Placental Mammals

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Introduction

The Eutheria, or placental mammals, are the dominant group of vertebrates on the Earth today, and they have ruled the planet ever since the extinction of the dinosaurs at approximately 65 Ma. At the latest count, there are over 4400 living species of mammal, classified into over 1000 genera, 140 families, and 18 orders. However, the number of extinct mammals is at least five times as great. Most living mammals are terrestrial, including large beasts, such as elephants, rhinoceroses, hippopotamuses, and giraffes, as well as a great diversity of smaller land animals. The largest known land mammal is the extinct 20 tonne hornless rhinoceros *Paraceratherium*. Many groups of mammals evolved from land-dwelling ancestors to life in the water. These include 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 (at 30 m in length and 150 tonnes) is by far the largest animal that has ever lived, surpassing even the largest dinosaurs. Mammals have also taken to the air, with almost 1000 living species of bat, as well as numerous gliding forms, such as the 'flying squirrels' and 'flying lemurs' or colugos. Mammals are even more successful when their body sizes are small, with hundreds of small species of rodent, rabbit, and insectivore. The smallest living mammal, the 1.5 g Kitti's hog-nosed bat, is at the lower limit of possible body size for mammals, since the physiology and anatomy of mammals 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 the possession of a number of unique characteristics. These include a body covered in hair or fur (secondarily reduced in some mammals, particularly aquatic forms); mammary glands in the females for nursing their 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 the production of metabolic heat. They have a four-chambered heart (two ventricles and two auricles), which 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 lifestyle, including specialized teeth (incisors, canines, molars, and premolars) for biting, tearing, and grinding up their food for more efficient digestion. These teeth are replaced only once in the lifetime of the animal (rather than continuously as in other toothed vertebrates). Mammals have a unique set of jaw muscles, which 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 them to breathe while they have food in their mouth. Ribs (found only in the thoracic region) are firmly attached to the breastbone, so that expansion of the lung cavity is accomplished by movement of a muscular wall in the abdominal cavity called the diaphragm.

All living mammals have relatively large brains for their body size. Most mammals have excellent senses, and some have extraordinary senses of sight, smell, and hearing. To accommodate their larger brains and more sophisticated development, most mammals are born alive (rather than from 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, which are 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 throughout their lives).

Reproduction and Classification

Living mammals are divided into three major groups: the monotremes (platypus and echidna), which still lay eggs, retain a number of reptilian bones in their skeletons, and have other primitive features in their anatomy and physiology; the marsupials (opossums, kangaroos, koalas, wombats, and their relatives), which give birth to an immature embryo that must crawl into its mother's pouch (marsupium), where it finishes its development; and the placentals (the rest of the living mammals), which carry their young through a long gestation until they give birth to relatively well-developed progeny. This last group derives its name from the placenta, the membrane that surrounds the developing embryos within the uterus of the female. The placenta is formed by the fusion of the two other embryonic membranes, the chorion, which surrounds the embryo, and the allantois, which holds the embryonic wastes in egg-laying vertebrates. The placental membrane attaches the embryo to the wall of the uterus, and exchanges nutrients, gases, and waste products with the circulatory system of the mother, so that no hard-shelled egg (or its associated features, such as the allantoic waste sac or the large yolk sac) is needed. The placenta allows the embryos to undergo more development within the uterus, and to be born more mature than in other groups of mammals. By contrast, in marsupials the lack of a placenta protecting the embryo means that, when the immune system develops, the embryo must be born prematurely and move to the pouch, otherwise the mother's immune system would reject the embryo as a foreign object within the uterus.

In addition to these three living groups, there were many other major groups, such as the squirrel-like multituberculates, which are 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, and 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)
          - Grandorder Ungulata (hoofed mammals)
            - Order Tubulidentata (aardvarks)
            - Order Artiodactyla (even-toed hoofed mammals: pigs, hippopotamuses, camels, deer, antelopes, cattle, giraffes, pronghorns, and their relatives)
            - Order Cete (whales and their extinct land relatives)
            - Order Perissodactyla (odd-toed hoofed mammals: horses, rhinoceroses, 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 on previous mammalian classifications, which listed 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 their evolutionary branching sequence (**Figure 1**).

In the past few years, molecular studies have suggested an alternative arrangement of placental relationships, which conflicts strongly with that indicated by the morphology and the fossil record. This classification groups the orders of placental mammals as follows:

- Subclass Placentalia
  - Superorder Xenarthra (edentates)
  - Superorder Afrotheria (African insectivores, such as the golden moles and tenrecs, plus elephant shrews, aardvarks, and the tethytheres, including elephants, sirenians, hyraxes)
  - Superorder Euarchontoglires
    - Infraorder Archonta (primates, colugos, tree shrews)
    - Infraorder Glires (rodents, rabbits)
  - Superorder Laurasiatheria
    - Infraorder Cetartiodactyla (whales plus artiodactyls)
    - Infraorder Ferungulata (perissodactyls, carnivores plus pangolins)
    - Infraorder Chiroptera (bats)
    - Infraorder Eulipotyphla (shrews, moles, hedgehogs)

Advocates of this molecular classification argue that it makes biogeographical sense for the African mammal groups (the 'Afrotheria') to be closely related, since Africa was an island continent isolated from the rest of the world during the Early Cenozoic. Likewise, the only placentals from the island continent of South America, the edentates, are in a separate group. The rest of the placental mammals, which have lived on the northern ('Laurasian') continents through most of their history, also cluster together. Critics of this classification point to a huge number

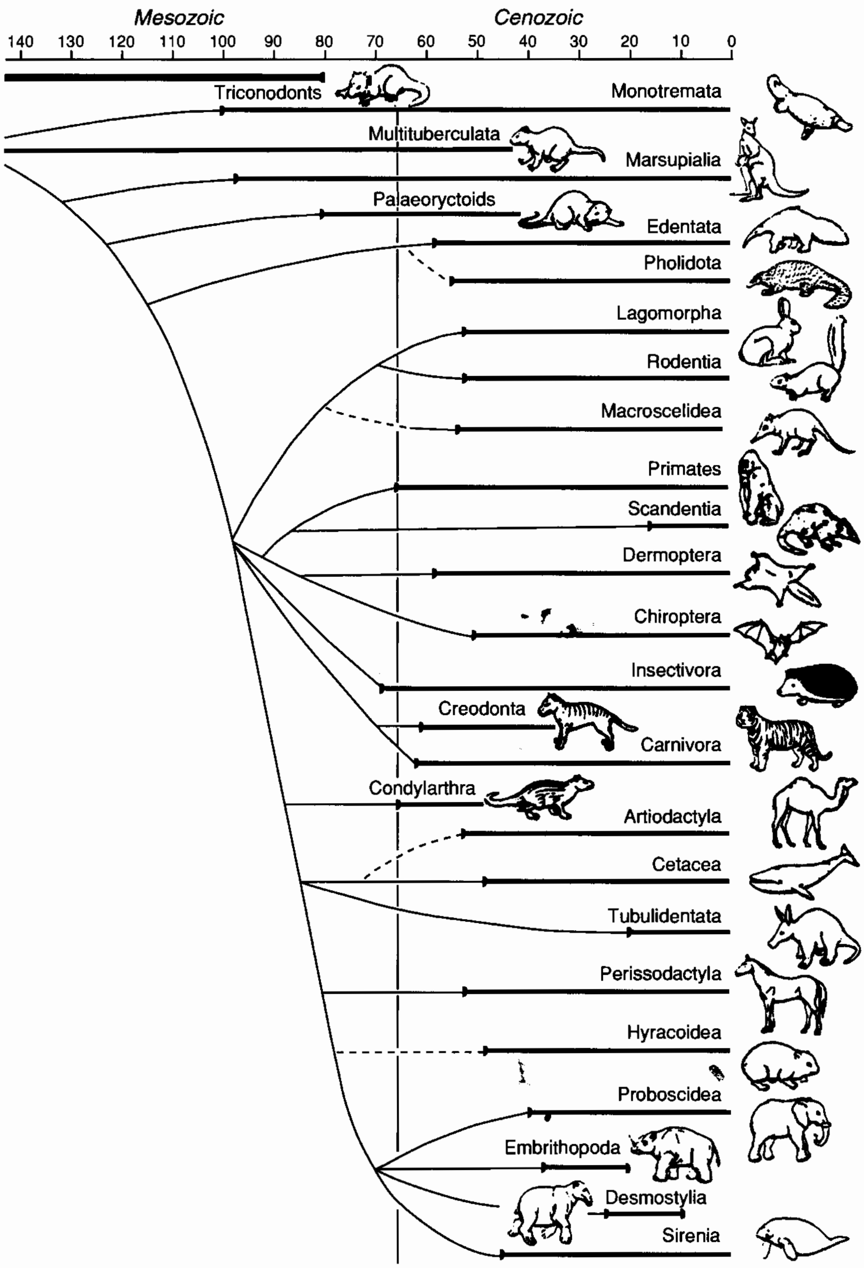

Figure 1 Evolutionary relationships and history of the major groups of mammals (modified from Novacek MJ (1994) The radiation of placental mammals. In: Prothero DR and Schoch RM (eds.) *Major Features of Vertebrate Evolution*, pp. 220–238. Paleontological Society Short Courses in Paleontology, no. 7. Paleontological Society, Lawrence, Allen Press).

of conflicts with well-established morphological evidence. For example, it breaks up the hoofed mammals by placing elephants and hyraxes in the Afrotheria, whereas the morphological evidence and the fossil record strongly suggest that they are related to the rest of the hoofed mammals (perissodactyls and artiodactyls plus whales). Likewise, good morphological evidence links at least some of the African insectivores with the true lipotyphlan insectivores, so most palaeomammalogists view the new molecular phylogenies with scepticism. They have good reason to do so, for molecular biologists have been claiming that they have 'the answer' to placental phylogeny in each new molecular system they examine, but, over the years, they have produced wildly varying results, so their classifications are not stable or reproducible enough yet to justify reordering the entire taxonomy of placental mammals.

Evolution

Mammals evolved from the Synapsida, an early branch of the terrestrial amniotes that has been erroneously called the 'mammal-like reptiles'. This name is inappropriate, because synapsids were never reptiles. Synapsids and reptiles originated independently about 320 Ma, and have evolved separately ever since. Early synapsids, such as the finback *Dimetrodon*, show relatively few mammalian characteristics, but, as their evolution progressed through the Late Palaeozoic, synapsids became progressively more and more mammal-like.

The first undoubted mammals appeared in the Late Triassic (about 210 Ma), and were tiny insectivorous forms much like living shrews. A number of different groups evolved over the next 145 Ma of the Jurassic and Cretaceous. Most remained tiny shrew-like 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 Ma, allowing mammals to emerge from their shadow.

Opossum-like marsupials are known from the Early Cretaceous (about 110 Ma), and they were more common than placentals just before the end of the age of dinosaurs. The first probable placental is the beautifully preserved skeleton (complete with hair impressions) from the Early Cretaceous of China known as *Eomaia scansoria*, which is about 125 Ma old. Although it is very primitive in most features, it had teeth for an insectivorous diet and limb proportions that suggest it was a tree dweller. By the Late Cretaceous (75 Ma), very primitive hoofed mammals (zhelestids) are known from Uzbekistan, and primitive members of the insectivore, carnivore, and primate lineages are known from the latest Cretaceous in both North America and Asia (65–70 Ma).

Although these early placentals are extremely primitive and hard to distinguish from early marsupials based on the limited evidence of their teeth and jaws, they can still be recognized by the trained palaeontologist. Early placentals had three upper and lower molars on each side of the jaw, and no more than five premolars (which reduces to four in later placentals). By contrast, early marsupials had four molars and usually only three premolars. In placentals, the last premolar has a tendency to be shaped like a molar (even though, as a premolar, it replaces a deciduous tooth, while a molar is never replaced). Primitive marsupial upper molars have a large expanded region on the outer edge of the tooth crown, whereas the upper molars of early placental mammals have little area outside the main cusps and instead are wider on the inside edge of the tooth. In the lower jaw of marsupials, the projection below the hinge (the angular process) flexes towards the midline, but in placentals it points straight back.

Between 65 and 55 Ma, a rapid adaptive radiation (**Figure 1**) yielded all the living orders of placental mammals and many extinct forms as well. The Xenarthra, or edentates, was the first group of placentals to branch off. Although the name 'edentate' means toothless, this is true only of anteaters; sloths and armadillos have simple peg-like teeth that lack 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 rod-like stapes in the middle ear. 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 tonnes), anteaters, and armadillos (including the giant glyptodonts, which were 2 m long and had 400 kg of body armour and a spiked club on the tip of the tail). The long period of isolation in South America ended about 3 Ma ago, and ground sloths and glyptodonts migrated to Central America and parts of North America, disappearing at the end of the last Ice Age.

The remaining (non-edentate) placentals, or epitheres, diversified primarily in Eurasia and North America, and spread throughout the world in the Early Cenozoic. The true lipotyphlan insectivores (represented by shrews, moles, and hedgehogs) continued to diversify throughout the Cenozoic all over the northern continents. Most remained small in body size and ate insects, worms, and other small animals, although the extinct giant hedgehog *Dinogalerix* was the size of a large dog and killed sizable prey. The smaller lipotyphlan insectivores, such as the shrews, are among the smallest living placentals. Their body size is so tiny that they are constantly losing body heat because of their large surface area relative to their tiny mass. Consequently, they must eat almost continuously, or they will starve to death in a matter of days. This makes them extremely active and voracious predators, attacking not only worms and arthropods, but also animals much larger than themselves. They are fearless and will fight much larger animals when cornered.

The archontan radiation began with an enormous expansion of primitive lemur-like 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 became restricted to Africa (Old World monkeys and apes) and South America (New World monkeys). From the Old World monkeys evolved the great apes. About 15 Ma, apes were more diverse than monkeys in the Old World. Today only four groups of living great apes are known: the gibbons, the orang-utans, the gorillas, and the chimpanzees. They diverged from our own family, the Hominidae, about 7 Ma. This timing was originally established by molecular evidence, but recently a hominid fossil of that age, *Sahelanthropus tchadensis*, has been described from rocks 6–7 Ma in Chad in western Africa. In the past 5 million years, there have been dozens of species of hominid, divided into many genera: *Orrorin, Ardipithecus, Paranthropus, Australopithecus*, and our own genus, *Homo*, which appeared about 2.5 Ma. Fossils that are recognizably members of our own species, *Homo sapiens*, are known from South Africa in rocks about 100 000 years old.

The earliest bats (known from about 50 Ma) already had fully developed wings. They are the second most diverse group of mammals after the rodents, with almost 1000 living species and many more fossil species. They are divided into two main groups, the insectivorous Microchiroptera (which use echolocation to find their prey on the wing) and the fruit bats, or Megachiroptera (which fly during the day, eating fruit in the trees of the tropics, and do not echolocate).

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. Rodents and rabbits are both characterized by chisel-like ever-growing front incisors that are used in gnawing. These incisors have a band of enamel only on the front edge; the rest of the tooth is made of softer dentin. The rodent keeps the teeth sharp by continuous gnawing, so that the more resistant enamel edge is worn and kept sharper than the dentin behind it. If the incisors are not worn down, but are misaligned by malocclusion, they will grow around in a curve until they pierce the skull.

Although rodents and rabbits are closely related, they form two different orders within the Glires and can be easily distinguished. 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 ranging in size from the pig-sized capybara down to the many 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 kin, seals and sea lions, raccoons, and many extinct groups). All Carnivora are distinguished by their distinctive shearing teeth, the carnassials, developed between the last upper premolar and the first lower molar. True Carnivora began as weasel-like 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 bear-like ancestors. Carnivorous mammals show remarkable convergence on a limited number of body forms. For example, sabertoothed forms evolved four times, once in the creodonts, once in the true cats, once in the extinct cat-like nimravids, which are related to dogs, and one extinct sabertoothed marsupial that has been found in South America. 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 Ma in central Asia. In the latest Cretaceous and the 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. Today there are over 190 living species of artiodactyl, and at least twice that number of fossil species are known. Artiodactyls include the suoids (pigs, peccaries, hippopotamuses), 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 in the later Cenozoic and grasslands expanded.

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. However, some of these fossils also show the 'double pulley' ankle bones found in all artiodactyls, which lends weight to the suggestion by molecular biologists that whales are descended directly from artiodactyls, rather than from mesonychids. By the Oligocene, whales had diversified into the predatory toothed whales (dolphins, orcas, sperm whales) and the filter-feeding baleen whales (blue, right, humpback, grey and many other whales).

The Perissodactyla, or odd-toed ungulates, have one or three toes on each foot. Today they include horses, rhinoceroses, and tapirs, but they were much more diverse in the past, with huge two-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 are so named because they originated from Late Paleocene ancestors that once lived along the Tethys seaway (which stretched from Gibraltar to Indonesia). Although sea cows had spread around the world by the Eocene, their earliest evolution was a mystery. Then a nearly complete specimen of *Pezosiren* was described from the Eocene of Jamaica, which showed what their earliest evolutionary transitions looked like. This fossil has a fully sirenian skull and teeth, and thick ribs for ballast, but retains fully functional legs and feet, rather than flippers.

The remaining tethytheres include the elephants, the huge two-horned extinct arsinoitheres, and the hippopotamus-like desmostylians from the Miocene of the Pacific Rim. The earliest relative of the elephant is *Paschatherium*, known from teeth from the Paleocene of Morocco. By the Eocene, the elephant family was represented by *Moeritherium*, which looked like a small pig or hippopotamus, although it had the beginning of a trunk or proboscis. The evolution of most of these groups was restricted to Africa until the Middle Miocene, when both groups (proboscideans and arsinoitheres) spread to Eurasia, and mastodonts even reached North America.

See Also

Evolution. **Fossil Vertebrates:** Mesozoic Mammals; Hominids. **Tertiary To Present:** Paleocene; Eocene; Miocene.

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