

Mammalian Evolution

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INTRODUCTION

The evolution of certain mammalian lineages has become the favorite examples of nearly every introductory textbook in historical geology, paleontology, and evolutionary biology. The evolution of the horse is the most frequently used, since it emerged in 1851 and has been reproduced many times in nearly 150 years (see Gould, 1987, and MacFadden, 1992). Occasionally, one sees a revival of one of Osborn's (1929) evolutionary sequences of brontotheres, and some books may show a sequence of mammoths and mastodonts. In most historical geology books, the discussion of fossil mammals usually consists of just these selected examples, since the authors seem to think that a fuller account of Cenozoic mammal evolution is beyond the level of their readers. Children's books, trade books, and museum displays typically show little more than the evolution of the horse and few selected pictures of spectacular beasts such as saber-toothed cats, ground sloths, mammoths, and the gigantic hornless rhinoceros *Paraceratherium* (called by the obsolete names *Baluchitherium* or *Indricotherium* in virtually every caption). Given these conditions, one cannot fault students or the general public for thinking that only horses have a good fossil record, or that there are no other well-studied groups of fossil mammals.

Even worse is the fact that most of these treatments are shamelessly copied from one another, right down to the typographical errors, the poses and coloration patterns of the animals, and the outdated metaphors (such as the "fox terrier" analogy for the earliest horses—see Gould, 1988). Most of the diagrams, such as the orthogenetic sequences of horses or brontotheres, have been obsolete for over sixty years, yet they are reproduced again and again long after paleontologists abandoned them. If any phylogenetic relationships of mammals are shown, they are either vaguely drawn or outright wrong. One only need look at some of the recent historical geology and paleontology textbooks (e.g., Wicander and Monroe, 1993, Fig. 19.8; Levin, 1992, Figs. 15-28, 15-33, 15-40; Stearn and Carroll, 1989, Fig. 12-7) to see mammal phylogenies based on 40-year old work, with no sign of the last several decades of progress made in the subject. This is in spite of several recent volumes on mammal phylogeny (e.g., Benton, 1988; Szalay, Novacek, and McKenna, 1993), and many papers in widely read scientific journals such as *Nature* (e.g., Novacek, 1992).

The most annoying sign of an obsolete secondhand treatment is the recycling of long-abandoned taxonomic concepts or invalid names. For the mammalian paleontologist, it is jarring to read an account that still uses names like "Palaeodonta" (an early twentieth-century grouping of primitive artiodactyls), "Amblypoda" (a nineteenth-century grouping of uinatheres and pantodonts), and "Acreodi" or "Pseudocreodi" (left over from the early twentieth century, when some paleontologists thought creodonts were related to archaic carnivorous ungulates, such as arctocyonids and mesonychids). These taxa have been abandoned

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for at least forty to sixty years, and not used by mammalian paleontologists in generations. Non-specialists who don't keep up with the literature might be excused for using taxa that have been invalidated in the last twenty years. These include the "Pantotheria" (a wastebasket for primitive non-tribosphenic Mesozoic mammals—Prothero, 1981), "Deltatheridia" (a group for creodonts and some insectivores created by Van Valen in 1966, which never caught on), "Proteutheria" (a wastebasket for primitive insectivorous mammals), or "Condylarthra" (a wastebasket for archaic ungulates—see below). Finally, the credibility of textbook authors would be greatly enhanced if they just spelled the taxonomic names right, and checked to see that the generic names (such as "*Baluchitherium*") are not long out of date.

Admittedly, a non-specialist might be intimidated by the literature, and not sure where to turn. It doesn't help that even some recent textbooks on fossil vertebrates (e.g., Colbert and Morales, 1991; Stearn and Carroll, 1989) perpetuate archaic notions, and are not as up-to-date as they could have been. One of the main purposes of the Paleontological Society short courses is to make up-to-date information accessible to non-specialists. Hence, this chapter and talk will focus on the most common misconceptions that need clarification, and will try to offer an alternative to the overused and inaccurate accounts of horse and brontothere phylogeny that passes for a discussion of mammalian evolution in most textbooks.

CONCEPTUAL CHANGES

The obsolescence of many of the older treatments of mammalian evolution comes from several conceptual changes in the profession, as well as from a wealth of new fossil discoveries. The oldest and most difficult to eradicate is the notion of orthogenesis. As pointed out by Gould (1987, 1989), MacFadden (1992), and many others, this turn-of-the-century idea was popular when the fossil record yielded only a few members of a given family, so they appeared to form a straight line of evolution. In addition, many paleontologists of a century ago were raised with a notion of "the scale of nature" and "progressive evolution," causing them to emphasize the overall trends at the cost of oversimplifying the data. The last century of additional collecting has made orthogenesis obsolete, not only because the notion of linear evolutionary progress is inappropriate, but also because the fossil record itself has yielded complex, bushy branched phylogenies where simple linear trends were once dogma. In each of the examples I will discuss, this trend is apparent: the proper metaphor for the family tree of nearly every mammalian group is "bushes," not "ladders."

Another important conceptual change has been the revolution in systematics known as cladistics, or phylogenetic systematics. First formulated by the German entomologist Willi Hennig (1965, 1966), it spread throughout zoology in the 1970s, and first shook up mammalian systematics with McKenna's classic 1975 paper. Today, virtually all phylogenetic research on fossil mammals is done with cladistic methods, as shown by the program of the Society of Vertebrate Paleontology meeting, or by recent books and symposia on mammalian phylogeny (e.g., Benton, 1988; Szalay, Novacek and McKenna, 1993). The focus on shared derived characters and explicit, testable phylogenetic hypotheses has shed light on previously intractable problems in mammalian phylogeny. Most of the new insights presented here would not have been possible without clearing away the confusing overgrowth of shared primitive characters and paraphyletic "wastebasket" taxa.

In a short course chapter such as this, it is not possible to update every aspect of mammalian evolution. The preceding chapter by Novacek reviews our current understanding of the relationships of the major placental groups. But most historical geology textbooks usually

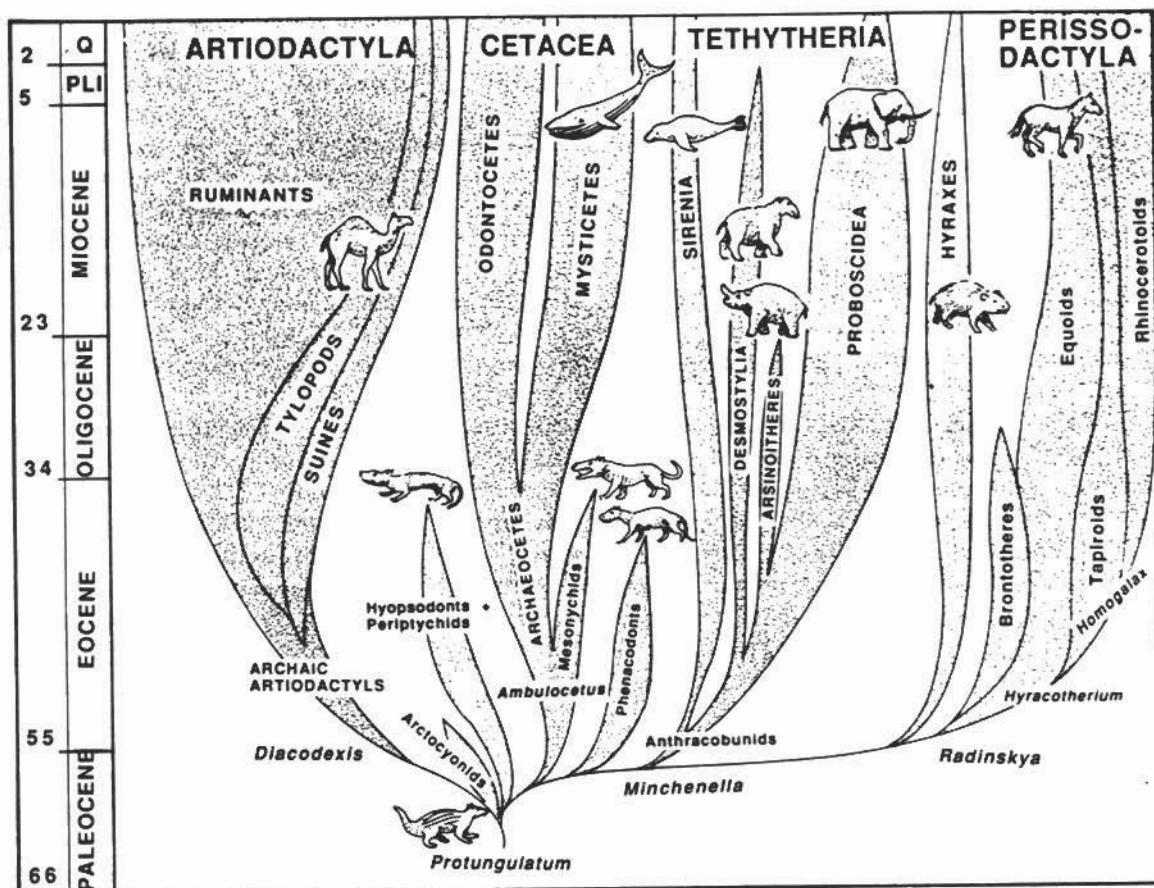


FIGURE 1—Phylogeny of hoofed mammals (after Prothero et al., 1988).

show a series of phylogenies, or "family trees," of some familiar fossil mammals. Typically, this includes a horse phylogeny, possibly a brontothere orthogenetic sequence, and frequently diagrams of the radiation of odd-toed or even-toed hoofed mammals cribbed from the first edition of Colbert (1955). These represent phylogenetic thinking of four decades ago, and have been rendered obsolete (both in their factual details, and also in their philosophy) by the Benton (1988) or Szalay, Novacek, and McKenna (1993) symposia. Although I cannot update every detail of mammal phylogeny in this short chapter, it is worth reviewing some of the most common examples, since they are vastly different from the way they are usually portrayed.

HOOVED MAMMALS

The ungulates, or hoofed mammals, make up about 33% of the living and extinct mammalian genera. Because they are typically large-bodied herbivores with robust bones, most ungulates have an excellent fossil record in the Cenozoic (see Prothero and Schoch, 1995). Today, the ungulates include the even-toed artiodactyls (pigs, hippos, camels, deer, giraffes, antelopes, cattle, sheep and goats), the odd-toed perissodactyls (horses, rhinos, tapirs, and their extinct relatives), the tethytheres (elephants, sirenians, and several extinct groups), and the controversial hyraxes, or conies (which have been allied with either tethytheres or perissodactyls—see Prothero et al., 1988; Prothero and Schoch, 1989; Fischer and Tassy, 1993; Shoshani, 1993; and Novacek, this volume). Whales are also ungulates, since they are descended from mammals that clearly possessed hooves.

The phylogeny of ungulates was long obscured by one of the worst of all the taxonomic wastebaskets, the "Condylarthra." The term was originally coined by Cope (1881) as a catch-all for several groups of archaic ungulates (phenacodonts, periptychids, and hyopsodonts). He originally used "Condylarthra" as a subdivision of the perissodactyls, since he thought they were ancestral to that group, but later raised the "condylarths" to their own, independent ordinal rank. In 1884, Cope threw more archaic ungulates, including arctocyonids and meniscotheres, as well as the primitive artiodactyl *Diacodexis*, and non-ungulates such as the taeniodont *Conoryctes*, in this convenient but meaningless taxon. In the last 110 years, different authors have added to or subtracted various other groups from the "Condylarthra." Through it all, however, it was clear that the group had no phylogenetic meaning. It was just a miscellaneous collection of archaic ungulates that were not clearly related to any living group.

When textbook authors use the word "condylarth" in their text or diagrams, it is usually a shorthand for the vague cloud of possible ancestors to the living ungulate groups (e.g., Wicander and Monroe, 1989, p. 484). The implication of the term was that "condylarths" were all "adaptively unified" (in the terminology of Van Valen, 1978a) primitive hoofed mammals that could not be distinguished except by specialists. Nothing could be further from the truth. Although they retain many shared primitive similarities, some "condylarths" (e.g., the arctocyonids) were quite dog-like or raccoon-like omnivores, whereas others were apparently small herding herbivores (e.g., *Meniscotherium*) or dachshund-shaped herbivores (e.g., hyopsodonts), and yet others were huge bear-like beasts (e.g., mesonychids).

Although the lack of "adaptive unity" in the "Condylarthra" would be grounds enough to abolish it, far worse was its effect on ungulate systematics. The phylogeny of the living groups would be traced back to "condylarth" ancestors, without any detailed analysis of exactly which of the many different "condylarths" was relevant. When someone uses the term "condylarth," do they mean arctocyonids, or meniscotheres, or hyopsodonts, or mesonychids, or periptychids, or phenacodonts? Each of these groups is so different from the others that comparing a given animal to a "condylarth" is a meaningless statement. Finally, the convenience of the "condylarth" wastebasket essentially stymied any attempt to analyze the relationships within the "Condylarthra," or see if some of its components might be more closely related to other living ungulates. Van Valen (1978b) presented some outlines of interrelationships of "condylarths," but did not support these with a detailed character analysis.

When cladistic methods came along, they demanded that paraphyletic groups like the "Condylarthra" be dissected to see where its components belonged (Cifelli, 1982; Prothero et al., 1988; Prothero, 1993b). Sure enough, it turned out that there was an interesting phylogenetic pattern beneath the obscuring blanket of "condylarths" that no one could detect while the term was used as a smoke screen for ignorance. For example, some of the "condylarths" (e.g., phenacodonts and meniscotheres) were closely related to the cluster of higher ungulates (the perissodactyls, hyraxes, and tethytheres), while others (e.g., periptychids and hyopsodonts) were related to the earlier clades (Fig. 1). More importantly, the poorly understood relationships of the living ungulates became clear with the analysis. Artiodactyls must have split off very early from the ungulate radiation; in some features, the earliest artiodactyls are among the most primitive of ungulates. Hyopsodonts plus periptychids split off next, followed by the mesonychid-whale clade, then the phenacodonts plus meniscotheres, and finally the higher ungulates.

Perissodactyls.—Among the living ungulate orders, the one most often mentioned in textbooks is the perissodactyls, or odd-toed ungulates. Today, they include the horses, rhinos and tapirs, and in the past there were many other groups, including the huge brontotheres and the bizarre clawed chalicotheres. They are called "odd-toed" because most perissodactyls

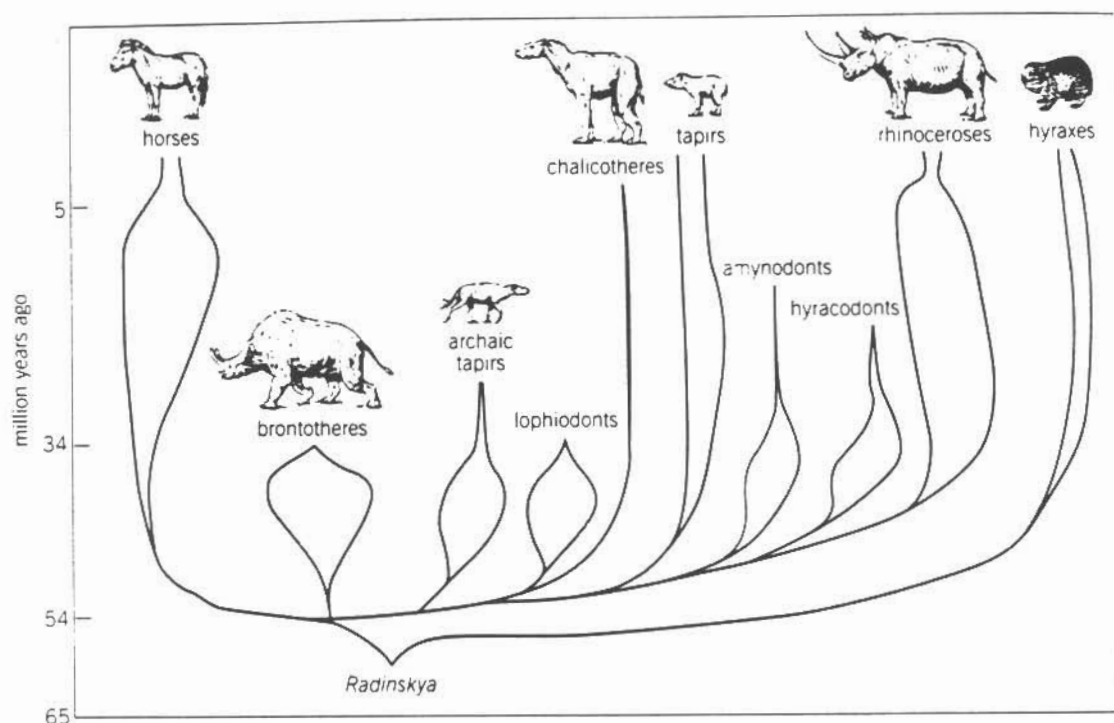


FIGURE 2—Phylogeny of perissodactyls (after Prothero and Schoch, 1989).

have either one or three toes on each foot, although tapirs and many primitive perissodactyls had four toes on the forefeet. Regardless of the actual number of toes, the axis of weight bearing is the central digit of the hand and foot (the third finger or toe, equivalent to your middle finger). Typically the second and fourth (index finger and ring finger) digits are retained on either side. A number of other synapomorphies unite the perissodactyls (Prothero et al., 1988; Prothero and Schoch, 1989), but they will not be reviewed here.

Great strides have been made in our understanding of perissodactyls, but sadly most of the treatments found in introductory texts (e.g., Wicander and Monroe, 1993, Fig. 19.20; Levin, 1992, Fig. 15-33; Cooper et al., 1990, Fig. 17-14) are grossly out of date. Some of these diagrams are derived from figures of Colbert (1955), which were not updated even in the most recent edition (Colbert and Morales, 1991, Fig. 28-5). The current understanding of perissodactyl evolution was summarized by Prothero and Schoch (1989). It is not possible to review all the new developments here, but a few of the more common errors need to be corrected:

1. The closest relatives of perissodactyls are the tethytheres (proboscideans, sirenians, arsinoitheres, and desmostylians), not the creodonts (e.g., Cooper et al., 1990, Fig. 17-14) nor the phenacodont "condylarths" (e.g., Sloan, 1987; Colbert and Morales, 1991; Carroll, 1988; and most texts which follow them). This has been shown not only by cladistic analysis (McKenna and Manning, 1977; Novacek, 1986; Prothero et al., 1988; Fischer and Tassy, 1993; Prothero, 1993b), but also by *Radinskya*, the earliest relative of perissodactyls, known from the upper Paleocene beds of China (McKenna et al., 1989). Although not formally placed in the Perissodactyla by McKenna and others, *Radinskya* makes a good sister-group to the Perissodactyla, and is extremely similar to the oldest known tethythere, *Minchenella* (Domning, Ray, and McKenna, 1986), and the arsinoithere *Phenacolophus* from the same beds (McKenna and Manning, 1977). From these late Paleocene ancestors in China, in the early

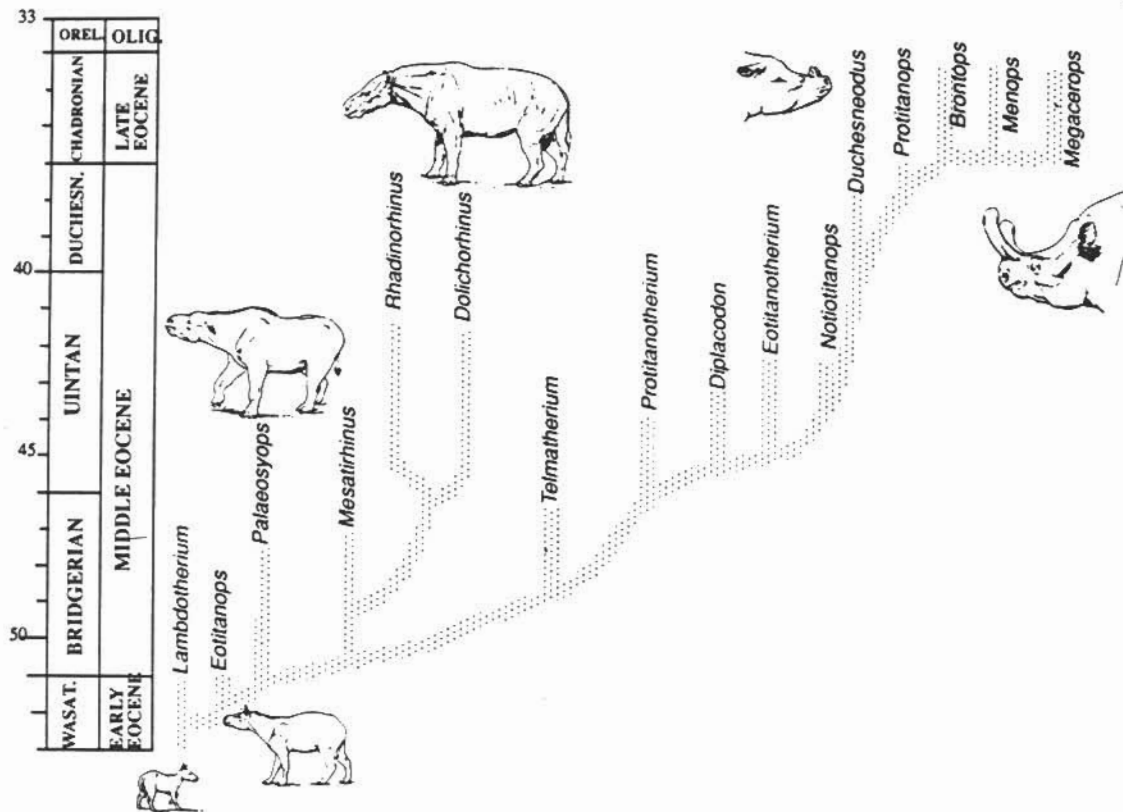


FIGURE 3—Phylogeny of the the brontotheres (modified from Mader, 1989).

Eocene perissodactyls migrated into other parts of the world, including North America, where they largely replaced the phenacodonts.

2. Most diagrams show the five major perissodactyl suborders in an unresolved pentachotomy (e.g., Wicander and Monroe, 1993, Fig. 19.20; Stearn and Carroll, 1989, Fig. 12-40) or unite brontotheres and chalicotheres (e.g., Cooper et al., 1990, Fig. 17-14), or place brontotheres and horses together in the Hippomorpha, with the chalicotheres isolated in the Ancylopoda (e.g., Colbert and Morales, 1991, Fig. 28-5). The latest research (Hooker, 1989; Schoch, 1989) clearly shows that chalicotheres are among the primitive "tapiroid" groups that are sister-taxa to living tapirs and rhinos, and do not merit such phylogenetic isolation, or their own suborder Ancylopoda (Fig. 2). Nor is there any strong evidence uniting brontotheres and horses (Hooker, 1989). In summary, the three major clades of Perissodactyla (as traditionally construed, excluding hyraxes—see Prothero and Schoch, 1989) are the horses plus palaeotheres (the Hippomorpha), the brontotheres (the Titanotheriomorpha), and the tapirs, chalicotheres, rhinos, and their extinct relatives (the Moropomorpha).

3. *Brontotheres*: Perhaps the most widely misunderstood group of perissodactyls are the brontotheres, or titanotheres. This is largely due to the fact that they were used as classic examples of "orthogenesis" by Henry Fairfield Osborn (see Schoch, this volume). Unfortunately, Osborn was a hyper-splitter whose notions of systematics and evolution were outmoded even in his own lifetime (Rainger, 1991), and most of the information in his imposing two-volume titanother monographs (1929) was invalid or obsolete before it was published. Yet because these monographs had so many impressive illustrations, people have recycled Osborn's ideas for over sixty years (e.g., Wicander and Monroe, 1989, Fig. 16-34). Indeed, the sheer bulk of the titanother monographs, and the inaccessibility of many important new brontother specimens in the Frick Collection of the American Museum of Natural History in

New York, have discouraged most scientists from tackling a long-overdue revision of the group, although for decades vertebrate paleontologists (e.g., Scott, 1941; Simpson, 1945) knew that Osborn's work was badly in need of a modern analysis.

A complete revision of the Brontotheriidae is still not published, but some of the more important myths were debunked by Bryn Mader (1989). He recognizes only 18 North American genera (Osborn recognized over two dozen) in two subfamilies (Osborn had oversplit them into *twelve* subfamilies!). Instead of the orthogenetic sequence of brontotheres with their gradually enlarging horns, Mader's review showed that brontothere phylogeny is very bushy, with many contemporaneous genera of differing horn lengths (Fig. 3). Brontothere evolution culminated in the late Eocene (*not* early Oligocene) with the long-horned, elephant-sized beasts so popular in museum displays and dioramas. These animals are usually called by obsolete names such as *Titanotherium*, *Brontotherium*, *Titanops*, *Diploclonus*, or *Menodus*. According to Mader, the only valid genera of late Eocene North American brontotheres are *Megacerops*, *Menops*, and *Brontops*.

Finally, brontotheres became extinct at the end of the late Eocene (*not* the early Oligocene, as seen in most books) because new correlations have shown that the formerly "lower Oligocene" beds of North America and Eurasia are actually upper Eocene (Swisher and Prothero, 1990; Prothero and Swisher, 1992; Berggren and Prothero, 1992). *There are no Oligocene brontotheres!* In addition, brontotheres did not die out because their evolution was driven by some intrinsic factor that was uncontrolled by natural selection, as Osborn (1929) thought. Instead, their extinction occurred when a global cooling and drying event at the end of the Eocene greatly reduced their habitat of leafy forests, and expanded the open scrublands with little soft-leaved browse upon which brontotheres (with their very low-crowned teeth) probably fed (Retallack, 1983; Prothero, 1994a).

4. *Horses*: Horses are by far the most popular exemplar of mammalian evolution in textbooks, tradebooks, museum displays, and just about every other medium which reaches the general public. However, most of what is presented about them is badly out of date. As MacFadden (1992) points out, they were one of the first examples of a supposedly orthogenetic sequence (starting with the pre-evolutionary ideas of Richard Owen in 1851). Most nineteenth-century diagrams emphasized the apparently progressive reduction in side toes, or increase in tooth crown height, or changes in body size and proportions. Since Matthew's (1930) work, however, paleontologists have come to realize that horse phylogeny is actually very bushy, with many genera coexisting (especially in the Miocene). This was further shown by Stirton (1940), Simpson (1951), and many authors since then. Yet textbooks continue to reproduce ancient diagrams of orthogenetic horse evolution (e.g., Matthew, 1926) as though that geometry were still valid.

A modern version of horse phylogeny (Fig. 4) is extremely bushy, with over a dozen branches in the Miocene alone. Indeed, the bushiness extends back throughout horse evolution. For example, Prothero and Shubin (1989) showed that the supposedly unbranched Eocene-Oligocene "trunk" of horse evolution of the allegedly sequential genera *Mesohippus* and *Miohippus* is actually composed of multiple species of the two genera (five species occur at the same level in Wyoming); moreover, the two genera overlap by at least five million years. Although placed in the same genus, the early Eocene horse (usually called *Hyracotherium*) also has multiple species coexisting side-by-side, along with the closely related "tapiroid" *Homogalax* (Gingerich, 1980). Indeed, wherever large samples of fossil horses are found, their evolution is bushy rather than orthogenetic.

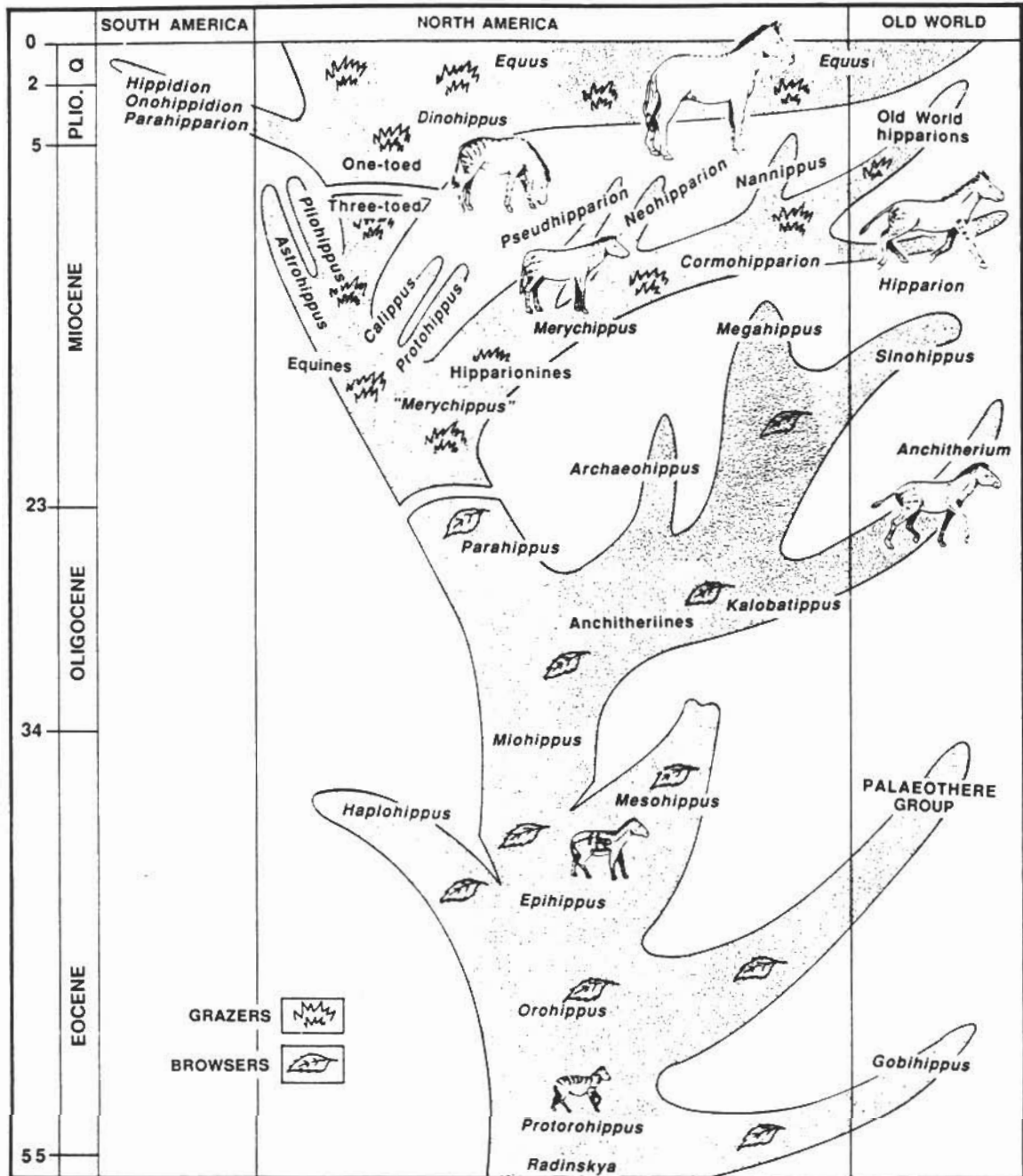


FIGURE 4—Updated phylogeny of horses (based on MacFadden, 1992, and Prothero and Shubin, 1989; see Prothero and Schoch, 1995).

There are many other aspects of horse evolution that need updating. The oldest known horses from the early Eocene of North America are neither *Hyracotherium* nor "eohippus." Jeremy Hooker (1989) showed that the early Eocene European type species of *Hyracotherium*, *H. leporinum*, is a palaeothere, and is unrelated to North American horses. The correct name for early Eocene horses has not yet been determined. It seems likely that *Protorohippus* (Wortman, 1896) may turn out to be the first available generic name for early Eocene North American horses, since the type specimen of "eohippus" is not a horse, either.

Another common mistake is to show *Merychippus* as the ancestor of all middle and late Miocene horses, treating the genus as a "wastebasket" ancestral group. As Skinner and Taylor (1967), MacFadden (1984, 1992), Hulbert (1989), and others have shown, *Merychippus insignis* (the type species) is actually within the hipparionine lineage. "*Merychippus coloradense*" and "*Merychippus republicanus*" are actually related to *Neohipparion* or *Pseudhipparion*, "*Merychippus goorisi*" and "*Merychippus sphenodus*" to *Cormohipparion*, and "*Merychippus stylodontus*" and "*Merychippus carrizoensis*" to the equines *Pliohippus*, *Dinohippus* and *Equus*. "*Merychippus isonesus*" and "*Merychippus sejunctus*" are also related to hipparionines. Only "*Merychippus primus*" and "*Merychippus gunteri*" cannot be clearly related to any one specific late Miocene group of horses. Eventually, these incorrectly allocated horses will be renamed something besides *Merychippus*, and then the bushiness of Miocene horse evolution will be even further accentuated.

For decades, the appearance of hipparionine horses in Europe was used as an indicator of the Miocene-Pliocene boundary (Colbert, 1935). Subsequent downward shifting of that boundary (Berggren, Kent, and Van Couvering, 1985), as well as major revision of the hipparionines (Woodburne, 1989), has shown that there were at least two separate migrations of hipparionine horses from North America to the Old World at 12 and 10 Ma, both well before the end of the Miocene at 5 Ma.

Many horse phylogenies based on Simpson (1951) or earlier works show *Pliohippus* as ancestral to *Equus*. For over 50 years paleontologists used the name "*Pliohippus*" as a wastebasket for one-toed horses with fairly advanced teeth. In 1950, John Lance noticed that some specimens of "*Pliohippus*" were very different from the true members of that genus, but closer to *Equus*. In 1957, Jim Quinn formalized this distinction by creating the genus *Dinohippus* for these specimens which had erroneously been called *Pliohippus*. Since then, many scientists have shown that *Dinohippus* and *Equus* not only have similar teeth (different from those of true *Pliohippus*), but *Dinohippus* and *Equus* are even more similar in their great reduction of the facial fossa. This shared specialization is carried on in all *Equus* from the Pliocene onward. *Pliohippus* is thus an extinct side branch of Miocene horses which independently evolved a one-toed foot. *Dinohippus* and *Equus simplicidens* are the most primitive members of the living horse radiation.

5. *Rhinoceroses*: Horses are not the only group of mammals with a long, distinguished history—they are just the most familiar. Rhinoceroses have an equally impressive fossil record on several continents, but research in this group has been stagnant since the 1930s and is now just beginning to catch up with all the research into horse evolution (Prothero, Manning, and Hanson, 1986; Prothero, 1987; Prothero, Guérin, and Manning, 1989; Prothero, 1993a). In some ways, rhino evolution is more interesting than the horse story, since rhinos have exploited nearly every ecological niche available to large-bodied herbivores, from the largest land mammal that ever lived (the 22-ton, 18-foot-tall *Paraceratherium*, usually mislabeled *Baluchitherium* or *Indricotherium*, according to Lucas and Sobus, 1989), to small running forms the size of a Great Dane, to multiple experiments in the hippopotamus lifestyle. Several rhinos had mastodon-like or tapir-like trunks. Few had horns.

Like horses, brontotheres, and tapirs, the earliest rhinocerotoid *Hyrachyus* from the early middle Eocene was a small, primitive dog-sized browsing animal barely distinguishable from other primitive perissodactyls. Like horses, rhinos started with low-crowned teeth and four toes on their forefoot. Hypsodonty and reduction to three front toes occurred independently several times in the rhinocerotoids. By the late middle Eocene, however, three lineages diverged: the aquatic amynodonts (some of which were hippo-like; others had a tapir-like proboscis); the long-limbed, running hyracodonts (ranging from the Great Dane-sized

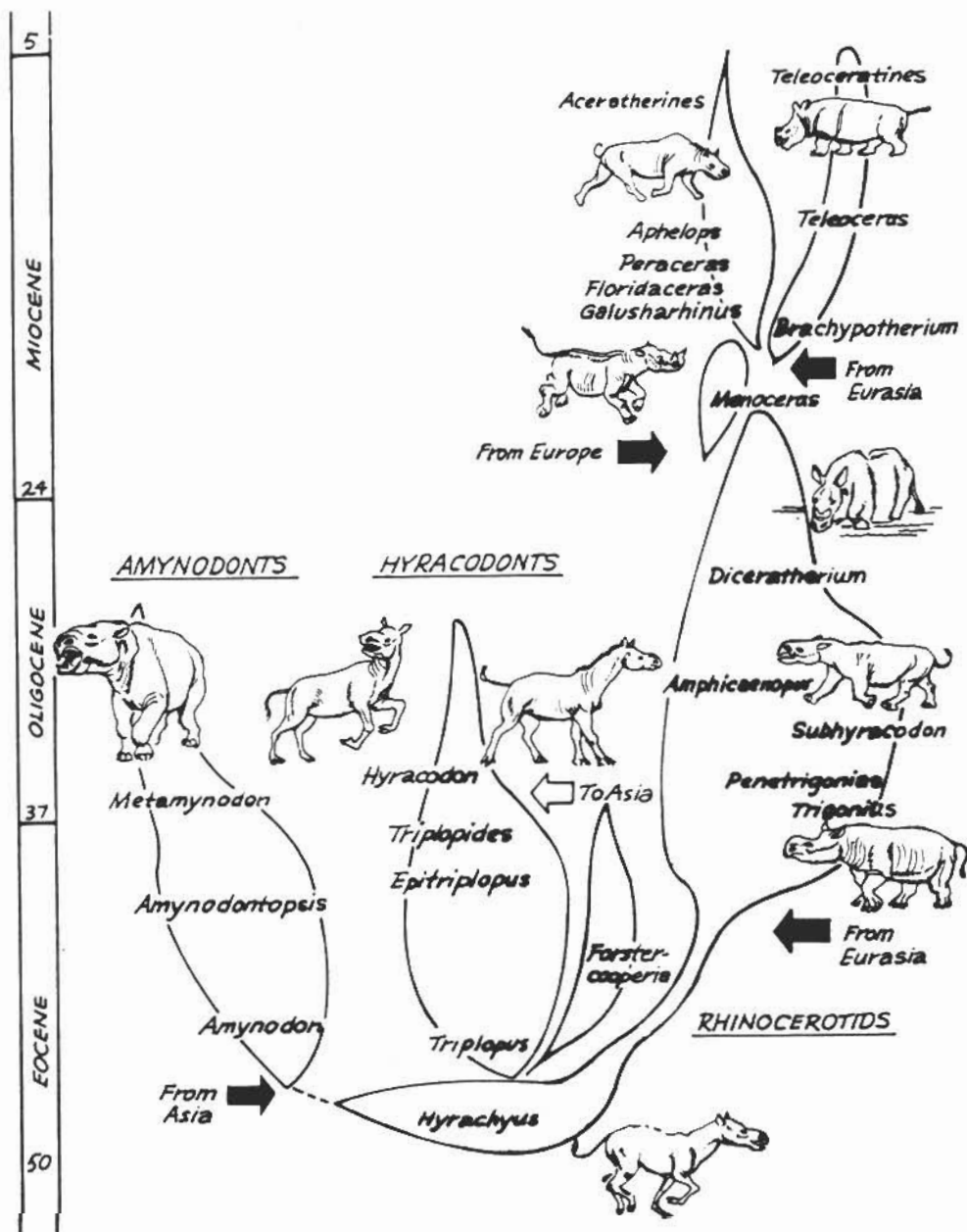


FIGURE 5—Evolution of the North American rhinocerotoids (based on Prothero et al., 1986, 1989; Prothero, 1993a).

Hyracodon to the gigantic *Paraceratherium*); and the true rhinoceroses of the living family Rhinocerotidae. Only the last group developed horns, and only later in their evolution. In fact, the first horn combination was paired horns side by side on the tip of the nose. This arrangement appeared independently in two different genera in the late Oligocene. *Diceratherium* had broad, flange-like nasal bones supporting its paired horns. *Manoceras* (the common early Miocene rhino from Agate Springs Quarry, usually mislabeled as *Diceratherium*) had rounded nasal bosses supporting its paired horns. *Manoceras* was a European immigrant to North America which converged on the paired horn condition in American *Diceratherium*.

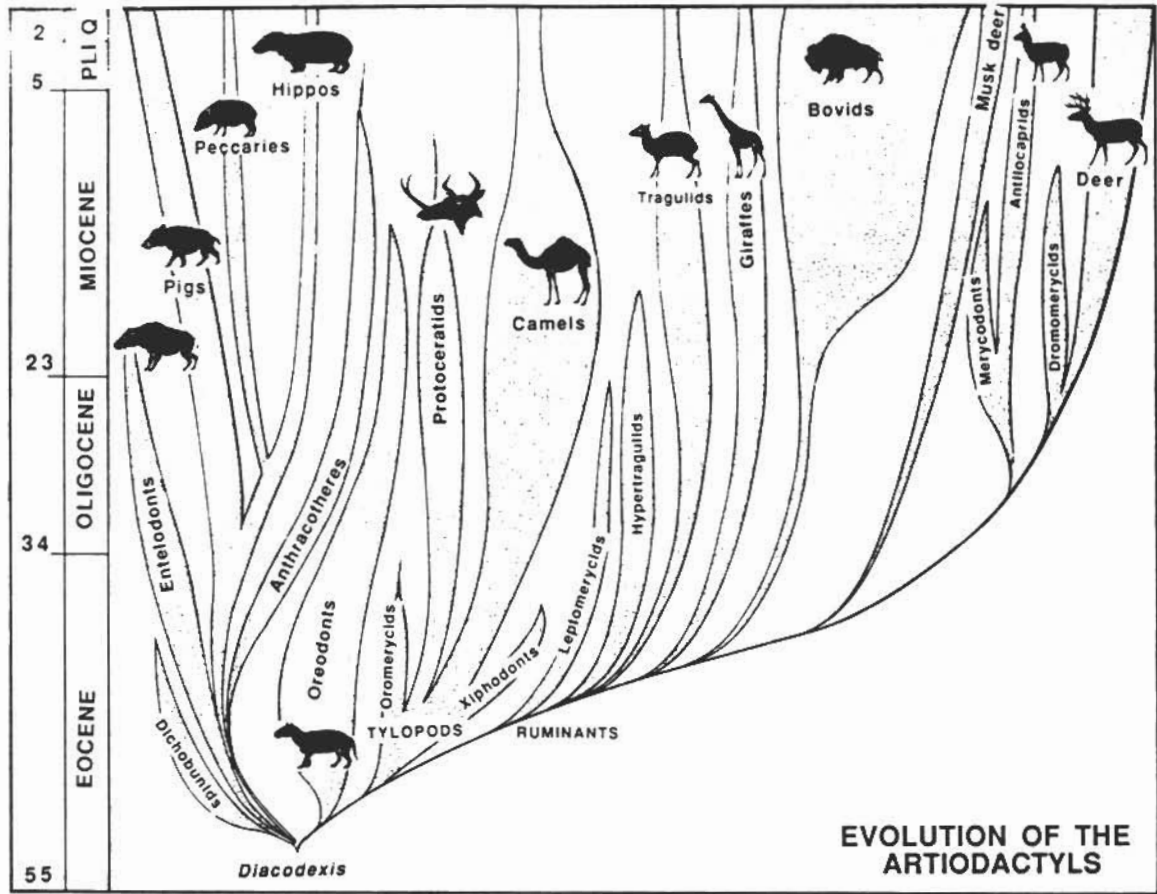


FIGURE 6—Phylogeny of the artiodactyls, based on Gentry and Hooker (1988) and Janis and Scott (1987, 1993).

During the spread of Miocene savannas which so favored the horses and other cursorial grazing hoofed mammals around Holarctica, rhinos were very successful too. Typically, they occurred in pairs in a given Miocene fauna: one was a browsing (leaf-eating) aceratherine rhino with a prehensile lip, like the living black rhinoceros; the other was a short-limbed, hippo-like grazing (grass-eating) teleoceratine rhino, that apparently dozed in the rivers during the day and came out at night to graze, like living hippos do. These browser-grazer pairs may be represented by different genera in different parts of the world throughout the Miocene (Prothero et al., 1989; Prothero, 1993a), but they are a characteristic feature of Miocene savannas.

At the end of the Miocene, rhinos disappeared from their ancestral homeland in North America (except for one isolated specimen known from the early Pliocene of Texas). Their extinction may have been a response to the climatic change which caused the extinction of so many other native North American horses, ruminants, camels, and other ungulates typical of the Miocene. However, rhinos continued to thrive in the Old World, especially during the Pleistocene, when the woolly rhino was one of the most common denizens of the ice margin habitat. Strangely, woolly rhinos did not cross the Bering land bridge back into North America, although woolly mammoths had no problem doing so. Today, only tiny populations of the five living species of rhinos remain, and due to the enormous price their horns bring, they

are on the brink of extinction—a sad remnant of one of the most distinguished and diverse families of mammals on earth.

Artiodactyls.—The artiodactyls, or even-toed hoofed mammals, are the most successful large mammals on land today, 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. Most domesticated ungulates, including cows, water buffalo, yaks, sheep, goats, camels, llamas, and even pigs, are artiodactyls. Virtually all meat (whether beef, pork, or more exotic fare such as goat or venison) comes from artiodactyls. In addition, artiodactyls produce all our milk (whether from a cow, goat, or camel), and all of our wool. In the natural world, artiodactyls are equally dominant. Just think of the common large mammals found in North America. Deer, moose, elk, bison, bighorn sheep, mountain goats, peccaries, pronghorns—they are all artiodactyls. On your average safari, nearly every large herbivorous mammal you would encounter would be an artiodactyl. These include the treetop-browsing giraffes, the huge hippos in the river, the ugly warthogs, the dangerous Cape buffalo, and a tremendous diversity of antelopes—wildebeest (or gnus), impalas, gazelles, bushbucks, elands, sable antelopes, hartebeests, kudus, gerenuks, and even tiny klipspringers and dik-diks.

Artiodactyls share many specializations, but the most obvious one is in their feet. All artiodactyls are “cloven-hoofed” in the biblical sense. Their feet are divided into an even number of toes (usually two or four), since the axis of the foot runs between the third and fourth fingers and toes (equivalent to your big finger and ring finger). The first digit (thumb or big toe equivalent) is lost completely. As they become more specialized for running, the finger and toe bones lengthen, giving their limbs an extra segment. The side toes (digits 2 and 5, equivalent to your index finger and pinky) become shorter than digits 3 and 4, and in many specialized artiodactyls, the side toes nearly disappear. The most specialized artiodactyls run on two elongate toes, digits 3 and 4, as you can see by examining any camel, deer, antelope, or cow. These two toe bones are usually fused together into a single bone, the “cannon bone,” which makes them less likely to break while running. Correlated with this specialized foot structure is a highly distinctive “double-pulley” ankle bone, or astragalus, that was a key adaptation early in artiodactyl history.

Most textbooks (e.g., Levin, 1992, Fig. 15-40; Wicander and Monroe, 1989, Fig. 16-24; Wicander and Monroe, 1993, Fig. 19.17) recycle the outdated family trees of Colbert (1955; not updated even in Colbert and Morales, 1991, Fig. 29-5), which show an unresolved, vague radiation of artiodactyl families during the Eocene with no character analysis. Since the work of Gentry and Hooker (1988) and Janis and Scott (1987, 1988), considerable progress has been made (Fig. 6). For example, turn-of-the-century paraphyletic “wastebasket” groups like the “Palaeodonta” (for primitive dichobunid artiodactyls) and “Ancodonta” (for anthracotheres and some other archaic artiodactyls) have long been abandoned. The earliest artiodactyls occur in the early Eocene of Pakistan (Thewissen et al., 1983), suggesting that they originated in the Old World and then spread rapidly around the world (as did perissodactyls, too) in the early Eocene; they are not descended from North American Paleocene “condylarths,” as once thought (e.g., Sloan, 1987).

Hippos were long thought to be related to pigs or the extinct anthracotheres, but Pickford (1983) argued that hippos are descended from peccaries, the North American pig analogue. Among the most common fossils in the middle Cenozoic of North America are the ubiquitous oreodonts, which are usually erroneously described as “pig-like” or “sheep-like.” In fact, they have been shown to be tylopods, related to the camels. The slingshot-horned protoceratids, long allied with the ruminants, have also been shown to be tylopods.

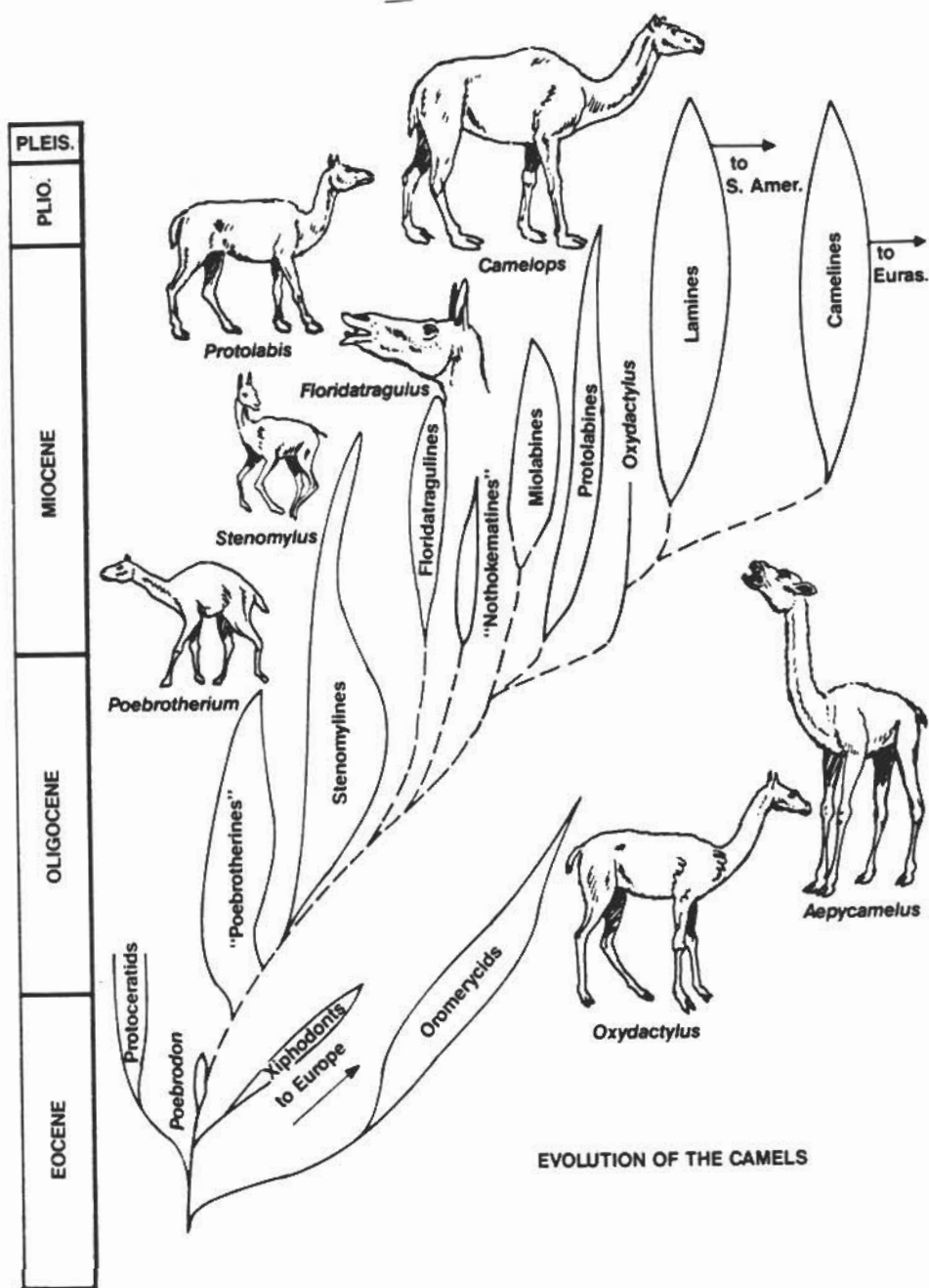


FIGURE 7—Evolution of the camels (based on Honey et al., 1995).

The relationships within the ruminants are more controversial, with the deer and giraffes usually placed in one group, and the pronghorn "antelopes" (which are not true antelopes, but an endemic North American family with a long and diverse Miocene-Pliocene record) and bovids (cattle, sheep, goats, antelope, etc.) in another (Colbert and Morales, 1991; Geraads et al., 1987; Gentry and Hooker, 1988). When the parallelism in cranial appendages, tooth hypsodonty, and limbs is filtered out, however, the unique features considered least likely to be homoplastic support an alliance of deer with pronghorns, and giraffes with bovids (Leinders and Heintz, 1980; Groves and Grubb, 1987; Janis and Scott, 1987, 1988; Scott and Janis, 1993).

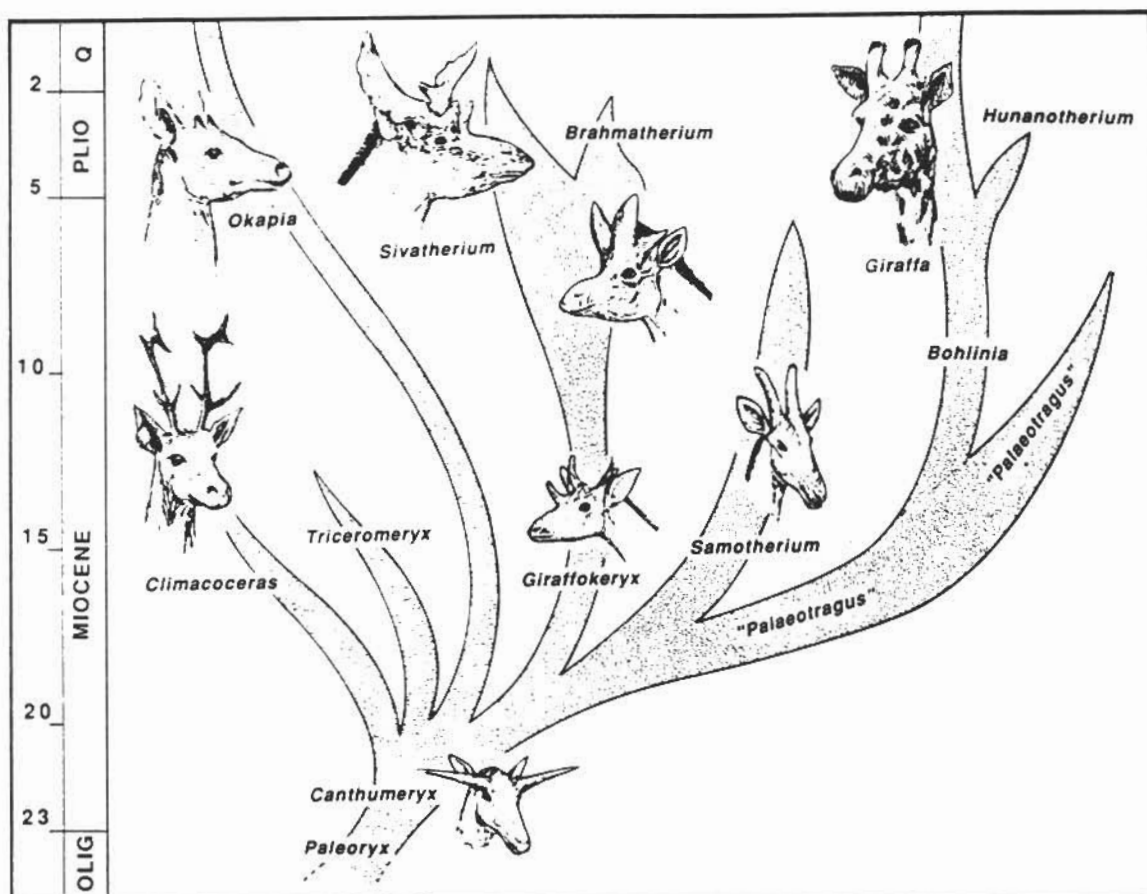


FIGURE 8—Evolution of the giraffe family (based on Hamilton, 1978).

Among the artiodactyls, there are groups with truly spectacular fossil records that rival that of the horse. Like the example of rhinos, however, they have not been studied or published as extensively, so they do not get into the textbooks. It's time to put the old gray mare out to pasture and put in some new beasts for a change. The evolution of camels, for example, is truly a textbook case (Fig. 7). A few textbooks (e.g., Wicander and Monroe, 1989, Fig. 16-26) show a turn-of-the-century orthogenetic sequence of camel skulls, teeth, and limbs, but then betray the antiquity of their sources by starting the sequence with the oromyrcid *Protylopus*, which was distinguished from the camels almost 40 years ago (Gazin, 1955).

Camels arose during the late middle Eocene in North America and were confined to this continent until the late Pliocene, when the ancestors of llamas, alpacas, guanacos, and vicuñas reached South America across the Panamanian land bridge. In the Pleistocene, the ancestors of dromedaries and Bactrian camels reached the Old World across the Bering land bridge. Like North American rhinos, camels were truly diverse on this continent because they occupied niches that ruminants dominated in the Old World. For example, during the Miocene there were gazelle-like camels, giraffe-like camels, plus a variety of other lineages with varying limb lengths and adaptations for different ecologies, much like antelopes of the African savanna (Honey et al., 1995). Like horses and rhinos, camels started out with relatively low-crowned teeth, and shorter limbs and toes, and both became longer during their evolution. Like rhinos, the stereotypical feature of living camels—the hump—was a late addition; most extinct camels lacked humps, just as most extinct rhinos lacked horns. Like rhinos, camels were

decimated at the end of the Miocene on this continent, but they did survive until the end of the last Ice Age, when they were among the many groups that disappeared from North America in the early Holocene (whether by overkill by human hunters, or by climatic change).

If you don't like rhinos or camels to replace the tired old horse diagram, how about the amazing story of giraffes (Fig. 8)? Once again, the stereotyped feature of the living species—the long neck—was a late addition in their history (Hamilton, 1978). Fossil giraffes show an amazing variety of cranial appendages and body proportions. In fact, most resembled moose or antelopes, and the living okapi is a much better analogue for typical fossil giraffids. Unfortunately, complete articulated skeletons with the neck vertebrae rarely fossilize, so we do not have a good record of how the giraffe actually got its long neck.

Tethytheres.—After perissodactyls and artiodactyls, the third major group of living ungulates are tethytheres, including the elephants and their relatives (the Proboscidea), the manatees and dugongs (the Sirenia), and two extinct groups, the aquatic desmostylians, and the horned arsinoitheres. Almost all the textbooks and trade books fail to mention the connection between these groups, usually listing them as four unrelated orders. But their close relationship has been clear since Malcolm McKenna named the group in 1975, and further corroborated by later studies (Domning et al., 1986; Tassy and Shoshani, 1988; Fischer and Tassy, 1993; Shoshani, 1993). Tethytheres have number of distinctive synapomorphies: a single pair of teats on the breasts (like humans and apes), not on the belly or groin as in other mammals; a heart which is subdivided at the top and bottom; eyes which are shifted far forward on the skull; cheekbones which contain a broadly expanded portion of the rear skull bones, and a number of other features in common. Their most unusual specialization, however, is in their teeth. In most mammals (including humans), when the baby teeth eventually drop out, they are replaced by adult teeth erupting from beneath the roots. Elephants and manatees, on the other hand, replace their teeth from the back of the jaw, pushing the old worn teeth out the front of the jaw in a sort of "conveyor belt" replacement. This "horizontal tooth replacement" mechanism is a specialization developed independently in elephants and sirenians, since it is not found in their ancestors, or in other tethytheres.

As the name implies, most of the early history of the group took place around the ancient Tethys seaway in Eurasia and northern Africa. The earliest tethytheres were *Minchenella* and *Phenacolophus* from the late Paleocene of China, and the anthracobunids from the early Eocene of Pakistan were also very primitive tethytheres. A number of primitive proboscideans occur in the Eocene beds of North Africa. By the middle Eocene, sirenians were abundant in Egypt and Libya, and also known from Alabama, Florida, Jamaica, Somalia, Rumania, France, Hungary, and India.

Arsinoitherium was long considered a zoological puzzle, with its huge elephantine body and pointed paired horns on the nose. For a long time, it was placed in its own order, the Embrithopoda, for lack of any clear evidence of relationship to other mammals. Recent work by Nick Court (1990), however, has clearly established that arsinoitheres were tethytheres, not far from the proboscideans in their origin. Arsinoitheres were originally known only from *Arsinoitherium*, which occurs in the Eocene-Oligocene transition beds of the Fayum in Egypt. However, recent specimens from the late Eocene of Rumania and Turkey, plus *Phenacolophus* from the late Paleocene of China, have considerably expanded their temporal and geographic range (McKenna and Manning, 1977). Yet books as recent as Colbert and Morales (1991, p. 413) completely fail to mention these new discoveries, and treat arsinoitheres as if no progress had been made since 1955.

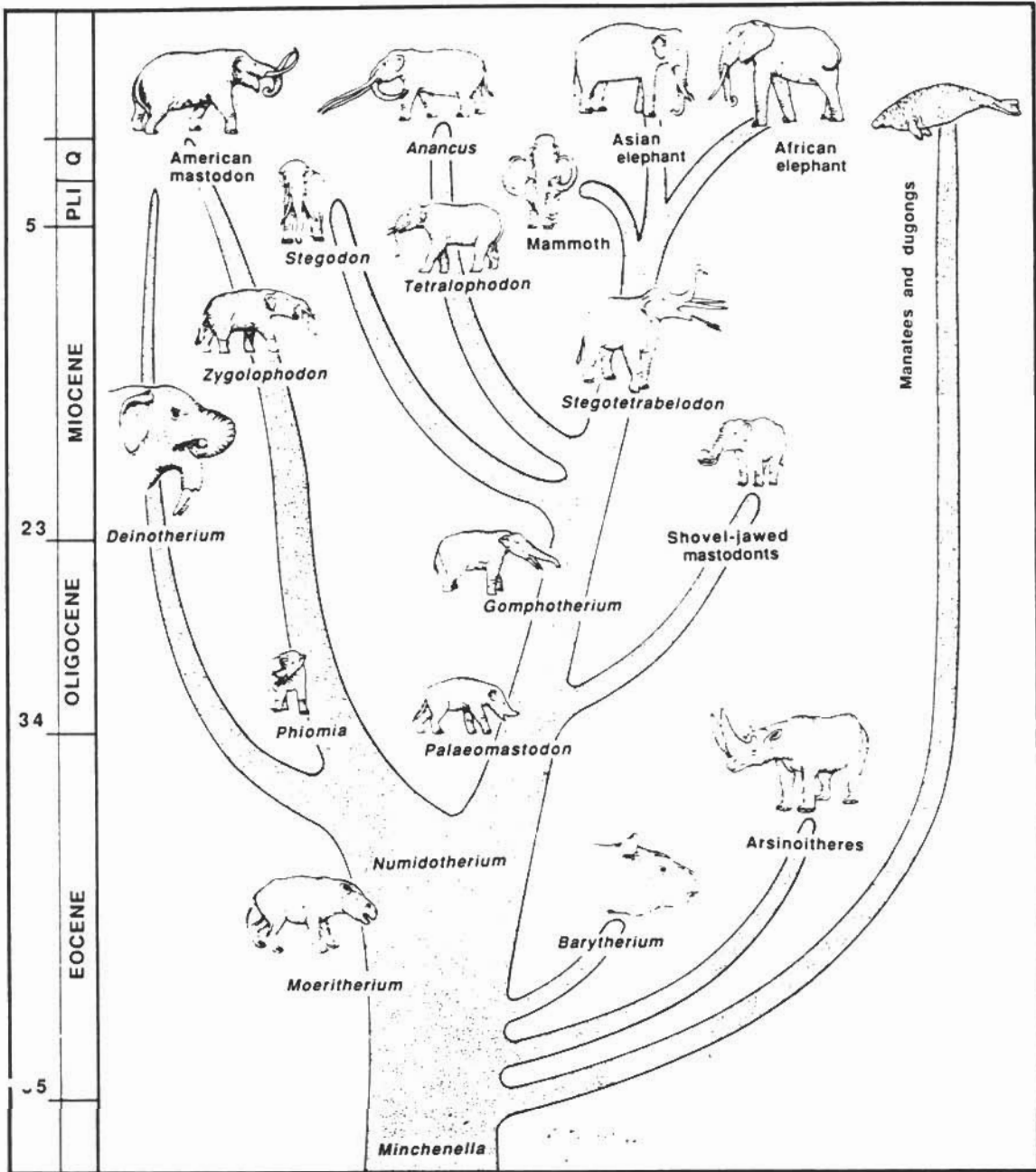


FIGURE 9—Evolution of the Tethytheria (based on Domning et al., 1986; Tassy and Shoshani, 1988; Shoshani, 1992).

One of the most spectacular and underutilized examples of mammalian evolution is the Proboscidea. Because their huge bones fossilize readily, we have an excellent record of their evolution from beasts with no trunks, tusks, or other stereotypical elephant features (Fig. 9). Most historical geology textbooks mention mastodonts and mammoths, but few really discuss their evolution as well as they should. The proboscideans display an amazing evolutionary history, particularly in the development of the trunk, the variations in their upper and lower tusks, and in the modifications of their teeth and skulls (Tassy and Shoshani, 1988; Shoshani, 1992). Starting with North African Eocene beasts such as *Barytherium* and *Moeritherium*,

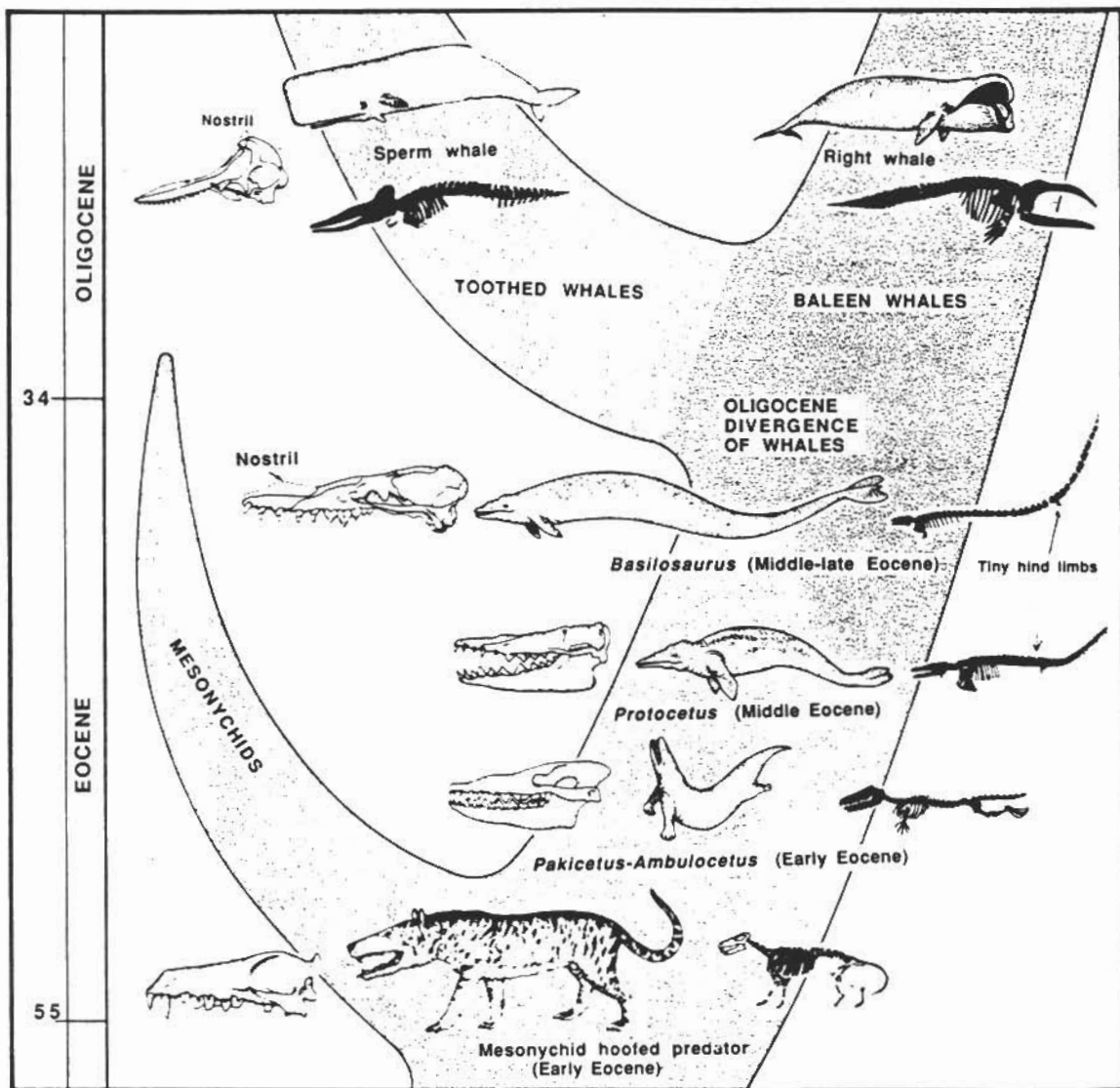


FIGURE 10—Evolution of the whales from mesonychids (based on Fordyce and Barnes, 1994; Thewissen et al., 1994).

which lacked trunk or tusks and looked more like a pygmy hippo, the next step is represented by the recently described *Numidotherium* from lower Eocene beds of Algeria, which had the beginning of the shortened skull and trunk (Mahboubi et al., 1984). In the Oligocene through Pleistocene, there were several major branches of the Proboscidea, including the deinotheres, with their downward-curved lower tusks, and the mammutids, which culminated in the Pleistocene American mastodon. The main line of elephant evolution through the gomphotheres and shovel-tuskers to the four-tusked stegotetrabelodonts led ultimately to mammoths and living elephants.

Whales.—Perhaps the most amazing story of mammalian evolution is how land dwelling hoofed mammals evolved into the fully aquatic whales and dolphins (Fordyce and Barnes, 1994) (Fig. 10). A few historical geology textbooks show typical Eocene archaeocete whales, but completely fail to mention all the recent evidence for their origins. For example, Levin (1992, p. 573) writes that “whales first appeared quite suddenly about 50 million years ago as already fully developed oceanic creatures.” No textbook says much about their four-legged ancestors, the huge predatory hoofed mesonychids, even though the origin of whales from hoofed mammals was first suggested by W.H. Flower in 1883, and connected to mesonychids by Leigh Van Valen (1966, 1968; Barnes and Mitchell, 1978).

This is even more surprising considering all the new discoveries of fossils which show the transition from mesonychids to fully aquatic whales (Gould, 1994). In 1983, Philip Gingerich, Donald Russell, and their colleagues discovered a transitional animal, *Pakicetus*, from the early Eocene of Pakistan. Although it had an archaeocete braincase, it still had very primitive ears that were incapable of echolocation. In addition, its teeth were intermediate between those of mesonychids and more advanced archaeocetes. Finally, it occurs in river sediments bordering on shallow seaways. Gingerich and his colleagues reconstructed this animal as partly aquatic and partly terrestrial, although the skeleton is unknown.

In 1990, new specimens of the archaeocete whale *Basilosaurus* from the Eocene deposits of northern Egypt were described by Gingerich and others. They were more complete than previous specimens, and showed that *Basilosaurus* had functional hind limbs complete with toes. However, the limbs were so tiny they could not have supported the animal's weight on land. The discoverers suggest that the limbs might have been used to help the male hold the female during mating, as many aquatic organisms do. It is just as likely, however, that these tiny hind limbs were simply useless vestiges with no function. Eventually, whales lost these limbs completely, and only their vestiges remain within their bodies.

Then in 1994, the best “transitional” fossil whale yet discovered was described by Hans Thewissen and colleagues. Dubbed *Ambulocetus natans* (“walking swimming whale”), it was found in lower Eocene river sediments in Pakistan not far from the locality that yielded *Pakicetus*. Its skull and teeth have the shape typical of mesonychids and primitive archaeocetes. The most exciting part of the find, however, was the skeleton. The front limbs are developed into flippers, clearly indicating an aquatic lifestyle. The hind limbs are still relatively long, however, with long toes that probably supported webbed feet. In this respect, the animal was more like an otter or a seal than a whale. Clearly, *Ambulocetus* was capable of walking on land better than a whale. However, the hind limbs could not support the body, but must have sprawled out to the side. The peculiarities of its back vertebrae suggest it was not as good a land walker as its ancestors, but may have wriggled along as do modern seals. This up-and-down wriggling of the spine suggests that that whales developed their up-and-down tail motion early in evolution. Unlike archaeocete whales (and like seals and otters), its primary propulsion came from the hind feet, and not from a tail fin.

CARNIVOROUS MAMMALS

Hoofed mammals provide some of the best documentation of mammalian evolution, since their robust bones tend to be more abundant. Some textbooks also discuss their predators as well. Once again, however, these books reproduce diagrams that are at least two decades out of date. Some (e.g., Cooper et al., 1990, Fig. 17-11) show carnivorans, whales, and ungulates as descended separately from the creodonts. This notion has not been seriously entertained since

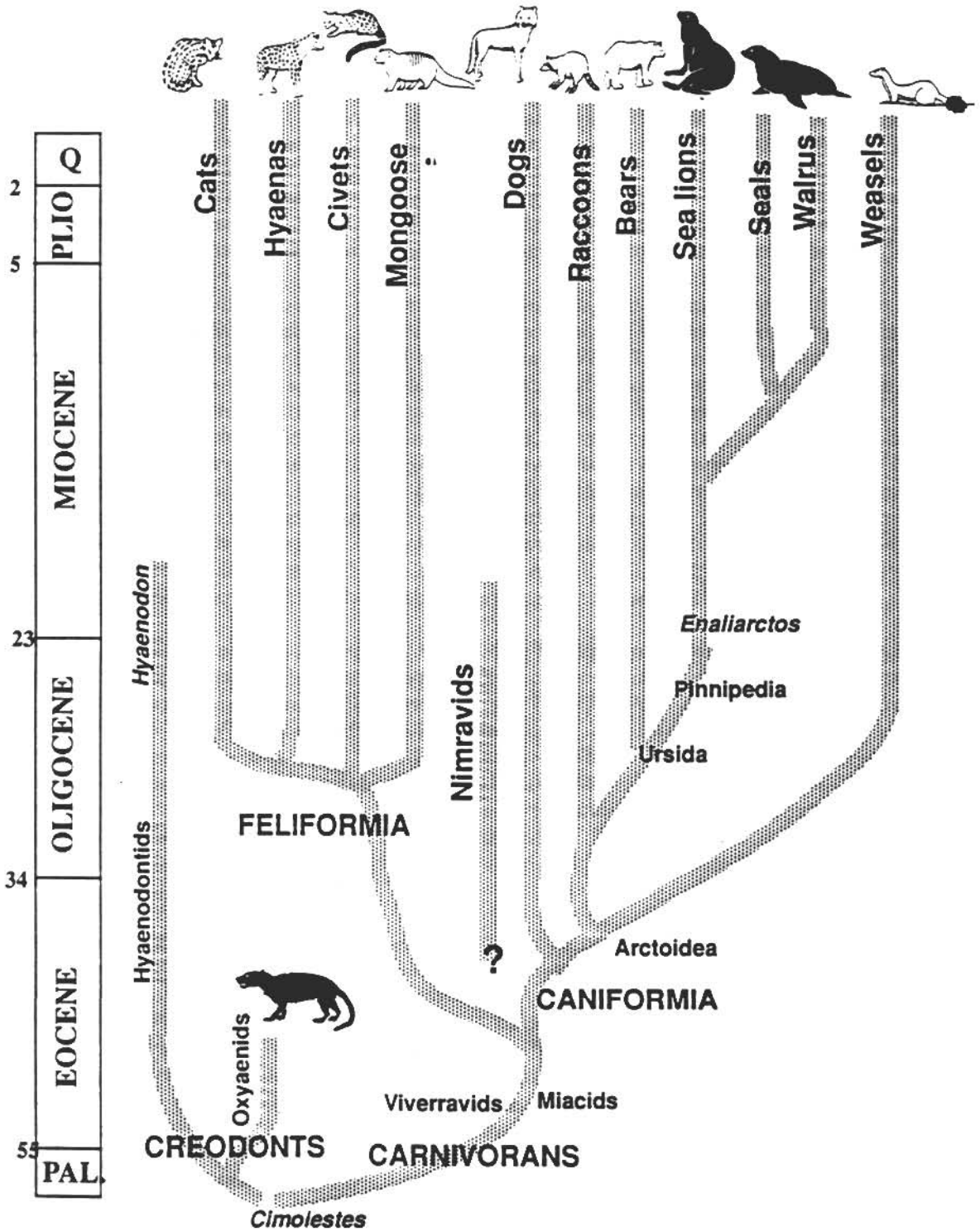


FIGURE 11—Relationships of the carnivorous mammals (Creodonta and Carnivora) (based on Flynn et al., 1988; Wyss and Flynn, 1993).

the 1930s, when "creodont" was used as a wastebasket for archaic hoofed mammals such as mesonychids and arctocyonids. Others (e.g., Wicander and Monroe, 1993, Fig. 19.14; Levin, 1992, Fig. 15-28) follow Colbert (1955), which was not even updated by Colbert and Morales (1991, Fig. 25-3). These diagrams show the carnivorans descended from a lineage separate from creodonts, but then leave their interrelationships unresolved. Today, we distinguish the carnivorans (members of the living order Carnivora, including all living carnivorous mammals) from the extinct Creodonta (the sister-group of Carnivora) by their shearing teeth, or carnassials. Carnivorans are most easily defined by the carnassial shear between their last upper premolar and first lower molar, whereas creodonts had carnassial shear between their first upper and second lower molars, or second upper and third lower molars.

Considering the recent vintage of these textbooks, it is surprising that they do not reflect the tremendous amount of new research on carnivorans (e.g., Tedford, 1976; Flynn and Galiano, 1982; Hunt, 1987; Flynn et al., 1988; Wyss and Flynn, 1993). At the very least, they could discuss some of the important conclusions about carnivoran phylogeny that have emerged in the last 15 years. Instead of an unresolved polytomy originating from a paraphyletic wastebasket family "Miacidae," these texts should show the fundamental arrangement of the carnivoran families (Fig. 11). After all, everyone is familiar with cats, dogs, bears, weasels, raccoons, hyaenas, and the rest. Recent research has clearly established that there are two main branches of carnivorans, the cat-like Feliformia (including cats, hyaenas, genets, civets, mongooses and their kin) and the more dog-like Caniformia. Within the Caniformia, the dogs split off first, followed by a fundamental split between the weasel clan (otters, skunks, wolverines, minks, ferrets, and weasels) and the bear clan (raccoons, pandas, and bears plus pinnipeds).

Most of these diagrams also incorrectly show the pinnipeds (seals, sea lions, and walruses) as a branch of carnivorans separated from the "fissipeds" (a wastebasket for all non-pinniped carnivorans). As early as 1869, W.H. Flower suggested that pinnipeds were related to the ursoids (bear-like group), and this was conclusively established by Wyss (1987; Wyss and Flynn, 1993). Yet Levin (1992, p. 573) writes, "Seals, sea lions, and walruses are known as pinnepeds [*sic*]. They are probably descended from semiaquatic mammals somewhat similar to present-day otters, but the transitional forms are as yet undiscovered." This statement is very dated for a book published in 1992. Archaic transitional pinnipeds from the early and middle Miocene, such as the enaliarctines, have been known since 1973 (Mitchell and Tedford, 1973; Barnes, 1979).

Another common mistake found in textbooks and tradebooks concerns the nimravids, or "paleofelids." These animals were extremely cat-like, so when the Big Badlands saber-toothed nimravid *Hoplophoneus*, or the dirk-toothed nimravid *Dinictis* are portrayed in reconstructions, they are usually mislabeled as "cats" (e.g., Levin, 1992, p. 551). However, recent research (Flynn and Galiano, 1982; Neff, 1983; Flynn et al., 1988; Bryant, 1991) has clearly shown that nimravids had nothing to do with true cats of the family Felidae; all of their cat-like features were extraordinary examples of convergence. Some (e.g., Flynn and Galiano, 1982) have argued that nimravids were related to the Caniformia, or dog-bear clade, and others (e.g., Bryant, 1991) have argued that they were feliforms, although there is still much controversy over where they belong within the Carnivora. Whatever nimravids were, *they were not cats!*

GLIRES

Students are usually overwhelmed by just a few diagrams of horses and other better-known examples from the Mammalia, so most textbooks neglect small mammals altogether. Rodents and rabbits just aren't as glamorous as sabertoothed cats, mammoths, or giant ground sloths. Yet over 40% of mammalian species (at least 1700 living today) are rodents, and one only need think about the reproductive rates of rats or rabbits to quickly realize that they easily outnumber all other mammals on earth by a large margin. If numbers or diversity were of prime importance, textbooks would focus on rodents and relegate most other mammals to brief sentences!

Given the general lack of interest among the public or the students, it is not surprising that rodents and rabbits get so little coverage. Nevertheless, some important basic ideas should be conveyed in the beginning textbooks. At very least, the basic arrangement of rodent anatomy, particularly with their distinctive chisel-like, ever-growing incisors, ought to be mentioned. Most students have watched a pet mouse or a hamster and have seen (and sometimes felt!) these teeth for themselves. If the instructor is more ambitious, the next step is to describe the different jaw muscle arrangements (Carroll, 1988, p. 490), and describe the fundamental separation between sciuriforms (squirrels, beavers, and their kin), myomorphs (rats and mice, hamsters, gophers, and their kin), and hystricomorphs (porcupines plus the South American rodents, or caviomorphs, such as the chinchilla, capybara, agouti, and Guinea pig). Further details of rodent phylogeny and systematics can be found in the symposium edited by Lockett and Hartenberger (1985).

Another important recent discovery is the close relationship of rodents and rabbits, and their common origin in the Paleocene of Asia. Most people are startled to find out that rabbits are *not* rodents, but the fundamental distinction between the two orders has been well known for over a century. Although rabbits also have chisel-like gnawing incisors, they have two pairs of them (only one pair in rodents), and there are many other important details in the skull and skeleton that distinguish the two orders. Nevertheless, there are a number of features in the skeletons and fetal development (Novacek et al., 1988; Lockett, 1985) that support the close relationship of rodents and rabbits, although some of the molecular evidence seems to contradict this conclusion (see discussion in Novacek et al., 1988, and Novacek, this volume).

Further corroborating the close relationship of the Glires (rodents plus rabbits) are a number of recent discoveries from the Paleocene and Eocene beds of China and Mongolia (Li and Ting, 1985, 1993; Li et al., 1987). Although the details of the relationships between eurymylids, mimotonids, and the later Glires are still controversial, there seems little doubt that these specimens demonstrate that both rodents and rabbits had a common origin in the Paleocene of east Asia. In the early Eocene, rodents then dispersed widely over the rest of the world, apparently displacing some rodent-like groups, such as the multituberculates and archaic primates (Krause, 1986; Maas et al., 1988). By the Oligocene, most of the living families of rodents and rabbits had become established, and since then they have become (by almost any standard) the most successful mammals on this planet. Rats will probably be around long after humans are extinct!

CENOZOIC FAUNAL EVOLUTION

Most treatments of Cenozoic mammals conclude with the examples of horses and brontotheres mentioned above, and completely ignore the extinct orders (particularly those of the early Cenozoic). Yet students often find it much easier to see the "big picture" of mammalian evolution, especially when it is presented in the context of the major Cenozoic climatic changes (Fig. 12) that are now becoming better understood (Stucky, 1990; Wing and Sues, 1992; Potts and Behrensmeyer, 1992; Janis, 1993; Dott and Prothero, 1994). In a nutshell, the history of Cenozoic climates, and the organisms that depend upon them, is a story of the deterioration of the Mesozoic greenhouse once ruled by the dinosaurs. Global cooling and drying events changed land vegetation from dense subtropical jungles to mixed forests, then to mosaics of woodland and scrubland, and eventually to grassland savanna and steppes (Webb, 1977; Wolfe, 1978; Retallack, 1990; Prothero, 1994a, 1995).

The climates of the Paleocene and early Eocene were warm and subtropical in most latitudes, with alligators, monitor lizards, pond turtles, and broadleaved evergreens (including palms and cycads) found even above the early Tertiary Arctic Circle (Estes and Hutchison, 1980; Wolfe, 1980; Schweitzer, 1980). Clearly, there were no polar ice caps, and the conditions at such high latitudes had to be mild for most of the year to allow these animals to survive. Inhabiting these subtropical forests at almost all latitudes were typical Paleocene faunas of western North America or Eurasia (Savage and Russell, 1983; Archibald et al., 1987), which contain a high percentage of tree-dwelling mammals (including the squirrel-like multituberculates and plesiadapids, and a variety of insectivorous mammals). On the ground beneath them were leaf-eating (browsing) mammals with low-crowned teeth, including a number of archaic ungulates ("condylarths") and the pantodonts. Their predators were mostly archaic wolf-like creodonts and the earliest true carnivorans (mostly weasel-sized), along with gigantic predatory birds 8 feet tall (see Feduccia, this volume). Most of these animals were no larger than a dog, and the largest mammals of the early Eocene, such as the pantodont *Coryphodon*, were cow-sized at best.

The Paleocene-Eocene transition in both Europe and North America is marked by the immigration of several groups that originated in Asia, including the perissodactyls, artiodactyls, and rodents. Krause and Maas (1990) suggested that these three orders evolved in isolation on the floating "Noah's ark" of the Indian subcontinent, and escaped to the Northern Hemisphere when India docked with Asia. In the early Eocene, dispersal between Eurasia and North America reached its peak, with many genera in common between the continents. This was probably due to the fact that both Beringia and the North Atlantic were traversed by land bridges (McKenna, 1983; Krause and Maas, 1990). The early-middle Eocene greenhouse, with its pandemic mammals, represents a peak in diversity of Cenozoic mammals, and diversity has been in decline ever since (Stucky, 1990).

At the climax of the early-middle Eocene, the earth began a slow, steady climatic change that culminated in Antarctic glaciers by the early Oligocene (Berggren and Prothero, 1992; Prothero, 1994a, b). The first major cooling event occurred at the end of the middle Eocene about 40-37 Ma, resulting in widespread extinction of temperature-sensitive marine organisms. Toward the end of the middle Eocene (late Uintan in North America), there was mass extinction (25% of the genera of North American land mammals). Most of the victims were archaic groups that can be associated with arboreal or browsing habitats. For example, the Uintan marked the last appearance in North America of such characteristically Paleocene to middle Eocene groups as mixodectids, microsypids, taeniodonts, achaenodonts, uintatheres, nyctitheriids, anatomorphine primates, sciuravid rodents, dichobunid artiodactyls, limno-

cyonid and "miacid" carnivorans, mesonychids, hyopsodonts, and isctolophid tapiroids. By the late Eocene (Chadronian), their places had been taken by a number of new groups of mammals known as the "White River Chronofauna." Many of these have living descendants, including the earliest dogs, camels, rhinos, pocket gophers, beavers, squirrels, rabbits, and shrews.

This late Eocene-Oligocene "White River Chronofauna" (Emry et al., 1987; Prothero, 1994a) is best represented in the White River Group of the Big Badlands of South Dakota. In most respects, it is transitional between the forest-dwelling Paleocene-Eocene faunas, and the savanna faunas of the late Miocene. Archaic groups with low-crowned teeth lived alongside more advanced groups, including oreodonts, camels, deer-like leptomerycids, horses, rhinos, and several kinds of advanced rodents and rabbits. Their predators included some of the first dogs and weasels, along with the cat-like nimravids (including saber-toothed *Hoplophoneus*), and the last of the creodonts, *Hyaenodon*.

In the earliest Oligocene (Orellan—33 Ma), another extinction event wiped out some of the last of the archaic Eocene groups, such as brontotheres, multituberculates, oromerycids, and several kinds of archaic rodents. According to Retallack's (1983, 1992) analysis of the Badlands paleosols, this extinction was due to a shift from mostly forested habitat to wooded grasslands and scrublands. The earliest Oligocene climatic change was even more severe in the reptiles and amphibians, with the aquatic crocodylians, pond turtles, and salamanders replaced by dry land tortoises (Hutchison, 1982, 1992). Even the land snails show a trend toward cooling and drying, with subtropical snails replaced by drought-tolerant types (Evanoff et al., 1992). Wolfe (1978, 1992) considered this the most extreme cooling event in the entire history of North American land plants. According to his methods of leaf margin analysis, mean annual temperature declined by 10°C and the annual range of temperature increased from 3-5°C to almost 25°C. In botanical terms, the subtropical late Eocene floras (found today in Central America) were replaced by broadleaved deciduous forests (found today in New England).

The ultimate cause of this earliest Oligocene cooling and drying was a global climatic change, formerly mislabeled the "Terminal Eocene Event." As now defined, however, the Eocene/Oligocene boundary (at 34 Ma) was relatively uneventful, and the biggest climatic change occurred about a million years later, in the earliest Oligocene (Prothero, 1994a). Many lines of evidence (summarized in Berggren and Prothero, 1992) indicate that this climatic change was caused by the growth of the first significant Antarctic ice caps. These ice sheets caused cold Antarctic bottom waters (the "psychrosphere") to form, and radically altered oceanic circulation and ultimately global climate. The cause of this Antarctic glaciation is usually attributed to the growth of circum-Antarctic circulation, as Australia and Antarctica separated sufficiently to allow deep-water flow between them (Murphy and Kennett, 1986; Kamp et al., 1990).

In the mid-Oligocene (Whitneyan—32-29 Ma), an even larger Antarctic glacial advance caused a major drop in sea level (Haq et al., 1987), and terrestrial climates were at their coolest and driest. In North America, the vegetation was mostly grassy scrublands, and eolian dunes were very common. Whitneyan faunas were low in diversity (Emry et al., 1987; Stucky, 1990), and dominated by a few groups, such as the leptachenine oreodonts, and the eumyine cricetid rodents, with higher-crowned teeth for eating tougher vegetation.

By the early Miocene, the Antarctic glaciers had retreated (until their ultimate return in the mid-Miocene, about 15 Ma), and climates had ameliorated somewhat. In North America, the early Miocene (late Arikareean-Hemingfordian—20-16 Ma) landscape (as shown by the

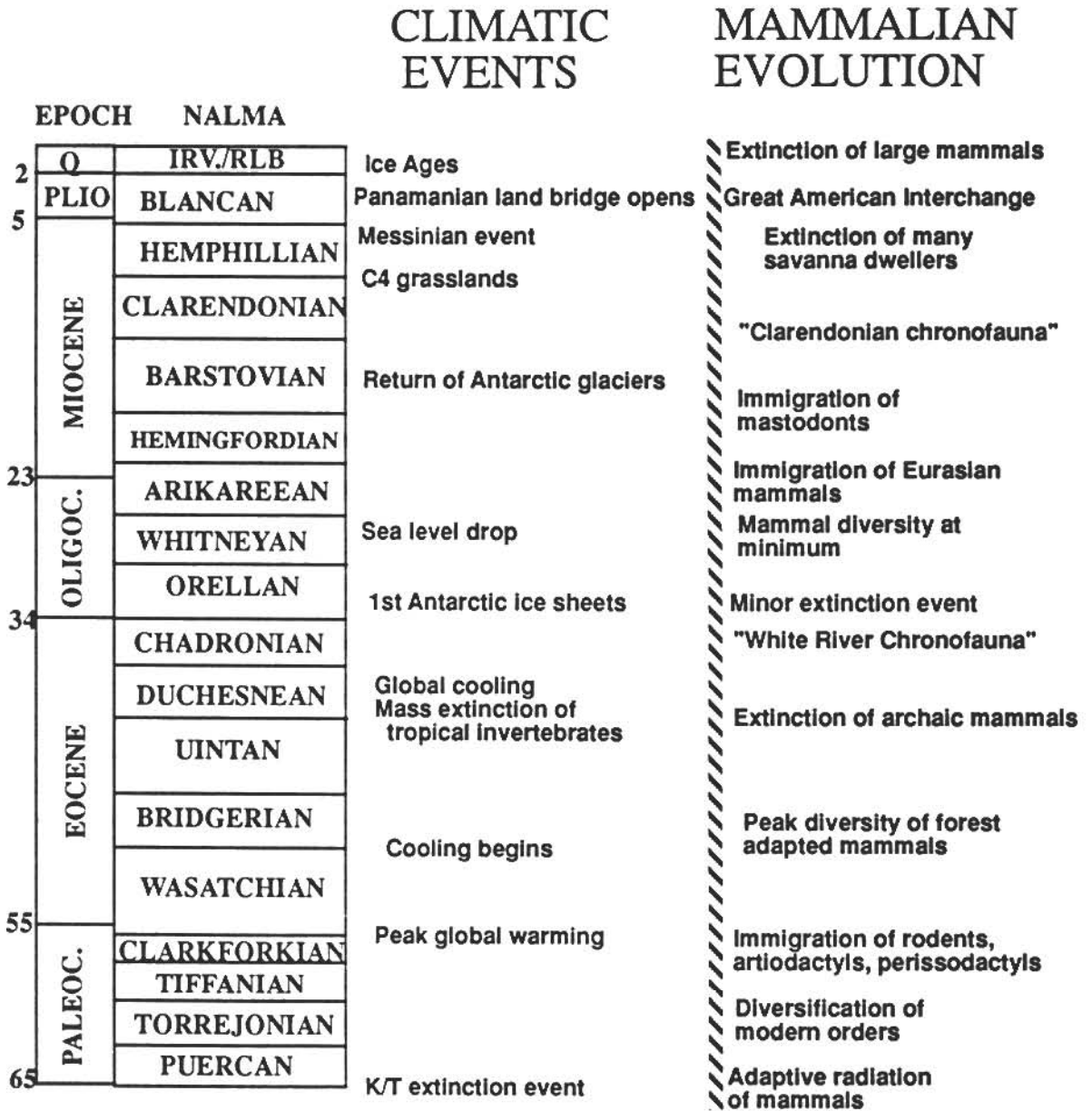


FIGURE 12—Summary of climatic events during the Cenozoic, and major events in North American mammalian history. Abbreviations: NALMA = North American land mammal "ages"; IRV./RLB = Irvingtonian/Ranchlabrean.

famous Agate Springs Quarry in western Nebraska) was dominated by a variety of browsing horses, camels, rhinos, deer-like ruminants, and some bizarre beasts, such as the huge pig-like entelodont *Dinohyus* and the clawed chalicothere *Moropus*. Many of these mammals were clearly related to Eurasian groups, indicating a significant increase in dispersal across the Bering corridor. Although many of the herbivores (especially the horses and camels) were clearly adapted for running, there is no evidence that they were adapted for grazing as well. According to Leopold et al. (1992), grasses were still rare, and most of the vegetation was open scrubland, although Retallack (1983, 1990, 1992) argues that there must have been extensive grasslands as well, based on the evidence from paleosols.

The mid-Miocene (Barstovian and Clarendonian—16–9 Ma) represents the flowering of the characteristic North American "Clarendonian chronofauna" (Webb, 1977, 1983, 1984), with its extraordinary diversity of ungulates. These included horses (12 different species in one locality), camels (including gazelle-like and giraffe-like forms), deer-like blastomerycids and dromomerycids, pronghorns, browsing and grazing rhinos (including the hippo-like *Teleoceras*), and immigrant mastodonts from the Old World. Preying upon them were a variety of dogs (including hyaena-like borophagines), amphicyonids ("bear dogs"), and some of the first true cats.

Traditionally, this fauna is compared to that of the modern African savanna, with its diversity of antelopes, cattle, zebras, giraffes, and their predators. However, the analogy may not be completely apt, since the isotopic signature of abundant C₄ grasses (warm season grasses typical of plains and savannas) in the soil carbonate does not begin until the late Miocene (around 8 Ma) in most parts of the world (Quade et al., 1989; Wang and Cerling, 1992). Yet a number of middle Miocene ungulates (especially horses—MacFadden, 1992, p. 240) had already developed high-crowned teeth, apparently for grazing. Solounias and Quade (1993) argue that the traditional scenario of early-middle Miocene savannas (e.g., Simpson, 1951; Webb, 1977, 1983) is a myth. Most middle Miocene mammals with hypsodont teeth apparently grazed within a mixed forest-C₃ grass habitat, and this is concordant with the palynological evidence of mixed habitats in the Miocene (Leopold and Denton, 1987). Only by the late Miocene did a grassy savanna prevail in Eurasia, Africa, and North America.

By the late Miocene (8 Ma), however, true grasslands were found throughout many of the continents. This late Miocene savanna fauna was decimated at the end of the Miocene (5 Ma), probably due to the climatic changes associated with the Messinian event. North American rhinos, horses, camels, dromomerycids, pronghorns, and many other groups were decimated, with few or no survivors to inhabit the steppe-like landscape of the Pliocene (Webb, 1984). Shortly thereafter, the world went into the fluctuating glacial-interglacial cycles of the Pleistocene. The dominant mammalian groups were adapted to living along the glacial margin, migrating with the changes in ice coverage (Kurtén, 1968, 1988; Kurtén and Anderson, 1980). The great Pleistocene megafauna included the familiar mammoths and mastodonts, giant bison, horses, camels, and ground sloths from South America. Their predators included saber-toothed cats, dire wolves, bears, lions, and smaller carnivorans, including weasels and raccoons.

Finally, the great Pleistocene megafauna was nearly extinguished at the end of the last glacial. Whether by human overhunting (Martin, 1984), or by abnormal climatic changes at the beginning of the present interglacial (Graham and Lundelius, 1984), or by some combination of both (Marshall, 1984), it left the continent depauperate in large mammals. Today, the small herds of bison, and a few deer and moose are the sole survivors of what was once a continent full of horses, camels, mammoths, and the like. Only in places such as East Africa can we see a diversity of mammals that approximates what North America or Eurasia supported through most of the Cenozoic.

CONCLUSION

Clearly, there is not enough space in a short course chapter such as this to update every aspect of mammalian evolution. The discussion above only brushes over the highlights of the evolution of the major groups of hoofed mammals, carnivorans, and rodents and rabbits (although these groups are by far the most common mammal fossils since the early Eocene). Many of these discoveries are relatively new, so non-specialists would not be expected to know about them. But that does not excuse trade books written by vertebrate paleontologists who should know better (e.g., Colbert and Morales, 1991; Stearn and Carroll, 1989), or textbook authors who should have done their homework (numerous examples given above). Moreover, many of these ideas are decades old, so it is even more disappointing to read descriptions of mammalian history that could have been written in 1955, as if nothing has been learned in the last forty years. Such outmoded ideas have no place in modern textbooks. We would reject any textbook that presented pre-1960 views of continental drift and plate tectonics. Why should our standards for mammalian paleontology in historical geology textbooks be any less strict?

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REFERENCES

- ARCHIBALD, J.D., W. A. CLEMENS, P.D. GINGERICH, D.W. KRAUSE, E.H. LINDSAY, AND K. D. ROSE. 1987. First North American land mammal ages of the Cenozoic Era, p. 24-76. *In* Cenozoic Mammals of North America, Geochronology and Biostratigraphy. M.O. Woodburne (ed.). University of California Press, Berkeley.
- BARNES, L.G.. 1979. Fossil enaliarctine pinnipeds (Mammalia, Otariidae) from Pyramid Hill, Kern County, California. Contributions to Science of the Natural History Museum of Los Angeles County 218.
- , AND E. D. MITCHELL. 1978. Cetacea, p. 582-602. *In* Evolution of African Mammals. V. J. Maglio and H.B.S. Cooke (eds.). Harvard University Press, Cambridge.
- BENTON, M.J. (ed.) 1988. The Phylogeny and Classification of the Tetrapods. Vol. 2: Mammals. Clarendon Press, Oxford, 326 p.
- BERGGREN, W.A., AND D.R. PROTHERO. 1992. Eocene-Oligocene climatic and biotic evolution: an overview, p. 1-28. *In* D.R. Prothero and W.A. Berggren (eds.), Eocene-Oligocene Climatic and Biotic Evolution. Princeton University Press, Princeton.
- , D.V. KENT, AND J.A. VAN COUVERING. 1985. The Neogene: Part 2. Neogene geochronology and chronostratigraphy. Geological Society of London Memoir 10: 211-260.
- BRYANT, H.N. 1991. Phylogenetic relationships and systematics of the Nimravidae (Carnivora). Journal of Mammalogy, 72: 56-78.
- CARROLL, R.L. 1988. Vertebrate Paleontology and Evolution. W.H. Freeman, New York, 698 p.
- CIFELLI, R.L. 1982. The petrosal structure of *Hyopsodus* with respect to that of some other ungulates, and its phylogenetic implications. Journal of Paleontology, 56: 795-805.

- COLBERT, E.H. 1935. Siwalik mammals in the American Museum of Natural History. *Transactions of the American Philosophical Society* 26:1-401.
- . 1955. *Evolution of the Vertebrates* (1st ed.). John Wiley, New York.
- , AND M. MORALES. 1991. *Evolution of the Vertebrates* (4th ed.). John Wiley, New York, 470 p.
- COOPER, J.D., R.H. MILLER, AND J. PATTERSON. 1990. *A Trip Through Time: Principles of Historical Geology* (2nd ed.). Merrill, Columbus, Ohio, 544 p.
- COPE, E.D. 1881. On some Mammalia from the lowest Eocene beds of New Mexico. *Proceedings of the American Philosophical Society*, 19: 484-495.
- . 1884. The Condylarthra. *American Naturalist*, 18: 790-805.
- COURT, N. 1990. Periotic anatomy of *Arsinoitherium* (Mammalia, Embrithopoda) and its phylogenetic implications. *Journal of Vertebrate Paleontology*, 10: 170-182.
- DOMNING, D. P., C. E. RAY, AND M. C. MCKENNA. 1986. Two new Oligocene desmostylians and a discussion of tethytherian systematics. *Smithsonian Contributions to Paleobiology* 59:1-56.
- DOTT, R.H., JR., AND D.R. PROTHERO. 1994. *Evolution of the Earth* (5th ed.). McGraw-Hill, New York, 569 p.
- EMRY, R.J., P.R. BJORK, AND L.S. RUSSELL. 1987. The Chadronian, Orellan, and Whitneyan land mammal ages, p. 118-152. *In* *Cenozoic Mammals of North America, Geochronology and Biostratigraphy*. M.O. Woodburne (ed.). University of California Press, Berkeley.
- ESTES, R., AND J.H. HUTCHINSON. 1980. Eocene lower vertebrates from Ellesmere Island, Canadian Arctic Archipelago. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 30: 325-347.
- EVANOFF, E., D.R. PROTHERO, AND R.H. LANDER. 1992. Eocene-Oligocene climatic change in North America: The White River Formation near Douglas, east-central Wyoming, p. 116-130. *In* *Eocene-Oligocene Climatic and Biotic Evolution*. D.R. Prothero and W.A. Berggren (eds.), Princeton University Press, Princeton.
- FISCHER, M.S., AND P. TASSY. 1993. The interrelation between Proboscidea, Sirenia, Hyracoidea, and Mesaxonia: the morphological evidence. p. 217-234. *In* *Mammal Phylogeny. Vol. II: Placentals*, F. S. Szalay, M. J. Novacek, and M. C. McKenna (eds.). Springer-Verlag, New York.
- FORDYCE, R.E., AND L.G. BARNES. 1994. The evolutionary history of whales and dolphins. *Annual Reviews of Earth and Planetary Sciences*, 22: 419-455.
- FLOWER, W.H. 1869. On the value of the characters at the base of the cranium in the classification of the Order Carnivora and the systematic position of *Bassaris* and other disputed forms. *Proceedings of the Zoological Society of London*, 1869: 4-37.
- . 1883. On whales, past and present, and their probable origin. *Notes and Proceedings of the Royal Institute of Great Britain*, 10: 360-376.
- FLYNN, J.J., AND H. GALIANO. 1982. Phylogeny of early Tertiary Carnivora, with description of a new species of *Protictis* from the middle Eocene of northwestern Wyoming. *American Museum Novitates*, 2725: 1-64.
- , N.A. NEFF, AND R.H. TEDFORD. 1988. Phylogeny of the Carnivora. p. 73-116. *In* *The Phylogeny and Classification of the Tetrapods*. M.J. Benton (ed.), vol. 2. Oxford: Clarendon Press.
- GAZIN, C. L. 1955. A review of the upper Eocene Artiodactyla of North America. *Smithsonian Miscellaneous Collections*, 128: 1-96.
- GENTRY, A. W., AND J. J. HOOKER. 1988. The phylogeny of the Artiodactyla. p. 235-272. *In* *The Phylogeny and Classification of the Tetrapods*. M.J. Benton (ed.), vol. 2. Oxford: Clarendon Press.
- GERAADS, D., G. BOUVRAIN, AND J. SUDRE. 1987. Relationships phyletiques de *Bachitherium* Filhol, ruminant de L'Oligocène d'Europe occidentale. *Palaeovertebrata*, 17 (2): 43-73.

- GINGERICH, P.D. 1980. Evolutionary patterns in early Cenozoic mammals. *Annual Reviews of Earth and Planetary Sciences*, 8: 407-424.
- , B. H. SMITH, AND E. L. SIMONS. 1990. Hind limbs of Eocene *Basilosaurus*: evidence of feet in whales. *Science*, 249:154-157.
- , N. A. WELLS, D. E. RUSSELL, AND S. M. IBRAHIM SHAH. 1983. Origin of whales in epicontinental remnant seas: new evidence from the early Eocene of Pakistan. *Science*, 220:403-406.
- GOULD, S.J. 1987. Life's little joke: the evolutionary history of horses and humans share a dubious distinction. *Natural History*, 96: 16-25.
- . 1988. The case of the creeping fox terrier clone. *Natural History*, 97(1): 16-24.
- . 1989. *Wonderful Life: The Burgess Shale and the Nature of History*. Norton, New York.
- . 1994. Hooking Leviathan by its past. *Natural History*, 103 (5): 8-15.
- GRAHAM, R. W. AND E. L. LUNDELIUS, JR. 1984. Coevolutionary disequilibrium and Pleistocene extinctions, p. 223-249. *In Quaternary Extinctions, A Prehistoric Revolution*. P.S. Martin and R.G. Klein (eds.). University of Arizona Press, Tucson.
- GROVES, C.P., AND P. GRUBB. 1987. Classification of living cervids, p. 21-59. *In The Biology and Management of the Cervidae*, C. Wemmer (ed.) Smithsonian Institution Press, Washington, D.C.
- HAMILTON, W. R. 1978. Fossil giraffes from the Miocene of Africa and a revision of the phylogeny of the Giraffoidea. *Philosophical Transactions of the Royal Society, Series B*, 283: 165-229.
- HAQ, B.U., J. HARDENBOL, AND P.R. VAIL. 1987. The chronology of fluctuating sea level since the Triassic. *Science*, 235: 1156-1167.
- HENNIG, W. 1965. Phylogenetic systematics. *Annual Review of Entomology* 10: 97-116.
- . 1966. *Phylogenetic Systematics*. University of Illinois, Urbana.
- HONEY, J. G., J. A. HARRISON, D. R. PROTHERO, AND M. S. STEVENS. 1995. Camelidae. *In Tertiary Mammals of North America*, K. M. Scott, C. Janis, and L. Jacobs (eds.). Cambridge University Press, Cambridge.
- HOOKER, J.J. 1989. Character polarities in early perissodactyls and their significance for *Hyracotherium* and infraordinal relationships. p. 78-101. *In The Evolution of Perissodactyls*. D. R. Prothero and R. M. Schoch (eds.). Oxford University Press, New York.
- HULBERT, R. C., JR. 1989. Phylogenetic interrelationships and evolution of North American late Neogene Equidae. p. 176-196. *In The Evolution of Perissodactyls*. D. R. Prothero and R. M. Schoch (eds.). Oxford University Press, New York.
- HUNT, R.M. 1987. Evolution of the aeluroid Carnivora: significance of the auditory structure in the nimravid cat *Dinictis*. *American Museum Novitates*, 2930: 1-32.
- HUTCHISON, J.H. 1982. Turtle, crocodylian and champsosaur diversity changes in the Cenozoic of the north-central region of the western United States. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 37: 149-164.
- . 1992. Western North American reptile and amphibian record across the Eocene/Oligocene boundary and its climatic implications, p. 451-463. *In Eocene-Oligocene Climatic and Biotic Evolution*. D.R. Prothero and W.A. Berggren (eds.), Princeton University Press, Princeton.
- JANIS, C. M. 1993. Tertiary mammal evolution in the context of changing climates, vegetation, and tectonic events. *Annual Reviews of Ecology and Systematics*, 24: 467-500.
- , AND K. M. SCOTT. 1987. The interrelationships of higher ruminant families with special emphasis on the members of the Cervoidea. *American Museum Novitates*, 2893: 1-85.
- AND ———. 1988. The phylogeny of the Ruminantia (Artiodactyla, Mammalia). p. 273-282. *In The Phylogeny and Classification of the Tetrapods*. M. J. Benton (ed.), vol. 2. Clarendon Press, Oxford.

- KAMP, P.J.J., D.B. WAGHORN, AND C.S. NELSON. 1990. Late Eocene-early Oligocene integrated isotope stratigraphy and biostratigraphy for paleoshelf sequences in southern Australia: paleoceanographic implications. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 80: 311-323.
- KRAUSE, D.W. 1986. Competitive exclusion and taxonomic displacement in the fossil record: the case of rodents and multituberculates in North America. *Contributions to Geology, University of Wyoming, Special Paper 3*: 95-117.
- , AND M. C. MAAS. 1990. The biogeographic origins of late Paleocene-early Eocene mammalian immigrants to the Western Interior of North America. *Geological Society of America Special Paper*, 243: 71-105.
- KURTÉN, B. 1968. *Pleistocene Mammals of Europe*. Columbia University Press, New York.
- . 1988. *Before the Indians*. Columbia University Press, New York.
- , AND E. ANDERSON. 1980. *Pleistocene Mammals of North America*. Columbia University Press, New York.
- LANCE, J. F. 1950. Paleontología y estratigrafía de Plioceno de Yepómera, Estado de Chihuahua. 1ª parte: Equidos, excepto *Neohipparion*. *Universidad Nacional Autónoma de México Instituto de Geología*, 54:1-81.
- LEINDERS, J.J.M., AND E. HEINTZ. 1980. The configuration of the lacrimal orifice in pecorans and tragulids (Artiodactyla; Mammalia) and its significance for the distinction between Bovidae and Cervidae. *Beaufortia*, 30: 155-160.
- LEOPOLD, E.B., AND M.F. DENTON. 1987. Comparative age of grassland and steppe east and west of the northern Rocky Mountains. *Annals of the Missouri Botanical Garden*, 74: 841-867.
- , G. LIU, AND S. CLAY-POOLE. 1992. Low-biomass vegetation in the Oligocene? p. 399-420. *In* D.R. Prothero and W.A. Berggren (eds.), *Eocene-Oligocene Climatic and Biotic Evolution*. Princeton University Press, Princeton.
- LEVIN, H.L. 1992. *The Earth Through Time* (4th ed.). Saunders College Publishing, Orlando, Florida.
- LI C.K. AND TING S.Y. 1985. Possible phylogenetic relationships of Asiatic eurymylids and rodents, with comments on the mimotonids. p. 35-58. *In* *Evolutionary Relationships among Rodents*. W.P. Luckett and J.-L. Hartenberger (eds.). Plenum, New York.
- AND ———. 1993. New cranial and postcranial evidence for the affinities of the eurymylids (Rodentia) and mimotonids (Lagomorpha). p. 151-158. *In* *Mammal Phylogeny. Vol. II: Placentals*, F. S. Szalay, M. J. Novacek, and M. C. McKenna (eds.). Springer-Verlag, New York.
- , R.W. WILSON, AND M.R. DAWSON. 1987. The origin of rodents and lagomorphs. *Current Mammalogy*, 1: 97-108.
- LUCAS, S. G., AND J. SOBUS. 1989. The systematics of indricotheres. p. 358-378. *In* *The Evolution of Perissodactyls*. D. R. Prothero and R. M. Schoch (eds.). Oxford University Press, New York.
- LUCKETT, W.P. 1985. Superordinal and intraordinal affinities of Rodents: developmental evidence from the dentition and placentation. p. 227-276. *In* *Evolutionary Relationships among Rodents*. W.P. Luckett and J.-L. Hartenberger (eds.). Plenum, New York.
- , AND J.-L. HARTENBERGER (eds.). 1985. *Evolutionary Relationships among Rodents*. Plenum, New York, 712 p.
- MAAS, M.C., D.W. KRAUSE, AND S.G. STRAIT. 1988. The decline and extinction of Plesiadapiformes (Mammalia, ?Primates) in North America: displacement or replacement? *Paleobiology*, 14: 410-431.
- MacFADDEN, B. J. 1984. Systematics and phylogeny of *Hipparion*, *Neohipparion*, *Nannippus*, and *Cormohipparion* (Mammalia, Equidae) from the Miocene and Pliocene of the New World. *Bulletin of the American Museum of Natural History*, 179: 1-196.
- . 1988. Horses, the fossil record, and evolution. A current perspective. *Evolutionary Biology*, 22: 131-158.

- PROTHERO, D.R. 1981. New Jurassic mammals from Como Bluff, Wyoming, and the interrelations of the non-tribosphenic Theria. *Bulletin of the American Museum of Natural History*, 167(5): 277-326.
- . 1987. The rise and fall of the American rhino. *Natural History*, 96(8): 26-33.
- . 1993a. Fifty million years of rhinoceros evolution. p. 81-87. *In* Proceedings of the International Rhino Conference, O. A. Ryder (ed.). San Diego Zoological Society, San Diego.
- . 1993b. Ungulate phylogeny: morphological vs. molecular evidence. p. 173-181. *In* Mammal Phylogeny. Vol. II: Placentals, F. S. Szalay, M. J. Novacek, and M. C. McKenna (eds.). Springer-Verlag, New York.
- . 1994a. The Eocene-Oligocene Transition: Paradise Lost. Columbia University Press, New York, 391 p.
- . 1994b. The late Eocene-Oligocene extinctions. *Annual Reviews of Earth and Planetary Sciences*, 22: 145-165.
- . 1995. The stratigraphic, paleogeographic and paleoclimatic background to North American mammalian evolution, *In* Tertiary Mammals of North America, K.M. Scott, C. Janis, and L. Jacobs (eds.), Cambridge Univ. Press, Cambridge (in press).
- , C. GUÉRIN, AND E. MANNING. 1989. The history of the Rhinocerotidae. p. 322-340. *In* The Evolution of Perissodactyls. D. R. Prothero and R. M. Schoch (eds.). Oxford University Press, New York.
- , E. MANNING, AND M. S. FISCHER. 1988. The phylogeny of the ungulates. p. 201-234. *In* The Phylogeny and Classification of the Tetrapods. M.J. Benton (ed.), vol. 2. Clarendon Press, Oxford.
- , ———, AND C. B. HANSON. 1986. The phylogeny of the Rhinocerotidae (Mammalia, Perissodactyla). *Zoological Journal of the Linnean Society of London* 87: 341-366.
- , AND R. M. SCHOCH. 1989. Origin and evolution of the Perissodactyla: summary and synthesis. p. 504-529. *In* The Evolution of Perissodactyls. D. R. Prothero and R. M. Schoch (eds.). Oxford University Press, New York.
- AND ———. 1995. Horns, Tusks, Hooves, and Flippers: The Evolution of Hoofed Mammals and their Relatives. W.H. Freeman, New York.
- , AND N. SHUBIN. 1989. The evolution of Oligocene horses. p. 142-175. *In* The Evolution of Perissodactyls. D. R. Prothero and R. M. Schoch (eds.). Oxford University Press, New York.
- , AND C. C. SWISHER III. 1992. Magnetostratigraphy and geochronology of the terrestrial Eocene-Oligocene transition in North America, p. 46-74. *In* Eocene-Oligocene Climatic and Biotic Evolution, D.R. Prothero and W.A. Berggren (eds.), Princeton University Press, Princeton.
- QUADE, J., T.E. CERLING, AND J.R. BOWMAN. 1989. Development of Asian monsoon revealed by marked ecological shift during the latest Miocene in northern Pakistan. *Nature*, 342: 163-165.
- QUINN, J.H. 1955. Miocene Equidae of the Texas Gulf Coastal Plain. Bureau of Economic Geology, University of Texas Publication, 5516: 1-102.
- RAINER, R. 1991. An Agenda for Antiquity: Henry Fairfield Osborn and Vertebrate Paleontology at the American Museum of Natural History, 1890-1935. University of Alabama Press, Tuscaloosa.
- RETALLACK, G.J. 1983. Late Eocene and Oligocene paleosols from Badlands National Park, South Dakota. Geological Society of America Special Paper 193.
- . 1990. Soils of the Past: An Introduction to Paleopedology. Unwin-Hyman, London.
- . 1992. Paleosols and changes in climate and vegetation across the Eocene/Oligocene boundary, p. 382-398. *In* D.R. Prothero and W.A. Berggren (eds.), Eocene-Oligocene Climatic and Biotic Evolution. Princeton University Press, Princeton.
- SAVAGE, D. E., AND RUSSELL, D. E. 1983. Mammalian Paleofaunas of the World. Addison Wesley, Reading, Massachusetts.

- SCHOCH, R. M. 1989. A review of the tapiroids. p. 298-320. *In* The Evolution of Perissodactyls. D. R. Prothero and R. M. Schoch (eds.). Oxford University Press, New York.
- SCHWEITZER, H.J. 1980. Environment and climate in the early Tertiary of Spitsbergen. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 30: 297-311.
- SCOTT, K. M., AND C. M. JANIS. 1987. The phylogenetic position of the Cervidae, and the case for a superfamily Cervoidea. p. 3-20. *In* The Biology and Management of the Cervidae. C. Wemmer (ed.). Smithsonian Institution Press, Washington, D.C.
- , AND ———. 1993. Relationships of the Ruminantia (Artiodactyla) and an analysis of the characters used in ruminant taxonomy. p. 282-302. *In* Mammal Phylogeny. Vol. II: Placentals, F. S. Szalay, M. J. Novacek, and M. C. McKenna (eds.). Springer-Verlag, New York.
- SCOTT, W.B. 1941. The mammalian fauna of the White River Oligocene. Part V. Perissodactyla. *Transactions of the American Philosophical Society*, 28: 747-790.
- SHOSHANI, J. (ed.) 1992. Elephants, Majestic Creatures of the Wild. Rodale Press, Emmaus, Pennsylvania.
- . 1993. Hyracoidea-Tethytheria affinity based on myological data. p. 235-256. *In* Mammal Phylogeny. Vol. II: Placentals, F. S. Szalay, M. J. Novacek, and M. C. McKenna (eds.). Springer-Verlag, New York.
- SIMPSON, G.G. 1945. The principles of classification, and a classification of mammals. *Bulletin of the American Museum of Natural History*, 85: 1-350.
- . 1951. Horses. Oxford: Oxford University Press.
- SKINNER, M.F., AND B.E. TAYLOR. 1967. A revision of the geology and paleontology of the Bijou Hills, South Dakota. *American Museum Novitates*, 2300: 1-53.
- SLOAN, R.E. 1987. Paleocene and latest Cretaceous mammal ages, biozones, magnetostratigraphic zones, rates of sedimentation and evolution. *Geological Society of America Special Paper*, 209: 165-200.
- SOLOUNIAS, N., AND J. QUADE. 1993. The savanna myth of the Miocene. *Journal of Vertebrate Paleontology*, 13 (3): 58A (abstract).
- STEARNS, C.W., AND R.L. CARROLL. 1989. Paleontology: the record of life. John Wiley, New York, 453 p.
- STUCKY, R.K. 1990. Evolution of land mammal diversity in North America during the Cenozoic. *Current Mammalogy*, 2: 375-432.
- STIRTON, R.A. 1940. Phylogeny of the North American Equidae. *University of California Publications in Geological Sciences*, 25: 165-198.
- SWISHER, C.C., III, AND D.R. PROTHERO. 1990. Single-crystal $^{40}\text{Ar}/^{39}\text{Ar}$ dating of the Eocene-Oligocene transition in North America. *Science*, 249: 760-762.
- TASSY, P., AND J. SHOSHANI. 1988. The Tethytheria: elephants and their relatives. p. 283-315. *In* The Phylogeny and Classification of the Tetrapods. M.J. Benton (ed.). vol. 2. Clarendon Press, Oxford.
- THEWISSEN, J.G.M., S. T. HUSSAIN, AND M. ARIF. 1994. Fossil evidence for the origin of aquatic locomotion in archaeocete whales. *Science*, 263: 210-212.
- , D. E. RUSSELL, P. D. GINGERICH, AND S. T. HUSSAIN. 1983. A new dichobunid artiodactyl (Mammalia) from the Eocene of north-west Pakistan. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen B*, 86: 153-180.
- TEDFORD, R.H. 1976. Relationships of pinnipeds to other carnivores (Mammalia). *Systematic Zoology*, 25: 363-374.
- VAN VALEN, L. 1966. Deltatheridia, a new order of mammals. *Bulletin of the American Museum of Natural History*, 132: 1-126.
- . 1968. Monophyly or diphily in the origin of whales. *Evolution*, 22: 37-41.
- . 1978a. Why not to be a cladist. *Evolutionary Theory*, 3: 285-299.
- . 1978b. The beginning of the age of mammals. *Evolutionary Theory*, 4: 45-80.

- WANG, Y., AND T. CERLING. 1992. Dietary evolution of horses: evidence from carbon isotopes in fossil tooth enamel. *Journal of Vertebrate Paleontology*, 12(3): 58A (abstract).
- WEBB, S.D. 1977. A history of savanna vertebrates in the New World. Part I: North America. *Annual Reviews of Ecology and Systematics*, 8: 355-380.
- . 1983. The rise and fall of the late Miocene ungulate fauna in North America, p. 267-306. *In* *Coevolution*. M. D. Nitecki (ed.). University of Chicago Press, Chicago.
- . 1984. Ten million years of mammal extinction in North America, p. 189-210. *In* *Quaternary Extinctions, A Prehistoric Revolution*. P. S. Martin and R. G. Klein (eds.). University of Arizona Press, Tucson.
- WICANDER, R., AND J.S. MONROE. 1989. *Historical Geology: Evolution of the Earth and Life through Time*. (1st ed.) West Publishing, St. Paul, Minnesota.
- , AND ———. 1993. *Historical Geology: Evolution of the Earth and Life through Time*. (2nd ed.) West Publishing, St. Paul, Minnesota.
- WING, S.L., AND H.-D. SUES. 1992. Mesozoic and early Cenozoic terrestrial ecosystems. p. 327-416. *In* *Terrestrial Ecosystems through Time*. A.K. Behrensmeyer, J.D. Damuth, W.A. DiMichele, R. Potts, H.-D. Sues, and S.L. Wing (eds.), University of Chicago Press, Chicago.
- WOLFE, J.A. 1978. A paleobotanical interpretation of Tertiary climates in the Northern Hemisphere. *American Scientist*, 66: 694-703.
- . 1980. Tertiary climates and floristic relationships at high latitudes in the Northern Hemisphere. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 30: 313-323.
- . 1992. Climatic, floristic, and vegetational changes near the Eocene/Oligocene boundary in North America, p. 421-436. *In* D.R. Prothero and W.A. Berggren (eds.), *Eocene-Oligocene Climatic and Biotic Evolution*. Princeton University Press, Princeton.
- WOODBURNE, M. O. 1989. Hipparion horses: a pattern of endemic evolution and intercontinental dispersal. p. 197-233. *In* *The Evolution of Perissodactyls*. D. R. Prothero and R. M. Schoch (eds.). Oxford University Press, New York.
- WORTMAN, J.L. 1896. Species of *Hyracotherium* and allied Perissodactyla from the Wahsatch and Wind River beds of North America. *Bulletin of the American Museum of Natural History*, 8: 81-110.
- WYSS, A.R. 1987. The walrus auditory region and the monophyly of pinnipeds. *American Museum Novitates*, 2871: 1-31.
- , and J.J. FLYNN. 1983. A phylogenetic analysis and definition of the Carnivora. p. 32-52. *In* *Mammal Phylogeny. Vol. II: Placentals*, F. S. Szalay, M. J. Novacek, and M. C. McKenna (eds.). Springer-Verlag, New York.