P. germanicus* from the Astaracian, and a poorly known species from the Upper Vallesian. *Prosantorhinus* is known only from western Europe and became extinct at the end of the Vallesian (Heissig, 1972a; Guérin, 1980b; Antunes and Ginsburg, 1983).

Another important rhino lineage in the European Miocene was the *Dicerorhinus* group (Fig. 16.1Q, S). The lineage may have originated in the poorly known species "*Ceratorhinus*" *tagicus* Roman, a taxon badly in need of revision. Common in the lowermost Aquitanian to upper Burdigalian, some of the material referred to this species should be classified in the genera *Protaceratherium* and *Prosantorhinus*. The first unquestionable *Dicerorhinus* is the medium-sized, cursorial, brachyodont *D. (Lartetotherium) sansani-*

ensis from the Orleanian. It was dominant in Astaracian sites of western Europe and Turkey, and survived until the early Vallesian. *D. leakeyi* from the Middle Miocene of East Africa seems to be anatomically very similar. *Dicerorhinus steinheimensis* from the Astaracian and the lower Vallesian of western Europe may be the smallest rhino ever known in the Neogene, since dwarfing is never observed in Old World rhinos. Possibly derived from the middle Orleanian *Dicerorhinus montesi* (Santafé-Llopis *et al.*, 1987), the large west European *Dicerorhinus schleiermacheri* and its east European relative *D. orientalis* are among the largest rhinos of the Vallesian and Turolian. All of these Miocene *Dicerorhinus* were tandem-horned, cursorial, brachyodont, and had well-developed tusks. Apparently all were browsers.

There were other rhinos in the European Miocene, but they were rare and apparently had limited success in spreading widely over Europe after immigrating from Asia or Africa. This was probably due to competition from indigenous species. Such rhinos include east Asian *Gaindatherium*, forerunner of the modern one-horned *Rhinoceros*. One isolated species, *G. rexmanueli*, is known from the Portuguese Orleanian. Three species of African tandem-horned rhino *Diceros* (the genus of the living black rhino) occur in the upper Miocene of Spain, Italy, and the Near East (Fig. 16.1U). The best known of these non-African *Diceros* is *D. pachygnathus* from Greece and Spain. Wagner (1848) originally based the taxon on juvenile material, but Gaudry (1862-1867) fully described it, and all subsequent identifications of *D. pachygnathus* have been based on these descriptions. Heissig (1975) found that the original material of Wagner belongs to the contemporary species *Dicerorhinus orientalis*, and suggested swapping the original definitions of the two taxa. Until the status of these taxa has been further studied and clarified, we pre-

fer to preserve Gaudry's (1862-1867) concept of the taxon. *Diceros neumayri* from the Near and Middle East, and *D. douariensis* from Tunisia and Italy are the other two species of non-African *Diceros*.

Finally, the immigrant *Hispanotherium* group, a very hypsodont, medium-sized representative of the Iranotheriinae, arrived in Europe in the Miocene. It originated in the lower Miocene of Asia, and is known from Portugal, Spain, Anatolia, the Caucasus, the Siwaliks, Mongolia, and China. The genera *Begertherium*, *Caementodon*, and *Beliajevina* are junior synonyms of *Hispanotherium* (Antunes and Ginsburg, 1983). In Europe, *Hispanotherium* is never found north of the Pyrenees.

Miocene rhinocerotids of Asia and Africa

East Asian Miocene rhinos are closely related to those of Europe. The first Chinese Neogene rhino is an Agenian *Brachypotherium* sp. from Tibet. In the Orleanian and Astaracian, aceratheriines were represented by *Aceratherium* sp., *Plesiaceratherium* (*P. gracile*, *P. shanwangensis*), and *Chilotherium* sp. Rhinocerotines are represented by the Orleanian *Dicerorhinus cixianensis* from Shanxi, and iranotheres by the Orleanian *Hispanotherium lingtungensis* (Li, Wu, and Qiu, 1984). Vallesian and Turolian species are well known from the Siwaliks of India and Pakistan (Heissig, 1972b; Guérin, 1979), from Turkey (Heissig, 1972b, 1974, 1975, 1976), and from Iran and China (Li, Wu, and Qiu, 1984). *Gaindatherium browni* from the uppermost Astaracian and lowermost Vallesian of the Siwalik Hills was replaced by *G. vidali* from the Nagri level (Vallesian). This genus was eventually replaced by *Rhinoceros* in the Pliocene and Pleistocene.

The other recent Asian genus *Dicerorhinus* (now represented by the living Sumatran rhino) is known from *D. abeli* from the middle Chinji (uppermost Astaracian/lowermost Vallesian) of India, from *D. ringstroemi* from the Vallesian and

Turolian of Turkey and South China, and from *D. orientalis* from the Turolian of the Near East and North China (Fig. 16.1S). *Coelodonta*, the woolly rhino (Fig. 16.1Q), is the most derived of the Dicerorhininae, probably appears in the Ruscinian of North China. Many species of *Chilotherium* are known from the Near and Middle East, including Turkey, India, and China. The last species is *Chilotherium yunnanensis* from the lower Villafranchian. The Iranotheriinae are represented by the large species, *Iranotherium morgani*, from the upper Miocene of Iran, and by several species of *Hispanotherium*. These, in turn, occurred with the first representatives of another very hypsodont rhino group, the Elasmotheriinae (Fig. 16.1R), represented by *Sinotherium* from the Turolian of North China. The very large *Brachypotherium permense* was a long-lived Indian species which ranged from the Burdigalian to the upper Turolian (Dhok Pathan). Another Asiatic teleoceratine was the small- to medium-sized *Aprotodon fatehjangense*, which lived in India from the Burdigalian to the lower Vallesian.

In Africa, rhinocerotids first appeared in the lower Miocene. The earliest are known from the early Miocene of Libya and Egypt (Hamilton, 1973) with *Aceratherium campbelli* and *Brachypotherium snowi*. In the middle and upper Miocene, the same genera were represented by *A. acutirostratum* from Kenya, Uganda, and Zaire, and *B. heinzlini* from Kenya, Zaire, and South Africa. Other African taxa include the teleoceratine *Chilotheridium pattersoni* from Kenya and Uganda, the dicerotines *Paradicerus mukirii* from Kenya and Morocco, and *Diceros douariensis* from Tunisia, and the iranotheres *Kenyatherium bishopi* from Nakali, Kenya. The dicerorhinines were represented by *Dicerorhinus leakeyi* from East Africa and *Dicerorhinus primaeus* from Algeria (Guérin, 1980a; Hooijer, 1966, 1968, 1971, 1973; Aguirre and Guérin, 1974).

In general, Miocene Old World rhinoceroses show several interesting features. Like North American *Aphelops* and *Teleoceras*, they show increased hypsodonty associated with the increase in grassland habitats. Hypsodonty arises independently in several rhinocerotid groups, mostly in the aceratheres *Chilotherium* and *Chilotheridium*, the teleoceratines *Teleoceras* and *Brachypotherium*, all the iranotheres (*Hispanotherium*, *Kenyatherium*, *Iranotherium*) and elasmotheres (*Sinootherium* and *Elasmotherium*). The most hypsodont cheek teeth also acquire highly infolded enamel to increase their efficiency. Second, high diversities of rhinos from the same deposit are common in the Miocene. For example, at La Grive Saint Alban (Astaracian of France), *Aceratherium* (*Alicornops*) *simorrense*, *Dicerorhinus sansaniensis*, *D. steinheimensis*, and *Brachypotherium* sp. occur together. In the lower Vallesian of Can Ponsic, Spain, there are *Aceratherium incisivum*, *A. simorrense*, *D. sansaniensis*, and *D. steinheimensis* in the same deposit. In the middle Miocene of Kenya, *A. acutirostratum*, *D. leakeyi*, *B. heinzlini*, and *Chilotheridium pattersoni* occur on Rusinga Island. Associations of four rhino species are not rare, as they are in North America, and in some cases, five species occur together. In some cases, one of the associated species is a grazer; the rest are usually browsers.

At the end of the Miocene, there was a worldwide faunal crisis probably associated with the Messinian salinity event in the Mediterranean, and the associated worldwide climatic changes. Many groups of animals went extinct, including all the aceratherines and most of the teleoceratines. In North America, this meant that the entire rhino fauna was severely decimated, with only one known specimen from the Blancan. In Eurasia, only the rhinocerotines and dicerorhinines survived. In Africa, only dicerotines survived (with

two isolated exceptions).

Plio-Pleistocene rhinocerotids

In Europe and northern Asia, only two rhino lineages are found during the Pliocene and Pleistocene. The first lineage is composed of the genera *Dicerorhinus* and *Coelodonta*. Many Palearctic rhinos are referred to *Dicerorhinus*, the genus of the living Sumatran rhino, but this usage makes the genus a paraphyletic "wastebasket" taxon for a long series of dicerorhinines. The European lineage starts with a Miocene form very near the Sumatran rhino (*Dicerorhinus sumatrensis*), and then the group undergoes many changes. These changes include total loss of incisors, acquisition of an ossified nasal septum with co-ossification of the premaxillae, maxillae, and distal nasal bones, and teeth with increased hypsodonty and complex enamel patterns. Guérin (1980b) proposed the subgenus *Brandtorhinus* for the species without functional incisors or partially ossified nasal septum. The very large *Dicerorhinus megarhinus* from the Ruscinian (lower and middle Pliocene of Europe) possessed visible but non-functional incisors and no bony nasal septum. The larger, but more slender *Dicerorhinus jeanvoireti* from the lowermost Villafranchian, and *D. etruscus* from the Villafranchian and early middle Pleistocene, have completely lost their incisors and have an ossified anterior nasal septum. Both of these species were brachyodont browsers.

Other members of the *Dicerorhinus* lineage show an even more completely ossified septum. The very large *D. mercki* (= *D. kirchbergensis*) was an open forest form from the early middle to upper Pleistocene. The medium- to large-sized *D. hemitoechus* was the end of the line, appearing during the end of the middle Pleistocene. Unlike the previous species, *D. hemitoechus* was a semi-hypsodont grazer. All of these Pleistocene species were widespread in Europe, northwest Asia, and the Middle East. *D.*

etruscus and *D. mercki* had relatives in the Far East, *D. yunchuchenensis* and *D. chokoutienensis* from China, and *D. japonicus* from Japan.

Coelodonta had the same cranial characters of the most derived *Brandtorhinus*, only highly exaggerated. Its teeth were very hypsodont, and the limb skeleton was fully graviportal. The genus seems to have originated in the Upper Villafranchian of northern China and migrated westward. *Coelodonta antiquitatis*, the woolly rhino, arose in China in the Pleistocene and arrived in Europe during the penultimate glaciation. In the Upper Pleistocene, *C. antiquitatis* had the largest range of any known rhino, living or extinct. It extended from South Korea to Scotland to Spain. It was a steppe grazer, well adapted to cold climates, with a broad front lip and a laterally flattened nasal horn well suited for brushing away snow to find grass. Its soft anatomy is well known, since many frozen or mummified carcasses have been found. Many of its anatomical features converge on the white rhino of Africa, even though it belongs to an entirely different lineage. For some reason not yet understood, *C. antiquitatis* never crossed the Bering Land Bridge to North America, even though its frequent companions—such as the woolly mammoth, bison, yak, saiga antelope, and humans—did.

It is not unusual to find three rhino species at the same level in the same site. For example, the cavern of La Fage (Corrèze, France), filled during the Riss glaciation, includes the open forest *Dicerorhinus mercki*, the parkland *Dicerorhinus hemitoechus*, and the steppe *C. antiquitatis* (Guérin, 1973).

The second Eurasian lineage is that of *Elasmotherium*, which originated in China from its sister-taxon *Sinootherium*. *E. caucasicum* occurred in southeastern Europe and adjacent Asia during the Villafranchian. *E. sibiricum* is known from the middle and upper Pleistocene. *Elasmoth-*

erium was a huge beast, as large as a male Asiatic elephant (*Elephas maximus*), with domed frontal bones and a single frontal horn (Fig. 16.1R). Its cheek teeth were the most specialized of any perissodactyl, and in some ways resemble the specialized teeth of certain rodents. It had only a single premolar, and its three molars were quadrangular in shape, extremely hypsodont with folded enamel and no roots. *Elasmotherium sibiricum* was geographically restricted to the Volga Basin and other tributaries of the Caspian and Black Seas, with possible incursions to central and western Europe. Both the *Dicerorhinus* lineage and the elasmotheres disappear at the end of the Pleistocene with the general extinction of large mammals around 13,000–10,000 years ago.

In southeast Asia, there were two Plio-Pleistocene lineages also, now represented by the genera *Rhinoceros* and *Dicerorhinus*. The one-horned genus *Rhinoceros* (Fig. 16.1T) originated in the Miocene with *Gaindatherium*, and includes the Pliocene *R. sivalensis*, the large Pleistocene *R. paleindicus*, *R. platyrhinus*, *R. sinensis*, and the two living species (*R. unicornis* and *R. sondaicus*). *R. unicornis* appeared in the Middle Pleistocene and includes the peculiar Pleistocene form from Indonesia, *R. unicornis kendengindicus*. *R. sondaicus*, the Javan rhino, can be traced back to the lower Pleistocene with *R. sondaicus siva-sondaicus*, and *R. sondaicus guthi*, respectively, as Indonesian and Indochinese Pleistocene sidebranches. *R. unicornis* and *R. sondaicus* still survive in southeast Asia, the first in Assam and Nepal, and the second in Java, Borneo, Malaya, Burma, and Indochina (Groves and Guérin, 1980). *R. unicornis* now occurs in about 19 locations with a total world population (1985 estimate) of less than 2,000 individuals. *R. sondaicus* is mainly restricted to the Ujung Kulon Reserve in western Java, with an estimated population of only 50 individuals left on earth (1987 estimate).

The tandem-horned rhinoceros, *Dicerorhinus sumatrensis*, presently survives in Sumatra, Borneo, Malaya, Burma, and Indochina. It is known from about 18 locations, with a total world population of about 400-900 (1987 estimate). This species is known from the lowermost Pleistocene, and is apparently a relict of the Miocene Dicerorhininae. *R. unicornis* is semi-hypsodont, and is able to graze. *R. sondaicus* and *D. sumatrensis* are brachydont browsers, inhabiting swamps and dense forests. *R. unicornis* is being bred in several zoos, but *R. sondaicus* and *D. sumatrensis* are both extensively poached and are highly endangered species.

In the Plio-Pleistocene of Africa, there was a different assemblage of rhinos. Besides the dicerotines, which were almost exclusively African, some exotic taxa are also found. The large *Brachypotherium lewisi*, the last of the Teleoceratinae, survived into the Pliocene. The Dicerorhininae made two incursions into North Africa: the Villafranchian *Dicerorhinus africanus*, an African endemic, and the Upper Pleistocene *Dicerorhinus hemitoechus*, a Eurasian species that may have immigrated across Gibraltar. The Dicerotinae, however, were the dominant African group, presently represented by the black rhino, *Diceros bicornis* (Fig. 16.1U), and the white rhino, *Ceratotherium simum* (Fig. 16.1V).

Diceros originated from African *Paradiceros* during the Middle Miocene, and was widespread during the Upper Miocene. It occurred from the Middle East (*D. neumayri*) to Italy (*D. douariensis*) to Spain (*D. pachygnathus*). *Diceros bicornis* appeared in the Pliocene and covered all of sub-Saharan Africa, but never reached North Africa or Eurasia. It can be traced back over 4 million years, making it among the most stable and long-lived species on the African savannah. A browser that prefers rugged, hilly, brushy terrain, it once had a clinal distribution of seven subspecies (Groves, 1967), and used to be the

most numerous rhino alive, with a population of about 65,000 in 1970. Since that time, however, it has been the most heavily poached, and has been wiped out in all but a few reserves, leaving fewer than 4,000 individuals alive in 1986, and only a few hundred in 1988 (Penny, 1988).

The grazing "white" (or wide-lipped) rhino, *Ceratotherium*, has very hypsodont teeth and a longer skull with an exaggerated occiput that allows it to graze with its head down. The genus appeared in the Pliocene with the long-legged *C. praecox*. The graviportal *C. simum* appeared in the Middle Pleistocene, with two extinct subspecies: *C. simum germanoaffricanum* of eastern and southern Africa, and *C. simum mauritanicum* of the Maghreb (surviving there until the Holocene). There are two living subspecies, *C. simum simum* of South Africa, and *C. simum cottoni* of Central Africa. Only 17 individuals of *C. simum cottoni* survive today in Zaire. On the bright side, however, the South African efforts to save *C. simum simum* are beginning to work. After reaching a low of about 3,000 individuals in 1980, the world population of this subspecies is now up to nearly 4,000 (Penny, 1988).

Next to horses, rhinos have been the most successful group of perissodactyls on this planet. From the Oligocene onward, most terrestrial habitats in the Northern Hemisphere had one or more rhino species as a normal part of the fauna. It is tragic that the rhinoceroses, which have survived so many other crises of environmental change and competition with repeated diversification and migration, may not survive their last crisis—their encounter with humans.

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Bibliography

- Abel, O. (1910): Kritische Untersuchungen über die paläogenen Rhinocerotiden Europas. -*Abh. k.k. Reisanst.* 20 (3): 1-52.
- Aguirre, E., and Guérin, C. (1974): Première découverte d'un Iranotheriinae (Mammalia, Perissodactyla, Rhinocerotidae) en Afrique: *Kenyatherium bishopi* nov. gen. nov. sp. de la formation vallésienne (Miocène supérieur) de Nakali (Kenya). -*Estudios Geológicos, Madrid*, 30: 229-233.
- Antunes, M.T., and Ginsburg, L. (1983): Les Rhinocerotidés du Miocène de Lisbonne—Systématique, écologie, paléobiogéographie, valeur stratigraphique. -*Ciencias da Terra (UNL), Lisboa*, 7: 17-98.
- Antunes, M.T., Viret, J., and Zbyszewski, G. (1972): Notes sur la géologie et la paléontologie du Miocène de Lisbonne. -*Bol. Mus. Lab. Miner. Geol. Fac. Ciencias, Lisboa*, 13: 5-23.
- Bonis, L. de (1973): Contribution à l'étude des mammifères de l'Aquitainien de l'Agenais: rongeurs, carnivores, perissodactyles. -*Mem. Mus. nat. Hist. natur., Paris*, C, XXVIII: 1-192.
- Brunet, M. (1979): Les grands mammifères chefs de file de l'immigration oligocène et le problème de la limite Eocène-Oligocène en Europe. -*Fond. Singer-Polignac édit., Paris*, 1-192.
- Cooke, H.B. S. (1968): Evolution of mammals on southern continents. II. The fossil mammal fauna of Africa. -*Quart. Rev. Biol.* 43 (3): 234-264.
- Cope, E.D. (1880): The genealogy of American rhinoceroses. -*Amer. Natur.* 14: 540.
- Duvernoy, G.-L. (1853): Nouvelles études sur les rhinocéros fossiles. -*C.R. Acad. Sci. Paris*, 36: 117-125.
- Eisenmann, V., and Guérin, C. (1984): Morphologie fonctionnelle et environnement chez les Périssodactyles. -*Geobios, Mém. Spéc.* 8: 69-74.
- Gaudry, A. (1862-1867): *Animaux fossiles et géologie de l'Attique*. -Paris, 475 pp.
- Gaudry, A. (1888): *Les Ancêtres de nos Animaux dans les Temps Géologiques*. -Paris (Bibliothèque scientifique contemporaine), 1-296.
- Ginsburg, L., and Guérin, C. (1979): Sur l'origine et l'extension géographique du petit Rhinocerotidé miocène *Aceratherium (Alicornops) simorreense* nov. subgen. -*C.R. Somm. Acad. Sci. Paris, D*, 288: 493-495.
- Gregory, W.K., and Cook, H.J. (1928): New material for the study of evolution: a series of primitive rhinoceros skulls (*Trigonias*) from the lower Oligocene of Colorado. -*Proc. Colo. Mus. Nat. Hist.* 8(1): 3-39.
- Groves, C. (1967): Geographic variation in the black rhinoceros *Diceros bicornis* (L., 1758). -*Z. f. Säugertierk.* 32 (5): 267-276.
- Groves, C. (1983): Phylogeny of the living species of rhinoceros. -*Zeit. Zool. Systematik Evolutionforschung*, 21 (4): 293-313.
- Groves, C., and Guérin, C. (1980): Le *Rhinoceros sondaicus annamiticus* (Mammalia, Perissodactyla) d'Indochine: distinction taxonomique et anatomique, relations phylétiques. -*Geobios*, 13(2): 199-208.
- Guérin, C. (1973): Les trois espèces de rhinocéros (Mammalia, Perissodactyla) du gisement pléistocène moyen des Abîmes de La Fage à Noailles (Corrèze). -*Nouv. Arch. Mus. Hist. Nat. Lyon*, 11: 55-84.
- Guérin, C. (1979): Intérêt biostratigraphique des Rhinocéros du Miocène supérieur d'Europe Occidentale. -*Soc. Géol. Fr. édit.*, p. 236.
- Guérin, C. (1980a): A propos des rhinocéros (Mammalia, Perissodactyla) néogènes et quaternaires d'Afrique: essai de synthèse sure les espèces et sur les gisements. -*Proc. 8th Panafr. Cong. Prehist. Quat. Stud.*, p. 65-83.
- Guérin, C. (1980b): Les rhinocéros

- (Mammalia, Perissodactyla) du Miocène terminal au Pléistocène supérieur en Europe occidentale. -*Docum. Lab. Géol. Lyon*, 79: 1-1185 (3 vols.).
- Guérin, C. (1982): Les Rhinocerotidae (Mammalia, Perissodactyla) du Miocène terminal au Pléistocène supérieur en Europe occidentale comparés aux espèces actuelles: tendances évolutives et relations phylogénétiques. -*Geobios*, 15(4): 599-605.
- Hanson, C. B. (1989): *Teletaceras radinskyi*, a new primitive rhinocerotid from the late Eocene Clarno Formation, Oregon (this volume, Chapter 20).
- Hamilton, W. (1973): North African lower Miocene rhinoceroses. -*Bull. Brit. Mus. Nat. Hist.*, 24(6): 351-395.
- Harrison, J.A., and Manning, E.M. (1983): Extreme carpal variability in *Teleoceras* (Rhinocerotidae, Mammalia). -*J. Vert. Paleont.*, 3: 58-64.
- Heissig, K. (1969): Die Rhinocerotidae (Mammalia) aus der oberoligozänen Spaltenfüllung von Gaimersheim bei Ingolstadt in Bayern und ihre phylogenetische Stellung. -*Bayer. Akad. Wiss. Abh.*, 138: 1-133.
- Heissig, K. (1972a): Die obermiozäne Fossil-Lagerstätte Sandelzhausen. 5. Rhinocerotidae (Mammalia), Systematik und Ökologie. -*Mitt. Bayer. Staatssamml. Paläont. Hist. Geol.*, 12: 57-81.
- Heissig, K. (1972b): Paläontologische und geologische Untersuchungen im Tertiär von Pakistan. 5. Rhinocerotidae (Mamm.) aus den unteren und mittleren Siwalik-Schichten. -*Bayer. Akad. Wiss. Abh.*, 152: 1-112.
- Heissig, K. (1973): Die Unterfamilien und Tribus der rezenten und fossilen Rhinocerotidae (Mammalia). -*Säugetierk. Mitt.*, 21: 25-30.
- Heissig, K. (1974): Neue Elasmotheriini (Rhinocerotidae, Mammalia) aus dem Obermiozän Anatoliens. -*Mitt. Bayer. Staatssamml. Paläont. Hist. Geol.*, 14: 21-35.
- Heissig, K. (1975): Rhinocerotidae aus dem Jungtertiär Anatoliens. -*Geol. Jahrb.*, 15: 145-151.
- Heissig, K. (1976): Rhinocerotidae (Mammalia) aus der Anchitherium-Fauna Anatoliens. -*Geol. Jahrb.*, 19: 3-121.
- Heissig, K. (1981): Probleme bei der cladistischen Analyse einer Gruppe mit wenigen eindeutigen Apomorphien: Rhinocerotidae. -*Paläont. Zeit.*, 55: 117-123.
- Heissig, K. (1989): The Rhinocerotidae (this volume, Chapter 21).
- Hooijer, D.A. (1966): Miocene rhinoceroses of East Africa. -*Bull. Brit. Mus. Nat. Hist.*, 13(2): 119-190.
- Hooijer, D.A. (1968): A rhinoceros from the late Miocene of Fort Ternan, Kenya. -*Zool. Mededel.*, 43(6): 77-92.
- Hooijer, D.A. (1971): A new rhinoceros from the late Miocene of Loperot, Turkana District, Kenya. -*Bull. Mus. Comp. Zool.*, 142 (3): 339-392.
- Hooijer, D.A. (1973): Additional Miocene to Pleistocene rhinoceroses of Africa. -*Zool. Mededel.*, 46 (11): 149-178.
- Hugueney, M., and Guérin, C. (1981): La faune de mammifères de l'Oligocène moyen de Saint-Menoux (Allier). 2^e partie: Marsupiaux, Chiroptères, Insectivores, Carnivores, Périssodactyles, Artiodactyles. -*Rev. Sci. Bourbonnais*, p. 52-71.
- Hunermann, K.A. (1982): Rekonstruktion des *Aceratherium* (Mammalia, Perissodactyla, Rhinocerotidae) aus dem Jungtertiär vom Höwenegg/Hegau (Baden-Württemberg, BRD). -*Zeit. geol. Wiss.*, 10(7): 929-942.
- Li C., Wu W., and Qiu Z. (1984): Chinese Neogene: subdivision and correlation. -*Vert. Palasiatica*, 22(3): 171-178.
- Lucas, S.G., Schoch, R.M., and Manning, E. (1981): The systematics of *Forstercooperia*, a middle to late Eocene hyracodontid (Perissodactyla: Rhinocerotidae)

- from Asia and western North America. -*J. Paleont.*, 55: 826-841.
- Lucas, S. G., and Sobus, J. (1989): The systematics of indricotheres (this volume, Chapter 19).
- Manning, E., Dockery, D.T. III, and Schiebout, J.A. (1986): Preliminary report of a *Metamynodon* skull from the Byram Formation (Lower Oligocene) in Mississippi. -*Miss. Geol.*, 6(2):1-16.
- Matthew, W.D. (1931): Critical observations on the phylogeny of the rhinoceroses. -*Univ. Calif. Publ. Geol. Sci.*, 20: 1-8.
- Matthew, W.D. (1932): A review of the rhinoceroses with a description of *Aphelops* material from the Pliocene of Texas. -*Univ. Calif. Publ. Geol. Sci.*, 20: 411-480.
- McKenna, M.C. (1975): Fossil mammals and early Eocene North American land continuity. -*Ann. Missouri Bot. Garden*, 62: 335-353.
- Pavlova, M. (1892): Études sur l'histoire paléontologiques des Ongules. VI. Les Rhinocéridae de la Russie et le développement des Rhinocéridae en général. -*Bull. Soc. Imp. Natur. Moscou*, 6: 137-221.
- Penny, M. (1988): *Rhinos, Endangered Species*. -New York (Facts on File).
- Prothero, D. R. (in prep.): The evolution of North American rhinoceroses.
- Prothero, D.R., and Manning, E. (1987): Miocene rhinoceroses from the Texas Gulf Coastal Plain. -*J. Paleont.*, 61(2): 388-423.
- Prothero, D.R., Manning, E., and Hanson, C.B. (1986): The phylogeny of the Rhinocerotidae (Mammalia, Perissodactyla). -*Zool. J. Linn. Soc.*, 87: 341-366.
- Prothero, D.R., and Sereno, P.C. (1982): Allometry and paleoecology of medial Miocene dwarf rhinoceroses from the Texas Gulf Coastal Plain. -*Paleobiology*, 8: 16-30.
- Prothero, D. R., and Schoch, R. M. (1989): The origin and evolution of perissodactyls: summary and synthesis (this volume, Chapter 28).
- Radinsky, L.B. (1966): The families of the Rhinocerotidae (Mammalia, Perissodactyla). -*J. Mamm.*, 47(4): 631-639.
- Radinsky, L.B. (1967): A review of the rhinocerotid family Hyracodontidae (Perissodactyla). -*Bull. Amer. Mus. Nat. Hist.*, 136(1): 1-45.
- Romer, A.S. (1966): *Vertebrate Paleontology* (3rd ed.). -Chicago (Univ. Chicago Press).
- Santafé-Llopis, J.V. (1978): Rhinocerotidos fosiles de España. -Thèse Fac. Sci. Géol. Univ. Barcelone, 1-501.
- Santafé-Llopis, J.V., Casanovas-Cladelas, M.L., and Belinchon-Garcia, M. (1987): Una nueva especie de *Dicerorhinus*, *D. montesi* (Rhinocerotidae, Perissodactyla) del yacimiento de Bunol (Orleanense medio) (Valencia, España). -*Paleont. Evol.*, 21: 271-293.
- Scott, W.B., and Osborn, H.F. (1898): On the skull of the Eocene rhinoceros, *Orthocynodon*, and the relations of this genus to other members of the group. -*Contrib. Mus. Geol. Archeol. Princeton Coll.*, 3(1): 1-22.
- Stevens, M.S., Stevens, J.B., and Dawson, M.R. (1969): New early Miocene formation and vertebrate fauna, Big Bend National Park, Brewster County, Texas. -*Pearce-Sellards Series Texas Mem. Mus.*, 15:1-53.
- Tanner, L.G. (1969): A new rhinoceros from the Nebraska Miocene. -*Bull. Univ. Nebraska State Mus.*, 8: 395-412.
- Tedford, R.H., Swinehart, J.B., Hunt, R.M., Jr., and Voorhies, M.R. (1985): Uppermost White River and lowermost Arikaree rocks and faunas, White River Valley, northwestern Nebraska, and their correlation with South Dakota. -In: Martin, J.E. (ed.), Fossiliferous Cenozoic deposits of western South Dakota and northwestern Nebraska. -*Dakoterra*, 2(2): 334-352.
- Troxell, E.L. (1921): A study of

- Diceratherium* and the diceratheres. - *Amer. J. Sci.*, 202: 197-208.
- Viret, J. (1958): *Perissodactyla*. -In: Piveteau, J. (ed.): *Traité de Paléontologie*, 6 (2): 368-475.
- Voorhies, M.R. (1981): Ancient ash fall creates a Pompeii of prehistoric animals. -*Nat. Geog.*, 159(1): 66-75.
- Voorhies, M.R., and Thomasson, J.R. (1979): Fossil grass anthoecia within Miocene rhinoceros skeletons: diet in extinct species. -*Science*, 206: 331-333.
- Wagner, J.A. (1848): Urweltliche Säugethiere-Überreste aus Griechenland. -*Abh. k. Bayer. Akad. Wiss. II Cl.*, 5(2): 335-378.
- Wall, W. P. (1982): Evolution and biogeography of the *Amyndontidae* (*Perissodactyla*, *Rhinocerotidae*). - *Proc. Third North Amer. Paleon. Conv.*, 2: 563-567.
- Wall, W. P. (1989): The phylogenetic history and adaptive radiation of the *Amyndontidae* (this volume, Chapter 17).
- West, R.M., Dawson, M.R., and Hutchinson, J.H. (1977): Fossils from the Paleogene Eureka Sound Formation, N.W.T., Canada: occurrence, climatic and paleogeographic implication. -In: West, R.M. (ed.): *Paleontology and plate tectonics*. - *Milw. Public Mus. Spec. Publ. Biol. Geol.*, 2: 77-93.
- Wood, H.E., II (1927): Some early Tertiary rhinoceroses and hyracodonts. -*Bull. Amer. Paleont.*, 13(50): 5-105.