

## Phylogenies of Flying Squirrels (Pteromyinae)

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The phylogeny of flying squirrels was assessed, based on analyses of 80 morphological characters. Three published hypotheses were tested with constraint trees and compared with trees based on heuristic searches, all using PAUP\*. Analyses were conducted on unordered data, on ordered data (Wagner), and on ordered data using Dollo parsimony. Compared with trees based on heuristic searches, the McKenna (1962) constraint trees were consistently the longest, requiring 8–11 more steps. The Mein (1970) constraint trees were shorter, requiring five to seven steps more than the unconstrained trees, and the Thorington and Darrow (2000) constraint trees were shorter yet, zero to one step longer than the corresponding unconstrained tree. In each of the constraint trees, some of the constrained nodes had poor character support. The heuristic trees provided best character support for three groups, but they did not resolve the basal trichotomy between a *Glaucomys* group of six genera, a *Petaurista* group of four genera, and a *Trogopterus* group of four genera. The inclusion of the small northern Eurasian flying squirrel, *Pteromys*, in the *Petaurista* group of giant South Asian flying squirrels is an unexpected hypothesis. Another novel hypothesis is the inclusion of the genus *Aeromys*, large animals from the Sunda Shelf, with the *Trogopterus* group of smaller “complex-toothed flying squirrels” from mainland Malaysia and southeast Asia. We explore the implications of this study for future analysis of molecular data and for past and future interpretations of the fossil record.

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**KEY WORDS:** flying squirrels, phylogeny, taxonomic history

### INTRODUCTION

Flying squirrels comprise 38–45 species of Recent mammals, placed in 15 genera, and a number of fossil species placed in 13 additional genera (Corbet and Hill, 1986, 1992; Hoffmann *et al.*, 1993; McKenna and Bell, 1997; Thorington *et al.*, 1996). They are commonly, but not universally, placed in the family Sciuridae with the tree and ground squirrels, which comprise another 35 genera and 230 species.

Flying squirrels occur in North America and Eurasia, ranging from northern coniferous forest to the tropical lowlands, with most species occurring in southeast Asia (Hoff-

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mann *et al.*, 1993). A diverse fauna of flying squirrels is reported from the European Oligocene and Miocene (Mein, 1970; Bruijn and Uenay, 1989). Contrary to tree squirrels, there are no fossil or recent records of flying squirrels in South America or Africa. All flying squirrels are nocturnal, as opposed to the diurnal habits of all tree squirrels. They range in size from the pygmy flying squirrel *Petaurillus* (24 grams), to the giant flying squirrel *Petaurista* (1.5 kilograms) (Thorington and Heaney, 1981). They constitute the most diverse radiation of gliding mammals. Other extant gliding mammals include two species of *Dermoptera* (Wilson, 1993), six species of African “flying squirrels” (Dieterlen, 1993), and three families of gliding marsupials, which include a total of seven species (Groves, 1993).

There are a number of disagreements and uncertainties about the phylogeny of flying squirrels. One is the rooting of the phylogenetic tree—whether flying squirrels evolved from ancestral tree squirrels or whether they evolved from the Eocene paramyid rodents independently (Mein, 1970; Bruijn and Uenay, 1989). A second is whether gliding evolved twice, perhaps in two different tribes of tree squirrels (Black, 1963, 1972; Hight *et al.*, 1974), or whether flying squirrels form a monophyletic group (Thorington, 1984). The latter hypothesis, based on morphological data, has not been contested, although we and others have searched for evidence to the contrary (Thorington and Darrow, 2000; Thorington *et al.*, 1997). A third uncertainty is the grouping of the 15 recognized genera of Recent flying squirrels (McKenna, 1962; Mein, 1970; Thorington *et al.*, 1996; Thorington and Darrow, 2000) and their affinities with the recognized genera of fossil forms. In this paper we first review the taxonomic history of flying squirrels, which forms the basis for all subsequent work. Taxonomic judgments frequently represent phylogenetic hypotheses that have subsequently been supported or refuted by further morphological and molecular studies. Second, we review the phylogenetic histories of this group and present three hypotheses based on morphological data. Finally, we test these three by presenting the first character-based cladistic analysis of flying squirrel relationships.

### Taxonomic History

The taxonomic history of flying squirrels is convoluted. Linnaeus described two flying squirrels in 1758: the European flying squirrel as *Sciurus volans* and the North American flying squirrel as *Mus volans*. Because he gave them both the species name *volans*, and both were soon considered to belong to the genus *Sciurus*, another species name, *volucella*, was given to the North American squirrel by Pallas in 1778 and was used for 137 years, until 1915.

An additional four flying squirrels were described during the rest of the 18<sup>th</sup> century, three of them being placed in the genus *Sciurus*. The fourth was placed in a new genus, *Petaurista*, by Link (1795), but this generic name was lost and not used again for more than a century. In 1800, George Cuvier introduced the name *Pteromys* for flying squirrels, separating them from the non-gliding squirrels placed in the genus *Sciurus*. He placed two species in *Pteromys*, the European flying squirrel and one of the giant flying squirrels from Southern Asia. Disagreements about which should bear the name *Pteromys* bedeviled the literature for 150 years. In 1825 Frédéric Cuvier introduced a second generic name, *Sciuropterus*. These two generic names were used for all but one of the 77 species named during the 19<sup>th</sup> century. Initially, *Pteromys* was used for the large flying squirrels of southern Asia, and *Sciuropterus*

for the small to medium-size squirrels. (During most of the 19<sup>th</sup> century, *Sciuropterus volans* (Linnaeus, 1758) was the accepted name of the European flying squirrel and *Sciuropterus volucella* (Pallas, 1778) was the name of the southern flying squirrel of North America.)

The one species not included in these two genera was the distinctive woolly flying squirrel, *Eupetaurus cinereus*, named by Thomas (1888). Thus in Major's (1893) classification of squirrels, only three genera—*Pteromys*, *Sciuropterus*, and *Eupetaurus*—were listed. At that time, *Pteromys* included the large flying squirrels. Subsequently Thomas (1896) resurrected the name *Petaurista* for these large flying squirrels. *Sciuropterus* included all the other, mostly smaller, flying squirrels, a diversity of forms as noted by Major.

The generic subdivision of the flying squirrels was furthered by Heude (1898), who placed the complex-toothed flying squirrel *Pteromys xanthipes* in a new genus: *Trogopterus*. Then in 1908, Thomas reexamined "the *Sciuropterus* group" and divided it into six genera: *Trogopterus*, *Belomys*, *Pteromyscus*, *Sciuropterus*, *Petaurillus*, and *Iomys*, based on features of teeth and crania. He further divided the genus *Sciuropterus* F. Cuvier, 1825, into four subgenera: *Sciuropterus* (the small North Eurasian flying squirrels), *Glaucomyss* (both the Himalayan and the North American flying squirrels), and *Hylopetes* and *Petinomys* (small to medium-size flying squirrels of Southern Asia).

These four subgenera were subsequently raised to full generic rank. Howell (1915) named the Himalayan flying squirrel, *Eoglaucomyss*, and separated it from *Glaucomyss*, the North American flying squirrels, recognizing both as full genera. With this action, he also separated the north Eurasian and North American flying squirrels at the generic level, which caused the name of the North American squirrel to change from *Sciuropterus volucella* (Pallas, 1778) to *Glaucomyss volans* (Linnaeus, 1758). Pocock (1923) elevated *Hylopetes* and *Petinomys* to full genera, based on differences between their bacula and the baculum of *Glaucomyss volans*. Subsequently, Ellerman (1947) combined *Eoglaucomyss* with *Hylopetes*, but Thorington *et al.* (1996) reported anatomical evidence that demonstrated this was inappropriate.

When Thomas (1896) resurrected the name *Petaurista* Link, 1795, for the large Asian flying squirrels, he considered the name *Pteromys* G. Cuvier, 1800, to be a junior synonym, but Miller (1914) subsequently noted that *Pteromys* should be used for the small Eurasian flying squirrel, with *Sciuropterus* F. Cuvier, 1825, as a junior synonym. These changes led to a plethora of ways in which generic names were used in the first half of the 20<sup>th</sup> century, when an additional 131 species and subspecies of flying squirrels were described. The name *Sciuropterus* was still used by Simpson (1945), but Ellerman and Morrison-Scott (1951) affirmed Miller's (1914) conclusion that the name *Pteromys* should be used for the north Eurasian flying squirrel, based on Cuvier's (1800) original description and a subsequent clarification by Fleming (1822).

With the delineation of three additional genera, *Aeromys* Robinson and Kloss, 1915, *Aeretes* G. M. Allen, 1940, and *Biswamoyopterus* Saha, 1981, the current taxonomic arrangement was reached of approximately 40 species of flying squirrels allocated to 15 genera (Hoffmann *et al.*, 1993, with the additional recognition of *Eoglaucomyss*).

The taxonomic name of the group, at the family level, expresses how closely related flying squirrels are thought to be to other squirrels. Brandt (1855) separated them from other squirrels, naming them the subfamily Pteromyinac, but he kept them in the squirrel family Sciuridae. Major (1893) suggested that flying squirrels are not closely related to other squirrels, but he did not formally recognize this idea, including both in the subfamily Sciurinae.

Because Miller (1912) considered *Pteromys* to be a junior synonym of *Petaurista*, he gave the flying squirrels the new name Petauristidae, and he raised them to a family separate from the Sciuridae, stating, "The Petauristidae are so sharply differentiated from the Sciuridae, that it seems preferable to recognize the two groups as families." When the name *Pteromys* was accepted as a senior synonym for *Sciuropterus*, the name Pteromyinae became the valid family-level name again, but the family versus subfamily question remains open (Corbet and Hill, 1992; Hoffman *et al.*, 1993.)

### Phylogenetic Hypotheses

From a review of the taxonomic history, a number of phylogenetic hypotheses become evident. First, those who have carefully reviewed the flying squirrels have considered them to be a monophyletic group (Major, 1893; Thomas, 1908; Ellerman, 1940). This was questioned by Black (1963) and by Hight *et al.* (1974), but supported by Thorington (1984). Second, the relationship of the flying squirrels to the other squirrels is ambiguous (Emry and Korth, 1996): whether they evolved from an Oligocene tree squirrel or are more distantly related, having been derived independently from Eocene paramyids.

Certain phylogenetic hypotheses of inter-generic relationships are clearly indicated in the taxonomic literature. Thomas (1908) considered the three genera *Trogopterus*, *Belomys*, and *Pteromyscus* to form a monophyletic group. This was supported by McKenna (1962) and has not been seriously questioned. Corbet and Hill (1992) even proposed that *Trogopterus* and *Belomys* should be congeneric.

Thomas (1908) maintained a genus *Sciuropterus* that included the current genera *Glaucomyss*, *Eoglaucomyss*, *Pteromys*, *Hylopetes*, and *Petinomys*, implying a hypothesis of monophyly for the group. Within it, he treated *Glaucomyss* and *Eoglaucomyss* as sister taxa. The latter hypothesis was not accepted by Ellerman (1961), who considered *Eoglaucomyss* and *Hylopetes* to be congeneric. Thorington *et al.* (1996) argued that all three genera should be recognized but their evidence could not distinguish between the two competing sister-group relationships, *Glaucomyss-Eoglaucomyss* or *Eoglaucomyss-Hylopetes*.

A sister-group relationship between *Petaurista* and *Aeretes* is suggested by the relative recency of separation of *Aeretes* (Allen, 1940) from the genus *Petaurista*. Earlier authors considered them to be congeneric.

More explicit phylogenetic hypotheses were presented by McKenna (1962) and Mein (1970). McKenna (1962) grouped the genera of flying squirrels in two different ways. He presented a diagram with the genera assorted into eight boxes connected by arrows. The meaning of this diagram is obscure. He combined boxes to provide a supra-generic grouping of flying squirrels into five groups, which we take to be hypotheses of monophyly (Figure 1):

1. The *Glaucomyss* group, consisting of *Glaucomyss*, *Eoglaucomyss*, *Pteromys*, *Olisthomys* (= *Petinomys setosus*), and *Petaurillus*.
2. The *Iomys* group consisting of only *Iomys*.
3. The *Petinomys* group including *Aeromys*, *Petinomys* (exclusive of *P. setosus*), "*Petinomys*" *vordermanni*, and *Hylopetes*.
4. The *Trogopterus* group including the three genera *Trogopterus*, *Pteromyscus*, and *Belomys*.
5. The *Petaurista* group consisting of *Petaurista*, *Aeretes*, and *Eupetaurus*.

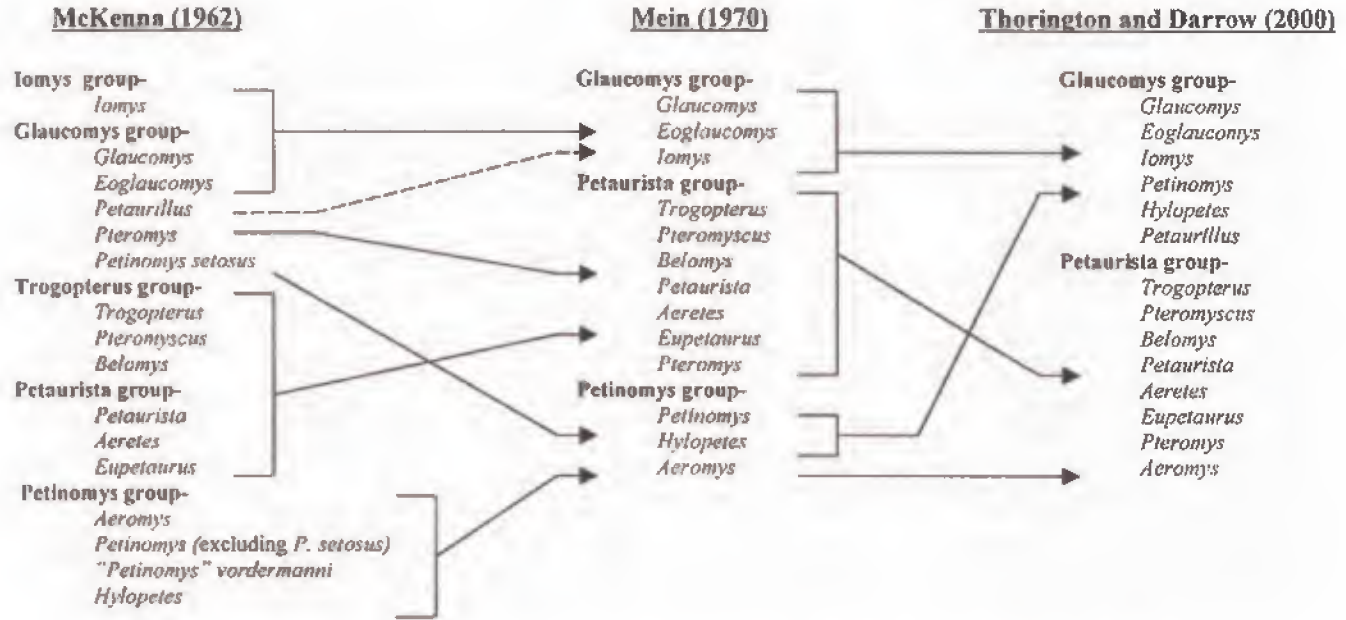


Fig. 1. Three phylogenetic hypotheses. Arrows indicate reallocation of genera to groups. Dashed line indicates probable reallocation of *Petaurillus* by Mein (see page 104).

Mein (1970) reviewed McKenna's characters and came to different conclusions about the supra-generic groupings of flying squirrels (Figure 1), listing the features of each of his groups (Figure 2).

I. The *Glaucomys* group consisting of *Glaucomys*, *Eoglaucomys*, and *Iomys*. This combined McKenna's *Glaucomys* and *Iomys* groups, while excluding *Pteromys*. Mein did not examine *Petaurillus*, but he surely would have included it in this group, because it exhibits the diagnostic characters. The features that he listed to diagnose this group are the combination of smooth enamel and absence of lophules, with other common characters being absence of the metaloph on M3, no mesostyle, presence of an anterior sinuside, and absence of anteroconid.

II. The *Petaurista* group, including McKenna's *Trogopterus* group and *Pteromys*, consists of the genera *Pteromys*, *Trogopterus*, *Pteromyscus*, *Belomys*, *Aeretes*, *Petaurista*, and *Eupetaurus*. It is characterized by the combination of smooth enamel and presence of lophules. Other common characters are presence of a metaloph on M3 and presence of a mesostylid in the form of a crest attached to the metaconid.

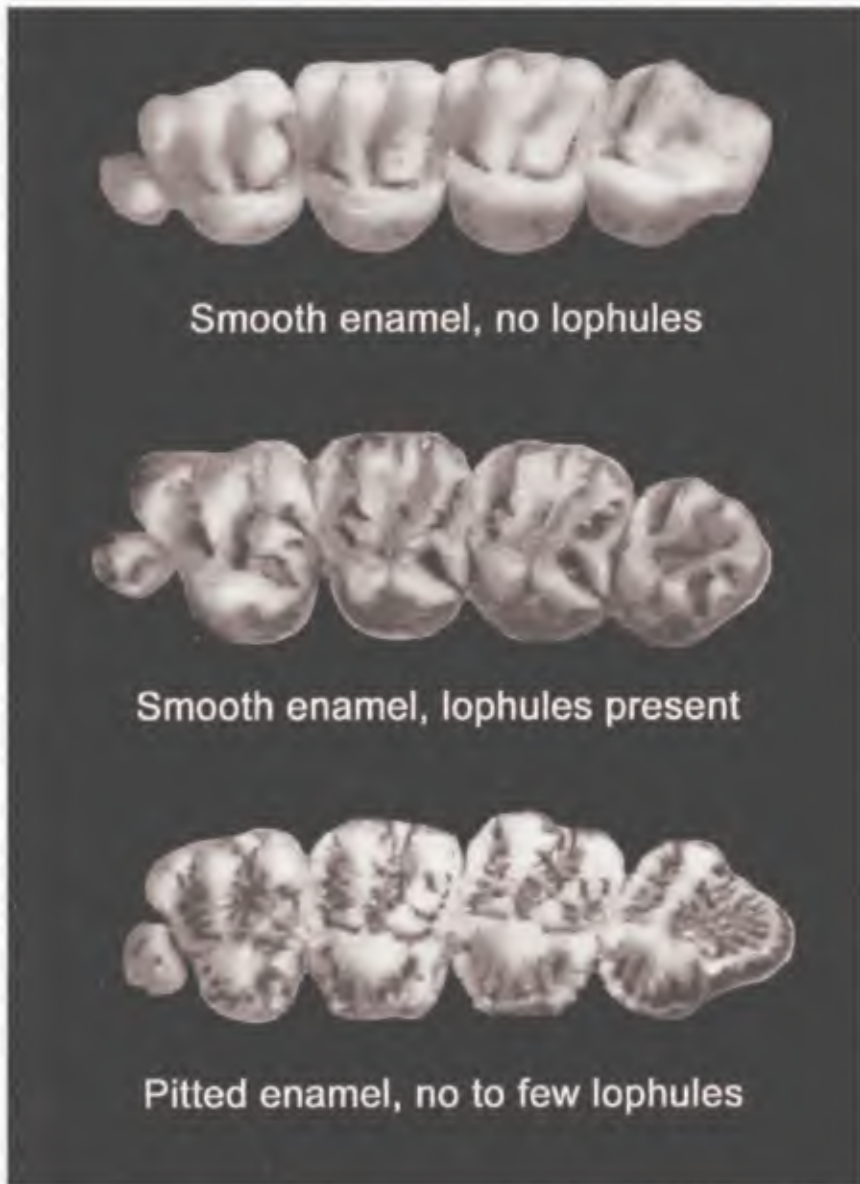
III. The *Petinomys* group, which is almost the same as McKenna's, includes *Petinomys*, *Hylopetes*, and *Aeromys*. It is characterized by pitted enamel and no or few lophules. Other common characters are the absence of a hypolophid and of a metaloph on M3.

Thorington and Darrow (2000) noted that flying squirrels could be divided into two groups (Figure 1), based on differences in detail of the wrist articulations and the insertion of the tibiocarpalis muscle at the ankle. They hypothesized that the gliding membrane evolved very early in the history of the subfamily (Thorington *et al.*, 1998), followed shortly by the evolution of these modifications at wrist and ankle. Later, flying squirrels adapted to various feeding niches, with concomitant evolution of the teeth and skulls. Therefore, they hypothesized that these postcranial features are primary and diagnose two basal clades, while the cranial and dental features diagnose subsequent clades. Their *Glaucomys* group includes Mein's groups I and III together, but with *Aeromys* excluded. Their *Petaurista* group includes Mein's group II, with the addition of *Aeromys*.

## MATERIALS AND METHODS

Of the 15 recognized genera of flying squirrels, we have studied all except *Biswamoyopterus*, and we have examined 35 of the 40+ species. These are listed in Appendix 1. Those that have been dissected are indicated with (d). Other material studied includes skulls (s), teeth (t), and postcranial (p) skeletal material. Dental features were examined on all teeth and recorded for each tooth independently. However, some features are present or absent consistently on more than one tooth. These were not considered to be independent of one another and were not treated separately. We chose characters that vary among the flying squirrel genera and excluded characters that vary among the species of a genus. Thus this study does not address the question of whether polytypic genera are monophyletic; for most relevant species we lacked postcranial data.

Of the 14 genera included, six are monotypic and four contain two species each. Another contains three species, but one of these is known only from the type specimen. The remaining genera, *Petaurista*, *Hylopetes*, and *Petinomys*, each contain more than



**Fig. 2.** Enamel characteristics used by Mein (1970) to divide flying squirrels into three morphological groups that could be distinguished in the fossil record.

three species. Half of the genera were completely sampled at the species level (*Glaucomys* was represented by both species). Other genera were represented by the species with the most complete set of data. Seven taxa of tree squirrels, including one fossil

squirrel (Emry and Thorington, 1982; Emry and Korth, 1996, 2001), were included as outgroups to root the tree. These represent four tribes of squirrels (Sciurini: *Sciurus carolinensis*, *Sciurus vulgaris*, and the Eocene fossil, *Douglasciurus jeffersoni*; Protoxerini: *Protoxerus stangeri*; Callosciurini: *Callosciurus prevostii* and *Callosciurus notatus*; and Ratufini: *Ratufa bicolor*, *R. affinis*, and *R. indica* combined). This includes all the tribes of tree squirrels that have been suggested as ancestors of flying squirrels. *Douglasciurus* is the oldest known fossil squirrel and probably pre-dates the divergence of tribes.

Fifty-one multistate and twenty-nine binary characters (Appendices 2 and 3) were compiled for 22 taxa and analyzed with PAUP\* 4.0b4 (Swofford, beta test version). Character states noted with a question mark could not be determined with the specimens available. "Variable" refers to intraspecific variation and reflects the genetic and evolutionary intermediate state between always "obsolete" and always "present." Five uninformative characters were excluded from the analyses. Character states were coded at the generic level because of problems of missing data for a number of species, e.g. when specimens for dissection or skeletons were not available, and the pattern of missing data might present a consistent bias.

Maximum parsimony analyses were conducted using heuristic searches with 200 random addition sequence replicates, tree bisection and reconnection (TBR) branch swapping, and no limits on the number of trees found. Two measures of nodal support were calculated: Bremer support (Bremer, 1994) and bootstrap support (Felsenstein, 1985). Bootstrap support was calculated for 5000 replicates using heuristic searches of 20 random additions and TBR branch swapping within each replicate. We explored the consequences of treating our characters in three different ways (Appendix 2). First, all characters were unordered and equally weighted (Fitch parsimony). Second, 24 characters were unordered and 51 characters were ordered (Wagner parsimony). Characters were ordered with intermediate stages being intermediate morphologically. Third, 24 characters were unordered, 36 characters were ordered, and 15 characters were assumed to be uniquely derived and irreversible (Dollo parsimony). Characters were treated as uniquely derived only when the ancestral state was obviously the same, whether flying squirrels evolved from paramyids or from sciurid tree squirrels.

In addition, we evaluated the fit of our data to three prior hypotheses of the relationship among the flying squirrels. We enforced topological constraints based on the major groupings of genera in these hypotheses. The McKenna (1962) hypothesis postulates five groups of genera, the Mein (1970) hypothesis postulates three groups, and the Thorington and Darrow (2000) hypothesis distinguishes two groups. Within these groups and between the groups, no constraints were imposed. Each hypothesis was tested with the characters treated in the same three ways as in the maximum parsimony analysis (i.e., Fitch, Wagner, or Dollo parsimony).

We explored the differences between dental and non-dental characters by dividing the data set and conducting phylogenetic analyses. The dental subset included 42 informative characters. The non-dental subset (cranial and postcranial) included 33 informative characters. Both subsets were analyzed under assumptions of Fitch, Wagner, and Dollo parsimony. These analyses were conducted to explore whether the dental and non-dental characters contained different phylogenetic signals. This is of particular interest because the paleontological record of flying squirrels is predominantly based on teeth.



## RESULTS

### Characters Unordered

With the 75 characters unordered (Fitch parsimony) and with no constraints imposed, a parsimony analysis yielded nine most parsimonious trees of 328 steps (consistency index = 0.40; retention index = 0.55). When constrained by the McKenna (1962) hypothesis (Figure 1), the shortest trees were eight steps longer (four trees of 336 steps) than the unconstrained trees. Constrained by the Mein (1970) hypothesis (Figure 1), the shortest trees were seven steps longer (seven trees of 335 steps). Constrained by the Thorington and Darrow (2000) hypothesis (Figure 1), the shortest tree was one step longer (one tree of 329 steps) than those found in the unconstrained analysis.

The strict consensus tree shown in Figure 3 (based on the nine shortest trees) groups six genera—*Hylopetes*, *Petinomys*, *Petaurillus*, *Iomys*, *Glaucomys*, and *Eoglaucomys*—identical to the *Glaucomys* group of Thorington and Darrow. It also groups *Trogopterus*, *Belomys*, *Pteromyscus*, and *Aeromys*. This is the *Trogopterus* group of McKenna, but with the addition of *Aeromys*. *Petaurista* and *Aeretes* form a third group. Neither *Eupetaurus* nor *Pteromys* joins any group in the strict consensus tree.

### Characters Ordered

With 24 characters unordered and 51 characters ordered (Wagner parsimony), an unconstrained parsimony analysis yielded nine shortest trees of length 353 steps (consistency index = 0.37; retention index = 0.56). Constrained by the McKenna hypothesis, the shortest trees were ten steps longer (three trees of 363 steps). Constrained by the Mein hypothesis, the shortest tree was five steps longer (one tree of 358 steps). Constrained by the Thorington and Darrow hypothesis, the shortest trees were one step longer (15 trees of 354 steps).

The strict consensus tree shown in Figure 4 (based on the nine shortest trees) groups the same four genera of the *Trogopterus* group: *Trogopterus*, *Belomys*, *Pteromyscus*, and *Aeromys*. It also groups *Petaurista*, *Aeretes*, and *Eupetaurus*. *Hylopetes* and *Petinomys* form a third group. None of the other five genera form consistent groups. In four of the nine trees, eight genera form a monophyletic group, the same as the *Petaurista* group of Thorington and Darrow (Figure 1). In the other five trees, however, the eight genera are divided into two monophyletic groups: the *Trogopterus* group and a group composed of *Petaurista*, *Aeretes*, *Eupetaurus*, and *Pteromys*. These two groups are placed variously among the other flying squirrels. This analysis provides no support for a *Glaucomys* group, and flying squirrels do not form a monophyletic group in the strict consensus tree.

### Characters Uniquely Derived

With 24 characters unordered, 36 characters ordered, and 15 characters ordered and uniquely derived (Dollo parsimony), an unconstrained parsimony analysis yielded two shortest trees of length 373 steps (consistency index = 0.35; retention index = 0.62). Constrained by the McKenna hypothesis, the shortest trees were 11 steps longer (two trees of 384 steps, strict consensus tree in Figure 6). Constrained by the Mein hypothesis, the shortest tree was five steps longer (one tree of 378 steps, Figure 7). Constrained by the

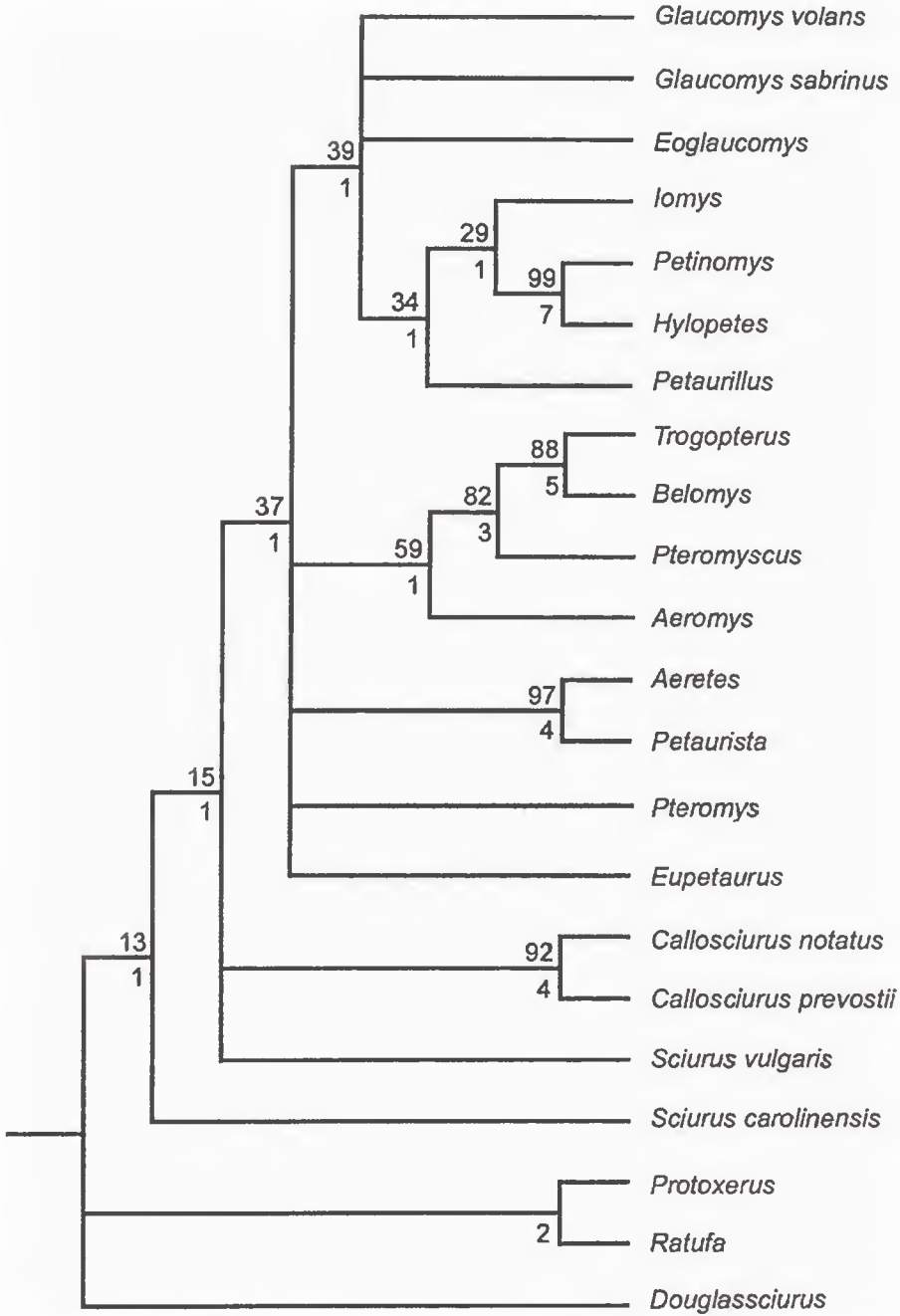


Fig. 3. Strict consensus tree based on unordered data (Fitch parsimony). Numbers above the line are bootstrap values; numbers below the line are Bremer support values.

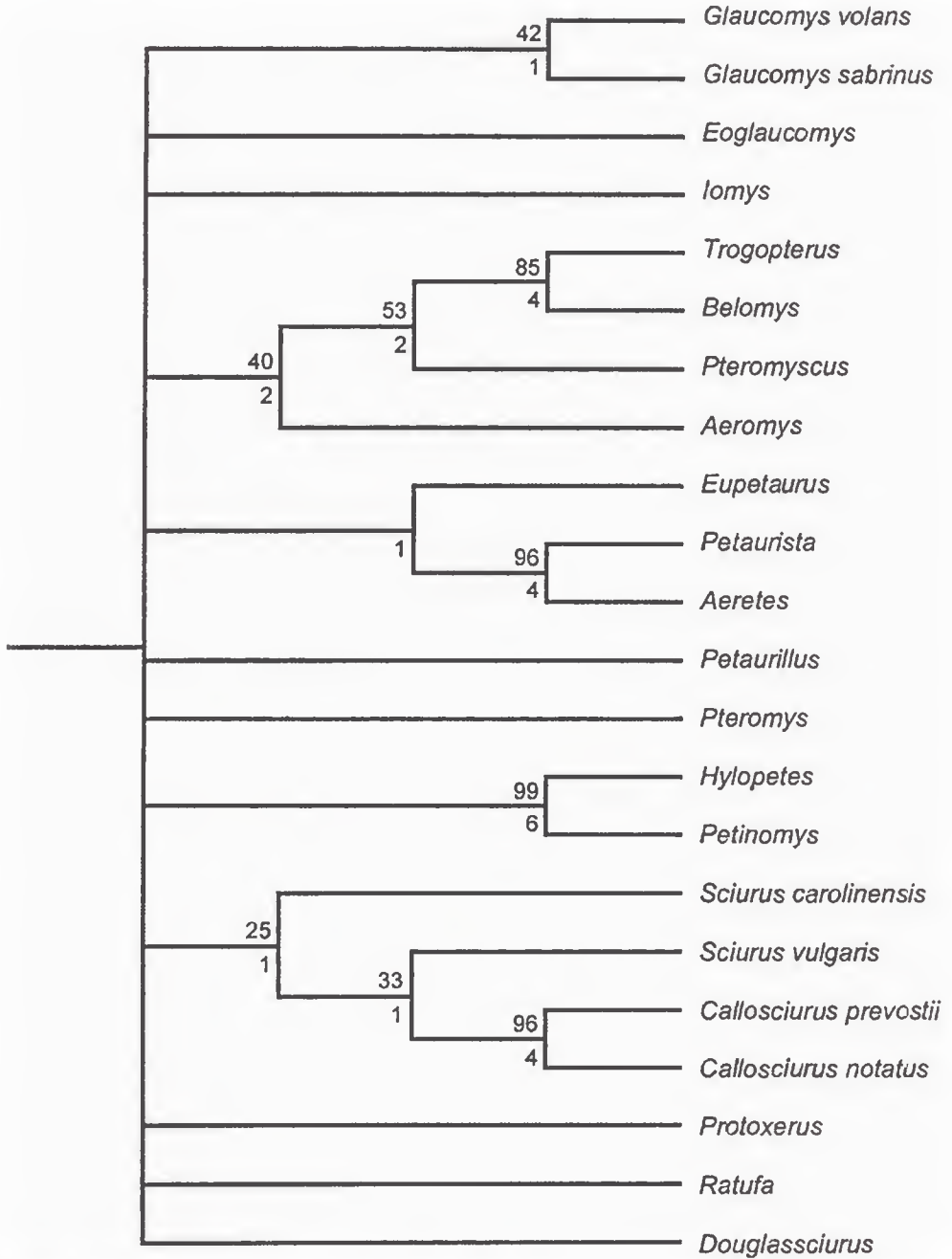


Fig. 4. Strict consensus tree based on ordered data (Wagner parsimony). Numbers above the line are bootstrap values; numbers below the line are Bremer support values.

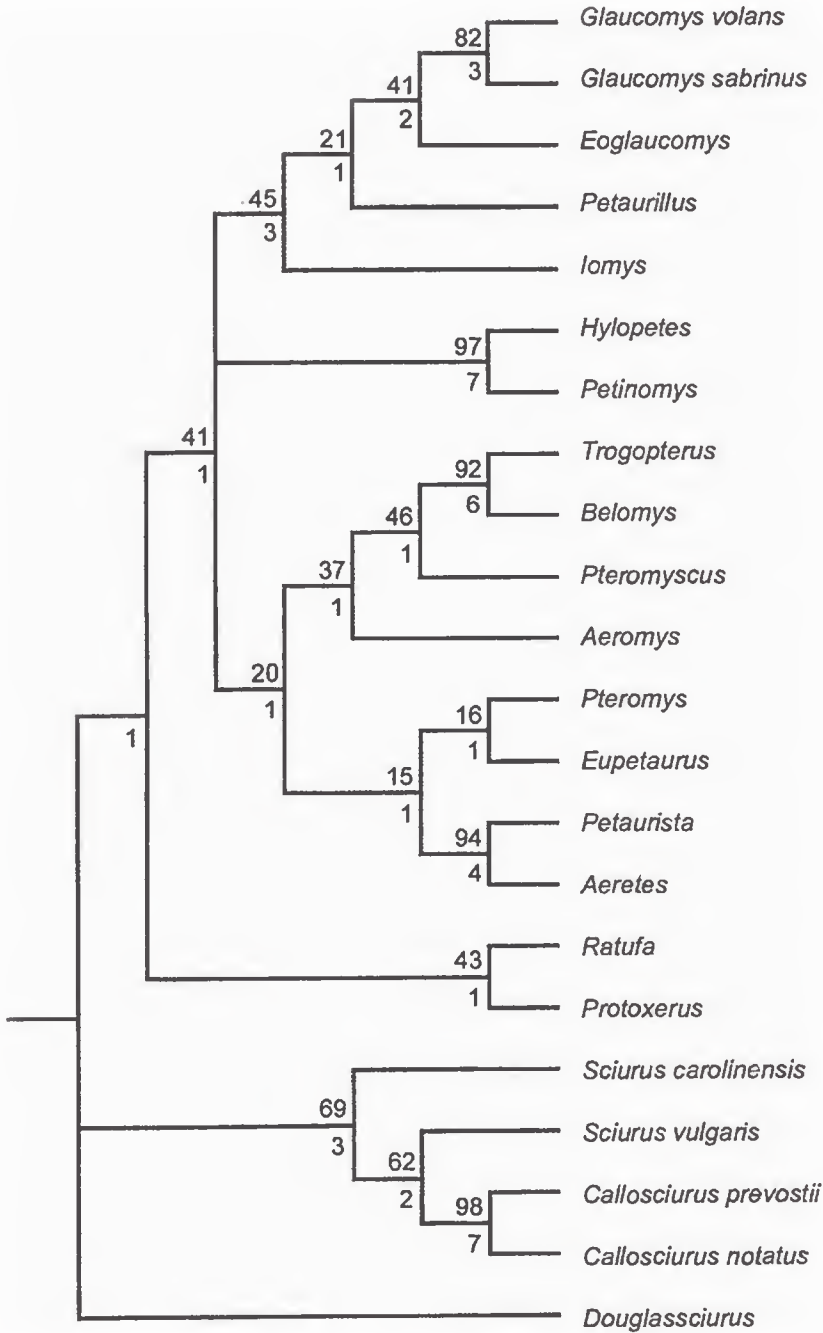


Fig. 5. Strict consensus tree based on ordered data with Dollo parsimony. Numbers above the line are bootstrap values; numbers below the line are Bremer support values.

Thorington and Darrow hypothesis, the shortest tree was the same length (one tree of 373 steps, Figure 8).

In the strict consensus tree (Figure 5), the flying squirrels are divided into three monophyletic groups. The first group contains the eight genera of the *Petaurista* group of Thorington and Darrow. The second group contains the genera *Glaucomys*, *Eoglaucomys*, *Petaurillus*, and *Iomys*. The third group contains *Hylopetes* and *Petinomys*. This is a consensus of two trees, one of which is like the Thorington and Darrow hypothesis and the other has the *Hylopetes-Petinomys* group as the out-group of all other flying squirrels. Thus the consensus tree differs from the Thorington and Darrow hypothesis by the separation of *Hylopetes* and *Petinomys* from the *Glaucomys* group. It differs from the Mein hypothesis by the placement of *Aeromys* in the *Trogopterus* group, instead of in the *Hylopetes* group.

### Constraint Trees

In all three of these analyses—with characters unordered, ordered, or uniquely derived—there is a consistent pattern that the McKenna hypothesis requires the most steps, the Mein hypothesis fewer steps, and the Thorington and Darrow hypothesis fewer yet. In the McKenna constraint tree (Figure 6), certain placements of taxa are not well supported in it or in the other trees recovered. In particular, the placement of *Pteromys* in his *Glaucomys* group, *Aeromys* in the same group with *Hylopetes*, and the placement of *Iomys* in its own group, is not well supported. Excluding *Pteromys* from the *Glaucomys* group reduces the length of the shortest tree by at least two steps. The placement of *Aeromys* in the *Hylopetes-Petinomys* group is not found in any of the unconstrained analyses, in which *Aeromys* is uniformly placed in the *Trogopterus* group. The case against the placement of *Iomys* in its own group is more equivocal, but *Iomys* joins the *Glaucomys* group in both the unordered and the uniquely derived analyses.

The Mein constraint tree (Figure 7) also places *Aeromys* in the same group with *Hylopetes*, on the basis of the shared character of enamel crenulation (Figure 2) and contrary to the parsimony analyses. Maintaining a *Hylopetes-Petinomys* group, separate from the *Glaucomys* group, is contradicted in the parsimony analysis of unordered characters, but it is in agreement with one of the two shortest trees of the analysis using Dollo parsimony, and hence with the strict consensus tree also.

The Thorington and Darrow constraint tree (Figure 8) divides the flying squirrels into two monophyletic groups: the *Glaucomys* group of six genera and a group of eight genera of the *Trogopterus* and *Petaurista* groups. In the analysis of unordered characters, the strict consensus tree (Figure 3) includes the six-genus *Glaucomys* group, but it does not include the eight-genus group. Both the six-genus and the eight-genus groups are recovered in one of the two shortest trees of the analysis with characters uniquely derived.

### Bootstrap and Bremer Support for Nodes

Bootstrap values are given in order below, for the strict consensus trees based on unordered data, ordered data, and ordered data with Dollo parsimony (Figures 3–5). Bootstrap values for nodes not found on the strict consensus trees are given in italics. On all three consensus trees, there is strong bootstrap support for three pairs of genera:

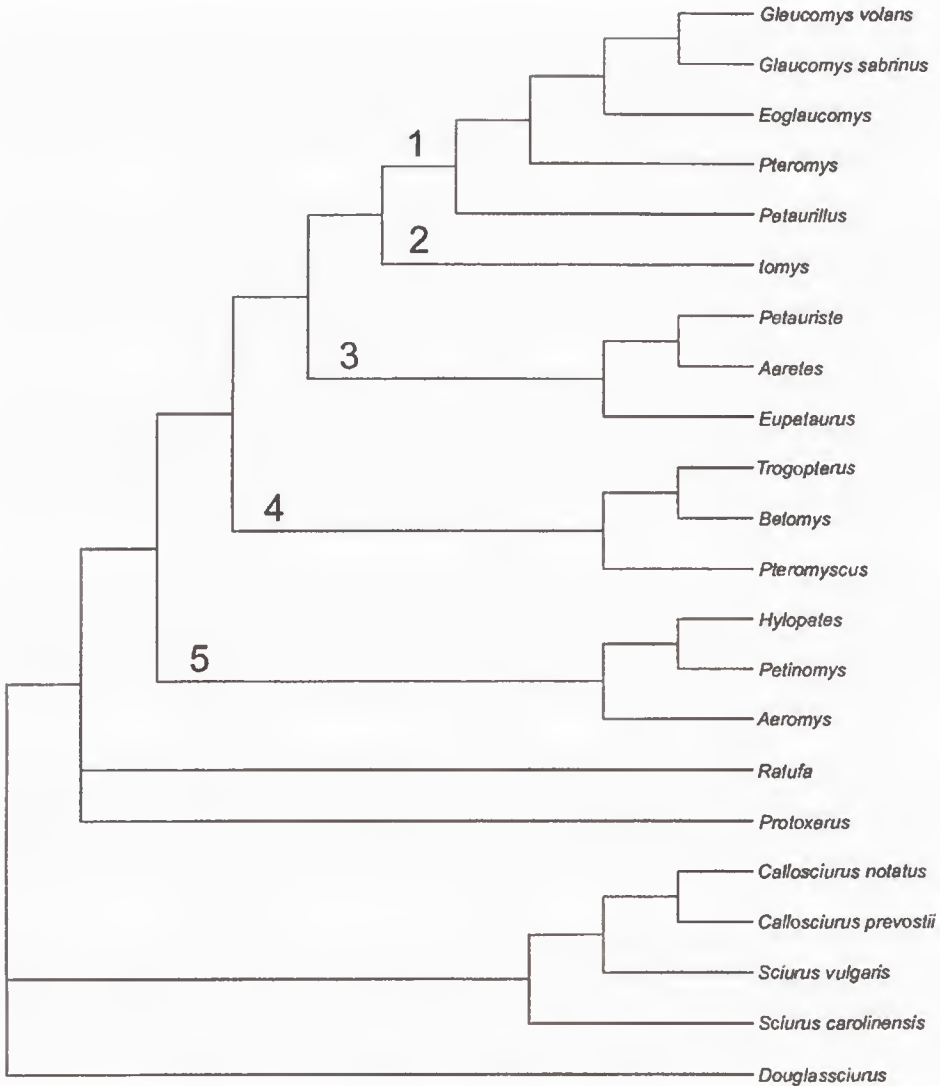


Fig. 6. Strict consensus tree for McKenna's (1962) hypothesis, with flying squirrels divided into five monophyletic groups, numbered 1-5. Analysis based on constraint tree of ordered data with Dollo parsimony.

*Trogopterus-Belomys* (88, 85, 92 percent), *Petaurista-Aeretes* (97, 96, 94 percent), and *Hylopetes-Petinomys* (99, 99, 97 percent). Bootstrap support for a clade comprising *Glaucomys volans* and *Glaucomys sabrinus* is much lower (48, 42, and 82 percent). There is variable support for the inclusion of *Pteromyscus* in the *Trogopterus-Belomys* group (82, 53, 46 percent) and weaker support for the further inclusion of *Aeromys* (59, 40, and 37 percent). Inclusion of *Eupetaurus* in a clade with *Petaurista-Aeretes* has support of 44, <5, and 19 percent.

The monophyly of flying squirrels receives bootstrap support of 37, 34, and 41 per-

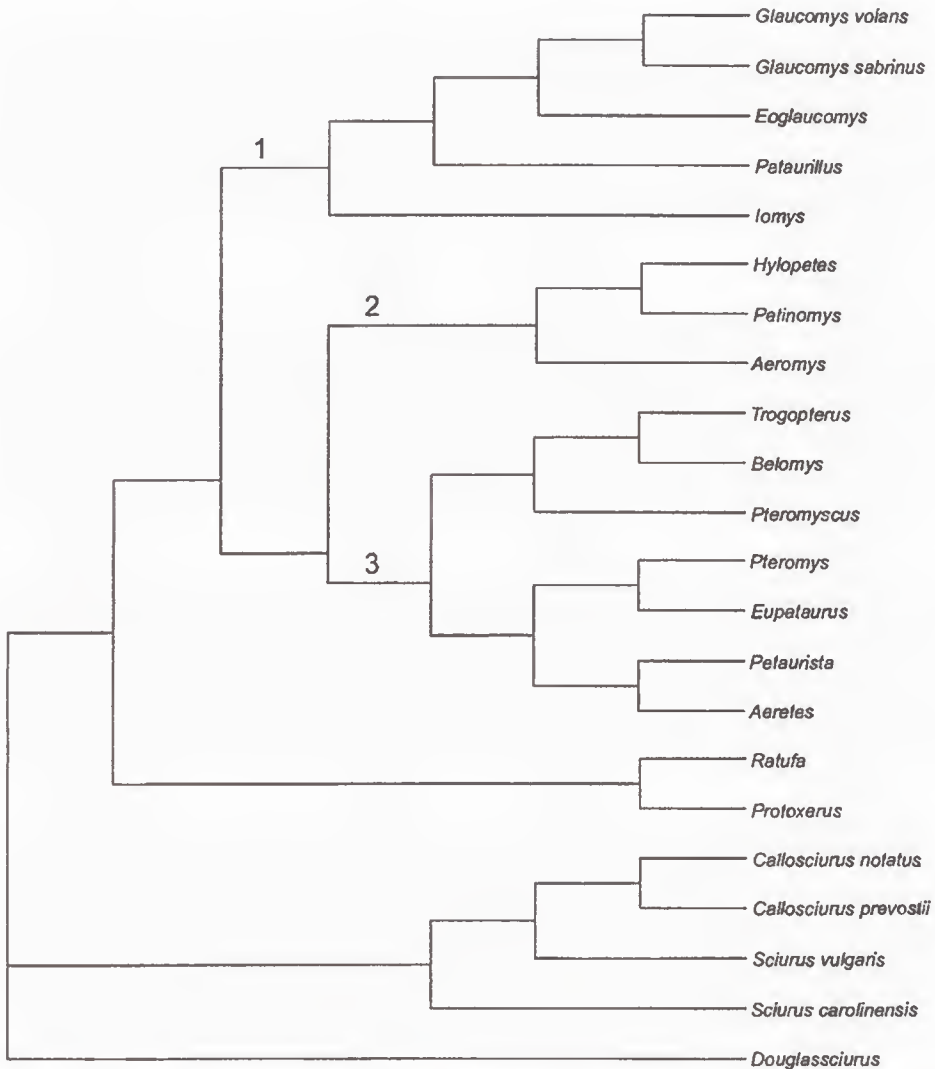


Fig. 7. Single most parsimonious tree for Mein's (1970) hypothesis, with flying squirrels divided into three monophyletic groups, numbered 1-3. Analysis based on constraint tree of ordered data with Dollo parsimony.

cent. Bootstrap support values of the *Glaucomys* group (including *Hylopetes* and *Petinomys* with *Glaucomys*, *Eoglaucomys*, *Petaurillus*, and *Iomys*) are 39, 31, and 21 percent. Bootstrap values for the combined *Petaurista* and *Trogopterus* groups (including also *Belomys*, *Pteromyscus*, *Aeromys*, *Aereles*, *Eupetaurus*, and *Pteromys*) are also lower (11, 38, and 20 percent).

In Tables I-III, we list characters that change at selected nodes and Bremer support for these nodes. Bremer support on the three trees ranges from 6-7 for *Hylopetes*-*Petinomys*, from 4-6 for *Trogopterus*-*Belomys*, to four for *Petaurista*-*Aereles*, and three or less

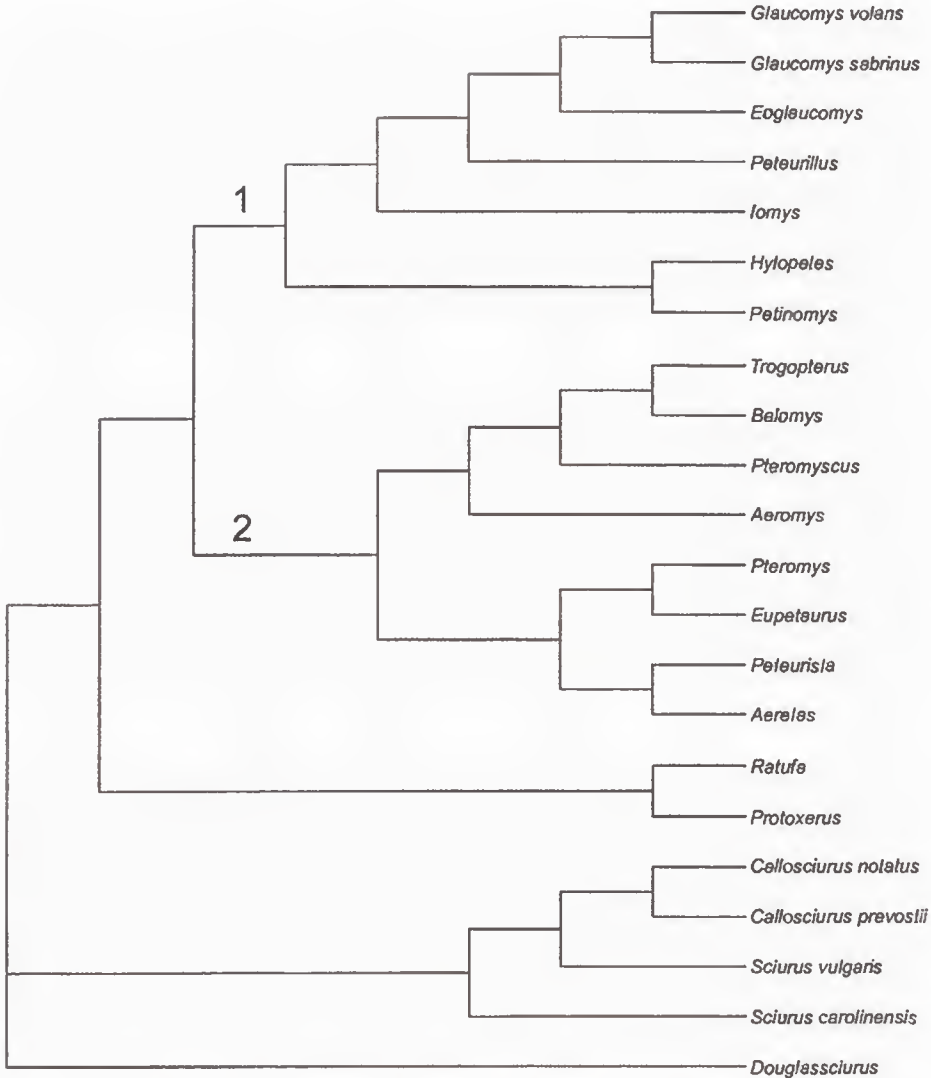


Fig. 8. Single most parsimonious tree for Thorington and Darrow's (2000) hypothesis, with flying squirrels divided into two monophyletic groups, numbered 1-2. Analysis based on constraint tree of ordered data with Dollo parsimony.

for other nodes. The support levels for these other nodes are given in the tables and in Figures 3-5.

### Synapomorphies

There are patterns among the synapomorphies listed. In the analysis of the unordered characters, dental and postcranial characters are approximately equally represented (Table I). In the analysis of the ordered characters, the dental characters are more strongly rep-



resented (Table II). In the analysis of the ordered characters using Dollo parsimony, the more basal nodes are characterized by changes in the postcranial characters and the more distal nodes are characterized more by changes in the dental characters (Table III).

### Analyses of Dental vs. Non-Dental Characters

We divided our data set into dental characters (42 informative characters) and non-dental characters (33 informative characters). In analyses of the dental characters alone, the strict consensus trees (not shown) did not include a monophyletic grouping of flying squirrels, whether the characters were treated unordered (117 trees, Length = 174, CI = 0.45, RI = 0.58), ordered (15 trees, Length = 183, CI = 0.43, RI = 0.60), or uniquely derived (20 trees, Length = 197, CI = 0.40, RI = 0.64). Instead, the following tree squirrels were included within clades of flying squirrels: *Callosciurus*, *Sciurus*, *Protoxerus*, and *Ratufa*. In analyses of the non-dental characters, the shortest consensus trees always included a monophyletic grouping of flying squirrels, with data ordered (212 trees, Length = 127, CI = 0.42, RI = 0.65), unordered (472 trees, Length = 138, CI = 0.38, RI = 0.65) or uniquely derived (276 trees, Length = 145, CI = 0.37, RI = 0.71). This is in agreement with the general observation that there is considerable variation among flying squirrels and among tree squirrels in diets and dental morphology, in contrast with the uniformity of postcranial features associated with gliding. With the reduced data sets, the internal structure of these trees was not well supported.

## DISCUSSION

### Hypotheses

A number of hypotheses drawn from the literature were explicitly tested in this study. In one respect, this separates hypothesis formulation from hypothesis testing. However, we cannot be sure that the data we used for testing these hypotheses were not used by the authors who formulated them, and in some cases we know that the same data were used for both, as undesirable as this is. Thomas (1908) based his hypotheses on cranial and dental characters; McKenna (1962) listed a larger variety of features, but relied mostly on dental characters. Mein (1970) was focused on the identification of fossils; therefore he purposely restricted himself to dental features. Thorington and Darrow (2000) emphasized postcranial characters. This study was deliberately restricted to morphological data based on Recent species, so that future studies of molecular data and paleontological data can provide independent tests of hypotheses.

### Clades

No two hypotheses agree on the genera to be included in the “*Glaucomys* group.” Thomas (1908) and McKenna (1962) included the Eurasian flying squirrel, *Pteromys*, but Mein (1970) excluded it on the basis of dental morphology, and Thorington and Darrow (2000) excluded it on the basis of postcranial anatomy. The combined data strongly support its exclusion.

The “*Glaucomys* group,” seen in the strict consensus tree based on unordered data (Figure 3), is the same as that recognized by Thorington and Darrow (2000). It includes

**Table 1.** Analyses of Unordered Data (Figure 3) With Character Changes and Bremer Support Values at Selected Nodes

---

**Node: *Glaucomys, Eoglaucomys, Petaurillus, Iomys, Hylopetes, Petinomys* (1)**

**Strict consensus tree:**

- 30: Protoloph connection to protocone  $M_3$ —(3) solid to (2) variable.  
 51: Size of supraorbital process—(2) long to (1) short.  
 64: Elevated scapholunate tuberosity on pisiform—(0) no to (1) yes  
 78: Distal tibial tuberosity present—(0) no to (1) yes

**Additional characters [most parsimonious trees #s given in square brackets]:**

- 5: Color of incisors—(0) deep orange to (1) yellowish orange. [1–3]  
 19: Protoconule  $P_4$ —(0) not evident to (1) incorporated into loph, but still evident. [1–3]  
 62: Semitendinosus III discrete or joined—(4) well separated from rest of musculature, deeply embedded in skin of uropatagium, to (2) joined by tendon to semitendinosus I, II. [4–6]  
 63: Insertion of tibiocarpalis—(3) Metatarsal II to (1) distal tibial tuberosity. [4–9]  
 75: Proximal falciform process on scapholunate—(0) absent to (2) present, not prominent. [1–3]
- 

**Node: *Trogopterus, Belomys, Pteromyscus, Aeromys* (1)**

**Strict consensus tree:**

- 17: Parastyle sub cone  $P_4$ —(0) absent to (1) present  
 23: Metaconule  $M_1$ ,  $M_2$ —(0) not evident to (2) pinched off from loph

**Additional characters [most parsimonious tree #s given in square brackets]:**

- 5: Color of incisors—(0) deep orange to (2) yellow. [4–9]  
 7: Hypocone—(0) no hypocone to (2) large protocone and smaller hypocone connected by a thin loph, but separated by some distance. [4–9]  
 8: Mesostyle  $P_4$ —(0) absent to (2) present. [2]  
 9: Mesostyle  $M_1$ ,  $M_2$ —(0) absent to (2) present. [2]  
 19: Protoconule  $P_4$ —(0) not evident to (1) incorporated into loph, but still evident. [1–6, 9]  
 48: Masseteric tubercles—(1) somewhat prominent to (0) not prominent. [1]  
 54: Zygomaticomandibularis fossa—(0) deep to (1) shallow. [4–5, 7–8]  
 69: Articulation between metacarpal II and centrale—(0) yes to (1) no. [2–9]  
 70: Scapholunate—capitate articulation—(1) yes to (0) no. [4–9]  
 74: Shape of pisiform facet on scapholunate—(0) circular to (1) grooved. [2–9]
- 

**Node: *Trogopterus, Belomys, Pteromyscus, Aeromys, Petaurista, Aeretes, Eupetaurus* (not on strict consensus tree)**

**Characters [most parsimonious tree #s given in square brackets]:**

- 6: Complexity of maxillary tooth pattern—(0) simple: no cross lophs to (2) complex: more than one cross loph. [1]  
 44: Complexity of mandibular tooth pattern—(0) simple or (1) somewhat complex to (2) complex. [1]  
 70: Scapholunate—capitate articulation—(1) yes to (0) no. [1–3]  
 71: Centrale—hamate articulation—(0) no to (1) yes. [1–3]  
 75: Proximal falciform process on scapholunate—(0) absent to (1) present, prominent. [1–3]  
 77: Angle between proximal falciform and body of scapholunate—(0) perpendicular to (1) acutely angular. [1–3]
- 

**Node: *Petaurista, Aeretes, Eupetaurus* (not on strict consensus tree)**

**Characters [most parsimonious tree #s given in square brackets]:**

- 2:  $P_4$  size relative to  $M_1$  size—(0) smaller to (2) larger. [4–9]  
 34: Posterior flexus—(0) absent to (1) present. [4–9]  
 48: Masseteric tubercles—(2) prominent to (1) somewhat prominent. [4–9]  
 70: Scapholunate—capitate articulation—(1) yes to (0) no. [4–9]  
 73: Size of triquetral facet on scapholunate—(0) short to (1) long. [4–9]

Table I. (Continued)

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<b>Node:</b> <i>Petaurista</i> , <i>Aeretes</i> , <i>Eupetaurus</i> , <i>Pteromys</i> (not on strict consensus tree)
<b>Characters [most parsimonious tree #s given in square brackets]:</b>
33: Metaloph connection to protocone / hypocone $M_3$ —(0) NA to (4) solid. [4–9]
36: Metacone on $M_3$ —(0) absent to (1) present. [4–9]
61: Origin of semitendinosus III—(1) Caudal vertebrae 5–8 to (2) Caudal vertebrae 9–15. [4–9]

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the genera *Glaucomys*, *Eoglaucomys*, *Iomys*, *Petaurillus*, *Petinomys*, and *Hylopetes*. Monophyly of the group is not well supported. Within the group, all historic hypotheses have linked the North American *Glaucomys* and Himalayan *Eoglaucomys*, usually implicitly as sister taxa (explicitly by Thomas, 1908; and by Thorington and Darrow, 2000), but this analysis provides weak support for a sister-group relationship. Instead, it places them basal to the radiation and suggests that the North American branch of flying squirrels diverged early from the Asian members of the *Glaucomys* group. The *Hylopetes-Petinomys* group is strongly supported (bootstrap values, 97–99%), in agreement with all hypotheses, but it is excluded from the *Glaucomys* group in the two other strict consensus trees (on ordered data with Wagner or with Dollo parsimony, Figures 4 and 5, respectively), in partial agreement with Mein's (1970) hypothesis. In the analysis based on Dollo parsimony, this seems to result from the Dollo requirement that crenulation of the molars evolved only once, consonant with Mein's hypothesis. Even with this requirement, one of the two most parsimonious trees includes the *Hylopetes-Petinomys* group within the *Glaucomys* group. Bootstrap values for the inclusion of the *Hylopetes-Petinomys* group within the *Glaucomys* group, as hypothesized by Thorington and Darrow (2002), are 37, 25, and 20 percent. We conclude that structure within the "*Glaucomys* group" is not well defined by this study, except for the *Hylopetes-Petinomys* node. In a phylogenetic study based on cytochrome *b*, Oshida *et al.* (2000) found that *Glaucomys* and *Hylopetes* formed a clade separate from a *Petaurista-Pteromys* clade, as in our strict consensus tree based on unordered data. Their study included no other flying squirrels, so it is consistent with both Mein's and Thorington and Darrow's hypotheses but contradicts McKenna's hypothesis.

A "*Petaurista* group" is recognized in the strict consensus tree using Dollo parsimony (Figure 5). It includes four genera: the wide-spread Asian giant flying squirrels, *Petaurista*, the monotypic Chinese *Aeretes*, the woolly flying squirrel of the Himalayas, *Eupetaurus*, and the northern Eurasian *Pteromys*, a grouping not suggested in any previous hypothesis based on morphology, but with bootstrap support of only 15 percent. The *Petaurista-Aeretes* pair has bootstrap values of 97, 96, and 94 percent.

A new "*Trogopterus* group", comprising four genera of eastern Asian squirrels, *Trogopterus*, *Belomys*, *Pteromyscus*, and *Aeromys*, is recognized in all three strict consensus trees (Figures 3–5), with bootstrap values of 59, 40, and 37 percent. The first three genera form a monophyletic group, as first hypothesized by Thomas (1908) and later by McKenna (1962), with bootstrap values of 82, 53, and 46 percent. The *Trogopterus-Belomys* pair, the complex-toothed flying squirrels, has bootstrap values of 88, 85, and 92% in support of this generally accepted hypothesis.

The strict consensus tree based on Dollo parsimony shows a combined *Petaurista-Trogopterus* group of 8 genera, (including also *Belomys*, *Pteromyscus*, *Aeromys*, *Aeretes*,

**Table II.** Analysis of Ordered Data (Figure 4) With Character Changes and Bremer Support Values at Selected Nodes

---

**Node: *Trogopterus*, *Belomys*, *Pteromyscus* (2)**

**Strict Consensus Tree**

- 41: Hypoconule P<sub>4</sub>—(0) absent to (1) present.  
 42: Hypoconule M<sub>1</sub>, M<sub>2</sub>—(0) absent to (1) present.  
 55: Number of septa per bullae—(1) two to three, to (4) more than three, sliver pattern.

**Additional characters [most parsimonious tree #s given in square brackets]:**

- 1: P<sub>3</sub>—(0) absent to (1) very small to small. [1–2, 4–7]  
 6: Complexity of maxillary tooth pattern—(0) simple: no cross lophs to (1) somewhat complex: one cross loph. [1–3, 8–9]  
 10: Mesostyle M<sub>3</sub>—(0) absent to (2) present. [4–7]  
 11: Mesostyle position P<sub>4</sub>—(3) discrete to (1) associated with paracone. [1–3, 8–9]  
 12: Mesostyle position M<sub>1</sub>, M<sub>2</sub>—(3) discrete to (1) associated with paracone. [1–3, 8–9]  
 13: Mesostyle position M<sub>3</sub>—(0) NA to (1) associated with paracone. [4–7]  
 41: Hypoconule P<sub>4</sub>—(0) absent to (1) present. [4–7]  
 42: Hypoconule M<sub>1</sub>, M<sub>2</sub>—(0) absent to (1) present. [4–7]  
 44: Complexity of mandibular tooth pattern—(0) simple to (1) somewhat complex. [1–3, 8–9]  
 55: Number of septa per bullae—(1) two or three to (4) more than three, sliver pattern. [4–7]  
 72: Lesser multangular—scapholunate articulation—(0) no to (1) yes. [4–7]
- 

**Node: *Trogopterus*, *Belomys*, *Pteromyscus*, *Aeromys* (2)**

**Strict consensus Tree:**

- 17: Parastyle sub cone P<sub>4</sub>—(0) absent to (1) present.

**Additional characters [most parsimonious tree #s given in square brackets]:**

- 5: Color of incisors—(0) deep orange to (2) yellow.  
 7: Hypocone—(0) no hypocone to (2) large protocone and smaller hypocone connected by a thin loph, but separated by some distance. [1–3, 8–9]  
 8: Mesostyle P<sub>4</sub>—(0) absent to (2) present. [4–7]  
 9: Mesostyle M<sub>1</sub>, M<sub>2</sub>—(0) absent to (2) present. [4–7]  
 19: Protoconule P<sub>3</sub>—(0) not evident to (1) incorporated into loph, but still evident. [4–7]  
 22: Metaconule P<sub>4</sub>—(1) incorporated into loph, but still evident to (2) pinched off from loph.  
 40: Anterior flexus—(0) absent to (1) present. [1–3]  
 45: Length of rostrum—(2) long to (0) short or (1) intermediate. [4–9]  
 50: Openness of distal half of eye orbit—(0) mostly open to (1) somewhat open. [1–3, 9]  
 54: Zygomaticomandibularis fossa—(0) deep to (1) shallow.  
 65: Triquetral process on pisiform—(0) no to (1) yes. [1–3, 8]  
 69: Articulation between metacarpal II and centrale—(0) yes to (1) no. [4–7, 9]  
 74: Shape of pisiform facet on scapholunate—(0) circular to (1) grooved. [4–7]  
 76: Distal falciform process on scapholunate—(0) absent to (1) present, prominent.
- 

**Node: *Petaurista*, *Aeretes*, *Eupetaurus* (1)**

**Strict consensus Tree:**

- 2: P<sub>4</sub> size relative to M<sub>1</sub> size—(0) smaller to (2) larger  
 6: Complexity of maxillary tooth pattern—(1) somewhat complex: one cross loph to (2) complex: more than one cross loph.  
 34: Posterior flexus—(0) absent to (1) present  
 44: Complexity of mandibular tooth pattern—(1) somewhat complex to (2) complex.

**Additional characters [most parsimonious tree #s given in square brackets]:**

- 46: Width of rostrum—(2) narrow to (1) intermediate. [1–3, 8]  
 48: Masseteric tubercles—(2) prominent to (1) somewhat prominent. [8]  
 52: Size of jugal process—(0) none to (1) small. [8]  
 70: Scapholunate—capitate articulation—(1) yes to (0) no. [1–3, 8]  
 73: Size of triquetral facet on scapholunate—(0) short to (1) long. [8]  
 75: Proximal falciform process on scapholunate—(1) present, prominent to (0) absent. [2–3]

Table II. (Continued)

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**Node: *Glaucomys*, *Eoglaucomys*, *Petaurillus*, *Iomys* (not on strict consensus tree)**

**Characters [most parsimonious trees #s given in square brackets]**

- 3: Crenulation—(1) low to (0) none. [9]
  - 8: Mesostyle  $P_4$ —(2) present to (0) absent. [9]
  - 9: Mesostyle  $M_1$ ,  $M_2$ —(2) present to (0) absent. [9]
  - 10: Mesostyle  $M_3$ —(2) present to (0) absent. [9]
  - 11: Mesostyle position  $P_4$ —(3) discrete to (0) NA. [9]
  - 12: Mesostyle position  $M_1$ ,  $M_2$ —(3) discrete to (0) NA. [9]
  - 22: Metacnule  $P_4$ —(2) pinched off from loph (1) incorporated into loph. but still evident. [1,3]
  - 60: Mastoid process inflated—(0) no to (1) yes. [1, 3, 9]
  - 64: Elevated scapholunate tuberosity on pisiform—(0) no to (1) yes. [1,3]
  - 78: Distal tibial tuberosity present—(0) no to (1) yes. [1,3]
- 

**Node: *Glaucomys*, *Eoglaucomys*, *Petaurillus*, *Iomys*, *Petaurista*, *Aeretes*, *Eupetaurus*, *Pteromys* (not on strict consensus tree)**

**Characters [most parsimonious tree #s given in square brackets]:**

- 3: Crenulation—(1) low to (0) none. [1, 3]
  - 8: Mesostyle  $P_4$ —(2) present to (0) absent. [1–2]
  - 9: Mesostyle  $M_1$ ,  $M_2$ —(2) present to (0) absent. [1–3]
  - 10: Mesostyle  $M_3$ —(2) present to (0) absent. [1–3]
  - 12: Mesostyle position  $M_1$ ,  $M_2$ —(3) discrete to (0) NA. [1–3]
  - 13: Mesostyle position  $M_3$ —(3) discrete to (0) NA. [2–3]
  - 48: Masseteric tubercles—(0) not prominent to (1) somewhat prominent or (2) prominent. [1–2]
- 

**Node: *Trogopterus*, *Belomys*, *Pteromyscus*, *Aeramys*, *Hylapetes*, *Petinomys* (not on strict consensus tree)**

**Characters [most parsimonious trees #s given in square brackets]:**

- 5: Color of incisors—(0) deep orange to (2) yellow. [1, 3]
  - 19: Protoconule  $P_3$ —(0) not evident to (1) incorporated into loph. but still evident. [1–2]
  - 69: Articulation between metacarpal II and centrale—(0) yes to (1) no. [1, 3]
  - 70: Scapholunate—capitate articulation—(1) yes to (0) no. [1, 3]
  - 74: Shape of pisiform facet on scapholunate—(0) circular to (1) grooved. [1, 3]
  - 75: Proximal falciform process on scapholunate—(0) absent to (1) present, prominent. [2–3]
- 

**Node: *Trogopterus*, *Belomys*, *Pteromyscus*, *Aeramys*, *Petaurista*, *Aeretes*, *Eupetaurus* (not on strict consensus tree)**

**Characters [most parsimonious trees #s given in square brackets]:**

- 20: Protoconule  $M_1$ ,  $M_2$ —(0) not evident to (1) incorporated into loph. but still evident. [4–5]
  - 46: Width of rostrum—(2) narrow to (1) intermediate. [4–6]
  - 48: Masseteric tubercles—(2) prominent to (1) somewhat prominent. [4–6]
  - 52: Size of jugal process—(0) none to (1) small or (2) large. [4–6]
  - 54: Size of jugal process—(0) none to (1) small. [4–6]
  - 70: Scapholunate—capitate articulation—(1) yes to (0) no. [4–6]
  - 75: Proximal falciform process on scapholunate—(0) absent to (1) present, prominent. [6]
- 

**Node: *Trogopterus*, *Belomys*, *Pteromyscus*, *Aeramys*, *Petaurista*, *Aeretes*, *Eupetaurus*, *Pteromys* (not on strict consensus tree)**

**Characters [most parsimonious trees #s given in square brackets]:**

- 6: Complexity of maxillary tooth pattern—(0) simple: no cross lophs to (1) somewhat complex: one cross loph. [4–7]
  - 22: Metacnule  $P_4$ —(1) incorporated into loph. but still evident to (2) pinched off from loph. [4–5, 7]
  - 44: Complexity of mandibular tooth pattern—(0) simple to (1) somewhat complex. [4–7]
  - 51: Size of supraorbital process—(1) short to (2) long. [4–5, 7]
  - 60: Mastoid process inflated—(1) yes to (0) no. [4–5, 7]
  - 62: Semitendinosus III discrete or joined—(2) joined by tendon to semitendinosus I, II to (4) well separated from rest of musculature, deeply embedded in skin of uropatagium. [4–5, 7]
  - 64: Elevated scapholunate tuberosity on pisiform—(1) yes to (0) no. [4–5, 7]
  - 65: Triquetral process on pisiform—(0) no to (1) yes. [4–5, 7]
  - 78: Distal tibial tuberosity present—(1) yes to (0) no. [4–5, 7]
-

Table III. Dollo Parsimony Analyses (Figure 5) With Character Changes and Bremer Support Values at Selected Nodes

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**Node: *Trogopterus*, *Belomys*, *Pteromyscus* (1)**

**Strict Consensus Tree**

- 3: Crenulation—(2) heavy to (1) low.  
 11: Mesostyle position  $P_4$ —(3) discrete to (1) associated with paracone.  
 12: Mesostyle position  $M_1$ ,  $M_2$ —(3) discrete to (1) associated with paracone.  
 41: Hypoconule  $P_4$ —(0) absent to (1) present.  
 42: Hypoconule  $M_1$ ,  $M_2$ —(0) absent to (1) present.  
 55: Number of septa per bullae—(2) more than three, not honeycomb pattern to (1) two to three.

**Additional characters [most parsimonious tree #s given in square brackets]:**

- 10: Mesostyle  $M_3$ —(0) absent to (2) present. [2]  
 12: Mesostyle position  $M_1$ ,  $M_2$ —(3) discrete to (1) associated with paracone. [2]
- 

**Node: *Trogopterus*, *Belomys*, *Pteromyscus*, *Aeromys* (1)**

**Strict Consensus Tree**

- 7: Hypocone—(0) no hypocone to (2) large protocone and smaller hypocone connected by a thin loph, but separated by some distance.  
 17: Parastyle sub cone  $P_4$ —(0) absent to (1) present.  
 40: Anterior flexus—(1) present to (0) absent.  
 45: Length of rostrum—(2) long to (0) short or (1) intermediate.  
 64: Elevated scapholunate tuberosity on pisiform—(1) yes to (0) no.

**Additional characters [most parsimonious tree #s given in square brackets]:**

- 5: Color of incisors—(0) deep orange to (2) yellow. [1]
- 

**Node: *Petaurista*, *Aeretes*, *Eupetaurus*, *Pteromys* (1)**

**Strict Consensus Tree**

- 3: Crenulation—(2) heavy to (0) none.  
 19: Protoconule  $P_4$ —(1) incorporated into loph, but still evident to (0) not evident.  
 33: Metaloph connection to protocone / hypocone  $M_3$ —(0) NA to (4) solid.  
 36: Metacone on  $M_3$ —(0) absent to (1) present.  
 48: Masseteric tubercles—(0) not prominent to (1) somewhat prominent.  
 61: Origin of semitendinosus III—(1) Caudal vertebrae 5–8 to (2) Caudal vertebrae 9–15.
- 

**Node: *Trogopterus*, *Belomys*, *Pteromyscus*, *Aeromys*, *Petaurista*, *Aeretes*, *Eupetaurus*, *Pteromys* (1)**

**Strict Consensus Tree**

- 2:  $P_4$  size relative to  $M_1$  size—(1) equal to (2) larger.  
 6: Complexity of maxillary tooth pattern—(1) somewhat complex: one cross loph to (2) complex: more than one cross loph.  
 22: Metaconule  $P_4$ —(1) incorporated into loph, but still evident to (2) pinched off from loph.  
 65: Triquetral process on pisiform—(0) no to (1) yes.

**Additional characters [most parsimonious tree #s given in square brackets]:**

- 46: Width of rostrum—(2) narrow to (1) intermediate. [2]  
 51: Size of supraorbital process—(1) short to (2) long. [2]  
 62: Semitendinosus III discrete or joined—(3) separate, but lies just caudal to other heads of semitendinosus to (4) well separated from rest of musculature, deeply embedded in skin of uropatagium. [1–2]  
 63: Insertion of tibiocarpalis—(1) distal tibial tuberosity to (3) Metatarsal II. [2]  
 66: Twisting of pisiform—(1) no to (0) yes. [2]  
 76: Distal falciform process on scapholunate—(0) absent to (1) present, prominent. [1]

Table III. (Continued)

---

**Node: *Glaucomys*, *Eoglaucmys*, *Petaurillus*, *Iomys* (3)**

**Strict Consensus Tree**

- 3: Crenulation—(2) heavy to (0) none.  
 11: Mesostyle position  $P_4$ —(3) discrete to (0) NA.  
 12: Mesostyle position  $M_1$ ,  $M_2$ —(3) discrete to (0) NA.  
 60: Mastoid process inflated—(0) no to (1) yes.  
 62: Semitendinosus III discrete or joined—(3) separate, but lies just caudal to other heads of semitendinosus to (2) joined by tendon to semitendinosus I, II.  
 69: Articulation between metacarpal II and centrale—(1) no to (0) yes.  
 73: Size of triquetral facet on scapholunate—(1) long to (0) short.

**Additional characters [most parsimonious tree #s given in square brackets]:**

- 6: Complexity of maxillary tooth pattern—(1) somewhat complex: one cross loph to (0) simple: no cross lophs. [1]  
 8: Mesostyle  $P_4$ —(2) present to (0) absent. [1]  
 9: Mesostyle  $M_1$ ,  $M_2$ —(2) present to (0) absent. [1]
- 

**Node: *Glaucomys*, *Eoglaucmys*, *Petaurillus*, *Iomys*, *Hylopetes*, *Petinomys* (not on strict consensus tree)**

**Characters [most parsimonious tree #s given in square brackets]:**

- 2:  $P_4$  size relative to  $M_1$  size—(0) smaller to (1) equal. [1]  
 61: Origin of semitendinosus III—(0) Not present to (1) Caudal vertebrae 5–8. [1]  
 64: Elevated scapholunate tuberosity on pisiform—(0) no to (1) yes. [1]  
 67: Enlarged surface for pisiform-triquetrum articulation: ulnar flange—(0) absent to (1) present, not prominent. [1]  
 68: Enlarged surface for pisiform-triquetrum articulation: radial flange—(0) absent to (2) present, prominent. [1]  
 69: Articulation between metacarpal II and centrale—(0) yes to (1) no. [1]  
 70: Scapholunate—capitate articulation—(1) yes to (0) no. [1]  
 71: Centrale—hamate articulation—(0) no to (1) yes. [1]  
 75: Proximal falciform process on scapholunate—(0) absent to (1) present, prominent. [1]  
 79: Patagium present—(0) no to (1) yes. [1]
- 

**Node: all flying squirrels minus *Hylopetes* and *Petinomys* (not on strict consensus tree)**

**Characters [most parsimonious tree #s given in square brackets]:**

- 61: Origin of semitendinosus III—(0) Not present to (1) Caudal vertebrae 5–8. [2]  
 62: Semitendinosus III discrete or joined—(0) Not present to (3) separate, but lies just caudal to other heads of semitendinosus. [2]  
 63: Insertion of tibiocondylar process—(0) Not present to (1) distal tibial tuberosity. [2]  
 64: Elevated scapholunate tuberosity on pisiform—(0) no to (1) yes. [2]  
 66: Twisting of pisiform—(0) yes to (1) no. [2]  
 68: Enlarged surface for pisiform-triquetrum articulation: radial flange—(0) absent to (2) present, prominent. [2]  
 69: Articulation between metacarpal II and centrale—(0) yes to (1) no. [2]  
 70: Scapholunate—capitate articulation—(1) yes to (0) no. [2]  
 71: Centrale—hamate articulation—(0) no to (1) yes. [2]  
 74: Shape of pisiform facet on scapholunate—(0) circular to (1) grooved. [2]  
 75: Proximal falciform process on scapholunate—(0) absent to (1) present, prominent. [2]  
 79: Patagium present—(0) no to (1) yes. [2]
- 

**Node: all flying squirrels (1)**

**Strict Consensus Tree**

- 3: Crenulation—(1) low to (2) heavy.  
 6: Complexity of maxillary tooth pattern—(0) simple: no cross lophs to (1) somewhat complex: one cross loph.  
 19: Protoconule  $P_4$ —(0) not evident to (1) incorporated into loph, but still evident.  
 62: Semitendinosus III discrete or joined—(0) Not present to (3) separate, but lies just caudal to other heads of semitendinosus.
-

*Eupetaurus*, and *Pteromys*), as hypothesized by Thorington and Darrow (2000). But bootstrap support is poor—20 percent.

The monophyly of flying squirrels also has poor bootstrap support (37, —, and 41 percent), in part because we emphasized postcranial characters of flying squirrels, not those that distinguish tree squirrels. This was particularly true of the analysis based on ordered data with Wagner parsimony (Figure 4), in which more clades of flying squirrels than tree squirrels were recognized, hence PAUP\* found it more parsimonious to treat gliding as primitive for all squirrels.

### Implications

If the three main clades of flying squirrels (*Glaucomys*, *Petaurista*, and *Trogopterus* groups) found with Dollo parsimony (Figure 5) are each monophyletic, there are interesting ecological and paleontological implications. First, it is evident that complex teeth associated with folivory evolved in the *Petaurista* and the *Trogopterus* groups, but not in the *Glaucomys* group. It seems likely that there have been dental simplifications in the evolution of the *Glaucomys* group as well as increased dental complexity in the evolution of the other two groups. Mein recognized three groups of flying squirrels in the European fossil record, distinguishing them by their dental morphology. The analyses based on Fitch and Wagner parsimony (Figures 3 and 4, respectively) do not agree with his hypothesis, but the Mein hypothesis (Figure 1) is similar to the tree based on Dollo parsimony (Figure 5), with the exception of the placement of *Aeromys*. The placement of *Aeromys* in the *Trogopterus* group in the Dollo tree is a major problem for the Mein hypothesis, however, because *Aeromys* has crenulated enamel, which Mein designated as the key character for identifying his *Hylopetes* group. In fact, because a phylogenetic tree based just on dental characters does not separate all tree squirrels from all flying squirrels, in spite of the evidence for monophyly of flying squirrels (Thorington, 1984), the identification of fossils as flying squirrels, based solely on dental characters, needs to be reexamined. In particular, our study documents that crenulation of the enamel occurs in a disparate group of squirrels: the African tree squirrel *Protoxerus*, the Asian giant squirrels, *Ratufa*, and four genera of flying squirrels, *Aeromys*, *Pteromyscus*, *Hylopetes* and *Petinomys*. This casts doubt on the use of crenulate enamel as the primary means by which fossil flying squirrels are identified. Accordingly, we concur with Emry and Korth (1996) that there is inadequate evidence that Oligocene teeth assigned to the Pteromyinae were actually the teeth of flying squirrels.

The morphological data do not allow us to resolve the early phylogeny of flying squirrels. We suspect that this results from rapid speciation after the original evolution of the gliding membrane. The morphological differences in the attachment of the gliding membrane at the wrist and ankle probably document early divergence within the group, but it is unclear from these data alone how the three groups identified in this study are related to one another and whether *Pteromys* should be considered a fourth monophyletic group, independent of the other three. For example, the pisiform bones of the wrist (Figure 9) exhibit morphologies that can be arranged in three phylogenetic groups. *Pteromys* and *Eupetaurus* do not fit into one of these three groups (*Aeromys* has a slight triquetral tuberosity and could be placed in the *Trogopterus* group). If molecular studies cannot resolve the early phylogeny of flying squirrels any better than can the morphological



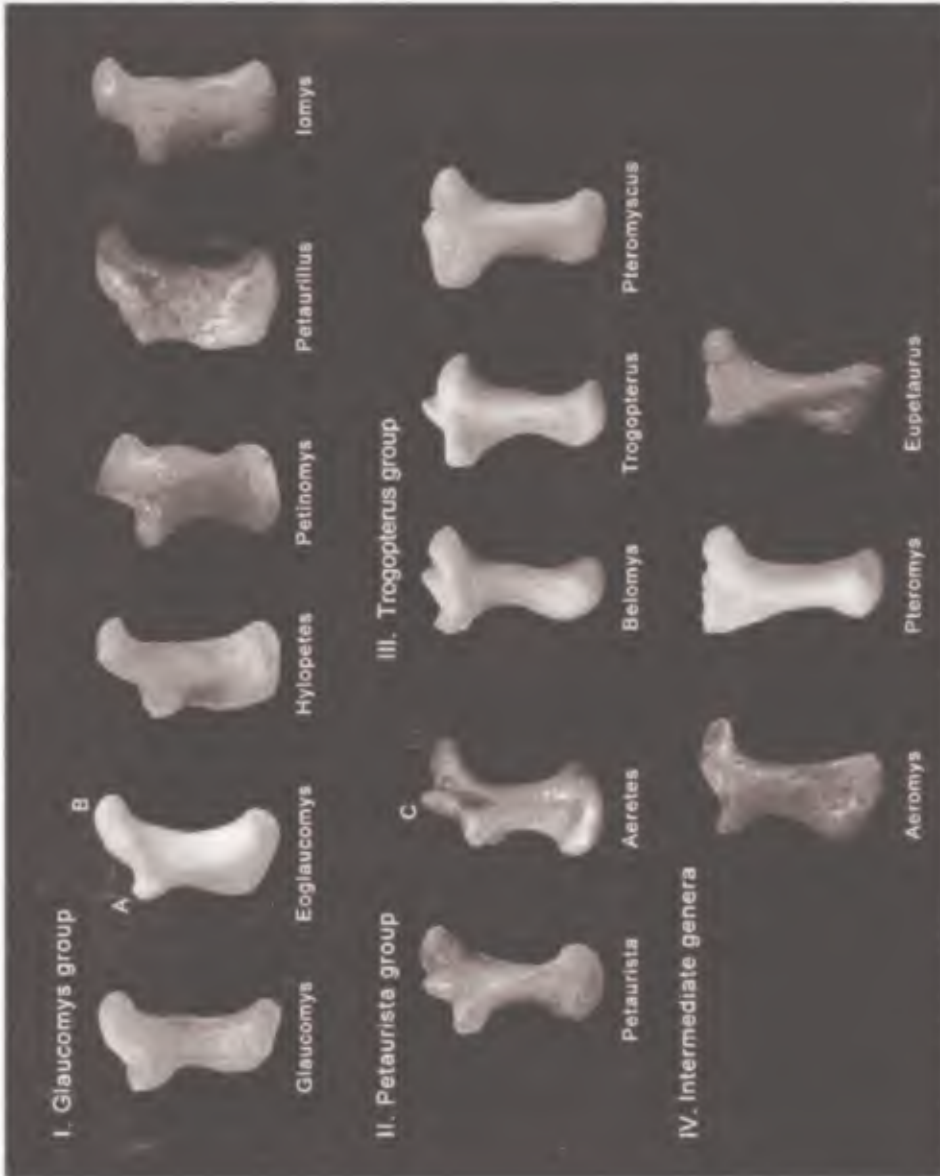


Fig. 9. Pisiform bones of flying squirrels showing the morphology of the *Glaucomys*, *Petaurista*, and *Trogopterus* groups, as well as intermediate genera. A, Ulnar tuberosity; B, Scapholunate tuberosity; and C, Triquetral tuberosity.

data, it will increase our confidence in the scenario that the group evolved very rapidly after the initial evolution of the gliding membrane. In theory, this could be documented in the fossil record, but currently that record is too poor to support or contradict evolutionary hypotheses.

### Size and the Evolution of Gliding

Because of our interest in the polarity of some of the character changes, we have debated whether gliding evolved among small squirrels (<500 g) or among large squirrels (~1500 g). (The argument is dichotomized for heuristic purposes.) Larger animals are expected to have higher terminal velocities and to land with more momentum. Therefore, larger squirrels are more likely to injure themselves in a fall, and there should be stronger selection for the evolution of gliding among large squirrels than among small squirrels. The counter argument favoring small size is based on the contention that falls are not a major source of morbidity or mortality among any squirrels, compared with the mortality caused by inadequate resources, principally food, in bad seasons. The availability of food resources is presumed proportional to home range size, which in turn is a positive function of body size. Gliding enables animals to maintain larger home ranges, which in turn means more food resources. Because food resources are more critical for small squirrels, there should be stronger selection for the evolution of gliding among small squirrels than among large squirrels.

There is a striking and consistent difference in tail morphology between small and large flying squirrels. Small flying squirrels have broad tails with the lateral hairs much longer than the dorsal and ventral hairs, and they have little or no uropatagium between the hind limbs and the tail. Large flying squirrels have a uropatagium with a long round tail extending beyond it. The lateral hairs of the tail are approximately the same length as the dorsal and ventral hairs. The transition between these two morphologies occurs at approximately 1 kg mass.

The morphology of the semitendinosus muscle (Character 61) roughly parallels the development of the uropatagium. In all tree and ground squirrels, the semitendinosus muscle has two heads. The first head takes origin on the ischium, the second takes origin on the first two caudal vertebrae (Bryant, 1945). The two heads merge and insert on the lateral surface of the tibia. In flying squirrels, a third head has evolved (Figure 10). The origin of this head has migrated distally on the tails of all flying squirrels, but most distally on those with a uropatagium. The muscle itself runs along the trailing edge of the uropatagium and inserts onto the lower leg. We examined seven genera and found that the origin and the insertion of this muscle were variable between genera. The North American *Glaucomys* is the only genus to have insertion of semitendinosus III solely onto the other two heads of the semitendinosus, which insert into the knee. *Eoglaucmys* and *Petinomys* have an additional insertion on the calcaneus. In *Hylopetes*, the third head does not join the other two heads of the semitendinosus and it inserts solely on the calcaneus. However, the muscle is not embedded in the skin of the uropatagium, but simply runs caudal immediately adjacent to the rest of the leg musculature in the thigh and calf. In *Petaurista* and *Belomys*, the semitendinosus III inserts solely on the calcaneus and is deeply embedded in the uropatagium. It has no attachment to the other two heads of semitendinosus and its course is more separated from the other leg muscles. The comparative

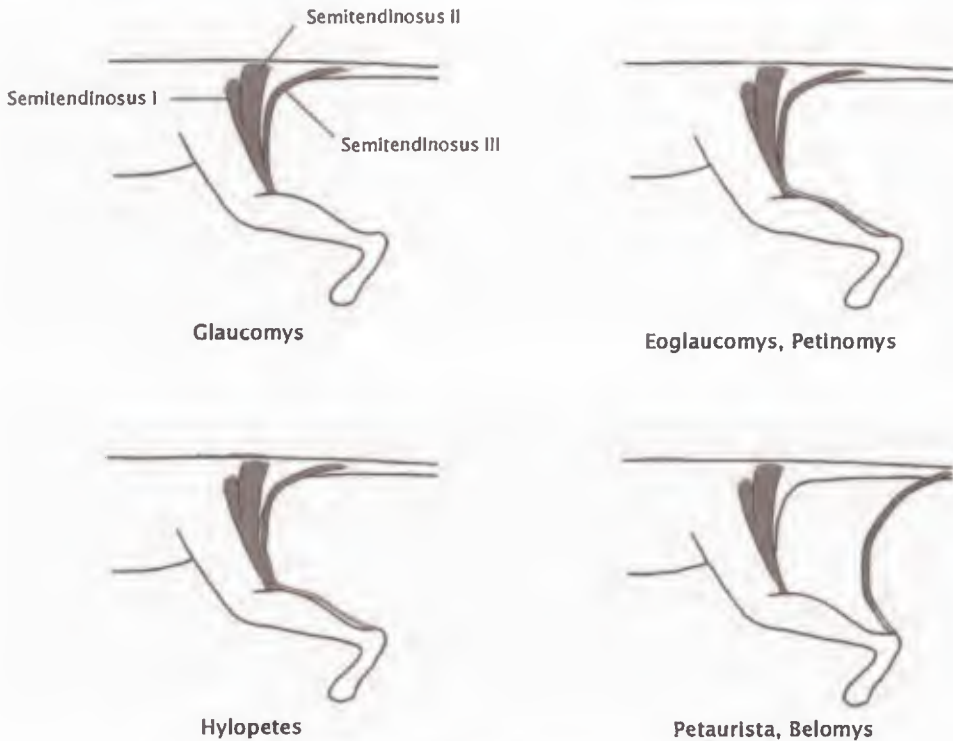
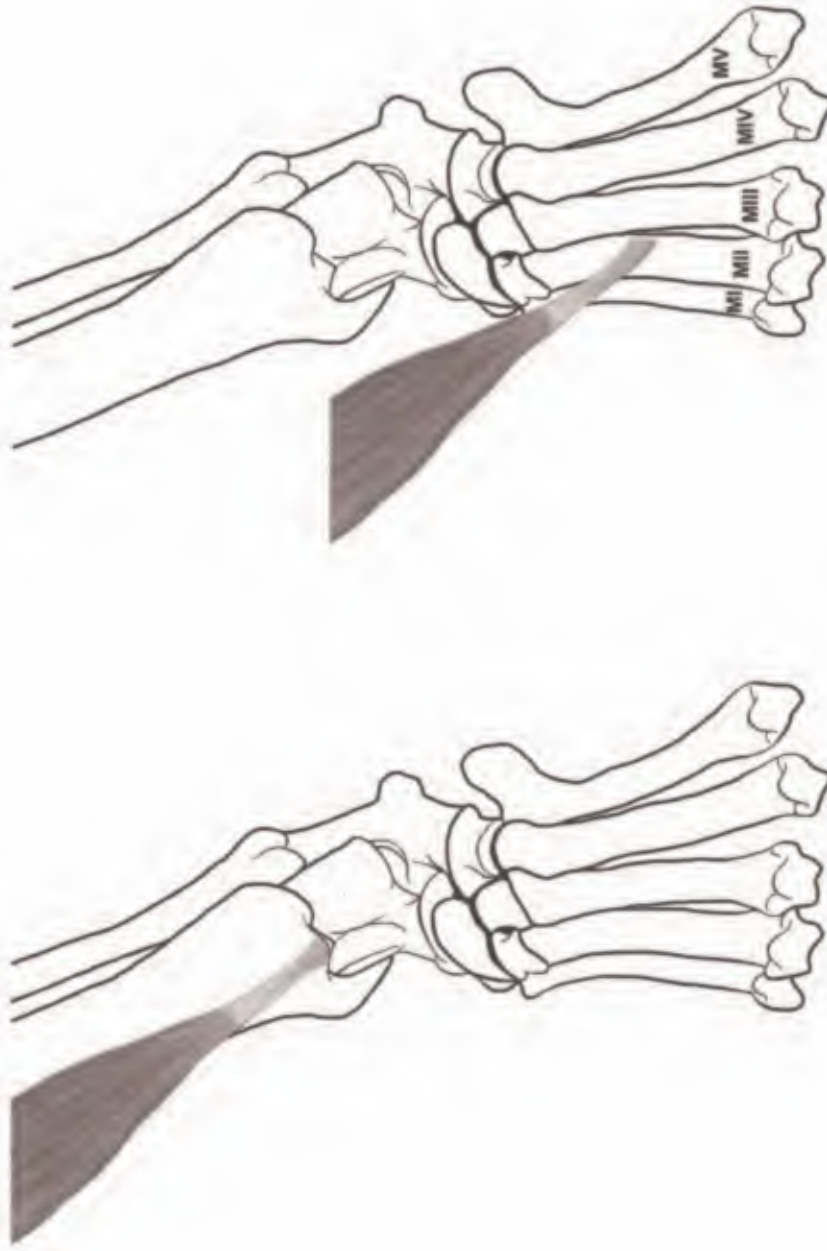


Fig. 10. Variation in the origin and insertion of the semitendinosus III muscle.

anatomy and anatomical relationships of this muscle suggests that our description parallels the evolutionary progression of the origin, course, and insertion. Under this scenario, the origin of the muscle migrated distally, down the tail, with the most distal origin being most derived. Also, the course of the muscle became more separated from the other heads of the semitendinosus muscle, and the insertion migrated from the crest of the tibia to the calcaneus. In all these features, the largest flying squirrels are the most derived anatomically, consonant with a hypothesis that large flying squirrels are derived from ancestors with morphology that now characterizes only small flying squirrels.

The tibiocarpalis muscle runs from the ankle to the tip of the styloid cartilage, through the edge of the gliding membrane, the plagiopatagium (Character 63). It is not found in other squirrels. The origin of this muscle at the ankle differs among genera of flying squirrels (Figure 11). In *Glaucomys*, *Eoglaucomys*, *Petinomys*, and *Hylopetes*, the tibiocarpalis takes origin from the medial tuberosity of the anterior surface of the distal tibia. *Iomys* and *Petaurillus* also have the medial tuberosity and probably the same tibiocarpalis origin. In contrast, in *Petaurista*, *Aeretes*, and *Belomys*, the muscle originates from the dorsum of metatarsal II of the foot. In *Pteromys*, the tibiocarpalis also originates on the foot, but on the dorsum of metatarsal I. Of the genera that we did not dissect, *Aeromys*, *Trogopterus*, and *Pteromyscus* lack a medial tibial tuberosity for origin of this muscle, suggesting that the tibiocarpalis arises from the foot in these genera. The



**Petaurista**

**Eoglaucomyys**

Fig. 11. Origin of the tibiocarpalis muscle in two genera of flying squirrels. MI-MV, metatarsals 1-5.

most distal origin, on the foot, would appear to be the most derived. In this respect also, the largest flying squirrels are the most derived and might be expected to have evolved from ancestors with less derived morphology like that seen in the small flying squirrels. Morphology thus provides some suggestive evidence that gliding first evolved in small squirrels.

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## APPENDIX 1.

## Specimens Examined

Material studied: p = postcranial, s = skull, t = dental, d = dissected, and <sup>l</sup> foot only

*Sciurinae*

*Callosciurus notatus*: USNM 113128 (s,t), 113158 (s,t), 292300 (p), 317219 (p), 396642 (p), 396643 (p), 396647 (p), 574902 (p), 521141 (d), USNM uncatalogued (IMR 84702, 86338, 86351) (d)

*Callosciurus prevostii*: USNM 155689 (p), 259034 (p), 545016 (p), 548412 (p), 300947 (s,t), 300949 (s,t)

*Douglassciurus jeffersoni*: USNM (Paleobiology) 243981 (p,s,t) 214936 (t); FAM 79301-6 (t), 79307 (s,t)

*Protoxerus stangeri*: USNM 465982 (s,t), 465984 (s,t), 465991 (s,t), 465996 (s,t), 481817 (d), 481821 (d), 539438 (s,t), 539440 (s,t), 539443 (s,t)

*Ratufa affinis*: USNM 151757 (p), 198121 (p), 115527 (s,t), 300928 (s,t), 522980 (d)

*Ratufa bicolor*: USNM 464512 (p), 49703 (p), 124238 (s,t), 124239 (s,t), 546334 (d)

*Ratufa indica*: USNM 308415 (p), 355785 (s,t), 38010 (s,t), 548661 (d)

*Sciurus carolinensis*: USNM 177903 (s,t), 177964 (s,t), 256047 (p), 297850 (p,s,t), 396002 (d), a 397180 (p), 497249 (d), 497250 (d), 505573 (p,s,t), 505575 (p,s,t), 522976 (d), 548048 (p,s,t)

*Sciurus vulgaris*: USNM 152693 (s,t), 152694 (s,t)

*Pteromyiinae*

*Aereetes melanopterus*: USNM 219205 (s,t), 240740 (p), 578592 (d<sup>l</sup>)

*Aeromys tephromelas*: USNM 196743 (p,s,t), 283511 (p), 291285 (s,t), 292649 (s,t), 292650 (s,t), 317237 (s,t), 481182 (s,t), 481187 (s,t), 481188 (p), 481190 (s,t), 481192 (t)

*Belomys pearsoni*: USNM 257845 (s), 308160 (s,t), 358354 (p,s,t), 358355 (s,t), 358356 (s,t), 359595 (d)

*Eupetaurus cinereus*: Uncatalogued specimen 1 (d<sup>l</sup>), specimen 2 (p)

*Eoglaucomys fimbriatus*: USNM 140501 (d), 173361 (s,t), 173362 (t), 173363 (p,s,t), 163364 (s,t), 173365 (p,s,t), 173367 (s,t), 173370 (s,t), 173371 (s,t), 173372 (s,t), 174082 (s,t), 326365 (s,t), 353232 (s,t), 353236 (s,t), 353238 (s,t), 353239 (s,t), 353243 (p)

*Glaucomys sabrinus*: USNM 25355 (s), 31674 (s), 37218 (s,t), 94309 (t), 193999 (t), 210155 (s), 235940 (p), 242129 (s), 242479 (s,t), 332334 (s), 332336 (s,t), 397067 (p), 397068 (p), 530557 (p)

*Glaucomys volans*: USNM 72934 (s), 194002 (s,t), 253944 (s,t), 263581 (t), 329701 (s,t), 329703 (s), 329705 (t), 364560 (s), 364638 (s), 397031 (p), 397077 (p), 398918 (s,t), 457978 (d), 457979 (d), 506226 (t), 525962 (p), 551843 (p), 585618 (p)

*Hylopetes alboniger*: USNM 20887 (s,t), 37875 (s,t), 253608 (s,t), 253610 (s,t), 253611 (p,s)

*Hylopetes bartelsi*: USNM 501690 (s,t)

- Hylopetes electilus*: USNM 259761 (s,t)  
*Hylopetes lepidus*: USNM 292651 (s,t), 292652 (s,t)  
*Hylopetes nigripes*: USNM 477994 (s,t), 477995 (s,t), 477998 (s,t), 478004 (p), 478005 (s), 478007 (p), 478009 (s,t)  
*Hylopetes phayrei*: USNM 260621 (p,s), 260622 (t), 260623 (s), 260024 (t), 294889 (s,t), 294890 (s), 294891 (s), 294892 (s), 297084 (t), 297085 (s,t), 297086 (s,t), 297087 (t), 297088 (s), 308156 (t), 355126 (p)  
*Hylopetes platyurus*: USNM 488616 (s,t), 488618 (s,t), 488619 (s), 488620 (s), 488623 (s,t), 488626 (t), 488627 (s,t), 488629 (t), 488630 (t), 488632 (p), 488637 (s,t)  
*Hylopetes spadiceus*: USNM 104627 (s,t), 292652 (t), 481109 (t), 481110 (t), 481114 (t), 488616 (t), 488638 (p,t), 488639 (s,t), 488643 (s), 488644 (s), 488645 (t), 488646 (s,t), 488647 (t), 488648 (s,t), 489456 (t), 489458 (s,t), uncatalogued specimen 1 (d), uncatalogued specimen 2 (d)  
*Iomys horsfieldi*: USNM 151792 (t), 252321 (s), 292653 (s), 292654 (p,t)  
*Petaurillus kinlochii*: USNM 488710 (s,t), 488711 (s,t), uncatalogued specimen 1 (p)  
*Petaurista alborufus*: USNM 311220 (s), 330196 (s), 330205 (s)  
*Petaurista caniceps*: USNM 240163 (s), 240165 (s)  
*Petaurista elegans*: USNM 292647 (s), 292648 (s), 307574 (s), 481189 (s), 481191 (s)  
*Petaurista leucogenys*: USNM 140876 (p), 140879 (s,t), 140880 (s), 140881 (t)  
*Petaurista magnificus*: USNM 290079 (s)  
*Petaurista petaurista*: USNM 34920 (s), 49660 (p), 104623 (s), 121500 (s,t), 121744 (s), 197320 (p,s), 253407 (s), 257713 (s), 307073 (p), 307579 (s), 353202 (s)  
*Petaurista philippensis*: USNM 240162 (s), 257844 (p), 258016 (s), 258876 (s,t), 259442 (s), 0297078 (s,t), 330228 (s), 332935 (s), 334352 (d), 334359 (d), 358351 (s,t)  
*Petaurista xanthotis*: USNM 144021 (s,t)  
*Petinomys fuscocapillus*: Uncatalogued specimen 1 (s,t)  
*Petinomys genibarbis*: USNM 488671 (s,t), 488672 (s,t)  
*Petinomys hagenii*: USNM 143344 (s,t), 143345 (s,t)  
*Petinomys lugens*: USNM 252318 (s), 252319 (s,t), 252320 (s), 252322 (s), 252323 (s,t), 252324 (s), 252326 (s,t)  
*Petinomys mindanensis*: USNM 254651 (s,t), 267975 (s,t)  
*Petinomys setosus*: USNM 481135 (p), 481136 (s,t), 488676 (s,t), 488678 (t), 488680 (s), 488681 (s), 488682 (s), 488683 (p,s,t)  
*Petinomys vordermanni*: USNM 481147 (s), 481148 (s,t), 481150 (s), 481151 (p), 481154 (s,t), 481156 (s,t), 481165 (s), 481166 (s), 481168 (s)  
*Pteromys volans*: USNM 172619 (s), 172621 (s), 172622 (s,t), 172623 (s), 172624 (s), 172625 (p,s,t), 172626 (s), 173367 (s), 173370 (s), 173371 (s), 173372 (s), 174082 (s), 237587 (s), 241271 (s), 254807 (s), 254934 (s), 258520 (s), 258980 (s), 268872 (s), 270545 (s), 353232 (s), 353236 (s), 546339 (p), 547926 (d)  
*Pteromyscus pulverulentus*: USNM 488692 (t), 488696 (p,s), 488697 (s,t), 488698 (s), 488699 (s,t), 488703 (s), 488704 (s,t), 489511 (t)  
*Trogopterus xanthipes*: USNM 241271 (s), 254807 (d,t), 258520 (p,s), 258980 (s), 268872 (p,s,t)



## APPENDIX 2

## Characters studied, Character states recorded, Character treatment

(U) = unordered; (O) = ordered; (D) = uniquely derived (with Dollo parsimony).

*Upper tooth row*

1. P3—(0) obsolete, (1) very small to small, (2) intermediate to large (O)
2. P4 size relative to M1 size—(0) smaller, (1) equal, (2) larger (D)
3. Crenulation—(0) none, (1) low, (2) heavy (D)
4. Enamel surface—(0) smooth, (1) folds: lumpy appearance, (2) pitting, (3) lophules (U)
5. Color of incisors—(0) deep orange, (1) yellowish orange, (2) yellow, (3) variable in color (U)
6. Complexity of maxillary tooth pattern—(0) simple: no cross lophs, (1) somewhat complex: one cross loph, (2) complex: more than one cross loph (D)
7. Hypocone—(0) no hypocone, (1) protocone and hypocone close together, but pinched off from each other with small groove in between them, (2) large protocone and smaller hypocone connected by a thin loph, but separated by some distance, (3) large, discrete hypocone, well separated from protocone (U)
8. Mesostyle P<sub>4</sub>—(0) obsolete, (1) variable, (2) present (U)
9. Mesostyle M<sub>1</sub>, M<sub>2</sub>—(0) obsolete, (1) variable, (2) present (U)
10. Mesostyle M<sub>3</sub>—(0) obsolete, (1) variable, (2) present (U)
11. Mesostyle position P<sub>4</sub>—(0) NA, (1) associated with paracone, (2) associated with metacone, (3) discrete (U)
12. Mesostyle position M<sub>1</sub>, M<sub>2</sub>—(0) NA, (1) associated with paracone, (2) associated with metacone, (3) discrete (U)
13. Mesostyle position M<sub>3</sub>—(0) NA, (1) associated with paracone, (2) associated with metacone, (3) discrete (U)
14. Mesoloph P<sub>4</sub>—(0) obsolete, (1) short, (2) lengthy (O)
15. Mesoloph M<sub>1</sub>, M<sub>2</sub>—(0) obsolete, (1) short, (2) lengthy (O)
16. Mesoloph M<sub>3</sub>—(0) obsolete, (1) short, (2) lengthy (O)
17. Parastyle sub cone P<sub>4</sub>—(0) obsolete, (1) present (O)
18. Parastyle sub cone M<sub>1</sub>, M<sub>2</sub>—(0) obsolete, (1) present (O)
19. Protoconule P<sub>4</sub>—(0) not evident, (1) incorporated into loph, but evident, (2) pinched off from loph (O)
20. Protoconule M<sub>1</sub>, M<sub>2</sub>—(0) not evident, (1) incorporated into loph, but evident, (2) pinched off from loph (O)
21. Protoconule M<sub>3</sub>—(0) not evident, (1) incorporated into loph, but evident, (2) pinched off from loph (O)
22. Metaconule P<sub>4</sub>—(0) not evident, (1) incorporated into loph, but evident, (2) pinched off from loph (O)
23. Metaconule M<sub>1</sub>, M<sub>2</sub>—(0) not evident, (1) incorporated into loph, but evident, (2) pinched off from loph (O)
24. Metaconule M<sub>3</sub>—(0) NA, (1) not evident, (2) incorporated into loph, but evident, (3) pinched off from loph (U)

25. Metaloph connection  $P_4$ —(0) protocone, (1) hypocone (U)
26. Metaloph connection  $M_1, M_2$ —(0) protocone, (1) hypocone (U)
27. Metaloph connection  $M_3$ —(0) NA, (1) protocone, (2) hypocone (U)
28. Protoloph connection to protocone  $P_4$ —(0) none, (1) weak, (2) variable, (3) solid (U)
29. Protoloph connection to protocone  $M_1, M_2$ —(0) none, (1) weak, (2) variable, (3) solid (U)
30. Protoloph connection to protocone  $M_3$ —(0) none, (1) weak, (2) variable, (3) solid (U)
31. Metaloph connection to protocone / hypocone  $P_4$ —(0) none, (1) weak, (2) variable, (3) solid (U)
32. Metaloph connection to protocone / hypocone  $M_1, M_2$ —(0) none, (1) weak, (2) variable, (3) solid (U)
33. Metaloph connection to protocone / hypocone  $M_3$ —(0) NA, (1) none, (2) weak, (3) variable, (4) solid (U)
34. Posterior flexus—(0) obsolete, (1) present (O)
35. Lingual cingulum—(0) obsolete, (1) present (O)
36. Metacone on  $M_3$ —(0) obsolete, (1) present (O)
37. Hypocone on  $M_3$ —(0) obsolete, (1) present (O)

#### Lower teeth

38. Formation of protolophid and metalophid on molars—(0) none, (1) protolophid & metalophid complete, join parametaconid (2) metalophid rejoins protolophid below parametaconid, (3) metalophid terminates in talonid basin (U)
39. Mesostylid distinct in all lower teeth—(0) no, (1) yes (O)
40. Anterior flexus—(0) obsolete, (1) present (D)
41. Hypoconule  $P_4$ —(0) obsolete, (1) present (O)
42. Hypoconule  $M_1, M_2$ —(0) obsolete, (1) present (O)
43. Hypoconule  $M_3$ —(0) obsolete, (1) present (O)
44. Complexity of mandibular tooth pattern—(0) simple, (1) somewhat complex, (2) complex (O)

#### Skull

45. Length of rostrum—(0) short, (1) intermediate, (2) long (O)
46. Width of rostrum—(0) wide, (1) intermediate, (2) narrow (O)
47. Length of incisive foramen—(0) short, (1) intermediate, (2) long (O)
48. Masseteric tubercles—(0) not prominent, (1) somewhat prominent, (2) prominent (O)
49. Shape of masseteric tubercles—(0) flat, (1) bulbous, (2) bulbous and tine-like (U)
50. Openness of distal half of eye orbit—(0) mostly open, (1) somewhat open, (2) slightly open (O)
51. Size of supraorbital process—(0) none, (1) short, (2) long (O)
52. Size of jugal process—(0) none, (1) small, (2) large (O)
53. Pterygoids—(0) parallel (1) pinched in (O)
54. Zygomaticomandibularis fossa—(0) deep, (1) shallow, (2) obsolete (O)

**Bullae**

55. Number of septa per bullae—(0) zero to one, (1) two to three, (2) more than three, not honeycomb pattern, (3) more than three, honeycomb pattern, (4) more than three, sliver pattern (U)
56. Width of bulla—(0) narrow, (1) intermediate, (2) wide (O)
57. Inflation of bulla—(0) inflated, (1) flat (D)
58. Distance between bullae—(0) narrow, (1) intermediate, (2) wide (O)
59. Size of bony process from opening of ear canal—(0) small, (1) large (O)
60. Mastoid process inflated—(0) no, (1) yes (D)

**Muscles**

61. Origin of semitendinosus III—(0) inseparable from origin of semitendinosus II, (1) Caudal vertebrae 5–8, (2) Caudal vertebrae 9–15 (D)
62. Semitendinosus III discrete or joined—(0) inseparable from semitendinosus I and II, (1) joined by muscle to semitendinosus I, II, (2) joined by tendon to semitendinosus I, II, (3) separate, but lies just caudal to other heads of semitendinosus, (4) well separated from rest of musculature, deeply embedded in skin of uropatagium (D)
63. Insertion of tibiocarpalis—(0) Not present, (1) distal tibial tuberosity, (2) Metatarsal I, (3) Metatarsal II (U)

**Carpal bones**

64. Elevated scapholunate tuberosity on pisiform—(0) no, (1) yes (D)
65. Triquetral process on pisiform—(0) no, (1) yes (D)
66. Twisting of pisiform—(0) yes, (1) no (D)
67. Enlarged surface for pisiform-triquetrum articulation: ulnar flange—(0) obsolete, (1) present, not prominent, (2) present, prominent (D)
68. Enlarged surface for pisiform-triquetrum articulation: radial flange—(0) obsolete, (1) present, not prominent, (2) present, prominent (D)
69. Articulation between metacarpal II and centrale—(0) yes, (1) no (D)
70. Scapholunate-capitate articulation—(0) no, (1) yes (O)
71. Centrale-hamate articulation—(0) no, (1) yes (D)
72. Lesser multangular-scapholunate articulation—(0) no, (1) yes (O)
73. Size of triquetral facet on scapholunate—(0) short, (1) long (O)
74. Shape of pisiform facet on scapholunate—(0) circular, (1) grooved (O)
75. Proximal falciform process on scapholunate—(0) obsolete, (1) present, prominent, (2) present, not prominent (U)
76. Distal falciform process on scapholunate—(0) obsolete, (1) present, prominent, (2) present, not prominent (U)
77. Angle between proximal falciform and body of scapholunate—(0) perpendicular, (1) acutely angular (O)
78. Distal tibial tuberosity present—(0) no, (1) yes (O)
79. Patagium present—(0) no, (1) yes (D)
80. Scapholunate fused—(0) no, (1) yes (D)



