

HORNS, TUSKS, & FLIPPERS



The Evolution of Hoofed Mammals

DONALD R. PROTHERO & ROBERT M. SCHOCH

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

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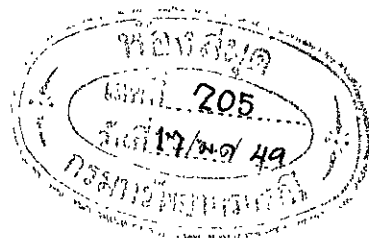
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Contents

Preface and Acknowledgments	xi
1. Introduction	1
American savanna	1
Names and dates	2
Hoofed mammals	6
Uinta beasts and the Cope-Marsh wars	9
The lost world	13
2. Cloven hooves	19
The kingdom of cloven hooves	19
Gut reactions	19
“Bunny deer”	23
Phosphate and fossils	25
Pseudopigs	26
Sui generis	27
“Nebraska man” and javelinas	35
The “river horse”	39
3. Tylopods	45
Camels without humps	45
Ships of the desert	53
“Mountain tooth”	56
4. Where the deer and the antelope play	61
Graveyard of the Amazons	61
Horns and antlers	63
“Mouse deer”	65
The “forest donkey”	66
The camelopard	67
Deer perfume	72
All-American—but not an antelope	74
Deer to us all	76
Abbé David and his deer	84
5. Hollow horns	87
A world of bovids	87
Bovines	90
Aurochs and wisent	92
Where the buffalo roam	94
Cattle call	97
Diving bucks	99
“Bright eyes”	100
Mountain monarchs	107

6. A whale's tale	115
Dr. Koch's "sea serpent"	115
Walking whales?	117
Andrews' giant "bear"	118
The pedigree of Leviathan	120
Life of a Leviathan	121
"So long, and thanks for all the fish"	124
Moby Dick, Flipper, and their kin	127
Filter-feeding monsters	133
Save the whales!	135
7. Out of Africa	141
The tethytheres	141
Mermaids	143
The "feeble folk"	149
8. The origin of Jumbo	157
Giants in the earth	157
Early tuskers	159
The "Great Missourium"	163
Shovel-tuskers and gomphotheres	166
Elephant grinders	169
Woolly wanderers	170
The mystery of the missing mammoths	176
9. Kingdom of ivory	179
Behold the behemoth	179
Behemoth biology	182
The sisterhood	185
God and slave	190
Blood and ivory	191
10. A horse of a different color (and shape)	197
The origin of perissodactyls	197
The "hyrax beast"	198
Cuvier's "ancient beast"	203
Halfway horses	204
Browsing anchitheres	205
Grazing horses	207
The hipparion controversy	209
11. <i>Equus</i>	213
One-toed horses	213
Stripes do not a zebra make	216
Wild asses	221
Wild and domesticated horses	223
12. Thunder beasts	229
The legend of the Thunder Beasts	229
Bone rush	230
Osborn, Asia, and orthogenesis	233
The biology of brontotheres	235

13. Proboscises and claws	241
Dragons' teeth	241
Hall of the mountain cow	242
Chalicotheres don't obey Cuvier's Law	247
Just what are chalicotheres?	250
Moropomorphs	252
14. Rhinoceroses without horns	255
"Ancient Dacians" and Siberian mummies	255
American rhinos	256
The amphibious amynodonts	257
Running rhinos and rhino giants	258
True rhinoceroses	262
Miocene invasions	264
Rhinoceros Pompeii	268
Hairy rhinos and giant "unicorns"	271
15. Thundering to extinction	277
Unicorn, monoceros, and rhinoceros	277
Black and white	280
One-horned rhinos	284
Horns of doom	287
Epilogue	293
References	297
Index	309

Preface and Acknowledgments

During the period 1983-1985 Schoch set about organizing a gathering of scientists that specialize in the evolution of perissodactyls (horses, rhinos, tapirs and their close living and extinct relatives). This culminated in a workshop on the evolution of perissodactyls (organized by Schoch and Jens Lorenz Franzen of the Forschungsinstitut Senckenberg, Germany) which was held as part of the Fourth International Theriological Congress in Edmonton, Canada, in August 1985. Both of us played major roles in this workshop, and we found that so many new discoveries and ideas were presented at the workshop that it would be a shame to have no permanent record of its proceedings. Consequently, we invited the contributors to the workshop, plus other selected scientists who were not able to attend the meeting, to write updated articles on their work. These technical articles were then collected in a volume entitled *The Evolution of Perissodactyls* (edited by D. R. Prothero and R. M. Schoch, Oxford University Press, New York, 1989, 537 pages).

After *The Evolution of Perissodactyls* was published we felt that the new ideas expressed in it should be made more readily accessible to a general audience. The evolution of horses in particular, as well as the evolution of other types of perissodactyls (such as brontotheres, see chapter 12 of this book) and their close relatives, the elephants, continue to provide classic examples of evolution in both textbooks and popular books on evolution and prehistoric life. Yet much of what is put forth in these popular books is badly outdated, or simply wrong. We find this appalling, yet it is understandable in that many authors of popular books are not scientific experts in all of the fields they address. Out of enthusiasm for our subject—we want scientifically up-to-date ideas about hoofed mammal evolution disseminated to the public—we decided to write this book. Initially we focused on the perissodactyls, but as the work progressed, the need for a book on all hoofed mammals and their close relatives (including whales and dolphins) became apparent. Eventually the book expanded to the present document. Such a book is timely, not only because of all the updated information, but also because most living hoofed mammals are now threatened by extinction. We find these animals to be intrinsically fascinating, and we hope that the reader will too. If more people come to appreciate these wonders of nature, perhaps their doom can be averted.

Although no one is an expert on all the hoofed mammals, we have taken on this project because we have learned from the best. We thank Earl Manning for his many insights about ungulates, especially rhinos, Rich Cifelli for his ideas on ungulate relationships, Jens Franzen for his work on the Perissodactyl Workshop, Spencer Lucas and Margery Coombs for their enthusiasm for large mammals, Bruce MacFadden for his untiring work on horses, and Christine Janis and Elisabeth Vrba for their insights on ruminants. We thank our graduate advisers, Malcolm McKenna and John Ostrom, for their guidance and inspiration over the years. The entire book was reviewed by the late Herb Brauer, Colin Groves, Teresa LeVelle, and the late Bob Savage. Individual chapters were reviewed by Larry Barnes, Rich Cifelli, Margery Coombs, Daryl Domning, Ewan Fordyce, William Franklin, John Harris, Christine Janis, Spencer Lucas, Tab Rasmussen, Hezy Shoshani, Lisa Spoon, Pascal Tassy, and Elisabeth Vrba. We are grateful to them all, and take complete responsibility, of course, for any errors of fact or interpretation.

This book would never have been completed without the patience and understanding of our families, Teresa LeVelle and Erik Prothero, and Cynthia, Nicholas, and Edward Schoch. Much of Prothero's portions of the book were written during a sabbatical in 1991, supported by grant EAR91-17819 from the National Science Foundation. The entire book was prepared by Prothero as camera-ready copy on a Macintosh PowerMac G4 computer, using Microsoft Word 8.0 and QuarkXpress 4.1 to lay out the book for the printer. We thank Edward Tenner of Princeton University Press for originally suggesting this book, and Trevor Lipscombe of the Johns Hopkins University Press for handling the final editorial details.

1. Introduction

AMERICAN SAVANNA

If you took a time machine back to Nebraska or Kansas or South Dakota seven million years ago, at first you might not notice a remarkable difference. Everywhere you looked, there would be grass as far as the eye could see. However, there would be numerous stands of trees, much denser than you'd find in the Great Plains of North America today. As you gazed around, the landscape would begin to remind you not of the modern Plains, but the African savanna, so familiar from countless nature documentaries (Fig. 1.1). Dense stands of trees, and areas of deep underbrush punctuate the mostly grassy landscape.

Looking again, the similarity to the modern African savanna would be further reinforced by the cast of characters that lived on the landscape. Tall giraffe-like animals stretched their necks to reach leaves in the high tree canopy. Elephant-like beasts push aside the undergrowth to strip leaves away from the greenest branches. Large herds of striped horses resembling zebras and hundreds of antelope-like animals move slowly along, grazing the tender green shoots in the open grasslands. Pig-like beasts scuttle out of the dense brush, and occasionally you catch a glimpse of impala-like creatures which live in the dense undergrowth as well. In the nearby waterhole, huge barrel-chested animals wallow in the deep end, much like living hippos. Lurking nearby are the predators and scavengers, including packs of wild dogs, cat-like beasts with saber teeth, and even skulking hyaena-like animals with bone-crushing teeth, waiting to move in on a carcass once the predators have finished.

But a closer look at these animals (especially if you could study their skeletons and teeth) would reveal that this similarity to animals of the modern African savanna is only superficial. Every one of the beasts we've just noticed is in reality unrelated to its modern counterpart in Africa. Take, for example, the hippo-like beasts wallowing in the water hole. They may have the barrel chest and short legs of a hippo, and live in the same habitat, but on the tip of their nose is a small horn—they are the hippo-like rhinoceros known as *Teleoceras*, not actual hippos. Further inspection would show that they have the three-toed feet of rhinos, not the four-toed feet of hippos, and details of their skull, teeth, skeleton, muscles, and other soft tissues would further confirm that their similarities to hippos are strictly convergence:

an unrelated group of animals evolves into a similar body form to occupy a specific niche. True hippos never came to North America, so a group of rhinos developed the same body form and ecological habitats to exploit this important niche of a semi-aquatic grazer. Indeed, if you were to watch *Teleoceras* feed, you would see even more similarities. Like hippos, *Teleoceras* did not eat water plants, but strolled around on the grassy meadows near their water holes (probably at night) eating grasses.

Today, African rhinos are strictly land-dwelling, large-bodied creatures who feed on either grasses (the white rhino) or green shoots and leaves in the bushes (the black rhino). North America also had a more normally proportioned rhinoceros known as *Aphelops*, which lived side-by-side with the hippo-like *Teleoceras*. Like the living black rhino, it probably spent most of its time browsing leaves in the undergrowth.

What about the giraffe-like beast browsing leaves from the tops of the trees? A closer inspection would show that the head lacks the two knob-like horns, and is all wrong for a giraffe. Instead, it has the distinctive face, eyes, and nostrils of a camel. Unlike any camel in the Old World, however, it lacks a hump (but so do the living South American camels, the llama, alpaca, guanaco, and vicuña), and it has an incredibly long neck (reaching over 22 feet, or 7 m, above the ground) and legs (some over 6 feet, or 2 m, in length). Once again, the niche for a long-necked treetop browser in North America had no occupant (since giraffes never reached this continent), so a native group (the camels) evolved a form to occupy it.

As you gaze at the herds of animals on the plains, you find more examples of this trend. The delicate, gazelle-like creatures with extremely long, thin legs can run as fast as any living antelope, but they're not antelopes. Not only do they lack horns that almost all antelopes have—but once again, you realize that you're looking at another kind of camel. In fact, looking around, you would find over a dozen different species of camels, some adapted for giraffe-like or gazelle-like existences, but others of the size and proportions of the South American camels. And none had humps.

The rest of the herd is also composed of mimics. Those horned beasts that resemble African antelopes? They're actually related to the American pronghorn, which is mis-

takenly called “antelope” but is unrelated to the true antelopes of Africa and Eurasia. In North America seven million years ago, there were over a dozen species of pronghorns in over eight genera, all with distinctively different horns (see Fig. 4.12).

And those zebra-like beasts are indeed related to zebras and other horses—but most of them are far more primitive than the living zebra. Most are much smaller, with simpler teeth, and they almost all have three toes on their feet. In some places, there are as many as a dozen different species of horses living side-by-side. Some hide in the underbrush, using their robust side toes on marshy ground; their simple, low-crowned teeth are only suited for soft leafy vegetation. Others are clearly plains dwellers, with greatly reduced side toes, longer more slender limbs, and ever-growing cheek teeth that allow them to eat gritty grasses without wearing their teeth down to the gums and starving to death.

What about the elephant-like animal breaking off branches from the trees? It does have a trunk and simple tusks, but it is smaller than any living elephant, with a long jaw and flat forehead—and it has four straight tusks, not the two long curved upper tusks of a living elephant. Instead, it’s a primitive mastodont, from which the living elephants and mammoths would one day evolve. Like the three-toed horses and zebras, this animal is indeed related to its living counterpart, but it is a much more primitive relative than the beast that lives in Africa today. Here we have a partial substitution of a remote ancestor in the role of its descendant, rather than the complete replacement of rhinos for hippos, camels for giraffes and antelopes, and pronghorns for antelopes that we saw earlier.

And the impala-like beast hiding in the bushes near the water? In Africa, we’d expect a true antelope like the impala or bushbuck, but in ancient North America that role is occupied by *Synthetoceras*, a member of an extinct group known as the protoceratids. Instead of paired spiral horns on their heads like impala, *Synthetoceras* has a slingshot-like horn on its nose, and a pair of unbranched horns curving upward and inward from above its ears. *Synthetoceras* has no living descendants, but is distantly related to the camels. Nearby is another extinct beast, *Cranioceras*, with short straight horns pointing straight up above its eyes, and a thick blunt horn curving up and forward from the back of its head. This animal also has no close living relatives, since it is a member of the extinct family, the dromomerycids, which are only distantly related to deer.

Scuttling in and out of the underbrush are pig-like beasts that might remind you of African hogs like the warthog or forest hog. But they are not true pigs at all, but peccaries, which live today in Central and South America, and even in the southwestern deserts of the United States. Peccaries resemble pigs in many superficial ways, but they are an entirely different family, restricted to North America, while true pigs and hippos were restricted to the Old World. But these extinct peccaries are much larger than the living javelinas of Mexico. They had longer snouts and flatter

heads, and much more prominent, dangerous-looking tusks.

This list of similarities could go on and on. The hyaena-like animals feeding on carcasses are not true hyaenas, but bone-crushing borophagine dogs. Some of the “saber-tooth cats” are not true members of the cat family, but an extinct group known as nimravids, which were related to dogs but had extremely cat-like bodies and teeth. Even the “bear” role is performed not by a bear, but by an extinct group of “beardogs,” or amphicyonids.

And this story is not restricted to the American savanna of seven million years ago. In Eurasia, there were similar savannas with ecological counterparts of the modern African savanna fauna, but with many substitutions. Indeed, this is a typical occurrence in the evolution of life: ecological niches are often occupied by unrelated groups of animals when the opportunity arrives, and the modern group was not present to occupy the niche. Throughout this book, this will be a common theme. Hoofed mammals have dominated the large bodied herbivorous niches on this planet for the past 65 million years, but many different, unrelated groups of hoofed mammals have evolved on many different continents. Frequently they develop body forms that converge on living animals when the same niche is available. And more often, they develop body forms which have no modern analog, making it very hard for the paleontologist to describe their lifestyle and ecology in terms of anything we’re familiar with in the living world.

NAMES AND DATES

Paleontologists work in a world with a time frame completely different from ordinary human life. From various methods, we now know that Earth is about 4.5 billion years old. That’s 4,500 million years, a number that is staggering in human terms. It is such an immense amount of time that some sort of analogy is necessary to make it comprehensible. Suppose we were to compress all 4.5 billion years of Earth history into a single calendar year. On this scale, each of the 365 “calendar days” equals twelve million years, and each minute of the “calendar” is 8561 years long! The formation of Earth would then take place on New Year’s Day in this “calendar.” The first recognizable life would not appear until February 21, and it would consist of tiny, single-celled blue-green bacteria. Complex, multicellular life, such as jellyfish, trilobites, and corals do not appear until November 12. The first amphibians crawled out on land on November 28. The first tiny mammals, and the first bird *Archaeopteryx*, appear during the peak of the age of dinosaurs, on December 17. The final extinction of the dinosaurs and the beginning of the age of mammals occur on the day after Christmas. The first ape-like primates that are members of our own family, the hominids, do not appear until eight hours before New Year’s Eve. Neanderthal man, the classic Stone Age “cave man,” appears ten minutes before New Year’s Eve, as the countdown begins in parties everywhere. Recorded history began less than one minute before New Year’s Eve, as the conductor raises his baton to

Ma	ERA	PERIOD	EPOCH	NALMA
2	CENOZOIC	Quat.	Pleistocene	IRV./RLB
5		Neogene	Pliocene	BLANCAN
24			Miocene	HEMPHILLIAN
				CLARENDONIAN
				BARSTOVIAN
				HEMINGFORDIAN
34		Oligocene	ARIKAREEAN	
			WHITNEYAN	
			ORELLAN	
		Eocene	CHADRONIAN	
			DUCHESNEAN	
			UINTAN	
			BRIDGERIAN	
			WASATCHIAN	
			CLARKFORKIAN	
		55	Paleocene	TIFFANIAN
				TORREJONIAN
				PUERCAN
	66			

Figure 1.2. Cenozoic time scale. "Quat." = Quaternary; "IRV./RLB" = Irvingtonian/Rancholabrean land mammal ages; "Ma" = million years before present; "NALMA" = North American land mammal ages.

start *Auld Lang Syne*. Within a second before midnight, Charles Darwin's *On the Origin of Species* was published, and the American Civil War was fought. Virtually all of human history, especially the last few millennia, is drowned out by the drunks who blew their noisemakers a fraction of a second too early!

On the scale of geologic time, human affairs appear pretty insignificant. The geologist is accustomed to dealing with such large amounts of time, and routinely deals with thousands and millions of years. For most geologic problems, events of less than thousands of years in duration cannot even be distinguished in the layers of sedimentary rocks. When dealing with events that occurred hundreds of millions or billions of years ago, even a million years here or there is negligible. A sense of "deep time" (as John McPhee labeled it) is very important to all of us, and not just to the geologists. Most geologists, however, find it practical to

deal with time not in absolute millions of years, but in relative time terms. Just as historians use "Elizabethan" or "Edwardian" to refer to periods in English history, so geologists use "Cambrian" and "Cretaceous" to refer to distinct episodes in Earth history.

For the purposes of this book, most of these time terms will not be necessary. The evolution of rhinos, horses, elephants and their relatives has taken place in the last 65 million years, known as the Cenozoic Era (Fig. 1.2). The Cenozoic is divided into a number of epochs, which began with the Paleocene approximately 65 million years ago and run to the present. The Paleocene, which lasted from 65 to 54 million years ago, is followed by the Eocene (54-34 million years ago), the Oligocene (34-24 million years ago), the Miocene (24-5 million years ago), the Pliocene (5-1.8 million years ago), and the Pleistocene or Ice Ages (1.8 million years ago to 10,000 years ago). The period since the last

retreat of the glaciers and present interglacial warming is called the Holocene, or Recent (10,000 years ago to present). Although these terms may seem intimidating at first, they are much easier to use than trying to estimate the age of an event in millions of years.

Paleontologists and biologists must also use different names for the animals, as well as for their ages. Most living mammals today have common names which are widely understood, so that we know a white rhino from a black rhino from an Indian rhino. Yet in many parts of the English-speaking world, the same common name can have different meanings. In most of the United States, for example, a "gopher" is a digging rodent. In the southeastern states, a "gopher" can be a tortoise. Many animals have different common names in different parts of the country. In countries which do not speak English, the animals have names in the local language. To get around this problem, biologists have long ago adopted a series of scientific names which is universal, regardless of region or native language. In 1758 when the system was first widely adopted, Latin was the universal language of scholars, so all scientific names are Latin in form, or Latinized words from Greek or some other language. A scientist will always understand *Geomys* to mean the rodent gopher, and *Gopherus* to mean the gopher tortoise. By convention, each species name is a compound of two words, always found together. These names are always italicized in print or underlined elsewhere. The first word is the genus name (plural: genera), which is always capitalized. The second word is the trivial name for the species, which is never capitalized. For example, the correct scientific name of our species is *Homo* (genus) *sapiens* (species), which means "thinking man." Another related species in our genus is *Homo erectus* ("erect man"), our probable ancestor. Similarly, the Indian and Javan rhinoceros are in the same genus (*Rhinoceros*), but in different species. The Indian rhino is *Rhinoceros unicornis*, and the Javan rhino is *Rhinoceros sondaicus*. The black rhino is in a different genus *Diceros*, which has only one living species, *Diceros bicornis*.

An example of the hierarchical classification of humans and Indian rhinos is shown below:

For most fossil mammals discussed in this book there are no popular names. The fossils are known only by their scientific names, and are always italicized in this book. At first, these long scientific names may seem hard to pronounce and remember. If you break them down syllable by syllable, however, they are not so intimidating.

Generic and specific (species) names are not the only names used to identify and classify an organism. Every genus belongs to a larger subdivision of life called a family. For example, humans belong in the Family Hominidae, and true rhinos in the Family Rhinocerotidae. All zoological family names can be recognized by the "-idae" ending. All the families, in turn, can be included in orders. Thus, the Hominidae can be grouped with the other families of apes, monkeys, lemurs, and tarsiers in the Order Primates. Rhinos belong with the tapirs, horses, and various extinct groups in the Order Perissodactyla, or the odd-toed hoofed mammals. Orders are subdivisions of a larger group, the class. Both perissodactyls and primates are mammals, or members of Class Mammalia. Classes are grouped into even larger groups, the phylum. For example, mammals, birds, amphibians, reptiles, and fishes are all members of the Phylum Chordata, which includes all animals with a spinal cord. Finally, the major phyla are grouped into the great kingdoms of life: the Kingdom Animalia, the Kingdom Plantae, the Kingdom Fungi, and so on. This hierarchical arrangement of classification not only serves as a useful tool, but also indicates closeness of evolutionary relationship. Animals in the same genus are more closely related to each other than they are to animals in any other genus, and so on. The division of kingdoms into phyla, and phyla into classes, and so on, is actually a reflection of the branching tree of life.

Of the mammals living today, most can be clustered into distinct, well defined groups that even a child can recognize. In most classifications of the mammals, these groups are ranked as orders. Many of the orders are obvious to the average zoo visitor. The bats comprise one order, the rodents another, the primates a third, and so on. Most of these orders have been recognized since the formalization of modern classification in 1758. Yet until recently, little was known about how these orders were related to one another, or from

KINGDOM	Animalia	Animalia
PHYLUM	Chordata	Chordata
CLASS	Mammalia	Mammalia
ORDER	Primates	Perissodactyla
FAMILY	Hominidae	Rhinocerotidae
SUBFAMILY	Homininae	Rhinocerotinae
TRIBE	Hominini	Rhinocerotini
GENUS	<i>Homo</i>	<i>Rhinoceros</i>
SPECIES	<i>sapiens</i>	<i>unicornis</i>

what kind of mammal they evolved. For over a century paleontologists tried to trace the ancestry of the major orders of mammals back to a common ancestor, but the quality of the fossil record was not good enough to do this. Most of the mammals of the late Cretaceous and Paleocene, when most of the orders must have differentiated, are not members of living orders, nor ancestral to them. Thus, mammal classifications have treated all orders as if they were independent and unrelated, when we know that there must be some orders which are close relatives of one another.

In the last decade, however, new approaches have made major advances in deciphering mammal relationships. Scientists have begun to look at the complete anatomy of the animal, not just the teeth (the most commonly preserved part for most fossil mammals). They looked in detail at other parts of the skeleton, particularly the details of the bones and canals in the skull and ear region. They also looked at the muscles and other soft tissues of the living mammals. Finally, they began to look at the various molecules found in mammal tissues, and discovered that the similarity of molecules can also give clues to relationships. All of this emphasis on complete anatomical analysis is not completely new. In fact, most of it was first done by German anatomists in the late nineteenth century, and much recent work has begun to rediscover how careful and perceptive those early German anatomists were.

However, the method of analyzing the data has changed. The traditional methods concentrated primarily on teeth and tried to find progressively more primitive teeth in older rock units. The new methods instead concentrate on shared specializations, or evolutionary novelties, that indicate close relationship. For example, there were many evolutionary novelties that appeared when mammals evolved. Some of these include the presence of hair (instead of scales or feathers), and mammary glands to nurse their young. These features are called shared derived characters, and are among those used to define the Class Mammalia. Other shared specializations can be used to define orders within the Mammalia. For example, the bats can be defined by their complex wing structure, formed by highly modified hands and fingers. The primates can be defined by a number of features, including their grasping hands and feet with opposable thumbs, nails instead of claws, or their forward-facing eyes with binocular color vision. Within the Order Primates, still smaller groups can be defined by their own evolutionary novelties. For example, the great apes (orangutan, gorilla, chimpanzee) and humans share a number of specializations, including the loss of a tail, complex nasal sinuses, five or six vertebrae in the hip, an elongated middle finger, and over two dozen other features in the skeleton alone.

Thus, the emphasis has shifted from seeking ancestral forms with their shared primitive similarity (which does nothing to indicate relationships—animals which share primitive characteristics may or may not be closely related) to seeking out only shared derived similarity. For example, hair and mammary glands are good indicators distinguish-

ing mammals from other animals, but are of no use in determining relationships *within* mammals (since all mammals have them, they are primitive characters within the mammals). In traditional mammal classifications, some orders were based on nothing but these shared primitive similarities. For example, the old definition of the order Insectivora (which properly includes moles, shrews, and hedgehogs) was broadened to include a wide variety of primitive insect-eating mammals unrelated to moles, shrews, or hedgehogs. To expand the meaning of "insectivore," the group was defined on characters such as having five toes on hand and foot (primitive not only for mammals, but even for their reptilian ancestors) or having 42 teeth, which is also primitive for all placental mammals.

By doing this, the Insectivora became a "wastebasket" group. All primitive placental mammals that retained the ancestral insectivorous ecology were thrown into this "wastebasket," even though they were not closely related. Usually, this was done because there was no better place for these problematic animals, and people like to have their classifications tidy. Everything in its place, and every mammal in its proper order! Unfortunately, these wastebasket groups had a negative effect as well. For those not familiar with the animals, it created the impression that all the problems were solved (which they were not), and that these problematic animals were closely related to moles, shrews, and hedgehogs (which they were not). In many cases, scientists could not find a particular fossil that was the perfect ancestor for later animals, and would construct a "hypothetical ancestor" based on a wastebasket assemblage of animals. In doing this, they would ignore the fact that each of the members of the wastebasket group had its own anatomical specializations that prevented it from being the actual ancestor. In short, the use of these "wastebasket" groups created concepts in people's minds of animals that never really existed.

Insectivores were not the only group to be made into a wastebasket. One of the worst wastebaskets was the archaic animals related to the hoofed mammals, or ungulates. Today, the living ungulates (Fig. 1.3) can be divided into at least six major groups of mammals, including the even-toed artiodactyls (pigs, camels, sheep, deer, antelope, cattle), the odd-toed perissodactyls (horses, rhinos, tapirs), the elephants, and three other groups (hyraxes, whales, and sea cows) we will discuss later. However, there are a number of extinct animals which have hooves and all the other hallmarks of ungulates. These could not be assigned to any of the living orders, mostly because their bodies were built on a very archaic plan. They shared no specializations with any living order, and so they were placed in the ultimate "wastebasket" group, the order "Condylarthra." The only thing that "condylarths" had in common was that they were archaic hoofed mammals that didn't belong somewhere else.

As in the case of other wastebasket groups, the "Condylarthra" made the classification appear neat and tidy, but it obscured all the problems and areas needing work.

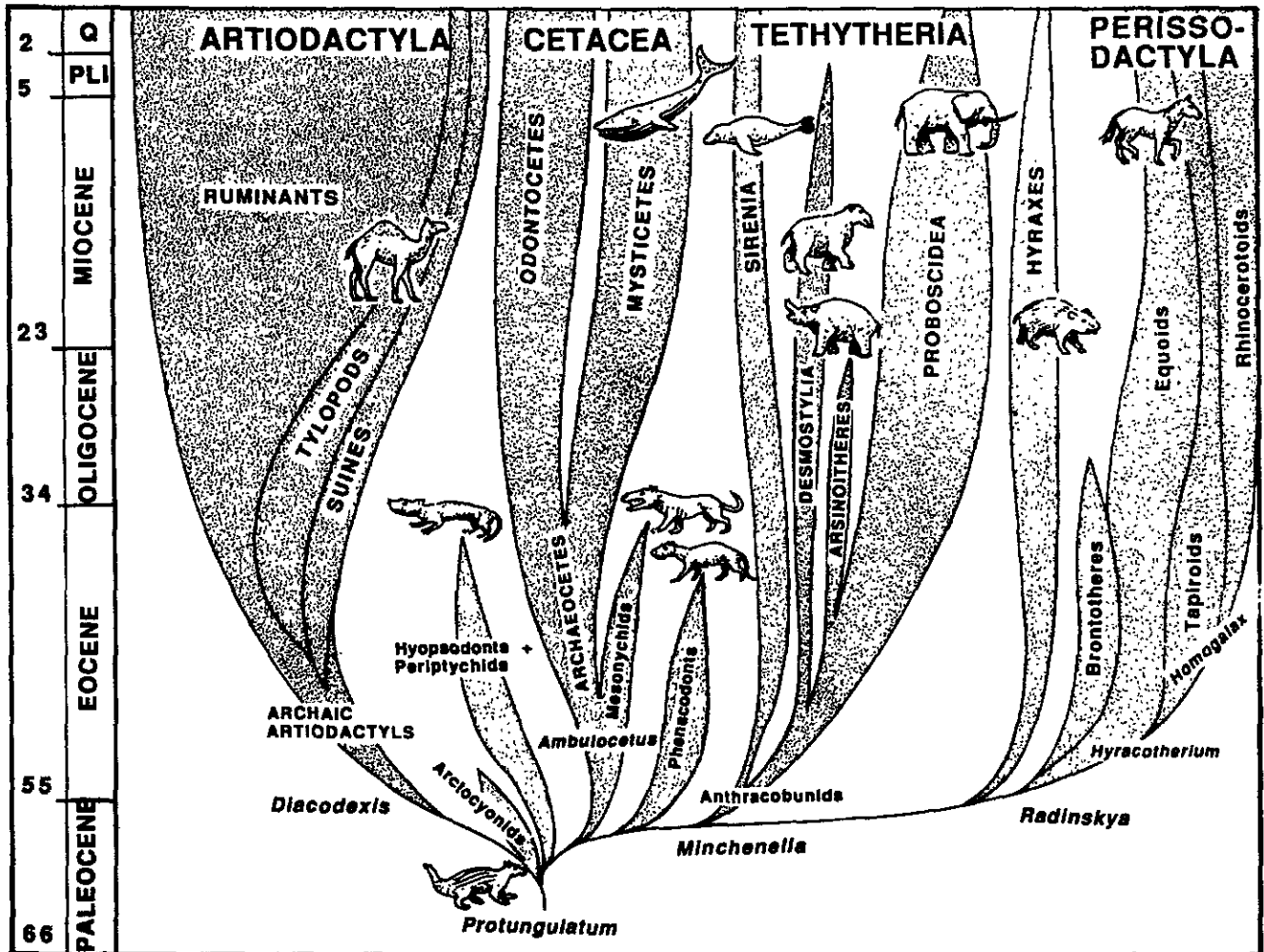


Figure 1.3. Relationships of the living and extinct ungulates. PLI = Pliocene; Q = Quaternary. (Drawn by C.R. Prothero, based on Prothero, Manning, and Fischer, 1988).

Scientists would suggest that one or more of the living ungulate orders evolved from a “condylarth ancestor,” a hypothetical creature with no basis in reality. Others would generalize about the ecology, or behavior, or extinction of “condylarths,” when in fact each of the “condylarth” groups had completely different ecologies and probably different behavioral patterns as well. Even worse, it misled anyone who did not know the fossils and got the mistaken impression that “Condylarthra” was as real a group as the order of bats or of whales. These people would make comparisons between “condylarths” and real groups, and the features they analyzed in the “condylarths” would not be true of most of its members. The “Order Condylarthra” obstructed the understanding of mammalian relationships for over a century, and finally it is being abandoned.

Indeed, once the living and extinct ungulate groups were analyzed, using only shared specializations to cluster groups together, it became apparent that the ungulates have a very rich, interesting history. This story, however, remained unknown for over a century because of the

“condylarth” veil. In this book, we will present the new ideas about hoofed mammals.

HOOFED MAMMALS

The hoofed mammals, or ungulates, are the largest, most anatomically diverse, and ecologically dominant group of mammals alive today. One need only to look at the huge variety of elephants, rhinos, hippos, antelopes, wildebeest, zebras, giraffes, and buffalo on the African savannah to realize that all of the large plant-eating mammals are ungulates. Ungulates make up about a third of the genera and families of living mammals, outnumbering even the abundant and diverse rodents. Since many ungulates feed on large quantities of low-quality vegetation, they can get big. Indeed, the largest mammals (both on land or sea) that ever lived, or are alive today, are all ungulates.

Even when housecat-sized ungulates first appeared at the end of the reign of the dinosaurs, they were larger than most of their rat-sized contemporaries among the mammals. The earliest ungulates are a group of extremely primitive

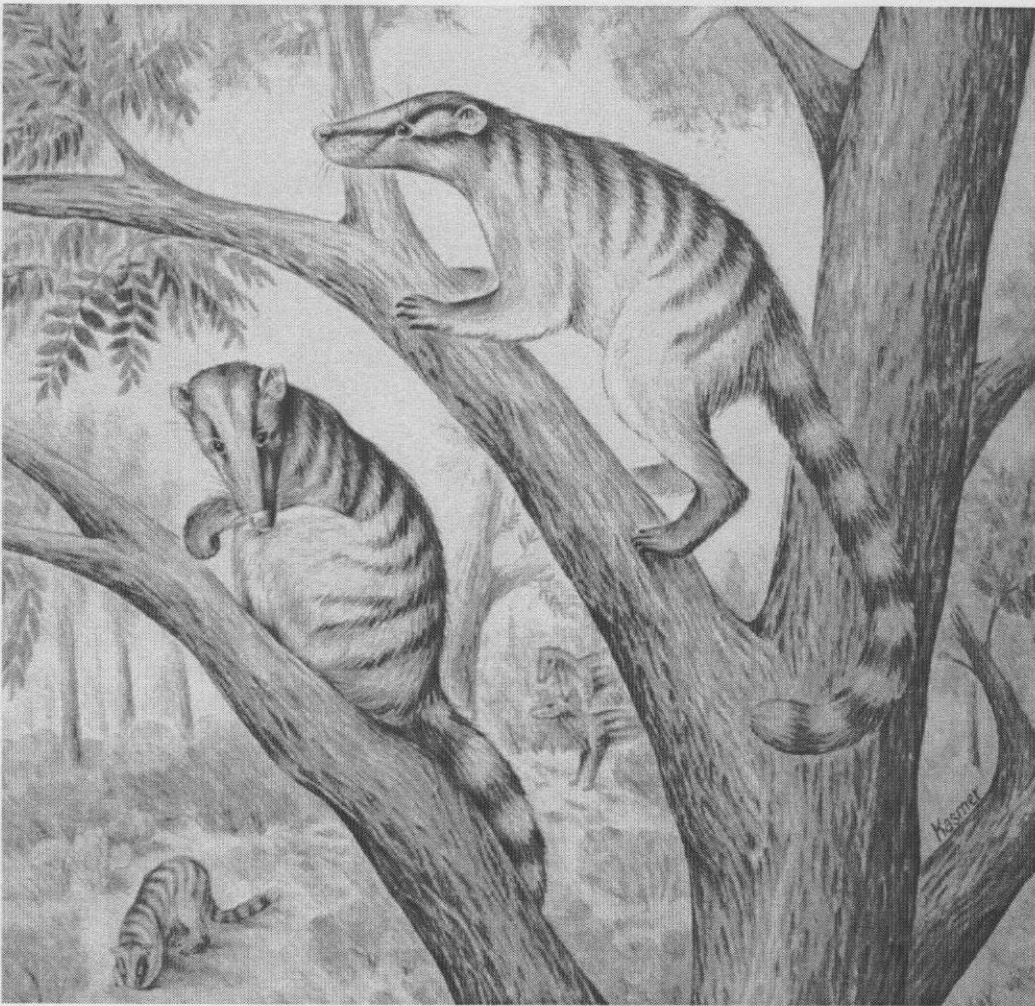


Figure 1.4. Restoration of the archaic ungulate *Chriacus*, an arctocyonid, emphasizing its superficial resemblance to the living coatimundis or raccoons. (Drawn by E. Kasmer, courtesy K. Rose).

forms known as the zhelestids, recently described by David Archibald and the late Lev Nesson from Late Cretaceous rocks almost 90 million years old from Uzbekistan, central Asia. Although these animals are known only from a few jaws, they already show that the hallmarks of ungulate teeth were well established at an extremely ancient time—about as far back as any of the recognized orders of placental mammals is known to have lived. Clearly, the ungulate branch of the Mammalia is one that goes back to the very beginning of the radiation of the placental mammals, some 30 million years earlier than they were once thought to have originated.

By the latest Cretaceous and earliest Paleocene, the zhelestids were replaced by the arctocyonids. The most complete skeletons known of these archaic ungulates (once called “condylarths”) from the Paleocene reveal an animal that had a body much like a raccoon or coatimundi (Fig. 1.4). The skeleton was not specialized for running, like most living ungulates. Instead, it is a very generalized mammal body, with flexible limbs and long fingers, suitable for both climbing and walking. The tail is also quite long, probably

for balance. The head had a long snout, much like a raccoon. In most cases, the teeth were unspecialized, suitable for an omnivorous diet.

However, there are a few features that tell us this animal is not related to raccoons. First, the relatively unspecialized teeth have a few advanced ungulate features compared to the other primitive mammals of the time. The cusps of the teeth are more bulbous than those of its insectivorous contemporaries, with low relief between cusps. These teeth were suited for a more grinding type of chewing, appropriate to an omnivorous diet of plants, seeds, and tubers, with some meat, eggs, fish or carrion. By contrast, most early mammals were insectivorous, with sharp, slicing crests on their teeth and very high relief between cusps. This kind of tooth pattern is suitable for chopping up the tough skins of insects, and shredding small prey animals.

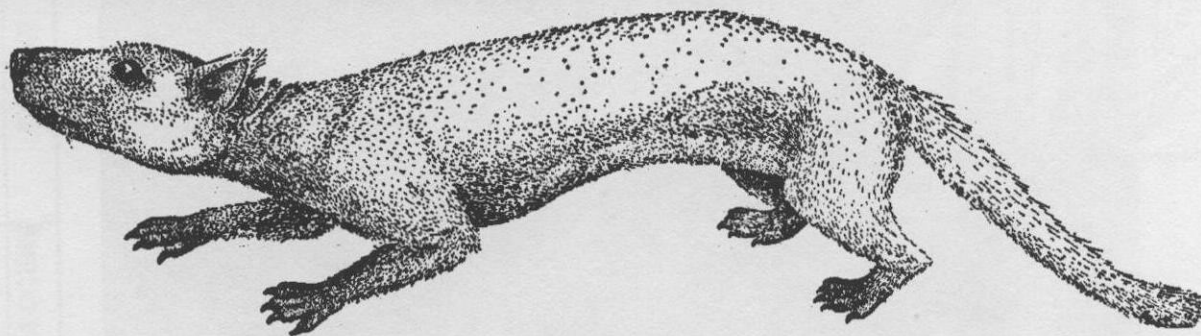
In addition to the teeth, there are several specializations of the skull openings for the arteries in the head, and in the bones that make up the ear region, which show that these arctocyonids are indeed ungulates. Finally, the ankle bones in even the most archaic ungulates are already adapted for

A



Figure 1.5. A. Restoration of the Paleocene peripitychid *Ectoconus* (painting by R. Bruce Horsfall, from Scott, 1913). B. Reconstruction of dachshund-like Eocene archaic ungulate *Hyopsodus* (After Gazin, 1968).

B



walking and bearing greater weight. Although the ankle is flexible, it is not as adapted for tree climbing as the ankle of primates or primitive carnivores.

Hooves, the feature most characteristic of ungulates, have not yet appeared. The most primitive ungulates still had claws, although they were relatively short and blunt. When hooves finally develop, they do so independently in several different groups. This can be seen by looking at the details of the anatomy of the hoof. It is constructed very differently in horses than in deer, for example. There must be a great evolutionary advantage to developing hooves in large animals which are adapted for running (as most living ungulates are). Clearly, hooves are valuable protection for running across hard ground without cutting the foot and bleeding profusely (as can happen to cats or dogs when they run, and certainly to humans!).

Recent research suggests that the first group to branch off from these earliest ungulates were the artiodactyls, or the even-toed hoofed mammals (Fig. 1.3). Today, the artiodactyls are the most abundant ungulates, with over 190 living species. They include pigs, peccaries, hippos, camels and llamas, deer, pronghorns, giraffes, sheep, goats, and dozens of species of antelopes and cattle. We will discuss the artiodactyls in greater detail in the next four chapters.

After the artiodactyls branched off from the ungulate common ancestor, the next groups were certain archaic ungulates (once called "condylarths") such as the extinct hyopsodonts and peripitychids (Fig. 1.5). Peripitychids became big, almost bear-like forms, with few anatomical specializations except in their teeth, which have highly wrinkled enamel surfaces. Hyopsodonts, on the other hand, developed a body form much like a weasel or dachshund. Although their skulls and teeth were primitive, they had very short limbs and a long trunk and tail. Many people have speculated about how hyopsodonts lived. Some think they may have burrowed, since they have strong digging limbs with claws. Others suggest that they were slinking along in the lower vegetation. Whatever they were doing, they were very successful archaic ungulates. While most archaic ungulates were dominant in the Paleocene and declined by the Eocene, hyopsodonts were some of the most common animals in the Eocene. They were also among the last archaic ungulates to die out at the end of the Eocene, long after all the others had gone extinct. In the older books, some scientists speculated that hyopsodonts were ancestral to artiodactyls. There are no shared specializations to support this idea, however, so it is no longer believed by paleontologists.

After the divergence of artiodactyls, and of the peripity-

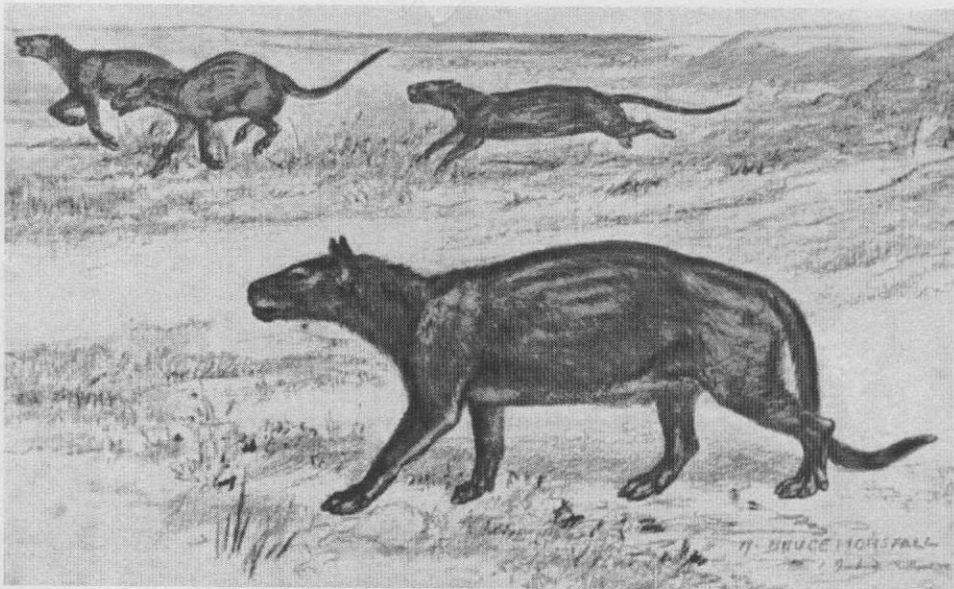


Figure 1.6. Restoration of the archaic Eocene ungulate *Phenacodus*, once thought to be related to perissodactyls (painting by R. Bruce Horsfall, from Scott, 1913).

chid-hypsodont group, the next step is a surprising one. A wide variety of evidence, both from fossils, and from anatomy and molecular biology, clearly indicates that whales are also ungulates (Fig. 1.3). “What?” you say, “whales don’t have hooves!” This is true, but remember that hooves are not the most important character that defines ungulates. When we trace whales back into the fossil record, we find progressively less specialized forms that look less like whales and more like other archaic ungulates. We will discuss the evidence for this surprising conclusion in Chapter 6.

Once the whale lineage had split off in the Paleocene, the next groups to diverge are archaic ungulates formerly lumped with the peripitychids and hypsodonts in the “condylarth” wastebasket. The best known of these are the phenacodonts (Fig. 1.6). Phenacodonts evolved into sheep-sized animals, with long faces and tails. However, their limbs are still unspecialized, along with the rest of their skull and skeleton. In the past, several scientists tried to show that phenacodonts were directly ancestral to the perissodactyls (horses, rhinos, and their relatives). However, as we shall see in Chapter 10, new discoveries suggest that phenacodonts are only distantly related to perissodactyls.

Finally, we come to the last major grouping of ungulates, the higher ungulates (the Altungulata). This includes not only the traditional perissodactyls (horses, rhinos, tapirs, and their relatives), but also the hyraxes (or conies), and the tethytheres (elephants, manatees, and their relatives), as well as a number of extinct forms. These animals are the subject of the latter half of the book.

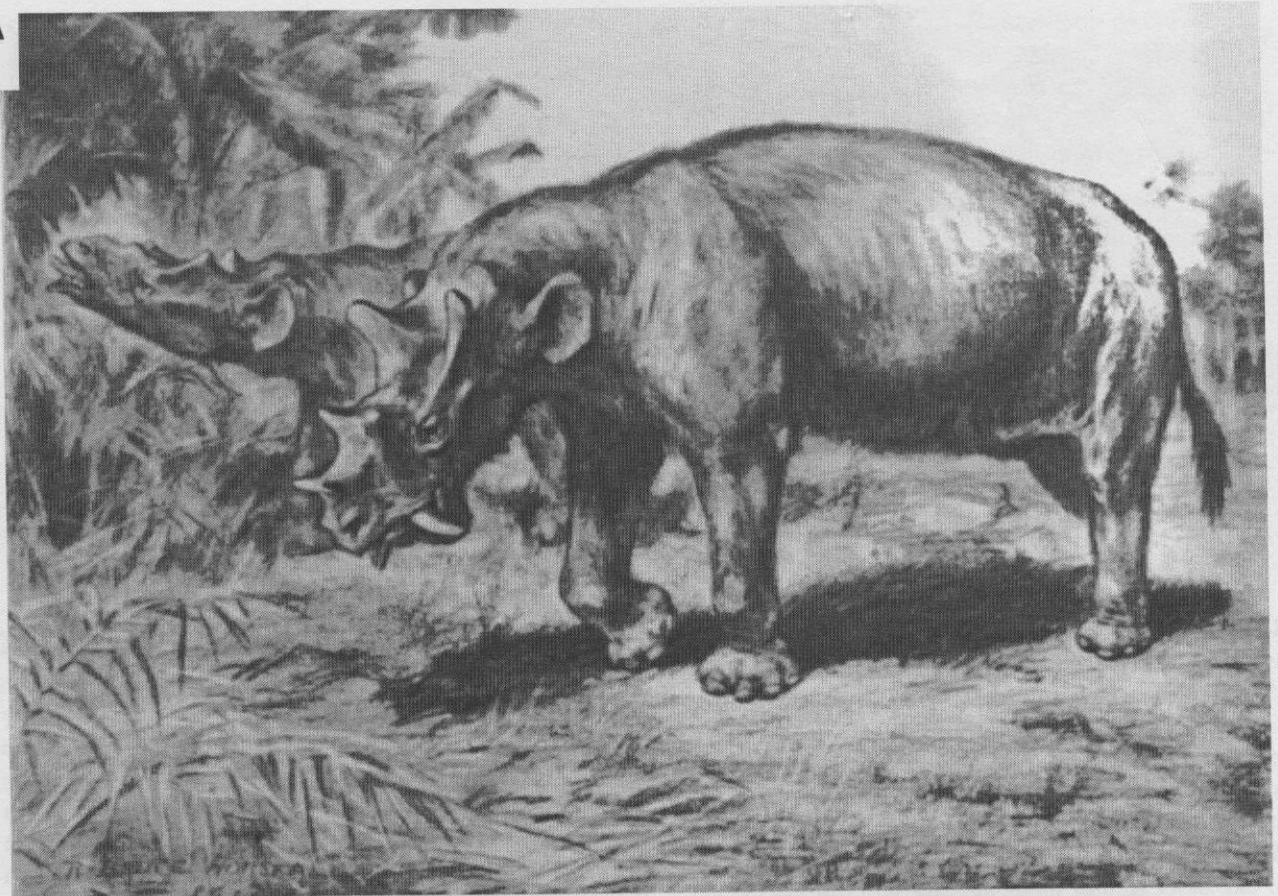
UINTA BEASTS AND THE COPE-MARSH WARS

One group often considered to be related to ungulates includes the bizarre animals known as the uintatheres (Fig. 1.7). Their name comes from the middle Eocene beds of the Uinta Basin of Utah, where they were first discovered. These animals reached elephantine size, yet they are not elephants. Their most distinctive features are the six knob-like

horns on the top of the head, and the huge protruding canine teeth protected by a flange on the lower jaw. It was a face only a mother could love! During the middle Eocene, they were the largest land mammals in both Asia and North America. By the late Eocene, they were extinct. Their role as a large, heavy-limbed herbivore was then taken over in North America by a succession of mammals: brontotheres in the late Eocene, rhinos in the Oligocene, and mastodonts in the middle Miocene. Some of the Mongolian uintatheres lack the knobs and canines; instead, *Gobiatherium* had a huge inflated bulb on its nose. What this structure was used for is anyone’s guess. Some have suggested that it was functionally similar to the bulbous nose of the saiga antelope, which uses it for warming cold air as it inhales. However, uintatheres were found mostly during the tropical climates of the Eocene, which rules out any need for warming inhaled air.

Uintatheres were large-bodied beasts that seem to have many specialized similarities to ungulates. For this reason, they have long been placed in ungulates, or in their own special order. In 1977, Earl Manning and Malcolm McKenna argued that uintatheres were ungulates related to the higher ungulate group, which includes perissodactyls and tethytheres. However, in 1982 Tong Yongsheng and Spencer Lucas proposed that uintatheres were related to a bizarre group of Chinese Paleocene mammals known as anagalids, which are distantly related to rodents and rabbits. This suggestion is rather startling, since uintatheres are rhino-sized, and anagalids are much like rabbits in size and skeleton. Most of this argument is based on uintathere teeth, which are abnormally small for the size of the beast, and have a peculiar V-shaped crest pattern seen in a lot of primitive mammals. We are not convinced that uintatheres are “giant bunnies,” but we admit that the evidence for their relationships to ungulates is also slim. Whatever uintatheres are related to, they are certainly among the most spectacular mammals in the middle Eocene of North America and Asia.

A



B

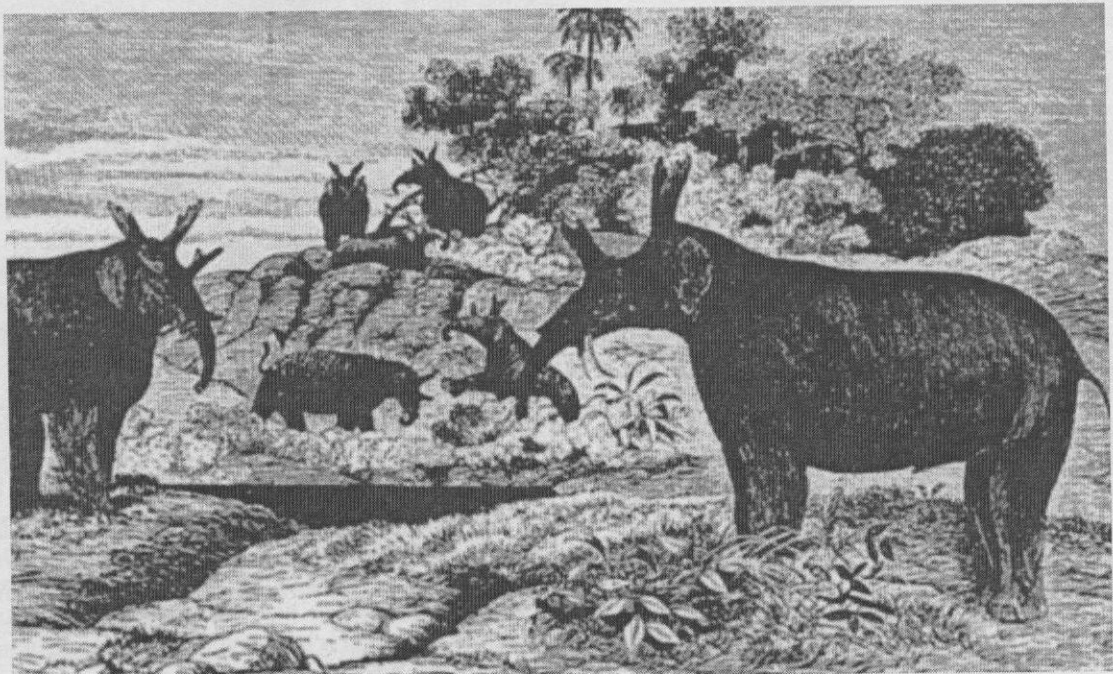


Figure 1.7. A. The rhino-sized uinatheres had six knobby horns on top of their skulls, and huge tusks. Whether or not they were truly ungulates, they were the largest land mammals during the middle Eocene in North America and Asia (painting by R. Bruce Horsfall, from Scott, 1913). B. Cope's reconstruction of uinatheres with elephant ears and trunks. (From *Penn Monthly*, August, 1873).

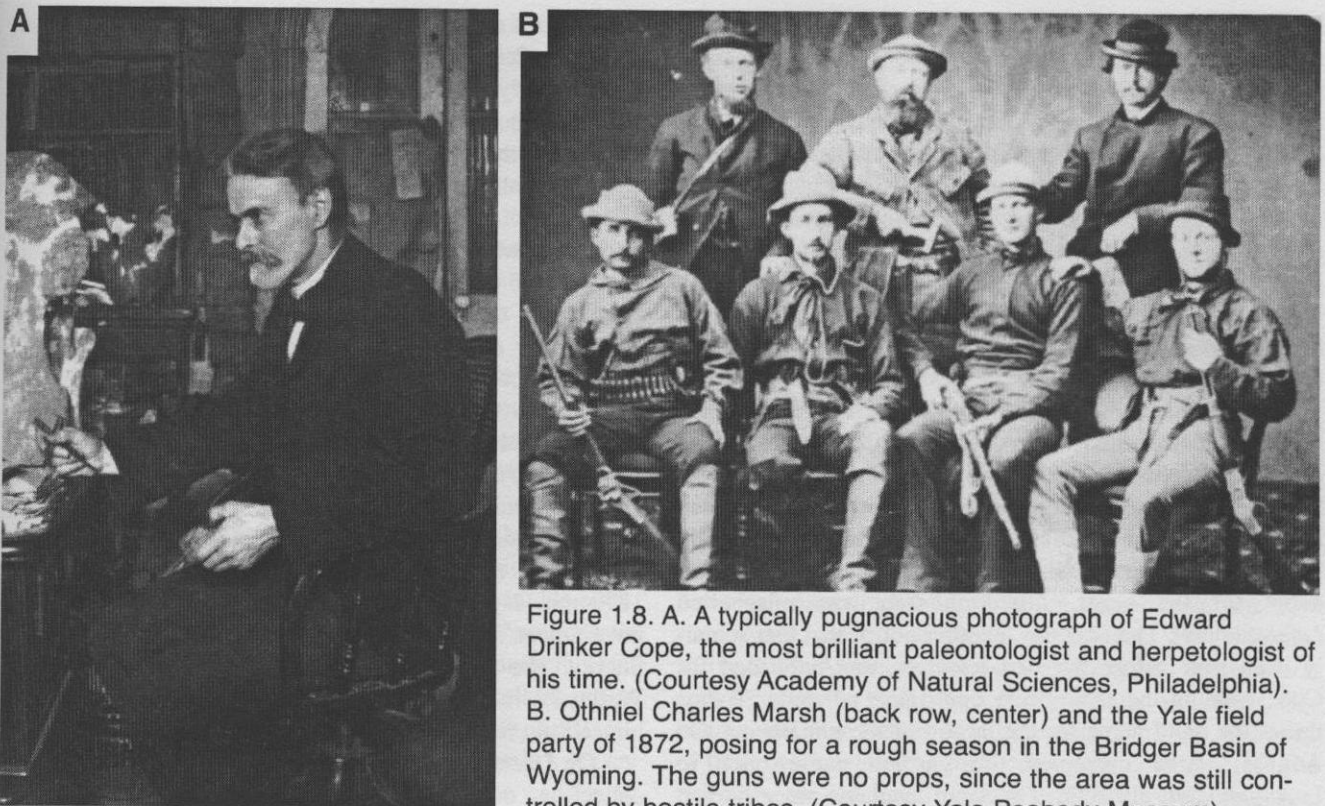


Figure 1.8. A. A typically pugnacious photograph of Edward Drinker Cope, the most brilliant paleontologist and herpetologist of his time. (Courtesy Academy of Natural Sciences, Philadelphia). B. Othniel Charles Marsh (back row, center) and the Yale field party of 1872, posing for a rough season in the Bridger Basin of Wyoming. The guns were no props, since the area was still controlled by hostile tribes. (Courtesy Yale Peabody Museum).

Uintatheres were such spectacular fossils that they became the focus of a major war between America's dominant late nineteenth-century paleontologists, Edward Drinker Cope and Othniel Charles Marsh (Fig. 1.8). Cope (1840-1897) was a brilliant, intense academic and political outsider of Pennsylvania Quaker heritage who never had a steady, respectable position until late in his life (from 1889 until his death he was a professor at the University of Pennsylvania). Often in need of money, Cope either lived off money he inherited or raised funds for his paleontological work as opportunity arose. In spite of these limitations, he had true paleontological genius, and managed to publish some 1,400 scientific papers during the course of his life. Cope married and had a single daughter. His personality was complex and often difficult. In particular, he held and expressed his opinions very adamantly and did not take orders from anyone, be it a college administrator, the council of a learned society, or an army officer or government official on a geological survey.

Although his immediate family was of a relatively humble New England background, Marsh (1831-1899) had the good fortune to be a nephew of the wealthy philanthropist George Peabody. Through his uncle's generosity (later inheritance), Marsh attended Yale University both as an undergraduate and graduate student, saw money donated to Yale for the Peabody Museum of Natural History, and from 1866 until his death was professor of paleontology at Yale. For most of his tenure he received no salary from Yale, but only an allowance from his uncle. Marsh remained a bachelor all of his life. He was alternately amicable and sociable,

or formal and aloof (more often the latter). He also had a secretive and suspicious nature, and could suffer from bouts of jealousy (such as when Cope beat him to the naming of new fossil species). Marsh was in no way as prolific as Cope; he published only 270 scientific papers in his lifetime. Unlike Cope, however, he was part of the establishment. Besides his position at Yale, Marsh often served as an officer of learned societies, such as holding the presidency of the National Academy of Sciences for a number of years.

In the late 1860s Cope and Marsh each decided separately to aspire to the position of being the foremost vertebrate paleontologist in America. Until then, this title was held by Joseph Leidy, whom we will discuss more in the next chapter. Initially on friendly terms, Cope and Marsh began to compete with each other for specimens and information as the vast fossil beds of the American West were opened up. Each wanted the best specimens for his own collection, and the recognition that came with being the first to describe and name the fantastic extinct animals that were being newly discovered by science. To these ends, both men organized and undertook personal expeditions to the West. At various times they associated themselves with various official government geological and paleontological surveys, and bought (and some say stole) fossil specimens, the rights to collect on certain lands, and the services of local collectors (the alliances of collectors often changed quickly as the rivals outbid each other).

The feud began in the summer of 1872 when Leidy, Cope, and Marsh were independently collecting fossils in the Bridger Basin and Washakie Basin of Wyoming. The

largest and most spectacular specimens they found were skulls of the bizarre uintatheres, which impressed all three scientists with their weird horns and tusks. Naturally, they rushed to describe their new finds before they left the field. Since all three men were in remote parts of the country, with limited access to civilization, they had to leave camp to send news east by way of telegraph. In those days, it was common practice to publish a short note of only a few paragraphs naming a new animal, so that one could get credit for being its discoverer and namer. Today, such slapdash methods are frowned upon, but they were common in 1872—especially when trying to beat a rival to press.

Leidy was the first to publish, when a short note he had sent east, dated August 1, 1872, described *Uintatherium robustum* (this is now the correct name for most of the specimens). On August 17 Cope sent a telegram from the Black Buttes in the Washakie Basin of Wyoming which was badly garbled when it was published two days later. His intended name for the beast, *Loxolophodon*, was misspelled *Lefalaphodon*. The next day, another notice that had actually been sent before the first telegram was published for Cope, naming the same beast *Eobasileus cornutus*. Today, this is the valid name for the largest of the uintatheres. On August 22 he corrected the garbled name back to *Loxolophodon*, although it was not available since he had already recklessly used it for another animal. Meanwhile, Marsh sent a note on August 20 naming his specimens *Dinoceras* and *Tinoceras* (they are now considered the same thing as Leidy's *Uintatherium*). All three were aware of the others nearby, and disputed their rivals' right to collect in "their" fossil field. Soon, this bitter rivalry drove Leidy into retirement from vertebrate paleontology as a field no longer fit for gentlemen.

When Cope and Marsh returned east and began to publish longer descriptions, they became convinced that they both had the same animal and that their own name for it was correct. Actually, Cope had an *Eobasileus*, and Marsh had a specimen of Leidy's *Uintatherium*, but at the time they considered the differences slight, or the result of their rivals' mistakes. In 1873, Cope compounded his errors by suggesting that uintatheres were related to elephants, even putting elephant ears and trunk on them (Fig. 1.7). Marsh disputed this, and instead placed them in their own order, the Dinocerata (a name still used today, even if his name of *Dinoceras* was invalid). Between August 1872 and June 1873 Cope and Marsh each published 16 articles on uintatheres, each ignoring his rival's names, and both ignoring Leidy's work. As a result, uintathere names reached a state of chaos, with multiple names for the same species. Marsh grew so bitter at Cope's actions that he lashed out in print: "Cope has endeavored to secure priority by sharp practice, and failed. For this kind of sharp practice in science, Prof. Cope is almost as well known as he is for the number and magnitude of his blunders ... Prof. Cope's errors will continue to invite correction, but these, like his blunders, are hydra-headed, and life is really too short to spend valuable

time in such an ungracious task, especially as in the present case Prof. Cope has not even returned thanks for the correction of nearly half a hundred errors ... he repeats his statements, as though the *Uintatherium* were a Rosinante, and the ninth commandment a windmill" (Marsh 1873).

Eventually, the uintathere wars died down as the rivals moved into conflicts over the naming of other beasts, such as the brontotheres discussed in Chapter 12. Fourteen years later, in 1884 Marsh finally published his huge scientific monograph on uintatheres, a 237-page volume entitled *Dinocerata: a monograph of an extinct order of gigantic mammals*, with giant folio pages and lavish plates. Meanwhile, Cope was losing ground politically. In the 1870s he had served under Ferdinand Hayden (see Chapter 12) on the U.S. Geological and Geographical Survey of the Territories, and from his collections made on those surveys, he had written a giant 1,009-page, 134-plate monograph for the Survey, now known as "Cope's Bible." However, in 1879 the Hayden Survey was merged with several other government surveys to form the present U.S. Geological Survey. The first directors were Clarence King and John Wesley Powell, both good friends of Marsh, and Cope found himself out in the cold.

On December 16, 1889, Cope was ordered to turn his collections over to the Smithsonian, even though he had made most of them from private expenditures, not on government surveys. Cope was so outraged that he lashed out and called a reporter, William Hosea Ballou of *The New York Herald*, and filled his ear with grievances against Marsh and his cronies King and Powell. He charged that they were "partners in incompetence, ignorance, and plagiarism," and that the Survey was a "gigantic politico-scientific monopoly next in importance to Tammany Hall." He leveled charges of every kind at Marsh, including scientific blunders, keeping the salaries of his employees, and that most of his work (especially the *Dinocerata* monograph) was actually the work of assistants. This accusation was later supported by some of Marsh's former assistants, including the famous paleontologist Samuel Wendell Williston.

Marsh defended himself by taking the train to Philadelphia and visiting the president and trustees of the University of Pennsylvania. He consoled them about "the shame that has befallen you," suggesting that "poor Cope" had cracked up and that Marsh would help locate "a more substantial scientist" to replace him. In the January 19, 1890 issue of the *Herald*, Marsh replied to Cope's accusations, charging that Cope had stolen his specimens, and that he had spied on Marsh's work when he was visiting Yale, and tried to publish it later. Ballou continued to play the feud out for several more columns, quoting and misquoting a number of paleontologists about the scientific competence and personal character of the two rivals. Eventually, this particular battle died down, leaving Cope and Marsh with egg on their faces. Cope retained his position and his fossils, as did Marsh and Powell.

Eventually, though, public scandals did hurt Marsh. When the budget of the U.S. Geological Survey came up before a House committee in 1892, fundamentalist congressman Hilary Herbert of Alabama discovered Marsh's recently published monograph, entitled *Odontornithes*, on toothed birds from the Cretaceous seas of Kansas. Waving it on the House floor, he shouted, "Birds with teeth! That's where your hard-earned money goes, folks—on some professor's silly birds with teeth." In terms similar to the recent science-bashing of William Proxmire and John Dingell, he stampeded Congress into cutting off funds from such "Godless" activities as monographs about impossibilities such as birds with teeth, and other creatures not mentioned in the Bible. Powell was finally forced to send Marsh a telegram: "Appropriations cut off. Please send your resignation at once."

By this point both Cope and Marsh were broken men, and the field soon moved on to a new generation: Osborn, Scott, Hatcher, and others discussed elsewhere in this book. Cope continued to teach at the University of Pennsylvania for five more years, visiting the Dakota badlands in 1892 and 1893, and died on a cot in his study amidst all his unfinished projects and unpublished specimens on April 12, 1897. Marsh had spent all Uncle George Peabody's legacy on his expeditions and lavish publications, so he was forced to live on a modest salary from Yale in a brownstone near the Peabody Museum. In 1896 he published his greatest work, *The Dinosaurs of North America*. Early in 1899, he caught pneumonia, and died on March 18, with less than \$100 to his name.

Although the Cope-Marsh feud generated a lot of bad blood, it catalyzed the collection of literally tens of thousands of vertebrate fossils and inspired a number of younger geologists and biologists to pursue this field. Even if done in a sometimes less than gentlemanly fashion (Cope and Marsh criticized and insulted each other in otherwise "objective" scientific papers), an amazing amount of research was accomplished during these years. Modern American vertebrate paleontology grew out of their work.

THE LOST WORLD

In his novel *The Lost World*, Sir Arthur Conan Doyle (creator of Sherlock Holmes) describes a plateau in the Amazon jungle which was a haven for dinosaurs still surviving today. Although this is science fiction, South America was a "lost world" in a very different sense. It was isolated from all the other continents during most of the Age of Dinosaurs, and during the first sixty million years of the Age of Mammals. Almost no mammals or birds from the Old World managed to penetrate this island continent during this entire time. Consequently, the few mammals and birds that originally colonized it had the entire continent to themselves for millions of years. As we saw at the beginning of this chapter, ecological niches occupied by typical Old World or North American animals on other continents had to be filled by South American substitutes. There were no cats,

dogs, or bears, so carnivorous marsupials and gigantic, flightless, predatory birds were the main flesh eaters. In some cases this led to remarkable cases of evolutionary convergence. One South American marsupial, *Thylacosmilus*, had the same saber-like canines as the saber-toothed cat, even though it was a pouched mammal like a kangaroo. Others, known as borhyaenids, did a remarkable job of mimicking the wolves, bears, and hyaenas we have today, even though they too were pouched mammals.

South America had three "old timer" groups inherited from the age of dinosaurs. The first include the marsupials, or pouched mammals, mentioned above. The second was the xenarthrans, or edentates (including the living tree sloths, armadillos, and anteaters), which eventually led to the giant ground sloths, and huge armadillo-like glyptodonts that were so characteristic of the Ice Ages. The third was hoofed mammals unique to South America, which evolved into the most amazing creatures of all. These South American experiments in evolution demonstrate just how stereotyped certain ecological niches are. For example, native South American ungulates evolved into beasts which converged on the body shape of horses, hippos, camels, elephants, and many other familiar beasts (Fig. 1.9). Yet none of these were related to their ecological counterparts—the resemblances are strictly due to evolutionary convergence, just as fish and dolphins have the same streamlined body shape even though they are unrelated in an evolutionary sense.

The origin of these South American ungulate groups is still controversial. Only a few scraps of mammals are known from the age of dinosaurs in South America, and they include no hoofed mammals. The earliest Paleocene Tiupampa fauna includes a diverse assemblage of extremely primitive ungulates. The most familiar of these is called *Peruherium*. It is difficult to say what this animal is, other than that the teeth look much like those of typical archaic ungulates from other continents. We next pick up the South American record in the late Paleocene, but by then mammal diversity had blossomed. There are a great variety of bizarre and unique forms whose relationships to mammals from the rest of the world are controversial. One group, the didolodonts, has long been placed in the "condylarth" wastebasket, but appears to be related to North American hyopsodonts. If so, then there was some sort of communication between North and South America during the Paleocene after all. Didolodonts flourished in the Eocene, but are not definitely known thereafter.

Another group which appear to be related to hyopsodonts were the litopterns. They evolved into a variety of body forms throughout the Cenozoic, with their greatest diversity during the Miocene, when South America had savannas similar to the rest of the world at that time. Some litopterns were truly amazing. The proterotheriids, for example, paralleled the trend toward limb elongation and side-toe reduction that we see in horses on other continents at the same time. *Diadaphorus*, from the early Miocene, had

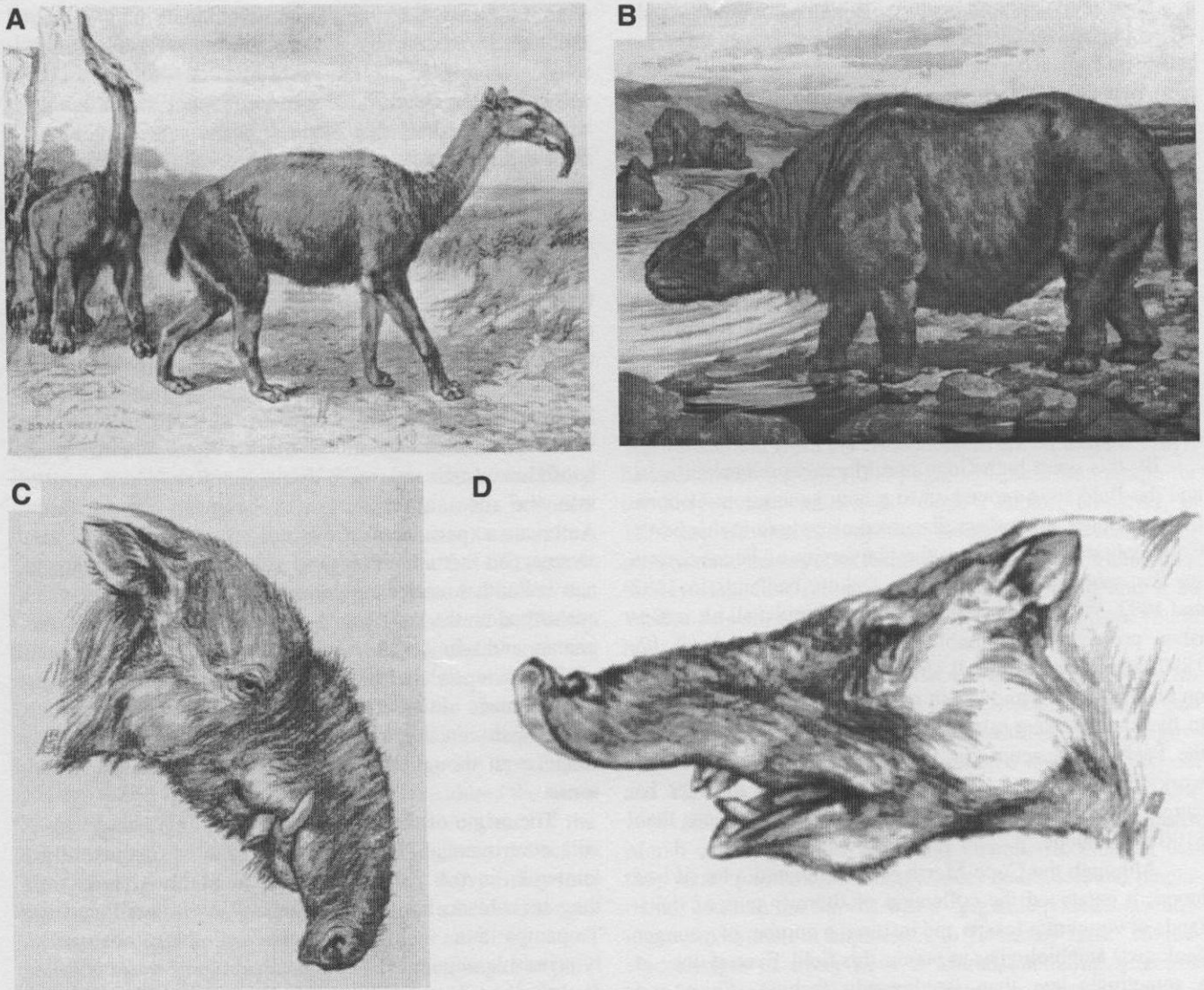


Figure 1.9. Reconstructions of typical South American ungulates. A. The camel-like litoptern *Macrauchenia*. B. The hippo-like notoungulate *Toxodon*. C. The tapir-like *Astrapotherium*. D. The mastodont-like *Pyrotherium*. (Paintings by R. Bruce Horsfall, from Scott, 1913).

a very horse-like build, but still retained three toes on each foot. *Thoatherium*, however, outdid even true horses—it had a single toe on each foot, with no vestiges of side toes like modern horses (Fig. 11.3)! As horse-like as their limbs and skeletons were, these animals were truly litopterns and not horses. Their teeth and skulls are completely unlike any mammal, horse or otherwise, from North America or the Old World.

One of the most unusual of the litopterns was a beast known as *Macrauchenia* (Fig. 1.9A). Darwin first discovered it during the voyage of the *Beagle*, and wrote of it:

“At Port St. Julian, in some red mud capping the gravel on the ninety-foot plain, I found half the skeleton of the *Macrauchenia Patachonica*, a remarkable quadruped, fully as large as a camel. It belongs to the same division of the *Pachydermata* with the rhinoceros, tapir, and

palaeotherium; but in structure of the bones of its long neck it shows a clear relation to the camel, or rather to the guanaco and llama” (Darwin 1839: 173).

Macrauchenia indeed had a camel-like neck, and primitive, heavy, rhinoceros-like feet, but its weirdest feature is the head. Unlike most advanced hoofed mammals, it still had all 44 teeth, with no gap between the front nipping teeth and the grinders, like horses and cattle have. To top it off, the nasal opening is up over the forehead, indicating that *Macrauchenia* had a long proboscis like a tapir or elephant. A “camel” with the feet of a rhino and the trunk of an elephant sounds like something out of Dr. Doolittle, but it was real and thrived during the Ice Ages in South America!

The dominant group of hoofed mammals was the notoungulates, literally “southern hoofed mammals.” They were by far the most diverse, with at least thirteen families

and well over 100 genera represented over their sixty million year history. They include peculiar beasts such as typotheres, which culminated in the beaver-like *Mesotherium* during the Pleistocene, and the hegetotheres, which converged on rabbits. The archaeohyracids, as their name implies, closely resembled the living hyraxes (which we will discuss in Chapter 7). The most diverse of notoungulates, however, were the toxodonts. Some toxodonts, like *Thomashuxleya*, looked much like warthogs; others, like *Rhynchippus*, converged on horses; still others resembled the primitive hornless rhinoceroses discussed in Chapter 14. *Homalodotherium* had robust limbs with claws on the toes, much like the chalicotheres we will discuss in Chapter 13. One of the most remarkable was *Toxodon* itself (Fig. 1.9B), which was also found by Darwin during the *Beagle* voyage:

"*Toxodon* [is] perhaps one of the strangest animals ever discovered. In size it equalled an elephant or megatherium; but the structure of the teeth, as Mr. Owen states, proves indisputably that it was intimately related to the Gnawers, the order which at the present day includes most of the smaller quadrupeds. In many details it is allied to the Pachydermata. Judging from the position of its eyes, ears, and nostrils, it was probably aquatic, like the dugong and manatee, to which it is also allied. How wonderfully are the different orders, at the present time so well separated, blended together in different points of the structure of the toxodon!" (Darwin 1839: 83).

Although Darwin was puzzled, we now know that *Toxodon* was not related to rodents, "pachyderms," manatees, or anything else outside South America; it is a native notoungulate. Its body form most closely converges on a hippopotamus, although its front teeth are chisels like those of gnawing rodents. Other toxodonts, such as *Trigodon*, had a single small horn in the center of the forehead, like one of the extinct rhinos; the sheep-sized *Adinotherium* also had a small horn on the forehead.

Despite their great diversity and abundance of excellent fossils, the affinities of notoungulates are still a mystery. In 1913 William Stein was collecting Paleocene mammals for the American Museum of Natural History in the Bighorn Basin of Wyoming. When his collections were sent to New York for study, the great paleontologist William Diller Matthew was startled to find a primitive notoungulate he named *Arctostylops*. At first, he thought there had been a mistake. Stein had recently been collecting in Patagonia—had the specimen gotten trapped in a pant cuff and then accidentally added to the Wyoming collections? Stein assured him that it was from Wyoming, and in subsequent years, more *Arctostylops* fossils have been found in the Bighorn Basin. Did the presence of a primitive notoungulate from the Paleocene of Wyoming indicate that these beasts had

escaped South America, or that they originated in North America and then spread south? The discovery of more arctostylopids from the Paleocene of China further complicated the story. Did they originate in Asia, pass through Wyoming, and then reach South America? Or was it the other way around? Philip Gingerich argues for the latter. The appearance of arctostylopids, along with edentate-like epoicotheres and the untathere-like forms (discussed below) is clear evidence to him of a migration from South America through Wyoming to China in the late Paleocene. More recently, Richard Cifelli, an expert on notoungulates, has become less convinced that arctostylopids are notoungulates. He suggests that the Wyoming arctostylopids may be immigrants from China, but he sees no concrete evidence that either is truly part of the great South American notoungulate radiation.

Besides the didolodont-litoptern-hypsodont group, and the notoungulates, there were two other important kinds of native South American hoofed mammals. One of the most puzzling are the "lightning beasts," or astrapotheres (Fig. 19.C), typical of the Miocene, and their primitive Eocene relatives, the trigonostylopids. *Astrapotherium* itself was rhino-sized, but had short feeble legs and small feet for so large an animal. It had large flaring tusks in both the upper and lower jaws, which closely mimic those seen in living hippopotamuses. The forehead was domed and full of air sinuses. Its most outlandish feature was a deep retraction of the nasal notch in the skull, indicating that it also had a tapir-like or elephantine trunk or proboscis (even more developed than the one seen in *Macrauchenia*). A weak-footed hippo with a trunk? The animals most similar to astrapotheres were the hippo-like amynodont rhinoceroses discussed in Chapter 14, which had stout aquatic bodies and well developed tusks, and heavy molar teeth. The relationships of astrapotheres and trigonostylopids are still a mystery. Their teeth bear some resemblance to those of notoungulates, but recent work by Richard Cifelli has shown that there are no true shared specializations.

The fourth odd South American ungulate group was the "fire beasts," or pyrotheres and their relatives (Fig. 1.9D). *Pyrotherium* itself comes from the late Oligocene of Patagonia and Bolivia, and is a truly amazing animal. The size of a small elephant, it had short upper and lower tusks and simple cheek teeth with cross-crests like primitive mastodonts. Like astrapotheres, its nasal bones are deeply notched to receive the muscles of a well-developed trunk. This animal is one of the best imaginable examples of convergence with mastodonts, since there is no question that it is not actually related to elephants or mastodonts. For a long time, it was said to have specializations of notoungulates, but recently this has been discounted. Although its teeth are highly specialized and stereotyped into tapir-like leaf-eating cross-crests, there is some evidence from more primitive beasts. Weird Eocene animals known as *Carolozittelia*, *Proticia* and *Columbitherium* have last molars like *Pyrotherium*, but their other teeth resemble the curious ani-

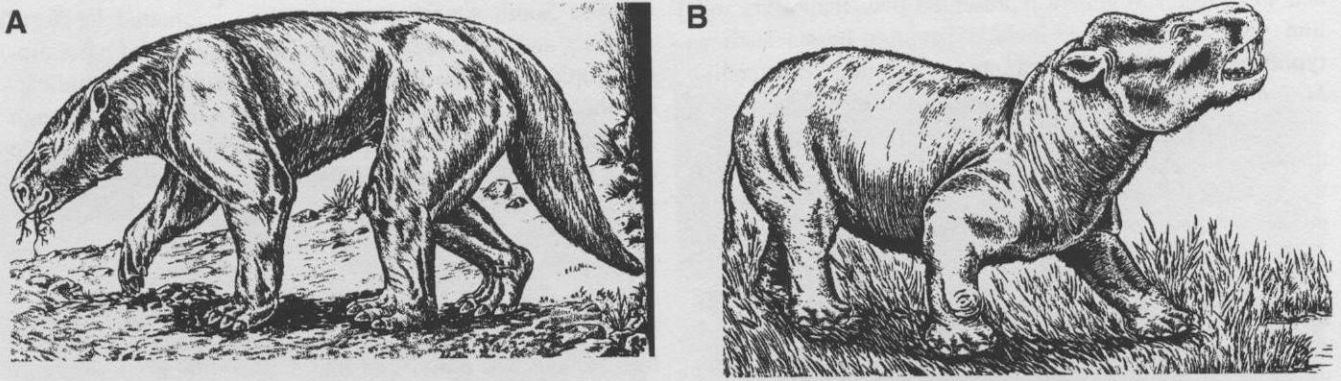


Figure 1.10. Although not related to ungulates, the pantodonts were the largest herbivores of the Paleocene and early Eocene. A. *Barylambda*, a sheep-sized beast of the late Paleocene. B. *Coryphodon*, one of the last of the pantodonts, and the largest beast of the northern continents in the early Eocene (From Fenton and Fenton, 1958).

mal called *Carodnia*, from the Paleocene of Brazil. *Carodnia* was a mystery for so long that it was placed in its own order, the Xenungulata ("strange ungulates"). However, a number of scientists have recently argued that *Carodnia* is very similar to primitive uinatheres, implying that the pyrothere-*Carodnia* group is part of the Dinocerata. If this is the case, then once again the question arises: did a uinathere-pyrothere group arise in Asia and spread to South America (passing through North America in the late Paleocene), or vice versa? As in the case of arctostylopids and epoicotheres discussed above, some would argue that all three groups originated in South America and ultimately reached China. However, if uinatheres are related to the higher ungulates (which began in Asia in the late Paleocene, as we shall see in Chapter 7), or to rabbits (as Tong and Lucas argue), then perhaps it was the other way around. Clearly, we need more fossils to test these hypotheses.

Recently, another group of animals has been found in South America that suggest a northern connection. They are known as pantodonts, big galumphing mammals common in the Paleocene of Asia and North America (Fig. 1.10). Although they were primitive in most skeletal features, they had very distinctive teeth, with molars which had distinctive "V"-shaped crests on the crowns. The last and largest of the pantodonts occurred in the Eocene, where the sheep-sized *Coryphodon* is the largest mammal in the early Eocene beds of North America and Europe (Fig. 1.10B), and the cow-sized *Hypercoryphodon* lived on until the middle Eocene of China.

Pantodonts were long thought to be a strictly Northern Hemisphere group, until 1987, when Christian de Muizon and Larry Marshall reported an extremely primitive pantodont they named *Alcidedorbignya* from the early Paleocene of Bolivia. Although it is the earliest pantodont known, it is less primitive than some later Paleocene pantodonts from China. Once again, this discovery poses a puzzle. Did pantodonts originate in China (where the most primitive species are found), then migrate through North America to South America, or vice versa?

This puzzle is further complicated by the most surpris-

ing discovery of all. In 1992, Henk Godthelp, Mike Archer, and others reported an early Eocene fauna from Australia. Prior to this report, there were no fossil mammals known from Australia earlier than the early Miocene (about 23 million years ago), and they were all pouched marsupials (like the kangaroo and koala), or egg-laying monotremes (like the platypus). For years, scientists have used this fact to argue that Australia was isolated from the rest of the world back in the Cretaceous, when marsupials and placental mammals were just differentiating. According to this hypothesis, placentals never reached Australia (until the Ice Ages), allowing the "island continent" to evolve marsupials in great abundance without placental competition for most of the Cenozoic. But this dogma came crashing down, since the early Eocene Tinga Marra fauna included not only primitive marsupials, but also a tooth of what appeared to be an archaic ungulate!

It now appears that in the late Cretaceous (about 70 million years ago), very archaic ungulates were present not only in North America and Asia, but also in South America and Australia (and probably in Europe and Africa, if we had fossils of the right age). For reasons not yet understood, they did not persist in Australia, ceding the dominance to marsupials. Ungulates flourished in the Northern Hemisphere, as detailed in the rest of the book. As we have seen, in South America they evolved in isolation to produce extraordinary ecological parallels with Northern Hemisphere ecological equivalents.

Returning to South America, these four bizarre groups of endemic hoofed mammals remain a great puzzle. Two groups seem traceable to animals found outside South America: didolodonts-litopterns to hyopsodonts, and pyrotheres-*Carodnia* to uinatheres. Arctostylopids may be notungulates, giving us a third instance of exchange between South American ungulates and the rest of the world. However, all of these possible cases are restricted to the Paleocene. By the Eocene, there is no further evidence that South America's native ungulates ever traveled to other continents, and they continued to flourish for almost 50 million years unmolested by outsiders. Secure on their island conti-

nent, they evolved startling examples of parallelism with horses, camels, rhinos, hippos, and elephants. Sometime in the late Oligocene, between 30 and 24 million years ago, rodents and primates arrived, possibly on rafts of floating vegetation or by island hopping. The rodents soon diversified into the great South American caviomorph radiation, producing everything from giant capybaras to agoutis to chinchillas and Guinea pigs. The primates became the prehensile-tailed New World monkeys, including the spider monkeys, howler monkeys and their kin. Raccoons and their relatives arrived sometime in the late Miocene, between 6 and 9 million years ago. However, none of these later arrivals seriously impacted the large ungulates, which continued to dominate the forests and grasslands.

The isolation of South America was finally broken in the Pliocene, about 3.5 million years ago. Continental collisions lifted up sea floor and triggered volcanic eruptions,

building the Central American land bridge. As it did so, nature began one of its greatest experiments, the "Great American Interchange." Waves of invaders swept down from the north and competed for the first time with their southern equivalents. These included horses, sabertooth cats, pumas and jaguars, wolves and dogs, bears, mastodons and mammoths, camels, tapirs, and deer. Some of these northern predators were undoubtedly more efficient than the native marsupial predators and giant predatory birds that had been there for millions of years. The native South American fauna was overwhelmed not only by the new predators, but also by competition from their ecological equivalents from the north. Most went extinct in a few thousand years, although some managed to survive well into the Ice Ages before finally disappearing, possibly due to hunting by the first humans to reach South America.