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*the* **TIMETREE** *of* **LIFE**

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# Mammals (Mammalia)

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## Abstract

Extant mammals (~5400 sp.) are divided into three groups: Prototheria (monotremes; platypus and echidnas), Metatheria (marsupials), and Eutheria (placental mammals). Traditionally, monotremes are considered the closest relatives of Theria (marsupials + eutherians), but analyses of mitochondrial sequences have advocated a grouping of monotremes with marsupials. Recent analyses of nuclear data firmly support the Theria hypothesis. The mammalian timetree indicates that monotremes diverged from therians in the late Triassic, ~220 million years ago (Ma), and that marsupials and eutherians diverged ~176 Ma, between the early and middle Jurassic. However, estimates of divergence times vary among studies, which points to the need for further investigations.

Mammals (Mammalia) comprise a diverse class of vertebrates characterized by three morphological characters: mammary glands, hair, and three middle ear bones. Mammals are divided into three well-established groups: the Subclass Prototheria (Fig. 1) (five species, e.g., platypus and echidnas); the Infraclass Metatheria (seven orders, ~330 species, e.g., kangaroos and opossums); and the Infraclass Eutheria (18–20 orders, ~5080 species, e.g., elephants, bats, anteaters, and humans) (1). The mosaic appearance of monotremes, with reptilian (e.g., egg-laying) and mammalian (e.g., mammary glands) characteristics, has placed them as remnants of an ancestral stock of mammals, classified into their own subclass, basal to Theria (marsupials and eutherians) (2). Here, the phylogenetic relationships and times of divergence of these three most basal mammalian groups are briefly reviewed.

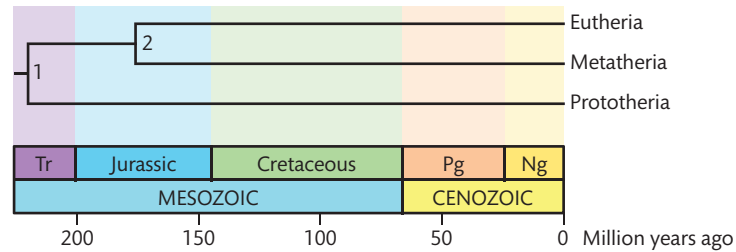
The traditional division of mammals in Prototheria and Theria is supported by a wealth of shared-derived morphological characters, which join eutherian mammals with marsupials (1, 2). An alternative grouping of

monotremes with marsupials, the Marsupionta hypothesis, has been suggested based on morphological characters (3, 4), but subsequent morphological analyses invalidated these characters as either ancestral or convergent, consequently rebutting the Marsupionta concept (2). Molecular phylogenetic analyses, however, rekindled the discussion whether monotremes or eutherians are the closest relatives of marsupials. Analyses of whole mitochondrial genomes have strongly supported the Marsupionta hypothesis (5, 6), but a recent study in which base composition and data partitioning were taken into account has favored Theria over Marsupionta (7).

While a few phylogenetic analyses of single nuclear genes have also supported Marsupionta (6, 8), the majority of nuclear gene phylogenies support the traditional Prototheria–Theria arrangement (9–13, 22, see 14 for a recent review), albeit that both scenarios display great variation in statistical support. Until recently, only a single study employed analyses of concatenated nuclear data (15). Two different data sets, one emphasizing broad taxon sampling, and the other sequence length, provided strong support for Theria. Besides the more traditional molecular phylogenetic analyses, independent support for Theria has also been obtained from rare genomic changes in the form of several informative indels (7, 15), and from the sex-determining system in platypus, being intermediate in having both reptilian- and therian-like features (16, 17).



**Fig. 1** The Platypus (*Ornithorhynchus anatinus*), one of the five species of extant monotreme mammals (Prototheria). Credit: Tourism Queensland, Mackay, Queensland, Australia.



**Fig. 2** A timetree of mammals (Mammalia). Divergence times are from Table 1. *Abbreviations:* Ng (Neogene), Pg (Paleogene), and Tr (Triassic).

Relatively few studies have dealt with the divergence times of the basal mammalian lineages (5, 7, 9, 11, 15, 18–22), and only five studies have simultaneously estimated timing of both divergences (11, 15, 20–22) (Fig. 2, Table 1). A synthesis of the results places the Prototheria–Theria divergence in the upper Triassic, 220 Ma and the Eutheria–Metatheria divergence between lower and middle Jurassic, 176 Ma. However, individual studies show some variation in the estimated times, with the Prototheria–Theria split ranging from 237 to 204 Ma, and the divergence between eutherians and metatherians dated between 195 and 130 Ma (Table 1). Therefore, additional analyses with larger data sets (both taxonomically and in sequence length) and more calibration points are required before final conclusions can be drawn about the most basal mammalian groups.

The molecular divergences times are in general older than current established paleontological evidence, with the oldest monotreme fossils from the early Cretaceous (~120 Ma) (23), and oldest eutherian and marsupial fossils from around 125 Ma (24, 25). But, some recent fossil analyses and new fragmented fossil remains, respectively, suggest older dates for both the therian split (~167 Ma) (20) and the oldest monotreme (~200 Ma) (2), dates close to the molecular estimates.

The divergence between marsupials and eutherians, between early and middle Jurassic, corresponds roughly with the initial breakup of Pangaea into Laurasia and Gondwana. This raises the possibility of an origin by continental vicariance (26), but the fossil record of mammals from this early time period is currently too fragmentary to either support or refute such a hypothesis.

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**Table 1.** Divergence times (Ma) and confidence/credibility intervals (CI) among mammals (Mammalia).

Timetree		Estimates								
Node	Time	Ref. (5)(a)		Ref. (5)(b)		Ref. (15)(a)		Ref. (15)(b)		Ref. (18)
		Time	CI	Time	CI	Time	CI	Time	CI	Time
1	220.2	-	-	-	-	213	262-164	233	306-160	-
2	176.1	143.0	176-110	130.0	149-111	192.0	238-146	195.5	257-135	176.0

Timetree		Estimates (Continued)									
Node	Time	Ref. (19)		Ref. (20)		Ref. (21)		Ref. (22)(a)		Ref. (22)(b)	
		Time	CI	Time	CI	Time	CI	Time	CI	Time	CI
1	220.2	-	-	237	263-212	206.8	228-187	204	218-190	227	251-203
2	176.2	173.0	197-149	186.0	232-150	190.8	212-172	178.5	192-166	196.0	218-174

Note: Node times in the timetree represent the mean of time estimates from different studies. Estimates are based on mitochondrial genomes (5, 18, 21), many nuclear genes (15, 19), and one or two nuclear genes (20, 22). A relaxed molecular clock was applied in some studies (15, 20-22) and rate constant genes were used in other studies (5, 18, 19). Estimates are based on the analysis of amino acids in refs. (5)(b), (15)(b), (18, 19, 22)(b)).

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