

The Evolution and Paleobiogeography of Flying Squirrels (Sciuridae, Pteromyini) in Response to Global Environmental Change

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Abstract Flying squirrels are strictly arboreal squirrels adopting a special gliding form of locomotion. This group of animals has a long history that has mirrored the vicissitude of forests. The discrepancy in the distribution between fossils and extant species indicates a mysterious evolution history requiring further exploration. This study compiles the worldwide fossils of Pteromyini to the species level in order to reproduce the spatiotemporal distribution pattern of flying squirrels and deduce the ancestral distribution according to dispersal-vicariance analysis of a phylogeny of the extant species. In addition, we reconstruct the paleoenvironmental background and find that flying squirrels probably originated in the Oligocene–Miocene transition from Europe and immediately dispersed to Asia and North America. Influenced by glaciation, CO₂ reduction, geologic movements and the Paratethys retreat, the Northern Hemisphere underwent climate deterioration and grassland expansion during the late Miocene, and thus the diversity of Pteromyini dramatically decreased. The uplift of the Tibet Plateau in addition to the strengthened Asian

monsoons intensified the aridity in central Asia, but brought sufficient water to the densely forested regions of South and Southeast Asia. These forests are likely both refugia and diversification center for flying squirrels during glacial periods in the Quaternary. The subsequent connection and separation events among these heterogeneous habitats has probably been a driving force in the speciation of flying squirrels. Based on this work, we predict a bleak future for the flying squirrels, one which is closely associated with the fate of forests in Asia.

Keywords Sciuridae · Pteromyini · Evolution · Paleobiogeography · Dispersal-vicariance analysis

Introduction

Flying squirrels (Sciuridae: Pteromyini) are an ancient rodent group adopting a peculiar gliding locomotion. There are about 44 extant species belonging to 15 genera. They mainly distribute in South and Southeast Asia with one genus (including two species) endemic to North America, and one widely distributed species inhabiting the northern part of Euroasia, ranging from North Finland to Korea and Japan (Thorington and Hoffmann 2005; Fig. 1a). Because of the strictly arboreal habit and high sensitivity to climate changes, flying squirrels are thought to be good indicators of the vicissitude of forests and also ideal study objects for investigating habitat changes and species diversification in the context of global environmental change (Arbogast 2007). Although the flying species account for only 15 % of the total extant Sciurids, the available fossil records suggest that millions of years ago in the Eurasian continent, they were more diverse than their non-gliding relatives, and their distribution area was greatly divergent compared with

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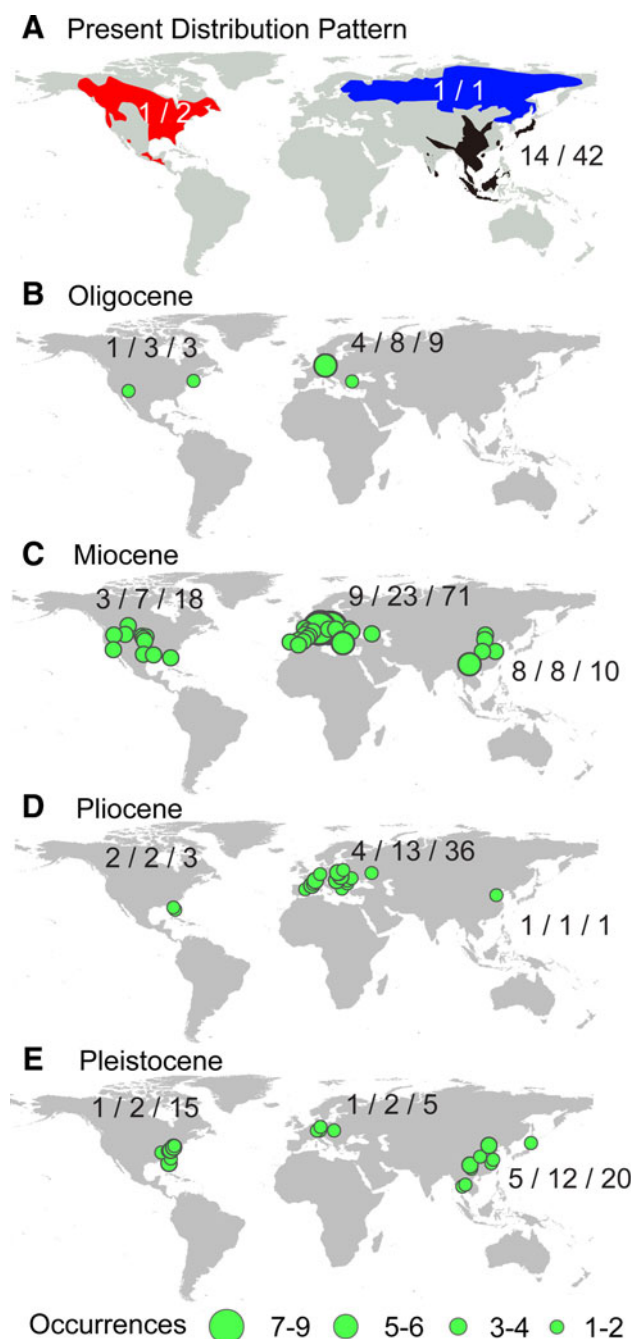


Fig. 1 The extant and fossil species distribution patterns of Pteromyini. **a** The present distribution; **b–e**, the fossil allocations from the late Oligocene to the Pleistocene. The amounts of genera/species (/occurrences) of each continent from different epochs are marked beside. The present distribution refers to the IUCN Red List (IUCN 2011) while the fossil allocations are generated from program ArcView GIS 3.2a (Environmental Systems Research Institute) on the basis of records collected here. The Antarctic continent is not shown

their present habitats (Korth 1994; McKenna and Bell 1997). These transformations indicate a complex evolution history of these animals under the combined influences of paleogeologic events and paleoclimatic changes.

Research on the evolution of flying squirrels is not only useful for understanding their history and providing information which may help in predicting their future, but also could provide valuable evidence for the impact of environment change on the evolution of other terrestrial organisms. However, the origin of flying squirrels has not been fully investigated. The only consensus on the origin of flying squirrels is that they are a monophyletic group evolved from arboreal squirrels, a view supported by studies of anatomy, molecular biology and morphology (Thorington and Heaney 1981; Thorington 1984; Thorington et al. 1998; Mercer and Roth 2003; Stepan et al. 2004). However, the time of origin and ancestral distribution of these animals, and the historical events that might have impacted their evolutionary dynamics, are less discussed. The refugia theory proposed by Haffer (1969) has been extensively used in interpreting the history of various organisms, especially the terrestrial rodents (Fedorov et al. 1999; Jaarola and Searle 2002; Haynes et al. 2003). But as for the arboreal populations or the flying squirrels, very few paleobiological studies [e.g. Russian flying squirrel *Pteromys volans* (Oshida et al. 2005) and North America flying squirrel *Glaucomys* (Arbogast 2007)] have been carried out.

Previous work on their fossils has focused mostly on the abundance and morphological diversification of different species (Mein 1970; Korth 1994; de Bruijn 1999), although a comprehensive review of these fossil records is still lacking. Through phylogenetic and molecular-clock analyses of extant species, Mercer and Roth (2003) established the divergence time for the major lineages of Sciuridae and revealed that Pteromyini probably branched out at around 23–18 million years ago (Ma). Yu et al. (2006) suggested that the major divergence of flying squirrels might have occurred on the northern part of Eurasia, but this hypothesis was proposed without substantial evidence nor a detailed exploration. The corroboration of fossil records and molecular data could provide more compelling evidence in tracing the history of different biological groups (Huchon et al. 2007; Kitazoe et al. 2007; Meredith et al. 2011), which is the motivation for our study on the evolution of Pteromyini based on both fossils and extant species.

Historical biogeographic reconstruction based on phylogenies is now an established approach to illuminate the history of organisms in space and time (Ali et al. 2012), with the dispersal–vicariance analysis (DIVA; Ronquist 1997) being one of the most widely used methods for inferring biogeographic histories (Yu et al. 2010). The aim of this study is to propose an evolutionary scenario for the evolution of flying squirrels in the paleoenvironmental background by compiling the worldwide fossils of the

Pteromyini to the species level, and reconstructing the spatiotemporal distribution pattern of these species.

Materials and Methods

Fossil Records Arrangement

The information from fossil records (including name, locality, paleobiological epoch) were mainly cited from original literatures and downloaded from the Paleobiology Database (<http://www.paleodb.org/cgi-bin/bridge.pl>). Further, to ensure the completeness of the fossil information, we also consulted the Zoological Record (from 1864 to 2011) provided by the Thomson Reuters' Web of Knowledge (<http://apps.webofknowledge.com/>).

Ancestral Distribution Inference

Dispersal-vicariance analysis is a parsimony “event-based” biogeographical method that optimizes ancestral areas on the internal nodes of a phylogeny by minimizing the number of duplication and extinction events required to explain the terminal distributions (Ronquist 1997). It has been extensively used in biogeographic inferences in the

past decade, although suffering known sensitivities, e.g. the inability to account for uncertainty in a phylogeny and uncertainty in ancestral area optimization. A new method, Bayesian-DIVA, was proposed more recently to overcome such limitations (Nylander et al. 2008). This Bayesian binary Markov Chain Monte Carlo (BB-MCMC) approach is implemented in the program RASP (reconstruct ancestral states in phylogenies; Yu et al. 2011).

DIVA reconstructs the ancestral distribution on a given phylogeny. In an attempt to obtain the widely accepted phylogenetic result of Mercer and Roth (2003), we repeated their analysis using the Bayesian method. One nuclear (interphotoreceptor retinoid-binding protein, IRBP) and two mitochondrial genes (12S and 16S ribosomal DNA) submitted by Mercer and Roth (2003) were downloaded from GenBank. Two additional species, *Petaurista petaurista* and *P. leucogenys*, each represented by one of the three genes (12S) were also added here. Taxon information and the accession number of each gene were listed in Table 1. We constructed the phylogenetic tree in the program MrBayes 3.1.2 (Huelsenbeck et al. 2001) and determined node support by the posterior probability. We set the main parameters as follows: two chains, both with two million generations, trees sampled every 1,000 generations, and the first 800 trees were discarded as burnin.

Table 1 Distribution and GenBank accession numbers of the representative species

Representative species	Distribution	Accession numbers in GenBank		
		IRBP	12S	16S
<i>Aeretes melanopterus</i> (Milne-Edwards, 1867)	ac	AY227593.1	AY227535.1	AY227481.1
<i>Aeromys tephromelas</i> (Günther, 1873)	a	AY227594.1	AY227536.1	AY227482.1
<i>Belomys pearsonii</i> (Gray, 1842)	ab	AY227595.1	AY227537.1	AY227483.1
<i>Eoglaucomyx fimbriatus</i> (Gray, 1837)	b	AY227597.1	AY227562.1	AY227485.1
<i>Eupetaurus ciereus</i> Thomas, 1888	b	AY227596.1	AY227538.1	AY227484.1
<i>Glaucomys volans</i> (Linnaeus, 1758)	d	AY227598.1	AY227559.1	AY227486.1
<i>Hylomys phayrei</i> (Blyth, 1859)	a	AY227599.1	AY227539.1	AY227487.1
<i>Iomys horsfieldii</i> (Waterhouse, 1838)	a	AY227600.1	AY227540.1	AY227488.1
<i>Petaurillus kinlochii</i> (Robinson & Kloss, 1911)	a	AY227602.1	AY227542.1	AY227490.1
<i>Petaurista alborufus</i> (Milne-Edwards, 1870)	a	AY227601.1	AY227541.1	AY227489.1
<i>Petaurista leucogenys</i> (Timminck, 1827)	c	Unavailable	D50280.1	Unavailable
<i>Petaurista petaurista</i> (Pallas, 1766)	ab	Unavailable	D50281.1	Unavailable
<i>Petinomys setosus</i> (Temminck, 1844)	a	AY227604.1	AY227544.1	AY227492.1
<i>Pteromys volans</i> (Linnaeus, 1758)	c	AY227605.1	AY227545.1	AY227493.1
<i>Pteromyscus pulverulentus</i> (Günther, 1873)	a	AY227603.1	AY227543.1	AY227491.1
<i>Troglodytes xanthipes</i> (Milne-Edwards, 1867)	ac	AY227606.1	AY227546.1	AY227494.1
Outgroups				
<i>Aplodontia rufa</i> (Rafinesque, 1817)		AF297284.1	AY227508.1	AY227451.1
<i>Graphiurus murinus</i> (Desmarest, 1822)		AB253960.1	AJ225118.1	AY227452.1
<i>Tamias sibiricus</i> (Laxmann, 1769)		AB253982.1	AY227531.1	AY227475.1
<i>Tamiops swinhoei</i> (Milne-Edwards, 1874)		AY227578.1	AY227522.1	AY227466.1

In the BB-MCMC procedure, the frequencies of an ancestral range at a node in the ancestral reconstructions were averaged over all trees obtained from the MCMC output. The MCMC chains were run with the Estimated (F81) state frequencies model. Among-site rate variation was set to Gamma (+G), and no outgroup defined (root distribution was set to NULL). Other parameters were all set as default. With regard to the regional divisions (realms) of fauna, the present distribution and diversity of flying squirrels and the presence of one or more endemic species, we predefined four areas for the extant genera and species (Nowak 1999; Thorington and Hoffmann 2005; Fig. 2c): (1) Southeast Asia (east Oriental realm, species richness hotspot); (2) South Asia (west Oriental realm,

second diverse region); (3) North Asia and Europe (Palearctic realm, excluding North Africa); (4) North America (Nearctic realm). These areas are listed in Table 1.

Results

Fossil Records and Extant Distribution

We report a total of 23 genera and nearly 70 fossil species in Pteromyini and list their names, occurrence time, and localities in the “Appendix”. The distribution patterns are displayed in Fig. 1b–e, showing the fossil succession on each continent. The time span of each fossil genus

Fig. 2 The phylogeny reconstruction and origin site inference of Pteromyini based on Bayesian-DIVA. **a** The reconstructed phylogenetic tree and the inference result. Posterior probabilities smaller than 1.00 are shown for the nodes. The ancestral node is labeled in a red circle, and asterisk represents unknown proportion; **b** the legend for the defined areas; **c** the predefined areas on the map of the world

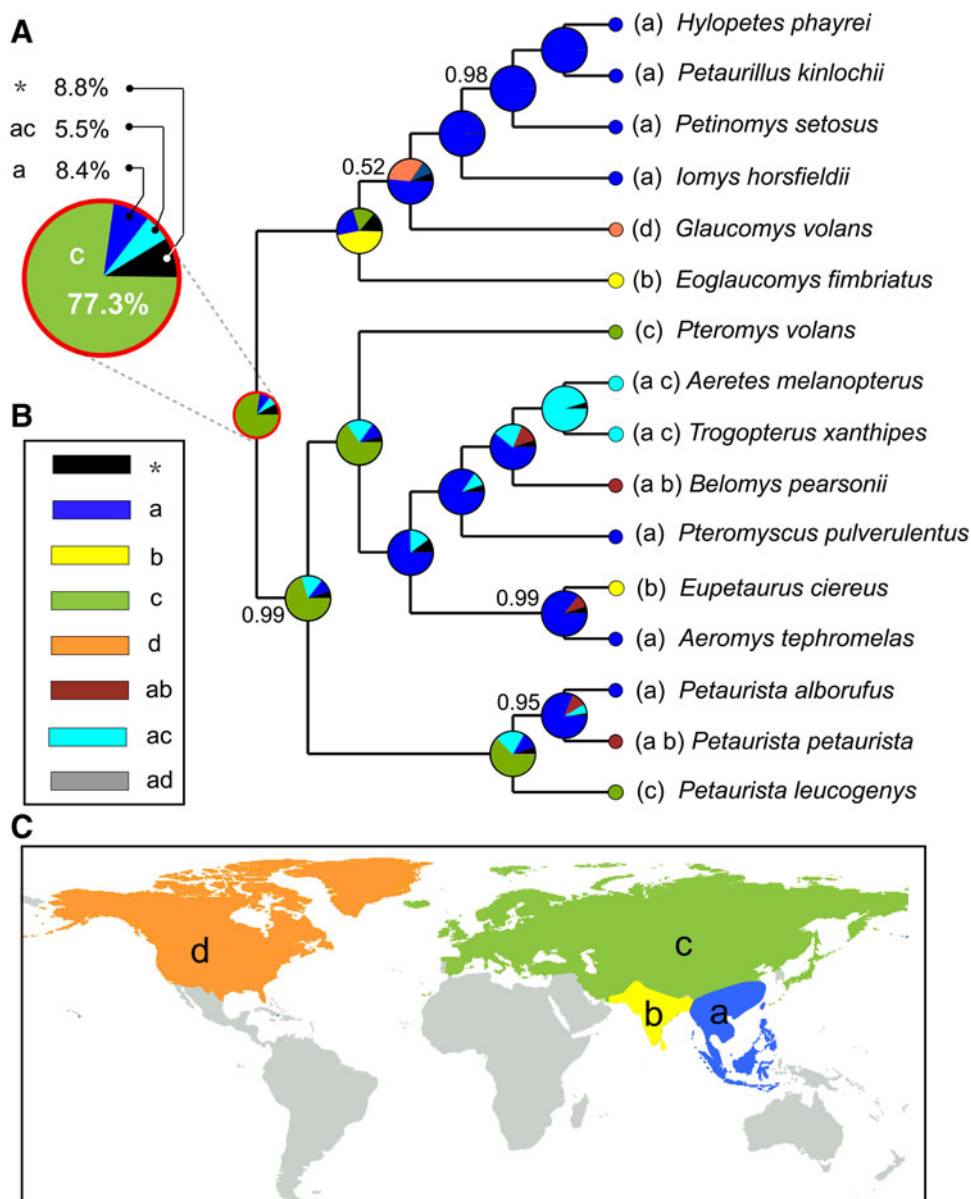
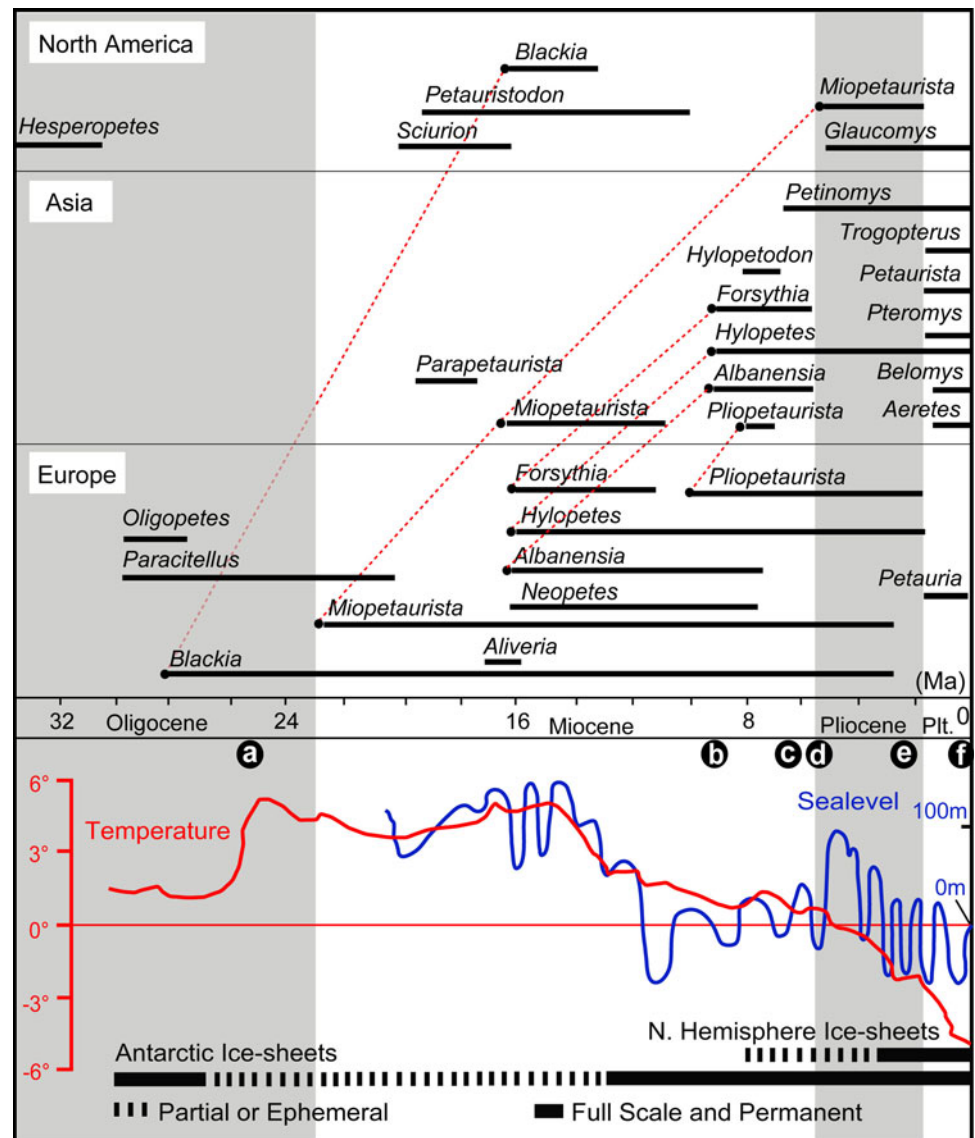


Fig. 3 The timespan of fossil genera of Pteromyini on the three continents and the eustatic, temperature and glacial changes since the late Oligocene. The *dotted curves* in red linking the same genera display the possible dispersal trends between continents. The $\delta^{18}\text{O}$ temperature changes (in red) and sea level fluctuations (in blue) are integrated. The *horizontal bars* below provide a rough qualitative representation of ice volume in each hemisphere relative to the LGM, with the *dashed bar* representing periods of minimal ice coverage ($\leq 50\%$), and the *full bar* representing close to maximum ice coverage ($>50\%$ of present). Several dramatic paleobiological and paleogeologic events are marked on the time scale: **a** Appearance of the earliest fossil gliding rodent; **b** Significant uplift of Himalaya and Tibetan Plateau; **c** The first open of Bering Strait; **d** Expansion of C4 grasslands; **e** Strengthening of Asian monsoon; **f** The Last Glacial Maximum. Modified from Haq et al. (1987), Mercer and Roth (2003), and Zachos et al. (2001)



occurring in North America, Europe and Asia are summarized and illustrated in Fig. 3.

The first fossil of Pteromyini appeared in the late Oligocene and greatly diversified in the Miocene, especially in Europe. This was followed by shrinkage of most populations in all three continents during the Pliocene, and then expansion of the Asian Pteromyini in the Quarternary. Some disputed genera occurring during the early stages of Pteromyini were taken into consideration here. Emry and Korth (2007) described genus *Hesperopetes*, which was found in the Oligocene in North America, as representing the earliest lineage leading to flying Sciurids. However, confidence of this was limited, and the genus was temporarily assigned to Sciuridae, not Pteromyini. *Oligopetes* was originally reported and known only from the early Oligocene of Europe as a genus of Aplodontidae (Heissig 1979) with a few occurrences, but McKenna and Bell

(1997) reassigned it to Pteromyini according to several prior studies (de Bruijn and Unay 1989; Cuenca and Canudo 1992). *Paracitellus* from the late Oligocene to the early Miocene (Dehm 1950) was considered to be the earliest flying squirrel (Thorington 1984), but recently it was transferred to Aplodontidae (Werner 1994; Kadlecova 2003) and Ischyromyidae (McKenna and Bell 1997).

Miopetaurista, *Blackia* and *Petauristodon* found in the early mid-Miocene and *Pliopetaurista* from the middle late Miocene to Pliocene were the most diverse fossil groups. They composed nearly half of the abundance on the three continents during the Miocene and the Pliocene. In Europe, there were two endemic genera (*Neopetes* and *Aliveria*) reported in the Miocene and one (*Petauria*) in the Pleistocene. Other populations originating here all had their subsequent appearances in Asia and North America. The extant genus *Hylopetes* originated early in the mid-Miocene in

Europe and survived there until the late Pleistocene, but at a low occurrence. In Asia, where most extant flying squirrels live, there were eight fossil genera found during the Miocene. These records were rich in species but poor in individual numbers: three endemic genera (each with one species and one occurrence) all reported from China, and the other five genera widely distributed in Eurasia. While in the Pliocene, there was only one occurrence of *Pteromys* reported from Asia (Jin et al. 1999). Genera which occurred in or after the Pleistocene all contained at least some extant lineages. Fossils unearthed in North America were fewer than Eurasia. The diverse genus *Petauristodon* and *Sciurion* (with one single occurrence) were reported as two endemic fossil genera of North America, while the other extant endemic genus *Glaucomys* occurred widely from the Pliocene to the present.

Molecular Phylogeny and Ancestral Distribution Inferences

The reconstruction of phylogeny confirmed the findings obtained by Mercer and Roth (2003), with the two additional species incorporated in this analysis having the relationship suggested by Yu et al. (2006) using the cytochrome *b* gene. The phylogenetic tree and the inferred historical biogeographic scenarios from the Bayesian-DIVA analysis are summarized in Fig. 2. Area ‘c’ is indicated to be the most probable ancestral distribution region with a support value of 77.3 %.

Discussion

Fossil Records and Ancestral Distribution of Flying Squirrels

The unearthed fossils that are classified as flying squirrels consist almost exclusively of teeth, with the postcranial skeleton, as the direct indicator of gliding ability, being virtually unknown (Thorington et al. 2005). This has brought many controversies in the identification and classification, especially of those fossils found in the early history of the group. As mentioned above, the fossil ‘flying squirrel’ *Paracitellus* (Dehm 1950) had been classified as the family Paramyidae (Black 1966), Sciuridae (Heissig 1979), Aplodontidae (Werner 1994) and Ischyromyidae (McKenna and Bell 1997), successively. So the early evolved genera such as *Hesperopetes*, *Oligopetes* and *Paracitellus*, were considered the lineages that might lead to ‘flying’ squirrels, while not necessarily being real gliders (Fig. 3). The real ancestor of flying squirrels may not be identified until more intact fossils appear (Korth 1994).

Although the problems raised by Thorington et al. (2005) about identifying flying squirrels from teeth (that features viewed as diagnostic can also be found in teeth of other squirrel groups) might also exist for the later fossils, it is necessary here to accept the fossil identifications from previous researches. On the basis of the existing fossil records (“Appendix”; Figs. 1, 3), we notice a prominent diversity of species during the Oligocene–Miocene transition in Europe, especially in Germany and France, etc. While in North America and Asia there is no fossil occurrence of Pteromyini reported within this time interval (24–20 Ma). But in the following mid-Miocene period, flying squirrels were abundant in both Eurasia and North America. The dotted curves linking the same genera on different continents (Fig. 3) show the possible dispersal events across Europe, Asia and North America. Apart from *Parapetaurista*, *Hylopetodon* and *Petinomys* (each with only one occurrence in China), all genera occurring in Asia during the Miocene could be traced back to their ancestors in Europe. Similar patterns are observed in North America. In Eurasia during the Pliocene, the fossil records dramatically decreased with no new genera reported, while the extant *Glaucomys* appeared in North America. However, the low occurrence of such fossils in Asia is probably attributed to sampling bias. Proceeding to the Pleistocene, fossils in Europe lost their dominance and declined sharply, with only one new genus *Petauria* reported (Dehm 1962), although some researchers consider this genus a synonym of the extant genus *Petaurista* (Thorington et al. 2005). While the genera in North America and Asia are all extant with some species of them extinct. Species in Asia became dominant during the Quarternary, and the present distribution pattern gradually formed in the Holocene.

Corresponding to the fossil explosion in Europe during the early Miocene, Mercer and Roth (2003) used molecular clock estimation to demonstrate that flying squirrels diverged from other tree squirrels 23–18 Ma years ago. And in the present study, the ancestral distribution inference based on the phylogeny indicates that the most possible area for the common ancestors of these animals is also northwestern Eurasia (Fig. 2a). After synthesizing these conclusions and inferences, we hypothesize that flying squirrel clade probably originated in Europe during the Oligocene–Miocene transition and dispersed to Asia and North America immediately after their origin.

This hypothesis is well supported from the dispersal pathways of specific taxa such as *Hylopetes*. Fossil species in this extant Asian endemic genus were largely reported in Europe in the late Miocene and the Pliocene, and the species in *Neopetes* reported in Europe were quite similar to *Hylopetes* (Daxner-Hoeck 2004), and were previously classified as the latter (de Bruijn 1998). These all suggest that some extinct species of *Hylopetes* previously lived in

Europe, and probably originated from that region. Besides, if the *Petauria* in Europe during the Pleistocene should actually be considered a synonym of the extant *Petaurista* in Asia as suggested above, we could consider a European origin of *Petaurista* as Oshida et al. (2000) and Yu et al. (2006) had proposed. Further, if our inference about the origin of flying squirrels is correct, then as some research suggests (Arbogast 2007), the disputed teeth found in North America and Europe in the early Oligocene probably could not be classified as flying squirrels.

Global Environmental Change and the Evolution of Flying Squirrels

The oldest complete fossil gliding rodent, *Eomys quercyi* (Eomyidae) was found in the late Oligocene, about 25.8 Ma ago in Germany (Storch et al. 1996). Abundant fossil leaves, fruits and seeds found around this fossil suggest a thick mesophytic forest setting. This forest was widespread in western and central Europe during the late Oligocene (Mai and Walther 1991) and probably afforded a suitable habitat for the gliding rodents. Compared to the Oligocene and the Pliocene, the Miocene was a warmer period during which the ‘Climatic Optimum’ appeared with the deep-sea temperature about 6°C higher in Eurasia (Flower and Kennett 1994) and sea level 100 m higher than the present (Haq and Al-Qahtani 2005; Fig. 3). Flying squirrels might owe their European Oligocene–Miocene radiation to this suitable environment, and the deciduous forests and bush woods which were abundant in the temperate zone of Eurasia (Bruch et al. 2007) might have provided habitats for the prosperous development and rapid dispersal of these gliders in the millions of years that followed.

However, flying squirrels were confronted with severe crises during the late Miocene. Huge and permanent Antarctic ice sheets began to form and accumulate, with the Alps–Himalayas orogenic movements, Paratethys tectonic reorganizations and related extensive volcanisms following (Bruch et al. 2007). These events dramatically affected the global geological and climatic patterns and triggered the seasonal climate fluctuations. The north hemisphere underwent a cooling phase and climate deterioration with temperature and precipitation greatly decreasing (Bruch et al. 2007). Probably because of the global CO₂ reduction (Raymo and Ruddiman 1992) and the frequent devastating fires (Keeley and Rundel 2005), the evergreen vegetation gradually changed to seasonal deciduous forest or open C₄ grassland during this period of 8–3 Ma (Edwards et al. 2010). The population of forest dwellers in these areas might have greatly contracted as a result of this habitat loss. Later in Asia, the accelerated uplift of the Tibet Plateau and the reinforcing Asian monsoons strongly

influenced the local environment (Guo et al. 2004). Climate in central Asia and northwest China changed to aridity and greatly promoted the expansion of gobi and desert (Sun et al. 2009). These dry and treeless regions were obviously not suitable for flying squirrels, while the forests in southeast Europe and southern Asia persisted, serving as refugia for these arboreal species (Turner 2001).

At the Pliocene epoch, a permanent ice sheet in the Arctic formed and induced a global cold crisis during which many cold-resistant mammals in the northern hemisphere went extinct, marmots for example (Mein 1992). During the same period, the aridity/humidity contrast between central and Southeast Asia was strengthened and persisted until present (An et al. 2001; Zhang et al. 2007). Flying squirrels were evidently affected by these disasters as their abundance dramatically decreased in Europe and Asia (Figs 1, 3). Other mammalian fossils found in north China during the early Pliocene also suggested that the fauna was dominated by grassland forms, scarcely containing woodland populations (Jin et al. 1999; Zhang 2006). The most recent factor that intensely shaped the present distribution pattern of Pteromyini was probably the Last Glacial Maximum (LGM, 25,000–15,000 BP). Proxy data from pollen for the LGM indicated substantial cooling at high latitudes of the Northern Hemisphere (Otto-Bliesner et al. 2006) with a southward displacement and major reduction in boreal forest (Bigelow et al. 2003). From the vegetation map of Eurasia (Fig. 4) during the LGM, it could be inferred that flying squirrels had been driven to their limited habitats in Eurasia at that time, which were mainly South and Southeast Asia.

As flying squirrels were gradually confined to southern Asia, the rise and decline of geographical barriers and high habitat heterogeneity of the region provided them with necessary environmental backgrounds for rapid radiation (Yu et al. 2006). There were two main geographic speciation ‘accelerators’: one being the profound complexity and dynamic motions in the Himalayan region, which resulted in the geological barriers among different species and their narrow distribution and small populations (mainly including genera *Biswamoyopterus*, *Eoglaucmys* and *Eupetaurus*); the other being probably the repeated connection and separation of different islands in Southeast Asia caused by glacier-driven sea level fluctuations. The low sea level permitted dispersal of squirrels while high sea level cut off their biological communications (Mercer and Roth 2003). This probably contributed to the rapid speciation of Pteromyini in Southeast Asia, with many genera (*Aeromys*, *Iomys*, *Petaurillus*, *Petinomys*, *Pteromyscus*, *Hylopetes* and etc.) rapidly diversifying here in this period.

Two distinctive genera have to be highlighted. The most diverse genus *Petaurista* might have originated 15 Ma (Mercer and Roth 2003) in northern Eurasia and then

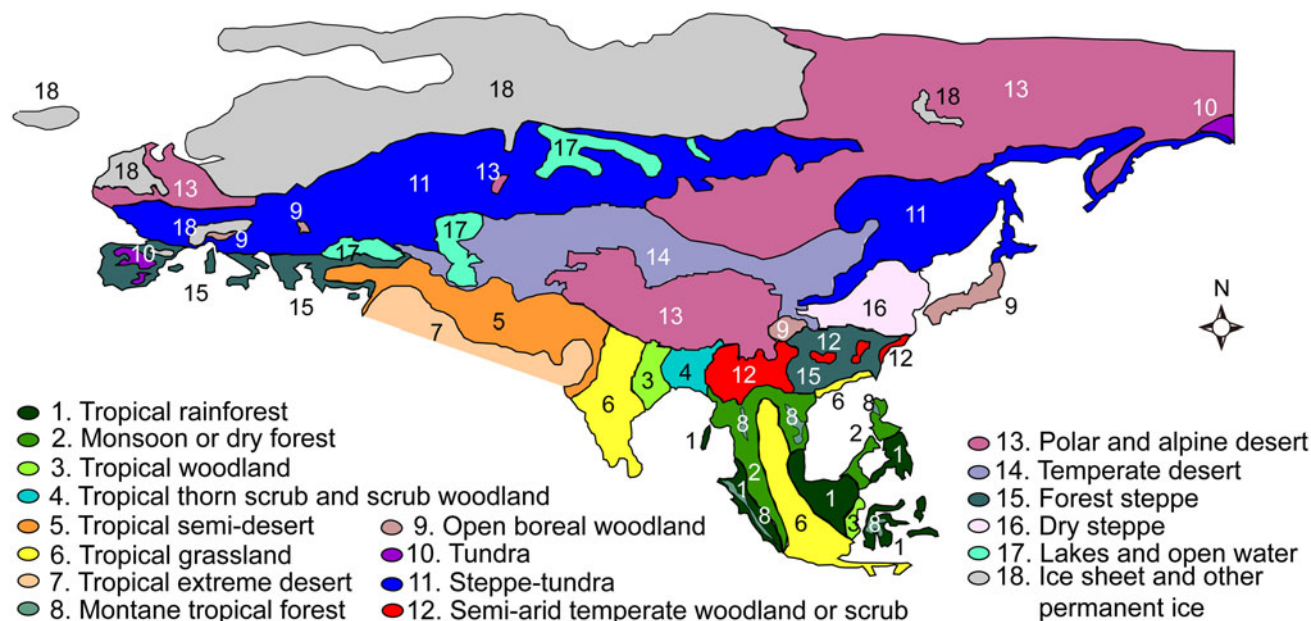


Fig. 4 The vegetation distribution pattern of Eurasia during the last glacial maximum (about 25,000–15,000 years ago). Modified from Ray and Adams (2001)

dispersed southwards into Asia (Yu et al. 2006). In this diverse genus, *P. leucogenys* is endemic to Japan, with some endemic species (taxonomically problematic) distributed in Taiwan, Hainan or other islands in southern Asia. These islands used to be connected with each other or with the mainland through land bridges during the Pleistocene glacial period, and those island populations probably arose in this period (Ho et al. 1997; Yu et al. 2006). *Pteromys volans* in the Eurasian boreal forests is the only species now existing in Europe. It likely survived in the scattered glacial refugia and then rapidly developed after the cooling period (Oshida et al. 2005).

The evolutionary history of flying squirrels in North America was similar to that occurring in Eurasia. Long before the Bering strait first opened (about 7.4–4.8 Ma) and separated the two continents (Marincovich and Gladenkov 1999), the ancestral branch of *Glaucomys* probably dispersed through the highly forested land bridge to North America 14 Ma (Wing 1998) and evolved there. Then North America also saw a course of climate deterioration and aridity during the Miocene-Pliocene transition, which resulted mainly from the cooling of the ocean as the Antarctic ice sheet spread (Mercer 1983), and from the uplift of the Rocky Mountain ranges that partially intercepted moisture-laden winter storms from the Pacific (Axelrod 1985). The initial rise of grasslands in this region probably commenced 7–5 Ma during the driest part of the Tertiary, an event which restricted forest and woodland coverage and encouraged the explosive evolution of grasses and forbs (Axelrod 1985).

These climate and vegetation upheavals undoubtedly impacted the biogeographic history of flying squirrels on this continent. The most recent glaciation (Wisconsinan Glaciation, 80,000–20,000 BP) also substantially impacted the present distribution of the single extant genus *Glaucomys* in North America (Arbogast 2007).

Fate of the Flying Squirrels

The evolution of flying squirrels was greatly affected by vegetation succession in the past few million years, and will continue to be tightly associated with the future development of forests in Asia. According to the latest version of the IUCN Red List of Threatened Species (IUCN 2011), at least 45 % of populations of the flying squirrels are currently under threat or have a negative development trend. Perhaps of greatest concern, forest loss rates are highest in the hotspots of arboreal squirrel diversity. The recent research on global vegetation claimed that the forests loss and deterioration rate in South and Southeast Asia are the highest when compared with other continents (Achard et al. 2002; Koprowski and Nandini 2008). For example, from 1985 to 2001, the protected lowland forests in Kalimantan, where many flying squirrels dwell, declined by more than 56 % (Curran et al. 2004). Since the degradation and fragmentation have threatened the integrity of forest ecosystems worldwide and the destroyed forests are hard to recover in the short term, the future of the flying squirrels is now of greater concern.

Conclusions

The evolutionary history of flying squirrels was seldom explored due to the paucity of well preserved fossils and systematic work from other perspectives. Evidence from fossil occurrence, molecular clock estimation and the present ancestral reconstruction indicate a possible origin of Pteromyini in the Oligocene–Miocene transition in Europe. Climate turbulence, organic movements, vegetation replacement and glaciation in the last twenty million years were the principle influences on their evolutionary history and have shaped the current distributional patterns. Evidence of the sensitivity to environmental changes from the past indicate a depressing future for the flying squirrels in the southern Asia, where large areas of

forest have been destroyed or are under critical threat in recent years.

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Appendix

See Table 2.

Table 2 Fossil records of flying squirrels

Fossil record	Time (Ma)	Location	Coordinates	Primary references
<i>Hesperopetes</i> Emry and Korth, 2007				Emry and Korth (2007)
<i>H. thoringtoni</i> Emry and Korth, 2007	38.0–36.0	Wyoming, USA	35.1°N, 111.5°W	Korth (2009)
<i>H. blacki</i> Emry and Korth, 2007	30	South Dakota, USA	41.5°N, 71.1°W	
<i>H. jamesi</i> Emry and Korth, 2007	30	South Dakota, USA	41.4°N, 71.1°W	
<i>Paracitellus</i> Dehm, 1950				Dehm (1950)
<i>P. eminens</i> Dehm, 1950	22.4–20.0	Germany	48.4°N, 9.9°E	Black (1966)
<i>P. eminens</i> Dehm, 1950	22.4–20.1	Bohemia, Czech	49.5°N, 13.3°E	Heissig (1979)
<i>P. cingulatus</i> Heissig, 1979	Early Oligocene	Germany	51°N, 10.3°E	Kadleceva (2003)
<i>P. marmoreus</i> Heissig, 1979	Early Oligocene	Germany	51°N, 10.4°E	
<i>Oligopetes</i> Heissig, 1979				Heissig (1979)
<i>O. lophulus</i> Heissig, 1979	Oligocene	Germany	51°N, 10.4°E	de Bruijn and Unay (1989)
<i>O. obtusus</i> Heissig, 1979	Oligocene	Germany	51°N, 10.4°E	Cuenca and Canudo (1992)
<i>O. radialis</i> Heissig, 1979	Oligocene	Germany	51°N, 10.4°E	Emry and Korth (2007)
<i>Aliveria</i> de Bruijn et al. 1980				de Bruijn et al. (1980)
<i>A. brinkerinki</i> de Bruijn et al. 1980	16.9–16.0	Greece	38.4°N, 24.0°E	
<i>A. luteyni</i> de Bruijn et al. 1980	16.9–16.1	Greece	38.3°N, 23.5°E	
<i>Sciurion campestre</i> Skwara, 1986				Skwara (1986)
<i>S. campestre</i> Skwara, 1986	20.6–16.3	Saskatchewan, Canada	49.6°N, 109.0°W	
<i>Petauristodon</i> Engesser, 1979				Engesser (1979)
<i>P. mathewsi</i> (James, 1963)	16.0–13.0	California, USA	34.4°N, 119.3°W	Barnosky (1986)
<i>P. uphami</i> (James, 1963)	13.0–10.0	California, USA	34.4°N, 119.3°W	Pratt and Morgan (1989)
<i>P. minimus</i> (Lindsay, 1972)	16.3–13.7	California; Texas, USA	34.4°N, 118°W	
<i>P. jamesi</i> (Lindsay, 1972)	16.3–13.6	California, USA	34.4°N, 117°W	
<i>P. pattersoni</i> Pratt and Morgan, 1989	20.0–16.0	Florida, USA	29.5°N, 82.5°W	
<i>P. sp.</i>	Miocene	Louisiana, USA	31.1°N, 93.1°W	
<i>P. sp.</i>	20.0–16.0	Texas, USA	31.6°N, 99.5°W	
<i>P. sp.</i>	16.3–13.6	Saskatchewan, Canada	49.2°N, 106.2°W	
<i>P. sp.</i>	16.3–13.6	Nebraska, USA	41.3°N, 99.5°W	
<i>P. sp.</i>	16.3–13.6	Oregon, USA	43.6°N, 117.5°W	
<i>P. sp.</i>	16.3–13.6	Texas, USA	31.6°N, 99.6°W	
<i>P. sp.</i>	16.3–13.6	Wyoming, USA	43.9°N, 110.8°W	
<i>P. sp.</i>	16.3–13.6	Nebraska, USA	42.9°N, 98.8°W	
<i>P. sp.</i>	16.3–13.6	Nebraska, USA	42.6°N, 98.0°W	
<i>P. sp.</i>	16.3–13.6	Nebraska, USA	42.8°N, 100.0°W	

Table 2 continued

Fossil record	Time (Ma)	Location	Coordinates	Primary references
<i>Blackia</i> Mein, 1970				Mein (1970a, b)
<i>B. miocaenica</i> Mein, 1970	Early Miocene	France	47.8°N, 1.9°E	Black and Kowalski (1974)
<i>B. miocaenica</i> Mein, 1970	16.9–16.0	Greece	38.4°N, 24.0°E	Daams (1977)
<i>B. miocaenica</i> Mein, 1970	28.4–23.0	Bayern, Germany	50.3°N, 9.8°E	de Bruijn et al. (1980)
<i>B. miocaenica</i> Mein, 1970	8.7–7.8	Niederösterreich, Austria	48.1°N, 16.3°E	Bulot (1980)
<i>B. miocaenica</i> Mein, 1970	16.9–16.0	Styrian Basin, Austria	47.1°N, 15.2°E	Bulot (1981)
<i>B. miocaenica</i> Mein, 1970	16.0–13.7	Schwaben, Germany	48.3°N, 10.1°E	de Bruijn and Unay (1989)
<i>B. miocaenica</i> Mein, 1970	16.0–13.7	Germany	50.9°N, 6.5°E	Werner (1994)
<i>B. miocaenica</i> Mein, 1970	16.0–13.7	Bayern, Germany	48.5°N, 10.6°E	de Bruijn (1999)
<i>B. miocaenica</i> Mein, 1970	13.7–12.8	Slovakia	48.2°N, 17.0°E	Dahlmann (2001)
<i>B. miocaenica</i> Mein, 1970	23.0–5.3	Valencia, Spain	39.4°N, 0.8°W	Venczel et al. (2005)
<i>B. miocaenica</i> Mein, 1970	20.0–16.9	Aragon, Spain	40.2°N, 0.7°W	Hir and Venczel (2005)
<i>B. miocaenica</i> Mein, 1970	12.8–11.1	Thurgau, Switzerland	47.6°N, 9.1°E	Daxner-Hoeck (2010)
<i>B. miocaenica</i> Mein, 1970	12.8–11.1	Baselland, Switzerland	47.5°N, 7.9°E	Nicoara (2011)
<i>B. miocaenica</i> Mein, 1970	16.3–13.6	Nebraska, USA	40.0°N, 98.5°W	
<i>B. miocaenica</i> Mein, 1970	16.3–13.6	Nebraska, USA	42.8°N, 100.0°W	
<i>B. wolfersheimensis</i> Mein, 1970	6.0–5.0	France	42.7°N, 2.9°E	
<i>B. wolfersheimensis</i> Mein, 1970	5.3–3.4	Rheinland-Pfalz, Germany	49.7°N, 8.2°E	
<i>B. wolfersheimensis</i> Mein, 1970	7.0–4.9	Leordoaia, Romania	47.3°N, 28.0°E	
<i>B. parvula</i> Baudelot, 1972	16.9–16.0	Greece	38.4°N, 24.0°E	
<i>B. polonica</i> Black, 1974	4.9–4.2	Poland	50.6°N, 19.5°E	
<i>B. polonica</i> Black, 1974	3.2–2.6	Poland	51.0°N, 18.9°E	
<i>B. polonica</i> Black, 1974	3.2–2.6	Poland	51.0°N, 19°E	
<i>B. polonica</i> Black, 1974	4.9–4.2	Poland	52.3°N, 22.2°E	
<i>B. ulmensis</i> Werner, 1994	28.4–23.0	Germany	48.4°N, 9.9°E	
<i>B. sp.</i>	Oligocene	Kesan, Turkey	40.9°N, 26.6°E	
<i>Miopetaurista</i> Kretzoi, 1962				Kretzoi (1962)
<i>M. gibberosus</i> Hofmann, 1893	16.0–11.6	Silesia, Poland	50.7°N, 17.9°E	Daxner-Hock (1975)
<i>M. lappi</i> Mein, 1958	16.0–13.7	Germany	50.9°N, 6.5°E	Daams (1977)
<i>M. lappi</i> Mein, 1958	16.0–13.7	France	47.5°N, 0.0°W	de Bruijn et al. (1980)
<i>M. diescalidus</i> Daams, 1977	23.0–14.0	Valencia, Spain	39.4°N, 0.8°W	de Bruijn and Unay (1989)
<i>M. dehmi</i> de Bruijn, 1980	20.0–16.9	Bavaria, Germany	48.9°N, 11.2°E	Aldana Carrasco (1992)
<i>M. dehmi</i> de Bruijn, 1980	16.0–13.7	Pyrenees Region, France	43.9°N, 0.7°E	Dahlmann (2001)
<i>M. dehmi</i> de Bruijn, 1980	16.9–16.0	Austria	47.1°N, 15.2°E	Qiu (2002)
<i>M. dehmi</i> de Bruijn, 1980	16.0–13.7	Bayern, Germany	48.3°N, 10.1°E	Shevyreva and Baranova (2003)
<i>M. dehmi</i> de Bruijn, 1980	16.9–16.0	Greece	38.4°N, 24.0°E	Daxner-Hoeck (2004)
<i>M. dehmi</i> de Bruijn, 1980	16.0–13.7	Bayern, Germany	48.5°N, 10.6°E	Markovic (2008)
<i>M. asiatica</i> Qiu, 2002	Late Miocene	Yunnan, China	25.1°N, 102.0°E	Casanovas-Vilar et al. (2010)
<i>M. crusafonti</i> (Mein, 1970)	4.9–4.2	Sabadell, France	41.4°N, 2.2°E	Nicoara (2011)
<i>M. gaillardi</i> (Mein, 1970)	4.9–4.2	La Grive, France	45.6°N, 5.2°E	
<i>M. gaillardi</i> (Mein, 1970)	16.0–11.6	Silesia, Poland	50.7°N, 17.9°E	
<i>M. gaillardi</i> (Mein, 1970)	13.7–12.8	Santarém, Portugal	39.3°N, 8.7°W	
<i>M. gaillardi</i> (Mein, 1970)	12.8–11.1	Baselland, Switzerland	47.5°N, 7.9°E	
<i>M. neogrivensis</i> (Mein, 1970)	4.9–4.2	La Grive, France	45.6°N, 5.2°E	
<i>M. thaleri</i> (Mein, 1970)	4.9–4.2	Hérault, France	43.6°N, 3.8°E	
<i>M. thaleri</i> (Mein, 1970)	3.2–2.6	Poland	51.0°N, 18.9°E	
<i>M. tobieni</i> (Mein, 1970)	4.9–4.2	Perpignan, France	42.7°N, 2.9°E	
<i>M. webbl</i> (Robertson, 1976)	4.9–1.8	Alachua, Florida, USA	29.8°N, 82.1°W	
<i>M. sp.</i>	7.0–4.9	Leordoaia, Moldova	47.3°N, 28.0°E	
<i>M. sp.</i>	16.9–16.0	Gers, France	44.0°N, 0.5°E	
<i>M. sp.</i>	11.1–9.7	Bavaria, Germany	47.9°N, 10.6°E	
<i>M. sp.</i>	16.0–13.7	Bayern, Germany	48.7°N, 12.0°E	

Table 2 continued

Fossil record	Time (Ma)	Location	Coordinates	Primary references
<i>M. sp.</i>	16.0–11.6	Nei Mongol, China	43.5°N, 112.0°E	
<i>M. sp.</i>	13.7–12.8	Zürich, Switzerland	47.3°N, 8.9°E	
<i>M. sp.</i>	16.9–16.0	Sankt Gallen, Switzerland	47.3°N, 8.8°E	
<i>M. sp.</i>	16.9–13.7	Sankt Gallen, Switzerland	47.3°N, 8.9°E	
<i>M. sp.</i>	8.7–7.8	Niederoesterreich, Austria	48.1°N, 16.3°E	
<i>M. sp.</i>	Oligocene	Kesan, Turkey	40.9°N, 26.6°E	
<i>Parapetaurista</i> Qiu and Lin, 1986				Qiu and Liu (1986)
<i>P. tenurugosa</i> Qiu and Lin, 1986	20.0–16.0	Jiangsu, China	33.2°N, 118.0°E	
<i>Hylopetodon</i> Qiu, 2002				Qiu (2002)
<i>H. dianense</i> Qiu, 2002	Late Miocene	Yunnan, China	25.2°N, 102.0°E	
<i>Forsythia</i> Mein, 1970				Mein (1970a, b)
<i>F. gaudryi</i> Gaillard, 1899	Mid-Miocene	La Grive, France	45.6°N, 5.2°E	de Bruijn et al. (1980)
<i>F. gaudryi</i> Gaillard, 1899	16.9–16.0	Midi-Pyrénées, France	44.0°N, 0.5°E	Daxner-Hoeck (2010)
<i>F. gaudryi</i> Gaillard, 1899	9.0–5.3	Yunnan, China	25.0°N, 102.1°E	
<i>F. gaudryi</i> Gaillard, 1899	9.0–5.3	Yunnan, China	25.0°N, 102.1°E	
<i>F. gaudryi</i> Gaillard, 1899	16.9–16.0	Baden, Germany	48.5°N, 10.1°E	
<i>F. gaudryi</i> Gaillard, 1899	12.8–11.1	Baselland, Switzerland	47.5°N, 7.9°E	
<i>Albanesia</i> Daxner-Höck and Mein, 1975				Daxner-Hock (1975)
<i>A. sansaniensis</i> (Lartet, 1851)	13.7–12.8	France	46.2°N, 2.2°E	de Bruijn et al. (1980)
<i>A. sansaniensis</i> (Lartet, 1851)	16.0–13.7	France	43.9°N, 0.7°E	Aldana Carrasco (1992)
<i>A. albanensis</i> (Major, 1893)	13.7–12.8	France	46.2°N, 2.2°E	Daxner-Hoeck (2004)
<i>A. albanensis</i> (Major, 1893)	12.8–11.1	Thurgau, Switzerland	47.6°N, 9.1°E	
<i>A. albanensis</i> (Major, 1893)	12.8–11.1	Cataluña, Spain	41.4°N, 1.6°E	
<i>A. albanensis</i> (Major, 1893)	13.0–11.0	Spain	40.4°N, 3.7°W	
<i>A. grimmeri</i> (Black, 1966)	13.0–11.0	Germany	51.1°N, 10.6°E	
<i>A. grimmeri</i> (Black, 1966)	8.7–7.8	Austria	48.1°N, 16.3°E	
<i>A. sp.</i>	9.0–5.3	Yunnan, China	25.0°N, 102.1°E	
<i>A. sp.</i>	13.7–12.8	Bayern, Germany	48.4°N, 11.1°E	
<i>A. sp.</i>	16.0–13.7	Bayern, Germany	48.7°N, 12.0°E	
<i>A. sp.</i>	13.7–12.8	Russian Federation	44.4°N, 41.8°E	
<i>Petauria</i> Dehm, 1962				Dehm (1962)
<i>P. helleri</i> Dehm, 1962	Mid-Pleistocene	Bayern, Germany	48.9°N, 11.2°E	Kretzoi (1965)
<i>P. voigtstedtensis</i> Kretzoi, 1965	Mid-Pleistocene	Thuringen, Germany	51.4°N, 11.3°E	Koenigswald (1973)
<i>P. sp.</i>	0.8–0.1	Sachsen, Germany	51.4°N, 11.3°E	
<i>P. sp.</i>	0.8–0.1	Baden, Germany	49.0°N, 9.2°E	
<i>P. sp.</i>	1.8–0.0	Poland	49.2°N, 19.9°E	
<i>Pliopetaurista</i> Kretzoi 1962				Mein (1970a, b)
<i>P. pliocaenica</i> (Deperet, 1897)	4.2–3.2	Perpignan, France	42.7°N, 2.9°E	Baranova and Konkova (1974)
<i>P. pliocaenica</i> (Deperet, 1897)	7.0–4.9	Spain	37.2°N, 3.6°W	Black and Kowalski (1974)
<i>P. pliocaenica</i> (Deperet, 1897)	5.3–1.8	Languedoc, France	42.7°N, 2.9°E	Baranova (1976)
<i>P. pliocaenica</i> (Deperet, 1897)	5.3–3.4	Rheinland, Germany	49.7°N, 8.2°E	Mein and Adrover (1977)
<i>P. pliocaenica</i> (Deperet, 1897)	5.3–1.8	Barany, Hungary	45.9°N, 18.2°E	Terzea (1980)
<i>P. pliocaenica</i> (Deperet, 1897)	3.4–1.8	Hungary	48.5°N, 20.8°E	Qiu (1991)
<i>P. pliocaenica</i> (Deperet, 1897)	4.2–3.2	Poland	50.8°N, 19.3°E	Shushpanov and Lungu (1993)
<i>P. pliocaenica</i> (Deperet, 1897)	3.4–1.8	Slovakia, Czech	48.3°N, 19.8°E	Dahlmann (2001)
<i>P. pliocaenica</i> (Deperet, 1897)	5.3–3.4	Aragon, Spain	40.4°N, 1.1°W	Popov (2004)
<i>P. pliocaenica</i> (Deperet, 1897)	7.0–4.9	Leordoia, Moldova	47.3°N, 28.0°E	Daxner-Hoeck (2004)
<i>P. pliocaenica</i> (Deperet, 1897)	9.0–5.3	Vinogradovka, Ukraine	45.9°N, 29.4°E	Nadachowski et al. (2006)
<i>P. dehneli</i> Sulimski, 1964	Late Pliocene	Romania	45.9°N, 24.9°E	Garcia-Alix et al. (2007)
<i>P. dehneli</i> Sulimski, 1964	9.7–8.7	Greece	41.1°N, 23.5°E	Menouret and Mein (2008)
<i>P. dehneli</i> Sulimski, 1964	4.9–4.2	Poland	50.6°N, 19.5°E	Nicoara (2011)
<i>P. dehneli</i> Sulimski, 1964	3.2–2.6	Poland	51.0°N, 18.9°E	Sinita (2011)
<i>P. dehneli</i> Sulimski, 1964	3.2–2.6	Poland	51.0°N, 19°E	

Table 2 continued

Fossil record	Time (Ma)	Location	Coordinates	Primary references
<i>P. dehneli</i> Sulimski, 1964	4.2–2.6	Siedlce, Poland	52.3°N, 22.2°E	
<i>P. dehneli</i> Sulimski, 1964	5.3–3.4	Romania	43.8°N, 24.9°E	
<i>P. dehneli</i> Sulimski, 1964	Mid-Pliocene	Moldova, Romania	47.1°N, 27.6°E	
<i>P. dehneli</i> Sulimski, 1964	Mid-Pliocene	Moldova, Romania	47.1°N, 27.6°E	
<i>P. schaubi</i> Sulimski, 1964	Pliocene	Poland	51.6°N, 19.1°E	
<i>P. bressana</i> Mein, 1970	Pliocene	Soblay, France	46.1°N, 5.3°E	
<i>P. bressana</i> Mein, 1970	8.7–7.8	Niederoesterreich, Austria	48.1°N, 16.3°E	
<i>P. bressana</i> Mein, 1970	8.7–7.8	Burgenland, Austria	47.1°N, 16.3°E	
<i>P. bressana</i> Mein, 1970	9.7–8.7	Greece	41.1°N, 23.5°E	
<i>P. meini</i> Black, 1974	4.9–3.2	Poland	51.1°N, 18.9°E	
<i>P. rugosa</i> Mein, 1970	Late Miocene	Nei Mongol, China	40.8°N, 111.7°E	
<i>P. kollmanni</i> Daxner-Höck, 2004	Late Miocene	Austria	47.1°N, 19.5°E	
<i>P. kollmanni</i> Daxner-Höck, 2004	8.7–7.8	Niederoesterreich, Austria	48.1°N, 16.3°E	
<i>P. sp.</i>	5.3–1.8	Russian Federation	50.7°N, 40.0°E	
<i>Petinomys</i> Thomas, 1908				Qiu (1991)
<i>P. auctor</i> Qiu, 1991	Late Miocene	Nei Mongol, China	40.8°N, 111.7°E	
<i>Hylomys</i> Thomas, 1908				Kretzoi (1959)
<i>H. hungaricus</i> (Kretzoi, 1959)	Pliocene	Csarnota, Hungary	45.9°N, 18.2°E	Danner-Hock (1970)
<i>H. hungaricus</i> (Kretzoi, 1959)	8.7–7.8	Niederoesterreich, Austria	48.1°N, 16.3°E	
<i>H. hungaricus</i> (Kretzoi, 1959)	5.3–1.8	Barany, Hungary	45.9°N, 18.2°E	
<i>H. hungaricus</i> (Kretzoi, 1959)	3.4–1.8	Hungary	48.5°N, 20.8°E	
<i>H. hungaricus</i> (Kretzoi, 1959)	4.9–4.2	Poland	50.6°N, 19.5°E	
<i>H. sp.</i>	7.0–4.9	Leordoaia, Moldova	47.3°N, 28.1°E	
<i>H. sp.</i>	9.0–5.3	Yunnan, China	25.0°N, 102.1°E	
<i>H. sp.</i>	16.0–13.7	Germany	50.9°N, 6.5°E	
<i>H. sp.</i>	9.0–5.3	Greece	41.2°N, 23.4°E	
<i>H. sp.</i>	5.3–3.4	Macedonia, Greece	40.5°N, 21.7°E	
<i>Neopetes</i> Daxner-Höck, 2004				Bouwens and de Bruijn (1986)
<i>N. macedoniensis</i> (Bouwens & de Bruijn, 1986)	8.7–7.8	Austria	48.1°N, 16.3°E	de Bruijn (1998)
<i>N. hoeckarum</i> (de Bruijn, 1998)	16.9–16.0	Styrian Basin, Austria	47.1°N, 15.2°E	Mein and Ginsburg (2002)
<i>N. debruijni</i> (Mein, 2002)	8.7–7.8	Austria	48.1°N, 16.3°E	Daxner-Hoeck (2004)
<i>Aeretes</i> Allen, 1940				Zheng (1993)
<i>A. melanopterus</i> Milne-Edwards, 1867	Late Pleistocene	Beijing, China	39.7°N, 115.9°E	Tong (2007)
<i>A. melanopterus</i> Milne-Edwards, 1867	Late Pleistocene	Beijing, China	39.6°N, 115.9°E	Tong et al. (2008)
<i>A. melanopterus</i> Milne-Edwards, 1867	0.04–0.03	Beijing, China	39.8°N, 115.6°E	
<i>A. grandidens</i> Zheng, 1993	Quaternary	Sichuan/Guizhou, China	28.0°N, 104.0°E	
<i>A. premelanopterus</i> Zheng, 1993	Quaternary	Sichuan/Guizhou, China	28.0°N, 104.0°E	
<i>Belomys</i> Thomas, 1908				Zheng (1993)
<i>B. pearsonii</i> Gray, 1842	Mid-Pleistocene	Kanchanaburi, Thailand	15.9°N, 101.0°E	Huang et al. (1995)
<i>B. pearsonii</i> Gray, 1842	0.8–0.1	Guizhou, China	25.6°N, 104.7°E	Chaimanee and Jaeger (2000)
<i>B. pearsonii</i> Gray, 1842	0.1–0.0	Hubei, China	33.1°N, 110.2°E	Liu et al. (2010)
<i>B. thamkaewi</i> Chaimanee, 2000	Late Pleistocene	Kanchanaburi, Thailand	14.7°N, 99.0°E	
<i>Glaucomys</i> Thomas, 1908				Martin (1974)
<i>G. volans</i> Linnaeus, 1758	1.8–0.3	Maryland, USA	39.6°N, 78.7°W	Ruez (2001)
<i>G. volans</i> Linnaeus, 1758	0.1–0.0	Georgia, USA	32.0°N, 81.1°W	Laub (2009)
<i>G. volans</i> Linnaeus, 1758	0.1–0.0	Florida, USA	29.6°N, 82.4°W	
<i>G. volans</i> Linnaeus, 1758	0.3–0.0	Florida, USA	29.1°N, 82.3°W	
<i>G. volans</i> Linnaeus, 1758	1.8–0.3	West Virginia, USA	38.7°N, 79.3°W	
<i>G. volans</i> Linnaeus, 1758	1.8–0.3	West Virginia, USA	38.7°N, 79.3°W	
<i>G. volans</i> Linnaeus, 1758	Pliocene	Florida, USA	27.6°N, 81.5°W	
<i>G. sabrinus</i> Shaw, 1801	0.1–0.0	Tennessee, USA	35.6°N, 86.9°W	
<i>G. sp.</i>	1.8–0.3	Florida, USA	28.8°N, 82.1°W	

Table 2 continued

Fossil record	Time (Ma)	Location	Coordinates	Primary references
<i>G. sp.</i>	4.9–1.8	Florida, USA	29.0°N, 82.7°W	
<i>G. sp.</i>	1.8–0.3	Virginia, USA	36.8°N, 82.8°W	
<i>G. sp.</i>	0.1–0.0	Virginia, USA	38.4°N, 79.1°W	
<i>G. sp.</i>	0.1–0.0	Virginia, USA	38.1°N, 79.7°W	
<i>G. sp.</i>	0.8–0.1	Virginia, USA	36.9°N, 80.9°W	
<i>G. sp.</i>	0.1–0.0	Virginia, USA	37.2°N, 80.8°W	
<i>G. sp.</i>	0.1–0.0	Virginia, USA	37.1°N, 81.3°W	
<i>G. sp.</i>	0.1–0.0	Virginia, USA	37.2°N, 80.7°W	
<i>Petaurista</i> Link, 1795				Jin et al. (2000)
<i>P. alborufus</i> Milne-Edwards, 1870	0.1–0.0	Hubei, China	33.1°N, 110.2°E	Liu et al. (2010)
<i>P. xanthotis</i> Milne-Edwards, 1872	0.1–0.0	Hubei, China	33.1°N, 110.2°E	
<i>P. sp.</i>	1.8–0.8	Anhui, China	31.1°N, 118.1°E	
<i>Pteromys</i> Cuvier, 1800				Young (1934)
<i>P. volans</i> Linnaeus, 1758	0.04–0.03	Beijing, China	39.8°N, 115.6°E	Young (1947)
<i>P. brachyodus</i> Young, 1934	~0.025	Beijing, China	39.7°N, 115.9°E	Jin et al. (1999)
<i>P. lopingensis</i> Young, 1947	Pleistocene	Jiangxi, China	28.9°N, 117.1°E	Tong et al. (2008)
<i>P. sp.</i>	Mid-Pliocene	Shandong, China	36.7°N, 117.0°E	
<i>P. sp.</i>	0.1–0.0	Aomori, Japan	41.4°N, 141.4°E	
<i>Trogopterus</i> Heude, 1898				Huang et al. (1995)
<i>T. parapearoni</i> (Zheng, 1993)	Quaternary	Sichuan/Guizhou, China	28.0°N, 104.0°E	Chaimanee and Jaeger (2000)
<i>T. xanthipes</i> Milne-Edwards, 1876	0.8–0.1	Guizhou, China	25.6°N, 104.7°E	Tong et al. (2008)
<i>T. xanthipes</i> Milne-Edwards, 1876	0.04–0.03	Beijing, China	39.8°N, 115.6°E	Jin et al. (2000)
<i>T. xanthipes</i> Milne-Edwards, 1876	1.8–0.8	Anhui, China	31.1°N, 118.1°E	

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