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# Rodents (Rodentia)

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## Abstract

The Order Rodentia is the most diverse group of mammals, represented by 34 extant families. Recent molecular data have helped to clarify relationships among these families, and provide a framework for the higher-level classification of rodents. Molecular time estimates among rodent families have been made in several studies, permitting a timetree of rodent evolution to be constructed. The timetree shows a partitioning of rodent families into three major clades and reveals three periods of diversification: The late Cretaceous, 88–66 million years ago (Ma), the Paleocene to early Eocene, 60–55 Ma, and the late Oligocene to early Miocene, 25–15 Ma.

The Order Rodentia (represented by squirrels, mice, rats, guinea pigs, and others) contains 42% (2277) of all species and 39% (481) of all genera described for the Class Mammalia (1) (Fig. 1). If one includes the recently discovered extant Family Diatomyidae (2), the order contains 34 families (1). All early classifications of mammals (3) and more recent cladistic analysis of morphological variation (craniodental, postcranial, fetal membrane) (4) support a monophyletic Rodentia. Although several early molecular phylogenetic studies questioned the validity of a monophyletic Rodentia (5, 6), more recent molecular data, based on either nuclear DNA (7–9) or a more thorough analysis of sequences of whole mitochondrial genomes (10), reveal support in favor of monophyly. In this review I will address phylogenetic relationships and divergence times for families within Rodentia.

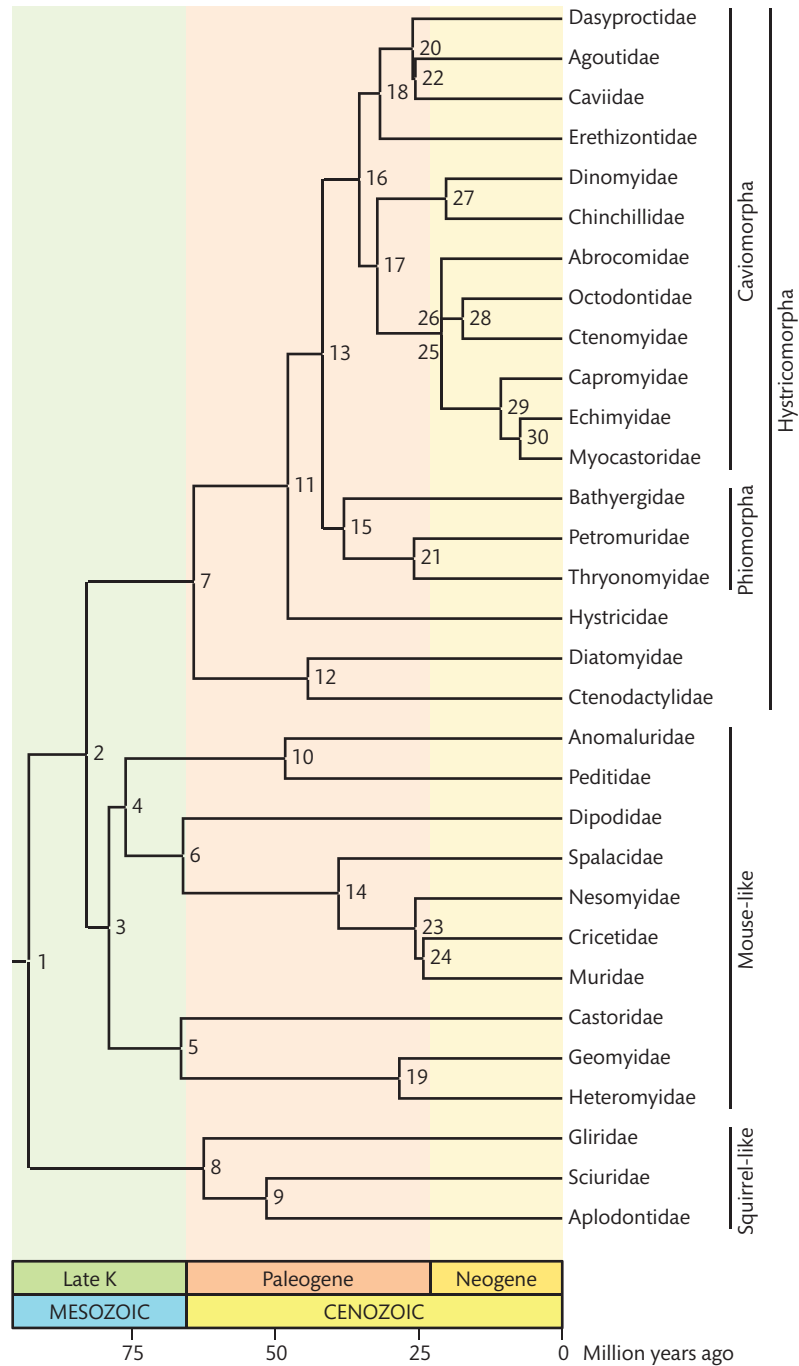
Even though the assignment of species and genera of rodents to specific families is well established (1), the derivation of a family-level phylogeny for rodents is more challenging (11–14). This problem has resulted in a variety of classifications that vary in terms of recognized suborders and the morphological features used to define monophyletic groups (1, 11, 15–17). Two of the major characteristics used to diagnose suborders relate

to either features of the zygomaseteric system (configuration of the infraorbital foramen and placement of the masseter muscles in the jaw) or the angle of the lower jaw relative to the plane of the incisors (15, 16). Tullberg's classification (15) identifies two suborders, Sciurognathi and Hystricognathi, based on the angle of the lower jaw, and the hystricognathous condition supports the monophyly of a clade containing phiomorph and caviomorph rodents (Fig. 2). Nevertheless, the phylogenetic distribution of features of the infraorbital foramen reveals evidence of parallel changes within Rodentia (17–19).

Detailed molecular phylogenetic studies contribute greatly to the resolution of the rodent evolutionary tree, and areas of congruence among the majority of these studies provide strong support for many interfamilial relationships among rodents (Fig. 2). For instance, two major monophyletic groups, Hystricomorpha and a squirrel-like clade, are supported by nuclear (2, 19–22)



Fig. 1 A capybara (*Hydrochaeris hydrochaeris*), Family Caviidae. Credit: R. L. Honeycutt.



**Fig. 2** A timetree of rodents (Rodentia). Divergence times are shown in Table 1. The muroid Families Calomyscidae (no divergence time data) and Platcanthomyidae (recently extinct) were not included. *Abbreviation:* K (Cretaceous).

and mitochondrial (18, 24, 25) sequences, and some nuclear markers (2, 7, 21), including the presence/absence of retrotransposon insertion loci (9), support a third mouse-like clade. Relationships among these three

clades are somewhat more tenuous, but many molecular studies place the squirrel-like clade at the base of the phylogeny (7, 8, 20, 21, 23). Recent molecular studies also help resolve the placement of several historically

**Table 1.** Divergence times (Ma) and their confidence/credibility intervals (CI) among rodents (Rodentia).

Timetree		Estimates											
Node	Time	Ref. (2)		Ref. (21)		Ref. (24)	Ref. (27)		Ref. (28)		Ref. (30)		Ref. (31)
		Time	CI	Time	CI		Time	CI	Time	CI	Time	CI	
1	92.9	-	-	96.9	105-85	-	-	-	-	-	-	-	-
2	82.8	72.1	80-64	93.5	106-77	-	-	-	-	-	-	-	-
3	78.9	67.8	76-60	90	101-68	-	-	-	-	-	-	-	-
4	76.0	66.5	75-58	85.4	101-65	-	-	-	-	-	-	-	-
5	66.4	63.3	72-55	84.9	93-66	50.9	-	-	-	-	-	-	-
6	66.0	65.4	73-57	87	82-53	45.7	-	-	-	-	-	-	-
7	64.2	61.3	63-54	83.7	97-67	47.6	-	-	-	-	-	-	-
8	62.4	57.3	65-50	78.8	90-62	51.2	-	-	-	-	-	-	-
9	51.5	50.8	59-43	65.3	82-53	38.3	-	-	-	-	-	-	-
10	48.3	56.8	65-49	-	-	39.7	-	-	-	-	-	-	-
11	47.8	45.4	51-40	43.1	51-29	-	55	63-46	-	-	-	-	-
12	44.3	44.3	51-38	-	-	-	-	-	-	-	-	-	-
13	41.7	42.7	47-37	38.1	54-16	-	49	54-43	-	-	36.6	39-34	-
14	39.0	-	-	-	-	-	-	-	-	-	-	-	39
15	38.0	38	43-33	-	-	-	45	48-41	-	-	30.5	34-27	-
16	35.3	34.3	37-30	-	-	-	-	-	37.7	40-35	33.8	36-32	-
17	32.2	33.3	36-29	32.8	47-24	30.4	-	-	-	-	-	-	-
18	31.7	31.7	35-27	-	-	-	-	-	-	-	-	-	-
19	28.4	27.3	33-22	-	-	-	27	29-25	-	-	31.4	33-29	-
20	26.0	-	-	-	-	-	24	26-21	-	-	27.9	30-26	-
21	25.8	24.5	43-20	-	-	-	27	28-25	-	-	-	-	-
22	25.6	24.1	28-20	-	-	-	-	-	-	-	26.5	29-24	-
23	25.5	-	-	-	-	-	-	-	-	-	-	-	25.5
24	24.2	-	-	-	-	-	-	-	-	-	-	-	24.2
25	21.3	18.6	22-15	-	-	-	-	-	27.4	32-23	17.5	20-15	-
26	21.0	-	-	-	-	-	-	-	-	-	20.6	23-18	-
27	20.2	21.4	26-18	-	-	-	-	-	-	-	19.1	22-16	-
28	17.3	-	-	-	-	-	-	-	19.6	23-17	15	17-13	-
29	10.7	12.4	15-10	-	-	-	9	10-7	-	-	-	-	-
30	7.3	-	-	-	-	-	6	7-5	-	-	8.6	10-7	-

Note: Node times in the timetree represent the mean of time estimates from different studies. In ref. (30), confidence interval is based on estimates of standard deviations provided. In ref. (27), divergence time represents an average of two estimates of the same gene (*VWF*) derived from nucleotide and amino acid sequences, and the CI refers to the range of these estimates. In ref. (21), divergence time represents an average of the *GHR* and *BRCA1* genes; only values derived from the rate-smoothing method were used; CI represents the combine rate of values for both genes. In ref. (28), divergence time represents an average of estimates derived from nuclear (*GHR*) and mitochondrial (*12S rRNA*) combined genes, and CI is the range of values. In ref. (31), estimates for Node 14 based on *GHR* gene, optimized with rate smoothing, and dates for Nodes 23 and 24 represented values from a concatenation of all genes and optimization with the penalized likelihood method.

problematic taxa, including the Families Pedetidae (Springhaas), Anomaluridae (scaly-tailed squirrel), Geomyidae/Heteromyidae (pocket gopher and pocket mouse), and Castoridae (beaver) (2, 7, 9, 21, 24).

Tullberg's (15) Suborder Hystricognathi, characterized by a hystricomorphous zygomasseteric system and a hystricognathous lower jaw, is strongly supported by molecular studies (2, 9, 18, 20, 21, 25). In addition,

monophyly of the South American Caviomorpha (guinea pigs and relatives) is strongly supported, suggesting a single invasion from African ancestors, represented today by the Phiomorpha (2, 7, 9, 20, 26). The placement of Old World porcupines (Hystricidae) is more controversial, yet the majority of data, based on nuclear and mitochondrial sequences, suggests a basal position for the family (2, 20, 21, 23, 27). Relationships among families within the Caviomorpha are well resolved with a combination of nuclear and mitochondrial sequences, and with few exceptions (e.g., clade containing Chinchilidae and Dinomyidae, Fig. 2) these results are similar to groups previously defined based on morphology (22, 23, 25, 27–29). The current classification of rodents assigns the 34 families to five suborders (1), and molecular data support the monophyly of these five suborders: Sciuromorpha, Castorimorpha, Myomorpha, Anomaluromorpha, and Hystricomorpha (Fig. 2). Three of these suborders comprise the mouse-like clade. As indicated earlier, placement of some of these major groups (e.g., basal squirrel-like clade and the clade uniting Muroidea, Dipodidae, Peditidae, and Anomaluridae, Fig. 2) is not well resolved at this time.

Divergence times for the rodent evolutionary tree (Fig. 2, Table 1) represent a compilation from several molecular studies based on the following combinations of genes: (a) portions of four nuclear protein-coding genes (*ADRA2B*, *GHR*, *IRBP*, *VWF*) and two mitochondrial genes (*cytochrome b* and *12S rRNA*) (2); (b) two mitochondrial genes (*Cyt b* and *12S rRNA*) (24); (c) a nuclear gene (*GHR*) (20); (d) two nuclear genes (*GHR*, *BRCA1*) (21); (e) one nuclear gene (*VWF*) (22, 27); (f) one nuclear (*GHR*) and one mitochondrial gene (*12S rRNA*) (28, 30); (g) four nuclear genes (*GHR*, *BRCA1*, *RAG1*, *c-myc*) (31); and (h) whole mitochondrial genomes (32). Calibration points and methods used to estimate divergence times vary across these studies. Nevertheless, all of these studies test for uniform rates before applying a molecular clock, and most provide dates estimated by methods that correct for rate heterogeneity across lineages (33–35). The beginning of the rodent radiations (Table 1) represents an average of two estimates: 96.9 Ma (21) and  $88.8 \pm 4.3$  Ma (32). The average date of 92.9 Ma obtained from these two estimates is larger than the basal diversification date of 85.3 Ma based on a recent supertree for extant mammals (36), yet is considerably less than the estimate of 110 Ma provided by Kumar and Hedges (37) for the split between the two major groups of rodents. All of these molecular dates are considerably older than the first appearance of rodents in the fossil record 60–55 Ma (38).

The timetree does provide a framework for testing hypotheses related to the distribution and diversification of rodents. The phylogeny in combination with estimates of divergence times (Fig. 2 and Table 1) reveals three major diversifications of rodents, one occurring in the late Cretaceous and early Paleocene, another in the Paleocene to early Eocene, and another that involved the diversification of African phiomorphs and South American caviomorphs in the late Oligocene to early Miocene. This pattern is similar to a recent proposal for mammalian radiations that suggests an early origin for many lineages followed by an increase in diversification during the Eocene and Oligocene (36). Many rodent families in the timetree also reveal long terminal branches and shorter internodes, features that make the resolution of the phylogeny more challenging.

The timetree also provides insight into the biogeography of hystricognath rodents. For instance, caviomorph rodents first appear in the fossil record of South America 37–31 Ma (39) and the oldest phiomorphs in Africa date to 37–34 Ma (38), and these dates are similar to those indicated in Table 1. Consequently, these dates are congruent with the hypothesis that the invasion of South America by African hystricognath ancestors involved overwater waif dispersal across an ~1700 km expanse of the Atlantic subsequent to the separation of these two continents at a much earlier date.

The classification of rodents has vacillated for well over a century, as a result of a lack of clear understanding of interfamilial relationships. Morphological comparisons of both extant and extinct forms have resulted in a host of phylogenetic hypotheses regarding not only the number of suborders but also the placement of several problematic taxa that are sometimes left as status undetermined in many classifications. Recent molecular studies contribute to the resolution of many problems, and they indicate that traditional morphological features used in earlier classifications have evolved independently in many cases. The timetree in Fig. 2 represents an interpretive framework for testing many hypotheses pertaining to behavioral and ecological evolution. Just as important is the observation that rates of molecular evolution vary across lineages and genes, thus influencing estimates of divergence times. Many of the estimates presented in Table 1 attempt to minimize the effects of rate heterogeneity by the inclusion of multiple calibration points and various types of rate-smoothing methods. The accuracy of these approaches is still debatable, and rodents provide an excellent model for investigating methods for deriving a molecular clock. In addition, rodents are diverse in terms of metabolic rates and body

size, and there is at least some information that suggests these features may be correlated with differences in rates across groups of rodents (29). Clearly, this is an area that needs further investigation.

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