h19 The descent of mammals < therians, protherians, prototherians >

> If paleontologists find an isolated femur or rib, they often can't say much about its owner, but if they find a bit of cracked, weathered enamel, the only pieces of bone left from a lost mammal dead for millions of years, they can declare it to be a tiger, a sloth, an opossum, a hominid. —Carl Zimmer.[1]

> Mammals were not abundant in the Mesozoic, but they were relatively diverse. Compared to the 547 known dinosaur genera, over 310 Mesozoic mammaliaform genera are now known. —Zhe-Xi Luo.[2]

John H. Burkitt's *Mammals*, 1995, lists ~16,000 (total of extant and extinct) species.[3] Living mammals (subclass Theria) are readily sorted into placentals and marsupials (embryos of which implant in the uterus, see ***Footnote h19.1***), and egg-laying monotremes.

Curiously, replacment every ~2.5 million years of small-mammal species is evidently synced to repeats of low orbital eccentricity.[4]

Living monotremes (infraclass Protheria) are of three species. Their lineages lack a fossil record. Physically, they are living fossils of otherwise-extinct primitive mammals (subclass Prototheria).

For placentals (infraclass Eutheria) and marsupials (infraclass Metatheria) there is an excellent fossil record. Both during the Cenozoic have been extremely successful and have diversified greatly. Several of the existing orders of mammals occupy the same ecological niche as did now extinct smaller-brained ancestors that had flourished in their day. According to David W. Krause, the arrival of true rodents in North American from Asia correlated with disappearance 30 Ma (million years ago) of multituberculates.[5]

The multituberculates, for which there is a good fossil record, were a diverse rodentlike group of prototherians (primitive mammals) that went extinct at the end of Eocene, although during that period they flourished and were survivors of the end-Mesozoic major extinctions (***Figure h19.1***). Much like them, but more widespread, were early orders of placentals (***Figure h19.2***) and marsupials. These two diverging radiations stemmed via *Eomaia* ("dawn mother") *scansoria* from a line of Early Cretaceous prototherians, the pantothers. The pantothers and two other lines of prototherians, the symmetrodonts and triconodonts, became extinct at the end of the Early Cretaceous.[6]

Mammalian teeth, incisors, premolars, and molars, are highly diagnostic of the animals' type and life style. Fortunate therefore is that the commonest fossil of mammals during the Mesozoic are their teeth. Except for some Early Cretaceous triconodonts species (opossum to Tasmanian-devil sized *Repenomamus robustus* that could dine on young dinosaurs),[7] Mesozoic mammals were shrew- or rat-sized insectivores with sand-sized teeth that often go unnoticed as fossils. These teeth can be recovered from sediments using graded-sieves. Multituberculate teeth often account for three-quarters of all found. From such evidence and, since 1991, from 400 Late Cretaceous multituberculate skulls and rare, complete, skeletons collected in the Gobi Desert, Mongolia, by American Museum of Natural History staff, the diverse life styles of these prototherians are reasonably well known. As colloquially described by Richard Monastersky: "Some multis scampered along the ground, whereas others lived in trees, using their reversible hindfeet to climb down headfirst, much like modern squirrels. Many multis had an herbivorous diet, while some apparently consumed insects."

Early Jurassic mammaliaforms from 193 Ma (oldest so far found) include the insectivore *Hadrocodium wui*, China, described by Zhe-Xi Luo in 2001.[8] Heavy in thought (or rather, olfactory ability), its genus name "large head" is for its ecephalization quotient 0.86 (braincase to skull sizes ratio) but light in weight (about 2 grams full grown) was this near-tiniest mammal of any period. It is distinctive for having, unlike other known mammals of the time, no groove at the rear of its jawbone. This, as in modern mammals, indicates that the three bones of the middle ear had long been separated from the mandible in *H. wui*'s ancestors. *H. wui* has allowed for an updated phylogeny of Mesozoic mammals in which the tribosphenic tooth condition with the reversed-triangle shearing between molar crowns may have evolved twice independently; most recently in the newly recognized Australosphenida and once before in Boreosphenida (tribosphenic marsupials and placentals).

Fossil evidence of Jurassic mammals in Pangea is sparse except for a group called *doconodonts*. These did not survive after the end of the Jurassic, but along with multituberculates, symmetrodonts, triconodonts, and haramiyids, they were present 210 Ma as the first evidence of class Mammalia members in the Late Triassic of Pangea. How these relate to each other in terms of branching from the common ancestor revealed by comparative anatomy, is not certain (***Figure h19.3***). By contrast, cladistic molecular phylogenetic analysis, reported by William J. Murphy in 2001, divides living eutherians into four clades: I) that includes elephants, manatees, hyraxes, tenrecs, aardvark and elephant shrews, II) that includes sloths, anteaters and armidillos, III) that includes two sister taxa: one with rodents and lagomorphs, and the other with primates, flying lemurs and tree shrews, and IV) that includes cetaceans, artiodactyls, perissodactyls, carnivores, pangolins, bats and core insectivores that date back to when dinosaurs were still in existence. Divergence of clades III and IV occurred on northern continents (then separated from the southern continents) near the end of the Mesozoic. Divergence of clades I and II occurred earlier in the Mesozoic in Pangea.[9]

Mammals evidently diverged in the Late Triassic from among the then going-extinct descendants of Permian cynodonts (advanced mammallike reptiles), and are included, therefore, in the clade Therapsida (advanced synapsids).[10] ❏

Figure ***h****19.1* [11] Evolutionary relationships among Mammals

The first announcement, in 1824, of the presence of mammals in Mesozoic strata (Middle Jurassic Stonesfield slates in England) ... challenged then-prevailing notions concerning the succession of life through geologic time. Additional discoveries through the 1860s, most also in England, quickly established the existence of a diversity of Mesozoic mammals, and in 1871 Richard Owen provided the first detailed study of these finds.[[12]]

—Hans Sues.[13]

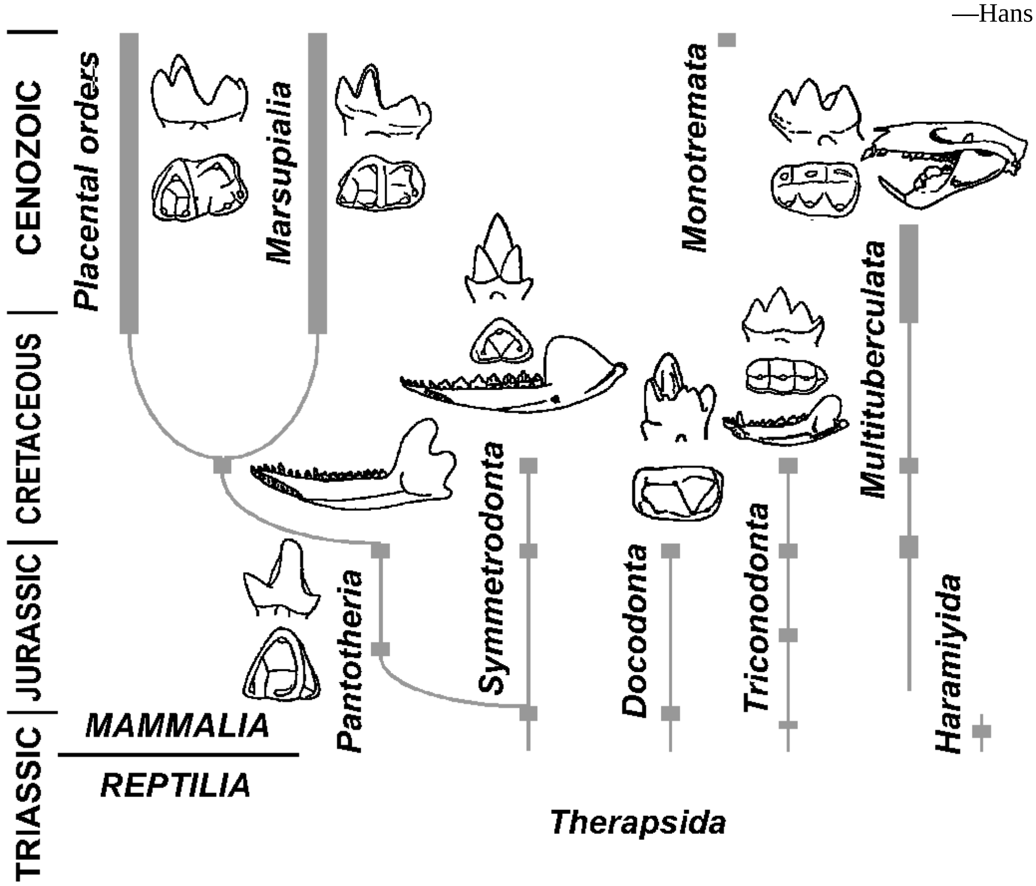


*Figure **h**19.2*[14] **Cretaceous marsupial jaws** are recognizable because adult mandible has three premolars and four molars, a condition still retained by living primitive marsupials. The type care of the young marsupial may also date from the Cretaceous. Living marsupials are born very immature. They wriggle to a lactating teat on their mother to which they attach and suckle for a prolonged period. This "period of fixation" selects for a modified pattern of baby (deciduous) teeth replacement. In all living marsupials, the deciduous third premolar (dp_3) is not replaced in the adult. Richard L. Cifelli has found this to be true also of the Upper Cretaceous marsupial *Alphadon* jaw (illustrated below).

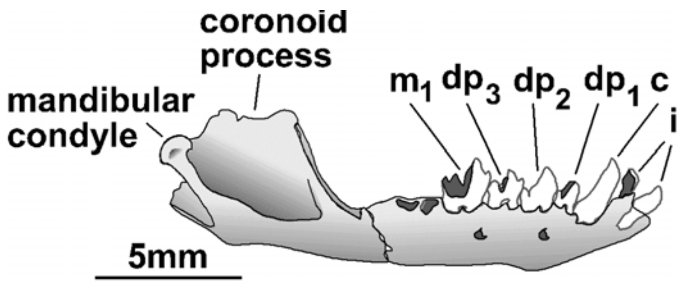
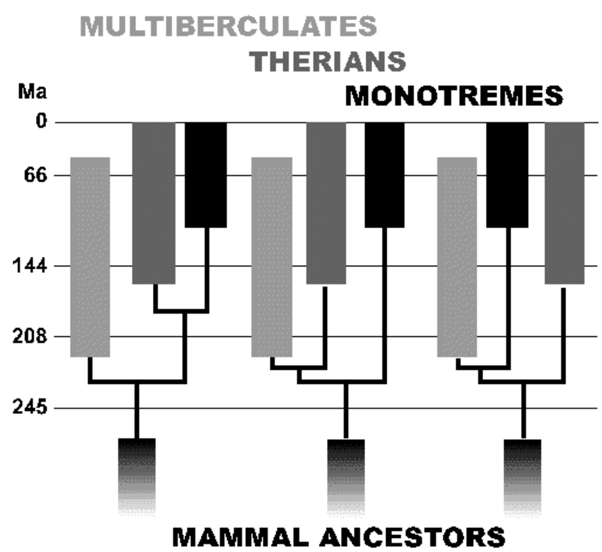


*Figure **h**19.3*[15] Cladistic phenotypic characters analyses of multituberculates fossils and other mammals, both living and extinct, have yielded equivocal results. Left to right:

The traditional view is that multituberculates evolved as a side branch distinct from both therians and monotremes .

Analysis by Paul C. Sereno and Malcolm C. McKenna in 1995 of the shoulder of a Mongolian multituberculate *Bulganbaatar*, placed multituberculates closest to the therians.

Analysis by Jin Meng and Andre R. Wyss in 1995 of the ear bones of the Chinese multituberculate *Lambdopsalis*, placed multituberculates closest to the monotremes.



*Footnote **h**19.1* Four homeotic genes are identified in making the reproductive systems of placentals and marsupials ("higher" mammals in which the young develop internally in the mother's uterus) different from monotremes (with incomplete uterine development).

In higher mammals, *Hox A-9, -10, -11, -13,* are expressed in the fallopian tubes, upper-uterus, lower-uterus, and vagina respectively. Unlike their expression in egg-laying mammals (and in all other animals and ancestral forms of the genes themselves back to possibly 640 million years ago), *Hox A-10* and *Hox A-11* genes in the higher mammals came to orchestrate thickening the uterine tissue and increasing the number of blood vessels serving it, to create a safe and well-oxygenated environment for embryonic implantation and development. For direct access to maternal nutrients, the embryo-placenta developed. In this development, *Hox A-13* genes came to orchestrate the formation of the blood vessels of the umbilical cord.[16]