Eutheria (Placental Mammals)

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Eutheria includes one of three major clades of mammals, the extant members of which are referred to as placentals.

Introductory article

Article Contents

Introduction

Eutheria (or Placentalia) is the most taxonomically diverse of three branches or clades of mammals, the other two being Metatheria (or Marsupialia) and Prototheria (or Monotremata). When named by Gill in 1872, Eutheria included both marsupials and placentals. It was Huxley in 1880 that recognized Eutheria basically as used today to include only placentals. McKenna and Bell in their *Classification of Mammals*, published in 1997, chose to use Placentalia rather than Eutheria to avoid the confusion of what taxa should be included in Eutheria. Others such as Rougier have used Eutheria and Placentalia in the sense used here. Placentalia includes all extant placentals and their most recent common ancestor. Eutheria is retained to include all extinct mammals that share a more recent common ancestor with placentals than they do with Metatheria.

Basic Design

Eutherians share with all other mammals some key innovations that differentiate them from other amniote vertebrates – Reptilia (including Aves). While in reptiles there can be many generations of teeth, in mammals there are at most two. Eutherians, if they have teeth, retain the ancestral mammal condition of two generations (deciduous and permanent) of teeth. Reptiles have a jaw joint composed of the articular (lower jaw) and quadrate (upper jaw), and have only one ear ossicle, the columnella. In all mammals the articular and quadrate become incorporated into the middle ear as the outermost two ear ossicles, the malleus and incus, respectively, which articulate with the intermost stapes (columnella). While prototherians lack teeth as adults, metatherians retain at most five upper and four lower incisors, one upper and one lower canine, three upper and three lower premolars, four upper and lower molars each. This condition is still found in the opossum, common to many areas of North America. Primitively, eutherians had a similar number of incisors and canines, but had five upper and lower premolars each and three upper and lower molars each. Except for placentals that have supernumerary teeth (e.g. some whales, armadillos, etc.), in extant placentals the number of teeth is at most three upper and lower incisors, one upper and lower canine, four upper and lower premolars, and three upper and lower molars. Except for one fewer upper molar, a domestic dog retains this pattern. Compared to reptiles, mammals have fewer skull bones through fusion and loss, although bones are variously emphasized in each of the three major mammalian taxa.

Physiologically, mammals are all endotherms of varying degrees of efficiency. They are also homeothermic with a relatively high resting temperature. These characteristics are also found in birds, but because of anatomical differences, the attainment of endothermy evolved convergently in mammals and birds. In mammals the large aorta leaving the heart bends to the left while in birds and their reptilian relatives the aorta bends to the right. Although both birds and mammals have diaphragms, they are formed very differently, again indicating convergent evolution.

Reproductively, mammals show all three major kinds of reproduction found in amniote vertebrates – oviparity or egg-laying, ovoviviparity where the embryo is retained internally by the mother but there is little maternal support, and euviviparity where the embryo is retained internally by the mother and much support is given by the mother. It is this last condition, euviviparity, that characterizes placentals. The name placental derives from the dominant extraembryonic structure of the same name found in this group. Both marsupials and placentals have a placenta but of considerably different structure. In marsupials two extraembryonic structures, the yolk sac and the chorion, fuse through part of their extent to form the choriovitelline placenta. In placentals, the allantois and chorion fuse to form the chorioallantoic placenta. Although the choriovitelline placenta of the marsupial compared to the chorioallantoic placenta of the placental does not produce as many hormones to sustain itself or provide as long a period of sustenance for the developing embryo, it should not be thought of as more primitive. Rather, because the two kinds of placenta are formed differently they almost certainly evolved convergently.

Taxonomic and Ecological Diversity

Almost 4700 genera of extinct and extant eutherians are recognized. Of these, some 1050 are extant and include almost 4400 extant species (**Table 1**). Although relatively low in taxonomic abundance, placentals (extant eutherians) arguably occupy one of the widest arrays of environments of any comparable group of vertebrates. They range in size from shrews to blue whales, from completely marine through terrestrial to fully volant. Three important factors that played a role in this considerable ecological diversity are mode of reproduction, level of metabolism, and an ancestral, generalized quadrupedal stance. The mode of reproduction in placentals, euviviparity, includes considerable *in utero* development of the embryo with all support and sustenance coming from the mother through the chorioallantoic placenta. This allows the mother to continue normal activities while pregnant. Placentals, like other mammals, are endothermic. This means they produce their heat through metabolic means. Perhaps as much as 80% of consumed food goes towards maintaining endothermy. The common ancestor of all mammals, as well as that leading to eutherians, was a small, insectivorous quadruped that maintained five digits on all four limbs. Such a generalized pattern of stance and locomotion permitted a greater diversity of stance and locomotion in later eutherians. For example, placentals have limbs greatly modified for swimming, flight, digging, fleet-footedness, capture of prey, brachiation, etc. In contrast, birds are represented by more species today (9000) than are placentals but show less diversity in locomotory patterns. This is because in contrast to mammals, the common ancestor of birds (a small theropod dinosaur) had already acquired a specialized habitus with hindlimbs used for locomotion and forelimbs for capture of prey (flight came later). Today placentals are found in every ocean and with a few exceptions on all landmasses. The landmasses that do not have naturally occurring placentals are Antarctica and many oceanic islands.

Table 1 Numbers of species of living eutherians (placental) (Wilson and Reeder, 1993; Vaughan *et al*., 2000)

Class Mammalia	
Subclass Prototheria	
Subclass Theria	
Infraclass Marsupialia	
Infraclass Placentalia	
Order Xenarthra	29 species
Order Pholidota	7 species
Order Lagomorpha	80 species
Order Rodentia	2024 species
Order Macroscelidea	15 species
Order Primates	236 species
Order Scandentia	19 species
Order Dermoptera	2 species
Order Chiroptera	928 species
Order Carnivora	271 species
Order Insectivora	429 species
Order Artiodactyla	220 species
Order Cetacea	78 species
Order Tubulidentata	1 species
Order Perissodactyla	18 species
Order Hyracoidea	6 species
Order Proboscidea	2 species
Order Sirenia	5 species

Fossil History and Distribution

The earliest known fossils of eutherians come from Asia and North America. These fossils are restricted to mostly dental and a few skull remains. The type and only known specimen of *Montanalestes* comes from beds of Aptian-Albian age (approx. 110 million years old) in Montana. *Prokennalestes* comes from slightly younger beds (approx. 105 million years old) in Mongolia, but is represented by numerous, mostly undescribed dental remains. Both taxa, as well some other slightly younger forms, also from Asia, show the typical eutherian pattern of at most five upper and lower premolars and three upper and lower molars. The last upper and lower premolars in the earliest eutherians as compared to metatherians already show trends towards molarization (i.e. adding extra cusps found on molars). The labial (cheek side) of the upper molars has a wide area called the stylar shelf that unlike in contemporary metatherians has few cusps. The back, lower margin of the lower jaw, the dentary, has a projection that points backwards in eutherians but internally in metatherians. These forms were all small, ranging in size from a shrew to an opossum. Diets were mostly carnivorous to insectivorous, but omnivory and probably even herbivory occurred in some eutherians by the time of dinosaur extinction 65 million years ago. Within about 15 million years of dinosaur extinction most of the 18 extant orders of placentals had appeared along with some 16 other orders that are now extinct. This was a truly explosive radiation and diversification. North America and Eurasia are known to have served as centres for much of the diversification of extant placental orders throughout much of the Tertiary. Although less is known about the early radiation of extant placental orders in Africa, both current diversity on this continent and recent molecular studies of endemic African clades indicate that this continent was also a major centre of placental evolution. Eutherians probably did not reach South America until about 65 million years ago. Except for possibly Xenarthra, no extant placental orders are believed to have originated in South America. This is not true of

extinct orders. At least five extinct orders are endemic to South America. These mostly herbivorous taxa flourished throughout much of the Tertiary, possibly rivalling the diversity among extant African herbivorous placentals. They ranged from rabbit- to rhino-sized. In Australia, except for bats, which reached Australia in the early Eocene (almost 55 million years ago), eutherians are not definitely known from this continent until about 5 million year ago, when rodents arrived. Today, bats and rats are the only placentals that reached Australia without the aid of humans. Madagascar has an unusual placental fauna, the best known being lemurs and relatives, which hark back to an early Tertiary African fauna. Oceanic islands, the largest being the islands of New Zealand, totally lack placentals (or any other mammals) except for the bats and the rare rodent species.

Phylogeny

Based upon anatomical and developmental studies of placentals (extant eutherians) and studies using fossil taxa, 18 orders of placental are usually recognized (**Figure 1**). Except for possibly Insectivora, which may have arisen in the late Cretaceous, all other extant orders appear in the early (14 orders) or late Cenozoic (2 orders). The late Cenozoic appearances are probably artefactual. In this scheme the earliest diverging order is the New World Xenarthra (or Edentata), the anteaters,

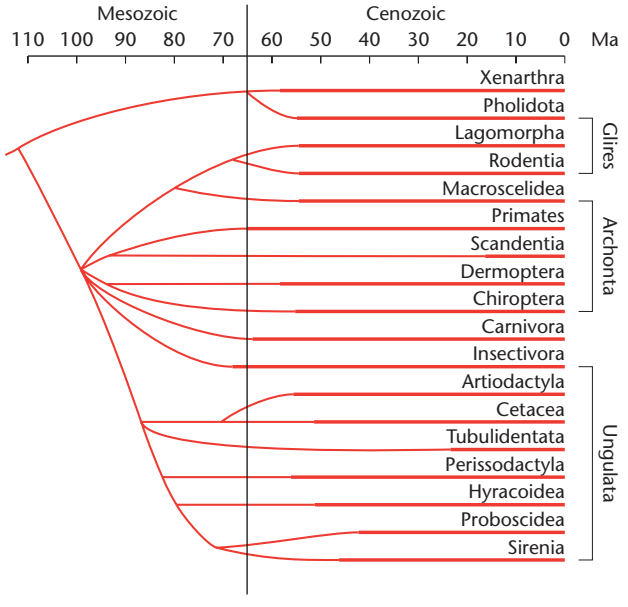

Figure 1 Phylogeny of placental (extant eutherian) orders showing approximate duration (bar) of each, based upon anatomy of extant species and the fossil record (modified after Archibald, 1996, and Novacek, 1992).

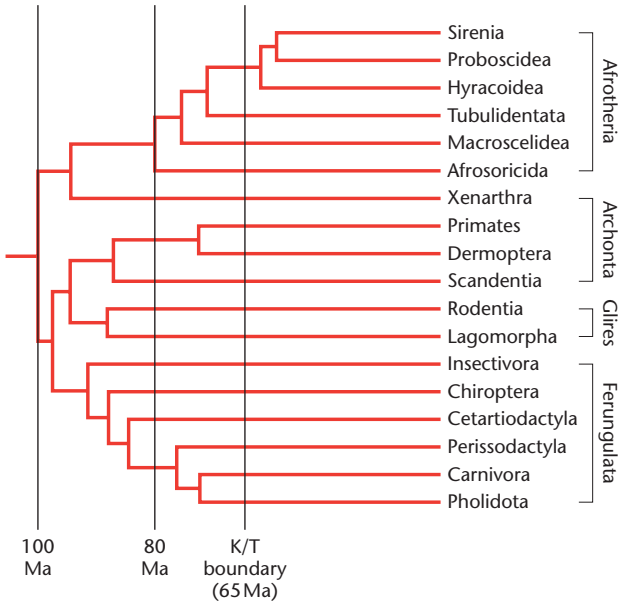

Figure 2 Phylogeny of placental (extant eutherian) orders showing timing of splits between orders, based upon various molecular data (modified after Waddell *et al.*, 1999).

armadillos and sloths. The pangolins (Pholidota) of the Old World are sometimes linked with Xenarthra. There is little consensus on which orders branched next, but some orders in this unresolved polytomy are often grouped together. Glires is a taxon that includes Rodentia and Lagomorpha (rabbits and pikas). Another order sometimes linked with this clade is Macroscelidea, the African elephant shrews. Archonta is another group, including four orders: the tropically distributed Primates, the Asian Scandentia (tree shrews) and Dermoptera (the so-called flying lemurs), and the globally distributed bats or Chiroptera. The globally distributed Insectivora and Carnivora are not clearly linked with other specific orders. Finally, a group of seven extant orders – Artiodactyla (even-toed ungulates such as deer, antelope, pigs, camels, hippos), Cetacea (whales and relatives), Tubulidentata (aardvark of Africa), Perissodactyla (odd-toed ungulates such as horses, rhinos, tapirs), Hyracoidea (hyraxes of Africa), Proboscidea (elephants) and Sirenia (the tropical marine manatees and dugongs) – are sometimes placed together in Ungulata. Within Ungulata are two more certain ordinal groupings. One includes Artiodactyla and Cetacea and the other includes Hyracoidea, Proboscidea and Sirenia (Paenungulata).

More recently, a number of molecular studies have argued for greatly altering parts of the traditional phylogeny while at the same time strengthening some traditionally based groups (**Figure 2**). Coincidentally, the molecular studies also recognize 18 orders, albeit with some different combinations. One of the major

new taxa is Afrotheria, which groups together six orders that are restricted to Africa (and Madagascar), or appear to have originated on this continent. Afrotheria includes the traditionally recognized Paenungulata of Hyracoidea, Proboscidea and Sirenia plus Tubulidentata, Macroscelidea, and also a new order, Afrosoricida, which includes tenrecs and golden moles, both formerly placed in Insectivora. Glires, including Rodentia and Lagomorpha, are linked with a modified Archonta, including Scandentia, Dermoptera and Primates but lacking Chiroptera. Insectivora (without afrosoricidans) and Chiroptera are combined with Ferungulata, a group sometimes recognized in traditional classifications. Ferungulata includes Pholidota, Carnivora, Perissodactyla, and a second new order, Cetartiodactyla. As the name suggests, this taxon includes cetaceans and artiodactyls, but unlike traditional phylogenies that link them as sister taxa, the new molecular studies indicate that the nearest relative of Cetacea is within Artiodactyla, specifically the family Hippopotamidae.

Further Reading

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