

FURRY FOLK: SYNAPSIDS AND MAMMALS

Of all the great transitions between major structural grades within vertebrates, the transition from basal amniotes to basal mammals is represented by the most complete and continuous fossil record, extending from the Middle Pennsylvanian to the Late Triassic and spanning some 75 to 100 million years.

—James Hopson, “Synapsid evolution and the radiation of non-eutherian mammals,” 1994

At the very beginning of their history, amniotes split into two lineages, the synapsids and the reptiles. Traditionally, the earliest **synapsids** have been called the “mammal-like reptiles,” but this is a misnomer. The earliest synapsids had nothing to do with reptiles as the term is normally used (referring to the living reptiles and their extinct relatives). Early synapsids are “reptilian” only in the sense that they initially retained a lot of primitive amniote characters. Part of the reason for the persistence of this archaic usage is the precladistic view that the synapsids are descended from “anapsid” reptiles, so they are also reptiles. In fact, a lot of the “anapsids” of the Carboniferous, such as *Hylonomus*, which once had been postulated as ancestral to synapsids, are actually derived members of the diapsids (Gauthier, 1994). Furthermore, the earliest reptiles (*Westlothiana* from the Early Carboniferous) and the earliest synapsids (*Protoclepsydrops* from the Early Carboniferous and *Archaeothyris* from the Middle Carboniferous) are equally ancient, showing that their lineages diverged at the beginning of the Carboniferous, rather than synapsids evolving from the “anapsids.” For all these reasons, it is no longer appropriate to use the term “mammal-like reptiles.” If one must use a nontaxonomic term, “protomammals” is a alternative with no misleading phylogenetic implications.

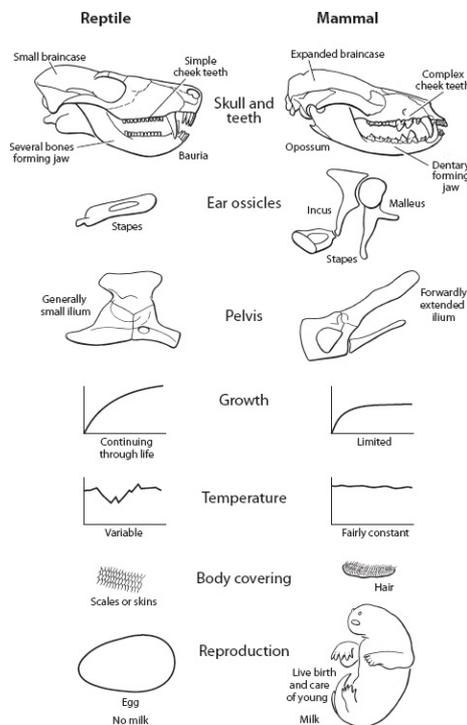


FIGURE 18.52 Some important anatomical and physiological differences between primitive amniotes and mammals. (Modified from E. H. Colbert and M. Morales, *Evolution of the Vertebrates* [4th ed.], copyright © 1991 Wiley-Liss, Inc. Reprinted by permission of Wiley-Liss, Inc., a division of John Wiley & Sons, Inc.)

From their origin in the Early Carboniferous, an amazing array of synapsid fossils shows the transition from early amniote to mammal in remarkable detail. Yet although the fossil record is excellent, many features that distinguish mammals from reptiles do not fossilize (fig. 18.52). Distinguishing features include:

1. **Physiological characters.** Mammals are usually defined as homeothermic (having constant body temperature) endothermic amniotes with hair. They also have other features related to their high metabolism and active lifestyles, such as a four-chambered heart, a diaphragm for actively pumping air in and out of the lungs, and a sophisticated brain with an enlarged neocortex. Most of these characters do not preserve in the skeleton. The internal molds of the brain cavity are known from many synapsids, so it is possible to determine when the enlargement of the neocortex occurs.
2. **Reproductive characters.** Another distinctive characteristic of mammals is their mode of reproduction. Most mammals (except the egg-laying platypus and echidna) give birth to live young, which the females then nurse with milk from their mammary glands. Instead of laying eggs and then abandoning them, mammals invest a lot of parental care in each offspring, so fewer are born, and they are born more helpless than hatchling reptiles or amphibians. Young mammals grow rapidly after birth, but their growth slows down to a terminal, adult growth stage (in contrast to most other animals, which grow continuously throughout their lives). The best way to detect a

pattern of terminal growth is by the presence of cartilaginous caps (**epiphyses**) on the ends of the long bones of juveniles, indicating that the animals underwent rapid growth as juveniles and then stopped growing when these caps fused to the shaft of the bone. Unfortunately, the other reproductive features have a very low fossilization potential, although there are indirect means of detecting some of them.

For paleontologists, the transformation to mammals must be detected in skeletal features that have at least some fossilization potential. Most of these give indirect evidence for mammalian physiology and reproduction. For example, there are many modifications of the skull and jaws for chewing and eating food more rapidly and efficiently, which is required for an animal with high metabolism. The teeth in early synapsids are simple cones or pegs for catching and puncturing prey, but later in synapsid evolution, the teeth become differentiated into nipping incisors in front, a large stabbing canine to catch and hold the prey, and multicusped cheek teeth (premolars and molars) for chewing up the food. Reptiles replace their teeth continuously throughout their lives, but mammals replace their deciduous teeth (“baby teeth”) only once, and the molars are never replaced. Many primitive amniotes have teeth on the palate and in the throat region for holding a struggling prey item, but mammals have teeth only on the margin of their jaws.

In reptiles, the nasal passage opens into the front of the mouth cavity, so that when a lizard is slowly swallowing a large prey item, it must hold its breath while there is food in its mouth. Clearly, the high metabolism of mammals would not allow them to hold their breath for long while eating or chewing. For this reason, the bones of the upper jaw grow toward the midline and form a **secondary palate** that roofs over the original amniote palate, so the internal nasal passage is enclosed and opens in the back near the throat. (If you feel the roof of your mouth with your tongue, you can detect the suture along the midline of your palate. Some babies have a birth defect called *cleft palate*, where the two halves of the secondary palate fail to grow together, making it difficult for them to eat and breathe.)

The primitive synapsid jaw was a simple snap-trap mechanism, with a strong temporal muscle pulling up on the jaw and inserting on the top of the skull behind the eyes. Numerous bones made up this primitive jaw: the dentary in front, which bore the teeth; the articular, which formed the jaw hinge with the quadrate bone of the skull; the coronoid, forming a ridge on the top of the back of the jaw; the angular and surangular, on the back lower corner of the jaw, and several others (fig. 18.53). Such a jaw was suitable for grabbing and crushing prey, but not for chewing. A single-element jaw is mechanically much stronger against the pressures and torque of the chewing motion than one with numerous elements that are sutured together; the sutures are lines of weakness under stress. Through synapsid evolution, the postdentary elements of the jaw become smaller and smaller as the dentary became the primary, and eventually the only, bone of the jaw. As the postdentary elements reduced in size and most of them disappeared, the dentary extended back and took their place as the main area of muscle attachment. Eventually, the dentary developed a tall coronoid process to which the temporal muscles attached, allowing these animals to have even greater bite strength. In addition, a pair of new muscles, the masseters, arose between the outer edge of the cheek bones and the outer side of the jaw, allowing front-back and side-to-side motion in chewing (fig. 18.54).

Eventually, the nondentary bones of the jaw were lost completely (although some persisted even in the earliest mammals) as the dentary expanded backward and took their place. In advanced synapsids, the dentary reaches far enough back to touch the squamosal bone of the skull and develop a dentary/squamosal jaw joint, replacing the old reptilian quadrate/articular jaw joint. In some specimens, such as *Diarthrognathus* (Greek: “double jaw joint”), both jaw joints operated side-by-side on each side of the head. Eventually, however, the dentary/squamosal joint took over completely, and then the quadrate and articular no longer functioned as a jaw joint. Instead of vanishing, however, they took over a new function. In reptiles, they served not only as a jaw hinge, but are also able to transmit sound to the ear, as most reptiles can hear with their lower jaws (fig. 18.55). (The snake charmer’s flute is for the spectators, not the cobra, as snakes cannot hear well when their jaw is up off the ground in a threat posture.) Once the quadrate and articular became detached from the jaw hinge, they took up a different role as bones of the middle ear. The quadrate became the incus, or “anvil” bone, and the articular became the malleus, or “hammer” bone. (The “stirrup” bone, or stapes, has been in the ear since the early tetrapods.) When sound vibrates your eardrum, the chain of bones—“hammer,” “anvil,” and “stirrup,” or malleus, incus, and stapes—that transmits this vibration to the inner ear is actually a remnant of your reptilian jaw apparatus. This amazing story is apparent not only in synapsid fossils, but also in mammalian embryology. When you began your development, your ear bones started out as part of your jaw, but were transferred entirely to your ear later in ontogeny.

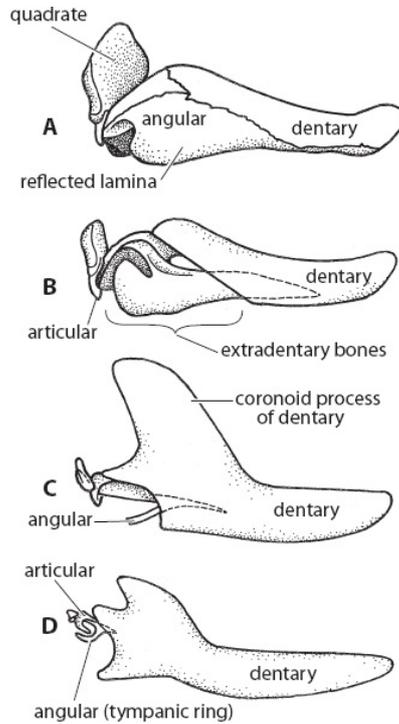


FIGURE 18.53 Transformation of the jaw and skull region during synapsid evolution. Primitive synapsids such as the finback *Dimetrodon* (A) had a lower jaw composed of many different bones hinged from the quadrate bone of the skull. In more advanced synapsids (B–D), the dentary expands until it becomes the only jaw bone, and the nondentary bones shrink and are eventually lost, except for the quadrate and articular bones of the jaw joint, which go to the middle ear. (From *Paleontology: The Record of Life*, by C. Stearn and R. L. Carroll, copyright © 1989 John Wiley & Sons, Inc. Reprinted by permission of John Wiley & Sons, Inc.)

Other skeletal modifications are apparent as synapsids became mammals. The early amniotes had a sprawling posture, resting on their bellies with the legs held out from the side of the body, but midway through synapsid evolution, the body adopted an erect posture, with the limbs held under the body and moving rapidly fore and aft. These skeletal changes are particularly evident in the shoulder blade, which flares out into a broad triangle with a ridge down the middle for more complex muscle insertions. The hips became long and narrow for greater flexibility, with forward expansions of the ilium bone for stronger leg muscles, and eventually the three bones of the pelvis fused into a single bone (not the multiple bones of the primitive amniote hip). The free ribs of the chest are linked together with a breastbone, forming a solid rib cage. This means that advanced synapsids could not breathe by flexing their ribs, but must have had a muscular wall in their chest cavity called a **diaphragm** to pump their lungs within the rigid rib cage. The ribs of the lower back, on the other hand, were lost, allowing the trunk to become more flexible. The small lower temporal opening of primitive synapsids became larger and larger as the jaw muscles expanded, until only a thin cheek bone, the zygomatic arch, remained. In many advanced synapsids and in most mammals, the temporal opening is so large that the bony bar between it and the eye is lost. The single ball joint that connects the skull to the vertebral column (the **occipital condyle**) in reptiles split into two small ball joints on either side of the spinal column, allowing much greater strength and stability in moving the head to catch and hold prey.

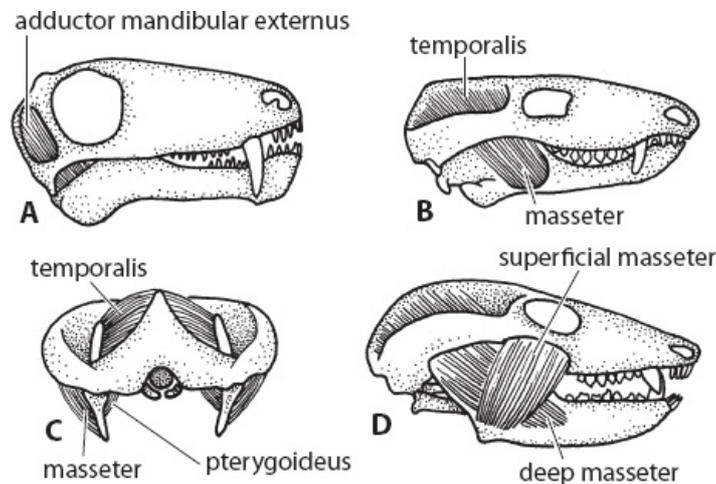


FIGURE 18.54 Primitive synapsids such as *Biarmsuchus* (A) had only a single jaw adductor muscle. *Thrinaxodon* (B and C) had both temporal and masseter muscles, and advanced cynodonts (D) divided the masseter into two branches for complex chewing

motions. (From *Paleontology: The Record of Life*, by C. Stearn and R. L. Carroll, copyright © 1989 John Wiley & Sons, Inc. Reprinted by permission of John Wiley & Sons, Inc.)

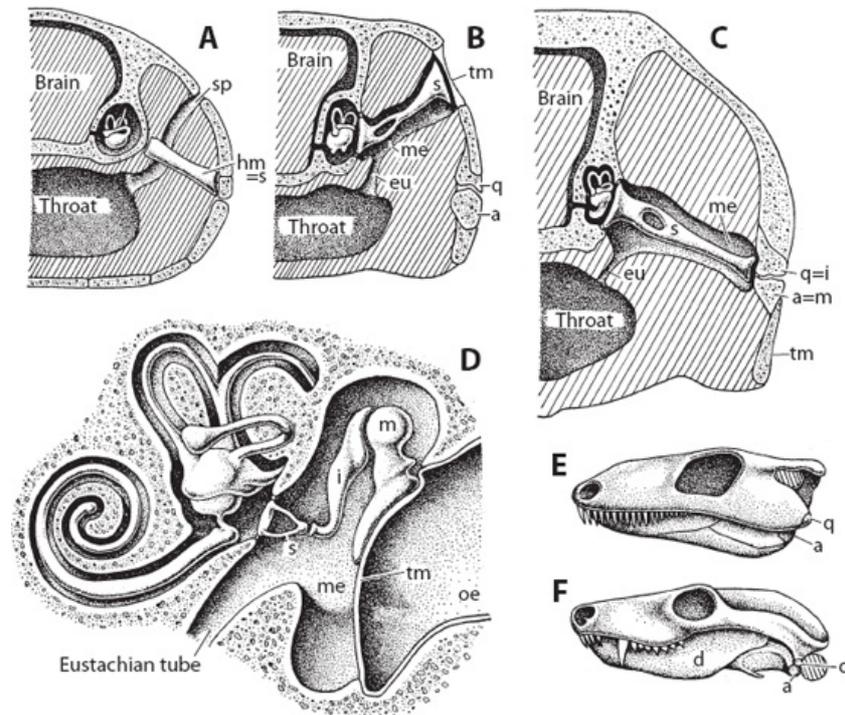


FIGURE 18.55 Evolution of the mammalian ear. In the fish (A), the hyomandibular bone (hm) acts as a bony strut, transmitting sound from the gill arches to the inner ear. In amphibians (B), it becomes the stapes (s), which vibrates with the eardrum (tm). In primitive amniotes (C), the stapes transmits sound from the jaw joint bones, the quadrate (q) and articular (a). These bones then become the incus (i) and malleus (m) of the middle ear of mammals (D). As these bones shift to the ear, the dentary (d) bone of the jaw contacts the squamosal bone of the skull to establish a new jaw joint (E and F). Other abbreviations: eu, eustachian tube; me, middle ear cavity; oe, outer ear cavity; sp, spiracle. (Modified from Romer, 1933.)

Most of these skeletal features can be traced through the course of synapsid evolution (figs. 18.56 and 18.57). For example, the earliest synapsids (mostly from the Pennsylvanian–early Permian) are known as the **pelycosaurs** (a paraphyletic group, unless it includes the rest of the synapsids), and include such familiar forms as the predatory finback *Dimetrodon* (often mistaken for a dinosaur). This animal and the herbivorous finback *Edaphosaurus* had large “sails” along their backs supported by long spines extending from their vertebrae. Many ingenious ideas have been proposed for the function of these fins, but the most plausible is that they served as heat gathering and dumping devices for thermoregulation. They have almost exactly the amount of surface area for an animal of that body volume to allow them to dump heat when the sail is out of the sun, and pick up heat when it is exposed broadside to the sun. This suggests that the earliest synapsids were not yet endotherms, but used sunning behavior to regulate their body temperature (as do most living reptiles). The “pelycosaurs” were primitive synapsids in many other aspects. They had a sprawling posture with a simple shoulder blade, a small iliac blade on the pelvis, and a simple thigh bone. Their teeth were simple conical pegs (although those in the canine position were a bit larger) replaced multiple times, and they had no secondary palate; instead, they had many teeth on their original, reptilian palate and in the throat region. They had a single ball joint in the back of the skull, a small brain, and a jaw composed of a small dentary and many accessory jaw bones. Indeed, the primary feature that earmarks the “pelycosaurs” as synapsids is the presence of the lower temporal opening, although it is small, indicating relatively small jaw muscles.

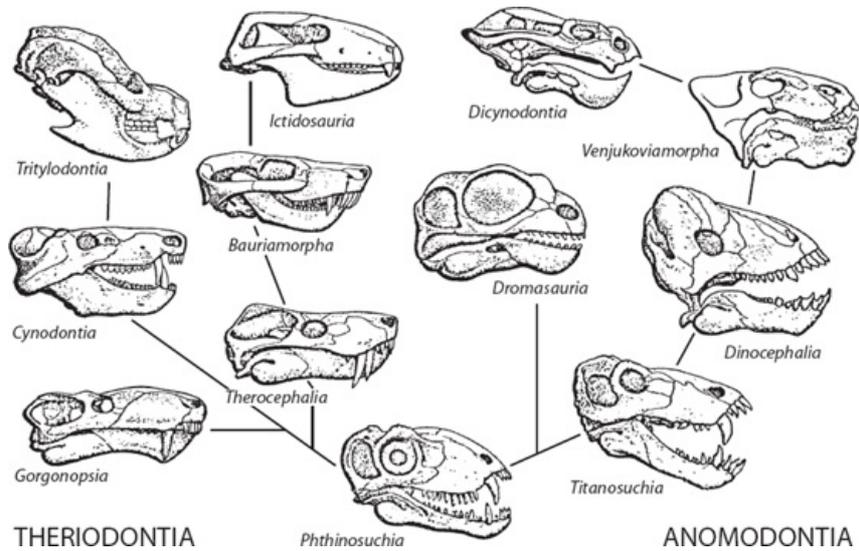


FIGURE 18.56 Variation in the skulls of therapsids and cynodonts. (Modified from Romer, 1966.)

By the Late Permian, the first radiation of “pelycosaurs” became extinct, and a “second wave” of synapsids, the **therapsids** (also a paraphyletic group, unless it includes the higher synapsids and mammals) came to dominate the landscape (fig. 18.57). Many of these “therapsids” (such as the biarmosuchids, gorgonopsians, and therocephalians) were wolf-sized or bear-sized predators, with huge canine teeth and much stronger jaws (as shown by the enlarged dentary and temporal openings). They also had a more upright posture, and the more advanced forms even had a short secondary palate. These predators could have killed and eaten not only more primitive reptiles of the Late Permian (such as the parieasaurs discussed in the anapsid section of this chapter), but also two groups of herbivorous “therapsids,” the dicynodonts and the dinocephalians. The dicynodonts (Greek: “two dog teeth”) had an almost toothless beak (except for large canines) for munching plants and a sliding jaw joint that gave them a chewing motion. With over 70 genera, they were the dominant herbivores of the Late Permian of Russia and South Africa, and some, such as the cow-sized *Kannemeyeria*, survived until the Late Triassic. The dinocephalians (Greek: “terrible head”) were huge (some up to 5 m long and weighing over a ton) sprawling, hippo-like “therapsids,” with a massive rib cage and thick, stocky limbs. The bone over the braincase was very thick, suggesting to some paleontologists that they engaged in head-to-head butting (Barghusen, 1975). Some genera, such as *Estemmenosuchus*, had bizarre crests, knobs, and flanges sticking out from their heads, probably for display to other members of their species. About 40 genera of dinocephalians are known from the Late Permian of Russia and South Africa, but they did not survive to the end of the Permian.

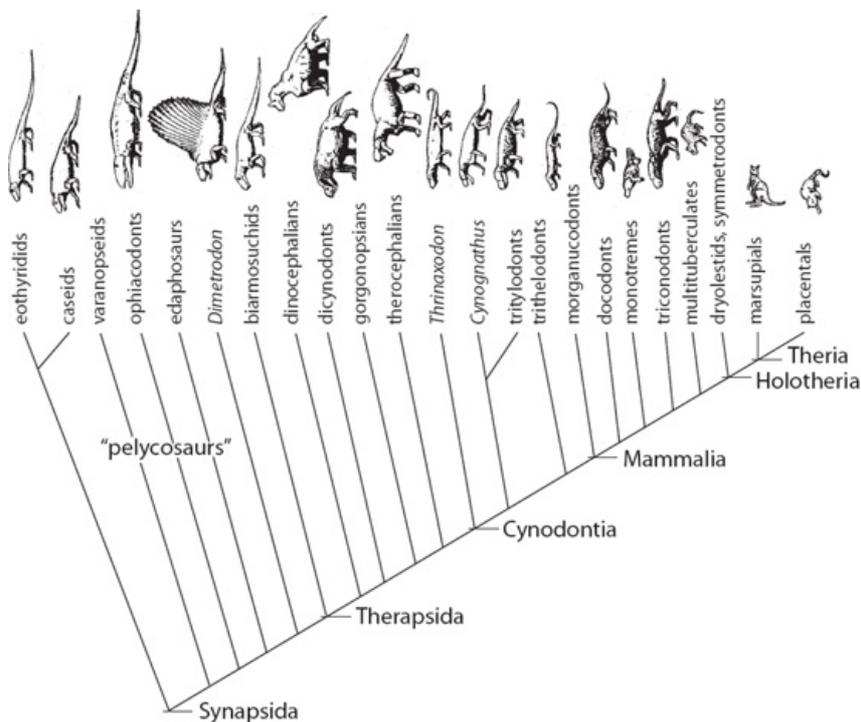


FIGURE 18.57 Phylogeny of the synapsids and primitive mammals.

The Permian catastrophe decimated most of the “therapsid” radiation, except the dicynodonts and the lineage that led to third radiation of synapsids in the Triassic, the **cynodonts** (again, a paraphyletic group, unless it contains the mammals). The “cynodonts” were mostly weasel- to dog-sized predators (although *Cynognathus* was bear-sized) with many advances toward the mammalian condition. As exemplified by *Thrinaxodon*, they had an upright posture, with a more advanced shoulder blade and pelvis and an additional muscle attachment point, the greater trochanter, on the thigh bone. *Thrinaxodon* had broad flanges on its ribs, which stiffened its trunk; it must have breathed with a diaphragm. In the skull, the teeth were almost fully differentiated into incisors, canines, and molariform cheek teeth, and were located only on the margin of the jaw. The secondary palate was now extended near to the end of the cheek tooth row, and the nondentary jaw elements were very small. *Thrinaxodon* also has small pits on its snout for whiskers, suggesting that it had at least some body hair. The temporal opening was already quite large in the therapsids, but there is good evidence that these animals also had masseter muscles, giving them complex chewing motions. Their brain was also quite a bit larger, and there was a double ball joint articulating with the neck vertebrae. In most respects, “cynodonts” were very close to mammals, except that they still had all the accessory jaw bones (although these are greatly reduced). In some “cynodonts,” the angular bone at the corner of the jaw form a hook-like process that apparently supported an eardrum, so the postdentary bones both supported the jaw and aided in hearing.

Hearing with Their Jaw Bones: The Mammals

With malleus Aforethought Mammals Got an earful of their ancestors' Jaw.

—John Burns, *Biograffiti*, 1975

The synapsids had been the dominant and most diverse land animals through most of the Permian and Triassic, but by the Late Triassic, they were largely replaced by the rapidly evolving archosaurs (especially the dinosaurs). Most of the “cynodont” lineages (along with the dicynodont stragglers from the Permian) were extinct. Instead, there were a number of very small-bodied, mammal-like “cynodont” lineages that approach mammals in most features, yet most paleontologists are unwilling to call them mammals. Some, like the tritylodonts, had a very rodent-like skull with long incisors, no canines, and rows of molars with multiple cusps for grinding; they had a long body shaped like a weasel. Others, such as the ictidosaur or trithelodonts, had very advanced jaws—*Diarthrognathus* (mentioned above) had both a dentary/squamosal and quadrate/articular jaw joint operating side-by-side. However, most paleontologists do not regard a fossil as mammalian until it had a robust dentary/squamosal jaw joint; others use the presence of an incus and malleus in the middle ear as their criterion for a mammal. This condition first appears in the latest Triassic and Early Jurassic with tiny, shrew-sized animals such as *Morganucodon* and *Sinoconodon* (fig. 18.58). Although they have a robust dentary/squamosal jaw joint, they retain vestiges of some of the other nondentary jaw bones on the inside and back of the jaw. They had an upright mammalian posture, with a long blade on the iliac portion of the fused pelvis, an advanced thigh bone with several bony processes for attaching muscles, and a broad shoulder blade with a spine down the middle (although the primitive amniote interclavicle bone was still present in the shoulder). Their teeth were specialized into incisors, canines, premolars, and molars, and had only a single replacement. However, they did not yet have the precise occlusion of the teeth seen in more advanced mammals.

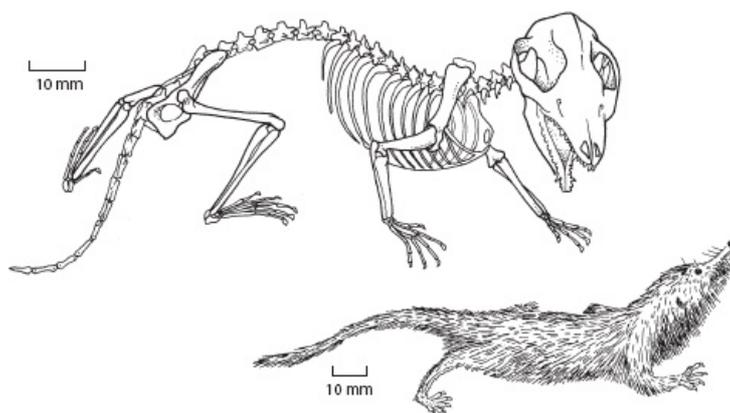


FIGURE 18.58 One of the earliest mammals was the shrew-sized *Morganucodon*. (Modified from M. Benton, 1995, *Vertebrate Palaeontology* [1st ed.]. Copyright © 1995 Wiley-Liss, Inc. Reprinted by permission of Wiley-Liss, Inc., a division of John Wiley & Sons, Inc.)

In the Jurassic, mammals remained small (rat- to shrew-sized) animals that may have hidden from the dinosaurs in the undergrowth and may have been mostly nocturnal. They remained as tiny, nocturnal animals under the feet of the dinosaurs, or in the trees above them, through about two-thirds of their history (the entire Jurassic and Cretaceous, spanning over 120 m.y.). Consequently, Mesozoic mammal fossils are also tiny, and tend to be fragmentary and hard to find. Most of what is known about Mesozoic mammals comes from tooth and jaw fragments, although in recent years, skeletal remains have been discovered for many the major groups. One important lineage is the morganucodonts and their relatives, including the triconodonts and docodonts (fig. 18.57). These mammals tend to have the main cusps of their cheek teeth oriented in a line. For example, a

typical triconodont tooth has a single main cusp, and shorter cusps in front and in back of it. These cusps occluded directly on top of, or just in front of, the corresponding cusps on the opposite tooth in the jaw. The other main lineage of Mesozoic mammals had a completely different occlusal pattern. The cusps of their teeth were arranged in a triangular fashion, with the triangles of the upper molars fitting into the V-shaped valleys between (rather than on top of) the reversed triangles of the lower molars. This is similar to the way the triangular teeth of a pair of pinkish shears occlude as you close the blades together. This “reversed triangle” condition is a derived feature found in all the higher mammals, variously known as the “Theria” or the “Holotheria” (Hopson, 1994).

The most primitive of these holotherians was *Kuehneotherium* from the Upper Triassic rocks of England. The best known of the holotheres were common in the Upper Jurassic dinosaur beds of North America and Europe, and were once known by the paraphyletic wastebasket taxon “pantotheres.” These primitive therians are sister-taxa to the living mammals and include the dryolestids, the symmetrodonts, and the paurodonts (Prothero, 1981). Some dryolestids and symmetrodonts still had tiny vestiges of the nondentary jaw bones, but in other respects they are fully mammalian. Their high-crowned triangular teeth were very compressed in the front-to-back direction, because there were as many as eight or nine molars on each side of the jaw (most living mammals only have three or four).

In addition to the triconodont lineage and the dryolestid–symmetrodont (therian) lineage, there were at least two other lines of mammalian evolution whose systematic position has been controversial. One group was the **multituberculates** (fig. 18.59). They looked somewhat squirrel-like with their chisel-shaped incisors in front and a gap between the incisors and cheek teeth. In some multituberculates, the skeleton was also quite squirrel-like, with a long, prehensile tail, and an ankle that could twist backward, allowing them to climb down trees headfirst. Multituberculates get their name from their complex molars, which are broad grinding mills with two or three rows of cusps (“tubercles”) for processing nuts and seeds. Most advanced multituberculates also had an enlarged, blade-like tooth in front of the lower cheek teeth, which may have been used for slicing open hard nuts, seeds, and fruits. Despite their rodent-like appearance, multituberculates were still primitive mammals in many features, so their rodent-like features are due to evolutionary convergence. The earliest multituberculates appeared in the Late Jurassic, long before rodents evolved, and the group persisted until the late Eocene, a span of over 180 m.y. By this criterion, they survived longer than any other order of mammals, living or extinct, and could be considered one of the most successful groups of mammals ever. Apparently, multituberculates finally met their doom in the Eocene due to climate changes that decimated their forest habitat or possibly from competition from the rodents, which apparently were more successful in occupying the same niche.

The position of the multituberculates within the mammals has long been controversial, with some arguing that they are prototherians, and others arguing that they are related to primitive therians. The latest consensus places them as a sister-group to the holotherians, between the triconodonts and dryolestids (fig. 18.57). Another line of mammalian evolution has also been a mystery, although a few fossils were left behind. This group is the **monotremes**, or the egg-laying mammals, such as the duckbilled platypus and the “spiny anteater” or echidna. Today, they are confined to Australia and New Guinea, but fossil monotremes are also known from the Paleocene of Argentina. Monotremes lay a pea-sized, soft-shelled egg, which has a sticky shell and is carried in a shallow slit (not quite a pouch) on the female’s belly. Once the egg hatches, the young lap up milk extruded from mammary glands without nipples. Monotremes have a much more primitive physiology than any other living mammal. For example, their body temperature is not very well regulated, but fluctuates with the environmental temperature (although not as much as does a true ectotherm). Their urogenital tract (fig. 18.60) is essentially a primitive amniote cloaca (Latin: “sewer”), into which both the reproductive openings and the waste openings from the kidney (the urethra) empty.



FIGURE 18.59 The squirrel-like multituberculates were the longest-lived group of mammals, ranging from the Jurassic to the Eocene. (From Dott and Prothero, 1994.)

So what are monotremes related to? The monotreme skeleton still has many primitive synapsid features, including archaic bones in shoulder and hip that are found in no other living mammal. These elements would suggest that monotremes are more primitive than dryolestids and are possibly related to the “prototherians.” Because Mesozoic mammals are known primarily from teeth, we need tooth fossils to make proper comparisons, but only juvenile monotremes have teeth, and they are so peculiar that for years no one could make sense of them. In 1975, a Miocene monotreme was described that gave a slightly better insight into the origins of their teeth, and in 1985 a Cretaceous monotreme preserved in opal was found in an mine and rescued just before it was made into jewelry. These specimens have teeth that are slightly more advanced than those of dryolestids, although they are not fully tribosphenic either. This evidence seemed to suggest that monotremes are in fact therian mammals that diverged sometime in the Middle Jurassic, possibly before dryolestids but after symmetrodonts, and have persisted with little change since then. However, more recent analyses of the ear region and skeleton suggest that monotremes are more primitive than triconodonts and are at the very base of the mammalian radiation. The most important implication of the relationships of monotremes is that they give us

a glimpse of the biology and physiology of their Mesozoic counterparts. Based on monotremes, it is likely that some other Mesozoic mammals laid eggs, but had mammary glands without nipples and very poor thermoregulation.

By the Early Cretaceous, mammals with more advanced teeth are known, living alongside the surviving archaic groups, such as the triconodonts, symmetrodonts, and dryolestids. These more advanced mammals have added a new cusp (the protocone) to the lingual corner of the upper cheek teeth, making it essentially a modern mammalian molar (known as the **tribosphenic** tooth). This basic tribosphenic prototype will be highly modified in later mammals, but the position and homologies of the primary cusps are the same, no matter what the tooth's purpose. By the late Early Cretaceous, the tribosphenic therian mammalian lineage had split into the two major living groups, the marsupials (Metatheria) and the placentals (Eutheria).

Pouched Life: The Marsupials

The opossum is a marsupial and marsupials are animals who carry their young around in an abdominal pouch or marsupium. As they have done this for millions and millions of years, they are not likely to stop, no matter how you and I feel about it. Baby opossums are born in a rudimentary or unfinished state, from four to twenty at once. They are only half an inch long and smaller around than a honey bee. This seems hardly worthwhile, but it suits the mother opossum, and she is the one directly involved. She thinks the other animals are crazy for having such enormous babies. If one of the children comes out before his time, she hisses, "You get right back in the marsupium." (The opossum language consists of faint hisses, growls and grunts. It is perfectly intelligible to insiders).

—Will Cuppy, *How to Attract the Wombat*, 1949

Most people are familiar with the opossum, kangaroo, koala bear, and (thanks to *Looney Tunes*) the Tasmanian devil. All these animals are **marsupials** (Metatheria), or pouched mammals, so called because they carry their young in a pouch. Marsupials are the dominant group of mammals only on the island continent of Australia, where there are few native placental mammals. In many instances where marsupials have been forced to compete with placental mammals, they have lost, and this has led people to think that they are more primitive and inferior to placentals. However, marsupials are not inferior, just very different. The most obvious difference is in their reproduction, which works very differently from that of a placental (fig. 18.60). A female marsupial has a pair of uteri (unlike the single uterus of a placental) that open into a vagina with three different branches, a central medial vagina (the birth canal), and two lateral vaginas that lead into it. The penis of many male marsupials is forked, so that it can deliver sperm to both lateral vaginas. Once fertilization occurs, the embryo develops for only a few weeks, after which the young is born essentially premature, with only its forelimbs functional. These limbs are important, because the embryo must crawl up the mother's belly fur and find the opening of the pouch. Once it reaches the pouch, it crawls in and clamps onto a nipple, where it completes its development.

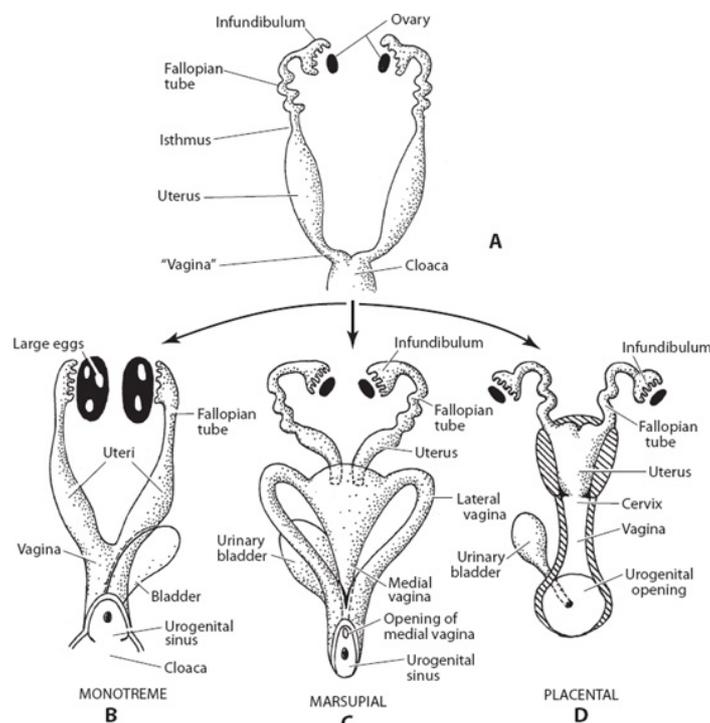


FIGURE 18.60 Basic differences in mammalian reproduction. At the top is the condition found in primitive amniotes, and presumably in synapsids and early mammals. The two horns of the uterus meet in a common cloaca. In the monotreme condition, uteri are fused into a short vagina. In marsupials, the horns of the uterus open into a vagina divided into a medial and two lateral branches. Sperm travels up the lateral vaginas to the uterus, but the medial vagina is the birth canal. In placentals, the uterine horns are fused into a single uterus with a muscular wall and a cervix for carrying the young until it is born. (Modified

from Pough et al., 1996.)

By contrast, a placental embryo has an organ, the **placenta**, which develops from the chorionic and amniotic membranes (also known as the “afterbirth”) and protects the embryo during development. The placenta also serves to pass gases, food, hormones, and waste products between mother and embryo. The placenta has another important function—it serves as a barrier against the mother’s immune system, so when the embryo develops its own immune signature, the mother’s system will not reject it as a “foreign object.” By contrast, marsupials have no such protection, so the young are born prematurely before they can suffer immune rejection. In addition, the membrane surrounding the embryo (the **trophoblast**) in a marsupial is nowhere near as efficient at supplying food and gases to the embryo as is a placenta, so the marsupial embryo must be born prematurely so that it can nurse.

Marsupial reproduction allows multiple generations of young to be raised at once. A marsupial mother can carry one baby in the pouch, an embryo in the uterus, and take care of a third generation still staying in her vicinity, so the generational turnover can be quite rapid. If a marsupial mother is in great danger from a predator or starvation, she can drop the babies in her pouch at minimal risk to herself and live to breed again. By contrast, a placental mother cannot abort her fetus without great risk to herself, so she is obliged to carry it to term, even if it means death for her. In other words, marsupial mothers make less parental investment in each young, but suffer less risk as a result. The main disadvantages of marsupial reproduction are that the young are born with a smaller neocortex in the brain, due to their abbreviated development, and therefore require a longer time to mature and be weaned from the mother. By contrast, some mammals (such as rabbits or rodents) can shorten their generation time until the young are weaned and thus can produce offspring faster than most marsupials.

Today, marsupials comprise most of the native fauna of Australia, and are restricted to that continent (except for the opossums and their South American relatives). In the Cretaceous, however, marsupials were widespread and found on most of the continents (they were the most common mammals in North America during the reign of *Tyrannosaurus*). After the KP event, however, the balance shifted to placentals on the northern continents, and only opossums persisted through much of the Cenozoic in Europe or North America. By contrast, the marsupials did very well on the southern continents of South America and Australia, where there was little placental competition (and also Antarctica, before it froze over). In South America, there were no large carnivorous placental mammals during the early Cenozoic, so marsupials occupied that niche. Some of them (the borhyaenids) were shaped much like wolves or hyaenas, while another (*Thylacosmilus*) was a sabertooth that closely resembles the placental sabertooth cat. Most of these marsupial predators disappeared as placental carnivores came from North America when the Panamanian land bridge opened in the Pliocene. However, South America still supports a large diversity of opossum-like marsupials.

In Australia, the situation was even simpler. Only one possible placental fossil is known from that continent before humans arrived with their animals in the Pleistocene, so Australia was apparently completely isolated from placentals during most of the Cenozoic. In the absence of such placental competition, marsupials evolved into a great variety of body forms to fill the niches occupied by placentals on other continents (fig. 9.1). There were marsupial equivalents of moles, mice, cats, flying squirrels, wolves, groundhogs, anteaters, and many other body forms. In addition, there are many body forms that placentals never invented. Kangaroos are the main herbivorous marsupials, but they get along by hopping, an innovation that hooved placental mammals never discovered. In the Australian Pleistocene, there were giant wombats the size of rhinos and kangaroos almost twice the size of any living species. There was even a marsupial “lion,” *Thylacoleo*, which had a peculiarly short skull with long cutting blades in its jaws, rather than the multiple shearing teeth found in a placental carnivore.

Most of these giant Pleistocene marsupials vanished as the ice ages ended and the climate changed. However, the most dangerous change for marsupials was the invasion of aborigines to Australia about 40,000 years ago, and with them their placental dogs (dingoes). When Europeans came about two centuries ago, they brought other destructive placentals, such as goats, rats, and rabbits. Today, many of the native Australian marsupials are endangered as their habitats disappear and placental mammals continue to take over. Australia has long been a “living museum” of unique animals that evolved in isolation through over 70 m.y., but that “museum” may vanish within another century.

The Placental Explosion

The placental or eutherian mammals comprise about twenty living orders and several extinct ones. The morphological and adaptive range of this group is extraordinary; diversification has produced lineages as varied as humans and their primate relatives, flying bats, swimming whales, ant-eating anteaters, pangolins, and aardvarks, a baroque extravagance of horned, antlered, and trunk-nosed herbivores (ungulates), as well as the supremely diverse rats, mice, beaver and porcupines of the order Rodentia. Such adaptive diversity, and the emergence of thousands of living and fossil species, apparently resulted from a radiation beginning in the late Mesozoic between 65 and 80 million years ago. This explosive radiation is one of the more intriguing chapters in vertebrate history.

—Michael J. Novacek, “The radiation of placental mammals,” 1994

Placentals make up about 95% of the fossil and living mammals. In Simpson’s (1945) classification of mammals, there were over 2600 placental genera, compared with a few hundred marsupials and a few dozen multituberculates, monotremes, and other Mesozoic forms. The number of described taxa has greatly increased in the last 50 years. Teeth that are recognizably placental are known from the late Early Cretaceous (about 110 Ma), and by the early Late Cretaceous (about 85 Ma), some of the main branches (such as the earliest hooved

mammals, or ungulates) had already differentiated. A diverse fauna of placentals is found in the uppermost Cretaceous (65 Ma) beds that entombed *Tyrannosaurus* and *Triceratops*, the Hell Creek Formation of Montana and the Lance Formation of Wyoming, as well as in the Upper Cretaceous beds of Mongolia. Although most of these animals are rat- to cat-sized insectivorous forms, it is already possible to recognize the earliest primate-like fossils (*Purgatorius*), several kinds of hoofed mammals (zhelestids and *Protungulatum*), insectivorans (*Batodon*), fossils that have been linked to the carnivorous mammals (*Cimolestes*), and others.

Once the nonavian dinosaurs were gone, however, placental mammals underwent an explosive adaptive radiation, so that by the early Eocene, nearly all of the 20 or so living orders, and numerous extinct ones, had appeared (fig. 18.61A). These include not only true carnivorans, insectivorans, rodents, primates, and several orders of hoofed mammals, but animals as different as bats and whales. Evolutionary biologists have long regarded this as one of the most spectacular adaptive radiations ever documented, although as we have seen, the same thing may have happened with early Cenozoic birds, and three times in the ammonites.

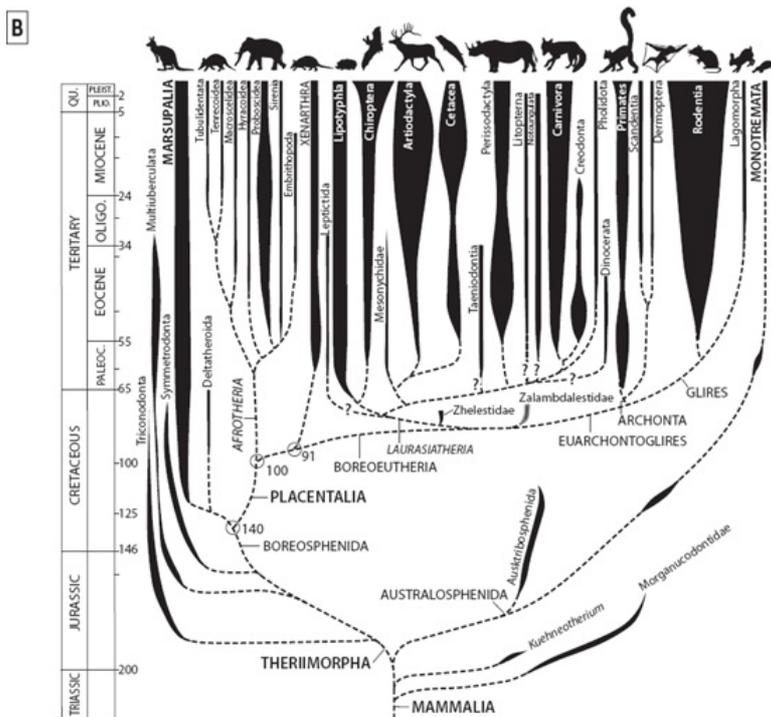
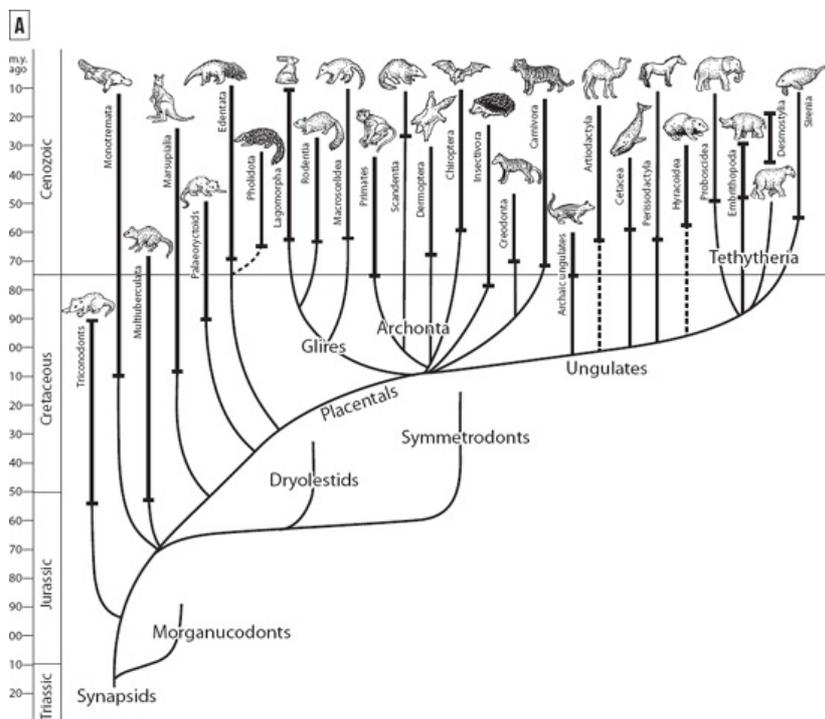


FIGURE 18.61 (A) Evolutionary radiation of the placental mammals, showing the probable branching sequence as deduced by anatomical analysis and molecular techniques, and the time ranges (solid bars) of the major groups of mammals. Most of the orders can be traced back to the Eocene, so their divergence must have occurred in the Cretaceous or Paleocene. Several supraordinal clusters of mammals are apparent, including the Glires, the Archonta, and the Ungulata (Modified from Novacek, 1994.). (B) Family tree of placental mammals based on the molecular data. (Modified from several sources.)

For over a century, paleontologists have tried to piece together the origin and early history of each of the orders of mammals, primarily by studying the scrappy teeth and jaws collected from the Cretaceous and Paleocene. Despite all this effort, however, little progress was made from the time of William King Gregory's (1910) massive monograph, *The Orders of Mammals*, until the late 1970s. This was due to several problems. For one thing, a lot of the important evidence is available from anatomy other than the teeth and jaws (especially from the braincase, ear region, and other parts of the skull and skeleton), and yet mammalian paleontologists persisted in trying to trace ancestral-descendant sequences of teeth back through the rocks. Another problem was that the most studied collections were primarily from North America and Europe, so paleontologists tended to try to link together fossils found in the same area, neglecting the possibility of immigration from other continents. When the excellent fossil record of the Paleocene of China finally became available for study by international scientists in the late 1970s and 1980s, many of the important "missing links" turned up in Asia, not in North America or Europe.

The breakthrough came in the 1970s due to two developments: cladistic analysis and molecular biology. Starting with McKenna's (1975) landmark paper on mammal phylogeny, paleontologists began to apply cladistic analysis to the problem of eutherian interrelationships and to go beyond teeth to use the neglected database of shared derived characters in the skull, ear region, skeleton, and nonskeletal anatomy. In addition, most of the orders of mammals have living representatives, so it is possible to analyze their molecular similarities as well. Together, these parallel research programs have made tremendous progress in understanding placental evolution and debunked many of the long-standing myths that persisted over the years. Some of the critical papers were published in volumes edited by Benton (1988), Szalay and colleagues (1993), and Novacek (1986, 1990, 1992, 1994). Novacek and Wyss (1986), Rose (2006), and Rose and Archibald (2005) summarized more recent research.

Molecular approaches to placental phylogeny date back to the early days of DNA hybridization and immunological distances and protein sequencing, but many of those early efforts were inconsistent or weakly supported by many molecular substitutions (Prothero, 1993). However, as the new millennium began, the PCR method of amplifying DNA (see [chapter 4](#)) made it possible to sequence large sections of the actual nuclear genome of many mammals. Indeed, the major achievement in this regard was the full sequencing of human DNA in the year 2000 by two different labs, as well as the full sequence of chimpanzees, lab rats and mice, and many others. Over the past decade, both nuclear genes and genes in the mitochondria of many groups of mammals have been sequenced, giving a much more robust and consistent molecular phylogeny than the ones of the 1980s and 1990s, which were based on protein sequences. Consequently, there is a wholly new supraordinal clustering of placental mammals ([fig. 18.61B](#)) based on these molecular data (Madsen et al., 2001; Murphy et al., 2001a, 2001b, 2004; Scally et al., 2001; Springer et al., 2004, 2007a, 2007b, 2011). More recently, the anatomical and molecular evidence have been analyzed together to produce a "supertree" that seems to resolve many of the problems and conflicts (O'Leary et al., 2013).

It's important to remember, before we discuss some of these taxonomic groupings in detail, that *they are supported by molecular evidence only*, and there are no anatomical or embryological characters that support them (Asher et al., 2008). Most mammalian paleontologists have adopted a "wait and see" attitude about molecular phylogenies for that reason, because earlier molecular studies led to many false notions and ridiculous ideas in the past (Prothero, 1993; Shoshani and McKenna, 1998). For purposes of this book, I'll place both phylogenies side-by-side ([fig. 18.61](#)) to allow the reader to compare their similarities and differences.

EDENTATES—One of the first myths to be debunked was the notion that insectivores were the ancestors of all other mammals. It is true that most Mesozoic mammals were small, insectivorous creatures that could not grow large and eat other kinds of food as long as the dinosaurs reigned (the multituberculates were the only important herbivorous mammals in the Mesozoic). But the well-defined monophyletic group known as the order Insectivora (composed of shrews, moles, and hedgehogs) was improperly expanded to include a whole zoo full of unrelated beasts, including tree shrews, elephant shrews, and many extinct Mesozoic and early Cenozoic mammals sometimes thrown in the wastebasket order "Proteutheria." Bats were supposedly derived from this amorphous cloud of animals, because some have an insectivorous diet; it turns out they are more closely related to primates. At one time or another, all of the rest of the mammalian orders were also traced to one or more "insectivores" of the Late Cretaceous.

When McKenna (1975) applied cladistic analysis to the problem, however, a surprising result emerged. Of the living placentals, one of the most primitive groups was not the Insectivora (shrews, moles, and hedgehogs), but the **edentates** (anteaters, sloths, and armadillos, known as the order Xenarthra). Although the name "edentate" implies that they are toothless, only anteaters fit that description; sloths and armadillos have simple teeth with no coating of enamel. Because they don't have an abundant fossil record of teeth and are known primarily from South America, edentates were long neglected in the analysis. But their remaining anatomical features show that they are very primitive placentals, lacking many of the specializations found in all other eutherians (the Epitheria of McKenna, 1975). For example, female edentates have a uterus simplex, which is divided by a septum and has no cervix. Edentate metabolism tends to be much slower and less well regulated than that of other placentals. Edentates still retain a few primitive amniote bones that all other placentals have lost, and their brain and neural development is also much less advanced. One of the most consistent characters found in all placentals except edentates is the stirrup-shaped stapes in epitherian placental mammals. Edentates have the primitive amniote rod-like stapes with no hole at the base for the stapedia artery to pass through. In addition, edentates have many unique synapomorphies of their own, including extra articulations between the vertebrae (the name Xenarthra refers to these "strange joints"), odd fusions of the hip region with the vertebrae of the back and tail, and many other unusual features in the shoulder, ankle, and skull. The molecular phylogenies ([fig. 18.61B](#)) also place the Xenarthra near the base of the placentals, along with the Afrotheria (see section on morphology and molecular phylogenies).

Part of the reason for the neglect of edentates is that they don't have teeth with enamel that preserve much

cuspid detail. In addition, most of their evolution took place in isolation in South America, so Northern Hemisphere paleontologists seldom studied them. Their Cretaceous ancestors were among the earliest mammals to evolve on that continent while it was mostly separate from the rest of the world, and consequently, through the Cenozoic, South America hosted a wide variety of edentates, including the huge ground sloths (elephant-sized *Megatherium* and *Eremotherium* towered over 6-m tall and weighed 3 tons) and giant relatives of the armadillos, the glyptodonts. These were the size of a Volkswagen Beetle, with the largest species over 2-m long. They weighed 2 tons, including 400 kg of bony armor, and had a spiked club at the tip of their tail. However, edentates were not always confined to South America. An anteater, *Eurotamandua*, is known from the middle Eocene Messel *Lagerstätten* of Germany, and a strange edentate-like animal, *Ernanadon*, has been described from the Paleocene of China. Edentates were among the few South American natives to successfully march north across the Panamanian land bridge in the Plio-Pleistocene against the tide of North American mammals heading south. Ground sloths, armadillos, and glyptodonts were all common in the Pleistocene of North America. The “scaly anteaters,” or pangolins (order Pholidota) are presently restricted to tropical Africa and Southeast Asia, but they are known from Eocene and Oligocene fossils in Europe, North America, and China. Although considered a separate order from edentates, some molecular data and anatomical analyses place them closer to the edentates than to anything else.

After the edentates branched off (sometime in the early Late Cretaceous before 85 Ma), the remaining placentals (Epitheria) split up into five supraordinal groups (fig. 18.61A): the Insectivora (moles, shrews, and hedgehogs); the carnivorous mammals (the true Carnivora, plus the extinct creodonts); the Glires (rodents, rabbits, elephant shrews, and their extinct relatives); the Archonta (primates, bats, tree shrews, colugos, and their extinct relatives); and the ungulates (the hoofed mammals, including whales). How these five supraordinal groups are related is still controversial. Some molecular and morphological data, for example, tend to support a relationship between ungulates and carnivores, but other information clusters insectivores, carnivores, and archontans. For example, the presence of a bony support in the male penis (the baculum bone) is known from Primates, Rodentia, Insectivora, Carnivora, and Chiroptera (= bats), suggesting a connection between archontans (Primates, Chiroptera), Insectivora, Carnivora, and Glires (Rodentia). However, this character could be primitive for the Epitheria, and then lost in the ungulates, which are the only epitheres lacking a baculum. The different hypotheses of the relationships of these supraordinal groups are shown in fig. 18.61. For the present, we will treat these five taxa as equal groups of supraordinal rank. Let us consider each in turn.

INSECTIVORA—Today, there are three main living groups of insectivorous mammals, the shrews, moles, and hedgehogs, which form a well-defined natural group, the order Insectivora (sometimes called the Lipotyphla). This taxon is easy to recognize by a number of features besides the sharp, high-crowned “reversed triangle” teeth used for their insectivorous diet. They lose several bones in their zygomatic arch and have several other modifications of the front of the skull. In their braincase, they have an unusual circulatory arrangement, and they exhibit many other unique anatomical features (such as the lack of a caecum, the blind digestive pouch branching off the intestine found in most mammals). Shrews are the most primitive of all the insectivores, yet there are some 245 living species, and they have an extensive fossil record. Despite their primitive body form, shrews have a number of specializations, including pigmented teeth. Shrews are fast-moving, active, voracious predators, eating almost continuously to feed their tiny bodies, which lose heat at a high rate due to their small size. They can use echolocation to find their prey, and they will attack animals much larger than they are. Their prey include not only insects and other arthropods, but also worms, small reptiles, birds, and mammals. Some have poison in their saliva that helps immobilize their prey.

Hedgehogs are mostly known from Eurasia and Africa today, but they once were common in North America as well. In Europe, these spiny little animals are well known for hunting insects and worms in the undergrowth and rolling up into a spiny ball when threatened. Not all hedgehogs are small, however. In the Miocene, some Mediterranean islands supported a giant hedgehog as big as a medium-sized dog, which had a robust skull with large incisors for killing sizable prey.

Moles are familiar for their tunnels, which serve not only for protection, but primarily to trap prey. When a worm drops into the tunnel and thrashes around, the mole runs to kill and eat it. Due to their subterranean habitat, moles have greatly reduced their eyes, and many are completely blind. They rely on their smell and hearing, and some have special organs on their nose to feel their way around in the darkness. Moles are also highly modified for digging, with robust, muscular forearms and large claws on their hands for pushing earth aside.

In addition to these groups, the insectivorous mammals include several other living oddities, including the golden moles and the otter shrews of Africa, and the tenrecs, a radiation of insectivores unique to Madagascar. Anatomical evidence seems to place these in the order Insectivora (fig. 18.61A), but molecular phylogeny places them elsewhere (fig. 18.61B). Another unique living fossil, the shrew-like solenodon, was once found on the islands of Cuba and Hispaniola, apparently isolated on those islands since they first rose out of the sea. Most are now thought to be extinct since the 1930s, thanks to humans and their accompanying rats.

CARNIVORANS AND CREODONTS—The earliest placentals (and most living insectivores) had molar teeth with a strongly “reversed triangle” pattern for chopping up the hard cuticle of insects and other arthropods. Cutting up flesh is another matter. It requires teeth that are modified into long, sharp points and blades. The upper blades must shear precisely against the edges of the lower blades in a scissor-like fashion to cut up muscles and tendons and to even break bones. This kind of dentition is so stereotyped for any fully carnivorous animal that several different groups have independently developed it (such as the carnivorous marsupials and even some hoofed mammals), and once it is developed, it is highly constrained and changes very little. Thus, we must look to other parts of the anatomy (especially the braincase) to decipher the relationships of carnivores and get past the convergent evolution of their teeth.

Once this is done, two main groups of carnivorous mammals are recognized: the extinct creodonts (an early experiment in carnivory that became extinct in the Pliocene) and the members of the living order Carnivora, or the carnivorans (fig. 18.62). (Note that *carnivore* describes a meat-eating diet in any animal, but *carnivoran* is a

taxonomic term referring to members of the order Carnivora; likewise for *insectivore* and *insectivoran*). Although the creodonts and carnivorans are closely related, there are some important differences that place them in separate orders. Both groups developed a pair of **carnassials**, enlarged teeth in their cheek tooth row that function as the main slicing and bone-breaking teeth. If you watch a dog eating, you will frequently see it eat with the side of its mouth, bringing the food up to cut or break it with the enlarged carnassials. In creodonts, the carnassial teeth tend to be toward the back of the jaw, typically between the first upper and second lower molars, or in some, between the second upper and third lower molars. Carnivorans, on the other hand, always use their last upper premolar and first lower molar as the carnassial pair. This distinction is important for a number of reasons. Not only is it a diagnostic feature that can be found consistently, no matter how carnivores modify their diets (e.g., bears and raccoons are omnivores, and pandas eat bamboo), but it is important for functional reasons as well. Creodonts had much less evolutionary flexibility, because the location of carnassials so far back in the jaw meant that they had to maintain a very standard, stereotyped dentition. Carnivorans, on the other hand, had the freedom to modify their postcarnassial molars in many different ways, or even lose them altogether, permitting many dietary specializations.

Creodonts were among the first mammals to occupy the niche of large predators during the Paleocene and Eocene. Most were shaped like dogs or weasels, with relatively robust unspecialized limbs, although *Patriofelis* from the Eocene was very bear-like, and *Hyaenodon* from the late Eocene and Oligocene was very hyena-like (as the name implies). The middle Eocene creodont *Apataelurus* developed saber-like canines, just as two groups of carnivorans and the marsupial *Thylacosmilus* did (see fig. 7.15). *Sarkastodon* from the late Eocene of Mongolia was a huge predator, larger than any bear, with enormous blunt teeth for bone crushing. Most of the creodonts were extinct by the late Eocene, but the hyaenodont lineage persisted well into the Pliocene in Eurasia and Africa. In Africa during the Miocene, there was a huge hyaenodont named *Megistotherium*, which had a skull twice as long as a tiger, with huge canines and enormous jaw muscles.

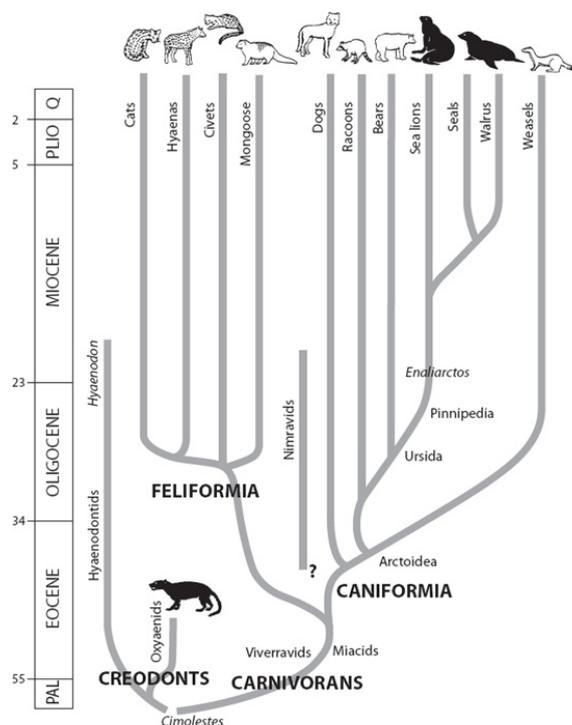


FIGURE 18.62 Evolution of the carnivorans and creodonts. (Redrawn by Carl Buell from Prothero, 1994.)

The oldest known carnivorans are weasel-like and raccoon-like animals from the Paleocene and early Eocene that have been loosely lumped into the wastebasket group called the “miacids.” As the creodonts declined in the late Eocene, the order Carnivora radiated into a variety of body forms and differentiated into two branches: the Caniformia (dogs, bears, raccoons, weasels, seals, and their relatives) and the Feliformia (cats, hyenas, civets, mongooses, and their relatives) (fig. 18.62). The caniforms differentiated very early, with the dogs (Canidae) appearing by the end of the middle Eocene and diversifying on many continents throughout the Cenozoic. In addition to the typical body forms of wolves, foxes, and coyotes, dogs have also come in weasel-like shapes, and one group, the borophagines, were huge, bone-crushing hyena-like predators in North America in the Miocene (North America never had true hyenas). Bears, raccoons, and the weasel clan (otters, minks, wolverines, badgers, skunks, and so on) appeared somewhat later, although they too were very diverse throughout the later Cenozoic on the northern continents.

Seals, sea lions, and walrus have long been placed in their own order “Pinnipedia,” but recent analyses show that they are closely related to primitive bears and should be a subgroup of the Carnivora. The transition from bears to seals can be demonstrated by the early Miocene *Enaliarctos*, which has many primitive bear-like features in the skull and teeth, even though it had flippers and other aquatic features like seals (and it is found in marine rocks).

The feliform branch of the Carnivora can probably be traced back in time to a group of Paleocene–Eocene “miacids” called the viverravids (fig 18.62). However, the first true cats are not known until *Proailurus* of the early

Miocene. From these roots, dozens of cat genera are known, including at least four different genera of saber-toothed cats found worldwide during the Plio-Pleistocene. The mongoose and civet lineages go back at least to the Oligocene, and the earliest hyena fossils are known from the Miocene.

In addition to these familiar living families, there was also an extinct family of carnivorans known as the nimravids. These animals were extremely cat-like in appearance, occupying the normal cat and sabertooth ecological niches during the late Eocene and Oligocene. They have long been called “paleofelids” or “false cats,” but this is misleading. All their cat-like features (especially the teeth and jaws) are due to evolutionary convergence. The details of their skull, braincase, ear region, and skeleton show that they are not cats at all. Some paleontologists argue that in fact they are closer to caniforms, while others place them as a distant relative of the feliforms. However, in nearly every textbook and illustration of the famous Badlands nimravids such as *Dinictis* and sabertooth *Hoplophoneus*, they are still mislabeled as “cats.”

ARCHONTANS—Many people are surprised (and sometimes uncomfortable) to learn that our own order, the Primates, is most closely related to the bats, tree shrews, and colugos. Yet that is the conclusion supported by a variety of anatomical characters (particularly in the braincase and foot region) that unite a supraordinal group called the Archonta by Gregory (1910). In addition, a great variety of molecular analyses seem to support the Archonta as well. Most archontans have features for living in the trees, and from there became gliders (colugos) or flying mammals (bats).

The oldest known archontans are the primates, starting with *Purgatorius* from the uppermost Cretaceous Hell Creek beds of Montana. During the early Cenozoic, lemur-like and squirrel-like primates were among the most common and diverse mammals in North America and Europe, because these regions were still covered by tropical jungle vegetation, even up to the Arctic Circle. As climates cooled and the forests retreated in the late Eocene and Oligocene, primates disappeared from most of their former habitats, eventually becoming restricted to Africa by the early Oligocene. From this origin, they again spread around the world. In the early Oligocene, the ancestors of New World monkeys apparently rafted from Africa to the island continent of South America, where they radiated into spider monkeys, howler monkeys, marmosets, and all the other New World monkeys (the family Cebidae). Meanwhile the Old World monkeys (baboons, rhesus monkeys, macaques, and their kin) continued to diversify in Africa through the Oligocene and Miocene. By the early Miocene, they competed with a great radiation of apes as well, and for much of the Miocene, apes were more common and diverse in Africa than were monkeys. By the Pliocene, one group of apes, the hominids, split off from the rest, and they were our ancestors.

The bat fossil record is not known until the middle Eocene, with extraordinary specimens of complete articulated bats from the Green River Shale of Wyoming, which entombed *Icaronycteris*, and from the Messel *Lagerstätten* of Germany. These earliest known bats already had wings supported by the elongated bones of all five fingers and exhibited the size and proportions of a modern bat. However, they still retained many primitive features lost in later bats, including a full placental dentition (modern bats have reduced dentitions), an unfused breastbone with no keel for the wing muscles, claws on the fingers, and a long tail that was free of the wing membrane. From this origin, bats quickly diversified into the tiny Microchiroptera (the insect-eating bats, which live in caves and hunt flying prey at night by echolocation) and the much bigger Megachiroptera (the fruit bats, which live in trees and fly during the day to seek fruit). By the Oligocene, most of the families of bats had differentiated. Today, bats are the second most diverse order of mammals alive, after rodents. There are over 780 species, 140 genera, and 17 families of Microchiroptera living today, and a smaller number of fruit bats.

The tree shrews (order Scandentia), as the name implies, were long lumped with the true shrews in the Insectivora, but in recent years their similarity to ancestral primates has been noted again and again. Tree shrews lack most of the derived characters of the true lipotyphlan insectivorans, but instead have a number of derived archontan features. Even though they live much like true shrews, they have become the models for what the ancestral archontan and early primates must have looked like.

The colugos, or “flying lemurs,” of the order Dermoptera are represented by a single living genus, *Cynocephalus*, which lives in Southeast Asia. The name “flying lemurs” is misleading, as they neither fly nor are they lemurs. Instead, they resemble primitive primates or insectivores, but have developed a gliding membrane between the front and hind limbs, which they use to sail from branch to branch like a flying squirrel (which also does not fly, but glides). The colugos were long an evolutionary mystery, a single genus in their own isolated order, until they were connected to some fairly common fossils from the Paleocene and Eocene of North America called **plagiomenids**. This group was also common in the Canadian Arctic in the early Eocene, when that region was warm and forested, and survived in North America until the late Oligocene. After that, there is no further fossil record of dermopterans, except for their sole living representative.

GLIRES—By far the most abundant, diverse, and successful group of placentals is the order Rodentia. They are incredibly diverse (over 40% of the living mammals, or at least 350 genera and 1700 species, are rodents), disparate (occupying body forms from the pig-sized capybara to aquatic beavers and muskrats; gliding, tree-climbing, and burrowing squirrels; spiny porcupines; subterranean gophers and naked mole rats; and hundreds of different kinds of rats and mice), and they are also incredibly abundant. One only needs to think about the ability of rats or mice or hamsters to multiply to realize why they are by far the most common mammals on the planet. If it were not for their predators, the earth would be a planet of rodents. Rodents are usually the dominant group in the small-body-size niche, but occasionally they become huge. The largest living rodent, the capybara, weighs about 40 kg, but the Miocene capybara *Telicomys* was the size of a rhinoceros, and the Pleistocene beaver *Castoroides* weighed about 200 kg and reach 2.5 m in length, as large as a bear.

Rodents have a number of unique features, but their most obvious is their pair of chisel-like (**gliriform**) upper and lower incisors, which are used to gnaw their hard-shelled food and vegetation, and in some groups, to cut down trees or dig tunnels or burrows. These incisors are constantly growing, with open roots, and must be continuously worn down into a sharp point by abrading them together (fig. 18.63). If there is a problem with occlusion such that the incisors are not sharpened down, they will continue growing in a curve until they curl around and puncture the top of the skull. There is a toothless gap (diastema) behind the incisors, and then a row

of premolars and molars that are adapted for grinding their diet of seeds, nuts, and vegetation.

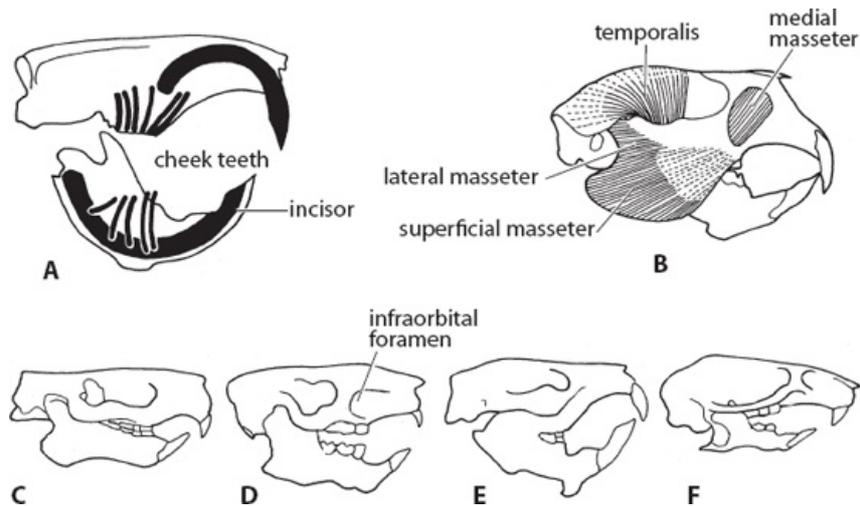


FIGURE 18.63 Rodents have many important specializations of the teeth and jaws. (A) Their ever-growing, chisel-like incisors have deep roots and must be constantly sharpened. (B) Configuration of the jaw muscles in a porcupine. A branch of the medial masseter passes through the infraorbital foramen on the front of the skull. The position of the masseter muscles is shown in the (C) protrogomorph, (D) hystricomorph, (E) sciomorph, and (F) myomorph conditions of the rodent skull. (From M. Benton, 1995, *Vertebrate Palaeontology* [1st ed.] Copyright © 1995 Wiley-Liss, Inc. Reprinted by permission of Wiley-Liss, Inc., a division of John Wiley & Sons, Inc.)

This small-bodied, seeds/nuts/vegetation-gnawing diet and lifestyle was very successful, as demonstrated by the fact that multituberculates occupied this niche for most of the Mesozoic, and several groups of primates also were built like rodents in the Paleocene. When rodents spread from Asia to North America and Europe in the early Eocene, however, they began to displace the earlier occupants, so that by the Oligocene, multituberculates and rodent-like primates were extinct. The early rodents had very primitive **protrogomorph** skulls (fig. 18.63), with the masseteric muscles attached only to a limited area along the base of the zygomatic arch (as in other mammals). By the late Eocene, they had diversified into three main lineages. The **sciomorphs** are only slightly more specialized than the ancestral protrogomorphs, with the masseter muscles extending up along the front of the zygomatic arch to the side of the snout. Sciomorphs are the squirrels and all their relatives, including chipmunks, woodchucks and marmots, and the beavers. In the second condition, known as **hystricomorph**, the masseter muscle passes up through the zygomatic arch and onto the snout through a hole for the passage of nerves called the infraorbital foramen. Hystricomorphs include not only the porcupines (both North American and African) and most other African rodents, but also the incredible radiation of native South American rodents, the caviomorphs (including the guinea pigs, capybaras, chinchillas, agoutis, and many less familiar animals). The caviomorphs first arrived in South America in the Oligocene, presumably from African hystricomorph ancestors that rafted there across the Atlantic. (The same scenario applies to the New World monkeys as well.) The most specialized condition is known as **myomorph**, and it combines a strand of the masseter passing along the front of the zygomatic arch with another passing through the infraorbital foramen. The vast majority of rodents, including the rats, mice, hamsters, voles, lemmings, and their kin, exhibit this condition.

Most people are surprised to learn that rabbits and hares are not rodents, but they have always been placed in their own order Lagomorpha, along with the hamster-like pikas which live only in high Rocky Mountain meadows above the treeline. Lagomorphs have two pairs of chisel-like incisors, in contrast to the single pair in rodents, and a number of other unique specializations. Although lagomorphs were originally classed with rodents, for most of the last century opinion swung away from this hypothesis, and attributed their similarities to parallelism. However, the last decade has seen opinion shift back again to the grouping of lagomorphs and rodents, called the Glires by Gregory (1910). Not only is there a lot of anatomical evidence to support it, but also much of the recent molecular data suggest a close relationship as well. In addition, recent studies of Chinese Paleocene eurymylids show that both rabbits and rodents probably originated from a eurymylid ancestor and then emigrated to other regions in the Eocene.

The third group assigned to the Glires is the elephant shrews, or Macroscelidea, which resemble hopping shrews with a long snout. They were long placed with the Insectivora because of shared primitive characters and their insectivorous diet. However, they have a number of anatomical specializations shared with rabbits and rodents, but recent molecular data support their inclusion in the Afrotheria.

UNGULATES—After rodents and bats, the third largest group of placentals is the hooved mammals, or ungulates. Hooved mammals make up about 33% of the living and extinct mammalian genera, and nearly all the large-bodied herbivores are ungulates. According to the anatomical and fossil-based phylogenies (figs. 18.61A and 18.64), they include the even-toed **artiodactyls** (pigs, hippos, camels, deer, antelopes, giraffes, cattle, sheep, and goats), the odd-toed **perissodactyls** (horses, rhinos, tapirs, and their extinct kin), the **tethytheres** (elephants, manatees, and their extinct relatives), the woodchuck-like hyraxes or conies, and, surprisingly, the whales. Ungulates have dominated not only the large herbivore niche through most of the Cenozoic, but also are the dominant aquatic predators and filter feeders, and some were even carnivorous. Some ungulates have long slender limbs for fast running (especially antelopes and horses), but others are large-bodied with robust

limbs (such as elephants, rhinos, hippos, and many extinct group). The tree hyraxes even climb trees. Ungulates have occupied a wide variety of ecological niches given the constraints of their body size and diet.

Until recently, the interrelationships of the major ungulate groups were obscured by a paraphyletic ancestral wastebasket group, the order “Condylarthra” (fig. 18.64). “Condylarths” had nothing in common, except that they were primitive ungulates that were not members of any of the living orders. As long as this wastebasket group covered up the evidence, there was no possibility that ungulate relationships could be deciphered. However, when cladistic analysis was applied to the group (Cifelli, 1983; Prothero et al., 1988), there was a clear pattern of branching among the ungulate groups that has withstood repeated testing from additional morphological and molecular analyses (Court, 1990; Thewissen and Domning, 1992; Prothero, 1993; Archibald, 1998). It turned out that throwing taxa into the “Condylarthra” wastebasket hid a phylogenetic pattern for over a century, but a focus on shared derived characters (plus the great increase in numbers of taxa and characters) was able to tease out that pattern.

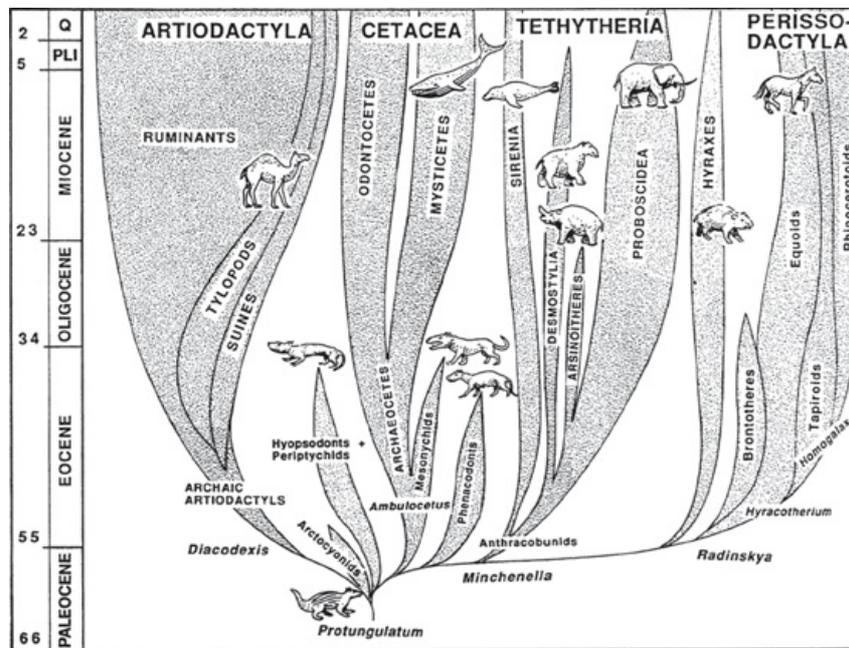


FIGURE 18.64 Evolution of the hoofed mammals, or ungulates. (From Prothero, 1994.)

The earliest ungulates are known from the early Late Cretaceous (about 85 Ma) of Uzbekistan (Archibald, 1996b), and show that the major placental divergences must have come quite early. Better specimens of ungulates are known from the latest Cretaceous, where *Protungulatum* is among the more common taxa. Although these Mesozoic ungulates are known mostly from isolated teeth and bones, they still have diagnostic ungulate features. Their molars are square and lower-crowned, with rounder cusps, for eating vegetation rather than insects, and they already have distinctive features of the ankle that are recognizably ungulate.

In the Paleocene, the ungulates split into a number of distinct clades. Some of these archaic ungulates (such as the arctocyonids, hypsodonts, and periplychids) have long been lumped into the order “Condylarthra,” but each is distinctive and related to a different part of the ungulate radiation. The Paleocene arctocyonids were the most primitive of the ungulates, about the size and shape of a raccoon, and probably with a similarly omnivorous diet. The hypsodonts, on the other hand, were most common in the Eocene, and were among the last of the surviving “condylarths.” They were shaped somewhat like dachshunds, except that their multicusped teeth were clearly adapted for grinding vegetation. Another group of “condylarths,” the phenacodonts, are not closely related to the other archaic ungulates, but are actually the sister-group of the clade that includes perissodactyls.

Surprisingly, one of the first ungulate groups to branch off was the even-toed ungulates, or artiodactyls. They are so called because the axis of symmetry in their hand and foot runs between the third and fourth digits, so they usually have either two or four toes. Artiodactyls also have a very distinctive ankle bone that has a pulley-like facet on each surface. This gives their feet very efficient movement in a fore-aft plane for rapid running, but restricts their ability to rotate their feet in a way that more generalized mammals can. Artiodactyls are the largest group of living ungulates, with over 190 living species, including most of the domesticated hoofed mammals (cattle, sheep, goats, camels, and pigs) and they are the source of most of our meat, milk, and wool.

The earliest artiodactyls are known from the lower Eocene rocks of Pakistan, and shortly thereafter they spread to the rest of Eurasia and North America. These early forms were very delicately built, resembling a small hornless antelope, and some had such long hind legs that they may have hopped. During the Eocene, these archaic artiodactyls quickly diversified into a great variety of lineages—the heavy-bodied, omnivorous pigs and their American relatives, the peccaries or javelinas; the aquatic hippos; and the early camels, which did not yet have humps, but were built more like deer. Camels were once a strictly North American group, playing the roles on this continent that were occupied by other groups elsewhere. For example, in the Miocene, there were long-necked, long-legged “giraffe-camels,” delicate “gazelle-camels,” and others that paralleled the shapes of many African antelopes (since North America never hosted true antelopes). In the Miocene, camels migrated to South America across the Panamanian land bridge, giving rise to the llamas, alpacas, guanacos, and vicuñas still living there today. In the Pleistocene, they also crossed the Bering Strait to the Old World, where they

evolved into dromedaries and Bactrian camels, the only groups with a hump. Then, about 10,000 years ago, they became extinct in their North American homeland.

In the late Eocene and Oligocene, another great evolutionary breakthrough occurred when a group of artiodactyls, the **ruminants**, developed a four-chambered stomach system. Ruminants first swallow their food and then let it ferment in the first stomach chamber, the rumen, where cellulose-digesting bacteria help break up the plant matter. When they have a chance, ruminants regurgitate food from the rumen and “chew their cud,” which helps break it down even further. (Their appearance of thoughtfulness during this time has led to the term “rumination” for someone “chewing over” an idea.) By the time the cud is swallowed again, most of the nutrients can be absorbed by the intestines, so ruminants get the maximum nutrition out of each bite of vegetation. By contrast, most other herbivorous mammals (horses, rhinos, elephants, rabbits) are hindgut fermenters, and have no specialized foregut fermentation chamber, so they can get only a limited amount of nutrition out of the relatively indigestible cellulose in the food as it passes rapidly through their intestine and caecum. Consequently, hindgut fermenters must eat much larger quantities of food than ruminants and are not as efficient or versatile. (Rabbits get around this by eating their feces, so the food goes through their digestive tract twice.) With this great innovation, the ruminants (especially the deer, giraffes, cattle, antelopes, goats, and sheep) eventually became the dominant hoofed mammals of the later Cenozoic and pushed out many other groups, such as the horses.

One of the most amazing stories in evolutionary biology is the origin of whales from land mammals (fig. 18.65). By the middle Eocene, there were archaic fossil whales with a fully whale-like body, including a horizontal tail fluke, forelimbs modified into flippers, and no hind limbs. Based on their distinctive triangular teeth, paleontologists had long looked for whale origins among a group of carnivorous hoofed mammals known as the *mesonychids*.

Mesonychids were the first group of mammals to become specialized meat-eaters, appearing in the middle Paleocene before more specialized carnivorous mammals (the creodonts, and eventually the true carnivorans) occupied that niche. Most mesonychids were the size and shape of large wolves or bears (although some were as small as foxes). They had a heavy robust skull armed with sharp canine teeth and huge round-cusped molar teeth suitable not only for eating meat, but also for bone crushing. Their body was also very wolf-like, with a long tail and limbs. Like many modern carnivores, they walked on the tips of their long toes, rather than flat-footed. Despite all these carnivorous adaptations, however, mesonychids were derived from hoofed mammals. The proof is in their toes, which had hooves rather than claws.

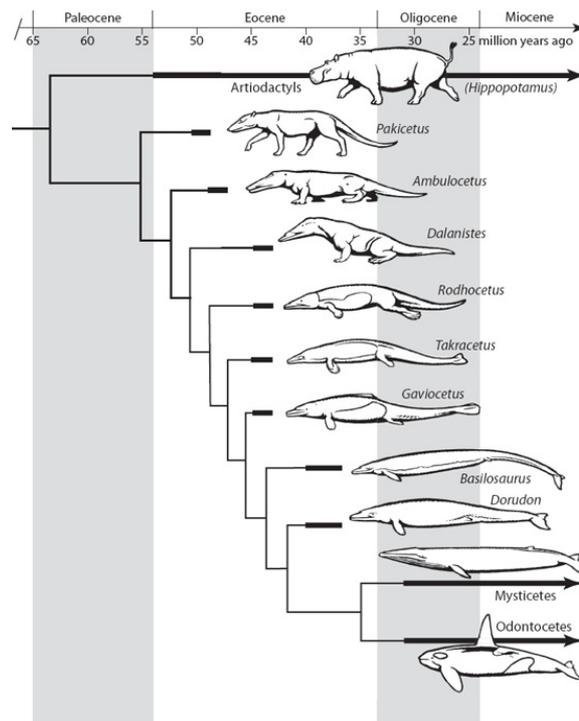


FIGURE 18.65 Evolution of the whales. (Drawing by Carl Buell.)

By the early Eocene, mesonychids had reached their peak of diversity, with wolf-sized beasts such as *Mesonyx* or *Harpagolestes* reigning as the largest carnivorous mammals of their time. However, they had to share their world with two other groups of carnivorous mammals: the creodonts (which soon surpassed them in size and diversity) and the true carnivorans (which were still weasel-sized, and did not become large dog-sized or cat-sized predators until the Oligocene). By the middle Eocene, the mesonychids rapidly declined in North America and Eurasia, where they had once dominated. The reasons for this decline are unclear. It was a time of major climatic change, with global cooling and drying that destroyed the dense forests that mesonychids had once ruled. With the coming of open habitats, the prey species became faster and more agile. Large, clumsy predators like mesonychids might have had difficulty finding cover to ambush their prey. In addition, some paleontologists speculate that mesonychids were not as efficient at eating meat as the creodonts or carnivorans, because the blunt, rounded cusps of mesonychid molars never developed the specialized, scissor-like carnassial shear found in more specialized carnivorous mammals. For whatever reasons, the mesonychids

were very rare in the late middle Eocene, and they disappeared from North America at the end of the middle Eocene, and from Asia in the late Eocene. The last of the Asian mesonychids, however, was a truly spectacular beast known as *Andrewsarchus*. Only one skull of this animal is known, but it is almost a meter long, more than twice the size of any bear or wolf that has ever lived! If the rest of the animal were also bear-like, it would have been about 4-m long, and 2-m high at the shoulder and would have weighed almost four times as much as the largest known bear. Mesonychids were long considered the sister-group of whales until more recent evidence has placed them as the sister-group of whales plus artiodactyls.

For years, the oldest known whales of the early middle Eocene were known only from fossils of fully aquatic animals without hind limbs. Recently, however, numerous transitional forms between whales and their ancestors have been found from the early Eocene of Africa and Asia. The most impressive of these is *Ambulocetus* from the early Eocene of Pakistan. Although it still has a mesonychid skull and teeth, its front and hind feet are both adapted for swimming, yet it does not yet have a tail fluke. Other fossil whales have even more specialized front flippers and have reduced their hind limbs to tiny vestiges and a tail with a horizontal fluke. Then in 2001, two groups of paleontologists working independently in Pakistan reported fossils of the earliest whales that had the distinctive “double-pulley” astragalus bone in their ankles, a feature unique to the artiodactyls. The idea that whales were descended from artiodactyls (specifically, the hippopotamus lineage and their extinct anthracothere ancestors) was long suggested by molecular evidence, but finally corroborated by fossils. The transformation from whale-like artiodactyls (the anthracotheres) to a fully aquatic whale is now one of the best-documented major evolutionary transitions in the fossil record.

By the Oligocene, the archaic archaeocete whales were extinct and were replaced by a radiation of the two modern groups of cetaceans, the odontocetes (toothed whales, including sperm whales, killer whales, dolphins, and porpoises) and the mysticetes (baleen whales, including the blue whale, right whale, humpback whale, gray whale, and many others). The more familiar toothed whales are predators, feeding on fish and squid with their many conical teeth. The baleen whales, on the other hand, are toothless, and their mouth is filled with screens of horny tissue called baleen, which is used to filter out small fish and plankton. Baleen whales such as the blue whale swallow a large mouthful of seawater, and as they close their mouths, they force out the water through the filter, leaving all the food trapped in their mouths.

After the branch points for the artiodactyls, the hyposodonts and periptychids, and the whales plus mesonychids, the remaining ungulates form a monophyletic group now known as the Altungulata (Prothero and Schoch, 1989), according to the anatomical and paleontological evidence (fig. 18.61A, 18.64). These include the sheep-like “condylarths” known as phenacodonts (fig. 18.64), and two major clades, the tethytheres and the perissodactyls. Tethytheres were not recognized as a group until McKenna named them in 1975, but they have a great variety of shared derived characters that unite them (Domning et al., 1986; Tassy and Shoshani, 1988; Fischer and Tassy, 1993; Shoshani, 1993). These include a single pair of teats on the breasts (like humans), eyes that are shifted far forward on the skull, cheekbones that contain a broadly expanded portion of the rear skull bones, and teeth that do not erupt from below, as in most mammals, but from the back, pushing the old teeth out the front of the jaw.

The most familiar tethytheres are the elephants and their kin, the order Proboscidea (fig. 18.66). The two living species of elephants are but a tiny remnant of a long, distinguished history of mammoths, mastodonts, and other unusual animals. The earliest proboscideans are known from the late Paleocene of Africa, and by the Eocene, they were shaped like small hippos, without trunks or tusks. In the Oligocene, they diverged into numerous lineages: the deinotheres, with their downward-deflected lower tusks; the true mastodonts; and the gomphotheres, with small upper and lower tusks. Some evolved into beasts with enormous broad tusks shaped like shovels, while others had various combinations of two and four tusks with different lengths and curvatures. In the late Pleistocene, only the true mastodonts and the diversity of mammoths remained, and most of these were driven to extinction at the end of the Pleistocene.

Closely related to the Proboscidea are several other groups that had long been zoological mysteries, placed in their own isolated orders. The order Sirenia includes the manatees and dugongs, or “sea cows.” These animals are completely aquatic, losing their hind limbs and developing a circular fluke on the tail and paddles for forelimbs. Living manatees have no hind limbs, but a fossil sirenian from the Eocene of Jamaica named *Pezosiren* not only had both front and hind limbs, but also typical ungulate hands and feet rather than flippers, a perfect transitional fossil between sirenians and their ancestors. Manatees are restricted to freshwater lakes, rivers, and estuaries, browsing the water plants, but they are so slow and docile that they are now on the endangered species list as a result of hunting and injuries from speedboats hitting them.

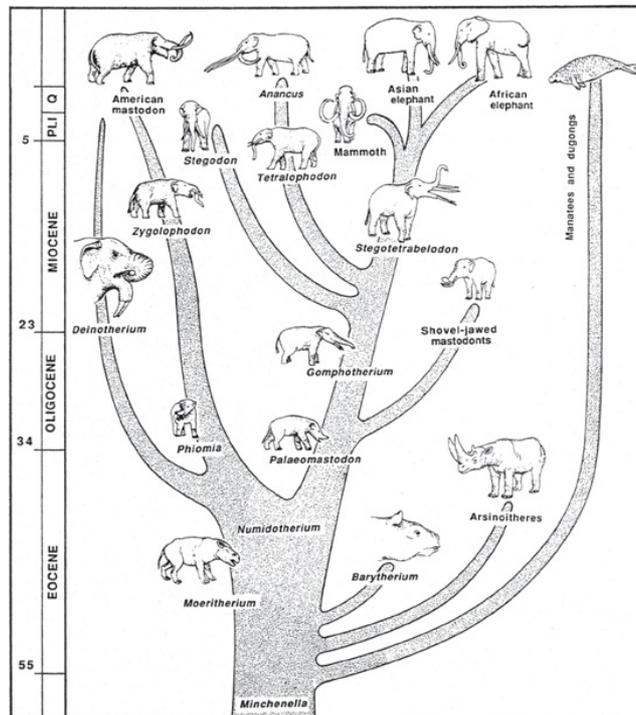


FIGURE 18.66 Evolution of the tethytheres (elephants, manatees, and their extinct relatives). (From Prothero, 1994.)

Another long-standing mystery was a peculiar rhino-like group from the African Oligocene known as arsinotheres, the order Embrithopoda. These elephant-sized animals had a pair of huge, sharp, recurved bony horns on their noses, and no one had a clue as to what they were related to. However, when more archaic Eocene arsinotheres were found in Mongolia and Turkey, McKenna and Manning (1977) suggested that they were tethytheres, and this has since been borne out (Court, 1990).

Yet another paleontological puzzle were the peculiar Pacific Miocene marine mammals known as desmostylians. These walrus-sized animals had hooved feet rather than flippers, with a broad shovel-like tusked jaw containing bizarre molars that look more like a bundle of barrels than anything else. They were long placed in their own order Desmostylia, with no apparent relationships to anything else, until Domning et al. (1986) described an unusually primitive specimen known as *Behemotops* and showed that desmostylians were actually tethytheres, distantly related to sirenians and proboscideans.

Still controversial are the woodchuck-like hooved mammals known as hyraxes or conies, the order Hyracoidea. These little animals are today restricted to rocky outcrops in east African and the Middle East, but during the early Cenozoic, they were among the most common hooved mammals in Africa, evolving into beasts with hippo-like bodies and many other shapes as well. Traditionally, they were allied to tethytheres, and that hypothesis is still supported by some (Novacek and Wyss, 1986; Novacek et al., 1988; Shoshani, 1993) and by the molecular evidence, while others place them with perissodactyls (Prothero et al., 1988; Fischer, 1989; Fischer and Tassy, 1993).

The perissodactyls are the order of herbivorous "odd-toed" hooved mammals that includes the living horses, zebras, asses, tapirs, rhinoceroses, and their extinct relatives (fig. 18.67). They are recognized by a number of unique specializations, but their most diagnostic feature is their feet. Most perissodactyls have either one or three toes on each foot, and the axis of symmetry of the foot runs through the middle digit. They are divided into three groups: the Hippomorpha (horses and their extinct relatives), the Titanotheriomorpha (the extinct brontotheres), and the Moropomorpha (tapirs, rhinoceroses, and their extinct relatives).

Perissodactyls were once thought to have evolved in Central America from the phenacodonts, an extinct group of archaic hooved mammals placed in the invalid taxon "Condylarthra." However, in 1989, a specimen recovered from upper Paleocene deposits in China was described and named *Radinskya*. This specimen shows that perissodactyls originated in Asia around 57 million years ago and were not closely related to North American phenacodonts. *Radinskya* is very similar to the earliest relatives of the tethytheres. This agrees with other evidence that perissodactyls are more closely related to tethytheres than they are to any other group of mammals.

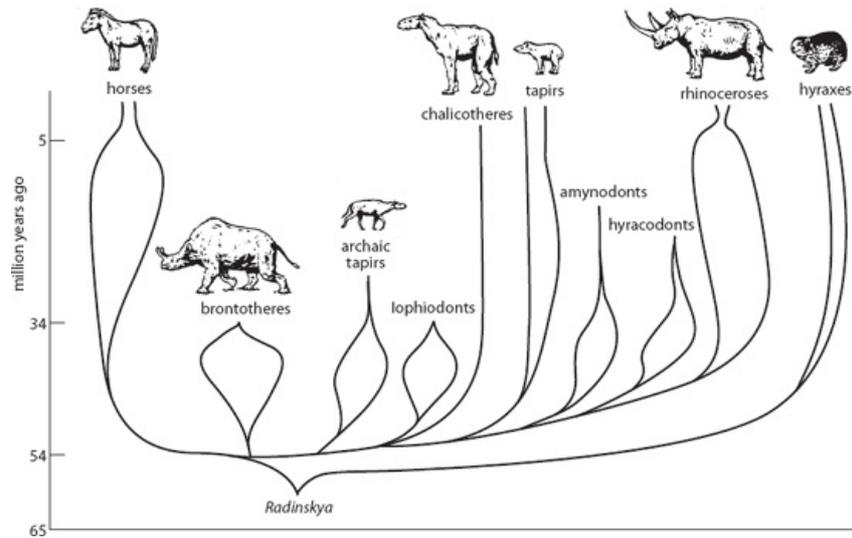


FIGURE 18.67 Evolution of the perissodactyls. (From Prothero, 1994.)

By the early Eocene, the major groups of perissodactyls had differentiated and migrated from Asia to Europe and North America. Before the Oligocene, the brontotheres and the archaic tapirs were the largest and most abundant hoofed mammals in Eurasia and North America. After these groups became extinct, horses and rhinoceroses were the most common perissodactyls, with a great diversity of species and body forms. Both groups were decimated during another mass extinction about 5 million years ago, and today only five species of rhinoceros, four species of tapir, and a few species of horses, zebras, and asses cling to survival in the wild. The niches of large hoofed herbivores have been taken over by the ruminant artiodactyls, such as cattle, antelopes, deer, and their relatives.

From their Asian origin, the hippomorphs spread all over the northern continents. In Europe, the horse-like palaeotheres substituted for true horses. North America became the center of evolution of true horses, which occasionally migrated to other continents. *Protorohippus* (once called *Hyracotherium* or *Eohippus*) was a beagle-sized horse with four toes on the front feet and lived in the early Eocene. Its descendants evolved into many different lineages living side-by-side. The late Eocene–early Oligocene collie-sized three-toed horses *Mesohippus* and *Miohippus* were once believed to be sequential segments on the unbranched trunk of the horse evolutionary tree. However, they coexisted for millions of years with five different species of the two genera living at the same time and place. From *Miohippus*-like ancestors, horses diversified into many different ecological niches. One major lineage, the anchitherines, retained low-crowned teeth, presumably for browsing soft leaves in the forests. Some anchitherines, such as *Megahippus*, were almost as large as the modern horse. *Anchitherium* migrated from North America to Europe in the late early Miocene, the first true horse to reach Europe.

In the middle Miocene, there were at least 12 different lineages of three-toed horses in North America, each with slightly different ecological specializations. This situation is analogous to the diversity of modern antelopes in East Africa. The ancestors of this great radiation of horses are a group of three-toed, pony-sized beasts that have long been lumped into the wastebasket genus “*Merychippus*.” However, recent analyses have shown that the species of “*Merychippus*” are ancestral to many different lineages of horses. True *Merychippus* was a member of the hipparion lineage, a group of three-toed horses that developed highly specialized teeth and had a distinctive concavity in the bone on the front of the face. Hipparions were a highly diverse and successful group of horses, with seven or eight different genera spread not only across North America, but also migrating to Eurasia. Merychippines were also ancestral to lineages such as *Calippus* (a tiny dwarf horse), *Protohippus*, and *Astrohippus*.

On two different occasions (*Pliohippus* and *Dinohippus*) three-toed horses evolved into lineages with a single toe on each foot. In the early Pliocene, most of these three-toed and one-toed horse lineages became extinct, leaving only *Dinohippus* to evolve into the modern horse *Equus*. The main lineage of horses that survived the latest Miocene extinctions were known as the equines. The living genus *Equus* first appeared in the Pliocene and was widespread throughout the northern hemisphere. When the Isthmus of Panama rose about 2.5 million years ago, horses also spread to South America, where they evolved into distinctive horses with a short proboscis known as the *hippidions*. At the end of the last Ice Age (about 10,000 years ago), horses became extinct in the New World. Columbus reintroduced horses to their ancestral homeland in 1493. Wild horses that have escaped from domesticated stock are known as mustangs.

Brontotheres or titanotheres began as pig-sized, hornless animals about 53 million years ago and quickly evolved into multiple lineages of cow-sized animals with long skulls and no horns. In the late middle Eocene (between 40 and 47 Ma), there were many different lineages of brontotheres (Mihlbachler, 2008). Some had long skulls, while others had short snouts and broad skulls. Still others had a pair of tiny blunt horns on the tips of their noses. Between 37 and 34 Ma, their evolution culminated with huge, elephant-sized beasts bearing large paired blunt horns on their noses. Throughout their history, brontotheres were the largest animals in North America. They also appeared in Asia in the late Eocene, where beasts such as *Embolotherium*, with a huge single “battering-ram” horn evolved. Recent research has shown that the extinction of brontotheres about 34 million years ago was due to a global climatic change (triggered by the first Antarctic glaciers) that caused worldwide cooling and drying of climates. This climatic change decimated the forests of the temperate regions

and eliminated most of the soft, leafy vegetation on which brontotheres fed.

The earliest moropomorphs, such as *Homogalax*, occur in lower Eocene strata. They are virtually indistinguishable from the earliest horses, such as *Protorohippus*. From this unspecialized ancestry, a variety of archaic tapir-like animals diverged. Most retained the simple leaf-cutting teeth characteristic of tapirs, and like brontotheres, they died out at the end of the Eocene when their forest habitats shrank. Only the modern tapirs, with their distinctive long proboscis, still survive in the jungles of Central and South America (three species), and Southeast Asia (one species). All are stocky, pig-like beasts with short stout legs, oval hooves, and a short tail. They have no natural defenses against large predators (such as jaguars or tigers) except fleeing through dense brush and swimming to make their escape.

The horse-like clawed chalicotheres are closely related to some of these archaic tapirs. When chalicotheres were first discovered, paleontologists refused to believe that the claws belonged to a hoofed mammal related to horses and rhinos. However, many specimens have clearly shown that chalicotheres are an example of a hoofed mammal that has secondarily regained its claws. There has been much speculation as to what chalicothere claws were used for. Traditionally, they were considered useful for digging up roots and tubers, except that the fossilized claws show no sign of the characteristic scratches due to digging. Instead, chalicotheres apparently used their claws to hook and haul down limbs and branches to eat leaves (much as ground sloths might have done), rather than for digging. *Chalicotherium* had such long forelimbs and short hind limbs that it apparently knuckle-walked like a gorilla, with its claws curled inward. Chalicotheres were always rare throughout their history in North America and Eurasia, but nevertheless survived in Africa until the ice ages.

Rhinoceroses have been highly diverse and successful throughout the past 50 million years. They have occupied nearly every niche available to a large herbivore, from dog-sized running animals, to several hippo-like forms, to the largest land mammal that ever lived, *Paraceratherium*. Most rhinoceroses were hornless. Unlike the horns of cattle, sheep, and goats, rhino horns are made of cemented hair fibers and have no bony core, so they rarely fossilize. The presence and size of the horn must be inferred from the roughened area on the top of the skull where the horn once attached.

The earliest rhinos, known as *Hyrachyus*, were widespread over Eurasia and North America in the early middle Eocene, and are even known from the Canadian Arctic. They apparently crossed back and forth between Europe and North America using a land bridge across the North Atlantic (before that ocean opened to its present width). From *Hyrachyus*, three different families of rhino diverged. One family, the amynodonts, was a hippo-like amphibious group, with stumpy legs and a barrel chest. In addition, amynodonts are usually found in river and lake deposits. They occupied this niche long before the hippo evolved. The last of the amynodonts, which had a short trunk like an elephant, died out in Asia in the middle Miocene.

The second family was known as the hyracodonts, or “running rhinos,” because they had unusually long slender legs compared with other rhinos. They were particularly common in Asia and North America in the middle and late Eocene. The last of the North American forms was *Hyracodon*, which was about the size and proportions of a Great Dane and survived until the late Oligocene. The second group of hyracodonts was the gigantic indricotheres (fig. 18.68), which were the largest mammals in Asia during the late Eocene and Oligocene (about 40 to 30 Ma ago). The biggest of all was *Paraceratherium* (once called *Baluchitherium* or *Indricotherium*), which was 6-m (18 feet) tall at the shoulder and weighed 20,000 kg (44,000 lb). It was so tall that it must have browsed leaves from the tops of trees, as giraffes do today. Despite its huge bulk, it did not have the massive limbs and short, compressed toes of most giant land animals, such as sauropod dinosaurs, brontotheres, or elephants. Instead, it reveals its heritage as a running rhino by retaining its long slender toes—even though it was much too large to run. Indricotheres were also the last of the hyracodonts, vanishing from Asia in the middle Miocene.

The third family is the true rhinoceroses, or family Rhinocerotidae. They first appeared in Asia and North America in the late middle Eocene and lived side-by-side with the hyracodonts and amynodonts on both continents. Up until this point, all the rhinoceroses we have mentioned were hornless. Rhinos with horns first appeared in the early late Oligocene; two different lineages independently evolved paired horns on the tip of the nose. Both of these groups became extinct in the late early Miocene, when two new subfamilies immigrated to North America from Asia: the browsing (leaf-eating) aceratherines and the hippo-like grazing teleoceratines. In the middle and late Miocene, browser-grazer pairs of rhinos were found all over the grasslands of Eurasia, Africa, and North America. The teleoceratine *Teleoceras* was remarkably similar to hippos in its short limbs, massive barrel-shaped body, and high-crowned teeth for eating gritty grasses.



FIGURE 18.68 Life-size restoration of the gigantic hyracodont rhinoceros *Paraceratherium*, the largest land mammal that ever lived. Its close relative, the running rhino *Hyracodon*, stands just below it to the right. The African elephants standing further to the right give a sense of scale. (Photo courtesy of University of Nebraska State Museum.)

A mass extinction event that occurred about 5 Ma wiped out North American rhinos and decimated most of the archaic rhino lineages (especially the teleoceratines and aceratherines) in the Old World. The surviving lineages diversified in Eurasia and Africa and even thrived during the ice ages. For example, the woolly rhinoceros was widespread in the glaciated regions of Eurasia, although it never crossed into North America (unlike the woolly mammoth or bison, which did). The five living species of rhinoceros are all on the brink of extinction due to heavy poaching for their horns.

Molecular Versus Morphological Phylogenies of the Placentals

Now that we have surveyed the major groups of placentals and discussed the morphological evidence for their relationships (fig. 18.61A), let us compare the arrangement of the traditional phylogeny with the molecular phylogeny of placentals that emerged over the past decade (fig. 18.61B). In many cases, the molecular and morphological data are congruent. For example, the Xenarthra separates out as one of the most primitive clades of placentals, and many long-accepted morphological groups and relationships (e.g., Glires for rodents plus lagomorphs; Archonta for primates, colugos, and tree shrews; lipotyphlan insectivores as a basal clade; whales descended from artiodactyls and artiodactyls closely related to perissodactyls; Tethytheria including proboscideans, sirenians, and hyraxes) emerge from the molecular data as strongly supported.

Other phylogenetic hypotheses are surprising. For example, molecular data cluster the tethytheres with an odd assortment of other isolated African orders, including aardvarks, tenrecs, golden moles, and elephant shrews in a clade called “Afrotheria.” This clade is claimed to have split off and become isolated in Africa from the remaining Eutheria (xenarthrans plus all other northern hemisphere groups, dubbed the “Boreoeutheria”). The “Boreoeutheria” also has a strong biogeographic component, with a clade called “Laurasiatheria” that includes insectivores, bats, and the “Ferungulata,” consisting of artiodactyls plus whales, perissodactyls, and, surprisingly, carnivorans and scaly anteaters. The other clade is less surprising, with the “Euarchontoglires” combining the Archonta and Glires.

Once again, the reader should be aware that groups like the Afrotheria, Boreoeutheria, Laurasiatheria, Euarchontoglires, and Ferungulata are supported by molecular evidence only (see the debate between Springer et al. [2007a, 2007b] and Asher et al. [2008]), and there are no anatomical or embryological characters that support them (and quite a few that conflict with them). However, when the relatively small number of anatomical character states is coded into a phylogenetic matrix along with the huge number of molecular changes, the molecular evidence always overwhelms any signal from the anatomy. Most mammalian paleontologists are still skeptical about molecular phylogenies for that reason, because they have led to many false notions and ridiculous ideas in the past (Shoshani and McKenna, 1998; Asher et al., 2008). Only time will tell whether these new phylogenetic arrangements reach acceptance and find any evidence from a data source other than molecular sequences. More recently, O’Leary and others (2013) produced a phylogeny that combined both morphological and molecular evidence and produced a “supertree” that resolved many of the conflicts. It was also calibrated with many different molecular clock dates, so it is consistent with the fossil record showing that most placental orders originated in the Paleocene, not much earlier in the Cretaceous, as suggested by purely molecular phylogenies.

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