HORNS, TUSKS, AND FLIPPERS: THE EVOLUTION OF HOOFED MAMMALS

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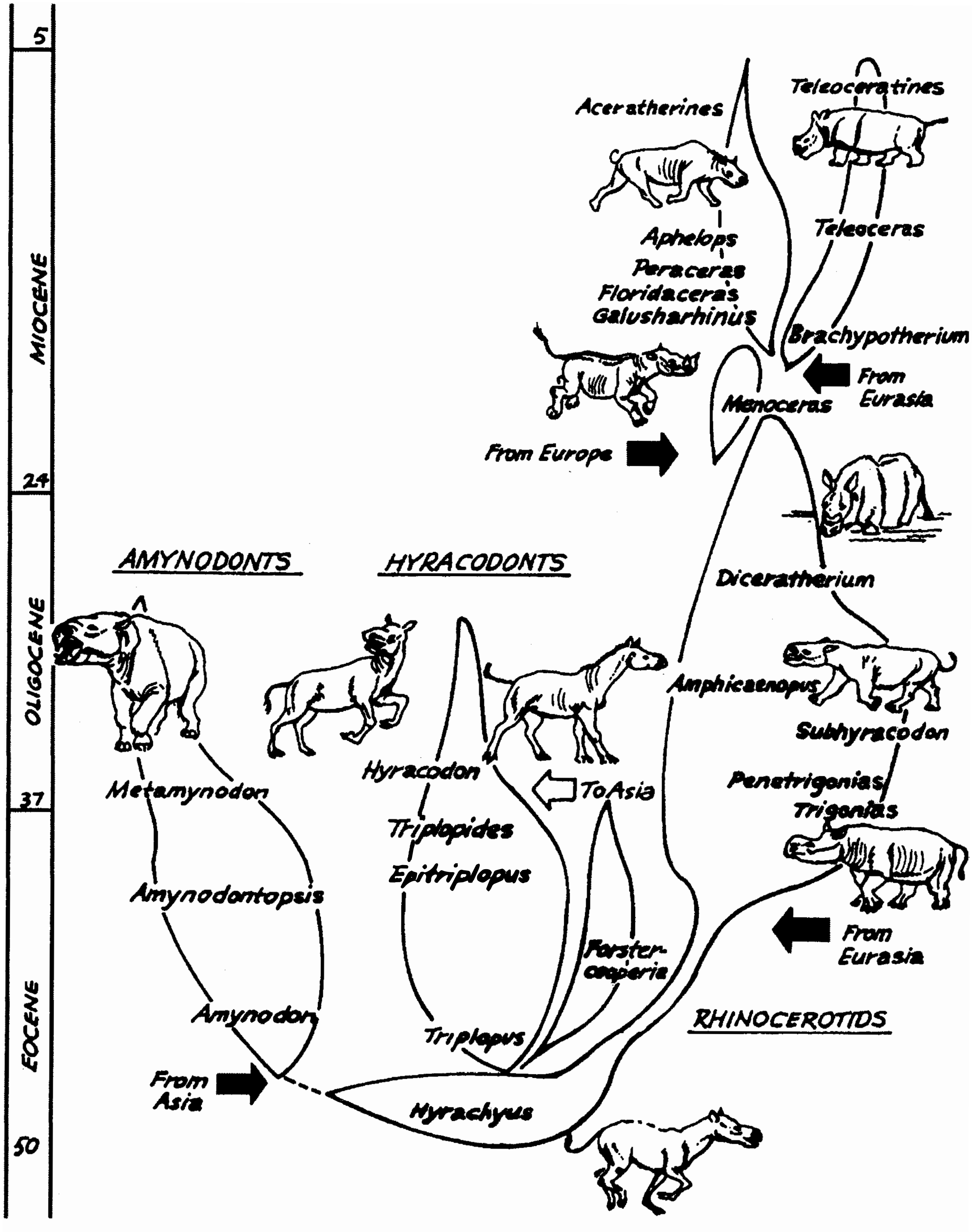


Figure 14.1. Family tree of rhinocerotoids in North America. (Drawn by C. R. Prothero).

14. Rhinoceroses without Horns

"ANCIENT DACIANS" AND SIBERIAN MUMMIES

Before the rise of modern comparative anatomy and paleontology, the giant bones found in the earth were a great source of wonder, mystery, and eventually legends. In Chapter 8, we saw how many of these "giants in the earth," interpreted as gigantic humans, were actually the remains of mastodonts or mammoths. The remains of fossil rhinoceroses (Fig. 14.1) were similarly misinterpreted. The horns of the woolly rhinoceros were thought by Siberians to be the claws of gigantic predatory birds and may have been responsible for the myth of the griffin (also spelled "gryphon").

The most amusing story of such myth-making was related in 1858 by the Finnish zoologist and explorer Alexander von Nordmann. In 1843 a number of large, mysterious bones were plowed up near the town of Kishinev in Moldova (now independent, but once part of the Soviet Union near the Romanian border). The Moldovan peasants lashed the bones together into an upright skeleton, and place the skull on top. In its "hand" was a staff with a colored rag tied to it like a flag. The local peasants flocked to see the wonder, which they considered one of their ancestors, the legendary ancient Dacian giants. They sang and danced around the skeleton, drinking plenty of the local firewater known as *buza*.

When the Imperial Military Governor heard of this wonder he went to see it for himself. He decided it was not an ancient Dacian, but an "old Roman grenadier" (equipped with unusually large molars!). An "anti-geological priest" thought the object a monstrosity and ordered the supposedly "saintly" bones chopped into pieces and buried. When Nordmann arrived a few months later no one could find the burial site under the head-high wheat. However, an old medicine woman had hidden away a piece of the jaw to cure the ills of her patients. Nordmann obtained it and found that it was a jaw fragment (Fig. 14.2) of the extinct steppe rhinoceros of the Ice Age, *Stephanorhinus hemitoechus*.

Fossil rhinoceroses had been found even earlier in many parts of Europe. The German naturalist Peter Simon Pallas (1741-1811) was invited to work for the St. Petersburg Academy of Sciences in 1767 by Catherine the Great. As a result, he was part of a long scientific expedition to Siberia between 1768 and 1774. When he published his results in 1777 and 1779 he described fossilized and mummified "large animals of India, "including elephants, rhinoceroses, and buffalos [now recognized as extinct Ice Age woolly rhinos and mammoths, and bison]. His most spectacular find was a mummy of a woolly rhinoceros, found with its skin intact in the frozen ground on the banks of the Viloui (also spelled Vilyuy) River. To Pallas this was "convincing proof that it must have been a most violent and most rapid flood which once carried these carcasses toward our glacial climates, before corruption had time to destroy their soft parts."

Pallas' insistence on the Indian origin of these Siberian mummies was a reaction to non-Biblical ideas proposed by Buffon in 1751. As we discussed in Chapter 8, Buffon regarded the presence of these "Indian" animals in Siberia, and similar animals in North America, as proof that Earth's climate had changed and elephants and rhinos had migrated in response. This implied that Earth was much older than orthodoxy was willing to admit, and that some of these beasts might be extinct. As we have seen, these heresies were not accepted until the nineteenth century, and most

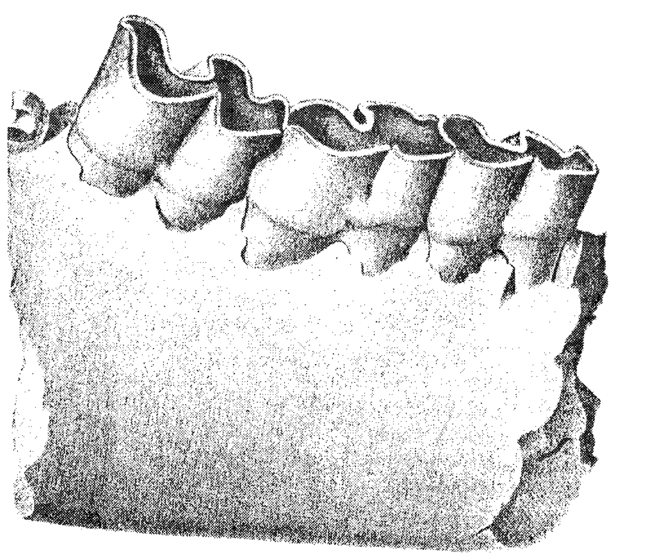


Figure 14.2. This jaw fragment of the steppe rhino, *Stephanorhinus hemitoechus*, is all that remains of the "ancient Dacian" or "Roman grenadier" revered by Moldavian peasants in 1843. (From Kurtén 1986).

eighteenth-century scientists tried to find Biblical explanations for these mysteries. Pallas, like most of his peers, thought that the Great Flood of Noah had moved these "Indian" animals to the perpetually cold regions of Siberia, where they could never have actually lived (in his view).

Along with fossil mammoths and mastodonts, fossil rhinos (especially the woolly rhinos) were described by many different scientists in Europe during the nineteenth century. Unfortunately, however, specimens from Oligocene and Miocene deposits tended to be very poor and incomplete, so very little progress was made in understanding rhinoceros evolution in Europe. Most specimens were simply isolated teeth and jaws, and these were usually assigned to one of the living genera. Not until 1832 did European scientists realize that some fossil rhinos did not have horns. Kaup created the new genus *Aceratherium* ("hornless beast") in recognition of this fact, and for the rest of the century nearly every hornless rhinoceros specimen was placed in this "wastebasket" genus. It soon turned out that through most of their history, rhinoceroses lacked horns. Only some of the lineages that started in the Miocene developed them, and by accident all of the species still living today have them. Most people think the horn is *the* characteristic feature of rhinos, but it is a late invention. Most extinct rhinoceroses were hornless. They can be recognized as rhinos by many other distinctive features of the skull, teeth, and skeleton. Since horns are made of cemented hair-like fibers, and not cored with bone like artiodactyl horns, we seldom find them fossilized. We can only deduce their presence by the roughened attachment surfaces they leave on the skull.

Because of the poor fossil record of European rhinoceroses, and the tendency to try to squeeze them into living genera, little progress was made in understanding their evolution in the Old World during the early nineteenth century. Ironically, it was scientists studying the excellent complete skulls and skeletons found in the western United States who were able to piece together their history and make sense of the Eurasian fossils.

AMERICAN RHINOS

One day early in December, 1850, Joseph Leidy received a surprising package in his Philadelphia study. Since 1847 Leidy had been receiving many shipments of fossils from the Indian Territories of Dakota and Nebraska out west, and his descriptions of these fossils had made him the foremost paleontologist in the country. Some of these fossils were of typically American beasts, such as dogs, cats, rabbits, peccaries, and deer, although they were of such archaic types that they could barely be recognized as related to their modern descendants. Other parcels held remains of animals (such as brontotheres) with no living descendants. Still other packages held the remains of animals never previously known from North America. He had already discovered that camels and horses had been all-American natives, but on this particular day he realized that he was looking at the first evidence of an American rhinoceros.

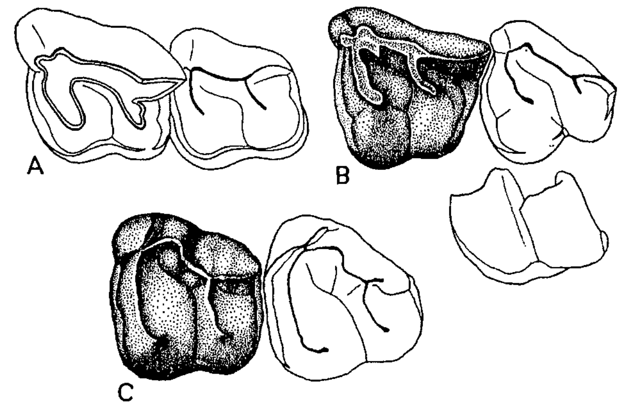
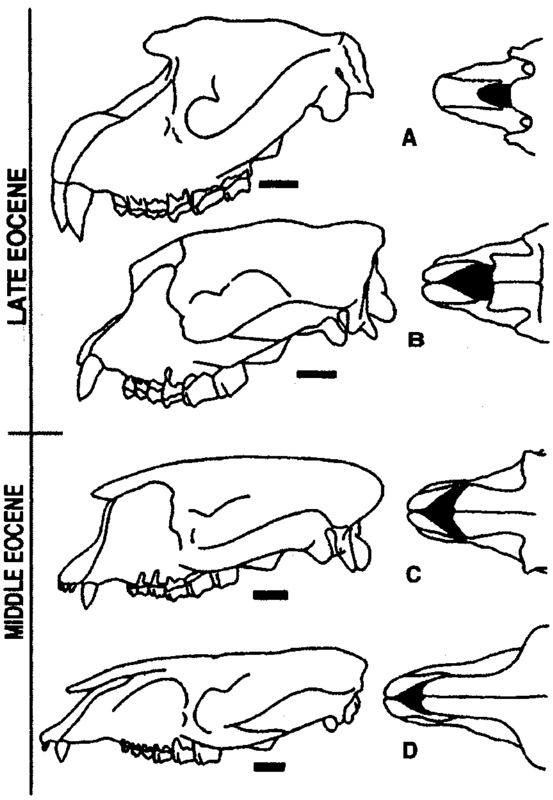


Figure 14.3. Occlusal view of second and third left upper molars of (A) *Amynodon*, the amphibious rhino; (B) *Hyracodon*, the running rhino; and (C) *Hyrachyus*, the most primitive rhinocerotoid. Note how the second molars form the shape of the Greek letter π, and the third molars (the ones on the right) lose the back crest and become more V-shaped. (From Radinsky 1966).

A few days later Leidy described the specimen at a meeting of the Philadelphia Academy of Natural Sciences. He christened it *Rhinoceros occidentalis*, the "Western rhinoceros" (now known as *Subhyracodon occidentalis*). In the remaining twenty years of his career he described many more rhinos from the Dakotas, Oregon, California, Nebraska, Texas, and even Florida. Cope and Marsh also began to describe rhinos from their collections out west. By the turn of the century it was clear that rhinoceroses had not only lived in North America, but they were the commonest large herbivore on this continent for most of the last fifty million years.

As we have seen in previous chapters, the oldest perissodactyls are known from the early Eocene. They include the first horse (?*Protorohippus*), and the most primitive relative of rhinos and tapirs, *Homogalax*. By the late early Eocene we find the oldest brontotheres and chalicotheres, as well as lophiodonts and palaeotheres. The diversification of the perissodactyls was taking place at a very rapid pace in the early Eocene, although it was "rapid" only in the geological sense. After all, the early Eocene spans six million years.

By the middle Eocene, the various lineages of "tapiroids," including the helaletids and isectolophids, diversified and became the dominant perissodactyls (see Chapter 13). The tapiroids already showed some of their characteristic specializations, such as strong cross-crests on the molars and a well-developed proboscis. Meanwhile, another lineage specialized in a different direction. This was the rhinocerotoids, the relatives of the true rhinoceroses, whose first representative is *Hyrachyus* (Fig. 13.14). Superficially, *Hyrachyus* is difficult to distinguish from



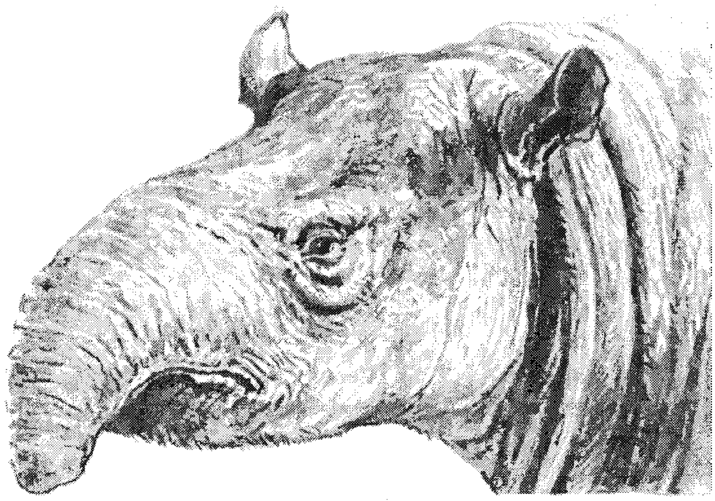


Figure 14.4. (left) Evolution of skull shape in Eocene Mongolian amynodonts from *Rostriamynodon* (D) to *Sharamynodon* (C) to *Amynodontopsis* (B), and culminating in *Cadurcodon* (A) with its deep nasal retraction indicating a sizable proboscis. (From Wall 1982).

Figure 14.5. (above) Restoration of *Cadurcodon*, the most tapir-like of all the amynodonts. (From Savage and Long 1986; by permission of the Natural History Museum, London).

some of its contemporaries among the horses and tapirs. It had a relatively slender body suited for running, and unspecialized features in the head and rest of the skeleton. But the teeth of *Hyrachyus* have already begun to show the hallmarks of rhino teeth. While both tapiroids and rhinocerotoids had strong cross-crests, the tapiroids began to reduce the ectoloph until only the cross-crests remain. *Hyrachyus* and later rhinocerotoids strengthen and straighten the ectoloph so that it joins with the cross-crests and forms the characteristic "pi"-shaped (π) upper molar (Fig. 14.3).

Hyrachyus was very successful in the middle Eocene, spreading from Asia to Europe and North America and even to Ellesmere Island in the Canadian Arctic. From an animal like *Hyrachyus*, three major branches of rhinocerotoids split off in the middle Eocene (Fig. 14.1). In one branch, the Family Amynodontidae, many species became specialized for amphibious life. Another branch, the Family Hyracodontidae, developed long legs suitable for running. The third, the Family Rhinocerotidae, was the lineage that led to the living rhinos. All three families can be distinguished by a number of skeletal features, but the quickest rule of thumb is to look at the last upper molar. In *Hyrachyus* the last upper molar has a very short crest in the rear outside corner of the tooth (Fig. 14.3). In amynodonts this crest is enlarged and points out and back. In hyracodonts the crest is enlarged, but points inward. In the true rhinoceroses this crest is lost altogether, and the last upper molar is triangular in shape. It seems like a subtle distinction to separate such different groups of animals, but it works. In this chapter, we will first look at the two families which went extinct and did not lead to living rhinos.

THE AMPHIBIOUS AMYNODONTS

In the middle Eocene, one of the descendants of *Hyrachyus* migrated from Asia to North America over the Bering land bridge. This was *Amynodon*, a tapir-sized animal that superficially resembled many of the other large perissodactyls (such as brontotheres and tapiroids) of the middle Eocene. However, it already showed some unique features that mark it for ancestry of a totally new group. Unlike most hoofed mammals, *Amynodon* had large canines, and these teeth became larger and larger until they formed a thick set of tusks in its descendants. There was a shallow depression on the facial region of the skull for attachment of the snout muscles. *Amynodon* probably had a prehensile lip like many modern rhinos. Finally, *Amynodon* had the square last upper molar characteristic of the group.

From an animal like *Amynodon* two groups emerged. One, the cadurcodonts, remained in Asia and developed a more mobile face and snout. We can see the stages of cadurcodont evolution in Asia, from early late Eocene *Amynodon* to latest Eocene *Sharamynodon* and *Amynodontopsis*, and culminating with the end of the line, *Cadurcodon* itself. In each of these stages, the nasal notch grew deeper and the nasal bones retracted (Fig. 14.4). This indicated a more and more flexible snout and upper lip. *Cadurcodon* has such extreme nasal retraction, and such deep pits for muscle attachment that it must have had a trunk larger than a tapir's

Figure 14.6. Reconstruction of *Metamynodon* in its typical hippo-like habitat, now represented by the lower Oligocene river channel sandstones of the Big Badlands of South Dakota. (Painting by R. B. Horsfall, from Scott 1913).

(Fig. 14.5). Along with these changes, the front tusks grew larger and larger, and the cheek teeth become more massive and high-crowned for a more specialized diet. As the expanding trunk took over the front of the face, the eyes moved lower on the skull.

While the cadurcodonts were probably forest dwellers that lived much like tapirs or elephants, the other group of amynodonts, the metamynodonts, were specialized for an amphibious lifestyle. They became massive animals built much like hippos, and reached sizes comparable to large hippos today. Like the cadurcodonts, most metamynodonts lived in Asia during the latest Eocene and early Oligocene. A few managed to migrate back to North America. The best known of these is *Metamynodon* itself, which was common in the early Oligocene river deposits of the Big Badlands of South Dakota. So many of their bones have been found that they are known as the "*Metamynodon* channels."

At first glance *Metamynodon* is very hippo-like (Fig. 14.6). It has both the broad, massive head and the stout, short-legged body that are associated with the hippo's amphibious existence. The eyes were high on the skull so it could see when its body and head were submerged. It had large tusks that the males must have used in combat. It also has impressively large, high-crowned molar teeth for grinding abrasive vegetation. It was probably a grazer. Modern hippos actually do most of their feeding in grassy meadows at night, and live in the water only when they're not grazing in the day. *Metamynodon* lived in the early Oligocene, just after the brontotheres had died out, and was the largest mammal in North America at the time. When *Metamynodon* died out in the late early Oligocene no large amphibious plant eater evolved to fill its hippo niche in North America until the middle Miocene when another rhino, *Teleoceras*, appeared.

After the early Oligocene, amynodonts became extinct in both Asia and North America. However, a metamynodont named *Cadurcotherium* survived in Europe in the late Oligocene, and in the early Miocene it is found in Asia. Its fossils have been found in early Miocene sediments of Pakistan and Burma. *Cadurcotherium* was truly a relict of the Eocene, surviving almost fifteen million years after all its relatives were gone. If we lived in the Miocene we would have recognized it as a "living fossil." Finally, it too succumbed to the competition from more advanced rhinos in Europe and Asia. About fifteen million years ago the last of the amynodonts joined its family in extinction.

RUNNING RHINOS AND RHINO GIANTS

While the amynodonts diverged from *Hyrachyus* in one direction, another group arose in the middle Eocene that was specialized for running (Fig. 14.1). These were the hyracodonts. Their earliest representatives included *Triplopus*, an animal built along much more slender lines than *Hyrachyus*. The name *Triplopus* refers to the three-toed front foot, since hyracodonts were quick to reduce digit 5 (the "pinky" finger). The amynodonts, on the other hand, retained the four-toed front foot, which must have been useful for traction in the mud. *Triplopus* and the hyracodonts

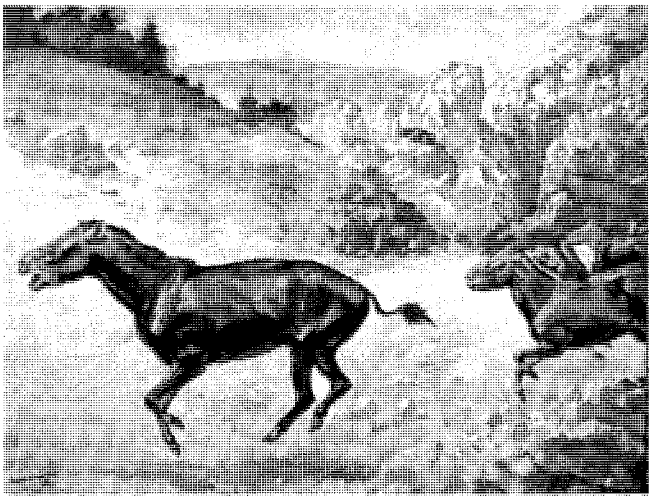


Figure 14.7. (above) Reconstruction of the Great-Dane-sized running rhino *Hyracodon*, one of the commonest mammals in the Big Badlands. (Painting by C.R. Knight, courtesy Department of Library Services, American Museum of Natural History).

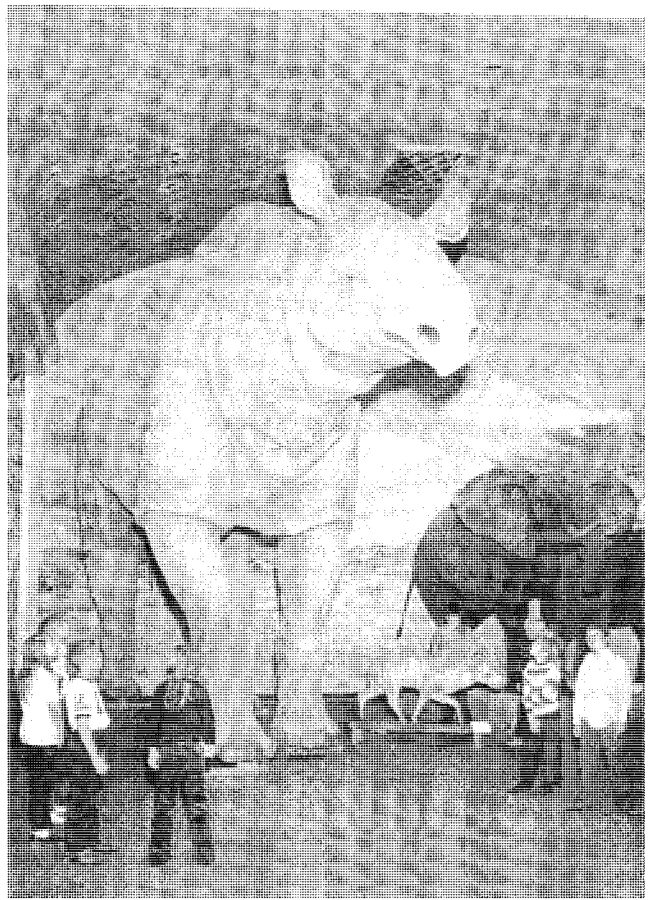


Figure 14.8. (right) Life-sized fiberglass reconstruction of the gigantic hyracodont *Paraceratherium*, now on display in the University of Nebraska State Museum. Note its small relative *Hyracodon* to the right, and the living and fossil elephants for scale. (Courtesy University of Nebraska State Museum).

not only lost the extra front toe, but developed much more slender limbs with a horse-like strong central toe. The late Eocene saw a number of small hyracodont genera in both Europe and Asia, but by the early Oligocene only a few remained.

The best known of these is *Hyracodon* itself, which is very common in the Big Badlands of South Dakota (Fig. 14.7). It was about the size of a Great Dane, and only slightly larger than *Mesohippus,* the horse of its time. The head was slender and unspecialized, but the body and especially the legs clearly show that it was an efficient runner. It had a neck proportionally longer than the horses of the time, but stronger because it had a much larger head. In behavior it may have seemed more like a pony or donkey than like any modern rhino. Its teeth, however, are not very high-crowned or complex. It probably browsed on shrubs and bushes that were still dominant in the mixed forest-grasslands of the early Oligocene.

By the late Oligocene the vegetation was changing to savanna grassland. There were fewer shrubs to browse on, and more and more animals that depended on them died out. *Hyracodon* survived until the very late Oligocene and then succumbed about 28 million years ago. It was the final member of its lineage anywhere in the world, surviving almost ten million years after the last of its relatives had died out in Asia and North America. Like *Cadurcotherium*, it was a "living fossil" that did not survive quite long enough. Neither hyracodonts nor amynodonts made it to our zoos. The third of the three families of rhinocerotoids, however, did make it (Fig. 14.1). They are the Family Rhinocerotidae.

Before we take up the story of the Rhinocerotidae, we should look at one of the most fascinating offshoots of the hyracodonts, the giant indricotheres. One of the descendants of *Triplopus* was a much larger hyracodont known as *Forstercooperia*. Its cumbersome name is an accident. It was first named *Cooperia* by Horace Wood in honor of the British paleontologist, Clive Forster Cooper, who described many of the indricotheres. In 1939 Wood discovered that the name *Cooperia* had already been given to a genus of roundworm, so it could not be used again. The rhino was renamed *Forstercooperia* to avoid confusion and duplication, even though this made the name unusually long and clumsy. *Forstercooperia* was about the size of a cow, although there was also a dwarf species about the size of a sheep. It migrated back and forth between China and North America freely during the middle Eocene. By the late Eocene, however, it disappeared from North America and the rest of the indricothere story takes place in Asia.

And what a story it was! Indricotheres quickly reached elephantine proportions with *Urtinotherium,* and then surpassed this standard. When they finished, they had produced the largest land mammal the world had ever known, *Paraceratherium* (or *Indricotherium*) (Fig. 14.8). This beast was almost 18 feet (6 m) high at the shoulder and probably

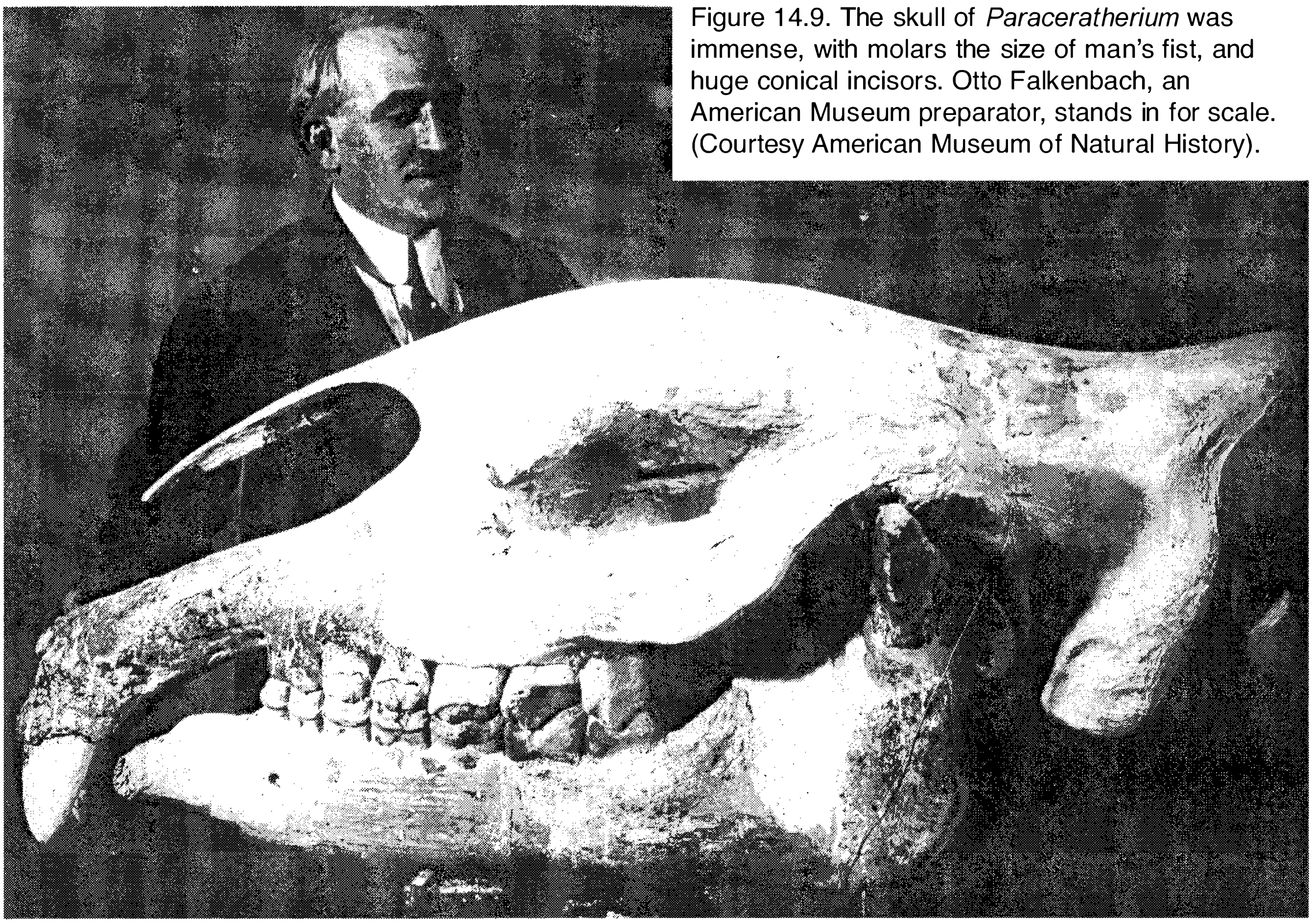


Figure 14.9. The skull of *Paraceratherium* was immense, with molars the size of man's fist, and huge conical incisors. Otto Falkenbach, an American Museum preparator, stands in for scale. (Courtesy American Museum of Natural History).

weighed 40 tons (35,000 kg). Its head was so high off the ground that it browsed on the tops of trees over 25 feet (7.5 m) high. Today we think of elephants and giraffes as giants, but *Paraceratherium* dwarfed them in both size and bulk. Its head was over five feet (1.5 m) long, with enormous tusks at the front end of its skull. As big as its head was, it seemed ridiculously small on such a large body.

In spite of these bizarre features, *Paraceratherium* still bears the hallmarks of its hyracodont ancestry. Its molar teeth show the same pattern as the hyracodonts, only they are enormous. Its incisors (Fig. 14.9), although large, are conical as they are in hyracodonts. Most importantly, its toe bones are still long and stretched out as if it were a runner. This is truly remarkable because most gigantic land animals, such as elephants and dinosaurs, shorten their foot bones until they are stubby, square blocks or even flattened like pancakes. The indricotheres outweighed any elephant, yet they retain the long toes as a hallmark of their running ancestry. An animal this large clearly had no need to run from any predator, and was much too large to run efficiently anyway. *Paracera-therium* is a good example of how animals can retain features of their ancestry long after they have outlasted their usefulness.

The proper name for this beast is a great source of confusion. The first name given to these gigantic hyracodonts was *Paraceratherium*, coined in 1911 by Clive Forster Cooper for specimens from Pakistan. Two years later Forster Cooper gave the name *Baluchitherium* to specimens of a large indricothere from the Baluchistan province of Pakistan. In 1915 the Russian paleontologist Borissiak described another giant rhino from the Turgai region of the Caucasus Mountains in southern Russia and called it *Indricotherium.* Although Borissiak's specimen is the most complete known, it was ignored because most scientists didn't read Russian and could not go to Russia to see the specimen during the First World War or the Russian Revolution. In 1922 the American Museum of Natural History made a highly publicized expedition to Mongolia where they found the largest and most spectacular specimens of a giant indricothere. It got enormous attention and was called *Baluchitherium*, since no one knew much about the Russian *Indricotherium.* As a result of all the publicity, nearly all the popular books have called this animal *Baluchitherium*, but this name is incorrect. This confusion over names is a good example of how politics and the sloppiness of popular science books can perpetuate names or ideas that are seventy years out of date.

Scientists have long realized that *Baluchitherium* is a junior synonym of *Paraceratherium*, but are *Paraceratherium* and *Indricotherium* the same beast? Some scien-

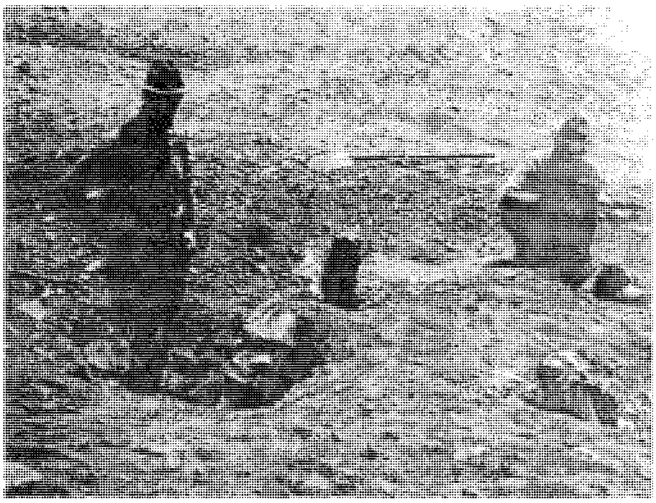


Figure 14.10. The leg bones of this Mongolian *Paraceratherium* were found standing upright, just as they were left when the animal died in quicksand. Here, Walter Granger stands next to the four pits where the leg bones were uncovered. (Courtesy American Museum of Natural History).

tists, such as Spencer Lucas, have studied all the large indricotheres called *Paraceratherium, Indricotherium*, and *Baluchitherium*, and have decided that they are all the same animal. The skull known as *Indricotherium* is thought to belong to the male and the skulls referred to *Paraceratherium* are thought to belong to females. If this is so, then the correct name for all these hyracodonts is *Paraceratherium*, the first name coined by Clive Forster Cooper in 1911, four years before Borissiak described *Indricotherium*. This reasoning makes some sense, since it is rare for such large animals to include many different species in a given area. Because of their large body size, their relatively small populations must have spread out over a large area, and there is not a lot of ecological space for such large animals to subdivide. On the other hand, very few specimens of these gigantic indricotheres are known, so it is difficult to tell if these skull differences are really due to differences in the sexes. We are divided over this dispute. One of us (Prothero) finds the argument convincing, but the other (Schoch) prefers to retain *Indricotherium*. In this book, we have followed the latter conservative course until some consensus is reached.

The American Museum Mongolian expeditions of 1922 and later years made a number of spectacular finds, including the first dinosaur eggs. But the gigantic bones of *Paraceratherium* were among the most exciting. Roy Chapman Andrews, the leader of the expedition, described it this way:

> "The credit for the most interesting discovery at Loh belongs to one of our Chinese collectors, Liu Hsi-ku. His sharp eyes caught the glint of a white bone in the red sediment on a steep hillside. He dug a little and then reported to [Walter] Granger [the chief paleontologist of the expedition] who completed the excavation. He was amazed to find the foot and lower leg of a *Baluchitherium*, STANDING UPRIGHT, just as if the animal had carelessly left it behind when he took another stride [Fig. 14.10]. Fossils are so seldom found in this position that Granger sat down to think out the why and wherefore. There was only one possible solution. Quicksand! It was the right hind limb that Liu had found; therefore, the right front leg must be farther down the slope. He took the direction of the foot, measured off about nine feet and began to dig. Sure enough, there it was, a huge bone, like the trunk of a fossil tree, also standing erect. It was not difficult to find the two limbs of the other side, for what had happened was obvious. When all four legs were excavated, each one in its separate pit, the effect was extraordinary. I went up with Granger and sat down upon a hilltop to drift in fancy back to those far days when the tragedy had been enacted. To one who could read the language, the story was plainly told by the great stumps. Probably the beast had come to drink from a pool of water covering the treacherous quicksand. Suddenly it began to sink. The position of the leg bones showed that it had settled slightly back upon its haunches, struggling desperately to free itself from the gripping sands. It must have sunk rapidly, struggling to the end, dying only when the choking sediment filled its nose and throat. If it had been partly buried and died of starvation, the body would have fallen on its side. If we could have found the entire skeleton standing erect, there in its tomb, it would have been a specimen for all the world to marvel at.
>
> I said to Granger: 'Walter, what do you mean by finding only the legs? Why don't you produce the rest?' 'Don't blame me,' he answered, 'it is all your fault. If you had brought us here thirty-five thousand years earlier, before that hill weathered away, I would have had the whole skeleton for you!' True enough, we had missed our opportunity by just about that margin. As the entombing sediment was eroded away, the bones were worn off bit by bit and now lay scattered on the valley floor in a thousand useless fragments. There must have been great numbers of baluchitheres in Mongolia during Oligocene times, for we were finding bones and fragments wherever there were fossiliferous strata of that age" (Andrews, 1932: 279-280).

Paraceratherium was probably as large as a land mammal can become. Only the whales are larger, and their weight is carried by the buoyancy of the water they live in. Some people have suggested that indricotheres were also amphibious to help bear their enormous weight, although

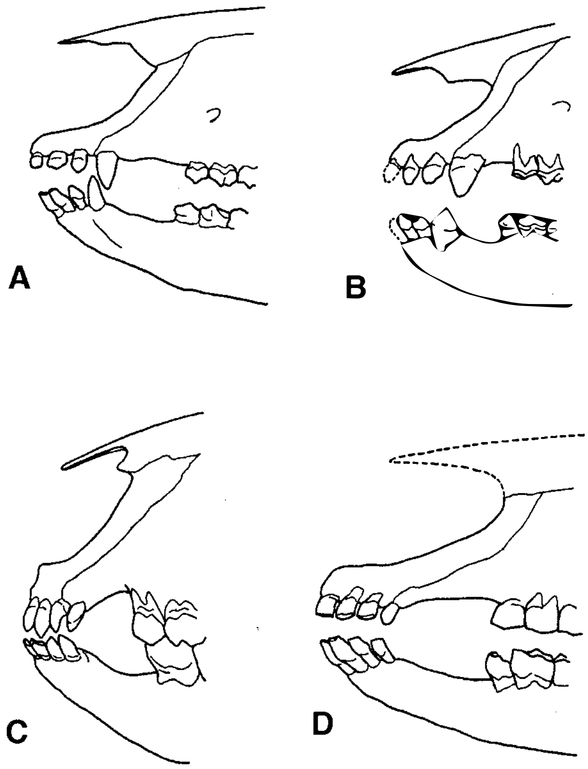


Figure 14.11. The front teeth of rhinocerotoids are diagnostic of their family groups. Starting with *Hyrachyus* (A), hyracodonts develop more spatulate incisors (C, *Hyracodon*). Amynodonts (B), on the other hand, developed prominent upper and lower tusks. True rhinoceroses, such as this rhinocerotid *Trigonias* (D), have an upper incisor chisel which occludes against a lower incisor tusk. The remaining upper incisors are lost in later rhinos. (From Radinsky 1966).

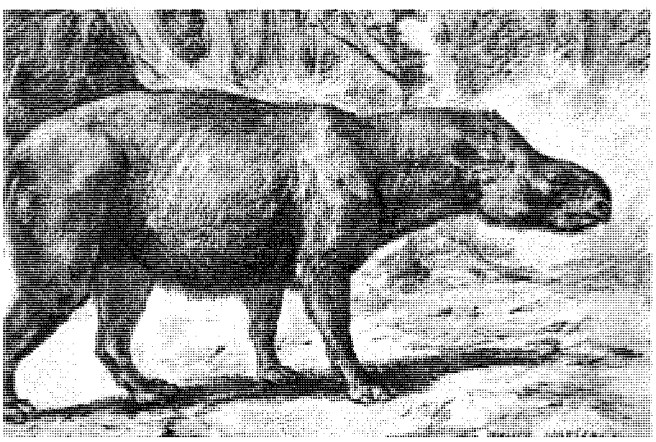


Figure 14.12. Restoration of the late Eocene-Oligocene rhinocerotid *Subhyracodon* (once known as *Caenopus*), typical of the Big Badlands of South Dakota. (Painting by R. B. Horsfall, from Scott 1913).

their bones were certainly stout enough to carry them. In addition, their enormous height and long necks only make sense if they browsed on treetops, as giraffes do. Gigantic animals, such as elephants and dinosaurs, have to consume an enormous amount of vegetation to feed such a large body. Living elephants today have to eat almost constantly to survive. Jim Mellett has shown that *Paraceratherium* was probably a hindgut fermenter, like other rhinos and elephants, and therefore was not as efficient at digestion as cows or giraffes that are ruminants with four-chambered stomachs. Instead, it had to pass large amounts of relatively low-quality forage through its gut quickly in order to get enough energy from its food intake. The largest dinosaurs, which were four times as big as *Paraceratherium*, all had peg-like teeth that cannot slice up vegetation. They had to swallow their food whole and digest large amounts of it quickly to survive. *Paraceratherium* was one of the few mammals that tried to make a living as the dinosaurs did. Not surprisingly, very few mammals have tried it before or since because it is a very difficult lifestyle in terms of bioenergetics. *Paraceratherium* was the largest land mammal ever seen, and it is unlikely that any mammal will ever top its record.

Another consequence of its large body size is that it has the same problems as elephants: its surface area for dumping heat is relatively small compared to its large volume, so it is always in danger of heat prostration. We have seen how elephants use the remarkable heat exchange network in their fanlike ears to dump heat, and must spend most of the hot parts of the day immersed in water or hiding in the shade. Indricotheres must have had the same problem, only more extreme, since they were about five times as large as an elephant. They certainly must have spent most of their daytime in the shade or the water, as elephants do, and fed mostly in the evening, at night, and in the morning. In addition, most reconstructions show indricotheres with fairly normal, relatively small ears. There is no bony structure to determine the size of the ears in extinct animals, but surely the indricotheres must have had much larger, almost elephantine ears, or some other fan-like structure in their body to help with dumping heat. The bony tubes at the base of the ear opening on the skull of indricotheres is very strongly reinforced, consistent with the idea that muscles and cartilages supporting a large fan-like ear must have attached there.

TRUE RHINOCEROSES

Life in the Oligocene looked very different from what we have seen in the Eocene. The climate was more temperate and arid than the subtropical world of the Eocene, with vegetation of mixed forest and savanna grasslands. These changes were effected by a number of causes we discussed in Chapter 12. Separation of Australia from Antarctica caused cold bottom waters to form and triggered climatic cooling. Rapid growth of Antarctic glaciers ultimately led to cooling and vegetational change, which caused the late Eocene extinctions that wiped out the brontotheres. Other animals felt the effects as well. The alligators, pond turtles, and other subtropical reptiles were replaced by land tortoises in great abundance. Tree-dwellers, such as lemur-like primates, vanished from North America as the forest canopy disappeared. Browsing animals with low-crowned teeth were becoming scarcer and were replaced by many modern groups of animals. These include shrews, squirrels, pocket mice and gophers, beavers, rabbits, dogs, camels, peccaries, elephants, true tapirs and rhinos, which first appear in the late Eocene. The grazing artiodactyls, especially the efficient ruminants, became more important, and most perissodactyl groups (especially tapirs and titanotheres) became scarce. The most common fossils in the Big Badlands of South Dakota are either artiodactyls (primarily oreodonts, deer, and camels) or tortoises. The only common Oligocene perissodactyls are the horses and hyracodonts, and they are far outnumbered by artiodactyls. The role of dominant herbivore had shifted from the perissodactyls to the artiodactyls. Today the artiodactyls are by far the most abundant of ungulates.

In the midst of this the true rhinoceroses (Family Rhinocerotidae) make their appearance (Fig. 14.1). They were first known from the middle Eocene of Asia and North America, and looked very much like hyracodonts. The oldest known species is *Teletaceras radinskyi*, recently described from the middle Eocene of Oregon. Two features distinguish true rhinoceroses from other rhinocerotoids. The last upper molar has completely lost the crest along the back (Fig. 14.3). In addition, the front teeth are no longer simple pegs or spatulas, but developed into a shearing upper incisor and tusk-like lower incisor (Fig. 14.11). This blade-tusk combination is not only efficient for feeding, but also served as an effective weapon. The living Indian rhino can use its tusks to slash very effectively, and elephants fear its tusks more than its horn.

Trigonias typified the early Rhinocerotidae. Known from the late Eocene, it was cow-sized and had a very saddle-shaped head. Although it had developed the advanced blade-tusk incisors, it still had the rest of the incisors and the canines in the upper jaw. Later rhinos would lose these useless, peg-like teeth, so that only the tusks and the cheek teeth remained. Although *Trigonias* died out by the early Oligocene, one of its close relatives, *Subhyracodon* survived until the late Oligocene and gave rise to later North American rhinos (Fig. 14.12). *Subhyracodon* is usually found in the ancient river channel deposits, so it was probably semi-amphibious like *Metamynodon*. Apparently, the amphibious lifestyle was popular among the rhinos. The teeth of *Subhyracodon* are not so high-crowned as those of *Metamynodon*, so it was probably a browser, not a grazer. *Subhyracodon* is not often found with *Hyracodon*, which lived on the grassy, open floodplains.

Incidentally, the name "*Subhyracodon*" has led to much confusion. First of all, it is a misnomer; the animal is a true rhinocerotid, not a hyracodont. It was the first American rhinoceros ever described (by Leidy in 1850), and he initially assigned it to the genus *Rhinoceros*, which includes the living Indian rhino. Secondly, most of the popular books incorrectly call this animal "*Caenopus*." The name *Subhyracodon* was proposed first in 1878, but the popular books have been unfortunately using the incorrect name for over a century.

As we saw in Chapter 2, Europe was an archipelago in the middle and late Eocene, isolated from the rest of the world and its mammals. Until the end of the Eocene the dominant large mammals were endemic palaeotheres and lophiodonts, which evolved in isolation from their tapir, horse, and rhino relatives found elsewhere. But the end of the Eocene marked the end of European isolation, and a great break ("Grande Coupure") in the mammals. Invaders from Asia took over the European continent and drove many of the natives, including the palaeotheres and lophiodonts, to extinction. The largest of these invaders were the rhinos. These included the smaller, primitive rhino *Epiaceratherium* (much like *Trigonias* in many features), and larger, more advanced rhinos like *Ronzotherium.*

In the late Oligocene the rhinos first developed horns. Rhino horns are nothing like the horns of deer, antelopes, or cattle. They have no bony core at all, but are made of a mass of hair-like fibers that is stuck together. They are attached to the skull at a roughened, raised area on the skull, and can break off. When they do so, they can grow back. Since rhino horns are made of hair-like fibers and not bone, they are very seldom fossilized. Paleontologists restore the size, shape and position of the horn based on the size and placement of its attachment point, but this is always approximate.

The first horned rhino was the direct descendant of *Subhyracodon* named *Diceratherium* ("two horned beast"). Instead of the familiar single horn on the tip of the nose, it had small horns that were paired on the nose (Fig. 14.13A). These horns were supported by broad ridges that ran along the side of the nasal bones. Only the males had horns; the females were completely hornless. Presumably these horns were short and stubby, and may have served more for impressing females than for defense. *Diceratherium* is a characteristic animal of the late Oligocene of North America, and was the only rhinocerotoid left after the extinction of the amynodonts and hyracodonts. For almost ten million years, there were no other large mammals (including rhinos) to compete with it. It was the largest herbivore around in the late Oligocene. As a result, there were several species of *Diceratherium* living side by side, differing primarily in size. At 77 Hill Quarry in eastern Wyoming there are thousands of bones of both males and females of two species of *Diceratherium*.

Diceratheriines were not restricted to North America. During the late Oligocene one of their descendants migrated to Europe, where it was named *Pleuroceros*. It too had broad flanges along the sides of its nasal bones, indicating broad paired horns. However, it was uncharacteristic of European rhinos. Instead, the ancestors of the dominant Miocene rhino groups were evolving in Europe. By the

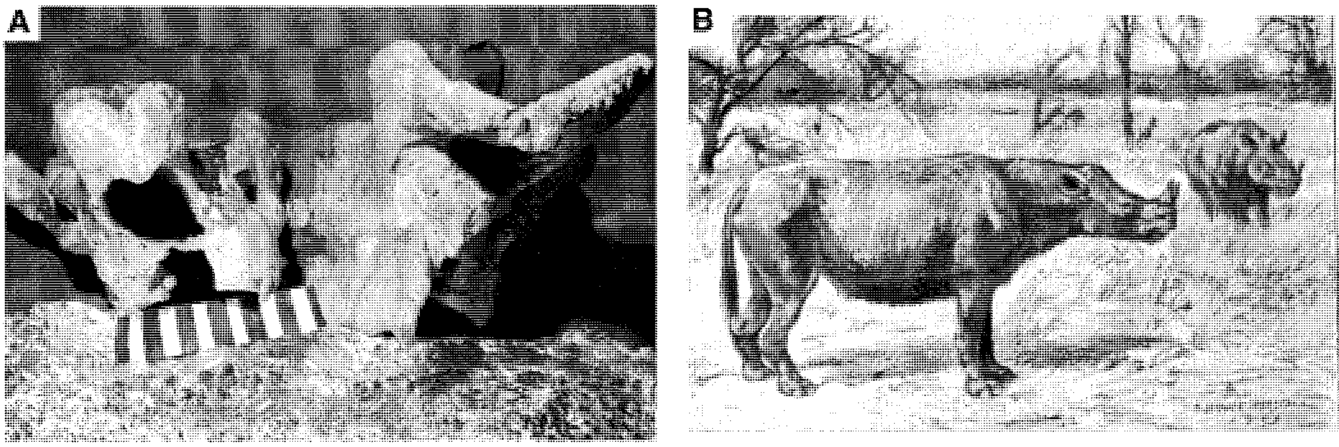


Figure 14.13. A. Front views of *Menoceras arikarense* (left) and *Diceratherium armatum* (right), showing the differences in their paired horns. The horns of *Menoceras* were supported by small, rounded bosses, while those of *Diceratherium* were underlain by long bony flanges. (Photo by D.R. Prothero). B. Restoration of *Menoceras*. (Painting by R. B. Horsfall, from Scott 1913).

early Miocene they migrated out of Europe and spread to Asia and North America, driving endemic diceratheriines to extinction.

MIOCENE INVASIONS

By the early Miocene, about 22 million years ago, the climate and vegetation had changed in North America. Savanna grasslands were now widespread as the climate had become much more arid than in the Eocene or Oligocene. The animals reflected these changes. Most of the oreodonts had become runners with high-crowned teeth (*Merychyus*) or tapir-like or hippo-like amphibious beasts with a trunk (*Promerycochoerus*). Horses (*Parahippus*) had become more efficient runners, and also had higher-crowned teeth. A number of different types of camels had evolved, including a slender one more like a gazelle (*Stenomylus*). The pig-like entelodonts that were important in the Oligocene had reached gigantic proportions. The early Miocene entelodont, *Daeodon,* was 7 feet (2.1 m) tall at the shoulder (see Chapter 2).

In the midst of all these native groups the first wave of immigrants since the early Oligocene gave the early Miocene mammals a new look. The chalicothere *Moropus* arrived from Asia. Musk deer, pronghorns, and dromomerycid cervoids all arrived shortly thereafter. A number of new types of carnivores, especially the bear-dog *Daphoenodon*, hunted the herbivores. Among these immigrants was a new rhino, *Menoceras* (Fig. 14.13B), which had arrived from Europe (Fig. 14.1) to challenge *Diceratherium.*

Descended from the late Oligocene *Protaceratherium, Menoceras* also had paired horns on its nose, but it was not closely related to *Diceratherium.* Unfortunately, because both rhinos had paired horns, people have confused the two for years. Direct comparison shows that the two paired horn combinations are not the same. True *Diceratherium* had broad ridges that pass along the side of the nasal bones. *Menoceras* had horn bases that were rounded knobs at the very tips of its nasal bones (FIg. 14.13A). The two animals are also very different in skull proportions, tooth features, and other features of the skeleton. *Menoceras* was much smaller, about three feet (1 m) high at the shoulder, or the size of a large hog. Yet many scientists today still refer to *Menoceras* as *"Diceratherium."* Most museum labels and popular books still have the name wrong, even though this mistake was corrected in 1921!

The most famous find of *Menoceras* was made in 1885 by "Captain" James Cook, a pioneer scout and rancher. He established Agate Springs Ranch on the banks of the Niobrara in western Nebraska while it was still roamed by hostile Indians. Cook, however, was on good terms with them, and was a personal friend of the great Sioux chief Red Cloud, who visited frequently. Cook found many fossil bones weathering out of a small hill, consisting of the deposits of an ancient river channel, on his ranch. In 1891 he showed the specimens to Dr. Erwin Barbour of the University of Nebraska, who became the first paleontologist to see the fossils. The University of Nebraska began to work the small conical hill to the north, which acquired the name "University Hill" (Fig. 14.14A). In the summer of 1904 Olaf Peterson, one of the principal paleontologists of the Carnegie Museum in Pittsburgh, visited the Cook Ranch. Peterson described it this way:

> "A day or two later Mr. Harold Cook, the eldest son of Mr. James H. Cook, accompanied the writer to a small elevation some four miles east of the farm buildings and immediately beyond the eastern limits of the land belonging to the ranch. The talus of this low hill was discovered to be filled with fragments of bones, and was afterwards designated as quarry A. On our return to the ranch I reported to Mr. James H. Cook that the place which his son had shown me was of much interest and importance to me and that I wished to start the work of

excavation on the prospect immediately. This was entirely satisfactory to Mr. Cook and his family. In fact there was evident satisfaction on the part of Mr. Cook that I had found something which I regarded as of interest and importance near his farm, and I was accorded every civility which I could possibly desire. As I wished to be near my work, Mr. Cook invited me to camp in his "lower field." Accordingly our first camp was pitched on the south bank of the stream close to the hill and the operation of excavating in quarry A was begun during the last few days of July. We had worked three or four days in this quarry when I decided to visit the two buttes (since named Carnegie Hill and University Hill by Prof. E. H. Barbour) which lie about three hundred yards to the south of the place where we were working. One may easily imagine the thrilling excitement of a fossil-hunter when he finds the talus of the hillside positively covered with complete bones and fragments of fossil remains.

It was with comparatively little effort that I was able to articulate portions of the feet of *Diceratherium cooki* [now known as *Menoceras arikarense*] and *Moropus* using the disassociated bones picked

A

B

C

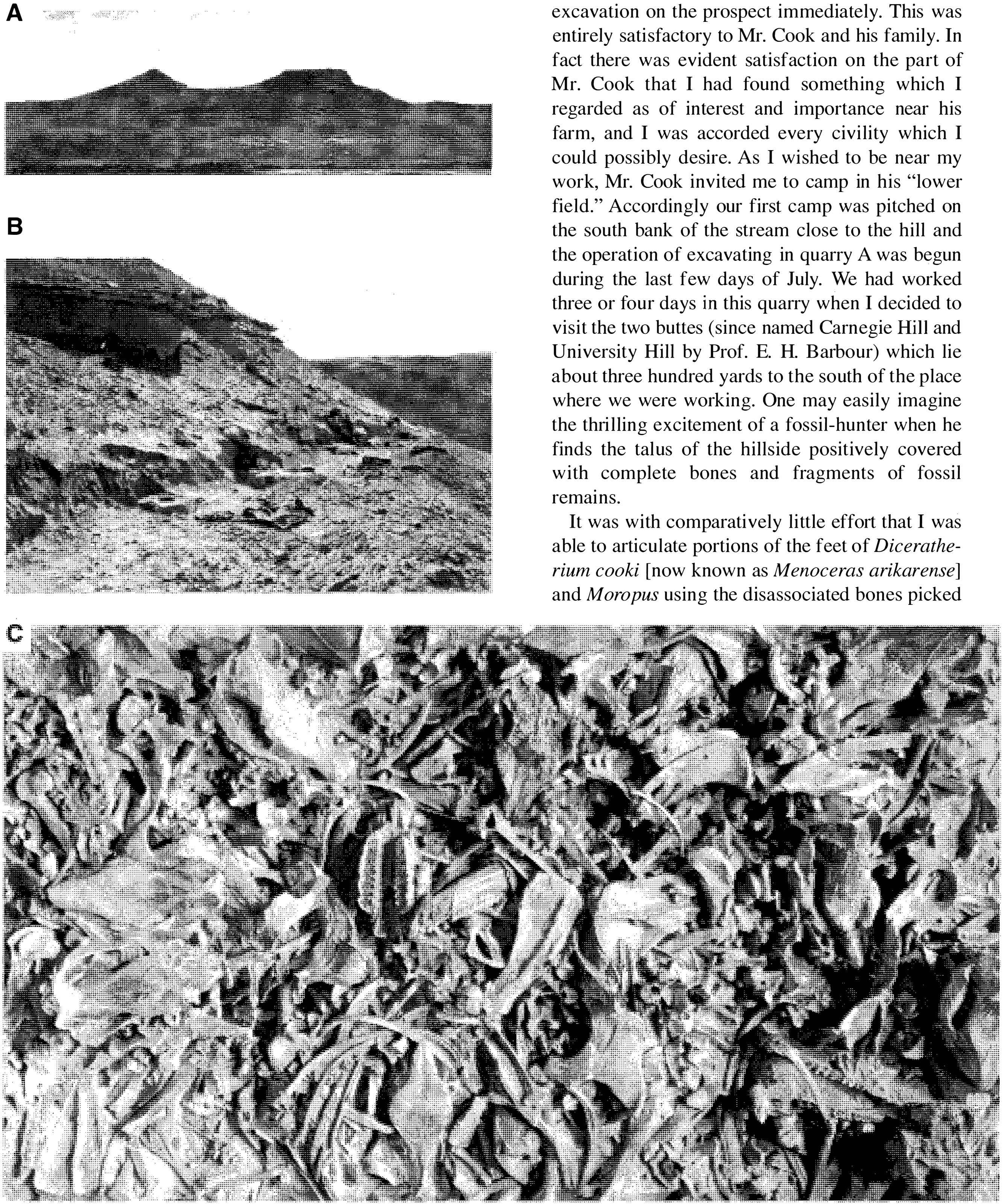


Figure 14.14. A. Agate Fossil Beds National Monument includes two hills known as University Hill (on the left) and Carnegie Hill (on the right). (Photo by D. R. Prothero). B. Quarrying operations at Agate were extensive. This is *Stenomylus* Quarry, worked by the American Museum of Natural History. (Neg. no. 18357, courtesy Department of Library Services, American Museum of Natural History). C. A typical slab of bones from Agate. It contains about 4300 bones and skulls, mostly of the rhino *Menoceras*. (Neg. no. 5594, courtesy Department of Library Services, American Museum of Natural History).

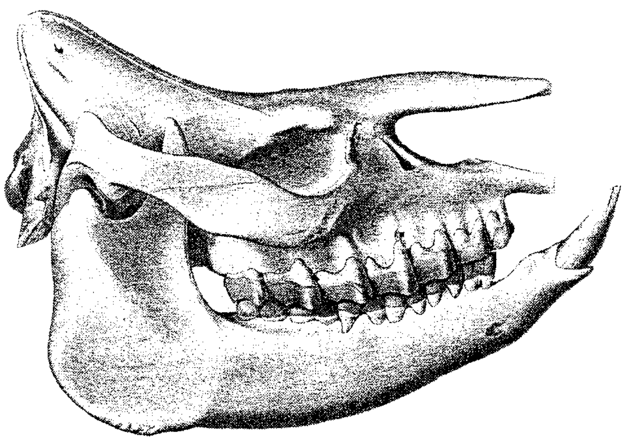


Figure 14.15. Side view of the skull of the Miocene aceratheriine rhinoceros *Aphelops*, showing the characteristic long nasal notch, and loss of the upper incisors. (From Cope and Matthew 1915).

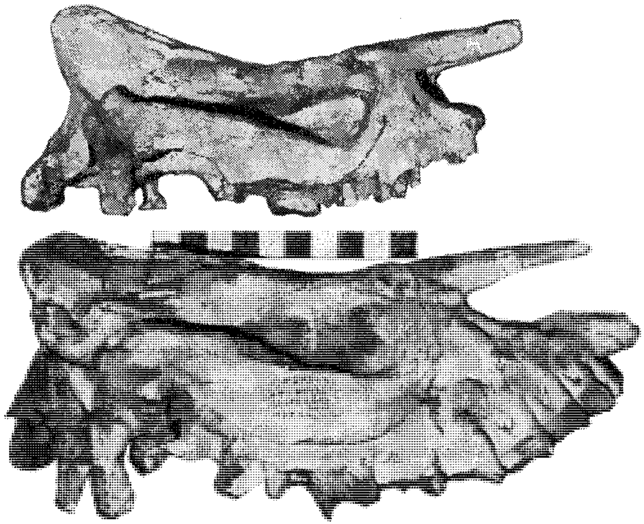


Figure 14.16. The aceratheriine rhinoceros *Peraceras* was also common in the Miocene. Here are the skulls of *Peraceras profectum* (bottom) and the dwarfed species from the Texas Gulf Coastal Plain, *Peraceras hessei* (top). (Photo by D. R. Prothero).

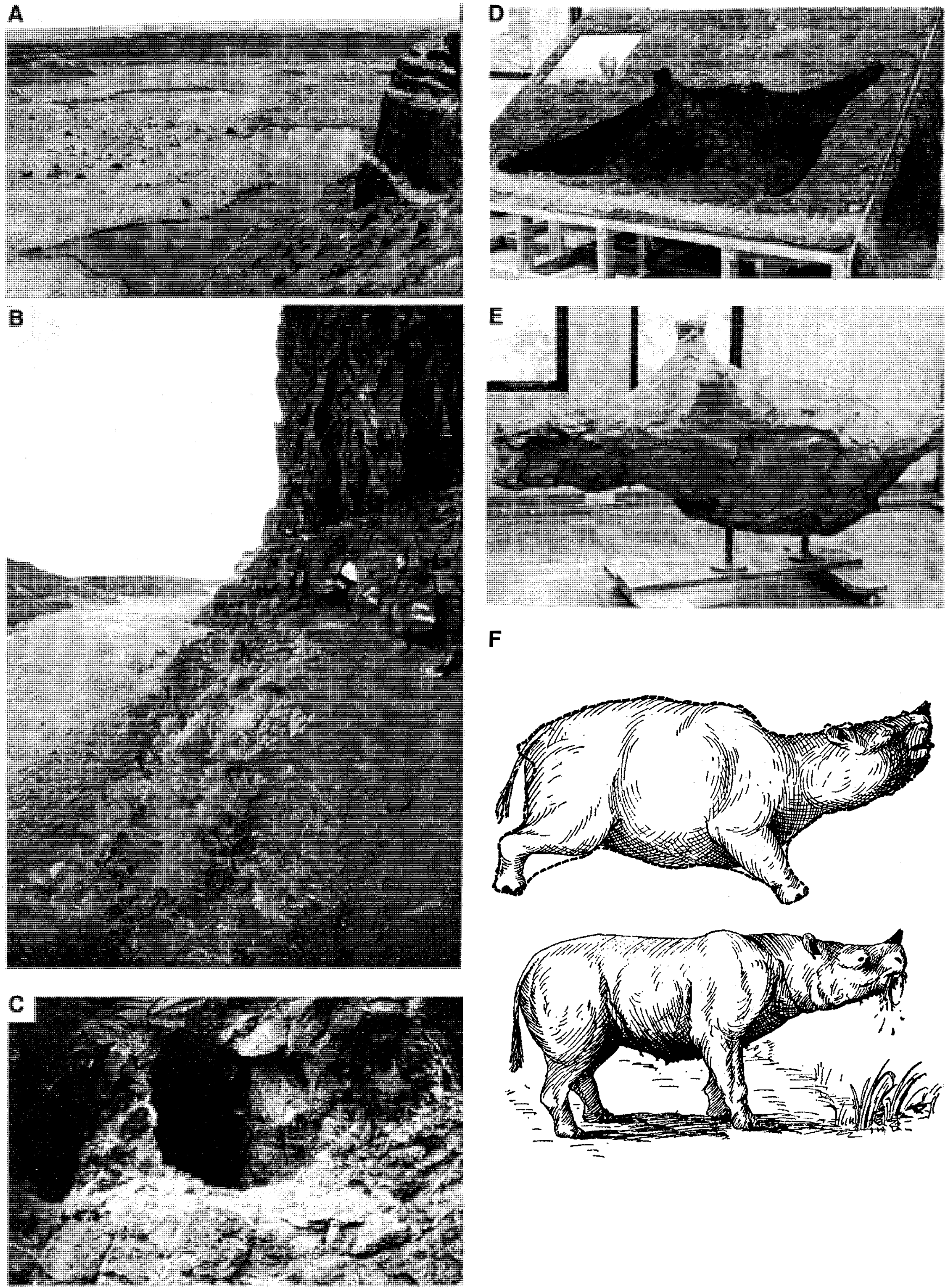
up in great abundance in the talus. Here then was a veritable wonderland!" (Peterson, 1909: 70-72).

Agate Springs bonebed was worked intensively by the Carnegie Museum from 1904 to 1908, and from 1911 to 1923 by the American Museum of Natural History in New York (Fig. 14.14B). Although only two small hills of the bonebed remained, an enormous number of fossil bones were concentrated there. One slab of sandstone with an area of 44 square feet contained 4300 skulls and separate bones (Fig. 14.14C). At that rate, one of the hills could contain 3,400,000 bones belonging to at least 17,000 skeletons! Over 16,000 of these belong to the little rhino, *Menoceras*. Since 1925 there have been only minor excavations. Most of the major American museums have large collections of Agate fossils. The entire area is now included in Agate Fossil Beds National Monument.

How did such an incredible concentration of bones get there? The skeletons are nearly all scattered about, with very few bones still articulated. They show relatively little breakage and abrasion, although in some areas the bones are quite abraded. The most important line of evidence comes from determining the age structure of the population. By looking at the wear on the teeth, the approximate age of each individual can be estimated. Bob Hunt has studied the age structure of Agate *Menoceras* and finds that there are far more old individuals than could be expected if they were all killed by a single, catastrophic event, such as a flood. Instead, this kind of population structure occurs with normal attrition due to the death of older individuals, and so represents a long term accumulation of rhino bones around an ancient waterhole, possibly due to droughts. If they had been killed by a catastrophic flood, there would have been far more juveniles and adults in the prime of their lives, and fewer old individuals.

The Agate bone bed records the first appearance of *Menoceras* in North America. Apparently it avoided competition with native *Diceratherium*, since quarries that contain one rhino in abundance have very little of the other, and vice versa. Soon afterward *Diceratherium* disappeared entirely, and *Menoceras* was the sole North American rhino. The early Miocene was a period of great mammal migrations throughout the world. For several million years many other mammal groups migrated back and forth between North America, Europe and Asia. Shortly after *Menoceras arikarense* appeared at Agate it evolved into a larger

Figure 14.17. (facing page) A. Panoramic view of the lava cliffs of the Grand Coulee region, where the lava cast rhino cave was found. (Photo by D. R. Prothero). B. Entrance to the lava cave, at the base of the lava flow to the right. C. Inside view of the lava cave, showing two cylindrical holes which are molds of the legs. D. Reconstruction of the lava cave, once on display at the Burke Memorial Museum of the University of Washington. E. Cast of the lava cave, showing the distinctive shape of the bloated rhino carcass floating upside down. (Photos B-E courtesy J. Rensberger, Burke Memorial Museum). F. Restoration of the Grand Coulee rhinoceros as it may have looked in life, and as a bloated carcass. (From Chappell et al. 1941; courtesy Geological Society of America).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species, *Menoceras barbouri*. This last species of *Menoceras* ran into competition from a whole new set of immigrants. By the end of the early Miocene two lineages of rhinos had become established in North America.

The first of these lines was the aceratheriine rhinos. These rhinos have long, straight skulls without any horns on the tips of the nasals. All of them have lost their upper incisors, so their lower tusks cut against horny pads on their upper lip. A few of them have secondarily regained digit 5 on the front foot, making them four-toed. Their long limbs and skeletal proportions are typical of most unspecialized rhinos.

Aceratheriines are first recognized in the late Oligocene of Eurasia with animals known as *Mesaceratherium* and *Alicornops*. Two genera of aceratheriines appeared in North America in the early Miocene. *Aphelops* remained the generalized, long-limbed browsing rhino through 12 million years of the North American middle and late Miocene (Fig. 14.15). *Aphelops* started out small and generalized, but as time went by, it became more specialized. Its teeth became higher-crowned and more complex, probably in response to tougher vegetation in the late Miocene. The notch below its nasal bones continued to retreat backward, indicating that it was developing a more flexible prehensile lip for browsing. By the end of its evolution the nasal notch was deeply retracted, and the last species of *Aphelops* was nearly twice the size of the first species.

The other North American aceratheriine was *Peraceras*, which diverged from *Aphelops* in the early Miocene. At first they are difficult to tell apart, but in the middle Miocene *Peraceras* begins to develop a broad, heavy skull common in hippo-like animals. Presumably, it followed an amphibious grazer lifestyle that we have already seen in *Metamynodon* and other rhinos. It soon came into competition with *Teleoceras* (discussed next) which perfected the hippo-rhino niche. *Peraceras* also evolved into a dwarf species, which is found primarily in the humid forests of the Texas Gulf Coastal Plain and not in the High Plains of Nebraska or Kansas, where other rhinos were abundant (Fig. 14.16). In this way, it is analogous to the dwarf species of many other large mammals living today, such as the pygmy hippopotamus, the dwarf Cape buffalo, and the smaller forest elephant.

One ancient rhino was fossilized in an extremely unusual manner. About fifteen million years ago there were immense eruptions of lava in the eastern half of the state of Washington. These eruptions covered thousands of square miles, flowing at speeds of 60 mph (100 km/hour) and more. They came from deep fissures, or cracks in the earth, rather than from volcanoes. The eruptions happened again and again, with each flow covering the last. Between eruptions, enough time passed that soils could form and forests grow on the old flows.

During one of these eruptions a bloated carcass of a rhino was floating in a small pond. Lava flowed into the water and immediately chilled into pillow-shaped blobs, which nestled against the carcass and compressed against it (Fig. 14.17). This made a natural mold of the rhino, preserving not only the bones, but the outline of the soft tissues of the body. Many more eruptions and millions of years later, rivers and glacial meltwater cut deep canyons into the flows, making the Grand Coulee. In 1935, three men were hiking along the steep walls of the lava-flow canyons near Blue Lake when they found an opening of a small cave. They crawled inside and recovered a jaw and a few leg bones in one of the side cavities. It seemed incredible, but they were crawling inside the natural mold of a rhinoceros! They must have felt a bit like Jonah, but in the belly of a rhino rather than a whale. The tubular side cavities which produced leg bones were clearly the impressions of the animal's legs. In 1948 several scientists returned and made a complete cast of the mold, so that it could be mounted for display. Using the cast, they also reconstructed the mold cave.

From the cast it is obvious that the animal had died and become bloated well before it was covered in lava. The torso is unnaturally fat, the legs are distended, and the neck is pulled back in rigor mortis. The rhino was floating upside down, since its legs were at the top of the cave. There were also a number of molds of trees preserved in the same lava flow. The lava impression is not very detailed, but some areas were well preserved. The shape of the rhino's head, with its prehensile lip, is very clear. But the tip of the nose and the area of the horns were not preserved, since they were in the gap between two lava pillows. The feet clearly show three blunt toes and a thick pad on the heel of the foot. By putting all these features together, the appearance of the animal in life can be restored. Unfortunately, the most important features that would distinguish between *Diceratherium, Menoceras*, or the dwarf *Peraceras* are not preserved. The Blue Lake rhino ranks as one of the most unusual examples of preservation in the fossil record. It is one of the few exceptions to the rule that fossils are not found in igneous rocks.

RHINOCEROS POMPEII

Besides the two aceratheriines, *Aphelops* and *Peraceras*, one other early Miocene rhino immigrant was common in the middle and late Miocene of North America. This was *Teleoceras*, probably the most hippo-like rhino ever (Fig. 14.18). *Teleoceras* and its relatives, the teleoceratines, were highly specialized for an amphibious existence. They had a stout, barrel-shaped body with extremely short, stumpy legs. Teleoceratines first appeared in Europe in the late Oligocene with an animal known as *Brachydiceratherium*. This animal still had a very generalized skull that looked more like aceratheriines or diceratheriines in most features. The limb shortening had not yet fully developed, but these animals were still much more short-limbed than aceratheriines. By the early Miocene, *Brachydiceratherium* was joined by another teleoceratine, *Diaceratherium* (not to be confused with *Diceratherium*), a slightly more advanced

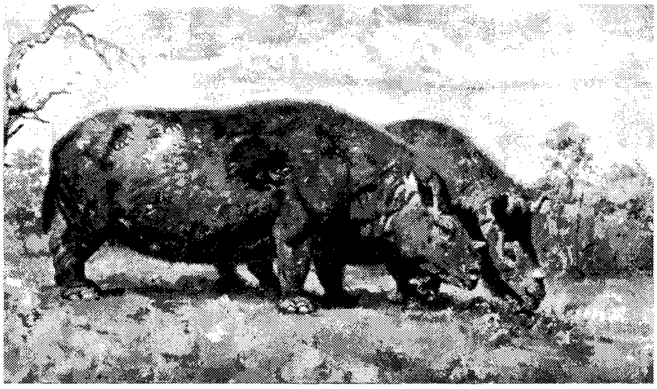
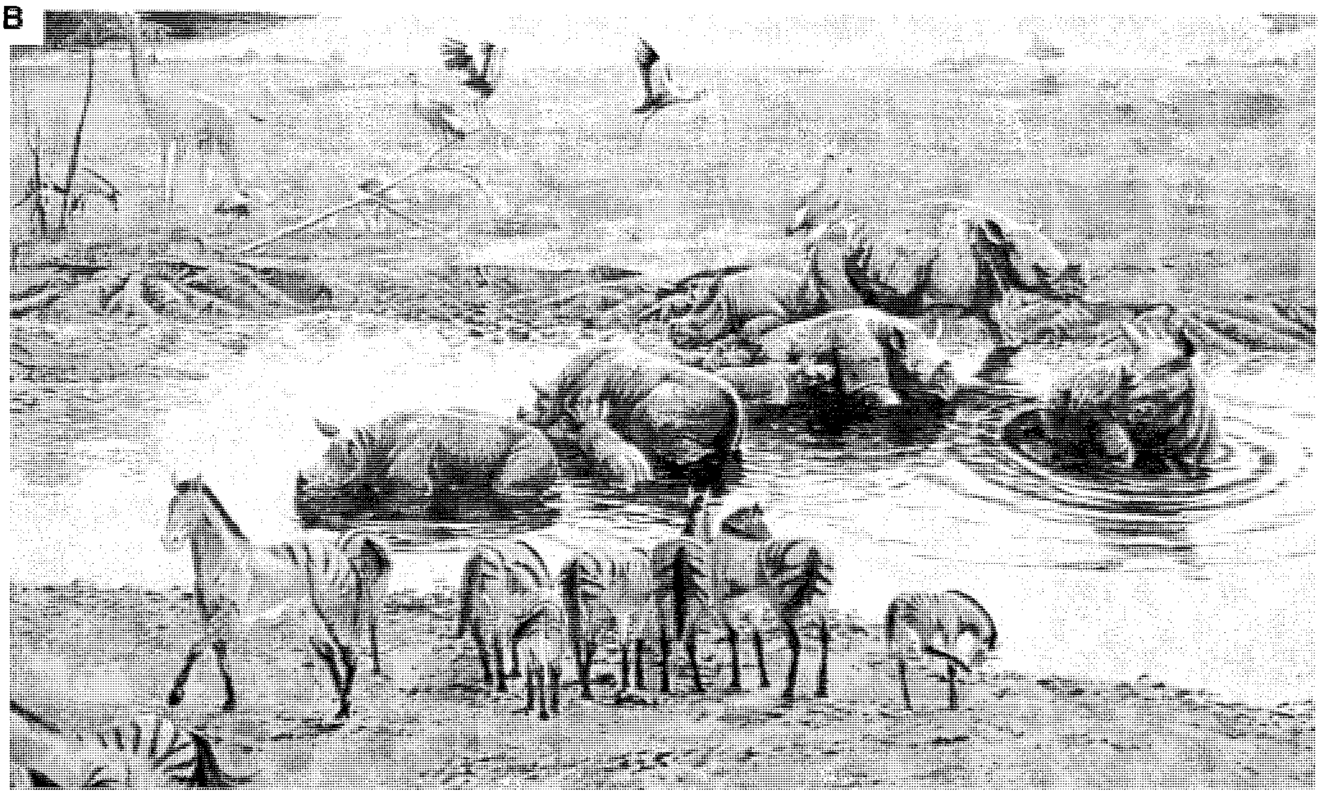


Figure 14.18. (above) Reconstruction of *Teleoceras*, the most hippo-like and amphibious of North American rhinos during the middle and late Miocene. Note the barrel chest, the short, stumpy legs, and the broad skull with huge grinding teeth for eating grass. (Painting by Z. Burian).

Figure 14.19. A. (right) Excavation of the "Rhino Pompeii," as it appeared in 1995. Several complete articulated skeletons of *Teleoceras major* can be seen, some with calves nursing at their sides. (Photo by D.R. Prothero). B. (below) Reconstruction of the Ashfall Fossil Beds water hole as it might have looked 10 million years ago. In addition to the rhinos, there are numerous three-toed horses, giraffe-camels, and other mammals. (Courtesy University of Nebraska State Museum).



form with shorter, more massive limbs. *Diaceratherium* underwent rapid evolutionary change in the early Miocene, developing very shortened legs, very high-crowned teeth, and still retaining the four-toed front foot. It died out in the middle Miocene, but according to Kurt Heissig, it spread to North America where it evolved into *Teleoceras*. Another of its descendants was a dwarfed form, *Prosantorhinus*, which had a very strong horn, but died out at the end of the middle Miocene in Europe. Yet a third descendant is an Asian form known as *Aprotodon*. This rhino developed a very broad snout with long, outward-flaring tusks, and also developed a deep nasal notch for attachment of a prehensile lip. Thus, it has an interesting mix of features found in the hippo-like grazing rhinos, and the prehensile-lipped browsing rhinos. *Aprotodon* disappears from the geological record in the late Miocene, where its last fossils are known from the Siwalik Hills of Pakistan.

By the middle Miocene *Brachydiceratherium* and *Diaceratherium* were replaced by a very successful animal, *Brachypotherium*. This teleoceratine was abundant and widespread throughout the Old World during the entire middle and late Miocene, and even managed to survive into the late Pliocene in East Africa. Although it had a huge, hippo-body with shortened legs like most teleoceratines, it never developed the extremely high-crowned teeth found in the teleoceratines adapted for eating grasses. Nevertheless, its molars are very large and broad, even if they are low crowned, and it had a heavy massive skull and jaws.

The early species of *Teleoceras* had relatively short legs already, but as they evolved, their legs became shorter and their limb bones became extraordinarily stumpy and compressed. The skull of *Teleoceras* was very large, with massive, high-crowned teeth that were almost certainly adapted for grazing on abrasive grasses. Unlike the aceratheriines, *Teleoceras* had a small horn on the tip of its nose, and still had its upper chisel-like incisors.

The extraordinarily hippo-like body of *Teleoceras* suggests that it lived much like a hippo, wallowing in the water in the day and coming out at night to graze on land. *Teleoceras* bones occur in great abundance in Miocene river channels, especially in Nebraska, Kansas, Texas, and Florida. For this reason, it is probably one of the commonest and best known of the North American rhinos, and many museums have a mounted skeleton on display. Many river channel deposits contain quarries of bones of both *Aphelops* and *Teleoceras*, which often lived together even though they had different ecologies. From these large quarry samples, we have additional evidence that *Teleoceras* was a hippo-like grazer. The Love Bone Bed of central Florida contains both *Aphelops* and *Teleoceras* in great abundance. By determining the age of each individual (estimated from tooth eruption and wear), it is possible to reconstruct the age profile of the rhino population. Dave Wright found that the age structure of the *Teleoceras* population was more like that of living hippos than rhinos. The age structure of the *Aphelops* population, on the other hand, was more like that of the browsing black rhinoceros.

The most remarkable of all the *Teleoceras* discoveries, however, was made recently by Mike Voorhies of the Unversity of Nebraska State Museum (Fig. 14.19A). In 1977, he was prospecting around Verdigre Creek, near the tiny town of Royal, in northeastern Nebraska. As he followed exposures of a silvery gray volcanic ash from one bank of the creek to another, he found the skull of a baby rhinoceros sticking out of the streambank. The next day, he excavated further, and found that it was a complete skeleton of a baby *Teleoceras*. Voorhies and his crew continued to dig back, finding 12 more rhino skeletons in an area the size of a living room. In the summer of 1978, they brought in a bulldozer and cleared off the overburden above the ash layer. Then the University of Nebraska State Museum crews began the slow, painstaking excavation of the bed with delicate brushes and scrapers. As they exposed the rhino skeletons, they treated them with preservative to protecct the brittle bone from shattering. They marked off the entire excavation in meter-square grids, so that the precise position of every bone could be recorded. The work was hot, tiring and especially dusty, since the powdery vocanic ash was lifted by the slightest breeze, and everyone had to wear dust masks and goggles for protection. The crews began to know what those rhinos once felt, choking to death on fine volcanic ash.

As they excavated further, the details began to emerge. Most of the skeletons were found intact, crouched down or lying on their sides in death poses. Even the most delicate bones of the throat and ear region (rarely preserved in most fossils) were in their correct anatomical position. Out of over 200 skeletons of *Teleoceras major* collected in the first few years, only 7 were adult males. The rest were adult females or their calves, many of whom were found in nursing position under the belly of their mothers. Some of the females had fetuses in their pelvic cavities. By studying the tooth wear, they found that most of the calves were in well defined age groups, as if they were born at the same season each year. Taken together, this suggests that *Teleoceras* formed large male-dominated herds, composed mostly of females and their calves, similar to many large ungulates today (Fig. 14.19B).

The nature of the deposit indicates that the rhinos were buried by ash blown all the way from the Rocky Mountains, and filling a bowl-shaped waterhole, 3 m deep at the center and thinning toward the edges. Most of the rhinos are found in the center of the water hole, where they slowly died or suffocated after being buried in ash. Studies of the bone pathology indicates that many died from a disease caused when their lung tissues were lacerated by inhaling the razor-sharp volcanic glass shards. Although most skeletons were buried intact, some of them were apparently exposed, and torn apart by scavengers. Others showed signs of rib cages that exploded when they died and became bloated.

Subsequent research on the rhinos has revealed even more details. In the midst of the well-preserved throat bones samples of grass seeds were found. They turned out to be seeds of the *Berriochloa*, a common grass in the late Miocene of Nebraska. These seeds were found only in the oral cavities or rib cages of the rhinos, and not in the surrounding ash, so they were unquestionably the "last supper" of this "Rhino Pompeii." This is the best possible proof that *Teleoceras* was a grazer, as its hippo-like build and population structure suggest.

After the initial excavation concluded in 1979, the storage floors of the Nebraska State Museum were filled with over 40 tons (2000 casts) of jacketed fossils, most of which have still not been prepared for study years later. But the rhino quarry extended further under the landscape. So many skeletons had already been removed that Voorhies and his crew decided to leave the rest in the ground, partially excavated, as a permanent exhibit. In 1991, the region was turned into a state park, with a modern visitor's center that helps guests interpret the fossils. The main excavation is now housed in a large "rhino barn" (Fig. 14.19A), which protects the fossils (and the crews) from the sun in the summer, and can be opened at both ends to allow ventilation. Visitors can walk along the edges and on catwalks to view the excavation up close. When October comes and the park closes down, the rhino barn can be locked up to protect the delicate fossils from the weather and vandals. Ashfall Fossil Beds State Historical Park is one of the great paleontological meccas, worth going out of one's way to visit.

As we saw in Chapter 3, the end of the Miocene was a period of great change around the world. In North America, oreodonts and the "slingshot-nosed" protoceratids were extinct, and horses, camels, mastodonts, deer, and pronghorns were reduced to a few species. As we discussed above, this great faunal change was caused by massive climatic cooling triggered by Antarctic glaciation and particularly by the Messinian drying of the Mediterranean. This Messinian event, which marked the beginning of the Pliocene, was also the beginning of the Ice Age world as well.

Among the victims of the changes at the end of the Miocene were the rhinos. By the latest Miocene, *Teleoceras* is very rare where it used to be abundant, and a dwarfed species appears in the panhandle of Texas. By contrast, latest Miocene river deposits are full of bones of the largest and final species of *Aphelops*. At the very end of the Miocene, however, both rhinos were virtually extinct. Only one scrap of a rhino tooth is known from a single early Pliocene quarry. After almost fifty million years as one of the dominant large mammals on this continent, rhinoceroses finally disappeared from North America, and would never return except as zoo animals.

In the Old World the crisis was just as severe. All the aceratheriines were decimated, with only a few species surviving into the early Pliocene of Asia. They were wiped out completely from Africa and Europe, as they were in North America. Teleoceratines disappeared entirely from Eurasia at the end of the Miocene, and only one lineage of *Brachypotherium* managed to persist into the Pliocene in Africa. The world of rhinos had been dominated by both aceratheriines and teleoceratines in the Miocene, but only a few straggled into the Pliocene before becoming extinct. They were replaced by three major groups which had arisen alongside them in the late Miocene: the dicerotines (the African black and white rhinos and their relatives); the dicerorhinines (the Sumatran rhino, woolly rhino, and their extinct relatives); and the rhinocerotinines (the Indian and Javan rhino and their extinct relatives). The first group came to dominate Africa, and the latter two were widespread in Eurasia, especially during the Ice Ages.

HAIRY RHINOS AND GIANT "UNICORNS"

As we saw at the beginning of the chapter, Ice Age rhino bones were responsible for many legends of "giants" and "dragons." Indeed, one of the earliest prehistoric restorations in sculpture was such a case. In 1590 the sculptor Ulrich Vogelsang built a huge winged dragon for the fountain in the main square in Klagenfurt, Austria. Although the body is conventionally dragon-like, with wings, scales, claws, and a long reptilian tail, the head looks peculiar. Disregarding the leaf-like ears, the head has the peculiar arched profile that can easily be traced to a skull of a woolly rhinoceros found in the area in 1335, and later placed on display in the Klagenfurt town hall.

The woolly rhinoceros is one of the best known members of a long and diverse group of rhinos, the dicerorhinines. Almost all members of the group clung to the primitive forest browsing niche, so their skeletons and teeth do not show very many specializations. Indeed, the living Sumatran rhino, *Dicerorhinus sumatrensis*, still survives in dense forests today. Consequently, the lack of distinguishing features makes it hard to tell many of the species of dicerorhinines apart, even though they have a history going back at least 25 million years in Europe. Most of the extinct species are placed in the Sumatran rhino genus, *Dicerorhinus*. But this overextends the meaning of the genus, and turns the genus into a taxonomic "wastebasket" for animals which are not really Sumatran rhinos, but are called "*Dicerorhinus*" for lack of a better name. Most of the eighteen or more extinct species should not be referred to the living genus. Some of these species have been split off into new genera, such as *Brandtorhinus*, *Lartetotherium*, and *Stephanorhinus*, but most of the fossil species should eventually be placed in their own genera. Wherever possible, we will use these new genera in place of invalid uses of "*Dicerorhinus*."

The earliest dicerorhinine is *Lartetotherium tagicum* from the early Miocene of Europe. It already had a small nasal horn like the living Sumatran rhino, and some specimens had a horn on the forehead as well. By the middle and late Miocene, *Lartetotherium sansaniensis* was widespread not only in Europe, but also in Africa where it evolved into *Lartetotherium leakyi*. In the late Miocene three different species of dicerorhinines coexisted in Europe, including the dwarf species "*Dicerorhinus*" *steinheimensis*, and the giant "*Dicerorhinus*" *schleiermacheri* and "*Dicerorhinus*" *orien-*

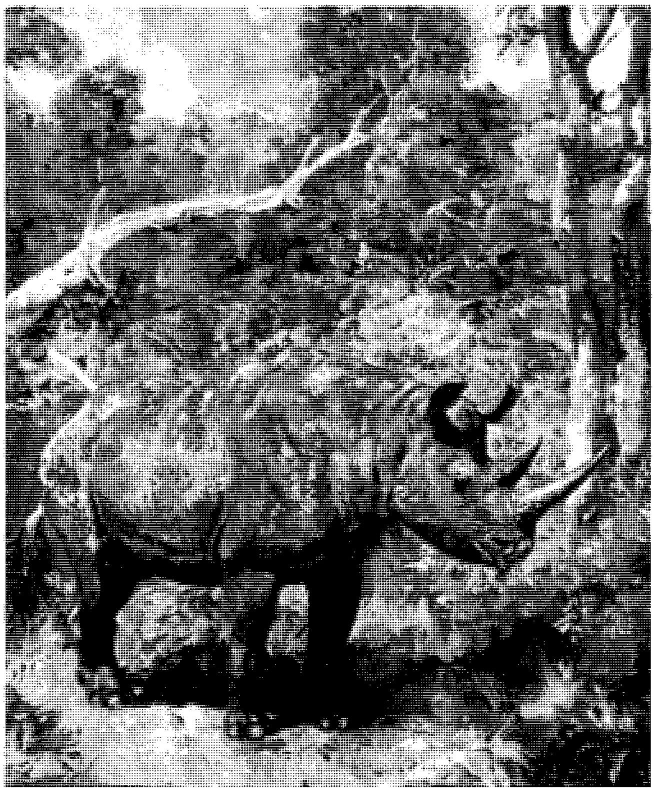


Figure 14.20. (left) A close relative of the woolly rhino was the Etruscan rhinoceros, *Stephanorhinus etruscus*. It lived in the early Pleistocene in southern Europe. (Painting by Z. Burian).

Figure 14.21. (above) Restoration of the woolly rhino, *Coelodonta antiquitatis*, one of the commonest mammals of Eurasia during the Ice Ages. (Painting by Z. Burian).

talis. Asia was the home not only of "*Dicerorhinus*" *orientalis*, but also of "*Dicerorhinus*" *abeli* from the late Miocene of India, and "*Dicerorhinus*" *ringstroemi* of Turkey and South China. All of these rhinos maintained the forest-browsing low-crowned teeth and long running limbs, but also had tandem horns on their noses and foreheads.

In the Plio-Pleistocene dicerorhinines continued to flourish. One Ice Age lineage, *Stephanorhinus*, can be traced back to "*Dicerorhinus*" *scheiermacheri* and *Stephanorhinus pachygnathus* from the Miocene of the Mediterranean region. The Etruscan rhinoceros, *Stephanorhinus etruscus*, was a primitive browser from the early Pleistocene (Fig. 14.20). In the middle Pleistocene it was succeeded by *Stephanorhinus hemitoechus*, the steppe rhinoceros. This beast had a low-slung head and high-crowned teeth like the living white rhino, and must have grazed on grasses of the parklands and steppes during the interglacials. Unlike the woolly rhino, however, it did not manage to colonize the tundra during cold periods. During the late Pleistocene the forest habitat was dominated by Merck's rhinoceros, "*Dicerorhinus*" *mercki*. This beast was named after the German writer Johann Heinrich Merck (a friend of the great poet Goethe), who was so fond of finding extinct rhino and mammoth bones that he called himself "elephant hunter and rhinoceros shooter." These rhinos were so characteristic of steppes and forests that the fluctuation between glacials and interglacials in Eurasia can be identified by the presence of either the steppe rhino or Merck's rhino.

The most successful of the dicerorhinines, however, was the woolly rhinoceros, *Coelodonta antiquitatis* (Fig. 14.21). This animal seems to have originated in the early Pleistocene from *Coelodonta nihowanensis* of northern China, and then migrated westward. The woolly rhino arrived in Europe about 200,000 years ago. By doing so, it had the largest range of any rhino, from Scotland to Spain to South Korea. It was clearly a steppe and tundra grazer, with a broad front lip for mowing grasses. One of its most peculiar features was the horn, which is flattened like a saber blade. Mikael Fortelius has studied these horns (which were once thought to be "gryphon" claws) and found that they have scratches and abrasion surfaces on the front edge. Like the tusks of the woolly mammoth and the antlers of caribou, the woolly rhino used its blade-like horn to brush snow away in a side-to-side motion and find tender grasses underneath. With its short legs, however, it probably did not spend much time in deep snowdrifts.

Unlike other extinct rhinos, we have an unusually complete picture of the woolly rhinoceros. A number of specimens frozen in permafrost have been found and they show that it had a thick woolly coat for protection against the Arctic cold. The most spectacular finds, however, were pickled in salty mineral wax, or ozocerite, in a natural seep near Starunia, Poland. Three complete carcasses, including the woolly hide, the flesh, the thick subcutaneous fat, and even the remains of the last meal, were found there in 1907 and 1929. The 1929 specimen had a last meal that included dwarf birches and small-leafed willows, typical of the tundra. This specimen has since been stuffed and is now displayed in the Natural History Museum of the Polish Academy of Sciences and Letters in Cracow (Fig. 14.22).

In addition to pickled specimens, we also have eyewitness drawings. Some of the best cave paintings in Europe, especially at Font de Gaume and Rouffignac, portray the woolly rhino as it was seen and hunted by Ice Age humans. Paleolithic artists always show it with a distinct shoulder hump and a downward inclined head. Many drawings showed that they were very furry, especially along the lower jaw, the back of the head, and the belly. Like most other dicerorhinines, they had tandem horns, with the nose horn much longer and more curved, but there was great variability in horn shape (as there is in living rhinos). Upper Paleolithic people in Siberia were great rhino and mammoth hunters, with some sites containing 3-4% rhino bones. Some rhinos are shown being speared with javelins and arrows in the cave paintings of La Colombière, France. Hunters may have also used pits dug across their habitual trails.

Despite their success on the late Pleistocene tundra from Scotland to Siberia, woolly rhinos never crossed the Bering land bridge into North America. It is still a mystery why they did not do so when their fellow tundra dwellers, such as the woolly mammoth, bison, yak, saiga antelope, elk, and humans, all crossed successfully and spread through the Americas.

The Siberian steppes were the home of another spectacular ice age rhino, *Elasmotherium* (Fig. 14.23). It was the true giant of the rhino family. As large as a living elephant, it had a huge skull almost 4 feet (1.2 m) long. Its most bizarre feature, however, was the horn. Instead of a typical nose horn, it had a gigantic horn over 6 feet (2 m) in length anchored to a huge bony boss on its forehead. In spite of the association of unicorn legends with other rhinos, *Elasmotherium* was more like the mythical unicorn in having a single horn on its forehead. Its cheek teeth were equally bizarre. They were rootless cylinders which had gotten so large that only a few were left in the jaw. As the tooth wore it became a thick cylinder of dentin surrounded by a thin layer of hard enamel. The worn surface of enamel formed a spectacular curlicue pattern that is totally unlike that of any other mammal known. These teeth, along with its steppe habitat, are clear indications of another great grazing beast.

According to Kurt Heissig, this creature originated from a tiny rhino known as *Caementodon* of the early Miocene of Pakistan. By the middle Miocene, there was a great diversity of relatives of *Caementodon*, including *Hispanotherium*, and several species of *Begertherium* found from China to Spain. Another branch began with *Iranotherium* (first described from the famous late Miocene Iranian locality of Maragheh). Middle Miocene *Beliajevina* from Siberia and Turkey and *Tesselodon* from China already had the distinctive elasmothere frontal horns and high-crowned teeth. In the late Miocene elasmotheres such as *Ningxiatherium* were restricted to central Asia, with lingering populations of *Caementodon* in Pakistan and *Kenyatherium* in Africa. Finally, in the Chinese early Pleistocene a beast known as *Sinotherium* gave rise to *Elasmotherium.*

Elasmotherium was restricted to Siberia and eastern

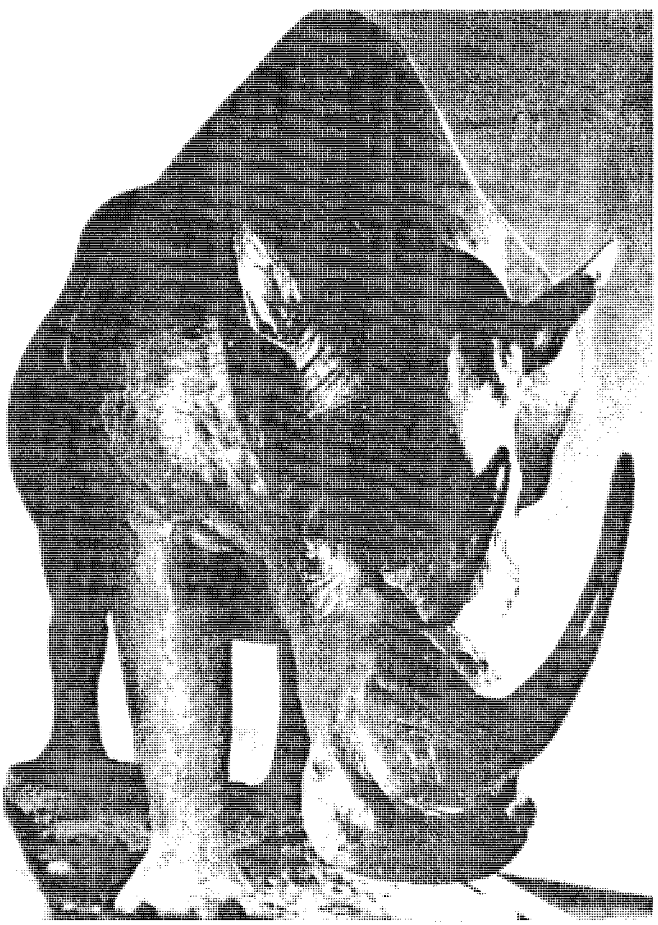


Figure 14.22. (left) The mummified carcass of a woolly rhino, pickled in petroleum in Starunia, Poland. It is now on display in the Institute of Systematic Zoology in Cracow. (From Kowalski 1967).

Figure 14.23. (above) Reconstruction of the elephant-sized rhino *Elasmotherium*, found in the steppes of Eurasia during the Pleistocene. Instead of a nasal horn, it had a single giant frontal horn. (Painting by Z. Burian).

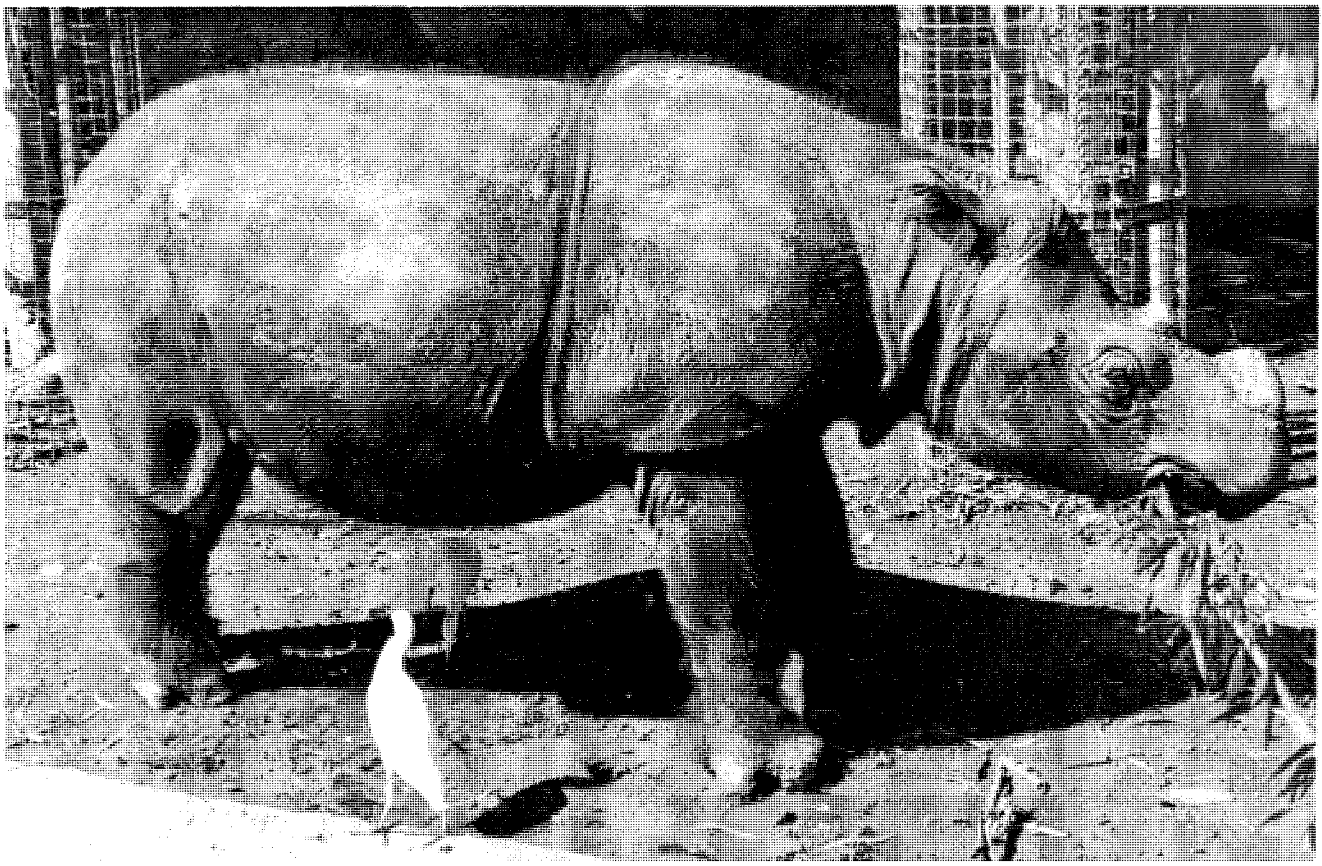


Figure 14.24. The living Sumatran rhino, *Dicerorhinus sumatrensis*, last of the lineage of the woolly rhino and its dicerorhinine kin. It is the smallest of living rhinos, and also retains the body hair typical of its tribe. (Photo by D. R. Prothero).

Europe (primarily the drainages of the Black and Caspian Seas), although one specimen is known from the Rhine Valley of Germany. It is not as common or as well known as the woolly rhino, although they both roamed the steppes of Siberia and eastern Europe. Both *Elasmotherium* and the woolly rhino died out about 10,000 years ago, at the end of the last glacial episode. Like the other great Ice Age mammals, their extinction was probably due to the climatic changes that destroyed their habitat. As we have seen, however, the great extinctions of the Ice Age megafauna are controversial, and many scientists attribute them to human hunting. Woolly rhinos were hunted during the last glacial without going extinct, and there is no evidence of humans hunting *Elasmotherium*. Clearly, the climatic explanation makes better sense for Ice Age rhinos.

Today the only remnant of the dicerorhinines is the Sumatran rhino, *Dicerorhinus* (formerly *Didermocerus*) *sumatrensis* (Fig. 14.24). In many ways it is a true living fossil. It retains the primitive forest browsing niche, and even has a significant amount of hair on its body (as most of the extinct dicerorhinines probably had). It is the smallest of the living species, weighing a little under a ton (about 550-750 kg). It is about 8-9 feet (2.5-2.8 m) long, and only 3-5 feet (1-1.5 m) high at the shoulder. Like other dicerorhines, it has tandem horns, although the forehead horn can be very small and give the impression that some individuals are one-horned. Their horns can be used for sparring or defense, but they are also used for breaking down saplings to feed. Like the one-horned rhino, its skin folds give the impression of armor plating, even though it is covered with long brown fur over much of its body.

Because Sumatran rhinos live in dense forests and are very secretive, very little is known about their biology. They spend most of the morning and evening browsing on leaves, twigs, bamboo shoots, and fruits such as wild mangoes and figs. With their prehensile lip, they are very adept at stripping off leaves and fruit. They will also eat lichens and fungus off a rotting tree, and occasionally eat grass. *Dicerorhinus* will step on a small tree and "walk it down" in order to reach fruit at the top. In the heat of midday, they sleep or wallow in the mud, and at night, they sleep in a concealed place.

Male Sumatran rhinos are usually solitary and non-territorial, but females may live in a territory 1-2 miles (2-3.5 km) in diameter. These territories are criss-crossed with well established trails in the underbrush that resemble green tunnels. Paths are used year after year, so even the bedrock can be worn smooth by rhino abrasion. In some places, rhinos mark their paths with dung heaps almost 3 feet (1 m) high and 5 feet (1.5 m) across. Sumatran rhinos are very mobile, moving into the steep highlands during the rainy season and down to the lowlands when the floodwaters recede and the weather is cooler. They are excellent climbers, clambering about in terrain too steep for elephants or gaur cattle, up to elevations of 6500 feet (2000 m). They are particularly adept at plunging through the steepest, thickest, thorniest vegetation to avoid being followed, which is why so few people have seen them or been able to study them. They are also excellent swimmers, and have been known to swim in the sea.

Their sense of hearing and smell is very acute, so it is very difficult to approach them although they have poor eyesight, as befits a forest animal with limited horizons. *Dicerorhinus* snorts when disturbed, brays like a donkey when alarmed, and squeaks when it is walking calmly. While it is wallowing it makes a variety of snorts, grunts, blows, and a low humming noise. Other than humans, *Dicerorhinus* is the only animal known to sing in the bath.

Given their secretive habits, even less is known about their reproduction. *Dicerorhinus* is a slow breeder, raising only one calf at a time, with a gestation period of about 15-18 months. One newborn baby was 50 pounds (23 kg) at birth, with a 20 mm long horn, and short, crisp, black hair all over its body. *Dicerorhinus* appears to reach adult size after about 3 years, although their teeth will not have fully erupted until 9 years of age. Little is known about their lifespan in the wild, although a captive animal lived for 32 years.

The Sumatran rhino is one of the most endangered of large animals. Although it once ranged all over southeast Asia, from India to south China to Sumatra and Borneo, today it is restricted to a very small portion of that original range. Poaching by humans seeking their horns is responsible for most of this decline, but today so few remain that they are only found in the densest forests, and are rarely seen by humans. The biggest threat to their survival is deforestation since they require large areas of dense forest and cannot be restricted to small reserves like other rhinos.

Since they are so elusive, it is very difficult to get an accurate count of how many still survive. According to 2002 estimates, there are fewer than 300 left, a 50% decline in just the past decade. There are 15 now held in captivity (5 males, 10 females), mostly in Indonesia and Malaysia. Too few are left in the wild to risk capturing more. The Malaysian government has begun a captive breeding program at the Sungai Dusun Rhino Facility on peninsular Malaysia, and this may hold the best hope for successful captive breeding. Several of the captive pairs have been mated, and one baby Sumatran rhino has been born in captivity (although it was conceived in the wild). A Global Propagation Group for the Sumatran Rhino was formed in 1991 to plan a conservation strategy. In addition to captive breeding, a studbook is now being maintained and efforts are being made to determine the genetics of the few available animals and avoid inbreeding. For the long term, however, the survival of *Dicerorhinus* depends upon halting the destruction of their habitat. The Sumatran rhino, because of its status as an exotic large endangered animal, could serve as an "umbrella" species to generate political momentum and funding for the preservation of large areas of its habitat and all the other endangered animals that share it.

Sadly, we know far too little about this fascinating living fossil which could give us a glimpse at the typical rhino of the prehistoric past. Yet our opportunities to learn more are rapidly diminishing. If deforestation is not slowed, captive breeding programs may not be enough to save this marvelous relict.

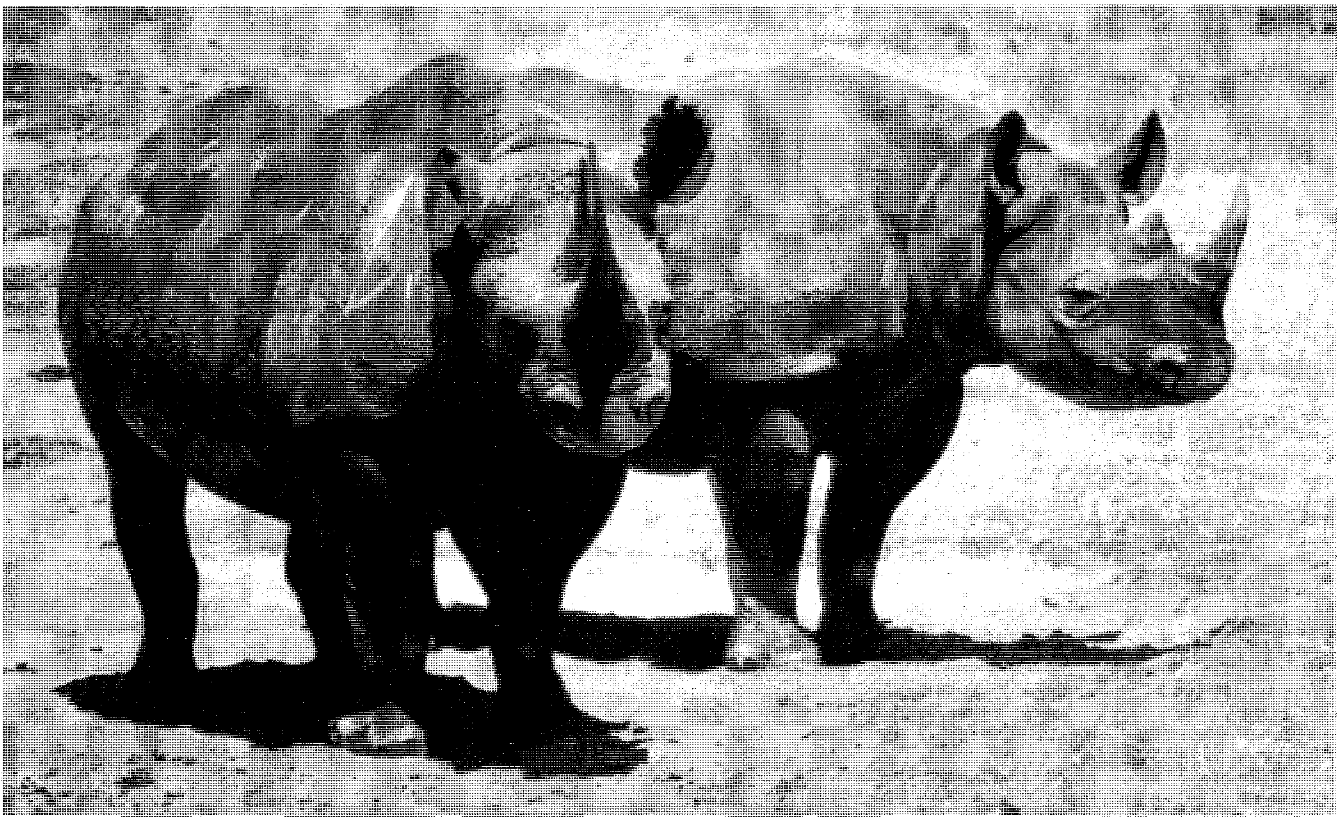


Figure 15.1. These two black rhinos were photographed in Ngorongoro Crater in 1973, and were poached soon afterwards. Today there are no rhinos in Ngorongoro Crater or most other East African national parks. (Photo by D.R. Prothero).

15. Thundering toward Extinction

Hearing and pre-eminently smell
Make far better sense
To rhinoceros, which sees dimly
(And wears a nosehorn well).
This all but hairless hulk
So enarmored of thick skin with folds
As to lack nonhuman predators of consequence
Thunders toward extinction [Fig. 15.1]
Blindly bold to man in self-defense.
Preferentially it holds
Itself apart, hoofing through reeds
And high grass, browsing by dusk
And dawn, solitary in its
Territory save when it breeds.
Communication faintly whiffs absurd:
Movement is action
Movements speak louder than words
Territory marks are piled turds.
(Burns, 1975)

UNICORN, MONOCEROS, AND RHINOCEROS

As we have seen in previous chapters, rhinoceros and mammoth fossils were responsible for many myths about great races of giants, or great extinct carnivorous beasts, or "ancient Dacians." The most persistent myth based on the rhinoceros, however, is the legend of the unicorn. A variety of one-horned beasts were common in ancient Chinese, Egyptian, Babylonian, and Assyrian mythology, and in the fables of the Greeks and Hebrews. In Job 39: 9-12, Yahweh asks Job, "Is the unicorn [*re-em* in Hebrew] willing to serve you? Will he spend the night at your crib? Can you bind him in the furrow with ropes, or will he harrow the valleys after you? Will you depend on him because his strength is great, or will you leave to him your labor? Do you have faith in him that he will return, and bring your grain to your threshing floor?" Herbert Wendt suggests that the familiar horse-like unicorn was a combination of legends of the recently domesticated ox in Asia (known to the Babylonians as the *rimu*, and to the Akkadians and Ugarites as the *remu*), the oryx of the Egyptians (known in Arabic as the *rim*), the wild ass or onager of central Asia (famous for its strength and ferocity), and the one-horned Indian rhinoceros.

Certainly, many ancient cultures were also aware of true rhinoceroses. The Indian rhinoceros was described by the Greek historians Ctesias, Strabo and Agartharcides, and by the Roman poet Martial, who remarked on how it flung bears away in combat in the Roman circuses. In his *Natural History*, Pliny the Elder writes that the *unicornis* was "the born enemy of the elephant that sharpens its horn on a stone and in combat aims at the elephant's belly, knowing well that it is soft." Both the Greeks and Romans assumed that the mysterious horse-like beast of Asia (known as *monoceros* to the Greeks and *unicornis* to the Romans) was something different from the rhinoceros, especially since there was a big market for the medicinal properties of unicorn horn from China (almost certainly taken from Indian rhinos).

In the Middle Ages, the lack of contact with Asia or Africa caused the classical knowledge of rhinoceroses to disappear into the unicorn legend. In almost all accounts, the unicorn is a powerful, wild beast, the size of a small horse but with a beard and cloven hooves. All were supposedly males. The unicorn was endowed with enormous strength, but all of its strength was concentrated in its horn. It was said to precede other animals to water and render it pure by dipping its horn into it. It could only be captured by a virgin sitting quietly in the forest with one breast bared. When the unicorn came, it could not resist her, but placed its head quietly in her lap. Once she plucked the horn from it, it lost its strength and was quite tame.

When mammoth tusks were dug up they were prized as the horns of unicorns, or *unicornum verum*. Sick people paid great sums to apothecaries for small shavings. Although most theologians discouraged this practice, fresh discoveries of mammoth tusks only perpetuated the myth. Even after the Middle Ages unicorns were illustrated and described in zoological textbooks by Gesner, da Vinci, Mercati, Leibniz, and even Linnaeus, none of whom doubted their reality. According to Leonardo da Vinci it was a mythical super-beast: "In its lack of moderation and restraint and the predilection it has for young girls, it completely forgets its shyness and wildness; it puts aside all distrust, goes up to the sitting girl, and falls asleep in her lap. In this way hunters catch it."

By the seventeenth century it had become a bearded horse-like animal with cloven hooves and a long, straight

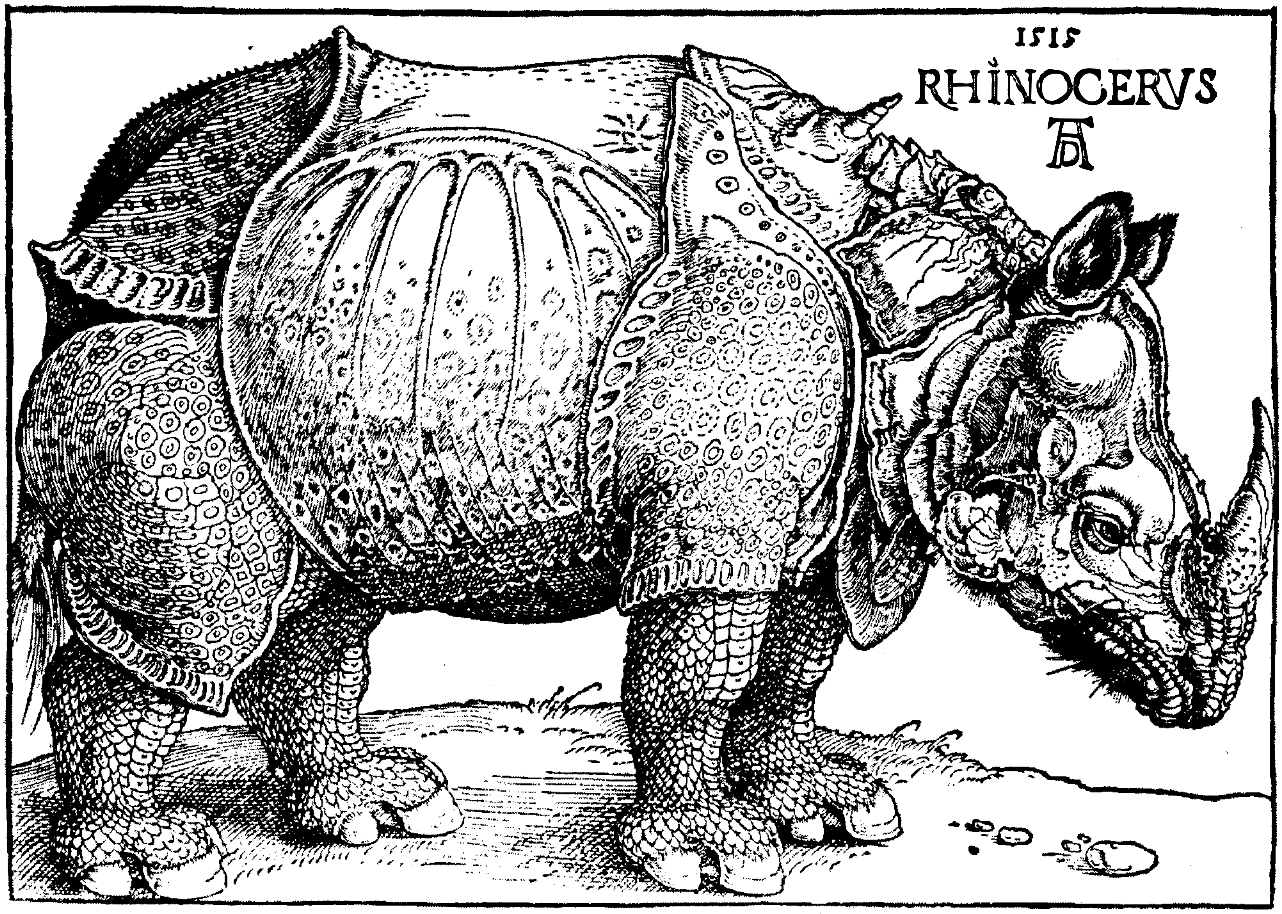


Figure 15.2. Albrecht Dürer never saw the Indian rhino on which he based this famous 1515 woodcut; nevertheless, it became the model for all rhino illustrations for over a century. The mythical element is still present in the unicorn horn protruding from the shoulder (From Wendt 1959).

horn with a spiral twist on its surface. This idea of the horn probably came from the imported tusks of narwhals, a small Arctic whale related to the white beluga whale. Male narwhals have an enlarged left incisor that protrudes as a tusk, sometimes reaching 10 feet (3 m) in length, which is used for social dominance. When Scandinavian fishermen brought these tusks back from the Arctic they were greatly prized by apothecaries for their supposed miraculous powers as unicorn horns. They were so valuable that the apothecary kept it on a chain, and scraped off only a few grains for a high price. A prince of Saxony paid a hundred thousand thalers for a single "alicorn," and Emperor Charles V discharged his imperial debt to the Margrave of Bayreuth with just two narwhal teeth. Other "unicorn horns" were probably Indian rhino horns, powdered and used for medicine. Queen Elizabeth I had one in her bedroom in Windsor, and as late as 1741 unicorn horn was still officially recognized as a drug in England. Just before the French Revolution in 1789 the French court still used "unicorn horn" to test if the royal food had been poisoned. Pope Gregory XIV was offered some on his deathbed in 1591, although he died right after consuming a potion made of the powder. It was so widely regarded as a symbol of apothecaries that today the trademark of Burroughs Wellcome, one of the world's largest drug companies, is a unicorn.

Skeptics called the narwhal tooth the *unicornum falsum*, and some even related accounts of a "toothed whale" from the Arctic. But the belief was so widespread that almost all accounts placed a long, straight narwhal tusk on their portraits of unicorns, the dominant image today. In the early nineteenth century, great anatomists such as Cuvier pointed out the biological impossibility of such a beast. No horse-like animal had cloven hooves like an artiodactyl!

The rediscovery of the rhinoceros after the Dark Ages caused almost as much excitement in Europe as the discovery of the elephant or giraffe. Instead of the delicate horse-like beast they had come to expect, they found a large, ugly beast with armor. In 1292 Marco Polo returned from his seven-year voyage bringing reports of a two-horned beast he had seen in Sumatra (probably the Sumatran rhino). He saw "lion-horns, which, though they have feet like elephants, are much smaller than the latter, resemble the buffalo in which, however, they harm no one … All in all, they are nasty creatures, they always carry their pig-like heads to the ground, like to wallow in mud and are not the least like the unicorn of which our stories speak in Europe. Can an animal of their race feel at ease in the lap of a virgin? I will say only one thing: this creature is entirely different from what we fancied."

Many of the European myths about rhinoceroses probably came from Chinese tales brought with the trade in rhino and elephant parts. These were liberally mixed with unicorn myths, and swallowed completely by credulous Europeans. The more ridiculous, the better. For example, rhinos supposedly had no joints in their legs and had to prop themselves against trees in order to sleep. If a rhino fell down it was helpless, so it could be captured by getting it to lean against a half-sawn timber. Once this collapsed it left the rhino immobilized on its side. Like unicorns, all rhinoceroses were said to be males. Rhinos were supposedly fond of music and perfume. To lure the rhinoceros a man should dress up as a virgin, reeking of perfume. If it charged, the man could climb a tree and drive the rhino off by urinating in its ear.

Not until 1513 did Europe actually see a live rhinoceros. It was captured in India after the Portuguese conquered the coastal city of Goa. Sent by King Muzaffar of Cambray to King Manuel the Great in Lisbon, it caused a sensation. After the Portuguese king had tired of it, he sent it as a gift to Pope Leo X. It was harnessed with a green velvet collar, studded with gold roses and carnations, and tethered to a gilt iron chain. When the ship docked in Marseilles, Francis I of France bribed the captain 5,000 gold crowns to display it to the French crowd. On its way to Rome a storm wrecked the ship, drowning all aboard. The rhino carcass washed ashore, where it was collected, skinned, stuffed, and sent to the Pope.

While it was in Lisbon it was described by the Italian naturalist Ulisse Aldrovandi, and a famous woodcut was made by the artist Dürer (Fig. 15.2) and copied by Gesner in 1551. The illustration emphasizes the folds of the skin, and showed horny spikes on the skin that were probably caused by the long confinement in the ship's hold. This early illustration was so influential that nearly every subsequent drawing of a rhino tried to show the same features, whether or not they were really there. When African black rhinos were found, they were shown with folded skin and armored spikes. Museum curators actually ironed some folds into their skins to make them "authentic."

The influence of myth and hearsay upon even the most authoritative accounts is demonstrated by Edward Topsell's 1607 *History of the Four-footed Beasts*. It was one of the first English-language accounts of the natural history of beasts published since the Renaissance, and was copied without change for centuries. Along with descriptions of dragons, manticores, unicorns, and many real animals, he gives a complete account of the mysterious rhinoceros.

> "We are now to discourse of the second wonder in nature: namely, of a beast every way wondrous both for outward shape, quantity, and greatness, and also for inward courage, disposition, and mildness. For, as the elephant was the first wonder of whom we have already discoursed, so this beast next unto the elephant fills up the number, being every way as admirable as he, if he does not exceed him, except in quantity or height of stature...
>
> Because of the horn in his nose, the Grecians call him *rhinoceros,* that is, "nose-horned beast." Although there are many beasts that have but one horn, yet there is none that has one horn growing out of the nose but this beast alone. All the rest have the horn growing out of their foreheads. There have been some people that have taken the rhinoceros for the *monoceros* (the unicorn) because of this one horn, but they are deceived.
>
> In quantity, the rhinoceros is not much bigger than an oryx. Pliny makes it equal in length to an elephant, and some make it longer than an elephant but say it is lower and has shorter legs. A rhinoceros that was seen at Alexandria had a color like that of an elephant; his quantity was greater than a bull's, or as that of the greatest bull; his outward form and proportion was like a wild boar's, especially in his mouth, except that out of his nose grew a horn, which he used instead of arms. He had two girdles upon his body like the wings of a dragon, coming from his back down to his belly, one toward his neck or mane and the other toward his loins and hinder parts.
>
> To this we may add descriptions out of Oppianus, Pliny, and Solinus. The color of the rhinoceros is like the rind or bark of a box-tree. (This does not differ much from an elephant). On his forehead there grow hairs which seem a little red, and his back is distinguished with certain purple spots upon a yellow ground. The skin is so firm and hard that no dart is able to pierce it, and upon it appear many divisions like the shells of a tortoise set over the scales, and there is no hair upon the back. Upon his nose there grows a hard and sharp horn, crooking a little towards the crown of his head but not so high. The horn is flat and not round, and it is so sharp and strong that whenever he sets to it, he either casts it up into the air or else bores through it though it be iron or stone. It is apparent by the picture that there is another horn not upon the nose but upon the withers (I mean the top of his shoulder next to the neck).
>
> Oppianus says that there was never yet any distinction of sexes in rhinoceroses, for all that have ever been found have been males and not females. But from hence let nobody gather that there are no females, for it is impossible that the breed should continue without females. Pliny and Solinus say that they engender or admit copulation like elephants, camels, and lions. When they are to fight, they whet their horn upon a stone. There is not only

discord between them and elephants for food, but there is also a natural enmity between the beasts. It is confidently affirmed that, when the rhinoceros which was at Lisbon was brought into the presence of an elephant, the elephant ran away from him.

How and in what place the rhinoceros overcomes the elephant was shown already in the story of the elephant; namely, he fastens his horn in the soft part of the elephant's belly.

All the later physicians do attribute the virtue of the unicorn's horn to that of the rhinoceros, but they are deceived. None of the ancient Grecians ever observed any medicines in the rhinoceros.

The rhinoceros is taken by the same means that the unicorn is taken, for it is said that above all creatures they love virgins and that unto them they will come, be the beasts ever so wild, and fall asleep before the virgins, and so being asleep, they are easily taken and carried away" (Topsell, 1607).

As exploration continued in the following centuries rhinoceroses occasionally made their way into the hands of scientists. Their rarity and difficulty of maintenance and transport, however, guaranteed that they were sensations fit for royalty. In the 1740s a Dutchman named Douvemont van der Meer took a rhino on a tour of the major European capitals, feeding it hay, beer, and wine. In Vienna, it received a full honor guard. It was so famous that Casanova mentioned it in his memoirs. Louis XV tried to purchase it after it had been to Versailles in a wheeled cage drawn by eight horses. But the owner wanted 100,000 écus for his prize, a fee even the King couldn't afford. Madame de Pompadour had to settle for tossing orange peels into its mouth.

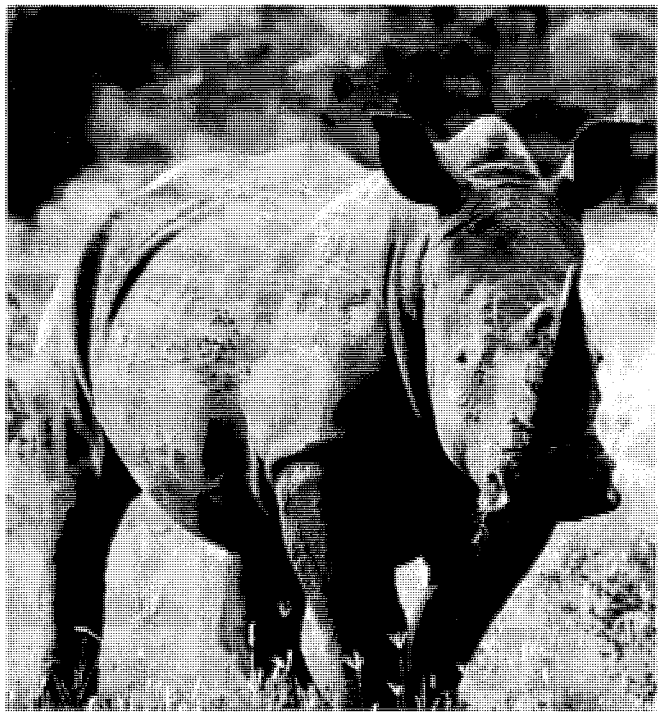


Figure 15.3. The white rhinoceros, *Ceratotherium simum* has a broad "lawnmower" mouth for mowing down grass. (Photo courtesy Nova Development Corporation).

BLACK AND WHITE

By 1868 the great zoologist Sclater had published the first accurate, modern zoological account of the black rhino, which had just been acquired by the Regent's Park Zoo in London. The Indian, Sumatran, and Javan rhinos were also described about this time by Sclater and other scientists. The white rhino (Fig. 15.3), however, was known only from the accounts of the English traveler Burchell, who crossed South Africa in 1817. [The plains zebra, *Equus burchelli*, is named after him]. The Boers called it the *wijd rhinoceros*, or "big rhinoceros," and Burchell's knowledge of Afrikaans was so poor that he confused this with "white rhinoceros." The "white" rhino got its name from a mistranslation before anyone had seen it and realized that it is the same gray color as the "black" rhino. Since "black" and "white" are both misnomers, some zoologists prefer to call them the "browse" and "grass" rhinos, or the "prehensile-lipped" and "square-lipped" rhinos, in reference to their diet or their lip specializations for that diet. Either set of names would be preferable to the misleading color names, but "black" and "white" are so entrenched now that it is impossible to change them. Most of what people know about rhinos is wrong. In addition to the misleading "black" and "white" distinction, we saw in the previous chapter that horns are a late addition in rhino evolution. Popular books are full of myths of rhinos as terrifying, short-tempered beasts who eagerly gore and impale humans at any opportunity. Hollywood loves to portray them as dark terrors of Africa, the "horned fury," a dangerous and diabolic beast. But white rhinos are relatively docile and timid, and black rhinos can either charge or flee, depending upon what their poor eyesight tells them. As described by the Belgian zoologist, Jean-Pierre Hallet,

"Africa's black rhino will, on occasion, "charge" a car without apparent provocation. He will also charge at tents, trees, bushes, rats, frogs, men, butterflies or grasshoppers. Sometimes he will even charge at the sound of his own dung dropping on a leafy scrub behind him. Much more often and for no good reason, he will flee from frogs, butterflies, and all the rest. There is no predictable pattern to his flights or aggressions; the same rhino who retreats in terror from a harmless native woman may gallop moments later toward a group of rifle-bearing white men. If the tourists hold their fire he will, almost invariably, come to a halt some twenty feet away, stare at them briefly, and then go trotting off to browse on a thorn bush. But they shoot, and most of them believe sincerely that they shoot and kill in self-defense.

> Loud-snorting bluffer and titanic blunderer, more easily stalked and killed than any member of the hunters' Big Five, the black rhino is a rebel without a cause, a chronic but incompetent delinquent. He is, even from the animals' point of view, a bull in Africa's china shop, rushing from one messy disaster to the next ... What could be more frantic, more maddened by frustration, more suspicious and aggressive, than a three-thousand pound animal, nearsighted to the point of blindness, who searches constantly for something he cannot see?
>
> Insatiably curious, the black rhino is at the same time extremely timid and equipped with only limited mentality. His hearing and his sense of smell are superb, but his vision is abysmally defective. Each of his tiny eyes, set on opposite sides of his bulky, elongated head, gives him a different picture to look at; each picture is tantalizing in its wide-angle perspective but horribly frustrating in its perpetual fuzziness. An animal Mr. McGoo, nearsighted Kifaru [the Swahili name for the black rhino] cannot tell a man from a tree at distances of more than thirty feet, cannot see any object distinctly if it is more than twenty or even fifteen feet away, and has to cock his head sideways to see, with one eye at a time, around the bulk of his muzzle and his massive front horn. Moving forward with horn lowered, he is running blind.
>
> By day as well as night, Kifaru hears and smells a whole world of fascinating objects which he cannot see. His curiosity drives him on to poke and probe among them, but his timid disposition makes him fear, and fear deeply, the very objects he wants to examine. He hesitates, agonized, while the two conflicting instincts boil within him. Usually he runs away but sometimes rushes forward to investigate with the world's most farcical display of bluff, noise, wasted energy, and sheer ineptitude—the notorious rhino 'charge'" (Hallet, 1968: 147-150).

Hallet goes on to describe how easy it is to dodge a rhino "charge" if you do not flee or make noise to give away your position. After a week of futile charges, a captive rhino was even tamed and taught to play games, and was harnessed and ridden. Hallet compares the rhino to its skittish relative, the horse, which will also shy away from a fluttering bit of paper or a butterfly, and stampede when panicked by a startling sight or sound.

The key to understanding rhinos is to realize that their senses are suited for dense vegetation, not the open savannas they now inhabit. In the dark forests where rhinos evolved, sight is nearly useless, and hearing and scent work at far greater distances. Douglas Adams made it clear in his description of a visit to the last remaining population of northern white rhinoceros in northern Zaire:

> "You need to know something about the way that a rhino sees his world before we go barging in," [the guide] whispered to us. "They're pretty mild and inoffensive creatures for all their size and horns and everything. His eyesight is very poor and he only relies on it for pretty basic information. If he sees five animals like us approaching him, he'll get nervous and run off. So we have to keep close together in single file. Then he'll think we're just one animal and he'll be less worried."
>
> "A pretty big animal," I said.
>
> "That doesn't matter. He's not afraid of big animals, but numbers bother him. We also have to stay downwind of him, which means that from here we're going to have to make a wide circle around him. His sense of smell is very acute indeed. In fact, it's his most important sense. His whole world picture is made up of smells. He 'sees' in smells. His nasal passages are in fact bigger than his brain."
>
> From here it was at last possible to discern the creature with the naked eye. We were a bit more than half a mile from it. It was standing out in the open, looking, at moments when it was completely still, like a large outcrop of rock. From time to time its long sloping head would wave gently from side to side and its horns would bob slightly up and down, as mildly and inoffensively, it cropped grass. This was not a termite hill...
>
> The animal is, of course, a herbivore. It lives by grazing. The closer we crept to it, the more monstrously it loomed in front of us, the more incongruous its gentle activity seemed to be. It was like watching an excavating machine quietly getting on with a little weeding.
>
> At about forty yards' distance, the rhinoceros suddenly stopped eating and looked up. It turned slowly to look at us and regarded us with grave suspicion while we tried hard to look like the smallest and most inoffensive animal we could possibly be. It watched us carefully but without apparent comprehension, its small black eyes peering dully at us from either side of its horn. You can't help but try and follow an animal's thought processes, and you can't help, when faced with an animal like a three-ton rhinoceros with nasal passages bigger than its brain, but fail.
>
> The world of smells is now virtually closed to modern man. Not that we haven't got a sense of smell—we sniff our food or wine, we occasionally smell a flower, and can usually tell if there's a gas leak—but generally it's a bit of a blur, and often an irrelevant or bothersome blur at that. When we read that Napoleon wrote to Josephine on one occasion, "Don't wash—I'm coming home," we are simply bemused, and almost think of it as deviant behavior. We are so used to thinking of sight, closely followed

by hearing, as the chief of the senses that we find it hard to visualize (the word itself is a giveaway) a world that declares itself primarily to the sense of smell ... For a great many animals, however, smell is the chief of the senses. It tells them what is good to eat and what is not (we go by what the packet tells us and the sell-by date). It guides them toward food that isn't within line of sight (we already know where the shops are). It works at night (we turn on the light). It tells them of the presence and state of mind of other animals (we use language). It also tells them what other animals have been in the vicinity and doing what in the last day or so (we simply don't know, unless they've left a note). Rhinoceroses declare their movements and their territory to other animals by stamping in their feces, and then leaving smell traces of themselves wherever they walk, which is the sort of note we would *not* appreciate being left.

When we smell something slightly unexpected, if we can't immediately make sense of it and it isn't particularly bothersome, we simply ignore it, and this is probably equivalent to the rhino's reaction to seeing us. It appeared not to make any particular decision about us, but merely to forget that it had a decision to make. The grass presented it with something infinitely richer and more interesting to the senses, and the animal returned to cropping it...

The animal measured about six feet high at its shoulders, and sloped down gradually toward its hindquarters and its rear legs, which were chubby with muscle. The sheer immensity of every part of it exercised a fearful magnetism on the mind. When the rhino moved a leg, just slightly, huge muscles moved easily under its heavy skin like a Volkswagen parking ...

The light breeze that was blowing toward us began to shift its direction, and we shifted with it, which brought us around more to the front of the rhino. This seemed to us, in our world dominated by vision, to be an odd thing to do, but so long as the rhino could not smell us, it could take or leave what we looked like. It then turned slightly toward us itself, so that we were suddenly crouched in full view of the beast. It seemed to chew a little more thoughtfully, but for a while paid us no more mind than that. . .

For the rhino, the sight of us was simply a clue that there was something he should sniff for, and he began to sniff the air more carefully, and to move around in a slow, careful arc. At that moment, the wind began to move around and gave us away completely. The rhino snapped to attention, turned away from us, and hurtled off across the plain like a nimble young tank" (Adams, 1990: 97-101).

Although they are very different in their size and ecology, black and white rhinos are closely related. Members of the tribe Dicerotini, they first appear in the middle Miocene deposits of Ft. Ternan, Kenya (an important locality for the earliest fossil apes described by Louis Leakey, such as *Proconsul* and *Kenyapithecus*). Known as *Paradiceros mukirii*, the earliest dicerotin was a short-limbed browsing form with tandem horns, much like a small version of the black rhino. *Paradiceros* was not restricted to Africa, but is also found in middle Miocene deposits of Turkey and Greece. In the late Miocene the black rhino genus, *Diceros*, is widespread from Spain to the Middle East, as well as Africa. By the early Pliocene, dicerotines were restricted to Subsaharan Africa. According to Dirk Hooijer, the living black rhino species, *Diceros bicornis*, can be traced back to about 4 million years ago, making it one of the few living mammal species to last so long.

The ancestor of the white rhino, *Ceratotherium praecox*, is found in southern and eastern Africa in late Miocene deposits about 7 million years in age. By about 3 million years ago the modern white rhino, *Ceratotherium simum*, could be found in Kenya. Like the black rhino, *Ceratotherium simum* has been around longer than just about any living species of mammal. Both are truly living fossils.

The white rhino is the second largest living land mammal after the elephant, reaching a weight of 5000 pounds (2270 kg) in males and 3750 pounds (1700 kg) in females (Fig. 15.3). Black rhinos are slightly smaller, weighing about 2100-3000 pounds (950-1370 kg). All dicerotins have tandem horns, one anchored on the nose, and the other on the forehead. Since these horns are made of compressed hair-like fibers, they grow continuously (at about the same rate as your fingernail grows), but are constantly worn by rubbing against the ground and trees. Occasionally they are torn off during digging, or during fights or other accidents. Then the animal must slowly grow another. The frontal horn is usually shorter than the nasal horn. Before heavy poaching, horns were typically 2-3 feet long, but are shorter in most living rhinos due to poachers. In the days before heavy poaching, the record holder had a horn 6 feet 6 inches (2 m) long, and it was probably a very old individual.

The most fundamental distinction between the two dicerotins is in their diet and ecology. The "black" rhino, or "prehensile-lipped" rhino, is a browser, subsisting on bushes and small trees. Consequently, it has features that we have seen in extinct browsing rhinos (Fig. 15.4). Its finger-like upper lip is highly flexible for grasping twigs and stripping off leaves. The black rhino eats a wide variety of leaves and twigs of different shrubs in the acacia woodland community; it also pulls up tree seedlings, and will eat fallen fruits and even long grasses and clover when available. The lip and lining of the mouth cavity are so tough that black rhinos can eat acacia branches with three-inch thorns. Hallet notes that "while nipping off some three bushels of leaves and twigs every day, he ingests a large number of vicious, flesh-ripping thorns. They never seem to bother him at all.

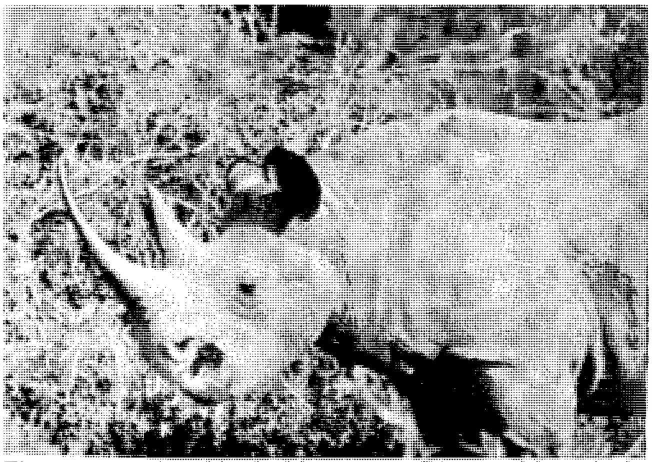


Figure 15.4. The black rhinoceros, *Diceros bicornis*, is distinguished by its prehensile lip, which enables it to pull down leaves, branches and other browse. Here it is eating long acacia thorns without difficulty. (From Guggisberg 1966).

Appallingly, he eats the fat thorny leaves of the euphorbia bushes whose acrid, milky-looking sap blisters human skin; and he even dines on fallen branches of the candelabra tree, a species of euphorbia whose juice is used by East African tribesmen to poison arrows which they use to hunt ... rhinoceros. While toxic enough if it gets into his bloodstream, Kifaru's cast-iron stomach can digest the poisonous euphorbia; in fact, it forms the major part of his diet in regions where it is used also to kill him" (Hallet, 1968: 164). Like other browsers, black rhinos have relatively low-crowned teeth, and walk with their head held horizontally to reach vegetation at a variety of levels. Because of their diets, they prefer the edges of forests and open scrublands, and avoid the open grasslands favored by white rhinos. Since the African savannas are predominantly scrubland, black rhinos were once common in all of Subsaharan Africa except the Congo Basin rain forests.

By contrast, the "white" rhino, or "square-lipped" rhino is a grazer, mowing grass with its broad, flat snout (Fig. 15.3). In addition to the broad snout it has a long, low-slung skull that always hangs down from the shoulder, so that it can feed easily on the ground. As we saw in other grazing mammals, they have very high-crowned teeth for chewing gritty grasses without wearing their molars down to the gums. Like other hindgut fermenters, they must eat enormous quantities of low-quality grass to make up for their inefficient digestion. During most of the year they feed almost constantly, with short periods of rest. During the wet season, they prefer the greener short grass, but they will settle for the medium-height (8 inches, or 20 cm) *Themeda* grass during the dry season, which they crop down to 1-2.4 inches (2-6 cm) in height. They feed by slowly swinging their head in a wide arc, cropping all the grass within reach as they step forward. In areas where they have been grazing, they manage to maintain the community of short grasses against invasion by other plant communities.

Both species are heavily dependent on water holes, although they can go 4-5 days without drinking. Their traditional trails to the water hole are well marked, and the availability of water often limits the rhino population in a given area. With their great body mass, they must use every possible resource to keep cool, and wallowing in the mud or taking dust baths is one of their favorite activities during the heat of the day. The coating of mud also helps keep down the bites from flies. Ticks and lice tend to fall off when the mud dries. These parasites also entice oxpeckers, tick birds and cattle egrets to ride on the rhino's back, picking off insects as they find them. The rhino tolerates this, and often the birds serve as a warning for threats the rhino cannot see.

Rhinos do not form large herds. Most often they travel alone, or females are accompanied by their immature offspring. Female black rhinos have home ranges covering 1-2 square miles in forest patches, and up to 35 square miles in arid territory. White rhinos occupy ranges of 3-6 square miles. The home ranges of individual females overlap completely, however, so they are not truly territorial. Their daily routine consists of traveling along well-worn trails within their home range between the water hole and the best feeding grounds. They spend the heat of the day in the water hole, or sleeping in the shade, and feed mostly in the morning and evening. Rhinos mark their trails with their urine and feces, and each rhino adds to the pile when it encounters the scent. These dung piles are particularly large along regularly used trails between their feeding areas and watering hole, and may indicate the population density in the area, or serve to mark a trail that is used once every few days. They also leave scent behind with the mud that constantly flakes off them.

Males, on the other hand, are highly territorial, patrolling an area and attempting to drive off any other competing males. However, the territorial male will tolerate several subordinate males as long as they are submissive and do not challenge him. White rhino territories are quite small, covering 200-600 acres, since their prime pasture is relatively rich and predictable. But black rhino males must patrol about 1.5 square miles, since the richest bushes are unpredictable and less dense than grass, and in thick vegetation other males are hard to detect. They mark their territories by kicking over and spreading out the dung piles with their feet, and spraying urine on just about every available bush and tree on the perimeter of their territory (Fig. 15.5). When they encounter another male, they practice several rituals before they resort to combat. They stand showing their profiles to each other to give their rival a sense of their size and maturity. (This behavior, which appears to be looking with one eye and then the other, has been misinterpreted to indicate that they do not have binocular vision). They may then stand horn to horn, staring each other down, and then back away to wipe their horn on the ground. This may be repeated for as long as an hour if they are at the boundary of their territory. If an intruding male does not back down, then they eventually get into a pushing match,

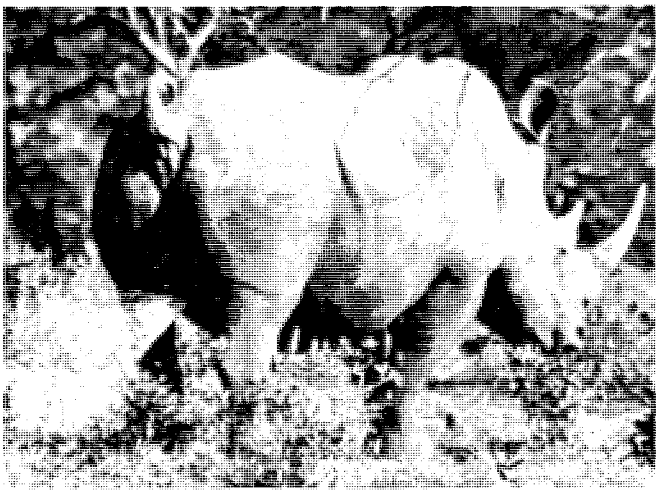


Figure 15.5. Rhinos mark territory by spraying urine on bushes and trees around the perimeter. (Photo courtesy N. Owen-Smith).

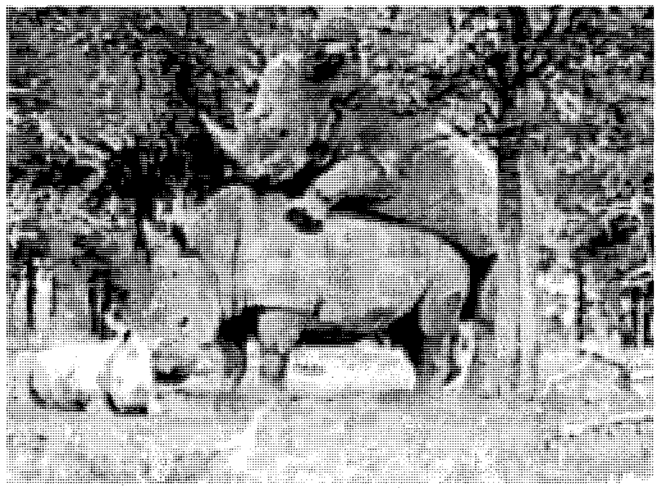


Figure 15.6. During the many minutes of copulation, the cow walks around while the bull tries to stay mounted on top of her. Her calf from a previous mating sits nearby. (Photo courtesy N. Owen-Smith).

wrestling with their horns, but they can get into serious fights that result in fatal injury, fighting with an upwards jab of their horns.

Females and subdominant males will adopt a submissive stance to ward off the aggression of the territorial male, and utter loud roars and shrieks to indicate their submission. The resident male, on the other hand, utters a deep growl, which is replaced by a fierce bellow if the fight becomes intense. Recent studies have shown that rhinos, like elephants, communicate with low frequencies below the range of human hearing. This enables them to be heard over long distances, since low-frequency long-wavelength sound carries much farther than sounds we can hear.

Females wander through the males' territories freely unless they are in heat. Then a male will try to consort with them, and attempt to confine them to his territory for as long as 1-2 weeks until they are ready for mating. However, if the female wanders into a neighbor's territory, the male will not trespass too far to keep her. Courtship is slow and cautious, taking 5-20 days to complete, since the female is frequently still with a possessive year-old calf, and can fight back herself. Once the male has overcome the female's reticence, he rests his head on her back, and then puts on a courtship display of brushing the ground with his horn, charging and shredding bushes, and darting back and forth on stiff legs, spraying urine. Eventually she allows him to mount her (Fig. 15.6). Copulation can take as long as eighty minutes, during which the male struggles to stay on top of the female as she walks along and ignores him.

Birth can take place at any time of the year, but conceptions usually peak during the rains so that birth peaks occur from the end of the rainy season through the middle of the dry season. Gestation takes between 15 and 16 months (longer in white rhinos than in black rhinos). Females first come into heat at 5 years of age, and begin breeding at 6-8 years, and intervals between offspring are typically 2-4 years. When the mother is about to go into labor she seeks seclusion in the bushes. Rhino calves are small at birth, weighing only 4 percent of the mother's mass—about 143 pounds (65 kg) in white rhinos and 88 pounds (40 kg) in black rhinos. Within about three days they are able to keep up with their mother. If danger threatens, the mother stands protectively over the calf, or places her body between the calf and the predator. When several females and their calves are together they will form a circle with horns pointed outward, sheltering the calves within the circle. The calf stays with its mother constantly for two or more years until a new calf is born, at which time the older sibling is driven away and must fend for itself. Since the normal life span is about 40-50 years, a female could produce 10-11 calves in her lifetime. This slow rate of reproduction is one of the major reasons that rhinos are so vulnerable.

ONE-HORNED RHINOS

The only living beasts to bear the scientific name *Rhinoceros* are the two larger Asian species, the Indian rhino (*Rhinoceros unicornis*) (Fig. 15.7) and the Javan rhino (*Rhinoceros sondaicus*) (Fig. 15.8). They are also known as the greater and lesser one-horned rhino because they are the only living rhinos with a single nasal horn. However the majority of extinct horned rhinos had only a single nasal horn as well, and the tandem-horned condition seen in the dicerotines and dicerorhinines is an exception to the rule. The single horn of the Indian rhino tends to be a foot long or less, and they tend to use their sharp lower tusks as their principal weapon. The Javan rhino has even a smaller nasal horn, found only in males. Adult male Indian rhinos weigh about 4000 pounds (2000 kg) and females about 1600 kg, about the same as the white rhino, and the Javan rhino weighs slightly less. Both are distinguished by their distinc-

Figure 15.7. The Indian rhino *(Rhinoceros unicornis)* has distinctive skin folds that were once thought to be “armor plating.” They also have a single nasal horn that is somewhat shorter than the nasal horns of the African species. (Photo by D. Prothero).

Figure 15.8. The Javan rhinoceros *(Rhinoceros sondaicus)* is slightly smaller than its Indian cousin, with a smaller horn. It is one of the rarest of all endangered mammals, with fewer than 50 left in the wild. (Photo courtesy Alain Compost)

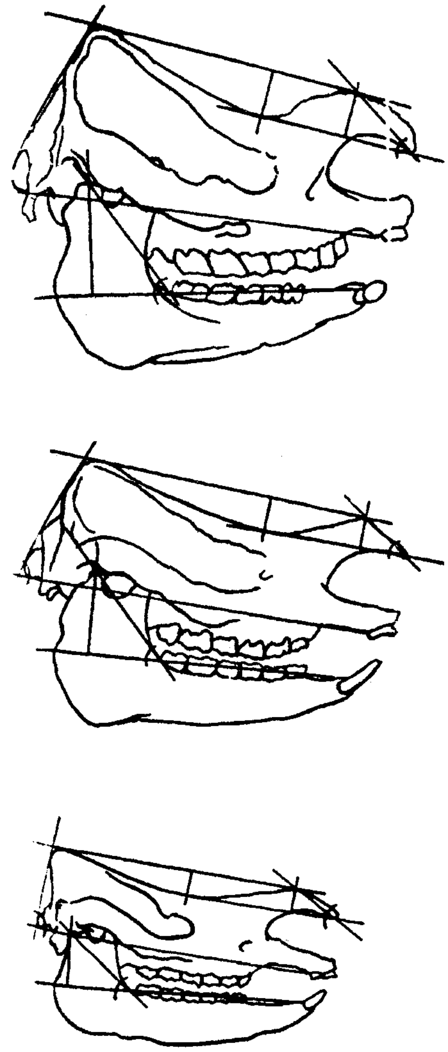


Figure 15.9. The genus *Rhinoceros* is descended from *Gaindatherium,* known from the Miocene of Pakistan (bottom skull). The Javan rhino *(Rhinoceros sondaicus,* middle skull) is a slightly more specialized version of *Gaindatherium,* and the Indian rhino *(Rhinoceros unicornis,* top skull) has the most extreme skull proportions. (From Colbert 1942).

tive skin folds that give them an “armored” appearance. This led many cultures to value rhino hide for making shields, although it is actually as soft and supple as any other large animal hide. The armor myth gave them their German name, *Panzernashorn*, and inspired the Ogden Nash rhyme:

> I shoot the bold rhinoceros with bullets made of platinum,
> Because if I use leaden ones, his hide is sure to flatten ‘em.

The *Rhinoceros* lineage has been distinct since at least the middle Miocene, about 16 million years ago. In 1934 Edwin Colbert described *Gaindatherium* from the middle Miocene of the Siwalik Hills in Pakistan (Fig. 15.9). Since that time *Gaindatherium* has been found in slightly older deposits in Portugal as well. Colbert showed that *Gaindatherium* already shows some of the characteristic features of *Rhinoceros*, including the arched nasal bones for the support of the horn, and the back of the skull is inclined forward. Fossils of these rhinos are rare in the late Miocene compared to dicerorhinines and relict aceratheriines and teleoceratines. By the Pliocene, they are represented by *Rhinoceros sivalensis* (also from the Siwaliks of Pakistan). Ironically, this animal is already more specialized than *Rhinoceros sondaicus*, the Javan rhino, which is built like a survivor from the late Miocene, but whose fossils are known only back into the early part of the Pleistocene. Several other species of *Rhinoceros* are also known from the Pleistocene of southeast Asia, including *Rhinoceros sinensis* from

Figure 15.10. Like many other ungulates, Indian rhinos lift their upper lip to expose the vomeronasal organ in a behavior called *Flehmen.* This allows them to pick up faint scents of pheromones in the air. (Photo courtesy A. Laurie).

Figure 15.11. The Indian rhino cow protects her calf by hiding in the 25-foot-tall elephant grass during the daytime. (Photo courtesy A. Laurie).

China, and a number of places in Indonesia, Burma, and India. Since the middle Pleistocene, *Rhinoceros unicornis* has inhabited the Ganges floodplain of India and the Himalayan foothills until recent poaching has restricted it to a few tiny refuges.

Unlike the browsing and grazing African rhinos, the Indian rhino is specialized for neither mode of feeding. Although it is mainly a grazer, it also has a flexible upper lip for grasping branches and bunches of grass. Andrew Laurie found 183 species of plants in its diet, but grasses accounted for 70-90%, depending on seasonal availability. The Indian rhino prefers swampy floodplains where it spends much of its time swimming and wallowing. Unlike the African species, the Indian rhino has a more leisurely daily routine, since water and shade are much more abundant in the forested floodplains of northern India and Nepal. From midday until late afternoon they remain almost completely submerged in their wallows; often in large, sleepy social groups. As evening approaches they move to their feeding areas and selectively pick out the youngest, greenest grasses in areas of recent grazing or burning, or along the edges of the river. Toward midnight they rest, with the adults sleeping wherever they feed, but females with young moving to the cover of the ten-foot tall elephant grass. In the morning, they continue to graze in more covered areas to keep cool, until it is time for their midday bath.

Indian rhinos do not show the marked territorial behavior of African rhinos. There is no urine-spraying or aggressive patrolling of boundaries. They do produce a huge communal dung-heap, which they use as a register; by defecating and leaving their scent they update the "directory" of which rhinos are in the area. Instead of rigid territories, they divide their range into "public" and "private" areas connected by paths. "Public" areas include wallows and bathing areas, which they share freely. Each rhino defends his or her own "private" area of about 5000 square yards of grazing territory for its own use, along with a private sleeping place in the elephant grass. When one Indian rhino intrudes on another's private grazing area, there can be conflict, although it is usually resolved by ritualized behavior, such as curling the lip to show their lower tusks, or advancing with head held low, snorting and honking. Sometimes they stand horn to horn and stare each other down, or exhibit close-up tusk displays. If these don't work in making one back down, then a charge can ensue. These fights can be severe, since their sharp lower tusks can slash through hide easily. Sometimes the victor will pursue the vanquished for kilometers, honking and bleating as it goes.

Urine-spraying is used, however, during courtship. Once a female reaches sexual maturity at about 3 years of age she can come into heat for a 24-hour period every five to eight weeks. In addition to spraying urine (whose pheromones advertise her breeding condition), she also makes a strange whistling sound with every breath. When the male catches the scent, he curls his upper lip in the *flehmen* gesture also seen in horses (Fig. 15.10). This exposes his vomeronasal organ and allows him to pick up pheromonal scents more easily. Once the male locates a female in heat he may follow her around for several days, attempting to approach her. For quite a while the female ignores him, or repels his advances, and sometimes this can lead to severe fights. Often they will get into horn-to-horn pushing matches lasting for hours until both are tired. If the female turns and runs the male pursues, making a "squeak-panting" noise while the female honks and bleats. Eventually they exchange love-bites with their tusks, and the male rests his head on the female's back. After several attempts at mounting, the male will copulate for up to an hour. The male may accompany the female for a few more days, probably to prevent any other male from mating with her.

Pregnant females are particularly wary and aggressive, and frequently hide out in the protection of the elephant grass. Like the white rhino, gestation lasts about 16 months, and the calf weighs about 65 pounds (30 kg) at birth. Since it consumes about 6.5 gallons (25 liters) of milk a day, it grows rapidly and gains about 5-7 pounds (2.2-3 kg) a day. It has all the skin folds of an adult Indian rhino when it is born. Mothers are very protective of their calves, since they are vulnerable to tigers (Fig. 15.11). Once an Indian rhino reaches subadult size it has no natural predators. By two or three months the calves begin to eat grasses to supplement their suckling, and by 18 months they are weaned. Calves stay with their mothers for about three years until the cow becomes pregnant again. About a week before the mother gives birth she drives off her subadult young to fend for themselves.

In contrast to the well-studied Indian rhino, the ecology of the Javan rhino is virtually unknown. This is largely because of their scarcity (only about 50-60 individuals are left), and to the fact that they inhabit the dense jungles of Udjung Kulon National Park on the western tip of Java. In the mid-1700s, they were so common in Burma, Thailand, Vietnam, the Malay Peninsula, Java, and Sumatra that they frequently damaged crops. Since that time, their numbers have been so reduced by poaching that they are the most endangered of all large mammals.

Their decline was so rapid that once the Javan rhino was known to science, few were available even for museum collections, and none has been held in captivity in a long time. In addition to the smaller horn, Javan rhinos can be distinguished from Indian rhinos in several ways. Their skin lacks the knobbly surface that gives the Indian rhino its "riveted" appearance. Javan rhinos have much more complex skin folds in the neck, and their shoulder folds join in the midline of the back, giving them a segmented look like an armadillo. In most other features they are so similar to Indian rhinos that zoologists did not distinguish them until 1822. Their skulls look like a more primitive or immature Indian rhino, so most people cannot tell them apart. For years the American Museum of Natural History in New York had sent out expeditions to collect a Javan rhino, spending millions without success. Ironically, when Edwin Colbert was studying fossil *Rhinoceros* from China in 1942, he found a specimen of *Rhinoceros sondaicus* that had been purchased from the hunting trophies of Prince Maximilian zu Wied almost a century before. It had been mislabeled as an Indian rhino by less observant curators. No one realized that all those expedition dollars were being spent in vain until a paleontologist began poking around the museum's dusty attic!

Like the Sumatran rhino, the Javan rhino prefers dense tropical jungles where it feeds on a variety of leaves and shrubs. It is restricted to the swampy lowlands, and apparently does not migrate to the higher regions of the Malay Archipelago like the Sumatran rhino. Javan rhinos are known to lean on a small tree and then "walk it down" to reach the leaves at the top; they are also known to eat bamboo, and stand in the ocean to eat mangroves. They create a series of green tunnels in the jungle with their preferred paths to food and water. Some of these are marked with urine spraying, and rarely they use a communal dung pile, although they are not territorial and do not use many kinds of scent marking. Their tracks were so well marked that many other animals and humans used them, and they eventually became the sites of roads; it is said that the roads of Java were originally surveyed and laid out by rhinoceros. Nineteenth-century explorers learned to follow a rhino track whenever they needed water.

Even less is known of their reproductive biology. They are said to have reproductive ages and gestations similar to Indian rhinos, although very little data support this. The rut is said to occur sporadically and non-seasonally, and bulls are said to produce "frightful roaring and aggressive behavior." The cow remains with the calf for about two years. Since they are not territorial they are rarely aggressive, but flee at the first opportunity. In the dense jungle they are so secretive that they are usually gone before a tracker has spotted them. Occasionally they can be surprised if a human comes at them downwind. Under these circumstances, they were known to charge humans and trample or bite or toss them in self-defense. However, today they are so scarce and gun-shy from intensive poaching that they rarely allow humans to see them. This is particularly sad, since they are a true relict of the Miocene that could give us much insight into what modern grazing rhinos evolved from.

HORNS OF DOOM

A rhinoceros horn is a wondrous thing (Fig. 15.12). Some can be 5 or 6 feet (1.5-2 m) long and weigh up to 12 pounds (5.4 kg). Unlike artiodactyl horns (which are made of bone), rhino horn is composed of compacted hair-like fibers made of keratin, the same protein in your own hair, fingernails, and skin. Like your fingernail, rhino horns grow continuously and are worn off during daily activities. They

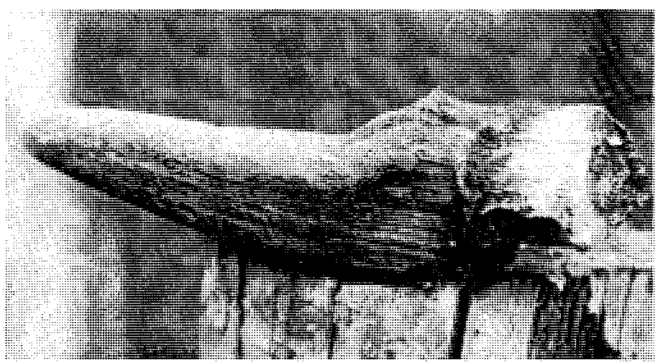


Figure 15.12. Rhino "horn" is not made of bone like bovid horns, but out of thousands of tightly compacted hairlike fibers. (Photo courtesy E. Bradley-Martin).

can also break off and grow back. Their size and shape is affected by the age of the animal, and daily wear and tear. As we have seen, they are used in defense and social interactions with other rhinos, although the rhino's body size protects it from most predation.

Sadly, the size and shape of the horn has given them value in folk medicines and cultural traditions that have no basis in science. Because of their phallic shape, some cultures have thought they had aphrodisiac properties. Others connected them with power and masculinity, and have used rhino horn for all sorts of objects, especially weapons. In the Far East, rhino horn has been a major part of folk medicine, primarily for reducing fever. Pound for pound, rhino horn is far more valuable than gold. In some places, prices have reached $27,000 a pound ($60,000 a kilo). Its value is so great that it has generated its own "Medellin cartel" of smugglers who shoot to kill, and operate as viciously as any drug lord. Indeed, it is far more valuable than heroin, cocaine, or any other illicit substance.

If that were not incentive enough, rhinos have the misfortune of inhabiting the poverty-stricken Third World where preserving wildlife has always been less important that feeding starving victims of the population explosion. Since rhinos require a lot of territory they do not do well in small reserves, and cannot be fenced in easily. Many African cultures view them as short-tempered, dangerous beasts who destroy their crops, and feel no remorse about killing them. Considering the fact that an African can make a year's salary from a single rhino horn, there are few taboos to prevent poaching. The rhino's biggest handicap is its total lack of fear. Until well-armed humans came along there was no predator that could threaten an adult rhino. However, evolution does not operate quickly enough to change fifty million years' worth of instinct overnight. Poaching has made most surviving rhinos extremely wary, but it is hard for a large, noisy, conspicuous animal with well-marked trails and dung heaps to hide from poachers for long.

The consequences have been truly catastrophic. In the 1700s, there were hundreds of thousands of rhinos, freely roaming most of Subsaharan Africa and much of southeast Asia. Sport hunting and poaching began to take their toll in the nineteenth century, but the last thirty years have been a true holocaust. Since about 1970 the skyrocketing price of rhino horn and the easy availability of automatic weapons imported for use in Africa's civil wars have resulted in rhino genocide. ***In the past thirty years over 85% of the world's rhinos have been exterminated***, leaving only about 16,000 left in the wild. Although 16,000 rhinos may seem sufficient, it is minuscule compared to their former numbers. It is even more alarming because those survivors are concentrated in only a few well-protected places, and most countries which once had rhinos in abundance now have none.

On a species-by-species basis, the statistics are even more alarming. We have already seen how the Javan rhinoceros population is reduced to 50-60 individuals in the Udjung Kulon reserve on the western tip of Java. Although they are very secretive and living in a protected area, they are still subject to poaching. This fragile population concentrated in a single reserve is very vulnerable to disease, or a local catastrophe such as a typhoon or volcano. Indeed, the 1883 eruption of Krakatoa (just offshore) virtually wiped out the area, and it became a national park because humans were afraid to move back into the devastation. Luckily, the jungle and wildlife (including Javan rhinos) were not so reluctant.

Some have suggested removing 30 animals from this population to start a captive breeding program. Unfortunately, so little is known about their biology that we cannot guarantee that captive breeding will succeed, or that capturing such a large part of the existing population won't cause the rest of the population to crash. In addition to the Udjung Kulon population, a small population of possibly 5-8 individuals was recently discovered near the Dong Nai River in Vietnam. It is amazing that these animals survived the devastation of the Vietnam war, but they may be survivors precisely because the war so greatly reduced farming and clearcutting of the jungle. Sadly, their limited population is very hard to study, and chasing them through the Vietnamese jungle with its live booby traps is dangerous.

The situation for the Sumatran rhino is only marginally better. Once found all over southeast Asia, they are now gone from India, China, Bangladesh, Cambodia, Vietnam, Laos, and nearly wiped out in Burma and Thailand. Most of the remaining 250 animals are dispersed over the Malay Peninsula, Sumatra, and Borneo. They are too scattered in remote areas to build up a protected population in a national park. However, a breeding program in Malaysia is just now taking effect. About 10% of the population are lost each year to poaching, even though they have minuscule horns. The greatest threat, however, is the rapidly escalating deforestation of the Malay Archipelago that is destroying their remaining habitat.

The Indian rhino has slightly better chances since its numbers are fairly stable in well protected reserves. At one time there were thousands of them along the Himalayan foothills from Pakistan to Burma. In the mid-1970s, its population was down to about 750 individuals. Since that time, however, aggressive protection (especially in the Royal Chitwan National Park in Nepal) has made a difference. As of 2002 there were about 600 in Nepal (mostly in Chitwan) and about 1800 in India (mostly in Kaziranga National Park), or about 2400 in the wild. There is also a zoo population of 140 individuals in 43 institutions, where there has been some success in breeding. However, poaching is still a serious threat. Indian rhino horn is typically valued at $20,000-$54,000 a kilo, more than twice the going rate for African horn. Apparently East Asian medicine considers Indian rhino horn to be more potent. A kilo of Indian rhino horn is also harder to obtain since they have smaller horns than African species. Consequently, the poaching pressure is tremendous—58 were killed in the northeastern Indian state of Assam in 1989. In recent years poachers have been resort-

Figure 15.13. In the Arabian Peninsula, rhino horn is prized for use in the handles of daggers called jambias. Here a Yemeni craftsman is filing a piece of rhino horn into a dagger handle. (Photo courtesy E. Bradley-Martin).

ing to a particularly gruesome method: electrocution.

At one time, African rhinos were abundant all over Subsaharan Africa except in the Congo jungle. The southern white rhino (*Ceratotherium simum simum*) was the first to suffer from hunters. In the 1830s they were so abundant in southern Africa that they were at the limit of their food supply, and a single day's march typically encountered between 100-500. Over the next forty years the slaughter (mostly by white hunters) was intense, and by 1900 there were only about 50-100 in South Africa; at one point, they were thought to be extinct. Then southern Africa began to take conservation seriously, and the southern white rhino population has recovered somewhat. As of 2002 there were 10,400 individuals in the wild, mostly in South Africa, Namibia, and Zimbabwe (all countries where the British colonial conservation ethic has dominated for years). However in struggling countries such as Botswana, Kenya, Swaziland, and Zambia, the population is critical. As of 2001 the southern white rhino is extinct in Angola and Mozambique.

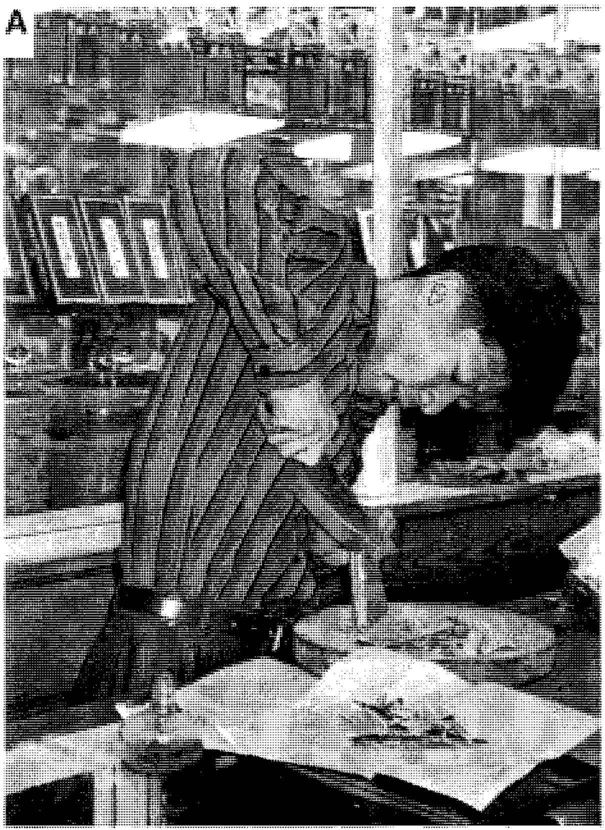
The northern subspecies of the white rhino (*Ceratotherium simum cottoni*) is even more endangered. They were once found in a belt north of the Congo Basin including Chad, the Central African Republic, Sudan, Uganda, and Zaire. Most of these were wiped out during bursts of poaching in the 1950s and 1960s, so only about 400 were left by 1970. During the 1980s when civil war spread over the region, virtually all of these were destroyed. Only 30 individuals are left in Garamba National Park in northern Zaire. Thanks to the heroic efforts of Kes Hillman-Smith, their population is slowly increasing, although it requires a massive effort patrolling a park over 5000 square kilometers in area (about the size of Delaware). Fortunately, where the white rhino is protected, it is such a docile grazer that foot patrols can stand guard over them 24 hours a day.

The saddest tale, however, is that of the black rhino. Before European exploration there were at least a million of them in Africa, inhabiting every country south of the Sahara. Due to their ecological versatility, they were found in more habitats than any other rhino. However, they were slaughtered for over a century, and by 1960 there were only about 65,000. They were still common enough, however, that they were regularly seen in the wild. Then because of civil unrest in Africa, they went through the most alarming decline of all. Uganda, for example, was once teeming with wildlife. The depredations of Idi Amin, and the chaos that accompanied his ouster by the Tanzanians, led to anarchy, and thousands of heavily armed poachers slaughtered all wildlife indiscriminately. Today Uganda has no rhinos. Kenya's rhino population dropped 98% between 1970 and 1985. The poaching was similarly intense in most other African countries, especially in the 1980s, so that while there were less than 15,000 in 1980, today there are less than 3100. More than half of these are in Zimbabwe, which has strong protection systems; the remaining populations are found mostly in Namibia, South Africa, Kenya, and Tanzania, where the European tradition of game parks is strong. However, black rhinos have been completely exterminated from Angola, Botswana, the Central African Republic, Chad, Ethiopia, Malawi, Mozambique, Rwanda, Somalia, Sudan, Swaziland, and Uganda.

What can be done to stop this slaughter before it is too late? The alarming acceleration of poaching during the 1970s and 1980s produced more than 100 metric tonnes of rhino horn, which is equivalent to at least 40,000 dead rhinos. In 1979 Esmond Bradley-Martin began to study the rhino horn trade in order to determine how to stop it. Contrary to common belief, he found that most countries (except India) did not use rhino horn as an aphrodisiac. Instead the two biggest markets were Yemen (a tiny country on the southwestern tip of the Arabian Peninsula), where they were carved into dagger handles (Fig. 15.13), and the Far East, where traditional medicine relied on their alleged powers to reduce fever and for other therapeutic applications (Fig. 15.14). In addition, rhino hide, nails, penises, dried blood, and even urine were thought to have medicinal power. Many cultures used rhino-horn cups to detect poison. There may have been some validity to this practice, since the keratin in rhino horn would react to strong alkaloid poisons.

The first crisis (and success) was in Yemen. Traditionally rich Arab nobles showed their wealth with a *jambia*, a huge curved dagger with a rhino-horn handle. When Yemenis became rich during the oil boom in the Persian Gulf, the demand for rhino horn increased. By the early 1970s they were importing three tons (equivalent to about 1000 dead rhinos) a year, more than 40% of the total market. A 1982 ban on rhino horn only increased the price

A



B

Figure 15.14. A. A pharmacist cuts a piece of rhino skin in a traditional Chinese medicine shop in Southeast Asia. The customer was buying it to treat a skin problem. B. Packages of rhino products sold in Chinese drugstores, mostly for fever reduction. (Photos courtesy WWF/ E. Bradley-Martin).

since bribery of corrupt customs officials resulted. Fortunately, the collapse in oil prices may have saved many rhinos, since most Yemenis could no longer afford rhino horn. In 1987 Yemen took steps to stop the flow of horns, and imports are now down to about 330 pounds (130 kg) per year. Water buffalo horn, camel nails, and plastic have been urged as a substitute, with great success. Similar pressure shut down the huge horn pipelines to Dubai, in the United Arab Emirates on the Persian Gulf. The tiny central African country of Burundi, which has no rhino or elephant of its own, was once the main shipping point for smugglers for horn and tusks; it is also virtually closed down now.

In 1987 the Convention on the International Trade in Endangered Species (CITES) banned all trade in rhino horn. International pressure began to take effect in Asian countries for the first time. By 1988 four major markets—Japan, Hong Kong, Malaysia, and Macao—were virtually eliminated by strong domestic enforcement policies. These successes, however, have been tempered by continuing difficulties in four other countries: China, South Korea, Taiwan, and Thailand. Because of the strong belief in rhino horn in Chinese medicine, it has been very difficult to close the market. Rhino horn is too expensive for most Chinese in the People's Republic now, but the Chinese government earned a record $700 million from exports of medicines in 1987. Although China joined CITES in 1981, it has not been very interested in controlling its trade. One of the sad consequences of this market fever is that priceless intricately carved rhino horn art objects from the Ming and Ch'ing dynasties are now being ground down into powder for medicine.

South Korea has been a difficult problem. Over 80% of its apothecary shops carry rhino horn products, even though the South Korean government outlawed them in 1983, and banned imports in 1986. The government has made no move to register their stock, so unregulated internal and black-market trading continues. They also refuse to join CITES, despite pleas from Britain's Prince Philip. Taiwan banned imports in 1988, but this raised the price to $54,000 a kilo for Asian rhino horn. Taiwanese self-made millionaires are notorious for their conspicuous consumption of endangered wildlife. The lack of enforcement made the ban meaningless, but there has been a recent movement to register their stocks.

The worst offender has been Thailand. Traditionally a country where any substance—drugs, guns, illegal wildlife products—can be obtained legally and illegally, Thailand is second only to China in the trade of rhino horn. Although a member of CITES, it has never passed the necessary legislation or funded its officers to enforce the laws. Consequently, Thailand is the main shipping point for most smugglers today. Bureaucratic inertia and a long tradition of graft and corruption make it unlikely that Thailand will cooperate in the near future.

Clearly, there have been some successes. There is also some hope of getting substitutes, such as saiga antelope horn, to replace rhino horn in Chinese medicine. But with demand from over a fifth of the world's population increasing, it is not realistic to think that the entire market can be shut down completely. So most recent efforts have been focused on eliminating the supply. We have seen how the situation is already hopeless in most African countries. In some cases they have resorted to desperate measures. Namibia, for example, has tried dehorning rhinos to see if poachers would leave them alone. Aside from the problems this causes for rhino socialization and defense, this measure would not work in countries with vegetation denser than that of the Kalahari Desert of Namibia. Most poachers shoot at any sound, and in thick brush they would not check to see if a rhino had been dehorned before shooting. Besides, the horn grows back, so the rhinos would have to be captured and disturbed every two years for dehorning.

The greatest successes have been in South Africa, Zimbabwe, and Namibia, where conservation enforcement and large national game reserves have been well funded for a long time. They now contain over 90% of the remaining African rhinos. These countries spend millions each year in salaries, guns, aircraft and vehicles, and in translocation efforts to move rhinos away from threatened border areas. Zimbabwe, for example, has captured hundreds of rhinos from the Zambezi River Valley where they were threatened by poachers from Zambia, and moved them into the country's interior. Rhino wars are costly not only in dollars, but also in human lives. The poachers are armed with automatic weapons and shoot to kill, so the rangers must do the same. Their efforts have been rewarded with growing populations in South Africa, so that some reserves now have a surplus of rhinos and are overgrazing their ranges.

Even with these successes, there are setbacks. As this book went to press in 2001, four rhinos were killed in Tsavo National Park in Kenya, one of the most protected parks in East Africa. After years of unrestricted poaching that reduced their black rhino population from 20,000 in 1970 to 350 in 1987, Kenya focused on concentrating the remaining rhinos in a few well protected national parks. They had succeeded in getting the population up to 420 before this recent setback had occurred. Clearly, the ban on the sale of rhino horn and some of the tightest anti-poaching measures in the world were not enough to save these rhinos.

Figure 15.15. Unless the appalling slaughter of rhinos is halted, few will be left in the wild by the next decade. Instead, future generations will find only skeletons covered by vultures, or bloated carcasses with the horns hacked off by poachers. (Photo courtesy WWF/E. Bradley-Martin)

At the International Rhino Conference in San Diego in 1991 controversy erupted between the representatives of the three successful southern African countries and the rest of the conservation community. Despite great effort and expense, most captive breeding programs have had limited success, and artificial insemination is still a long way off. The only effective use of conservation dollars is protection of wild populations. South African and Zimbabwean officials are faced with a dilemma: they have successfully increased their populations to the point of surplus, but cannot afford to continue with current conservation budgets. They argued that harvesting a few surplus rhinos and selling their horn legally would do more than anything to protect the remaining rhinos. The proceeds from a single horn would legally net $8000, and for a trophy-hunting expedition produces over $30,000. This money would go far to supplement their stretched conservation budgets.

This suggestion was met with horror by other conservationists and wildlife biologists. Although the idea sounds good in principle, they were concerned that releasing any legal horn to the market after the total ban in 1987 would make it easier for smugglers to operate. Once a rhino horn has been cut into shavings there is no way to identify where it came from. If all rhino horn trade remains illegal, then it is obvious that the horn is smuggled; poached horn could not be traded with forged documents as a legal horn. In addition, letting their guard down might discourage efforts to find horn substitutes in Asia, or to raise funds in the developed world. However, if conservationists are sincere about stopping the rhino horn trade, they must invest most of their dollars in South Africa, Zimbabwe, and Namibia to get the best results and decrease pressure for legal cropping and trade.

The future is dim for these great beasts, magnificent relicts of fifty million years of evolution. After successfully occupying every major ecological niche, from giraffe-like indricotheres to hippo-like teleoceratines, to tapir-like cadurcodonts and aceratheriines, to running hyracodonts, they are meeting their final crisis. Zoos cannot preserve enough of them to make a difference, and the Javan and Sumatran rhinos may already be doomed (Fig. 15.15). Only extraordinary efforts on behalf of the successful reserves will provide healthy, growing populations of rhinos for future generations to marvel at.

In many areas of Africa, there are more carcasses and bones of elephants and rhinos than there are living animals. This "elephant graveyard" is typical of the carnage all over Africa. (Courtesy J. Shoshani).

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