Eutheria (Placental Mammals)

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Introductory article

Article Contents

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

With almost 4800 extinct and extant genera, including 1135 extant (living) genera and over 5000 extant species arrayed in 20 extant orders, placentals (extant eutherians) are the most taxonomically diverse of the three branches of extant mammals. Eutherians appear in the fossil record by 105 Ma (million years ago) and possibly by 160 Ma. Extant orders of eutherians (placentals) do not occur in the fossil record until after dinosaur extinction 65–66 Ma. Molecular studies generally agree with these dates for the origin of placental orders, but place the origin of Eutheria at approximately 190 Ma and groups related to living orders of mammals by 100 Ma. Placentals vary greatly in size (whales down to shrews), in locomotion (flying, swimming, climbing, burrowing, running, etc.), and diet (meat, leaves, fruit, termites, etc.). They have a high resting temperature (homiothermy) and produce this heat internally (endothermy). They have a chorioallantoic placenta that allows a long gestation for development.

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 who recognised 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 *et al*. (1998) used Eutheria and Placentalia in the sense used here (see Rose and Archibald, 2005). Placentalia includes all extant eutherians 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. **See also**: Mammalia; Marsupialia (Marsupials); Monotremata

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Basic Body Plan

Eutherians share with all other mammals some key innovations that differentiate them from other amniote vertebrates – Reptilia (including Aves). Although 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 columella. 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 innermost stapes (columella). Whereas 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 (**Figure 1**). 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 (**Figure 1**). Pigs retain this pattern, and except for one fewer upper molars, a domestic dog does as well. Compared to reptiles, mammals have fewer skull bones through fusion and loss, although bones are variously emphasised in each of the three major mammalian taxa. **See also**: Digestive System of Mammals; Ingestion in Mammals; Mesozoic Mammals; Reptilia (Reptiles)

Physiologically, mammals are all endotherms with varying degrees of efficiency. They are also homoeothermic 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

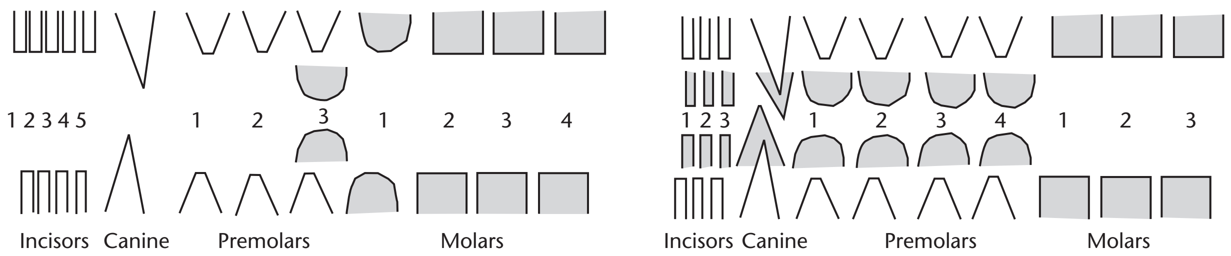

Figure 1 The maximum number of upper and lower teeth normally found in an extant marsupial such as opossum (left) and in an extant placental such as a pig (right). First generation teeth are shown in grey and second generation teeth are shown in white. Marsupials suppress their anterior first generation teeth. Molars are first generation teeth that erupt only as the jaws increase in size (by the author following Archibald and Averianov, 2012).

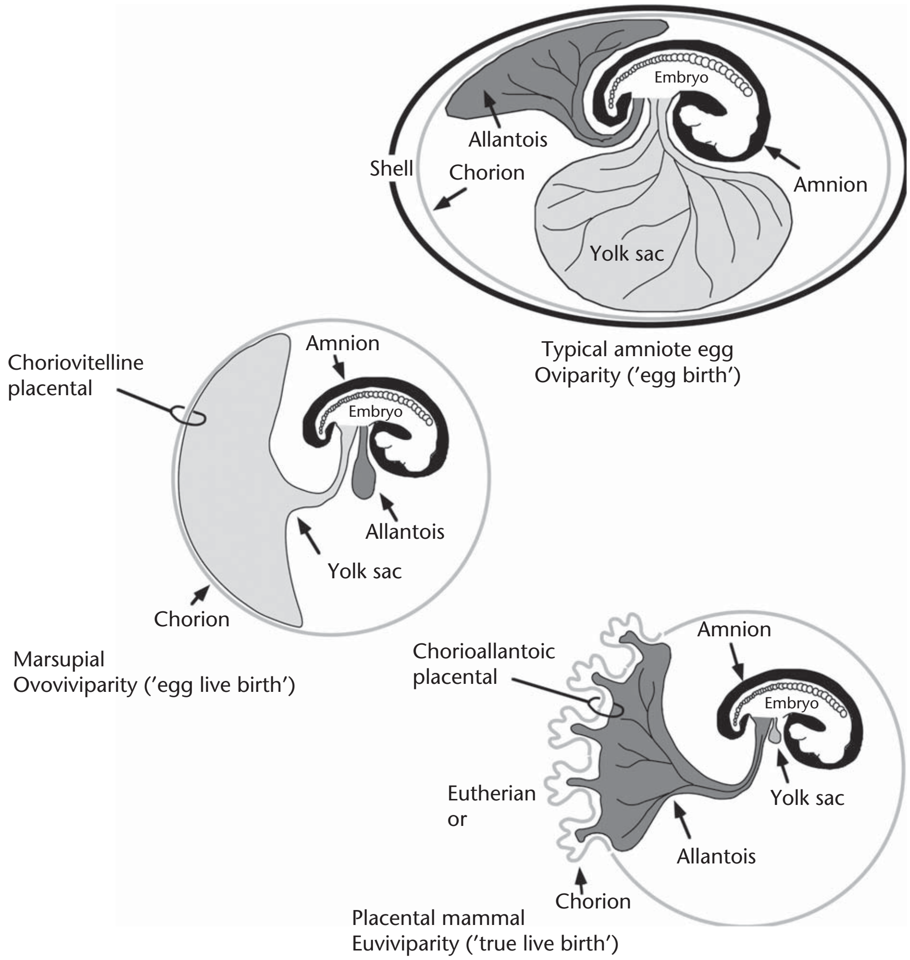

Figure 2 The three kinds of reproduction in mammals (by the author after a variety of sources).

bends to the left whereas 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. Placental mammals possess a corpus callosum, a bundle of neural fibers joining the two cerebral hemispheres of the brain. This is lacking in other mammals. **See also**: Thermoregulation in Vertebrates; Vertebrate Functional Morphology and Physiology

Reproductively, mammals show all three major kinds of reproduction found in amniote vertebrates – oviparity or egg-laying of monotremes, ovoviparity where the embryo is retained internally for only a short time by the mother as in marsupials, and euviviparity as in placentals where the embryo is retained for a longer time internally by the mother and much support is given by the mother (**Figure 2**). The name placental derives from the dominant extra-embryonic 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. **See also**: Reproduction in Eutherian Mammals; Reproduction in Mammals: General Overview; Reproduction in Monotremes and Marsupials

Taxonomic and Ecological Diversity

Almost 4800 genera of extinct and extant eutherians are recognised (McKenna and Bell, 1997; Wilson and Reeder, 2005). Of these, some 1135 are extant and include over 5000 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, generalised 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, similar to 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 generalised pattern 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. Even Antarctica has seals breeding on coastal beaches and bats have reached most oceanic islands. **See also**: Aves (Birds)

Table 1 Number of species of living eutherians (placental)

Class
Mammalia
Subclass
Prototheria
Theria
Infraclass
Marsupialia
Placentalia
Order (listed alphabetically, see **Figure 3** *for relationships)*
Artiodactyla (or Cetartiodactyla) (324 species)
Carnivora (286 species)
Chiroptera (1116 species)
Cingulata (21 species)
Dermoptera (2 species)
Erinaceomorpha (24 species)
Hyracoidea (4 species)
Lagomorpha (92 species)
Macroscelidea (15 species)
Perissodactyla (17 species)
Pholidota (8 species)
Pilosa (10 species)
Primates (376 species)
Proboscidea (3 species)
Rodentia (2277 species)
Scandentia (20 species)
Sirenia (5 species)
Soricomorpha (428 species)
Tenrecoidea or Afrosoricida (51 species)
Tubulidentata (1 species)

Source: Wilson and Reeder (2005).

Fossil History and Distribution

The earliest known possible fossils of eutherians come from Asia. Identifying which of these fossils are correctly identified as eutherians remains problematic in part because some have not been fully described and documented. Two such forms from China are *Juramaia* from the late Middle Jurassic (approximately 160 Ma) (Luo *et al*., 2011) and *Eomaia* from the Early Cretaceous (approximately 125 Ma) (Ji *et al*., 2002). *Juramaia* and possibly *Eomaia* may prove to be a stem therian lying outside of Eutheria, which is before the split between Eutheria and Metatheria. This was the case for another, *Montanalestes* from North America (Cifelli, 1999), which was first thought to be a eutherian, but is more likely a stem therian (Cifelli and Gordon, 2011). Another more clearly identified and better documented form is *Prokennalestes* (Kielan-Jaworowska and Dashzeveg, 1989) from slightly younger late Early Cretaceous beds (approximately105 Ma) in Mongolia, although it is known mostly from dental and a few skull remains. *Prokennalestes* and possibly the two taxa from China 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 which unlike in contemporary metatherians has few cusps. The back, lower margin of the lower jaw, the dentary, has a projection (angular process) that points backwards in eutherians but internally in metatherians. These forms were all small, ranging in size from a shrew to an opossum. *Eomaia* is argued to show both scansorial (climbing) and arboreal (tree-living) adaptations, compared to other Cretaceous eutherians that, when known, are terrestrial and sometimes cursorial (running). Diets were mostly carnivorous to insectivorous, but omnivory and probably even herbivory occurred in some eutherians by the time of dinosaur extinction 65 Ma. Within approximately 15 million years of dinosaur extinction most of the 20 extant orders of placentals had appeared along with some 16 other orders that are now extinct. This was a truly explosive radiation and diversification (Archibald, 2011). 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 for placental evolution. Eutherians probably did not reach South America until approximately 65 Ma. Except for possibly Cingulata and Pilosa, 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 (approximately 55 Ma), eutherians are not definitely known from this continent until approximately 5 Ma, 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. Except for bats, oceanic islands lack any nonmarine mammals, with the exception of a few species of rodents on the Galápagos. Even the largest oceanic islands such as those comprising New Zealand, today totally lack nonmarine placentals, except for a few species of bats. **See also**: Diversity of Life through Time; Fossil Record; Geological Time: Principles

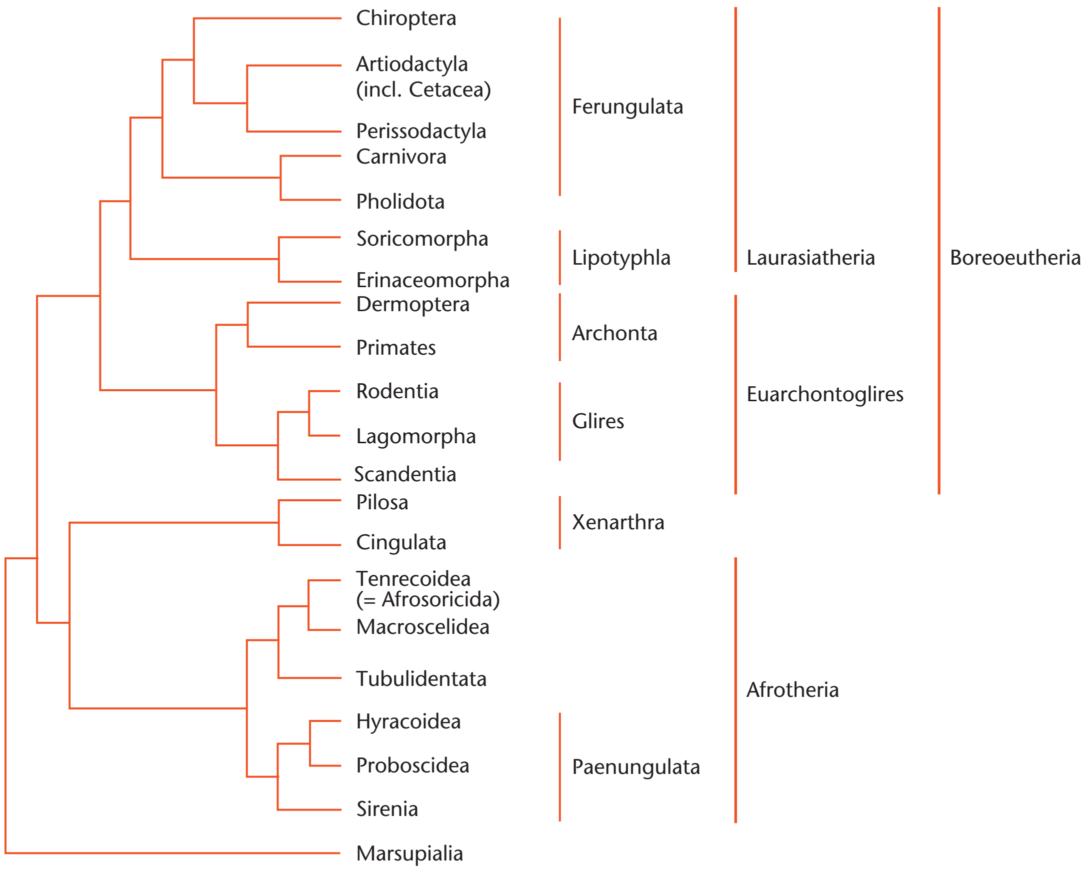

Figure 3 Phylogeny of placental (extant eutherian) orders showing timing of splits between orders, based upon various molecular data (ordinal relationships–modified after Meredith *et al.*, 2011. Copyright by American Association for the Advancement of Science).

Phylogeny

Based upon anatomical and developmental studies, the fossil record, and molecular studies, 20 orders of placental are now recognised (**Figure 3**). Most of the orders appear in the fossil record within the first 15–20 million years of the Cenozoic. Although ordinal and superordinal groupings of placentals based on molecular studies and those based on fossil and anatomical data agree in many ways (Archibald, 2003), a number of molecular studies have argued for greatly altering parts of the traditional phylogeny (Murphy *et al*., 2001). The earliest diverging major new taxon 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 recognised Paenungulata of Hyracoidea (hyraxes of Africa), Proboscidea (elephants), and Sirenia (the tropical marine manatees and dugongs), plus Tubulidentata (aardvark of Africa), Macroscelidea (African elephant shrews), and also a new order, Tenrecoidea (= Afrosoricida), which includes tenrecs and golden moles, both formerly placed in Lipotyphla. A second group is Xenarthra, which includes Cingulata (armadillos) and Pilosa (anteaters and sloths) with a history mostly found in South America. Finally are two groups, Euarchontoglires and Laurasiathera, together known as Boreoeutheria, reflecting a northern or boreal distribution earlier in their evolutionary history. Euarchontoglires includes Glires (Lagomorpha, the rabbits and pikas, as well as Rodentia), which are linked to a modified Archonta, including Scandentia (tree shrews), Dermoptera (the so-called flying lemurs), and Primates but lacking Chiroptera (bats). Laurasiastheria includes Lipotyphla (Erinaceomorpha and Soricomorpha), Chiroptera, Pholidota (pangolins), Carnivora, Perissodactyla (odd-toed ungulates such as horses, rhinos and tapirs), and a new ordinal grouping. This new ordinal grouping includes cetaceans (whales and relatives), and artiodactyls (even-toed ungulates such as deer, antelope, pigs, camels and hippos), and is called Artiodactyla or Cetartiodactyla. 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. **See also**: Molecular Phylogeny Reconstruction

References

Archibald JD (2003) Timing and biogeography of the eutherian radiation: fossils and molecules compared. *Molecular Phylogeny and Evolution* **28**: 350–359.

Archibald JD (2011) *Extinction and Radiation: How the Fall of the Dinosaurs Led to the Rise of the Mammals*. Baltimore: Johns Hopkins University Press.

Archibald JD and Averianov AO (2012) Phylogenetic analysis, taxonomic revision, and dental ontogeny of the Cretaceous Zhelestidae (Mammalia: Eutheria). *Zoological Journal of the Linnean Society* **164**: 361–426.

Cifelli RL (1999) Tribosphenic mammal from the North American Early Cretaceous. *Nature* **401**: 363–366.

Cifelli RL and Gordon C (2011) New information on tribosphenic mammals from the Cloverly formation, Montana and Wyoming. *Journal of Vertebrate Paleontology Program and Abstracts* **31**(suppl. 6): 89.

Ji Q, Luo Z-X, Wible JR, Zhang J-P and Georgi JA (2002) The earliest known eutherian mammal. *Nature* **416**: 816–822.

Kielan-Jaworowska Z and Dashzeveg D (1989) Eutherian mammals from the Early Cretaceous of Mongolia. *Zoologica Scripta* **18**: 347–355.

Luo Z-X, Yuan C-X, Meng Q-J and Ji Q (2011) A Jurassic eutherian mammal and divergence of marsupials and placentals. *Nature* **476**: 442–445.

McKenna MC and Bell SK (1997) *Classification of Mammals*. New York: Columbia University Press.

Meredith RW, Janecka JE, Gatesy J *et al*. (2011) Impacts of the cretaceous terrestrial revolution and KPg extinction on extant mammal diversification. *Science* **334**: 521–524.

Murphy WJ, Eizirik E, O'Brien SJ *et al*. (2001) Resolution of the early placental mammal radiation using Bayesian phylogenetics. *Science* **294**: 2348–2351.

Rose KD and Archibald JD (eds) (2005) *The Rise of Placental Mammals: Origin and Relationships of the Major Extant Clades*. Baltimore: Johns Hopkins University Press.

Rougier GW, Wible JR and Novacek MJ (1998) Implications of Deltatheridiun specimens for early marsupial history. *Nature* **396**: 459–463.

Wilson DE and Reeder DM (2005) *Mammal Species of the World: A Taxonomic and Geographic Reference*. Baltimore: Johns Hopkins University.

Further Reading

Agusti JD and Anton M (2005) *Mammoths, Sabertooths, and Hominids: 65 Million Years of Mammalian Evolution in Europe*. New York: Columbia University Press.

Attenborough D (2002) *The Life of Mammals*. Princeton: Princeton University Press.

Berta A (2012) *Return to the Sea: The Life and Evolutionary Times of Marine Mammals*. Berkeley: University of California Press.

Macdonald DW (2009) *The Princeton Encyclopedia of Mammals*. Princeton: Princeton University Press.

Prothero DR (2006) *After the Dinosaurs: The Age of Mammals (Life of the Past)*. Bloomington: Indiana University Press.

Rose KD (2006) *The Beginning of the Age of Mammals*. Baltimore: Johns Hopkins University Press.

Ungar PS (2010) *Mammal Teeth: Origin, Evolution, and Diversity*. Baltimore: Johns Hopkins University Press.

Wallace DR (2005) *Beasts of Eden: Walking Whales, Dawn Horses, and Other Enigmas of Mammal Evolution*. Berkeley: University of California Press.