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Phylogenetic Relationships among Six Flying Squirrel Genera, Inferred from Mitochondrial Cytochrome *b* Gene Sequences

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ABSTRACT—Petauristinae (flying squirrels) consists of 44 extant species in 14 recent genera, and their phylogenetic relationships and taxonomy are unsettled questions. We analyzed partial mitochondrial cytochrome *b* gene sequences (1,068 base pairs) to investigate the phylogenetic relationships among six flying squirrel genera (*Belomys*, *Hylopetes*, *Petaurista*, *Petinomys*, and *Pteromys* from Asia and *Glaucomys* from North America). Molecular phylogenetic trees, constructed by neighbor-joining and maximum likelihood methods, strongly indicated the closer relationship between *Hylopetes* and *Petinomys* with 100% bootstrap values. *Belomys* early split from other flying squirrels. *Petaurista* was closely related to *Pteromys*, and *Glaucomys* was most closely related to the cluster consisting of *Hylopetes* and *Petinomys*. The bootstrap values supporting branching at the deeper nodes were not always so high, suggesting the early radiation in the evolution of flying squirrels.

INTRODUCTION

Flying squirrels (Petauristinae), which are distributed throughout Eurasia and the North America, consist of 44 extant species in 14 recent genera (Corbet and Hill, 1991). However, phylogenetic study of flying squirrels has been superficial so far. Genetic analyses of intrageneric relathionships of the genus *Petaurista* (Oshida *et al*., 1992; 1996; 2000) and of the genus *Glaucomys* (Nadler and Sutton, 1967; Rausch and Rausch, 1982; Arbogast, 1999) have been reported. From the morphological perspective, the close phylogenetic relathionship between *Glaucomys* and *Hylopetes* was indicated by Burt (1960) and Thorington Jr. *et al*. (1996). Rausch and Rausch (1982) reported the phylogenetic relathionship between *Glaucomys* and *Pteromys* based on their chromosomal characterizations. Hight *et al*. (1974) described the phylogenetic relationships of four flying squirrel genera (*Iomys*, *Petaurista*, *Petinomys*, and *Pteromys*), based on immunological data. However, the phylogenetic relationships of flying squirrels remain poorly understood.

In the present study, molecular phylogenetic analyses using partial sequences (1,068 base pairs: bp) of the mitochondrial cytochrome *b* gene was conducted for ten flying squirrel species distributed in various areas of Asia and North America: *Belomys pearsonii*, *Hylopetes phayrei*, *Glaucomys volans*, *Petinomys setosus*, *Petaurista alborufus*, *Petaurista leucogenys*, *Petaurista petaurista*, *Petaurista philippensis*, *Pteromys momonga*, and *Pteromys volans*. We here discuss the phylogenetic relationships among the six flying squirrel genera.

MATERIALS AND METHODS

Flying squirrels examined in the present study are shown in Table 1. Muscle tissues of *Belomys pearsonii* and *Hylopetes phayrei* and the skin tissue of *Pteromys momonga* were collected. Samples of *Glaucomys volans* and *Petinomys setosus* were commercially obtained. Sequence data of *Petaurista alborufus*, *Petaurista leucogenys*, *Petaurista philippensis*, *Petaurista petaurista*, and *Pteromys volans* were quoted from our previous report (Oshida *et al*., 2000). These flying squirrels are representative species in each area: *Belomys* from Taiwan and Southeast Asia, *Petinomys* and *Hylopetes* from South and Southeast Asia, *Petaurista* from southern Eurasia and Japan, *Pteromys* from northern Eurasia and Japan, and *Glaucomys* from North America.

From homogenates of muscle or skin tissues, total DNAs were extracted according to the phenol/proteinase K/sodium dodecyl sulfate method of Sambrook *et al*. (1989). A partial nucleotide sequence (1,068 bp) of the mitochondrial DNA (mtDNA) cytochrome *b* gene was amplified with polymerase chain reaction (PCR) using the following two primers: L14724 5'-GATATGAAAAACCATCGTTG-3' and

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Table 1. Species of flying squirrels examined in this study

Species name	Code	Common name	Collecting locality	Accession No. of sequence**
Belomys pearsonii	BPE	Hairy-footed flying squirrel	Central Taiwan	AB030262
Hylopetes phayrei	HPH	Phayre's flying squirrel	Thailand	AB030259
Glaucomys volans	GVO	Southern flying squirrel	North America	AB030261
*Petaurista alborufus castaneus**	ALC1	Red and white giant flying squirrel	Southern China	AB023898
*Petaurista leucogenys leucogenys**	LEL1	Japanese giant flying squirrel	Kyushu island, Japan	AB023904
*Petaurista leucogenys nikkonis**	LEN1	Japanese giant flying squirrel	Honshu island, Japan	AB023906
*Petaurista petaurista melanotus**	PEM1	Red giant flying squirrel	Laos	AB023908
*Petaurista philippensis grandis**	PHG	Indian giant flying squirrel	Central Taiwan	AB023907
Petinomys setosus	PSE	White-bellied flying squirrel	Indochina peninsula	AB030260
Pteromys momonga	PMO	Japanese small flying squirrel	Honshu island, Japan	AB030263
*Pteromys volans orii**	PVO	Siberian flying squirrel	Hokkaido island, Japan	AB023910

* Data previously reported by Oshida *et al.* (2000).
** Sequence data will appear in the DDBJ nucleotide sequence databases with accession numbers.

H15910 5'-GATTTTTGGTTTACAAGACCGAG-3'. Primer names correspond to the light (L) or heavy (H) strand and the 3'end-position of the primers in the human mtDNA sequence (Anderson *et al.*, 1981). The former primer was synthesized from the sequence described by Kocher *et al.* (1989) and the latter was also done from the sequences reported by Oshida *et al.* (2000). The 50 μl of reaction mixture contained 100 ng of genomic DNA, 25 picomoles of each primer, 200 μM dNTPs, 10 mM Tris-HCl (pH 8.3), 50 mM KCl, 1.5 mM $MgCl_2$, and 2.5 unirs of r*Taq* DNA polymerase (Takara). Amplification was carried out for 35 cycles using the following cycle program: 94°C for 1 min, 53°C for 1 min, and 72°C for 2 min. The extention reaction was completed by incubation at 72°C for 10 min. PCR products were purified with the Qia-quick PCR purification kit (Qiagen) and directly sequenced using an automated DNA sequencer (SQ5500L, Hitachi).

After sequence alignment was made using GeneWorks (Intelligenetics), the phylogenetic trees were reconstructed with the neighbor-joining (NJ) method (Saitou and Nei, 1987) in Clustal W (Thompson *et al.*, 1994) and with the maximum likelihood (ML) method using DNAML in PHYLIP package program (Felsenstein, 1993). Numbers of nucleotide substitutions per site were estimated for multiple substitutions using Kimura's two-parameter method (Kimura, 1980). To estimate branching confidence, the bootstrap analyses (Felsenstein, 1985) were performed at 1,000 replications in NJ method and at 100 replications in ML method. *Rattus norvegicus* (Gadaleta *et al.*, 1989) was employed as an out-group for reconstructing trees. In addition, the transversional divergence rate (0.5%/million years, Myr) at the third codon positions of mammalian cytochrome *b* gene (Irwin *et al.*, 1991) was used for divergence time estimation.

RESULTS AND DISCUSSION

Phylogenetic relationships among flying squirrels

In the present study, the partial sequences (1,068 bp) of cytochrome *b* gene were determined for five species of flying squirrels: *Belomys pearsonii*, *Glaucomys volans*, *Hylopetes phayrei*, *Petinomys setosus*, and *Pteromys momonga*. Percentage differences corrected by Kimura's two-parameter model (1980) and numbers of transitions and transversions obtained from pairwise comparison are shown in Table 2. Data of transversional substitutions at the third codon positions are present in Table 3. Phylogenetic trees reconstructed using the NJ and the ML methods showed essentially identical branching patterns (Fig. 1a and b), although bootstrap values at the deeper nodes on both trees were not always high enough. The first dichotomy isolated *Belomys* from the other flying squirrels (bootstrap values: 64% for NJ tree and 42% for ML tree) and then two clusters were constructed: one cluster consists of *Glaucomys*, *Hylopetes*, and *Petinomys* (bootstrap values: 74% for NJ tree and 43% for ML tree) and another was formed by *Petaurista* and *Pteromys* (bootstrap values: 89% for NJ tree and 49% for ML tree). However, the low bootstrap values at the deeper nodes, especially in ML tree, indicated that the order of early divergence of flying squirrels was still unclear, suggesting their polychotomy consisting of five

Table2. Pairwise comparisons of cytochrome *b* nucleotide sequences (1,068 bp) between eleven flying squirrel specimens

	BPE	HPH	GVO	ALC1	LEL1	LEN1	PEM1	PHG	PSE	PMO	PVO
BPE		21.9	21.9	21.4	22.1	21.8	22.7	22.4	22.3	24.9	24.8
HPH	115/86		19.2	20.9	19.6	19.3	21.4	21.6	2.4	23.0	23.0
GVO	122/78	116/62		23.1	20.8	19.7	22.2	21.5	19.9	22.3	23.8
ALC1	113/84	118/74	138/70		14.3	14.1	13.7	13.9	22.2	22.1	21.5
LEL1	119/83	111/71	120/71	113/21		1.4	14.5	14.9	20.8	20.5	21.6
LEN1	116/84	108/72	113/70	112/22	14/1		14.8	14.9	20.8	20.2	20.9
PEM1	128/78	127/68	135/66	108/22	114/23	117/22		3.8	23.4	20.2	20.5
PHG	126/78	129/68	130/66	112/20	119/21	118/22	35/4		23.1	20.2	21.2
PSE	114/90	17/8	116/68	121/82	113/79	112/80	135/76	133/76		24.7	24.0
PMO	131/92	121/88	127/76	127/74	114/75	113/74	113/74	115/72	130/92		14.6
PVO	135/87	126/83	142/71	129/67	134/62	130/61	123/65	130/63	129/87	113/25	

Data above the diagonal represent percentage differences corrected by Kimura's two-parameter model (Kimura, 1980).
Data below the diagonal are the numbers of nucleotide substitutions (transition/transversion).

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Table 3. Transversional substitutions at the third codon positions of cytochrome *b* gene between eleven flying squirrel specimens

	BPE	HPH	GVO	ALC1	LEL1	LEN1	PEM1	PHG	PSE	PMO	PVO
BPE		16.3	18.0	19.9	18.0	18.0	17.7	18.0	16.3	21.1	19.7
HPH	58		14.3	18.0	17.7	17.1	15.7	16.3	1.1	20.2	19.4
GVO	64	51		15.5	15.7	15.5	14.9	15.2	14.6	16.3	14.9
ALC1	71	64	55		4.5	4.8	5.6	5.1	19.3	17.4	16.0
LEL1	64	63	56	16		0.3	5.3	4.2	18.3	17.7	14.0
LEN1	64	61	55	17	1		5.3	4.2	18.3	17.1	13.8
PEM1	63	56	53	20	19	19		0.6	17.1	18.0	15.2
PHG	64	58	54	18	15	16	2		17.4	17.4	15.2
PSE	58	4	52	69	65	65	61	62		20.2	19.4
PMO	75	72	58	62	63	61	64	62	72		5.9
PVO	70	69	53	57	50	49	54	54	69	21	

Data above the diagonal represent transversional percentage differences between specimens. Data below the diagonal are the numbers of transversions.

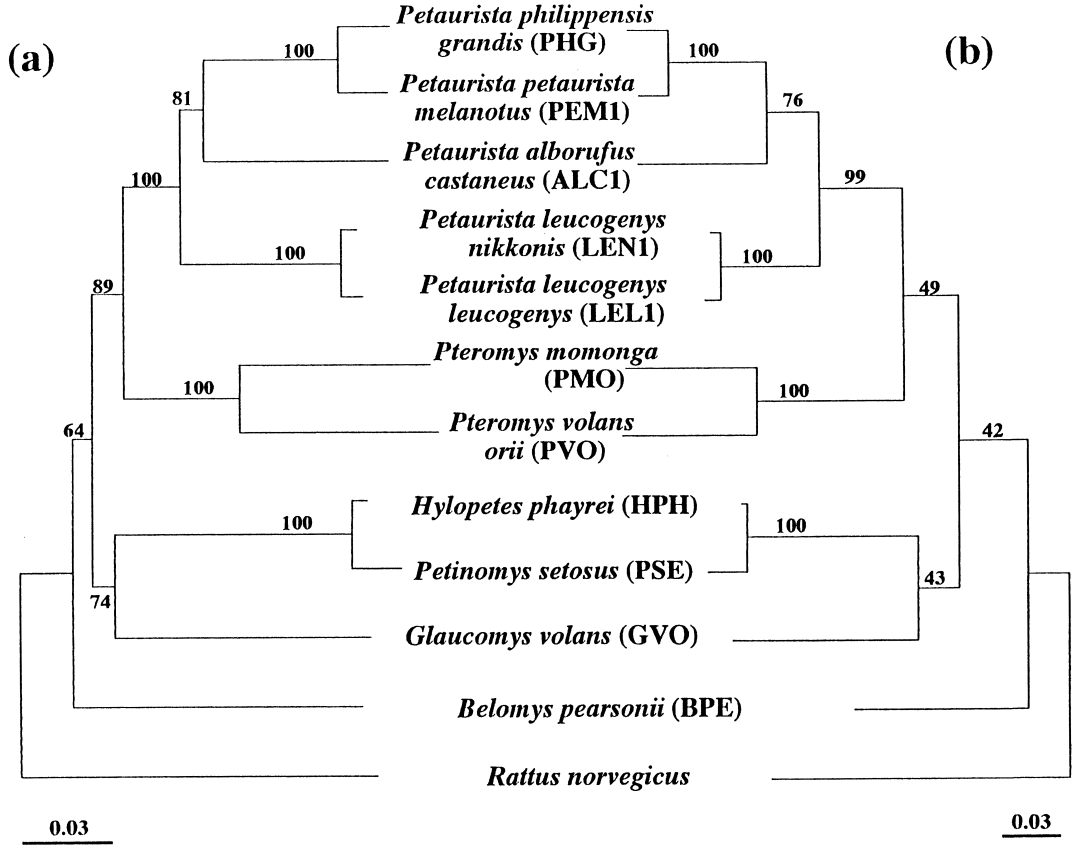


Fig. 1. Phylogenetic trees reconstructed by (a) the neighbor-joining (NJ) and (b) the maximum likelihood (ML) methods based on the cytochrome *b* nucleotide sequences. Scale bars for both trees represent branch length in terms of nucleotide substitutions per site. Numbers above branches indicate bootstrap values (%) derived from 1,000 replications for NJ tree and 100 replications for ML tree.

clusters: the genus *Belomys*, the genera *Hylopetes* and *Petinomys*, the genus *Glaucomys*, the genus *Petaurista*, and the genus *Pteromys*. Based on the fossil records, Mein (1970) and Black (1972) reported that flying squirrels were dominant in Europe in supplanting other squirrels during the Pliocene. Considering the abundant fossil records of flying squirrels from Europe and the unclear divergence order of flying squirrels in the present study, their divergence might have early occurred in the Eurasian Continent supplying ancestral stock.

Phylogenetic position of *Belomys pearsonii*

Belomys pearsonii is distributed in southern parts of the Eurasian Continent and Taiwan (Ellerman and Morrison-Scott, 1966; Mitchell, 1979; Lekagul and McNeely, 1988). This has been considered a monotypic genus (Corbet and Hill, 1991; Nowak, 1991), until recently. Whereas Corbet and Hill (1992) reclassified this species into the genus *Trogopterus*, renaming it *Trogopterus pearsonii*, the previous scientific name (*Belomys pearsonii*) seems to be generally adopted (e.g., Yu,

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1996) and is used in the present paper. Thus the classification of *Belomys pearsonii* is still controversial. Phylogenetic trees of the present study suggest an early divergence of *Belomys pearsonii* from other flying squirrels, although the bootstrap values were not so high (64% for NJ tree and 42% for ML tree). This is the first time that the phylogenetic relationships of this rare species has been examined. There are no analyses of fossil records, protein data, and morphological characteristics with which to compare our molecular data.

It has been reported that *Belomys pearsonii* inhabits dense forests (Lekagul and McNeely, 1988) and may not be as expert at gliding as some of the other genera of flying squirrels (Nowak, 1991). This behavioral data and our molecular data suggest that *Belomys pearsonii* is a specialized species in the group of flying squirrels.

Phylogenetic relationships between *Hylopetes* and *Petinomys*

There are 11 species in the genus *Hylopetes*. Flying squirrels belonging to this genus are widely distributed in southern Eurasia (Lekagul and McNeely, 1988; Corbet and Hill, 1991; 1992). *Petinomys* includes eight species and its distribution is similar to that of *Hylopetes*. Threfore, the two flying squirrel genera show the sympatric distribution (Lekagul and McNeely, 1988; Corbet and Hill, 1991; 1992). In the present study, *Hylopetes phayrei* was closely related to *Petinomys setosus* with high bootstrap iterations (100% for both trees), suggessting the recent divergence between them. Corbet and Hill (1992) described that *Petinomys* is closely related to *Hylopetes*, distinguishing the two genera by number of septa in the auditory bullae. Our data strongly supports their hypothesis. Using the available substitution rate at the third codon positions estimated from the mammalian cytochrome *b* genes (Irwin *et al*., 1991), the divergence between *Hylopetes* and *Petinomys* could have occurred approximately 2.2 Myr ago, suggesting that two flying squirrel genera diverged in Southeast or South Asia during the Pleistocene. Since Black (1972) reported that the Miocene fossil remains of *Petinomys* had been found in Europe, *Petinomys* may be considered ancestral to *Hylopetes*, especially.

Phylogenetic position of *Glaucomys*

The genus *Glaucomys*, which includes two species (*G. volans* and *G. sabrinus*), is the only flying squirrel genus found in the New World (Corbet and Hill, 1991). Compared with the Old World flying squirrels, *Glaucomys* has been carefully studied in detail (e.g., Wells-Gosling, 1985). However, the classification and the phylogenetic relationships of two *Glaucomys* species are still controversial (Burt, 1960; Muul, 1968; Thorington Jr., 1996; Arbogast, 1999). Several questions still remain concerning the phylogenetic position of *Glaucomys* within flying squirrels and the phylogenetic relationships between New World and Old World flying squirrels. Here we suggest that *Glaucomys* is most closely related to *Hylopetes* and *Petinomys* from Southeast Asia (Fig. 1), although the bootstrap values were low (74% for NJ tree and 43% for ML tree). Based on the immunological data, Hight *et al*. (1974) reported that *Petinomys* has a slightly greater affinity to *Glaucomys* than either *Petaurista* or *Pteromys*. Our cytochrome *b* data support the relationship supposed from the immunological data, and indicates that the divergence between *Glaucomys* and *Hylopetes* and that between *Glaucomys* and *Petinomys* occurred approximately 28.6 Myr ago and 29.2 Myr ago, respectively. Recently, based on the paleontological data, Marincovich Jr. and Gladenkov (1999) reported that the first break of the Bering Strait occured between 4.8 and 7.3–7.4 Myr ago. Considering the divergence time between *Glaucomys* and *Hylopetes* and that between *Glaucomys* and *Petinomys*, *Glaucomys* might have diverged from other flying squirrel genera much earlier than the formation of the Bering Strait. After the Oligocene-Miocene radiation of flying squirrels in Europe, the ancestral stock of *Glaucomys* may have migrated to North America, and at the same time the ancestor of *Hylopetes* and *Petinomys* might have migrated to South and Southeast Asia.

Phylogenetic relationships between *Petaurista* and *Pteromys*

The genus *Petaurista*, which includes ten species, is distributed in the southern parts of the Eurasian Continent, on many islands of Southeast Asia, and main islands of Japan excluding Hokkaido island (Corbet and Hill, 1991; 1992). The phylogenetic relationships within this genus has been studied by Oshida *et al*. (1992, 1996, 2000) using the mitochondrial DNA and chromosome data. On the other hand, flying squirrels belonging to the genus *Pteromys* are only two species and are widely distributed throughout the northern parts to the central parts of the Eurasian Continent and main islands of Japan (Corbet and Hill, 1991; Nowak, 1991). Only few attempts (Yanagawa *et al*., 1996) have been made for elucidating the intrageneric phylogeny of *Pteromys*.

The NJ tree (Fig. 1a) clearly indicates that *Petaurista* is closely related to *Pteromys* with a high bootstrap iteration (89%). In addition, the ML tree (Fig. 1b) confirms this close relationships, although the bootstrap value is not so high (49%). The mitochondrial 12S rRNA sequences data by Oshida *et al*. (1996) suggested that *Petaurista* is closely related to *Pteromys*. From cytochrome *b* data of the present study, we estimated that the divergence between *Petaurista* and *Pteromys* occurred approximately 28.0–36.0 Myr ago. The present geographic distribution of *Petaurista* does not overlap with *Pteromys*, except in Japan. Pleistocene fossils of *Petaurista* have been recorded in Europe (Black, 1972), China (Young, 1934; Young and Liu, 1950; Hsu *et al*., 1957; Hu and Qi, 1978) , and Japan (Hasegawa, 1966; Kowalski and Hasegawa, 1976; Kawamura, 1988). Accordingly, *Petaurista* may have been a dominant flying squirrel throughout the Eurasian Continent during the Pleistocene. Kawamura (1988) suggested that *Petaurista* may have expanded northward with the forests in the warmer periods of the middle Pleistocene. Pleistocene fossils of *Pteromys* have been found only from Japan (Kowalski and Hasegawa, 1976; Kawamura, 1988). Judging from the fossil records and the

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present distribution of these two genera, their biogeographic history could be described in the following manner. After the radiation in Europe during the Oligocene-Miocene, the ancestor of *Petaurista* might have occurred throughout the Eurasia until at least the middle Pleistocene. Its subsequent distribution was restricted to the southern parts of the Eurasian Continent by the southward shifting of its forest habitat. At the same time, the ancestor of *Pteromys* may have extended its distribution to northern and central parts of the Eurasia.

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