In Parker, S.P. (ed.) *McGraw-Hill Encyclopedia of Science and Technology* (9th ed.), McGraw-Hill, Inc., New York, 2002, v. 10, p. 359-362

Mammalia

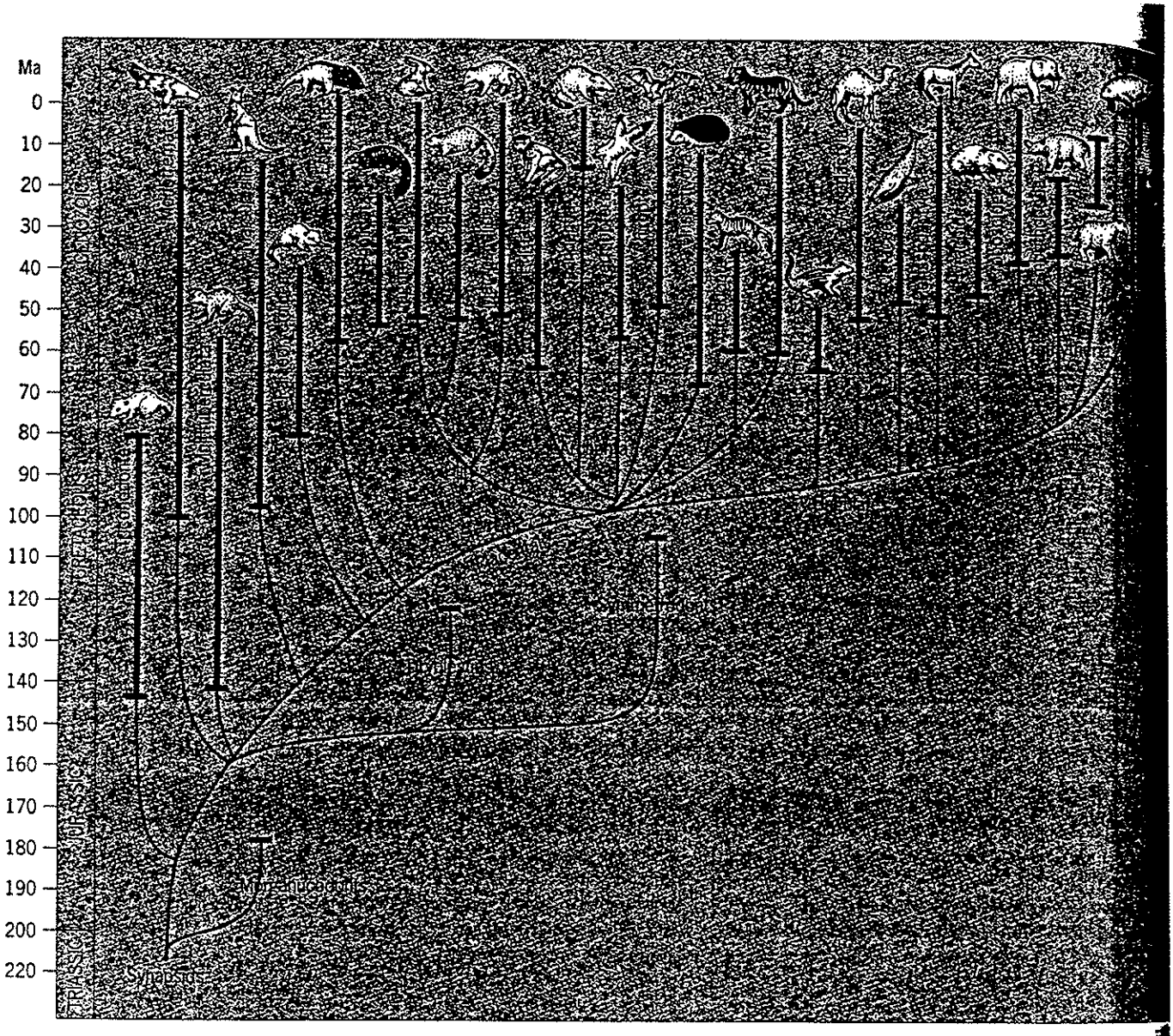
The class Mammalia is the dominant group of vertebrates today. They have ruled the planet since the extinction of the dinosaurs 65 million years ago. There are over 4200 living species of mammals, classified into over 1000 genera, 140 families, and 18 orders. However, the number of extinct mammals is at least five times that. Most living mammals are terrestrial, including such large beasts as elephants, rhinos, hippos, and giraffes, as well as a great diversity of smaller land animals. The largest known land mammal was the extinct 20-ton hornless rhino *Paraceratherium*. Many groups of mammals moved to the water from land-dwelling ancestors. These included manatees and dugongs (which are distantly related to elephants), otters (which are related to weasels), seals, sea lions, and walruses (which are distantly related to bears), and whales (which are distantly related to even-toed hoofed mammals), as well as numerous extinct groups. The living blue whale [reaching 30 m (100 ft) in length and 150 tons] is by far the largest animal that has ever lived. Mammals have also taken to the air, with over 920 living species of bats, as well as numerous gliding forms such as the flying squirrels, phalangerid marsupials, and flying lemurs or colugos. Mammals are even more successful at small body sizes, with hundreds of small species of rodents, rabbits, and insectivores. The smallest living mammal, the 1.5-g Kitti's hognosed bat, is at the lower limit of body size for mammals, since physiology and anatomy prevent them from thriving in the tiny-body-size niche inhabited by insects and other arthropods.

Anatomy and physiology. Mammals are distinguished from all other animals by a number of unique characteristics. These include a body covered with hair or fur (secondarily reduced in some mammals, particularly aquatic forms); mammary glands in the female for nursing the young; a jaw composed of a single bone, the dentary; and three middle ear bones, the incus, malleus, and stapes. All mammals maintain a constant body temperature through metabolic heat. Their four-chambered heart (two ventricles and two atria) keeps the circulation of the lungs separate from that of the rest of the body, resulting in more efficient oxygen transport to the body tissues. They have many other adaptations for their active life-style, including specialized teeth (incisors, canines, molars, and premolars) for biting, tearing, and grinding up food for more efficient digestion. These teeth are replaced only once in the lifetime of the animal (rather than continuous replacement, found in other toothed vertebrates). Mammals have a unique set of muscles that allow the jaw to move in many directions for chewing and for stronger bite force. Their secondary palate encloses the internal nasal passage and allows breathing while they have food in the mouth. Ribs (found only in the thoracic region) are firmly attached to the breastbone (sternum), so that expansion of the lung cavity is accomplished by a muscular wall in the abdominal cavity called the diaphragm. *See* CARDIOVASCULAR SYSTEM; DENTITION; GHOST IMAGE (OPTICS); HAIR; LACTATION; MAMMARY GLAND; THERMOREGULATION; TOOTH.

All mammals have large brains relative to their body size. Most mammals have excellent senses, and some have extraordinary senses of sight, smell, and hearing. To accommodate their large brains and more sophisticated development, mammals are born alive (except for the platypus and echidnas, which lay eggs), and may require considerable parental care before they are ready to fend for themselves. Juvenile mammals have separate bony caps (epiphyses) on the long bones, separated from the shaft of the bone by a layer of cartilage. This allows the long bones to grow rapidly while still having a strong, bony articulation at the end. When a mammal reaches maturity, these epiphyses fuse to the shaft, and the mammal stops growing (in contrast to other vertebrates, which grow continuously through their lives). *See* BRAIN; NERVOUS SYSTEM (VERTEBRATE); SKELETAL SYSTEM.

Reproduction and classification. The living mammals are divided into three major groups: the monotremes (platypus and echidnas), which still lay eggs, retain a number of reptilian bones in their skeletons, and have other primitive features of their anatomy and physiology; the marsupials (opossums, kangaroos, koalas, wombats, and their relatives), which give birth to an immature embryo that must crawl into the mother's pouch (marsupium), where it finishes development; and the placentals (the rest of the living mammals), which carry the young through a long gestation until they give birth to relatively well-developed progeny. In addition to these three living groups, there were many other major groups, such as the rodentlike multituberculates, now extinct. The most recent classification of the mammals can be summarized as follows:

Class Mammalia
- Subclass Prototheria (monotremes)
- Subclass Theriiformes
  - Infraclass Holotheria
    - Cohort Marsupialia (marsupials or pouched mammals)
    - Cohort Placentalia (placentals)
      - Magnorder Xenarthra (sloths, anteaters, armadillos)
      - Magnorder Epitheria
        - Grandorder Anagalida (= Glires) (rodents, rabbits, elephant shrews)
        - Grandorder Ferae (carnivores, pangolins, many extinct groups)
        - Grandorder Lipotyphla (hedgehogs, shrews, moles, tenrecs, and kin)
        - Grandorder Archonta
          - Order Chiroptera (bats)
          - Order Primates (lemurs, monkeys, apes, humans)
          - Order Scandentia (tree shrews)



Evolutionary relationships of the major groups of mammals.

Grandorder Ungulata (hoofed mammals)
- Order Tubulidentata (aardvarks)
- Order Artiodactyla (even-toed hoofed mammals: pigs, hippos, camels, deer, antelopes, cattle, giraffes, pronghorns, and relatives)
- Order Cete (whales and their extinct land relatives)
- Order Perissodactyla (odd-toed hoofed mammals: horses, rhinos, tapirs, and extinct relatives)
- Order Hyracoidea (hyraxes)
- Order Tethytheria (elephants, manatees, and extinct relatives)

This classification does not list all the extinct groups, which include at least a dozen more ordinal-level taxa. It is a considerable improvement over previous mammalian classifications, which used to list over 30 different orders with no indication of how they were related to one another. Although there are more ranks in this classification than is traditional, this nesting of groups within groups accurately reflects the evolutionary branching sequence (see **illus.**). *See* REPRODUCTIVE SYSTEM.

Evolution. Mammals evolved from the Synapsida, an early branch of the terrestrial amniotes that has been erroneously called the mammallike reptiles. This name is inappropriate because synapsids were never related to reptiles. Synapsids and reptiles originated independently from one another about 320 million years ago, and evolved separately ever since. Early synapsids, such as the finback *Dimetrodon*, show relatively few mammalian characteristics, but as their evolution progressed through the late Paleozoic, synapsids became progressively more mammallike.

The first undoubted mammals appeared in the Late

Triassic (about 210 million years ago), and were tiny insectivorous forms much like living shrews. Through the rest of the age of dinosaurs, a number of different groups evolved over the next 145 million years of the Jurassic and Cretaceous. Most remained tiny, shrewlike animals, hiding from the dinosaurs in the underbrush and coming out mostly at night. The first two-thirds of mammalian history had passed before the dinosaurs became extinct 65 million years ago, and this allowed mammals to emerge from their shadow.

Opossumlike marsupials are known from the Early Cretaceous (about 110 million years ago), and they were more common than placentals just before the end of the age of dinosaurs. Although opossums were found on most continents during the Cenozoic, other marsupials diversified primarily on the southern continents of Australia or South America, which were isolated from the main developments in placental evolution. On both of these continents, marsupials evolved in parallel with placentals, so that Australia has marsupials shaped like woodchucks (wombats), rabbits (bandicoots), flying squirrels (phalangers), monkeys (cuscuses), dogs (Tasmanian wolf), wolverines (Tasmanian devil), anteaters (myrmecobiids), cats (dasyurines), moles (notoryctines), mice (dasycercines), as well as extinct marsupial lions and rhino-sized diprotodonts. South America was once the home of marsupial sabertooths and hyaenalike marsupials known as borhyaenids, although they apparently became extinct about 3 million years ago when placental carnivores came from North America via the Panamanian land bridge.

Between 65 and 55 million years ago, a rapid adaptive radiation (see illus.) yielded all the living orders of placental mammals and many extinct forms as well. The Xenarthra, or edentates, were the first group of placentals to branch off. Although "edentate" means toothless, this is true only of anteaters; sloths and armadillos have simple peglike teeth lacking enamel. The archaic nature of edentates among the placentals is shown by a variety of characters, including a uterus simplex (divided by a septum and lacking a cervix), a slower, less well regulated metabolism, retention of several reptilian bones lost in all other placentals, and a primitive rodlike stapes in the middle ear. Like the marsupial carnivores, edentates evolved in isolation in South America throughout most of their history, developing into a variety of sloths (both tree sloths and huge ground sloths weighing up to 3 tons), anteaters, and armadillos [including the giant glyptodonts, which were 2 m (6.5 ft) long, had 400 kg (880 lb) of body armor, and a spiked club on the tip of the tail]. The long period of isolation in South America ended about 3 million years ago, and ground sloths and glyptodonts migrated to central America and parts of North America, but they disappeared at the end of the last ice age.

The remaining (nonedentate) placentals, or eutheres, diversified primarily in Eurasia and North America and spread throughout the world in the early Cenozoic. The true lipotyphlan insectivorans (represented by shrews, moles, and hedgehogs) continued to diversify all over the northern continents throughout the Cenozoic. Most remained small, and they ate insects, worms, and other small animals, although the extinct giant hedgehog *Dinogalerix* was as big as a large dog and killed sizable prey.

The archontan radiation began with an enormous expansion of primitive lemurlike primates in the early Cenozoic, when the world had dense jungle vegetation all the way to the Poles. Primates declined in the Oligocene, when their forest habitats disappeared, and they became restricted to Africa (Old World monkeys and apes) and South America (New World monkeys). The earliest bats (known from about 50 million years ago) already had fully developed wings. They are the second most diverse group of mammals, after the rodents.

The radiation of the Glires began in the Paleocene of Asia, where numerous primitive relatives of rodents and rabbits are found. In the Eocene, both groups migrated to Europe and North America, where they soon took over the niche of small-bodied fruit, seed, and nut eaters that had been occupied by multituberculates and primitive primates. Although rodents and rabbits are separate orders, they are both characterized by chisellike, ever-growing front incisors that are used in gnawing. However, rodents have only a single pair of incisors, while rabbits have two. The enormous diversification of the Rodentia since the Eocene has given rise to over 1700 species (about 40% of the Mammalia), with forms as large as the pig-sized capybara down to the tiny mice and voles.

Predatory mammals (the Ferae) include the extinct creodonts (an archaic group that were the dominant predators and scavengers of the early Cenozoic), and the living order Carnivora (cats, hyenas, mongooses, civets, dogs, bears, weasels and their kins, seals and sea lions, raccoons, and many extinct groups). All Carnivora are distinguished by distinctive shearing teeth, the carnassials, developed between the last upper premolar and first lower molar. True Carnivora began as weasellike forms in the early Eocene, but by the Oligocene they had taken over most of the predatory niches from the creodonts. By the Miocene, the ancestors of seals and sea lions had evolved from bearlike ancestors. Carnivorous mammals show remarkable examples of convergence on a limited number of body forms. For example, sabertoothed forms evolved four times: once in the creodonts, once in the true cats, and once in the extinct catlike nimravids, which are related to dogs (plus the extinct sabertoothed marsupial). In North America, the borophagine dogs converged on hyenas, with similar bone-crushing teeth.

The hoofed mammals, or ungulates, are first known from about 85 million years ago in central Asia. In the latest Cretaceous and Paleocene, archaic hoofed mammals ("condylarths") were among the most common forms in North America and Asia. From these roots, numerous orders evolved. The first

to branch off were the even-toed Artiodactyla, which have two or four toes on each foot and a distinctive ankle structure. First appearing in Pakistan in the earliest Eocene, artiodactyls quickly diversified into a number of different groups, including suoids (pigs, peccaries, hippos), tylopods (camels and their extinct relatives), and ruminants (deer, giraffes, pronghorns, cattle, sheep, goats, antelopes). With their four-chambered stomachs for more efficient digestion, the ruminants became the dominant group of large herbivorous mammals as global climates became drier and grasslands expanded in the later Cenozoic.

The ancestors of whales were large hoofed predators known as mesonychids. Recently, transitional forms between mesonychids and primitive whales have been found in the Eocene of Pakistan. By the Oligocene, whales had diversified into the predatory toothed whales (dolphins, orcas, sperm whales) and filter-feeding baleen whales (blue, right, humpback, gray, and many other whales).

The Perissodactyla, or odd-toed ungulates, have one or three toes on each foot. Today they include horses, rhinos, and tapirs, but they were much more diverse in the past, with huge slingshot-horned brontotheres and bizarre clawed chalicotheres. Closely related to perissodactyls are the hyraxes or conies, and the tethytheres (elephants, sea cows, and their relatives). Tethytheres originated from late Paleocene ancestors that once lived along the Tethys Seaway (which stretched from Gibraltar to Indonesia). Although sea cows spread around the world by the Eocene, the early evolution of hyraxes, and of elephants and their kin was restricted to Africa until the middle Miocene, when both groups spread to Eurasia, and mastodonts even reached North America.

Donald R. Prothero

Bibliography. J. F. Eisenberg, *The Mammalian Radiations*, 1981; J. H. Honacki, K. E. Kinman, and J. W. Koeppl, *Mammal Species of the World*, 1982; D. Macdonald, *The Encyclopedia of Mammals*, 1984; M. C. McKenna and S. K. Bell, *Classification of Mammals above the Species Level*, 1997; R. M. Nowak, *Walker's Mammals of the World*, 1991; D. R. Prothero and R. M. Schoch, *Horns, Hooves, and Flippers: The Evolution of Hoofed Mammals and Their Relatives*, 2000; R. J. G. Savage and M. R. Long, *Mammal Evolution: An Illustrated Guide*, 1986; F. S. Szalay, M. J. Novacek, and M. C. McKenna (eds.), *Mammal Phylogeny*, 1993; J. Z. Young, *The Life of Mammals*, 1975.