Chapter 7

Phylogeny and Divergence of Basal Glires

JIN MENG

ABSTRACT

Phylogenetic analyses based on morphological data support monophyly of Glires, but not a link between Glires and zalambdalestids. Glires are more closely related to several Tertiary taxa, including primates, leptictids, pseudictopids, anagalids, and macroscelideans. Phylogenetically constrained distributions of Glires support the conventional view for a post K-T boundary radiation of modern orders of placental mammals and disagree with conclusions of some molecular studies that divergence of Rodentia and Lagomorpha at infraordinal, ordinal, and certain supraordinal levels occurred in the Cretaceous. Current hypotheses employed to explain the discrepancy between the fossil record and the molecular clock hypothesis are not supported by phylogenetic and distributional evidence of Glires. There is no compelling evidence that close relatives of Glires were present in the Cretaceous.

INTRODUCTION

Glires (Linnaeus, 1758) encompasses two extant mammalian orders: Rodentia (rats, squirrels, guinea pigs, and relatives) and Lagomorpha (rabbits and pikas). Both orders are characterized by possessing a pair of enlarged, ever-growing incisors in both upper and lower jaws. Lagomorpha contains two living families (about 13 genera, 81 species) (Nowak, 1999) and 56 fossil genera (McKenna and Bell, 1997) that first appeared in the Paleocene of Asia (McKenna, 1982), although it is debatable whether some of these fossils are lagomorphs. Rodentia consists of 29 Recent families (about 468 genera, 2052 species) (Nowak, 1999) and 743 extinct genera (McKenna and Bell, 1997), and probably dates back to the late Paleocene of North America (Wood, 1962; Dawson et al., 1984; Korth, 1984; Dawson and Beard, 1996). Lagomorphs and rodents constitute nearly half of the diversity of extant mammalian species, and are frequent subjects for biological experiments in physiology, genetics, and molecular biology (Flynn, 1994). Two related issues concerning these two orders are currently under rigorous debate: whether Rodentia and Lagomorpha form a sister group, namely Glires; and when Glires, Rodentia, and Lagomorpha diverged from other principal mammalian clades during geological history. This study focuses on these issues.

The relationship of Rodentia and Lagomorpha is a long-standing problem in mammalian systematics (Tullberg, 1899; Gidley, 1912; Wilson, 1949; Wood, 1957; Dawson, 1967; Landry, 1999; Luckett and Hartenberger, 1985; Li and Ting, 1985; Novacek, 1985, 1990; Jaeger, 1988; Luckett and Hartenberger, 1993; Meng and Wyss, 2001), and the concept of Glires has not been always favored. For many years Landry (1970) was probably the only active defender in North America of a close relationship between lagomorphs and rodents (Li et al., 1987). Among those who disfavored the concept of Glires was Malcolm McKenna, who played a critical role in advocating alternative relationships for rodents and lagomorphs and an early divergence of gliroid mammals. McKenna (1961) proposed a close relationship between basal rodents and primates based on overall similarity of the cheek teeth of *Acritoparamys atavus*, *Plesiadapis*, and *Phenacolemur*, a conclusion subsequently supported by others (Van Valen, 1966; Lille-

graven, 1969; Wood, 1962, 1977; Patterson and Wood, 1982). Wood (1977) suggested that southeastern North America was the most probable area of origin for rodents, and that the order might have evolved from Primates in the middle Paleocene. In a later study, McKenna (1975) placed Rodentia as incertae sedis within eutherian mammals and Lagomorpha as the sister taxon to Macroscelidea within Anagalida. McKenna (1982) also conducted the first cladistic analysis of lagomorph interrelationships, which included 32 terminal taxa and 52 characters. He considered *Mimotona*, a gliroid taxon with two pairs of lower incisors, a lagomorph. He also called *Pseudictops*, a Paleocene genus with a typical eutherian dental formula, a lagomorph (Bleefeld and McKenna, 1985) and suggested a lagomorph-zalambdalestid link to the exclusion of rodents (Szalay and McKenna, 1971; McKenna, 1975). McKenna (1994: 58) stated that the Late Cretaceous *Zalambdalestes* (also *Barunlestes*) ''seems to me to be a distant relative of lagomorphs—closer to them than to many other kinds of mammals because it seems to share at least a few derived features with them.'' In his recent classification (McKenna and Bell, 1997) the concept of Glires was still not accepted, although Rodentia was placed with Mixodontia within Simplicidentata, and Lagomorpha with Mimotonida within Duplicidentata. Both Simplicidentata and Duplicidentata were placed together with Macroscelidea, Pseudictopidae, Anagalidae, and Zalambdalestidae within Anagalida.

Morphologists are not alone in challenging the monophyly of Glires. During the last decade, molecular biologists have proposed several hypotheses concerning Glires phylogeny, such as the polyphyly of Rodentia (Graur et al., 1991; Li et al., 1992); a primate + lagomorph clade (Easteal, 1990; Penny et al., 1991); a (lagomorph + tree shrew) + primate relationship (Graur et al., 1996); a primate + rodent + lagomorph relationship that is associated with tree shrews (Miyamoto and Goodman, 1986); and a primate supraordinal clade composed of Primates, Dermoptera, Scandentia, Lagomorpha, and Rodentia (Stanhope et al., 1993).

The notion of a lagomorph-zalambdalestid relationship (McKenna, 1994) necessarily rejects Glires monophyly or requires that the concept of Glires be greatly expanded. If the latter is true, then it would extend the known history of gliroid mammals into the Cretaceous. A similar hypothesis was proposed in a recent paleontological study that identified a clade containing zalambdalestids and Glires (Archibald et al., 2001). Given the presence of zalambdalestids in the 85–90 Ma faunas at Dzharakuduk, Archibald et al. (2001) argued that the superordinal clade including Glires and zalambdalestids had separated from other placental clades in the Cretaceous. The result was believed to be concordant with molecular-based estimates of the superordinal diversification of placental mammals 64–104 Ma.

Divergence time of rodent groups at the infra- and supraordinal levels based on molecular data has been estimated at about 110 Ma, making them the earliest placental group known except for Xenarthra (Kumar and Hedges, 1998). On the molecular time scale, Lagomorpha diverged from other placental mammals about 90 Ma (Kumar and Hedges, 1998). The statement that ''molecular divergence times among sciurognath rodents are roughly four times older than their fossil-based estimates'' (Kumar and Hedges, 1998: 918) may overestimate the time difference between the molecular clock and fossil record, because conventional sciurognath rodents (see Landry, 1999 for an alternative view of the terminology) are found in the early Eocene, at least 50 Ma. Still, the 110 Ma dating of rodent divergence is twice as old as what is indicated by the earliest fossil record. These molecular-based dates contradict the conventional view of a post Cretaceous-Tertiary boundary radiation of modern placental groups as shown by the known fossil record (Gingerich, 1977; Novacek, 1992; Archibald and Deutschman, 2001).

Gliroid mammals are an exemplary group for studying divergence times of modern placental mammals for several reasons. First, taken as a whole, Glires is one of the placental groups that display the greatest discrepancy in divergence time between the fossil record and molecular dating (Bromham et al., 1999). Second, they are the most diverse placental mammals and have the best represented fossil record, which extends from the

early Paleocene to the Recent. Finally, most of them are smaller than most known Cretaceous mammals, so that the preservation rate owing to body size is a less influential factor than in other mammals when the fossil record is concerned.

MATERIAL AND METHODS

The phylogenetic analysis herein is based on Meng and Wyss (2001). In addition to the 28 taxa used in that study, two additional taxa, *Matutinia* and *Sinomylus*, are added to the analysis in this study. *Sinomylus* was described recently by McKenna and Meng (2001) and was considered an outgroup taxon to other eurymylids plus rodents. *Matutinia* (Li et al., 1979), previously regarded as a junior synonym of *Rhombomylus* (Dashzeveg and Russell, 1988; McKenna and Bell, 1997), is now considered a valid taxon based on more completely preserved specimens (Ting et al., 2002). Other gliroid taxa represented only by fragmentary jaws and isolated teeth are not included in this study; their relationships have been explored in Meng and Wyss (2001). *Asioryctes* and *Kennalestes* are chosen as outgroups. Non-gliroid taxa include *Zalambdalestes*, *Barunlestes*, *Anagalopsis*, *Pseudictops*, *Elephantulus*, *Rhynchocyon*, *Plesiadapis*, *Adapis*, *Leptictis*, and *Tupaia*. These taxa have been commonly regarded as closely related to the Rodentia, Lagomorpha, or Glires.

Among the 91 characters used in this study, 82 were adopted from Meng and Wyss (2001). The data matrix and a list of the additional nine characters are provided in appendix 7.1. The numbering of those characters follows the same sequence of characters listed in Meng and Wyss (2001). Phylogenetic analyses employing PAUP* (Swofford, 2000) were conducted on the data set. The methods of the analyses are congruent with those used by Meng and Wyss (2001). Specific options chosen for PAUP* analyses include tree(s) rooted using outgroup method, all characters unordered, all characters equally weighted, multistate taxa interpreted as uncertain, and delayed transformation (DELTRAN) of character states.

RESULTS

A Branch-and-Bound Search discovered eight equally most parsimonious trees (MPTs). The strict consensus tree is illustrated in figure 7.1. The apomorphy list supporting each node is presented in appendix 7.2. Figure 7.2 illustrates the phylogenetically constrained geological distributions of the included taxa.

Although the number of most parsimonious trees discovered in this study is fewer than that (44 MPTs) in Meng and Wyss (2001: fig. 13), the consensus trees are congruent with respect to supporting the monophyly of Glires (node 43 in fig. 7.1); that is, Lagomorpha (node 33 in fig. 7.1) and Rodentia (node 39 in fig. 7.1) are more closely related to each other than either of them is to any other selected eutherian group that has been previously considered kin of either Rodentia or Lagomorpha. This result is also consistent with a study that includes extant rodents and lagomorphs (Meng et al., 2003). Within the Glires, ''eurymylids'' and ''mimotonids'' are paraphyletic stem taxa to rodents and lagomorphs, respectively. *Matutinia* is paired with *Rhombomylus*, and *Sinomylus* is the sister taxon of other simplicidentates, as predicted by McKenna and Meng (2001). Relationships outside the clade of the Glires are better resolved than in Meng and Wyss (2001), but the general topology remains the same.

DISCUSSION

Phylogeny of Glires

Conventionally, there is little doubt about the monophyly of either Rodentia or Lagomorpha. The monophyly of Glires, however, has proven to be one of the most controversial issues in higher-level mammalian systematics (Wilson, 1949; Wood, 1957; McKenna, 1975; Luckett and Hartenberger, 1985, 1993; Li and Ting, 1985; Novacek, 1985; 1992; Li et al., 1987; Meng and Wyss, 2001). Rodentia and Lagomorpha have been at one time or another related to a variety of mammalian groups, either together or individually, such as rodent + primate (McKenna, 1961), rodent + leptictid (Szalay, 1977, 1985), and lagomorph + zalambdalestid to

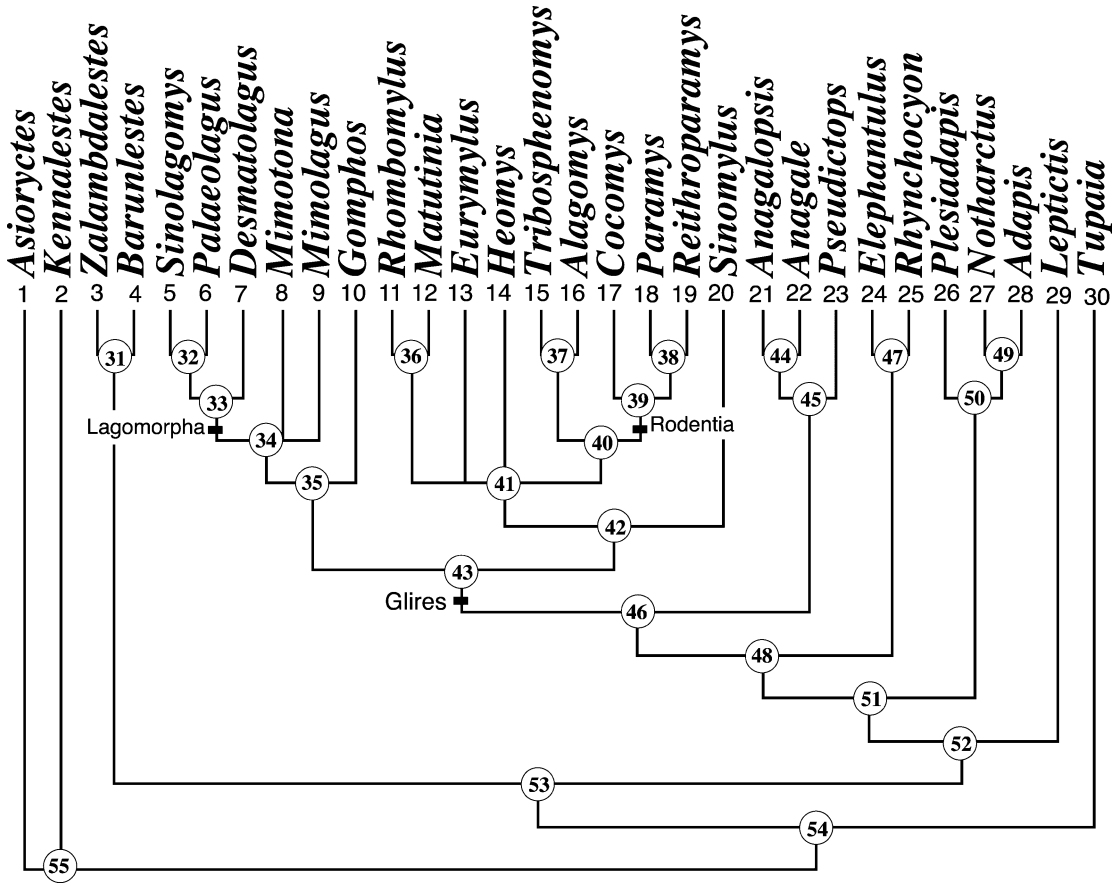

Fig. 7.1. The strict consensus of eight equally most parsimonious trees. Tree length = 235; consistency index = 0.6553; homoplasy index = 0.3447; retention index = 0.8724; and rescaled consistency index = 0.5717. Apomorphy list supporting each node is provided in appendix 7.2.

the exclusion of rodents (Szalay and McKenna, 1971; McKenna, 1975). All of these hypotheses would dismiss the similarities between rodents and lagomorphs as convergence. As pointed out elsewhere (Meng and Wyss, 2001), these hypotheses of convergence require identification of some third taxon that shares a unique common ancestry with one of the two groups but lacks the derived similarities common to both. Such a ''third taxon'' has never seriously threatened the sister-group relationship between lagomorphs and rodents. Several recent morphological studies favored monophyly of Glires (Li et al., 1987; Novacek, 1992; Luckett and Hartenberger, 1993; Shoshani and McKenna, 1998; Meng and Wyss, 2001). The present study supports this relationship.

During the last decade the challenges to the monophyly of Rodentia or Glires by some molecular studies have been severe. Based on analysis of amino acid sequence data, Graur et al. (1991) first questioned whether the guinea pig (*Cavia porcellus*) is a rodent. Their result suggested a closer grouping of the guinea pig with Primates, not with other rodents, which would make the conventional Rodentia, and therefore Glires, nonmonophyletic. Some molecular analyses also rejected the monophylies of Glires and Rodentia (Li et al., 1992; Graur et al., 1996; D'Erchia et al., 1996), while others were less certain with respect to the relationships of rodents and lagomorphs (Ma et al., 1993; Martignetti and Brosius, 1993; Honeycutt and Adkins, 1993; Porter et al., 1996; Stan-

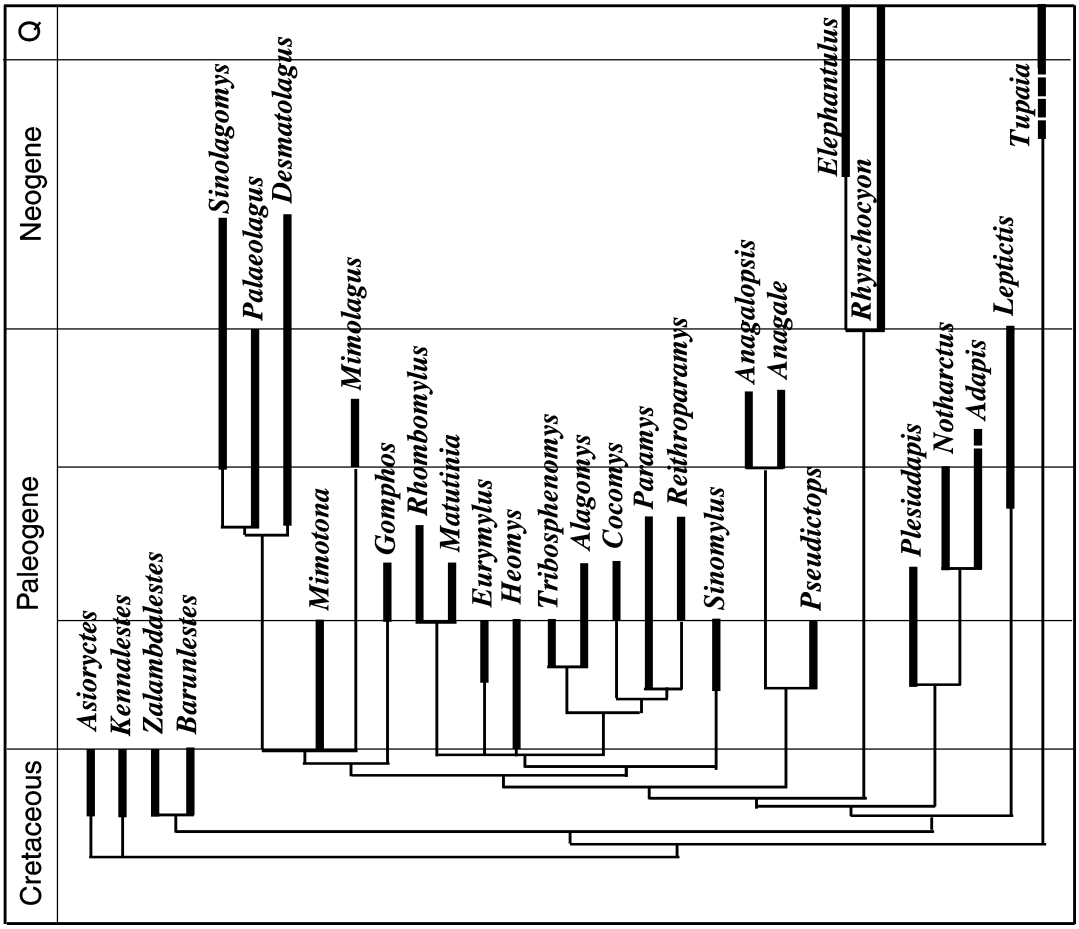

Fig. 7.2. Geologic distributions of the genera included in the phylogenetic analyses. Bold lines represent extensions of genera; fine lines indicate phylogenetic relationship as illustrated in figure 7.1. Age data were obtained from McKenna and Bell (1997), except those for *Sinomylus* (McKenna and Meng, 2001) and *Matutinia* (Ting et al., 2002).

hope et al., 1996; Huchon et al., 1999). As pointed out by several studies, earlier molecular studies that claimed the nonmonophyly of Glires may have been biased by inappropriate methods and deficient quality of data used in analyses (Allard et al., 1991; Hasegawa et al., 1992; Graur, 1993; Novacek, 1993; Catzeflis, 1993; Sullivan and Swofford, 1997). Recent molecular studies that include more taxa and sequence data (Madsen et al., 2001; Murphy et al., 2001a, 2001b), however, concur with recent morphological studies in supporting the Glires monophyly.

It has been questioned that some derived characters shared by rodents and lagomorphs, such as loss of canines, have been attributed to the evolution of gnawing function; therefore, they were regarded as parallelism (Graur et al., 1996). Gnawing, or incisor biting, is a common function in eutherian mammals, but the gnawing in gliroid mammals is unique in two aspects. First, the upper and lower cheek teeth must be distantly separated when the upper and lower incisors are engaged, or vice versa. Second, the lower incisors can be protruded anterior to the upper incisors so that the tips of the lower incisors can be honed against the tips of the upper incisors. Some other placental mammals, such as plesiadapids, have enlarged incisors, but they cannot gnaw the same way as do the gliroid mammals. Still,

some pleciadapids lack canines. It seems to me there is no evidence for the relationship between the loss of canines and the function of gnawing; nor is there reason to think, based on our current knowledge of relationships of gliroid mammals, that the enlarged incisors and other derived similarities shared by rodents and lagomorphs evolved independently.

Graur et al. (1996: 335) also suggested that

> One simple and intriguing possible resolution of the conflict between morphological and molecular data is to assume that many morphological ''synapomorphies'' used in support of Glires are actually ancestral character states that have been retained in some mammalian orders but were lost in others. If this reversal of character-state polarity proves valid, then the ancestral eutherian morphotype may have resembled a rodent species much more closely than is currently recognized in the morphopalaeontological literature.

Based on the phylogeny and distributions of gliroid and related eutherian mammals (Meng and Wyss, 2001; Meng et al., 2003), a rodentlike ancestral eutherian morphotype is not supported by paleontological data. Features, such as losses of the incisors, canines, and premolars, modification of the glenoid fossa, and enlarged upper and lower incisors, are apparently derived conditions evolved in the lineage toward rodents and lagomorphs and are not retention of a rodentlike eutherian morphotype that was present in the Cretaceous.

Divergence Times of Glires

On the molecular time scale, sciurognath rodents made their first appearance approximately 112 ± 3.5 Ma, followed by the divergence of hystricognaths (109 ± 3.2 Ma), Gerbillidae/Muridae (66.2 ± 7.6 Ma), Muridae/Cricetidae (65.8 ± 2.2 Ma), and mouse/rat (40.7 ± 0.9 Ma) (Kumar and Hedges, 1998; see also Janke et al., 1994). Lagomorpha would have appeared at 90.8 ± 2.0 Ma (Kumar and Hedges, 1998). Other molecular analyses also suggest that the common ancestor of rodents split from other eutherian orders in the Cretaceous (Janke et al., 1994; Huchon et al., 2000). However, there is no evidence in the fossil record supporting such an early date. The earliest rodent, *Acritoparamys* (which may be considered a sciurognath) occurred in the late Paleocene Clarkforkian of North America, about 57 Ma (Dawson and Beard, 1996). Its age is only half the divergence time for the Sciurognathi estimated by the molecular clock hypothesis (Kumar and Hedges, 1998). The earliest known fossil record of hystricognaths is in the early Eocene (McKenna and Bell, 1997), approximately 55 Ma. Clearly, the molecular clock hypothesis tends to push divergence times of the Glires at various levels deeper into history than what the fossils have documented. Five hypotheses for the divergence time of placental mammals and the discrepancy between fossil and molecular dates have been postulated: (1) the conventional view that placental radiation occurred after the K-T boundary, (2) poor preservation of Cretaceous mammals, (3) a lack of morphological diagnostic features in Cretaceous taxa, (4) hidden Cretaceous fossil records in southern continents, and (5) deep branching of superordinal clades of placental mammals (fig. 7.3).

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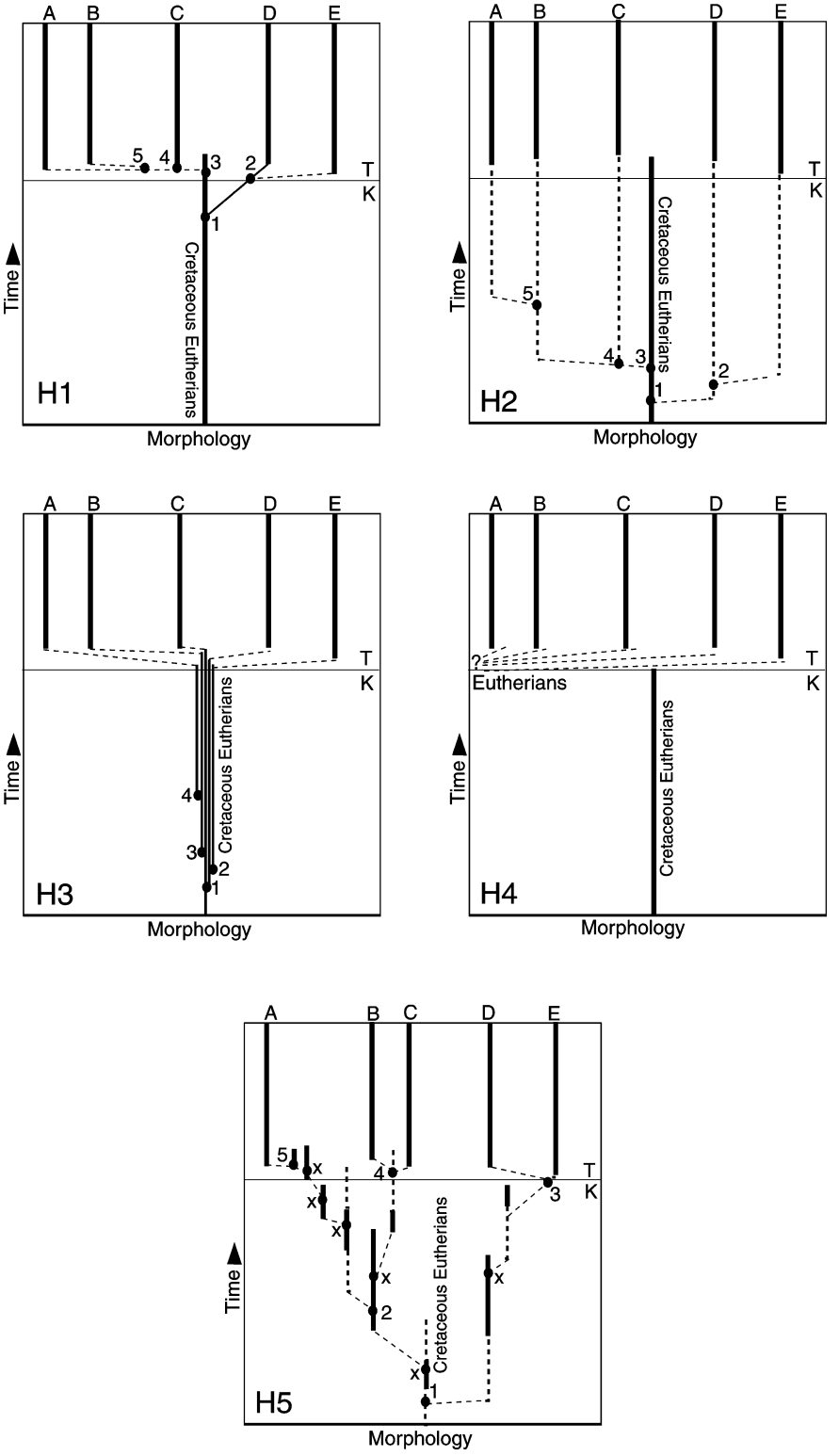
Fig. 7.3. Diagrams illustrate hypotheses (H) that have been proposed to explain discrepancies of divergence times of modern placental mammals between molecular dates and fossil records. Solid bars = presence of fossil records; dashed-line = missing durations in fossil record; A–E = modern placental orders; 1–5 = cladogeneses; X = stem taxa of crown groups in H5. **H1** represents conventional view that there is a post K-T boundary radiation of modern placental orders, although some higher taxa such as ungulates may have evolved in the Cretaceous. **H2** illustrates deep splits of placental orders in the Cretaceous; absence of these lineages in fossil records is attributed to lower preservation rates. **H3** shows that Cretaceous lineages of modern placental orders are morphologically not distinguishable until after the K-T boundary. **H4** suggests dispersal of modern placental orders originated in the Cretaceous from an unknown source area. **H5** suggests that stem taxa to modern placental orders were present in the Cretaceous; nodes 1–2 represent superordinal cladogeneses and nodes 3–5 are ordinal. See text for discussion.


A
B
C
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T
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Time
Morphology
Cretaceous Eutherians
H1
H2
H3
H4
H5
Eutherians
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The conventional view of the eutherian radiation (H1 in fig. 7.3; ''Explosive Model'' of Archibald and Deutschman, 2001) emphasizes a post K-T boundary radiation of modern eutherian orders, presumably having taken place in the empty niches left by the extinction of dinosaurs (Gingerich, 1977; Novacek, 1992). The geological distributions of the monophyletic Glires, including basal gliroid taxa such as eurymylids, mimotonids, and alagomyids, are found in the Paleogene (figs. 7.1, 7.2) and therefore support the conventional view. Moreover, the earliest occurrences of immediate outgroups to Glires, such as anagalids, pseudictopids, macroscelideans, and primates, are present only in the early Paleogene. These would indicate that the cladogenesis of rodents and lagomorphs took place no earlier than the K-T boundary and contradict the much earlier divergence times for rodents and lagomorphs estimated from some molecular studies. If the fossil record roughly reflects cladogenesis of gliroid mammals, then one has to question the accuracy of the molecular clock. Problems concerning the vagaries of the molecular clock have been reviewed elsewhere (e.g., Ayala, 1997; Bromham et al., 1999; Rodríguez-Trelles et al., 2001) and are beyond the scope of this study.

Hypothesis 2 (H2 in fig. 7.3., which is similar to the ''Short Fuse Model'' of Archibald and Deutschman, 2001) suggests that the split of modern placental orders occurred early in the Cretaceous and may be concurrent with the breakup of continents (Hedges et al., 1996), but that fossils of presumably Cretaceous placental mammals did not show up in the record because these early forms were small and fragile, so that their preservation as fossils was less likely (Cooper and Fortey, 1998; Foote et al., 1999a). As Foote et al. (1999a, 1999b) demonstrated, however, assuming even very low preservation rates for Cretaceous mammals, the gap between the earliest fossil record and the divergence time based on molecular data is unacceptably large. Several major groups of mammals, including ''triconodonts'', symmetrodonts, multituberculates, therians, and eutherians (Lillegraven et al., 1979; McKenna and Bell, 1997; Novacek et al., 1998) flourished in the Cretaceous. It seems unreasonable that these taxa, most of which were small, would be preserved as fossils while placental taxa were not. Although Cenozoic mammals are usually larger than Cretaceous mammals, and preservation rates of Cenozoic fossils are often greater than those of Cretaceous fossils (Cooper and Fortey, 1998; Foote et al., 1999a, 1999b), these generalizations do not seem applicable to the Glires because early gliroid mammals are generally small and many are smaller than most Cretaceous mammals.

It should also be noted that the molecular clock hypothesis extends not only the divergence times of the sciurognath and hystricognath rodents into the Cretaceous, but also those of lower-level rodent groups into much earlier periods of the Tertiary, such as the mouse-rat split at about 41 Ma. Fossil records show that *Mus* and *Rattus* diverged at about 8 to 14 Ma (Jacobs and Pilbeam, 1980; Jaeger et al., 1986), with *Mus* not appearing until 5.7 Ma (Jacobs and Downs, 1994). The argument of poor preservation for Cretaceous mammals does not seem applicable for these Tertiary rodents.

Hypothesis 3 (H3 in fig. 7.3; phylogenetic fuse of Cooper and Fortey, 1998) implies that cladogeneses of modern placental orders took place about 110 Ma, but the lineages remained morphologically cryptic until they evolved diagnostic characters after the K-T boundary (Cooper and Fortey, 1998; Foote et al., 1999a). Hypotheses 1 and 3 both imply rapid morphological modifications during a short period of time. The difference between them is that in hypothesis 1 the morphological changes are coeval with cladogeneses, whereas in hypothesis 3 cladogeneses occur throughout the Cretaceous and are decoupled from morphological changes. The relationship of molecular and morphological evolution is not fully understood, but some studies suggest that they are generally correlated, not decoupled (Omland, 1997). Moreover, lack of diagnostic characters is a poor argument for the absence of a subgroup of rodents, such as *Mus*, in early Tertiary records. This is particularly so when the cladogenesis of *Mus* and its sister taxon was recognized in fossil records (Jacobs and Downs, 1994).

Hypothesis 4 (H4 in fig. 7.3), or the ''Garden of Eden'' hypothesis (Foote et al.,

1999a), suggests that deep splitting of modern placental mammals took place in areas where fossil records of Cretaceous eutherians are unknown or sediments of relevant ages are not preserved (Foote et al., 1999a). Potential areas of this kind include Africa, Australia, and Antarctica. This hypothesis further assumes that in the early Tertiary, about 65 to 60 Ma, early members of placental orders dispersed to northern continents and were recognized as the post–K-T radiation (Bromham et al., 1999). This hypothesis implies that known Cretaceous eutherians from northern continents are unrelated to modern orders, which contrasts with studies that suggest that higher-level taxa such as ungulates may have evolved from these northern eutherians (Archibald, 1996). Nonetheless, the ''Garden of Eden'' hypothesis can be tested with fossil finds from southern continents (Foote et al., 1999a). *Ausktribosphenos nyktos* from the Early Cretaceous in Australia (Rich et al., 1997, 1999) was considered to be a possible erinaceid and thus evidence corroborating the ''Garden of Eden'' hypothesis (Rich et al., 2001). However, the status of *A. nyktos* as a genuine erinaceid remains controversial (Kielan-Jaworowska et al., 1998; Musser and Archer, 1998; Archer et al., 1999; Rich et al., 2001). Additional material from the cranial and postcranial skeleton of *A. nyktos* would help clarify its taxonomic identification.

The phylogeny and distribution of basal gliroid mammals show that their early divergence area, if not their center of origin, was in Asia. All basal gliroid taxa, such as *Mimotona*, *Mimolagus*, *Gomphos*, *Rhombomylus*, *Matutinia*, *Eurymylus*, *Heomys*, *Tribosphenomys*, and *Alagomys* are known only from Asia, except for one species of *Alagomys* that was found in North America (Dawson and Beard, 1996). Assuming gliroid mammals originated in the southern continents during the Cretaceous, the large bodies of water present between Asia and the southern continents (Smith et al., 1994) were obvious geographic barriers for the migration of gliroid mammals in the Late Cretaceous. Finds of basal gliroid mammals in areas that are possible dispersal routes may also test the ''Garden of Eden'' hypothesis. However, the absence of basal Glires, such as mimotonids and eurymylids, in Tertiary sediments outside Central Asia challenges the theory of the origin of the Glires in southern continents. To reiterate, the ''Garden of Eden'' hypothesis does not explain the absence of subgroups of rodents, such as *Mus* and *Rattus*, in the early Tertiary as predicted by the molecular clock hypothesis. Given that rodents and lagomorphs have a relatively dense fossil record since the early Eocene, hidden origin centers for various subgroups of rodents are difficult to defend.

Hypothesis 5 (H5 in fig. 7.3; the ''Long Fuse Model'' of Archibald and Deutschman [2001]) predicts a deep branching of superordinal clades of eutherian mammals. It argues that although members of modern placental orders are not present in the Cretaceous, stem taxa to the modern placental orders can be found in the Cretaceous. This hypothesis may be supported by the relationship of zhelestids and ungulates (Archibald, 1996; Archibald et al., 2001), but that relationship has been put in doubt by other studies (Novacek et al., 1998, 2000). More recently, Archibald et al. (2001: 64) presented another case study of the Long Fuse Model that included zhelestids, ungulates, zalambdalestids, and Glires. These authors concluded that the results of their analysis ''support a superordinal clade including zalambdalestids and Glires'' and that the presence of zalambdalestids in the 85–90 Ma faunas at Dzharakuduk ''argues that the superordinal clade including Glires had separated from other superordinal placental clades by this time'' (Archibald et al., 2001: 64). Archibald et al. (2001) considered that the result of their study was concordant with molecular-based estimates for the superordinal diversification of placentals, and thus called zalambdalestids Late Cretaceous relatives of rabbits and rodents, a scenario once favored by McKenna (1982, 1994).

However, although Archibald et al. (2001) considered zalambdalestids to be more closely related to Glires than other Cretaceous eutherians selected for their analysis, they did not sufficiently test whether Glires, represented by *Tribosphenomys* and *Mimotona* in their analysis, is the Tertiary group that is most closely related to zalambdalestids. As mentioned above, rodents and lagomorphs

have been frequently related to primates, leptictids, tree shrews, pseudictopids, anagalids, macroscelideans, zalambdalestids, eurymylids, and mimotonids. All these groups, except zalambdalestids, are Tertiary mammals and an appropriate phylogenetic analysis to test Glires relationships should include them. Only two Tertiary ungulates, *Protungulatum* and *Oxyprimus*, in addition to *Tribosphenomys* and *Mimotona*, were included in Archibald et al.'s (2001) study. Because these ungulates are distantly related to the Glires, the zalambdalestid-Glires link (Archibald et al., 2001) is insufficiently supported. When relevant taxa are included in the analyses (Meng and Wyss, 2001; Meng et al., 2003; this study), zalambdalestids are not the closest group to Glires.

Nonetheless, because zalambdalestids were nested within crown placentals in this and previous studies (Meng and Wyss, 2001), it is not impossible to think that at a certain level of mammalian phylogeny, such as the clade of ''Euarchontoglires'' of Murphy et al. (2001b), placentals may have occurred within the Cretaceous. Murphy et al. (2001b) actually suggested that zalambdalestids may be early representatives of ''Euarchontoglires'', which is congruent with McKenna's (1982: 215) earlier suggestion that ''If one accepts a broad association with lagomorphs of rodents (including eurymylids), living elephant shrews, anagalids, pseudictopids, and zalambdalestids, then the clade that includes them all dates from some much earlier time in the Cretaceous.'' The scenario of a Cretaceous split of higher-level placental clades, however, needs further testing in the broader scope of mammalian phylogeny.

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The first time I met Malcolm was at his summer camp at Lance Creek, Wyoming, in July of 1985, after I was accepted as a graduate student by Columbia University. Malcolm promised me my Ph.D. when I arrived at his camp because I had been able to find him using a fuzzy copy of a topographic map on which he had marked his camp and a contact telephone number that had been disconnected when I arrived in Cheyenne after a long flight from Beijing and a long journey on a Greyhound bus from San Francisco. In New York, Malcolm insisted on my taking calculus so that I could understand that the earth is but a rounded cube. He sent me without mercy to the fossil mammal collection spread over seven floors of the Frick Wing to dig out my own dissertation project from the millions of specimens, a mission almost impossible for one who knew nearly nothing of vertebrate paleontology. When Malcolm said to me ''you made it'' at my defense meeting five years later, I realized that I had learned more than just paleontology from him. It is my fortune to have been his student and my honor to be his colleague.

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APPENDIX 7.1

DATA MATRIX

Taxon	1111111111222222222233333333334444444444555555555566666666667777777777888888888899 12345678901234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901
Asioryctes	0?000000000?000000000000000000000000000000000000000000000000000000000000000000000000000000000000000
Kennalestes	0?100000000?000000000000000000000000000000000000000000000000000000000000000000000000000?????000000000?
Zalambdalestes	0?110100000?000100110000000010000000000000000000000001000100000000010000000001100?0010000?0
Barunlestes	??110100000?00??011101100000100000000000000000000000100010000?00?001000000000?????001000000
Tupaia	0?110000000000?111111000000100000000000000010021000000000000000000000100002020100000110000
Sinolagomys	12111?1?11111?022?2?111020233020111?1?2100202121112022132111323111021311?1?0??????40?0?????
Desmatolagus	12111?1?11111?022?2?111020233020111100221002021211120221321113231110213 11?1?0??????40???????
Palaeolagus	12111?1?11111?022?2?111020233020212100221002021211120221321113231110213111110410010403?01010
Mimotona	12111?1?2111010 12?2?111010112001021000110020112111200211211 1??30100?1??1?1?04?????21???????
Mimolagus	12111?1??101??012?2??1?01??1???1011000?1002?1121?????21?211???31?00????????0?0111A2????????
Gomphos	11111???2??101??2?2?111??01?2201011000110020112111200211???????????1??0?????????20???????
Rhombomylus	1C111?1?21011?1?2?2?1111?0112010011000110020112111200211112222300001111101104010013020111 10
Eurymylus	11111?1?21011?1?2?2?1111?0112010011000110020112111200211110 02??0?0??1?1001????????D0???????
Heomys	11111?1?21011?1?2?2?1111?0112010011000110020111111200211110 0??30000?1?1001????????20???????
Tribosphenomys	10111?1?21011?1?2?2?1111?1?220B000000011000110111211112121 10?????????1112?1???0100?11??????0
Alagomys	11111???2??11?????2?1111?1?2210000100011000110111221 1?12???????????11112?????????01???????
Cocomys	11111?1?21011?1?2?2?1111?1?2200000100112100010111221121312002230000 11?1101004?????104001 01?
Paramys	11111?1?21011?1?2?2?1111?1?2212000100112100010111221121312002230000111120100401001114001010
Reithroparamys	11111?1?21011?1?2?2?1111?1?2212000100112100010111221121312002230000111120100401001114001010
Anagalopsis	????????????????01010000001032000110001110100220 11A000010000000000000000000104?1?0?01?0000??
Anagale	0?110000000000000101000000103200011000111010022011100001000000000000000000104 0??0?00?0000??
Leptictis	0?11001?000000000111000000001120000000100000000000000000000000002A0000000010100A101100001
Elephantulus	0?110000000000001111000000432202A11100300100104110000 0?0000111000210200000051000050120000 1
Rhynchocyon	0?11001?0??000000110000000432202A11100300100104110000 0?0000111000210200000051000050120000 0
Pseudictops	0?110000000000000101000 0?0?032100110001110100121010000010000 0?0000010??00000?0001000??????0
Plesiadapis	0?11010100001?1?B12111A0100000100000001100000003100 00CA1000000200011200000 00D0100011?000000
Notharctus	0?11000000001?1?0101000010001010000000110102000310000001000000000011201000213010001A?000000
Adapis	0?11000000001?1?0101000010001020100000110102000310000001000000000011201001213?000?1A?000000
Matutinia	1?111?1?21011?1?2?2?1111?0112010011000110020112111200211112222300001111101104 0???1302011110
Sinomylus	10?1??1??1?1??1?2????1?01??12?00011?00?10020112 1?????2??11????30000??????1?0??????10?0?????

A = 0, 1; B = 0, 2; C = 1, 2; D = 2, 3.

APPENDIX 7.1 (*continued*)

Description of Data Matrix

The data matrix is derived from Meng and Wyss (2001). A total of 30 terminal taxa and 91 characters were selected for analyses. The first 28 taxa in the data matrix were from the primary analysis of Meng and Wyss (2001). The first 82 characters were adopted from Meng and Wyss (2001) in the same order as listed therein. Two modifications were made to scores of *Rhombomylus*. Character 60 (zygomatic fossa for masseter lateralis) was originally coded as ''0'' and character 76 (orbit orientation) ''?'' for *Rhombomylus*; these were changed to ''2'' and ''0'', respectively. The first change is based on the observation that the fossa on the zygomatic plate formed by the maxilla and jugal in *Rhombomylus* and *Matutinia* is unique. The second change represents an error in original data matrix. Discussions on these characters were presented in Meng and Wyss (2001). Characters 83–91 are additional to those used in Meng and Wyss (2001) and are listed below.

83. Upper molar hypocone: (0) weak or absent, (1) small with slim postcingulum, (2) large with strong posteroloph, (3) shelflike, (4) posterior and short loph, or (5) posterior and long lobe of the molar.
84. Mental foramina: (0) two or more, or (1) single (Dashzeveg et al., 1998).
85. Postglenoid foramen: (0) medial to glenoid process, (1) on ventral side of basicranium and posterior to postglenoid process, (2) in glenoid fossa within the squamosal, (3) on lateral side of skull and between squamosal and ectotympanic or petrosal, or (4) on lateral side of skull within squamosal (Rougier et al., 1998; Landry, 1999).
86. Posterior maxillary notch: (0) weak, (1) closed to form a foramen, or (2) forming a deep socket (Wahlert, 1974).
87. Dorsal process of jugal: (0) absent, or (1) present.
88. Glenoid fossa: (0) nearby the auditory region, or (1) shifted anterodorsally.
89. Mastoid of petrosal: (0) small, or (1) inflated.
90. Squamosal contribution to the epitympanic recess: (0) present, or (1) absent.
91. Distal ulna: (0) complete, or (1) reduced.

APPENDIX 7.2

Apomorphy List

node 55 to *Asioryctes*. 3 (character): 1 (consistency index), 1 to 0 (change of character state).
node 55 to node 54. 4: 1, 0 to 1; 18: 0.333, 0 to 1; 19: 0.4, 0 to 1; 20: 1, 0 to 1; 29: 0.6, 0 to 1; 79: 0.2, 0 to 1; 85: 1, 0 to 1.
node 54 to node 53. 68: 0.667, 0 to 1.
node 53 to node 31. 6: 0.5, 0 to 1; 16: 0.667, 0 to 1; 54: 0.667, 0 to 1; 58: 0.667, 0 to 1; 78: 0.333, 0 to 1.
node 31 to *Zalambdalestes*. 18: 0.333, 1 to 0.
node 31 to *Barunlestes*. 22: 0.25, 0 to 1; 23: 0.5, 0 to 1.
node 53 to node 52. 31: 0.25, 0 to 2; 39: 0.667, 0 to 1; 67: 0.667, 0 to 2; 77: 1, 0 to 1; 83: 0.556, 0 to 1.
node 52 to node 51. 19: 1, 0.4, 1 to 0; 40: 1, 1, 0 to 1; 48: 1, 0.8, 0 to 1; 49: 1, 0.333, 0 to 1; 56: 1, 0.75, 0 to 1; 77: 1, 1, 1 to 3.
node 51 to node 48. 29: 0.6, 1 to 3; 30: 0.333, 0 to 2; 34: 0.5, 0 to 1; 35: 0.5, 0 to 1; 43: 0.667, 0 to 1; 46: 0.667, 0 to 1; 50: 1, 0 to 1; 77: 1, 3 to 4; 83: 0.556, 1 to 0.
node 48 to node 46. 27: 1, 0 to 1; 31: 0.25, 2 to 0; 47: 0.667, 0 to 2; 67: 0.667, 2 to 0; 75: 0.4, 0 to 1; 85: 1, 1 to 2; 90: 1, 0 to 1.
node 46 to node 43. 1: 1, 0 to 1; 5: 1, 0 to 1; 7: 0.333, 0 to 1; 9: 1, 0 to 2; 10: 1, 0 to 1; 12: 1, 0 to 1; 14: 1, 0 to 1; 16: 0.667, 0 to 1; 17: 0.667, 0 to 2; 19: 0.4, 0 to 2; 21: 0.333, 0 to 1; 22: 0.25, 0 to 1; 23: 0.5, 0 to 1; 25: 0.667, 0 to 1; 28: 1, 0 to 1; 29: 0.6, 3 to 2; 43: 0.667, 1 to 2; 45: 0.667, 0 to 1; 51: 0.667, 0 to 2; 54: 0.667, 0 to 2; 55: 1, 0 to 1; 57: 1, 0 to 1; 58: 0.667, 0 to 1; 61: 1, 0 to 2; 62: 1, 0 to 2; 63: 1, 0 to 3; 69: 1, 0 to 1; 70: 0.75, 0 to 1; 71: 0.5, 0 to 1; 74: 0.5, 0 to 1; 83: 0.556, 0 to 2; 88: 1, 0 to 1.
node 43 to node 35. 11: 0.5, 0 to 1; 32: 1, 0 to 1; 57: 1, 1 to 2; 59: 1, 0 to 1; 60: 1, 0 to 1; 61: 1, 2 to 3; 64: 0.5, 0 to 1; 65: 1, 0 to 1; 68: 0.667, 1 to 2; 70: 0.75, 1 to 3; 73: 1, 0 to 1; 81: 0.5, 0 to 1; 85: 1, 2 to 3.
node 35 to node 34. 2: 0.667, 1 to 2; 72: 0.5, 0 to 1.
node 34 to node 33. 9: 1, 2 to 1; 13: 0.333, 0 to 1; 16: 0.667, 1 to 2; 25: 0.667, 1 to 2; 27: 1, 1 to 2; 28: 1, 1 to 3; 29: 0.6, 2 to 3; 33: 0.667, 0 to 1; 38: 1, 0 to 2; 39: 0.667, 1 to 2; 45: 0.667, 1 to 2; 53: 1, 0 to 2; 56: 0.75, 1 to 3; 66: 1, 0 to 1; 78: 0.333, 0 to 1; 79: 0.2, 1 to 0; 83: 0.556, 2 to 4.
node 33 to node 32. 32: 1, 1 to 2.
node 32 to *Sinolagomys*. 37: 0.5, 0 to 1.
node 32 to *Palaeolagus*. 34: 0.5, 1 to 2.

node 34 to *Mimotona*. 30: 0.333, 2 to 0; 34: 0.5, 1 to 2; 64: 0.5, 1 to 0; 84: 0.2, 0 to 1.
node 34 to *Mimolagus*. 11: 0.5, 1 to 0; 80: 1, 0 to 1.
node 43 to node 42. 13: 0.333, 0 to 1; 15: 0.333, 0 to 1; 30: 0.333, 2 to 0; 82: 1, 0 to 1.
node 42 to node 41. 24: 1, 0 to 1; 31: 0.25, 0 to 1.
node 41 to node 36. 59: 1, 0 to 2; 60: 1, 0 to 2; 72: 0.5, 0 to 1; 83: 0.556, 2 to 3; 87: 1, 0 to 1; 89: 1, 0 to 1.
node 41 to *Heomys*. 47: 0.667, 2 to 1.
node 41 to node 40. 26: 1, 0 to 1; 28: 1, 1 to 2; 31: 0.25, 1 to 0; 34: 0.5, 1 to 0; 43: 0.667, 2 to 0; 46: 0.667, 1 to 0; 47: 0.667, 2 to 1; 50: 1, 1 to 2; 52: 1, 0 to 1; 53: 1, 0 to 1; 56: 0.75, 1 to 2; 72: 0.5, 0 to 2; 75: 0.4, 1 to 0; 83: 0.556, 2 to 1; 84: 0.2, 0 to 1; 85: 1, 2 to 4.
node 40 to node 37. 44: 1, 0 to 1.
node 37 to *Tribosphenomys*. 2: 0.667, 1 to 0; 35: 0.5, 1 to 0; 51: 0.667, 2 to 1.
node 37 to *Alagomys*. 30: 0.333, 0 to 1; 83: 0.556, 1 to 0.
node 40 to node 39. 38: 1, 0 to 1; 40: 1, 1 to 2; 41: 0.5, 0 to 1; 56: 0.75, 2 to 3; 58: 0.667, 1 to 2.
node 39 to *Cocomys*. 72: 0.5, 2 to 1; 84: 0.2, 1 to 0.
node 39 to node 38. 30: 0.333, 0 to 1; 31: 0.25, 0 to 2.
node 42 to *Sinomylus*. 2: 0.667, 1 to 0; 83: 0.556, 2 to 1.
node 46 to node 45. 41: 0.5, 0 to 1.
node 45 to node 44. 46: 0.667, 1 to 2; 48: 0.8, 1 to 0; 51: 0.667, 0 to 1; 68: 0.667, 1 to 0.
node 44 to *Anagalopsis*. 84: 0.2, 0 to 1.
node 44 to *Anagale*. 51: 0.667, 0 to 1.
node 45 to *Pseudictops*. 31: 0.25, 0 to 1; 49: 0.333, 1 to 0; 75: 0.4, 1 to 0; 79: 0.2, 1 to 0; 81: 0.5, 0 to 1.
node 48 to node 47. 19: 0.4, 0 to 1; 28: 1, 0 to 4; 33: 0.667, 0 to 2; 36: 1, 0 to 1; 37: 0.5, 0 to 1; 39: 0.667, 1 to 0; 40: 1, 1 to 3; 48: 0.8, 1 to 4; 61: 1, 0 to 1; 62: 1, 0 to 1; 63: 1, 0 to 1; 70: 0.75, 0 to 2; 77: 1, 4 to 5; 78: 0.333, 0 to 1; 79: 0.2, 1 to 0; 83: 0.556, 0 to 5; 86: 0.667, 0 to 2.
node 47 to *Elephantulus*. 17: 0.667, 0 to 1; 91: 0.5, 0 to 1.
node 47 to *Rhynchocyon*. 7: 0.333, 0 to 1; 18: 0.333, 1 to 0.
node 51 to node 50. 13: 0.333, 0 to 1; 15: 0.333, 0 to 1; 25: 0.667, 0 to 1; 31: 0.25, 2 to 1; 48: 0.8, 1 to 3; 67: 0.667, 2 to 1; 69: 1, 0 to 2; 84: 0.2, 0 to 1.
node 50 to *Plesiadapis*. 6: 0.5, 0 to 1; 8: 1, 0 to 1; 19: 0.4, 0 to 2; 21: 0.333, 0 to 1; 22: 0.25, 0 to 1; 29: 0.6, 1 to 0; 54: 0.667, 0 to{12}; 63: 1, 0 to 2.
node 50 to node 49. 42: 1, 0 to 1; 44: 1, 0 to 2; 71: 0.5, 0 to 1; 75: 0.4, 0 to 2; 76: 1, 0 to 1.
node 49 to *Adapis*. 31: 0.25, 1 to 2; 33: 0.667, 0 to 1; 74: 0.5, 0 to 1; 79: 0.2, 1 to 0.
node 52 to *Leptictis*. 7: 0.333, 0 to 1; 30: 0.333, 0 to 1; 86: 0.667, 0 to 1; 91: 0.5, 0 to 1.
node 54 to *Tupaia*. 15: 0.333, 0 to 1; 17: 0.667, 0 to 1; 21: 0.333, 0 to 1; 22: 0.25, 0 to 1; 45: 0.667, 0 to 1; 48: 0.8, 0 to 2; 49: 0.333, 0 to 1; 70: 0.75, 0 to 1; 75: 0.4, 0 to 2; 77: 1, 0 to 2; 86: 0.667, 0 to 1.