MAMMALS

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Mammals are not a diverse group, and yet they have achieved a dominant position in many ecosystems. There are estimated to be 4000 species of mammals alive today, a low number compared to the insects or flowering plants, and indeed only two-thirds of the current diversity of reptiles. The success of the mammals is measured rather in their wide adaptability, and by the sheer abundance of some species, such as humans and rats.

Class Mammalia is divided into three unequal groups, the Subclasses Monotremata, Marsupialia (or Metatheria), and Placentalia (or Eutheria). The monotremes, the duck-billed platypus and the echidnas of Australasia, are characterized by the fact that they lay eggs, the retention of a primitive reptilian character. Marsupials, such as the opossums of the Americas and the kangaroos, koalas, and wombats of Australasia, generally give birth to tiny immature young which then complete their development in a pouch. The placental mammals, by far the largest group, and consisting of all other mammals from mice to elephants, aardvarks to zebras, and bats to whales, give birth to well-developed young which have been nourished by means of a placenta in the maternal womb.

The success of the mammals: chewing and homeostasis

It is impossible to point to a single feature of mammals that can explain their great success. Mammals are distinguished from their reptilian forebears by a number of anatomical and physiological characters, and some of these appear to have led to the great adaptability of the group.

Perhaps mammals owe their success to their teeth. Unlike reptiles, amphibians, and fishes, which have rather uniform teeth, mammals have differentiated teeth, snipping incisors at the front, pointed piercing canines to the sides, and broad crushing and shearing cheek teeth (premolars and molars) behind (Fig. 1). Tooth differentiation allows mammals to process their food efficiently: less is wasted and it is cut up or ground into fragments before it is swallowed. The jaws and teeth were modified in other ways.

Unlike reptiles, mammals generally have only two sets of teeth during their lives, a milk set and an adult set. Reptiles retain the primitive style in which teeth are inserted continuously as old ones wear out. This might seem to be a better system than ours; indeed, continuous tooth replacement means no visits to the dentist. However, mammals are forced to minimize the amount of tooth replacement because of the precise occlusion (fitting) between the upper and lower cheek teeth. The benefits of close interlocking between the crests (cusps) and troughs of the premolars and molars, the fact that this arrangement allows mammals to chew and comminute their food, thereby aiding digestion, far outweigh the advantages of being able to shed worn-out teeth.

Reptiles cannot chew; their jaws generally merely open and shut in a single orientation, rather like a simple hinge. Mammals have complex rotatory and sliding jaw joints, and the mandibles (lower jaws) may move sideways and back and forwards over considerable distances. Parents and nannies used to urge children to chew their food one hundred times before swallowing; this injunction was intended to instill good manners and to prevent indigestion, but chewing means that the digestive processes begin even while the food is in a mammal's mouth. Reptiles and birds gulp their food down and hence lose much nutritive value.

The mobile jaw joint and differentiated teeth of mammals have been cited as a major reason for the success of the group as a whole, and as an explanation for their wide diversification. Mammals have a wide range of diets, including fish, shellfish, plankton, flying insects, ants, worms, snails, other land vertebrates, grass, leaves, roots, wood, fruit, seeds, and nectar. The teeth are highly variable and specifically adapted for the diet: needle-like piercers in insectivores, filtering curtains in plankton-eating whales, broad ever-growing crushers in grass-eaters, and even no teeth in some ant-eaters (Fig. 1).

The second major adaptive complex of mammals concerns their control of body temperature. Mammals, independently of birds, evolved endothermy, commonly called warm-bloodedness. In other words, mammals produce a great deal of heat within their bodies by physiological means: indeed it is estimated that fully nine-tenths of what we eat is devoted to temperature control (which is why a crocodile consumes one-tenth of what a human does). The heat production is closely monitored to maintain a precisely constant body temperature. In other words, mammals are endothermic ('internal heat') homeotherms ('constant temperature'). Different species of mammals maintain different temperature set points, but generally in the range 35-40oC, and small deviations may be fatal. The adaptive advantage of such constancy of body temperature is in terms of biochemical functioning; mammalian enzymes have evolved to act at peak efficiency at the normal set-point temperature, whereas reptilian enzymes must be able to cope with wide fluctuations in body temperature, and they can rarely function ideally. The maintenance of constant body temperatures involves a complex array of homeostatic (feed-back) mechanisms: when you are too hot, you sweat, you turn red (blood flows in the skin layers), and you seek a cool place; when you are cold, you seek a warm place, you shiver, your peripheral blood vessels close off, and your body generates internal heat as fast as it can.

The advantages of endothermic homeothermy are seen in the wide range of habitas occupied by mammals, wider than for any other group of animals of similar diversity. Mammals uniquely live from the Equator to the poles, in the depths of the oceans, underground, and in the tree tops and skies. Mammals operate at night and during the day.

The third major reason for the success of the mammals is clearly their relatively large brains. In proportion to body size, mammals have brains about ten times the size of reptilian brains. Large parts of the brain are, admittedly, devoted to the homeostatic control of body temperature, but the bulk of the new brain volume is concerned with intelligent functioning. Many mammals live complex lives, for example in trees, and they must learn how to move around and find a diverse array of food. Most mammals show better abilities to solve problems than do reptiles.

The large brain and intelligence of mammals requires a learning period after birth. Reptiles generally abandon their nests after the eggs have been laid, but mammals devote long periods to feeding and caring for their young. Indeed, reptiles typically produce large numbers of eggs, perhaps twenty to fifty, and their evolutionary strategy is to invest in quantity rather than quality (r-selection strategy). Mammals do the opposite, producing few young, typically one to eight, and devoting effort to protecting them while they grow to adulthood (K-selection strategy). The large brain and need to learn require parental care. Parental care includes feeding, and a characteristic feature of mammals is that the mothers feed their young on milk produced by mammary glands (mammae, hence, mammal, and indeed 'mama').

The origin of the mammals

Teeth, warm-bloodedness, and brains: which came first? All three adaptive complexes seem to have evolved in parallel in the ancestors of the mammals, but warm-bloodedness may have come last. The ancestry of mammals can be traced back to the mid Carboniferous, when the great vertebrate group, the Amniota arose. Amniotes are the fully land-living vertebrates, including reptiles, birds, and mammals, that broke away from the dependence on water shown by the amphibians. The Amniota divided early on into three lineages, the Anapsida (leading to turtles), the Diapsida (leading to lizards, crocodiles, and birds), and the Synapsida (leading to mammals).

The pre-mammalian synapsids, often called mammal-like reptiles, showed hints of mammalian characters from the start. Tooth differentiation was well advanced by the Late Permian. In addition, brain expansion was also underway. Reptile skulls are typically in two parts, a large outer portion that supports the jaws and sensory organs, and a small braincase fitted fairly loosely inside at the back. The best analogy is a shoebox with a cigarette packet placed inside at one end. Permian and Triassic mammal-like reptiles showed various stages in a process of brain enlargement. The bones surrounding the brain moved outwards, and fused with the outer skull bones. In the end, in mammals, the brain dominates the back half or more of the skull, and the sense organs are concentrated in front.

Mammals arose from within a major clade of synapsids termed the Cynodontia. Cynodonts included a number of lineages in the Triassic, many of which probably looked very mammal-like (Fig. 2). The teeth were fully differentiated, the braincase bulged at the back of the head, and many of them walked in an upright manner, instead of the primitive sprawling gait of other reptiles. Later cynodonts may have had hair, an insulating layer, which is a necessary part of warm-bloodedness. These animals still laid eggs, and indeed all Mesozoic mammals probably did. The oldest mammal is Adelobasileus from the Late Triassic of Texas, and the transition from mammal-like reptile to mammal may seem rather subtle.

The key feature that is traditionally taken to define the Class Mammalia is the full expression of the mammalian jaw joint (Fig. 2). In reptiles, the jaw hinges between the articular bone at the back of the lower jaw, and the quadrate. In mammals, the jaw joint has shifted bodily to the dentary in the lower jaw and the squamosal. This extraordinary shift did not occur in one dramatic step: some later cynodonts had both joints close together and in operation at the same time. The old articular-quadrate joint of the reptiles did not disappear, but it changed function and became part of the chain of three ear ossicles ('little bones') of mammals. Reptiles have a single ear ossicle, the stapes or stirrup bone. Mammals have three, the stapes, the malleus (hammer), and incus (anvil), the last two being the old reptilian jaw joint still conserved deep within our ear. Ears and jaw joints are still closely associated; you can 'hear' yourself chewing.

Mammal evolution

The oldest mammals (Fig. 2) originated at the same time as the dinosaurs. However, the dinosaurs rose to dominate the earth for the remainder of the Mesozoic, a span of some 155 million years. During this time, the mammals radiated and evolved, but they could not make the breakthrough to becoming large or to diversifying their modes of life. Most were rat- or mouse-sized, and they filled nocturnal niches, mainly as insectivores. One group, the multituberculates ('many cusps'), were highly succcessful gnawing herbivores, and they outlasted the Mesozoic, surviving until the Oligocene. The multituberculates had gnawing incisors, a deep cutting premolar, and broad multi-cusped molars.

The monotremes, marsupials, and placentals arose in the Early Cretaceous. These modern groups were relatively rare during the Cretaceous, the monotremes known by only isolated specimens from Australia and South America, and the marsupials and placentals from North and South America, with some superbly preserved placentals from Central Asia. Even these mammals of modern aspect, although diversifying to some extent, did not exceed cat size, and they would have been unimpressive when seen beside the larger and more abundant dinosaurs with which they shared their habitats.

As is well known, the dinosaurs died out 65 million years ago, at a time of numerous other extinctions at the Cretaceous-Tertiary (KT) boundary. Several groups of Mesozoic mammals also disappeared, and the marsupials nearly died out. Little is known of the evolution of monotremes, beyond the fact that they appear to have existed always at low diversity, and essentially restricted to Australasia.

The marsupials that survived the KT event radiated in North and South America. They diversified particularly successfully in South America, giving rise in time to a wide diversity of carnivores, from opossums to marsupial sabre-toothed cats and dogs. Marsupials some time in the Eocene traversed Antarctica to reach Australasia. As Gondwana broke up, the link was broken, and the Australasian marsupials evolved in isolation, giving rise to the modern groups of koalas, bandicoots, wombats, and kangaroos. From North America, marsupials migrated to Europe, and from there to Central Asia and Africa. Those radiations were short-lived, and marsupials died out all over the northern hemisphere by mid-Tertiary times. The South American marsupials radiated back into Central and North America when the Panamanian land bridge was formed 3 million years ago, but many of the more dramatic South American forms eventually died out at the end of the Pleistocene.

The placentals seemingly diversified through the KT mass extinction, and the modern orders virtually all originated within the first 10 million years of the Tertiary, essentially during the Paleocene and Early Eocene. The oldest bats, whales, proboscideans (elephants), perissodactyls (horses, rhinos), artiodactyls (cattle, pigs, camels), primates (monkeys, humans), insectivores (shrews, hedgehogs), rodents (rats, squirrels), and carnivores (cats, dogs) are known from this early phase of radiation. In addition, there were numerous other major groups of Paleocene and Eocene mammals, some plant-eaters, others meat-eaters, that radiated, some succcessfully, but died out during mid Tertiary times, as the modern orders became established.

The radiation of the placental mammals (Fig. 3) is often chosen as a classic example of an adaptive radiation, in other words, a rapid diversification of a clade that is apparently driven by, or facilitated by, some adaptation or adaptations. To a large extent, the radiation was opportunistic: the extinction of the dinosaurs vacated large volumes of ecospace on land, and at first it was not clear that the mammals would prevail. In certain parts of the world, huge hunting birds or fast-running crocodiles dominated the Paleogene scene. The radiation can be dissected into several phases: (1) the opening of ecospace; (2) the initial diversification when new species seem to have arisen rapidly and with minimal competition from others; (3) a later phase when the ecospace was filling up, and more stable food chains and competitive interactions became established; and (4) a final phase when many groups died out and modern ecosystems became established.

Modern terrestrial mammalian ecosystems perhaps owe their shape to two further major environmental changes that occurred in the mid to late Cenozoic. During the Oligocene and Miocene, climates worldwide became more arid, an areas that had formerly been covered by lush tropical and subtropical forests, opened up and became grasslands. Great savannas spread over much of the Americas, Europe, Asia, and Africa. Mammals that had formerly lived secretive lives in the forests either died out or adapted. Horses adapted: they had previously been small terrier-sized animals that fed on leaves, and they evolved into taller long-legged animals that fed on grass.

The second major events were the Pleistocene ice ages. In the northern hemisphere, ice sheets several times advanced over much of North America, as well as northern Eurasia. Pluvial and arid climatic changes affected the whole world. Land mammals underwent numerous large-scale migrations as climates changed, and some groups died out. Other ice-adapted species evolved, such as mammoths and woolly rhinos, and perhaps Neanderthal humans. At the end of the Pleistocene, some 11,000 years ago, large mammals died out in many parts of the world, perhaps as a result of environmental changes, perhaps partly as a result of the rapid worldwide spread of human hunters.

Current human activities are threatening the futures of some endemic mammalian species, for example certain primates that occur in small populations in Madagascar, the African apes, pandas, elephants, and other specialists. The majority of mammalian species, however, seem to be highly adaptable and rather immune to such dramatic environmental modification.

Mammals can never rival insects or microbes in terms of abundance or diversity, but their large body size and adaptability have made them highly successful over the past 65 million years, and presumably for a long time into the future.

Further reading

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Figure 1. Mammal teeth. Mammals (A) have differentiated teeth, while reptiles (B) generally have uniform teeth throughout the jaws. Mammalian teeth have diversified into a wide range of forms (C) which relate to diet. Based on several sources.

Figure 2. The mammal jaw joint. The mammalian jaw joint evolved from the standard reptilian condition (A), where the joint is between the articular and quadrate, through an intermediate condition in many cynodonts (B), to the mammalian dentary-squamosal joint (C). The early cynodonts, such as *Thrinaxodon* (D), were mammal-like in many respects in comparison to the oldest mammals, such as *Morganucodon* (E). Based on Kemp (1982).

Figure 3. The radiation of the placental mammals in the Cenozoic is often treated as a classic 'adaptive radiation'. Placentals radiated rapidly after the extinction of the dinosaurs, and the modern diversity of form was established within the first 10 million years of the Tertiary. Based on Gingerich (1984).