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# HOW TO MAKE A FLYING SQUIRREL: *GLAUCOMYS* ANATOMY IN PHYLOGENETIC PERSPECTIVE

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Molecular evidence strongly supports the derivation of flying squirrels from tree squirrels, with the sister group being the Holarctic tree squirrels (*Sciurus*) and their close relatives. We present a rationale for the hypothesis that the transition occurred among small squirrels, and we propose using the northern flying squirrel (*Glaucomys sabrinus*) and the southern flying squirrel (*Glaucomys volans*) as models. Thus, we compare their morphologies with similar-sized tree squirrels (the Central American dwarf squirrel [*Microsciurus alfari*] and the western dwarf squirrel [*M. mimulus*]). We compare body proportions of *Glaucomys* with those of *Microsciurus*, considering differences as potential adaptations for gliding associated with wing loading, aspect ratio, and parasitic drag. We use the following measurements: lengths of the centra of the thoracic, lumbar, sacral, and caudal vertebrae; and lengths of the long bones (humerus, radius, femur, and tibia), metacarpals, metatarsals, and proximal phalanges of the hands and feet. We then compare these proportions of *Microsciurus* with those of other species of Sciurini, and the proportions of *Glaucomys* with other species of Pteromyini, to determine if each is representative or derived within its clade. Members of the genus *Glaucomys* exhibit relative elongation of the lumbar vertebrae and the forearm, relevant to wing loading and aspect ratio, relative lengthening of the midcaudal vertebrae, and relative shortening of the more distal caudal vertebrae, perhaps of importance for stability and control. Members of the genus *Glaucomys* also have shorter hands and feet, but these appeared to be elongated in *Microsciurus*, rather than shortened in *Glaucomys*, leaving the issue of parasitic drag moot. Finally, we speculate on the genetic changes that have produced these morphological modifications and may facilitate the evolution of gliding flight.

Key words: anatomy, *Bmp2*, body proportions, flying squirrel, *Glaucomys*, gliding adaptations, *Hox* genes, *Microsciurus*, morphology

Strong evidence supports the thesis that flying squirrels (Pteromyini) are derived from a common ancestor shared with the Holarctic tree squirrels (Sciurini). Mercer and Roth (2003), Steppan et al. (2004), and Herron et al. (2004) reached this conclusion based on a total of 6 genes (respectively, a combination of nuclear and mitochondrial genes: *IRbp, 12S*, and *16S*, 2,659 base pairs [bp]; 2 nuclear genes: *c-Myc* and *Rag1*, 4,477 bp; and 1 mitochondrial gene: *Cytb*, 1,140 bp), and it is concordant with morphological features that are probably synapomorphies. We accept the common ancestry of the Pteromyini and the Sciurini (Thorington and Hoffmann 2005), figured in Arbogast (2007). This phylogeny is contradicted by some interpretations of paleontological evidence (de Bruijn and Ünay 1989; Major 1893; Mein 1970), and our study was initiated as a challenge to these interpretations. In a previous paper, Thorington et al. (2005) showed that the dental characters previously used to identify flying squirrels in the fossil record are seen in a number of nonflying squirrels as well, calling into question the identity of pre-Miocene "flying squirrels." They also suggested morphological features of the proximal and distal ends of long bones that are present or likely to be present in the fossil record of the Oligocene and Miocene and that would enable paleontologists to distinguish between flying squirrels and others. In the current study, we consider other morphological changes, particularly changes in proportions, required to transmute tree squirrel morphology into the gliding adaptations of flying squirrels.

The common ancestor of the Sciurini and the Pteromyini was most likely an animal with tree squirrel morphology. *Douglassciurus* of the late Eocene and *Palaeosciurus* of the early Oligocene, the 2 earliest squirrels in the fossil record, both with surprisingly complete skeletons, had postcranial anatomy that was remarkably like that of modern-day tree squirrels in proportions and details of their anatomy (Emry and Thorington 1982; Vianey-Liaud 1974). *Douglassciurus* was compared directly with the fox squirrel (*Sciurus niger*) and

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exhibited very similar proportions of limb bones, hind foot bones, and proximal caudal vertebrae (Emry and Thorington 1982). *Palaeosciurus goti* is suggested to be a ground squirrel, based on the relative lengths of its humerus and radius and of its femur and tibia. The illustrations accompanying the description of *P. goti* show that the hind limb and upper arm bones closely resemble those of Recent tree squirrels (Vianey-Liaud 1974). *Palaeosciurus feignouxi*, of the very early Miocene (Savage and Russell 1983), has long-bone ratios like those of tree squirrels. Accordingly, it is highly likely that the common arboreal ancestor of flying squirrels and tree squirrels, also of the early Miocene, was very similar morphologically to modern-day tree squirrels.

The polarity that we propose—that tree squirrel morphology is primitive and that flying squirrel morphology is derived—also is supported by comparative data from other sciurids. First, we propose the obvious, that flying squirrels were not derived from terrestrial squirrels. It does not seem logical that a means of getting from 1 tree to another without coming to the ground would evolve in a terrestrial squirrel. Second, all tree squirrels are remarkably similar in body proportions, and where they differ, none are similar to flying squirrels. Most relevant, the Callosciurinae tree squirrels of southern Asia and the Sciurini tree squirrels of northern Eurasia, North America, and South America are very similar (Thorington and Heaney 1981). Either this is due to a common ancestral morphology or to convergent evolution. If the former, then the morphology must be primitive for the divergence of the Sciurini and the Pteromyini, which occurred slightly later (Mercer and Roth 2003). The early Miocene fossil *P. feignouxi* is a candidate for that ancestor or a close relative of it. If convergent evolution is responsible for the similarities between the Callosciurinae and the Sciurini tree squirrels, then the convergence would be expected in the arboreal ancestor of the Pteromyini. Other cases that can be argued to result from convergent morphology strengthen this argument. They are the African tree squirrels and perhaps the Asian giant tree squirrels (*Ratufa*) and the South American pygmy squirrel (*Sciurillus*), whose limb and trunk proportions are reported by Thorington and Heaney (1981) and Thorington and Thorington (1989). It seems that arboreal squirrels have repeatedly converged on similar morphologies or retained ancestral tree squirrel proportions. Accordingly, we submit that the common ancestor of the Sciurini and Pteromyini most likely had the limb and trunk proportions of the former.

We suggest that flying squirrels evolved from tree squirrels that were small for the following reasons. First, very few Recent Sciurini tree squirrels weigh more than 1 kg, most species are 500 g or less, and many are 250 g or less. Early Miocene sciurines are likely to have exhibited the same size distribution, although there is little evidence for judgment. Second, tree squirrels are excellent leapers and easily transfer from 1 perch or tree to another by leaping, but maximum leaping distances scale with body size. A small tree squirrel cannot leap as far as a large one; thus the advantage of gliding increases with decreasing size. Third, smaller animals are less likely to be hurt in falling because they reach lower terminal velocities and have less momentum; small inept gliders face fewer risks than large ones. Fourth, wing loading increases with body size. Other factors being equal, mass increases with the cube of linear dimensions and wing area increases with the square; thus wing loading should be lower in small squirrels. Minimal gliding speed is expected to vary directly with wing loading, so smaller, more lightly loaded squirrels are expected to be able to glide more slowly—hence more safely (Thorington and Heaney 1981). Fifth, large flying squirrels are more specialized than small flying squirrels. Large squirrels eat more vegetable matter and have more complex teeth than do small squirrels, including all the Holarctic tree squirrels (Bryant 1945; McKenna 1962: with particular reference to groups B II and B III). Among features relevant to the aerodynamics of gliding, discussed below, the large flying squirrels have an additional patagial region, the uropatagium, stretching between the hind limbs and the tail; they have a hind limb muscle (the semitendinosis III) with a more derived morphology than that found in small flying squirrels, including its origin from the caudal vertebrae, its course along the edge of the uropatagium, and its insertion at the ankle; and they also have a more derived origin of the tibiocarpalis muscle on metatarsal III, not found in the small *Glaucomys* or *Petinomys* (Johnson-Murray 1977; Thorington et al. 2002).

Accordingly, we submit that the 2 North American flying squirrels (*Glaucomys sabrinus* and *G. volans*) are good models for comparison with similar-sized Sciurini tree squirrels for the study of basic gliding adaptations in the Pteromyini. We consider *Microsciurus* to be an appropriate model for the ancestral sciurine that gave rise to the flying squirrels because of its small size and because it is closely related to *Sciurus niger*, which has been called a living fossil because of its similarities to the Eocene *Douglassciurus* (Emry and Thorington 1984). Therefore, we compare these flying squirrels (*G. sabrinus* and *G. volans*) with similar-sized members of the Sciurini—2 species of dwarf squirrels of the genus *Microsciurus* (*M. alfari* and *M. mimulus*)—thereby minimizing allometric differences.

The appropriateness of these 2 genera as models for the evolution of flying squirrels can be questioned on the basis of their phylogeny. Mercer and Roth (2003) estimated that the Pteromyini and Sciurini diverged 23 million years ago, that the genus *Glaucomys* diverged from other flying squirrels 14 million years ago, and that *Microsciurus* evolved less than 3 million years ago. However, models that would appear to be more appropriate, such as *Eoglaucomys* and *Petaurista*, are not small. It is not possible to support our choice of models with evidence from the fossil record because most purported flying squirrels in the fossil record are represented by teeth only. However, our hypothesis would be strongly challenged by the finding of a large flying squirrel in the early Miocene (23–18 million years ago) based on a fossil bone or bone fragment identified by the anatomical details described by Thorington et al. (2005). We are able to test whether *Glaucomys* and *Microsciurus* are similar to other members of their clade in morphological features that distinguish the 2 genera from each other. This enables us to determine to what extent either or both genera are derived within their clade for these characteristics, which hence may be irrelevant to our more general thesis. Thus, we use the comparison of the 2 genera as a heuristic hypothesis to highlight the major differences in body proportions that may be elements of the flying squirrel adaptation, subject to further test.

Our hypotheses are based on several aerodynamic features, such as wing loading, parasite drag, and aspect ratio. Wing loading is mass per unit area, so to reduce wing loading, one must increase wing area or decrease body mass, or both. Thorington and Heaney (1981) showed that the ponderal index, a measure of mass versus body length, is inversely related to size in flying squirrels, but not in tree squirrels. This caused us to look at vertebral lengths and to question whether some vertebrae are more elongated than others in flying squirrels relative to tree squirrels. Exploratory analysis led to the hypothesis tested, that an elongation of the lumbar region in flying squirrels relative to the thoracic region characterizes *Glaucomys* versus *Microsciurus*.

We examined the relative lengths of the caudal vertebrae, knowing that tails and tail lengths vary greatly among flying squirrels. Small flying squirrels have shorter tails relative to body length than large flying squirrels and the tails are distichously haired (feather-tailed) as opposed to the teretely haired (round-tailed) large flying squirrels. Because tree squirrel tails also are distichous, we expected no difference in the relative lengths of the caudal vertebrae between *Glaucomys* and *Microsciurus*. Exploratory analysis suggested that this hypothesis was wrong and that the middle caudal vertebrae were relatively longer in *Glaucomys*, so we tested this as the alternative hypothesis. The presence of the uropatagium in large flying squirrels suggests that there are some major differences in tail function between large and small flying squirrels, so we expected the relative lengths of their caudal vertebrae to differ, but we had no clear concept of how they would differ.

Aspect ratio is the ratio of wingspan to wing area, and it is complexly associated with glide distance and issues of control. The higher the aspect ratio is, the further a glider can go per meter of altitude loss; but the higher the aspect ratio is, the more sensitive the wing is to stalling at higher angles of attack. A high-aspect wing will permit long glides but it will not permit landing on vertical tree trunks the way flying squirrels do. Wingspan is a function of forelimb length, so we tested the hypothesis that the forelimb (humerus + radius) is disproportionately lengthened in *Glaucomys* relative to *Microsciurus*. From previous work (Thorington and Heaney 1981), we know that the forearm (radius) is elongated in flying squirrels relative to callosciurine tree squirrels, so we focused on this relationship in our study of the more phylogenetically appropriate Sciurini–Pteromyini comparison. We then tested whether the radius was disproportionately lengthened relative to the humerus, as would be expected in order to keep muscle mass proximal on the limb, and lengthened disproportionate to the tibia, as hypothesized if the aspect ratio is a critical factor.

During glides, flying squirrels hold their hands and feet in positions that appear to reduce drag. Externally, *Glaucomys* appear to have shorter toes than *Microsciurus*. Using X-rays of skins, we measured the lengths of hand and foot bones to test this, including the metacarpal 4 and proximal phalanx of the 4th digit of the hand, and the metatarsal 4 and proximal phalanx of the 4th digit of the foot. The 4th is the longest digit of the hand and foot. The hypothesis is that flying squirrels reduce the length of the hand and foot to reduce parasite drag.

Gliding adaptations have evolved in Recent mammals at least 6 times: in the Pteromyini (the true flying squirrels, 15 genera including *Glaucomys*), the Asian Dermoptera (the flying lemurs, *Cynocephalus* and *Galeopterus*), the African Anomaluridae (the scaly-tailed "flying squirrels," *Anomalurus, Idiurus*, and *Zenkerella*), and 3 times in the Australian fauna (the feather-tailed gliders, *Acrobates*; the lesser gliding possums, *Petaurus*; and the greater glider, *Petauroides*). The fossil record documents 2 or 3 additional lineages of gliding mammals (Meng et al. 2006; Stafford et al. 2002). Among these, flying squirrels probably present the best opportunity for comparison with living species that retain the ancestral morphology. As genetic analyses become less expensive and we approach the era of $1,000 genomes (Service 2006), it may become possible to document the molecular basis for the adaptations of flying squirrels and hence for the evolutionary novelty of gliding flight, which provides an additional motivation for thorough anatomical study and comparison of the Pteromyini with the Sciurini.

## MATERIALS AND METHODS

We studied and measured skulls, postcranial skeletons, X-rays of hands and feet of museum skins, and scanned images of caudal vertebrae of Sciurini and Pteromyini squirrels. We also utilized measurements taken by collectors and recorded on the skin tags. Specimens used are listed in Appendix I. Skull lengths, lengths of limb bones, and lengths of segments of trunk skeletons were measured with digital calipers (Fowler Max-Cal, Newton, Massachusetts). X-rays and scanned images were measured from digital images on a computer using analySIS Soft Imaging System (Münster, Germany). All specimen measurements were made by the junior author.

Knowing that there is considerable geographic variation in size in the northern flying squirrel, we measured the greatest length of the skull in *G. sabrinus* from different parts of its range (Arbogast 2007; Hall 1981). We combined our measurements with those of Howell (1918), after measuring a number of specimens that he also measured, comparing our measurements with his, and concluding that differences appeared to be random and never exceeded 0.1 mm (his measurements were recorded to the nearest 0.1 mm). Because of the size variation within the species, we treated *G. sabrinus* in 2 different samples: the smaller eastern subspecies (*G. s. macrotis*, *G. s. fuscus*, and *G. s. coloratus*) versus the other larger western subspecies (*G. s. sabrinus*, *G. s. fuliginosus*, *G. s. gouldi*, *G. s. klamathensis*, *G. s. lascivius*, and *G. s. oregonensis*).

We used external measurements taken by the collectors and recorded on the skin labels for an initial test of differences between *Glaucomys* and *Microsciurus* in the relative lengths of the tail and hind foot. Tail length was subtracted from total

**Table 1.**—Trunk lengths in millimeters (thoracic + lumbar + sacral vertebrae; see Fig. 3), relative lengths of lumbar (L) and thoracic (T) vertebrae (L1–L7/T1–T12), and relative limb lengths (lengths of the forelimb [humerus + radius] and hind limb [femur + tibia] divided by trunk length [means and standard deviations, sample size in parentheses] of *Glaucomys* and *Microsciurus*. Other Sciurini and other Pteromyini are listed from small to large. The other genera are "*Microsciurus*," which is probably polyphyletic, *Sciurus*, *Tamiasciurus*, *Eoglaucomys*, *Hylopetes*, *Trogopterus*, *Petaurista*, and *Aeromys*. See text for definition of sample size. NS = not significant.

| Species | Trunk length | L1–L7/T1–T12 | Forelimb/trunk | Hind limb/trunk |
|---|---|---|---|---|
| *G. sabrinus* (west) | 100.6 ± 4.8 (6) | 1.15 ± 0.03 (6) | 0.73 ± 0.03 (6) | 0.87 ± 0.04 (6) |
| *G. sabrinus* (east) | 90.7 ± 5.6 (18) | 1.17 ± 0.07 (18) | 0.72 ± 0.03 (14) | 0.88 ± 0.03 (14) |
| *G. volans* | 72.2 ± 4.8 (65) | 1.07 ± 0.05 (65) | 0.78 ± 0.03 (54) | 0.91 ± 0.04 (54) |
| *M. alfari* | 74.5 (10) | 0.92 ± 0.01 (10) | 0.69 ± 0.03 (10) | 0.92 ± 0.04 (10) |
| *M. mimulus* | 74.3 (8) | 0.96 ± 0.03 (8) | 0.66 ± 0.02 (8) | 0.86 ± 0.03 (8) |
| *Glaucomys* versus *Microsciurus* | | | | |
| *F* | | 113 | 94.5 | 1.56 |
| *d.f.* | | 1, 105 | 1, 90 | 1, 90 |
| *P* | | < 0.00001 | < 0.00001 | NS |
| Other Sciurini | | | | |
| "*M.*" *flaviventer* | 82.0 (10) | 0.94 ± 0.02 (10) | 0.69 ± 0.03 (10) | 0.90 ± 0.03 (10) |
| *S. deppei* | 111 ± 5 (5) | — | 0.60 ± 0.03 (5) | 0.85 ± 0.03 (5) |
| *T. hudsonicus* | 121.2 ± 4.6 (15) | 0.91 ± 0.05 (15) | 0.53 ± 0.02 (12) | 0.73 ± 0.03 (12) |
| *S. vulgaris* | 127.9 ± 7.4 (2) | 1.01 ± 0.03 (2) | 0.60 ± 0.02 (2) | 0.85 ± 0.02 (2) |
| *S. carolinensis* | 150.2 ± 6.3 (14) | 0.92 ± 0.06 (14) | 0.56 ± 0.02 (13) | 0.79 ± 0.04 (13) |
| *S. niger* | 180.4 ± 5.9 (19) | 0.97 ± 0.04 (20) | 0.56 ± 0.02 (19) | 0.77 ± 0.03 (19) |
| Other Pteromyini | | | | |
| *E. fimbriatus* | 172.2 ± 2.26 (2) | 1.11 (3) | 0.63 ± 0.02 (2) | 0.84 ± 0.04 (2) |
| *H. nigripes* | 175.5 ± 2.4 (3) | — | 0.65 ± 0.03 (3) | 0.80 ± 0.04 (3) |
| *T. xanthipes* | 192.4 (1) | 1.24 ± 0.04 (2) | — | — |
| *P. elegans* | 225.8 (1) | — | 0.64 (1) | 0.86 (1) |
| *A. tephromelas* | 226.8 (1) | — | 0.68 (1) | 0.90 (1) |
| *P. petaurista* | 288 ± 30 (4) | — | 0.66 ± 0.04 (4) | 0.82 ± 0.02 (4) |

length to provide a measure of the length of head and body, which we used as an estimate of size.

Vertebral measurements were taken ventrally on dried, straightened backbones. The vertebral columns were straightened by moistening the specimens with water, pinning them on a foam block, and air drying them. Measurements of thoracic vertebrae T1 through T10 and T1 through T12, thoracic vertebra T11 through lumbar vertebra L7, lumbar vertebrae L1 through L7, and sacral vertebrae S1 through S3 include the lengths of the centra of all the vertebrae in each segment. For *Microsciurus*, these vertebral measurements were taken from Thorington and Thorington (1989). The ratio of lengths of lumbar vertebrae divided by lengths of thoracic vertebrae is used to test whether there is an elongation of the lumbar region in flying squirrels. The measurements were summed (thoracic vertebrae T1 through T12, plus lumbar vertebrae L1 through L7, plus sacral vertebrae S1 through S3) and these are the trunk lengths used to determine relative lengths of the limbs and the individual long bones. For these, the lengths of the limbs and long bones of each specimen were divided by the trunk length of the same specimen, and these ratios were averaged. We scanned the trunk vertebrae of 14 specimens and all the caudal vertebrae of 127 specimens using a digital scanner. We measured the vertebrae individually using the imaging system after calibrating each image with a scale on the scanned image. For each vertebra, we obtained the average. We summed these averages to obtain trunk length (thoracic 1–sacral 3) and tail length (caudal 1–21), and we obtained the relative lengths of the vertebrae by dividing the average length of each by the appropriate total, either trunk length or tail length. Sample sizes in Tables 1 and 2 are the numbers of vertebral columns that were complete (e.g., all caudal vertebrae 1–21 were present) or for which the relevant measurements could be obtained (e.g., lengths of both forelimb and trunk).

The following limb measurements were taken: the greatest length of the humerus, from the head to the medial margin of the trochlea; the greatest length of the radius from the medial edge of the head to the tip of the styloid process; the greatest medial length of the femur, from the head to the medial condyle; the greatest length of the tibia, from the proximal articular surface to the tip of the medial malleolus; and the medial width of the femur. All limb-bone measurements were taken using digital calipers. The length of the forelimb is defined as the summed lengths of the humerus and radius. The length of the hind limb is defined as the summed lengths of the femur and tibia. Southern flying squirrels (*G. volans*) have been reported to be sexually dimorphic (Robins et al. 2000). We combined sexes in our study because of the small sample sizes of *Microsciurus* available and because the 1–2% sexual dimorphism Robins et al. (2000) reported was expected to be small compared with the intergeneric differences.

The hands and feet of museum specimens were X-rayed, using a digital X-ray unit, and measured using the imaging system. Total lengths of metacarpals 2–5, metatarsals 1–5, and corresponding basal phalanges were measured, when their images were visible, that is, not blocked by other bones or the

**TABLE 2.**—Lengths of segments of caudal (C) vertebrae in millimeters and ratio of lengths of midcaudal vertebrae to summed lengths of the other caudal vertebrae in *Glaucomys* and *Microsciurus* (means and standard deviations, sample size in parentheses). Other Sciurini and other Pteromyini are listed from small to large. The other genera are *Tamiasciurus*, *Sciurus*, *Hylopetes*, *Eoglaucomys*, and *Aeromys*. Samples are described in text.

| Species | C1–C4 | C5–C13 | C14–C21 | (C5–C13)/(C1–C4 + C14–C21) |
|---|---|---|---|---|
| *G. sabrinus* (16) | 11.7 ± 1.1 | 82.9 ± 4.8 | 37.0 ± 4.9 | 1.71 ± 0.16 |
| *G. volans* (29) | 9.7 ± 0.76 | 61.7 ± 4.23 | 34.4 ± 3.0 | 1.40 ± 0.28 |
| *M. alfari* (4) | 10.8 ± 0.4 | 51.3 ± 2.8 | 50.5 ± 2.2 | 0.84 ± 0.03 |
| *M. mimulus* (11) | 10.2 ± 0.5 | 51.1 ± 4.3 | 43.7 ± 4.8 | 0.95 ± 0.09 |
| *Glaucomys* versus *Microsciurus* | | | | |
| *F* | | | 119 | |
| *d.f.* | | | 1, 58 | |
| *P* | | | $< 0.00001$ | |
| Other Sciurini | | | | |
| *T. hudsonicus* (10) | 14.4 ± 0.6 | 50.3 ± 3.5 | 67.2 ± 2.6 | 1.04 ± 0.07 |
| *S. vulgaris* (1) | 16.9 | 72.9 | 86.2 | 0.96 |
| *S. carolinensis* (12) | 21.4 ± 1.6 | 82.6 ± 5.2 | 86.6 ± 4.9 | 0.83 ± 0.06 |
| *S. niger* (15) | 26.6 ± 1.9 | 107.9 ± 6.5 | 112.3 ± 8.0 | 0.83 ± 0.08 |
| Other Pteromyini | | | | |
| *H. phayrei* (1) | 11.3 | 76.3 | 57.6 | 1.11 |
| *E. fimbriatus* (2) | 24.1 ± 0.6 | 159.2 ± 0.4 | 115.7 ± 5.7 | 1.14 ± 0.04 |
| *A. tephromelas* (1) | 25.5 | 174.7 | 148.9 | 1.00 |

supporting wire within the skin. Only the data for the 4th digits, the longest of the hand and foot, are presented here. The lengths of the foot bones were averaged and the relative lengths were computed by dividing this average and its standard deviation by an average trunk length. This was necessitated by the lack of axial skeletons for the specimens X-rayed. In most cases the average trunk lengths are listed in Table 1. For *Hylopetes spadiceus* and *Iomys horsfeldii* the trunk lengths were estimated from the measured trunk lengths of *Glaucomys* and the relative lengths of the head and body of *Hylopetes*, *Iomys*, and *Glaucomys*, as listed in Thorington and Heaney (1981). These computations should provide good estimates of the averages of relative lengths of the foot bones but are expected to overestimate their standard deviations if trunk and foot bone lengths are correlated.

Ratios sometimes have abnormal distributions. As in previous papers (Thorington and Heaney 1981; Thorington and Thorington 1989), we have found that the distributions of the ratios of body measurements do not differ greatly from normal. A slight skewness of the distributions probably causes the analysis of variance to underestimate the *F*-value and consequently the significance of the difference.

Analyses of the data all were conducted with Microsoft Excel (Microsoft, Redmond, Washington). In comparing 2 genera that probably have not shared a common ancestor for 20 million years, it is not surprising to find statistically significant differences. Confounding statistical analysis is the complexity of making Bonferroni adjustments on multiply correlated measurements and the 33% probability that both species of *Glaucomys* will be larger than both species of *Microsciurus*, or vice versa, in any particular comparison. Our solution to this problem is to consider only differences with extremely large significance values (e.g., cases in which *F*-values for analysis of variance [ANOVA] are much higher than those for $P = 0.001$, and usually probabilities are much much lower than 0.00001), in the hope that these modifications of tree squirrel anatomy are the meaningful ones for the evolution of gliding. We report the actual *F*-values for the ANOVA with 1 degree of freedom in the numerator (*Glaucomys* species combined versus *Microsciurus* species combined) and probability levels as low as 0.00001.

## RESULTS

Geographic variation in *G. sabrinus* in skull length caused us to divide the species into 2 samples (see "Materials and Methods"). We report the values for both samples, except for the hand measurements, in which we included only the eastern subspecies. The eastern subspecies (*G. s. coloratus*, *G. s. fuscus*, and *G. s. macrotis*) include the smallest animals. The largest animals are those of northern Idaho and western Montana (*G. s. latipes*). For more details, see Appendix II.

The relative lengths of the thoracic to lumbar vertebrae differ between flying squirrels and tree squirrels (Table 1), with the ratio of lumbar to thoracic vertebrae, (L1–L7)/(T1–T12), averaging 1.07–1.17 in *Glaucomys* and 0.92–0.96 in *Microsciurus* ($F = 131.4$, *d.f.* = 1, 113, $P < 0.00001$). In the length of the thoracic segment (T1–T12), the 2 species of *Microsciurus* are intermediate between the smaller *G. volans* and the larger *G. sabrinus*, ($F = 1.8$, *d.f.* = 1, 113, $P > 0.05$), whereas in the length of the lumbar segment (L1–L7) both species of *Microsciurus* are shorter than both species of *Glaucomys* ($F = 13.5$, *d.f.* = 1, 115 $P < 0.001$). The proportions of *Microsciurus* lie within the range of lumbar to thoracic ratios of other Sciurini and the proportions of *Glaucomys* are similar to those of other Pteromyini (Table 1). Therefore, we interpret the relative differences between *Microsciurus* and *Glaucomys* to result from elongation of the lumbar region in the flying

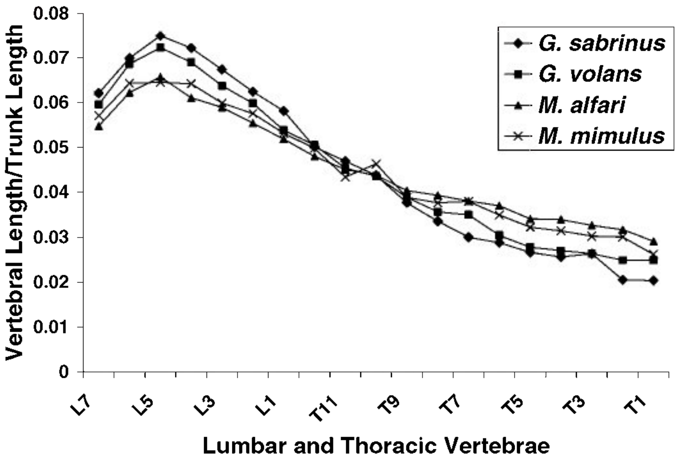

**FIG. 1.**—Relative lengths of thoracic and lumbar vertebrae of *Glaucomys* and *Microsciurus*. The vertical axis is the length of each individual vertebra, divided by the total trunk length (thoracic, lumbar, and sacral vertebrae). *G. sabrinus* ($n = 4$), *G. volans* ($n = 3$), *M. alfari* ($n = 3$), *M. mimulus* ($n = 4$). Symbols indicate means for each species; $n$ is the number of vertebral columns measured.

squirrels. *G. sabrinus* has the highest ratio (1.17) in contrast to *M. alfari* with the lowest ratio (0.92). The average ratio of *G. sabrinus* exceeds the average ratio of *Microsciurus* by 24% of the latter. The location of the elongation is demonstrated by measurements of the individual vertebrae. When the relative lengths of each vertebra (relative to the summed lengths of thoracic, lumbar, and sacral vertebrae) are graphed (Fig. 1), it is clear that the thoracic vertebrae of *Glaucomys* are slightly shorter than those of *Microsciurus*, lumbar vertebrae are longer, that the transition occurs in the vicinity of thoracic vertebrae 10–12, and that there is a graded change in the relative lengths of the lumbar vertebrae with the greatest differences in lumbar vertebrae 4 and 5. The elongation of the lumbar vertebrae causes approximately a 10% elongation of the length of the trunk vertebrae in *Glaucomys* versus *Microsciurus* and should account for approximately a 10% increase in the area of the gliding membrane. If one distinguishes between vertebrae with lumbar-type articulations versus those with thoracic-type articulations, a ratio of vertebrae T11–L7/T1–T10 also emphasizes the elongation of the lumbar vertebrae in the flying squirrels ($F = 121.6$, $d.f. = 1, 113$, $P < 0.00001$).

In the illustration of the trunks of the 4 species (Fig. 2), it is obvious that differences in lengths of the lumbar vertebrae are accompanied by diminution of their transverse processes. The transverse processes of *Glaucomys* are much smaller than those of *Microsciurus*, implying that the dorsal musculature is much reduced in the former and suggests that the mass of the animal does not increase as much as might be expected from the elongation of the vertebrae.

In an analysis of field-taken measurements (data not shown), relative tail length (tail length/length of head and body) was not consistently different between *Microsciurus* and *Glaucomys* ($F = 1.71$, $d.f. = 1, 97$, $P > 0.05$). These measurements taken by diverse collectors are variable and have large standard deviations, but the ranking of relative tail length (from largest to smallest)—eastern *G. sabrinus*, *M. alfari*, western *G. sabrinus*,

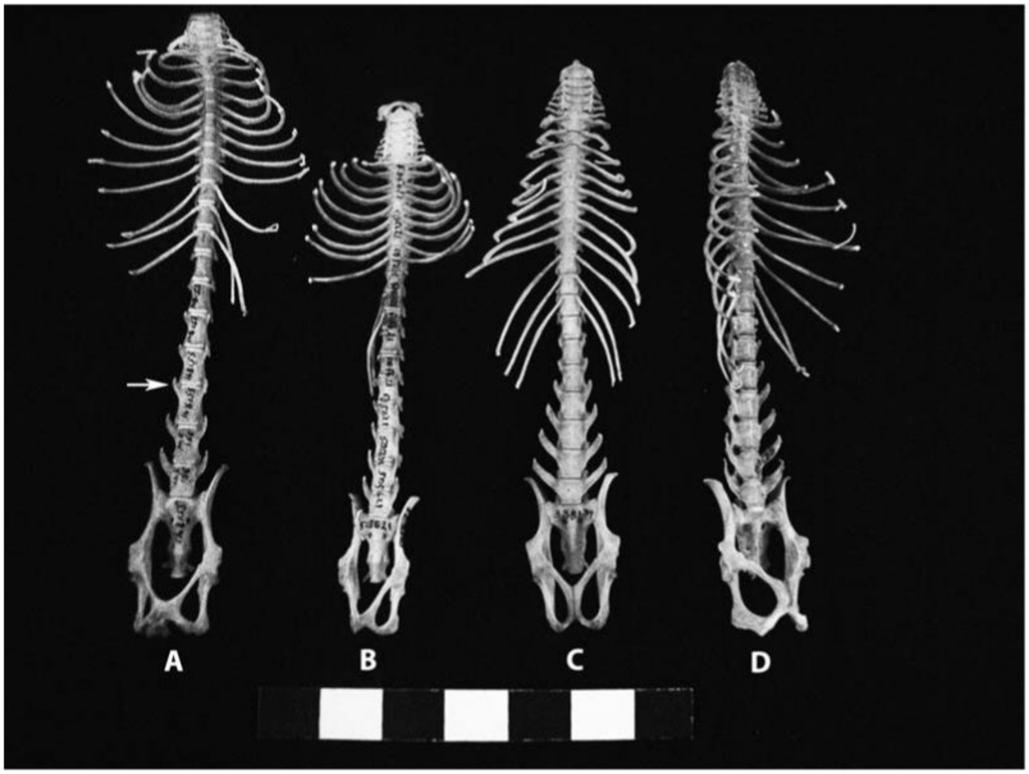

**FIG. 2.**—Trunk skeletons of A) *Glaucomys sabrinus*, B) *Glaucomys volans*, C) *Microsciurus alfari*, and D) *Microsciurus mimulus*. Note smaller size of transverse processes in *Glaucomys* than in *Microsciurus* (arrow). Scale: squares are 10 mm on a side.

*G. volans*, and *M. mimulus*—gives no reason to suspect a systematic difference between *Glaucomys* and *Microsciurus*.

However, measurements of the caudal vertebrae (Table 2) demonstrate significant differences between the tails of *Glaucomys* and *Microsciurus*. The tails of *Glaucomys* have slightly fewer vertebrae than those of *Microsciurus*, and the relative lengths of the individual vertebrae differ systematically between the flying squirrels and tree squirrels. The reduced number of vertebrae is difficult to quantify because of the frequency with which the distal vertebrae are lost during the preparation of specimens, but our samples of skeletons included *Glaucomys* with 21–23 vertebrae and *Microsciurus* with 25–27 vertebrae. The proximal 4 caudal vertebrae do not differ, but caudal vertebrae 5–13 are relatively longer in *Glaucomys* than in *Microsciurus*, and caudal vertebrae 14–21 are shorter (Fig. 3). The 9 caudal vertebrae C5–C13 average 60% of the length of C1–C21 in *Glaucomys* but only 48% in *Microsciurus*. A ratio of the lengths of the elongate middle vertebrae to the others (Table 1) emphasizes the difference between the flying squirrels and tree squirrels ($F = 119$, $d.f. = 1, 58$, $P < 0.00001$). *Microsciurus* does not differ from other Sciurini in this ratio, implying that *Glaucomys* is derived in this feature. *Hylopetes* and *Eoglaucomys* are similar to *Glaucomys* in this ratio, suggesting that it is characteristic of small to medium-sized flying squirrels, but a single large flying squirrel (*Aeromys*) is different.

The relative lengths of the limbs are presented in Table 1. *Glaucomys* has a significantly larger ratio of forelimb (humerus + radius) to trunk (thoracic + lumbar + sacral vertebrae) than *Microsciurus*, but not a significantly larger ratio of hind limb (femur + tibia) to trunk. In this case, the forelimb to trunk ratio of *Microsciurus* exceeds that of larger members of the Sciurini, being matched only by the ratio of another species of dwarf squirrel, "*M.*" *flaviventris*. The forelimb to trunk ratio of *Glaucomys* also exceeds that of larger species of Pteromyini. This suggests that there are 2 contributing factors to the elongation of the forelimb in *Glaucomys*—a "small squirrel factor" as well as a "flying squirrel factor," both increasing the aspect ratio of the wing. The lengths of the long bones are given in Table 3 and their proportions relative to trunk length are given in Table 4. There is little difference between *Glaucomys* and *Microsciurus* in the relative lengths of the humerus (humerus/trunk, $F = 7.36$, $d.f. = 1, 116$, $P < 0.01$), so most of

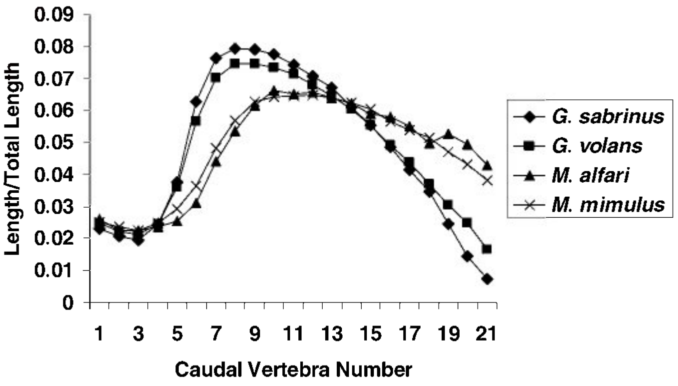

**FIG. 3.**—Relative lengths of caudal vertebrae 1–21 in *Glaucomys* and *Microsciurus*. The vertical axis is the length of each individual vertebra, divided by the summed lengths of caudal vertebrae 1–21. *G. sabrinus* ($n = 30$), *G. volans* ($n = 70$), *M. alfari* ($n = 9$), *M. mimulus* ($n = 13$). Symbols indicate means for each species; $n$ is the number of vertebral columns measured.

**TABLE 3.**—Lengths of long bones in millimeters (means and standard deviations, sample size in parentheses) of *Glaucomys* and *Microsciurus*. Other Sciurini and other Pteromyini are listed from small to large. The other genera are "*Microsciurus*," which is probably polyphyletic, *Tamiasciurus*, *Sciurus*, *Hylopetes*, *Eoglaucomys*, *Petaurista*, and *Aeromys*. Samples are described in text.

| Species | Humerus | Radius | Femur | Tibia |
|---|---|---|---|---|
| *G. sabrinus* (east) | 31.2 ± 1.2 (17) | 34.9 ± 1.3 (15) | 37.2 ± 1.1 (17) | 43.5 ± 1.3 (14) |
| *G. sabrinus* (west) | 34.2 ± 1.0 (8) | 37.9 ± 0.8 (8) | 40.1 ± 0.9 (9) | 46.4 ± 1.1 (8) |
| *G. volans* | 26.2 ± 1.0 (75) | 29.9 ± 1.1 (65) | 30.7 ± 1.3 (75) | 35.5 ± 1.3 (64) |
| *M. alfari* | 26.1 ± 0.7 (9) | 26.0 ± 0.6 (9) | 31.2 ± 0.8 (9) | 36.5 ± 1.1 (9) |
| *M. mimulus* | 25.5 ± 0.4 (10) | 24.2 ± 0.5 (10) | 29.9 ± 0.5 (10) | 35.1 ± 0.8 (10) |
| Other Sciurini | | | | |
| "*M.*" *flaviventris* | 28.4 ± 1.2 (10) | 28.4 ± 0.8 (10) | 33.8 ± 1.4 (10) | 39.7 ± 1.5 (10) |
| *T. hudsonicus* | 33.5 ± 0.8 (14) | 30.6 ± 0.6 (12) | 41.8 ± 0.9 (13) | 46.6 ± 0.7 (14) |
| *S. deppei* | 34.6 ± 0.4 (10) | 32.9 ± 0.9 (9) | 43.8 ± 1.1 (9) | 49.5 ± 1.4 (9) |
| *S. vulgaris* | 38.7 (2) | 38.5 (2) | 50.4 (2) | 58.2 (2) |
| *S. carolinensis* | 43.3 ± 1.2 (16) | 41.0 ± 1.2 (15) | 55.9 ± 1.6 (16) | 62.7 ± 1.7 (15) |
| *S. niger* | 51.8 ± 1.3 (20) | 48.5 ± 1.2 (20) | 65.3 ± 1.5 (20) | 73.1 ± 1.6 (20) |
| Other Pteromyini | | | | |
| *H. phayrei* | 29.5 (1) | 31.7 (1) | 34.9 (1) | 39.4 (1) |
| *E. fimbriatus* | 53.3 ± 1.2 (3) | 55.9 ± 0.5 (3) | 69.3 ± 1.6 (3) | 75.8 ± 3.2 (3) |
| *H. nigripes* | 54.7 ± 2.4 (3) | 58.7 ± 2.5 (3) | 66.2 ± 2.9 (3) | 73.6 ± 3.2 (3) |
| *P. elegans* | 71.7 (1) | 73.6 (1) | 95.1 (1) | 100 (1) |
| *P. petaurista* | 91.9 ± 7.2 (8) | 90.8 ± 8.3 (8) | 112.6 ± 10.7 (8) | 115.6 ± 11.7 (8) |
| *P. magnificus* | 94 (1) | 93.4 (1) | 119.1 (1) | 120.8 (1) |
| *A. tephromelas* | 94.0 ± 1.2 (2) | 95.4 ± 1.2 (2) | 114.8 ± 1.8 (2) | 116.4 ± 1.3 (2) |
| *P. philippinensis* | 106.6 ± 3.5 (5) | 104.2 ± 3.3 (5) | 131.1 ± 3.4 (4) | 134.8 ± 3.3 (5) |
| *P. alborufus* | 106.9 (1) | 108.5 (1) | 130.9 (1) | 140 (1) |

**Table 4.**—Lengths of long bones in millimeters relative to trunk length (means and standard deviations, sample size in parentheses) of *Glaucomys* and *Microsciurus*. Other Sciurini and other Pteromyini are listed from small to large. The other genera are "*Microsciurus*," which is probably polyphyletic, *Tamiasciurus*, *Sciurus*, *Eoglaucomys*, *Hylopetes*, *Petaurista*, and *Aeromys*. Samples are described in text. NS = not significant.

| Species | Humerus/trunk | Radius/trunk | Femur/trunk | Tibia/trunk |
|---|---|---|---|---|
| *G. sabrinus* (east) | 0.34 ± 0.01 (17) | 0.38 ± 0.01 (15) | 0.41 ± 0.01 (17) | 0.48 ± 0.01 (14) |
| *G. sabrinus* (west) | 0.34 ± 0.01 (8) | 0.38 ± 0.01 (8) | 0.40 ± 0.01 (9) | 0.46 ± 0.01 (8) |
| *G. volans* | 0.36 ± 0.01 (75) | 0.41 ± 0.02 (65) | 0.43 ± 0.02 (75) | 0.49 ± 0.02 (64) |
| *M. alfari* | 0.35 ± 0.01 (10) | 0.35 ± 0.01 (10) | 0.42 ± 0.01 (10) | 0.49 ± 0.01 (10) |
| *M. mimulus* | 0.34 ± 0.01 (8) | 0.33 ± 0.01 (8) | 0.40 ± 0.01 (8) | 0.47± 0.01 (8) |
| *Glaucomys* versus *Microsciurus* | | | | |
| $F$ | 7.36 | 184 | 3.55 | 0.95 |
| $d.f.$ | 1, 116 | 1, 104 | 1, 117 | 1, 102 |
| $P$ | < 0.01 | < 0.00001 | NS | NS |
| Other Sciurini | | | | |
| "*M.*" *flaviventer* | 0.35 ± 0.01 (10) | 0.35 ± 0.01 (10) | 0.41 ± 0.02 (10) | 0.48 ± 0.02 (10) |
| *T. hudsonicus* | 0.28 ± 0.01 (13) | 0.25 ± 0.01 (12) | 0.35 ± 0.02 (13) | 0.39 ± 0.01 (14) |
| *S. deppei* | 0.31 ± 0.01 (6) | 0.29 ± 0.01 (5) | 0.39 ± 0.01 (7) | 0.44 ± 0.02 (5) |
| *S. vulgaris* | 0.30 (2) | 0.30 (2) | 0.39 (2) | 0.46 (2) |
| *S. carolinensis* | 0.29 ± 0.01 (14) | 0.27 ± 0.01 (13) | 0.37 ± 0.02 (14) | 0.42 ± 0.02 (13) |
| *S. niger* | 0.29 ± 0.01 (19) | 0.27 ± 0.01 (19) | 0.36 ± 0.01 (19) | 0.41 ± 0.01 (19) |
| Other Pteromyini | | | | |
| *E. fimbriatus* | 0.31 ± 0.01 (2) | 0.32 ± 0.01 (2) | 0.40 ± 0.02 (2) | 0.44 ± 0.02 (2) |
| *H. nigripes* | 0.31 ± 0.01 (3) | 0.33 ± 0.01 (3) | 0.38 ± 0.02 (3) | 0.42 ± 0.02 (3) |
| *P. elegans* | 0.32 (1) | 0.33 (1) | 0.42 (1) | 0.44 (1) |
| *P. petaurista* | 0.33 ± 0.02 (4) | 0.33 ± 0.02 (4) | 0.40 ± 0.01 (4) | 0.42 ± 0.01 (4) |
| *A. tephromelas* | 0.34 (1) | 0.34 (1) | 0.44 (1) | 0.46 (1) |
| *P. philippinensis* | 0.34 (1) | — | 0.40 (1) | — |

the difference in the relative size of the forelimb is due to the elongation of the forearm (Table 4), as demonstrated by the relative length of the radius (radius/trunk, $F = 184$, $d.f. = 1, 104$, $P < 0.00001$). This is further demonstrated (Table 5) by the relative lengths of the humerus and radius (radius/humerus, $F = 492$, $d.f. = 1, 103$, $P < 0.00001$), a ratio that directly tests whether the forearm is elongated relative to the upper arm. In the hind limb, there is little to no difference between *Glaucomys* and *Microsciurus* in the relative lengths of femur and tibia (femur/trunk, $F = 3.55$, $d.f. = 1, 117$, not significant; tibia/trunk, $F = 0.95$ , $d.f. = 1, 102$, not significant); but the tibia is slightly longer than the femur in *Microsciurus* than in *Glaucomys* (tibia/femur, $F = 17.9$, $d.f. = 1, 101$, $P < 0.0001$). This ratio demonstrates that *Glaucomys* is not just elongating its distal limb bones relative to *Microsciurus*. The other ratios in Table 5 confirm that the main differences between *Glaucomys* and *Microsciurus* are in the elongation of the forearm of the former (radius/tibia, $F = 575$, $d.f. = 1, 96$, $P < 0.00001$; and forelimb/hind limb, $F = 333$, $d.f. = 1, 95$, $P < 0.00001$) and that there is little or no elongation of the humerus, femur, and tibia. However, the similar ratios of humerus/trunk, femur/trunk, and tibia/trunk conceal elongation of the long bones of flying squirrels commensurate with elongation of the lumbar region. The humerus, femur, and tibia, relative to trunk length, are not shorter in *Glaucomys* than in *Microsciurus*, in spite of the fact that the trunk length of *Glaucomys* is approximately 10% longer, due to the lumbar elongation. All of the larger Pteromyini species measured have a relatively longer radius than all of the larger Sciurini species, demonstrating that elongation of the forearm is a general feature of flying squirrels.

The long bones of flying squirrels are visibly more gracile than those of tree squirrels. The femora of *Glaucomys* have smaller midshaft diameters than those of *Microsciurus* ($F = 75.6$, $d.f. = 1, 117$, $P < 0.00001$) and the relative width (diameter/length) is much less ($F = 191.7$, $d.f. = 1, 116$, $P < 0.00001$). Because robustness of long bones is expected to be proportional to body mass, this implies that mass relative to linear measurements is reduced in *Glaucomys* compared with *Microsciurus*.

Field measurements of *Glaucomys* and *Microsciurus* suggest that the hind foot of the flying squirrels is relatively shorter (hind foot length/head and body length, means and standard deviations) than in the tree squirrels: *G. sabrinus*, eastern (0.25 ± 0.02); *G. sabrinus*, western (0.23 ± 0.03); *G. volans* (0.24 ± 0.02); *M. alfari* (0.28 ± 0.02); *M. mimulus* (0.26 ± 0.01; $F = 41.1$, $d.f. = 1, 97$, $P < 0.001$). Skeletal measurements support this observation (Table 6). The lengths of metatarsal 4 and proximal phalanx 4, relative to trunk length, are significantly shorter in *Glaucomys* than in *Microsciurus*. The sum of the 2, which comprise most of the length of the foot, is 22–23% of trunk lengths in *Glaucomys* and 26% in *Microsciurus* ($F = 117$, $d.f. = 1, 43$, $P < 0.00001$). In the hands, metacarpal 4 and proximal phalanx 4 also are significantly shorter in *Glaucomys* than in *Microsciurus*. As measured by the summed lengths of metacarpal 4 and proximal phalanx 4, the hands exhibit a greater difference than the feet—12–14% of trunk length in *Glaucomys* and 18% in *Microsciurus* ($F = 182$, $d.f. = 1, 24$,

**TABLE 5.**—Ratios of long-bone lengths (humerus [Hum], radius [Rad], femur [Fem], tibia [Tib], forelimb [Fore], and hind limb [Hind]; means and standard deviations, sample size in parentheses) of *Glaucomys* and *Microsciurus*. Other Sciurini and other Pteromyini are listed from small to large. The other genera are "*Microsciurus*," which is probably polyphyletic, *Tamiasciurus*, *Sciurus*, *Eoglaucomys*, *Hylopetes*, *Trogopterus*, *Aeromys*, and *Petaurista*. Samples are described in text. NS = not significant.

| Species | Rad/Hum | Tib/Fem | Hum/Fem | Radius/Tib | Fore/Hind |
|---|---|---|---|---|---|
| *G. sabrinus* (east) | 1.10 ± 0.02 (14) | 1.16 ± 0.02 (14) | 0.84 ± 0.02 (17) | 0.80 ± 0.01 (14) | 0.82 ± 0.01 (14) |
| *G. sabrinus* (west) | 1.11 ± 0.03 (8) | 1.16 ± 0.02 (8) | 0.85 ± 0.02 (8) | 0.82 ± 0.02 (8) | 0.83 ± 0.02 (8) |
| *G. volans* | 1.13 ± 0.02 (65) | 1.15 ± 0.02 (63) | 0.85 ± 0.01 (73) | 0.84 ± 0.01 (58) | 0.85 ± 0.01 (57) |
| *M. alfari* | 1.00 ± 0.02 (10) | 1.18 ± 0.01 (10) | 0.84 ± 0.01 (10) | 0.71 ± 0.01 (10) | 0.77 ± 0.01 (10) |
| *M. mimulus* | 0.95 ± 0.01 (8) | 1.17 ± 0.02 (8) | 0.85 ± 0.02 (8) | 0.69 ± 0.01 (8) | 0.76 ± 0.01 (8) |
| *Glaucomys* versus *Microsciurus* | | | | | |
| *F* | 492 | 17.9 | 1.72 | 575 | 333 |
| *d.f.* | 1, 103 | 1, 101 | 1, 114 | 1, 96 | 1, 95 |
| *P* | < 0.00001 | < 0.0001 | NS | < 0.00001 | < 0.00001 |
| Other Sciurini | | | | | |
| "*M.*" *flaviventer* | 1.00 ± 0.02 (10) | 1.18 ± 0.04 (10) | 0.84 ± 0.01 (10) | 0.71 ± 0.02 (10) | 0.77 ± 0.01 (10) |
| *T. hudsonicus* | 0.92 ± 0.01 (12) | 1.12 ± 0.01 (12) | 0.80 ± 0.01 (12) | 0.65 ± 0.01 (11) | 0.72 ± 0.01 (12) |
| *S. deppei* | 0.95 ± 0.01 (8) | 1.12 ± 0.01 (8) | 0.79 ± 0.01 (8) | 0.67 ± 0.01 (8) | 0.72 ± 0.01 (8) |
| *S. vulgaris* | 0.99 (2) | 1.16 (2) | 0.77 (2) | 0.66 (2) | 0.71 (2) |
| *S. aberti* | 0.95 ± 0.02 (6) | 1.12 ± 0.02 (6) | 0.78 ± 0.02 (6) | 0.66 ± 0.01 (6) | 0.72 ± 0.01 (6) |
| *S. carolinensis* | 0.95 ± 0.02 (15) | 1.12 ± 0.02 (15) | 0.77 ± 0.01 (16) | 0.65 ± 0.01 (15) | 0.71 ± 0.01 (15) |
| *S. niger* | 0.94 ± 0.02 (20) | 1.12 ± 0.01 (20) | 0.79 ± 0.02 (20) | 0.66 ± 0.01 (20) | 0.72 ± 0.01 (20) |
| Other Pteromyini | | | | | |
| *H. phayrei* | 1.07 (1) | 1.13 (1) | 0.85 (1) | 0.80 (1) | 0.82 (1) |
| *E. fimbriatus* | 1.05 ± 0.02 (3) | 1.09 ± 0.01 (2) | 0.77 ± 0.01 (3) | 0.74 ± 0.02 (2) | 0.75 ± 0.01 (2) |
| *H. nigripes* | 1.07 ± 0.01 (3) | 1.11 ± 0.02 (3) | 0.83 ± 0.04 (3) | 0.80 ± 0.01 (3) | 0.81 ± 0.01 (3) |
| *T. xanthipes* | 1.03 (1) | 1.05 (1) | 0.79 (1) | 0.78 (1) | 0.79 (1) |
| *A. tephromelas* | 1.01 ± 0.03 (2) | 1.01 ± 0.01 (2) | 0.82 ± 0.02 (2) | 0.82 ± 0.01 (2) | 0.82 ± 0.01 (2) |
| *P. petaurista* | 0.99 ± 0.02 (9) | 1.03 ± 0.02 (9) | 0.82 ± 0.03 (9) | 0.78 ± 0.02 (9) | 0.80 ± 0.02 (9) |

$P < 0.00001$). This is approximately a 15% difference in relative foot length, and 25% difference in relative hand length. However, a comparison of the relative hand and foot lengths in *Microsciurus* with other tree squirrels of the Sciurini suggests that *Microsciurus* has unusually long hands and feet for a tree squirrel, and that it, not *Glaucomys*, exhibits the derived morphology. Examination of our data for other Sciurini and other Pteromyini suggests that flying squirrels, in general, have shorter hands and feet, relative to trunk length, than tree squirrels (Table 6). However, these data are very dependent on the estimates of trunk length, and we are not confident of these estimates for flying squirrels other than *Glaucomys* because of small sample sizes (Table 1).

In summary, compared with *Microsciurus*, *G. sabrinus* and *G. volans* exhibit elongation of the lumbar vertebrae, the middle caudal vertebrae, and the long bones of the forearm. They exhibit shortening of the distal caudal vertebrae, the hands, and the feet, relative to *Microsciurus* (Fig. 4). However, the hands and feet are probably better considered to be elongated in *Microsciurus*, not shortened in *Glaucomys*.

## DISCUSSION

Contrasting the anatomy, behavior, and ecology of flying squirrels and tree squirrels provides us with concepts of the evolutionary changes required of and resulting from gliding flight. For example, all tree squirrels are diurnal, although crepuscular activity is not uncommon. In contrast, all flying squirrels are nocturnal, although also commonly crepuscular. We presume this behavioral change is in response to predation during glides by diurnal aerial predators in the Miocene, like present-day Cooper's hawks (*Accipiter cooperii*) and northern goshawks (*Accipiter gentilis*), which fly much more rapidly than flying squirrels glide. However, testing hypotheses about causation in the Miocene is very difficult. In turn, nocturnality has driven a number of anatomical changes, including relative eye size, a retina comprised largely of rods, and correlated neurological changes (Walls 1942). The patagium itself is the most obvious contrast between flying squirrels and tree squirrels. The leading edge extends from the cheek to the wrist and is lined by a muscle, the platysma II. The importance of the wing tip in flight—for stability, control, and reduction in drag—is reflected in a constellation of anatomical changes exhibited by flying squirrels (Thorington and Darrow 2000; Thorington et al. 1997, 1998). The major portion of the patagium extends from the body to the wrist and ankle and includes a number of thin muscles, including the tibiocarpalis muscle reaching from the wrist to the ankle (Bryant 1945; Johnson-Murray 1977). The uropatagium between the tail and the ankle is absent from *Glaucomys*, but very conspicuous in larger flying squirrels. The trailing edge of the uropatagium is supported by a 3rd head of the semitendinosis muscle of the thigh (Johnson-Murray 1977; Thorington et al. 2002).

The shape and size of the patagium determine important aerodynamic features, such as wing loading (body mass/wing area) and aspect ratio (wingspan/average wing chord), and we

TABLE 6.—Relative lengths of metapodial 4 and of proximal phalanx of *Glaucomys* and *Microsciurus* (means and standard deviations, sample size in parentheses). Hand Ph4 is the proximal phalanx of the 4th digit of the hand. MC4 is metacarpal 4. Foot Ph4 is the proximal phalanx of the 4th digit of the foot. MT4 is metatarsal 4. Other Sciurini and other Pteromyini are listed from small to large. The other genera are *Sciurus*, *Tamiasciurus*, *Hylopetes*, *Iomys*, *Eoglaucomys*, and *Petaurista*. Samples are described in text. NS = not significant.

| Species | Hand Ph4/trunk | MC4/trunk | Foot Ph4/trunk | MT4/trunk |
|---|---|---|---|---|
| *G. sabrinus* | 0.058 ± 0.003 (13) | 0.065 ± 0.004 (11) | 0.058 ± 0.002 (12) | 0.162 ± 0.007 (12) |
| *G. volans* | 0.065 ± 0.003 (13) | 0.075 ± 0.003 (6) | 0.067 ± 0.004 (15) | 0.164 ± 0.007 (14) |
| *M. alfari* | 0.082 ± 0.007 (8) | 0.099 ± 0.005 (7) | 0.089 ± 0.002 (10) | 0.175 ± 0.005 (10) |
| *M. mimulus* | 0.083 ± 0.004 (7) | 0.101 ± 0.006 (3) | 0.085 ± 0.005 (9) | 0.175 ± 0.011 (9) |
| *Glaucomys* versus *Microsciurus* | | | | |
| *F* | 181 | 182 | 240 | 29.0 |
| *d.f.* | 1, 39 | 1, 25 | 1, 44 | 1, 43 |
| *P* | < 0.00001 | < 0.00001 | < 0.00001 | < 0.00001 |
| Other Sciurini | | | | |
| *S. vulgaris* | 0.046 ± 0.009 (12) | 0.075 ± 0.006 (6) | 0.062 ± 0.003 (11) | 0.146 ± 0.005 (10) |
| *T. hudsonicus* | 0.070 ± 0.007 (20) | 0.091 ± 0.008 (20) | 0.076 ± 0.007 (20) | 0.176 ± 0.018 (17) |
| *S. carolinensis* | 0.071 ± 0.003 (12) | 0.094 ± 0.008 (12) | 0.077 ± 0.005 (14) | 0.169 ± 0.014 (12) |
| *S. niger* | 0.062 ± 0.003 (13) | 0.086 ± 0.004 (11) | 0.066 ± 0.004 (13) | 0.156 ± 0.006 (12) |
| Other Pteromyini | | | | |
| *H. spadiceus* | 0.063 ± 0.003 (15) | 0.070 ± 0.005 (15) | 0.057 ± 0.003 (14) | 0.118 ± 0.005 (14) |
| *I. horsfieldii* | 0.071 ± 0.008 (5) | 0.084 ± 0.001 (2) | 0.065 ± 0.002 (5) | 0.144 ± 0.003 (4) |
| *E. fimbriatus* | 0.056 ± 0.001 (11) | 0.064 ± 0.007 (8) | 0.058 ± 0.004 (13) | 0.130 ± 0.036 (12) |
| *P. philippinensis* | 0.070 ± 0.013 (6) | 0.084 ± 0.014 (6) | 0.061 ± 0.011 (6) | 0.139 ± 0.025 (6) |
| Other Sciurini versus Other Pteromyini | $F = 0.04$<br>$d.f. = 1, 92$<br>NS | $F = 55.9$<br>$d.f. = 1, 78$<br>$P < 0.00001$ | $F = 64.0$<br>$d.f. = 1, 94$<br>$P < 0.00001$ | $F = 102.3$<br>$d.f. = 1, 85$<br>$P < 0.00001$ |

hypothesized that changes in body proportions in flying squirrels would decrease wing loading and increase the aspect ratio. The observed elongation of the lumbar vertebrae, accompanied by a compensatory elongation of the limbs, should result in a decrease in the wing loading of flying squirrels. The observed elongation of the lumbar vertebrae by 20% results in an elongation of the trunk, and hence of the patagium, by approximately 10%. The compensatory elongation of the limbs, also approximately 10%, should result in an increase in patagium area on the order of 20% and would result in a similar decrease in wing loading. The reduction in the size of the transverse processes of the lumbar vertebrae in *Glaucomys*, and the greater gracility of the long bones, suggests that there is not an accompanying increase in body mass. Thus, we contend that these evolutionary changes decrease wing loading from what it otherwise would have been.

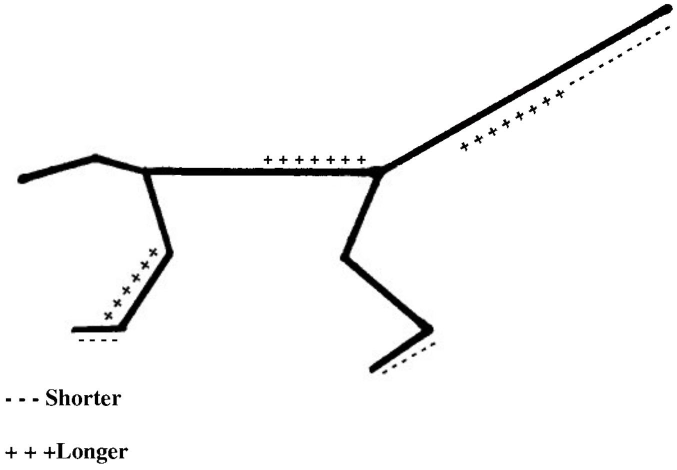

FIG. 4.—Stick figure of skeleton of *Glaucomys* showing areas of major differences in proportions of parts compared with *Microsciurus*. Lumbar vertebrae, midcaudal vertebrae, and forearm are longer; distal caudal vertebrae, hands, and feet are shorter.

The importance of wing loading to flying squirrels is unknown, but the morphological modifications of *Glaucomys* suggest that it is very important. Aerodynamically, wing loading is expected to affect the minimal speed of gliding, but not the distance (Thorington and Heaney 1981). In a study of *G. volans*, Bishop (2006) found a significant positive correlation between speed and coefficient of lift, which is anomalous, as she noted, because minimal speed is expected to be inversely proportional to the coefficient of lift, according to aerodynamic theory. This may result from the different gliding behaviors of her 2 animals—the more heavily loaded animal averaged a lower glide angle with a higher coefficient of lift, as well as a higher average velocity than the lighter animal. There was a significant correlation between wing loading and speed in Bishop's analyses of gliding in *G. volans*, but the correlation between speed and coefficient of lift was slightly larger, causing wing loading to be eliminated in her stepwise multiple regression analysis and leaving only coefficient of lift as a factor contributing to velocity. It seems unlikely to us that flying squirrels defy aerodynamic principles, so we still expect minimal airspeed to be directly proportional to the square root of wing loading divided by the coefficient of lift. Speed affects critical issues such as landing and control in flight. Rapid gliding requires rapid reactions; slow gliding increases vulnerability to gusts of wind. In nature, flying squirrel body mass varies with age, season, and pregnancy, so we know that flying squirrels cope with differing wing loadings. We do not know if there are critical issues of stability and maneuverability among young animals learning to glide or among gravid females, but the importance of wing loading for such animals could be tested in flight chambers.

Robins et al. (2000) suggested that the sexual dimorphism in *G. volans* is important because it reduces the wing loading of the females when pregnant. (Examination of their data shows that females average larger than males in long-bone lengths by 1.0–1.4%.) Their hypothesis seems counterintuitive because wing loading (mass/wing area) would be expected to be slightly larger in the larger females. In order to have lower wing loadings than males, nonpregnant females would need to be leaner. Unfortunately, we were unable to test this hypothesis with our data because mass is seldom recorded for older museum specimens.

We have considered other hypotheses involving the elongation of lumbar vertebrae. The elongation of vertebrae necessarily reduces flexibility by moving intervertebral joints further apart, so flying squirrels should be expected to have stiffer, less flexible lumbar portions of their spines. However, most of the flexibility of tree and flying squirrel spines is accomplished between the 10th thoracic vertebra and the 2nd lumbar vertebra (personal examination of X-rays), and there is very little elongation in this region in flying squirrels. Most of the elongation occurs in lumbar vertebrae 3–7. Accordingly, we think elongation of the lumbar vertebrae has minimal effects on the flexibility of the spine of flying squirrels.

In contrast, the relative elongation of caudal vertebrae 5–13 may well function to increase the stiffness of the tails of flying squirrels. The shorter vertebrae of *Microsciurus* result in more intervertebral joints per centimeter in this portion of the tail than are found in *Glaucomys*. We do not understand why this should be important, but we do suspect that flying squirrels while gliding and tree squirrels while leaping use their tails differently for balance and control (Scheibe et al. 2007, and videos 4 and 5, available online at http://dx.doi.org/10.1644/06-MAMM-S-331.s4 and http://dx.doi.org/10.1644/06-MAMM-S-331.s5).

The elongation of the forelimb has 2 consequences. One is that it will increase the area of the wing, and hence decrease the wing loading. Second, and perhaps more important, it will increase the wingspan and hence the aspect ratio (AR) of the wing ($AR = (\text{wingspan})^2/(\text{wing area})$ or (wingspan)/average chord length of wing). We hypothesized that evolution would favor elongation of the forelimb, because the aspect ratio is directly proportional to glide ratio (glide distance/vertical drop), so that the elongation should increase the distance of the squirrel's glides. We have pondered why flying squirrels do not have higher aspect ratios that would enable them to glide further yet. We suspect there are 2 trade-offs that account for this. First is the trade-off between the advantage of a higher glide ratio and the disadvantage of reduced agility in tree-trunk locomotion. The latter would be particularly important during mating chases, if these mating chases are similar to those of Holarctic tree squirrels (as seems likely, but is poorly documented). Second, there may be a trade-off between the advantage of a higher glide ratio and the disadvantageous attributes of higher aspect ratios on landing characteristics. Wings with low aspect ratios do not stall until they reach high angles of attack, allowing a flying squirrel to be nearly vertical when it lands on a tree trunk. This enables it to land on its feet, rather than on its nose. The 2nd hypothesis seems less probable, but it is more testable (with models in a wind tunnel) than is the 1st.

Because flying squirrels hold their hands and feet in positions that appear to minimize parasite drag, we hypothesized that a reduction in foot and hand length might also occur. We found that *Glaucomys* do have shorter hands and feet than *Microsciurus*, but this seems to be due to the fact that *Microsciurus* has especially long hands and feet, not that those of *Glaucomys* are short. Examination of our data suggests that other species of Pteromyini also have shorter hands and feet than the other species of Sciurini. However, because the data are scanty, we considered the issue moot.

In a perspective titled "How to make a limb?" Duboule (1994) described the development of vertebrate limbs in terms of what was then known about *Hox* genes. The understanding of biochemical pathways of vertebrate development has increased greatly since then (Forlani et al. 2003) and should in the future enable us to determine what modifications in DNA have led to specific morphological changes during evolution. A selective review of the burgeoning literature leads us to suggest some biochemical pathways that may be responsible for the differences we have observed between flying squirrels and tree squirrels. These pathways are the links between the mutations of DNA and the adaptive morphological features of the phenotype that permit or facilitate the evolutionary novelty of gliding flight.

During development, presomitic mesoderm gives rise to the somites, which then give rise to the vertebrae and skeletal musculature. The vertebral modifications we observe in the evolution of flying squirrels from tree squirrels are possibly driven by changes in the molecular pathways during these transitions, in particular *Hoxa, Hoxc*, and *Hoxd*, paralogs *10, 11,* and perhaps *13* (Deschamps and van Nes 2005). Wellik and Capecchi (2003) demonstrated that *Hoxa, Hoxc*, and *Hoxd 10* are active in the presomitic mesoderm of the lumbar region and determine that the lumbar vertebrae have no ribs, and that the paralogs *Hoxa, Hoxc*, and *Hoxd 11* are active in the presomitic mesoderm of the sacral vertebrae and determine their morphology. Carapuco et al. (2005) suggest that *Hoxa11* is active in the somites of the proximal caudal vertebrae as well.

As the presomitic mesoderm gives rise to the somites, the boundaries between the somites appear to be controlled by the Notch pathway in a clocklike manner, under the coordination of the *Wnt* signaling pathway (Dequeant et al. 2006). The fibroblast growth factor (*Fgf8* signaling pathway), coupled with the receptor for the fibroblast growth factor (Hajihosseini et al. 2004), is involved in determining the size of the somites

(Aulehla and Herrmann 2004). A gradient of *Fgf8* mRNA is established from the tail bud, which establishes a gradient of *Fgf8*, strongest toward the caudal end, weakest toward the rostral end (Dubrulle and Pourquie 2004), which determines the rate of inclusion of presomitic mesoderm in the somites as they are formed. This gradient, coupled with the timing of the somite boundaries by the Notch pathway, determines the size of the somites and could determine the size of the subsequently formed vertebrae. Another possibility is that the size differential between flying squirrel and tree squirrel vertebrae could be determined later in their embryology by different growth rates of the vertebrae, as described by Sears et al. (2006) for the phalanges in bat wings (discussed below). Because the embryology of tree and flying squirrels has not been studied, we cannot distinguish between these 2 possibilities.

Boulet and Capecchi (2004) demonstrated that *Hoxa11* and *Hoxd11* are active in the forearm during the development of the radius and ulna, and that lack of function of these 2 leads to decreased mesenchymal condensation through reduced expression of *Fgf8* and *Fgf10* and delayed limb development. However, the major effect was the malformation of the growth plates of both bones. In the growth plates, the chondrocytes failed to mature and rarely formed hypertrophic cells. Thus, modifications of the biochemical pathways controlled by these 2 homeobox genes in the development of the forearm are likely the cause of differing adult forearm morphology in tree squirrels and flying squirrels.

The *Hox* genes, *Hoxa* and *Hoxd 11*, *12*, and *13* are similarly important in the development of the hands and feet, particularly through the expression of *Fgf8* and *Fgf10* (Boulet and Capecchi 2004; Zakany et al. 1997). Knosp et al. (2004) demonstrated that *Hoxa13* is essential for the development of the digits of the hands and functions through the expression of the bone morphogenetic proteins *Bmp2* and *Bmp7*. Subsequently, Sears et al. (2006) demonstrated that the elongation of the digits of bats is affected by the up-regulation of *Bmp2*, which increases the rate of chondrogenesis during development. *Bmp2* causes great enlargement of the hypertrophic zone of the growth plate and elongation of the digits, whereas its antagonist, *Noggin*, reduces the rate of chondrogenesis and causes the digits to be shorter. Upstream regulation of levels of *Bmp2* or *Noggin* could therefore account for the different foot and hand lengths in *Glaucomys* and *Microsciurus*. As noted by Sears et al. (2006), this manner of control of the size of skeletal elements could be widespread in vertebrate development. If true, it also could be the basis of the lengthening and the shortening in the flying squirrel vertebral column and forearm.

Delineation of the DNA changes in the evolution of flying squirrels, the molecular pathways affected, and how these have led to their morphology and made gliding flight possible, will ultimately tell us how nature has built flying squirrels. The evolutionary novelty of gliding has evolved 6 different times among Recent mammals, but squirrels probably present the only opportunity to study these details of the evolutionary process, because of the persistence of the ancestral morphology among the American tree squirrels.

## ACKNOWLEDGMENTS

We're grateful to W. P. Smith for his invitation to participate in a symposium about northern flying squirrels, and to prepare this manuscript. The invitation provoked us to examine flying squirrel flying proportions in greater detail than before. The senior author has benefited greatly from discussions about the aerodynamics of gliding with B. J. Stafford and guidance from J. Maldonado about the molecular biology of flying squirrel development, and we have benefited from review of the manuscript by W. P. Smith, B. S. Arbogast, J. S. Scheibe, and P. D. Weigl.

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## Appendix I

*Specimens examined.*—Most specimens examined were from the collection of the National Museum of Natural History (USNM), Washington, D.C. Specimens also were examined from the Natural History Museum (BM), London, United Kingdom; and the Delaware Museum of Natural History (DelMNH).

### Sciurini

*Microsciurus alfari*

*Skeletons.*—USNM 305627, 305631, 305632, 310382, 310387, 338139, 338140, 338141, 338142.

*Skins.*—USNM 250272, 250273, 250481, 297769, 301296, 315918, 315919, 315920, 315921, 315922, 315923, 318363, 318364, 335510, 335511, 335512, 335513, 335514, 335515, 335516.

*X-rays.*—USNM 338140, 171244, 292134, 309027, 318364, 338138, 338139, 338142, 338149, 338154.

### *Microsciurus mimulus*

*Skeletons.*—USNM 305634, 310388, 338166, 338167, 338168, 338169, 338172, 338173, 338174, 338175, 338176, 338177, 499514.

*Skins.*—USNM 338169, 113311, 305633, 305634, 306897, 310388, 335167, 338166, 338168, 338170, 338171, 338172, 338173, 338174, 338175, 338176, 338177, 338178, 338179, 339054.

*X-rays.*—USNM 309028, 309029, 309031, 309032, 309033, 309073, 309074, 309075, 499514.

### *Sciurus carolinensis*

*Skeletons.*—USNM 396202, 396335, 396995, 396999, 397050, 397054, 397064, 397179, 397213, 397223, 397224, 398853, 503982, 505317, 536760, 536822.

*X-rays.*—USNM 396335, 396995, 396999, 397050, 397054, 397064, 397179, 397213, 397223, 397224, 398853, 503982, 505317, 536760, 536822.

### *Sciurus deppei*

*Skeletons.*—USNM 244934, 244935, 244937, 244938, 244939, 244942, 244952, 244953, 244954, 244956, 244958.

### *Sciurus niger*

*Skeletons.*—USNM 568156, 583319, 583320, 583325, 583326, 583327, 583327, 583328, 583328, 583329, 583332, 583333, 583333, 583335, 583337, 588360, 588363, 588374, 588387.

*X-rays.*—USNM 568156, 588362, 588363, 588364, 588374, 588387, 588389, 588390, 588392, 588394, 588395, 588398, 588399, 588402.

### *Sciurus vulgaris*

*Skeletons.*—USNM 581894, 581894, 582904.

*X-rays.*—USNM 548937, 548938, 548939, 548940, 548946, 548960, 548962, 548963, 548966, 548967, 548971, 548944.

### *Tamiasciurus hudsonicus*

*Skeletons.*—USNM 548945, 548949, 548965, 548969, 548970, 548979, 548989, 548995, 548997.

*X-rays.*—USNM 2273, 2274, 86921, 86922, 143669, 143670, 143671, 143672, 152690, 152694, 152695, 152703, 159623, 548945, 548947, 548950, 548965, 548969, 548970, 548979, 548989.

## Pteromyini

### *Aeromys tephromelas*

*Skeletons.*—USNM 229, 90437, 196743.

### *Eoglaucomys fimbriatus*

*Skeletons.*—USNM 173361, 173363, 173365.

*X-rays.*—USNM 326363, 353231, 353232, 353242, 353244, 353245, 353246, 410953, 413517, 413518, 413519, 416516, 513520.

### *Glaucomys sabrinus*

*Skulls.*—Eastern: USNM 260421, 260429, 267440, 292277, 311056, 332333, 332334, 332335, 332336, 338987; western: USNM 71035, 072960, 168243, 168662, 168663, 168693, 169169, 169170, 169171, 169172, 169173, 169725, 169918, 170507, 176902, 176903, 202776, 206017, 207709, 208318, 208319, 208320, 208321, 231939, 231940, 231941, 233399, 241799, 241800, 241801, 265900, 266093, 274347, 298548, 397017, 397020, 397022, 397023, 397040, 397041, 397065, 397067, 397068, 397069, 514256, 514257, 514258, 514259, 524543, 524544, 527619, 527620, 530553, 530554, 530555, 530556, 530557, 551840, 551841, 551842, 551843, 552249.

*Postcranial skeletons.*—Eastern: USNM 397021, 332333, 524543, 527620, 551841, 338987, 332336, 267440, 311056, 397040, 397068, 397022, 397023, 397065, 397067, 397069, 397020, 397017; western: USNM 006525, 038795, 049821, 049822, 141771, 141951, 235940, 398287, 398288.

*Skins.*—Eastern: USNM 292277, 64684, 71174, 71175, 76379, 86373, 96095, 260421, 260929, 267440, 289646, 311056, 332333, 332334, 332335, 332336, 338987, 528212, 530836; western: USNM 24270, 72960, 75178, 168693, 169169, 207709, 208318, 208319, 208320, 208321, 231939, 231940, 231941, 232230, 233399, 241800, 241801, 264949, 264950, 265900, 274347.

*X-rays.*—USNM 229020, 243062, 397017, 397023, 397041, 514256, 514258, 514259, 524543, 527620, 530553, 530557, 551842.

### *Glaucomys volans*

*Skeletons.*—USNM 003612, 025317, 194012, 252203, 25316, 256758, 293441, 301992, 348384, 348385, 348386, 360912, 360913, 397018, 397019, 397024, 397025, 397026, 397027, 397028, 397030, 397031, 397032, 397033, 397034, 397035, 397036, 397037, 397038, 397039, 397057, 397058, 397072, 397073, 397074, 397075, 397076, 397077, 397078, 397079, 397080, 397081, 397082, 397083, 397100, 397101, 397105, 397105, 503986, 505615, 505618, 505619, 505620, 505621, 505622, 505623, 505624, 506226, 506653, 525962, 525963, 536966, 536967, 536968, 564132, 564133, 567961, 568371, 568670, 569025, 569026, 589259, 589260, 589262; DelMNH: DRH349, JPC427.

*Skins.*—USNM 525963, 282245, 313318, 313944, 323319, 347760, 347761, 347762, 347763, 348384, 348385, 505615, 505617, 505618, 505619, 525962, 567671, 567672, 569025.

*X-rays.*—USNM 256758, 286627, 301992, 338986, 360913, 397025, 397028, 397034, 397036, 397039, 505615, 505620, 505623, 568371, 569026.

### *Hylopetes nigripes*

*Skeletons.*—USNM 63025, 63027, 63030, 63031.

### *Hylopetes phayrei*

*Skeletons.*—USNM 267267, 117635.

### *Hylopetes spadiceus*

*X-rays.*—USNM 311369, 48839, 481109, 481110, 481111, 481112, 481113, 481114, 481115, 481116, 488640, 488642, 488644, 488646, 488683.

### *Iomys horsfieldii*

*Skeletons.*—USNM 292645.

*X-rays.*—USNM 292653, 151792, 252321, 292653, 301024, 317240.

### *Petaurista spp.*

*Skeletons.*—BM 1858624168, 18791121239.

### *Petaurista alborufus*

*Skeletons.*—USNM 187082, BM 19686102.

### *Petaurista alborufus lena*

*Skeletons.*—USNM 332937.

*Petaurista elegans*

*Skeletons.*—USNM 292647.

*Petaurista leucogenys*

*Skeletons.*—USNM 307073.

*Petaurista magnificus*

*Skeletons.*—USNM 12528, BM 1848112011, BM?.

*Petaurista petaurista*

*Skeletons.*—USNM 32396, 46647, 68784, 98533, BM 1960845.

*Petaurista petaurista batuana*

*Skeletons.*—USNM 49660.

*Petaurista petaurista nitidula*

*Skeletons.*—BM 973103, 1879721.

*Petaurista petaurista rajah*

*Skeletons.*—USNM 197320.

*Petaurista philippinensis*

*Skeletons.*—USNM 112975.

*Petaurista philippinensis cineraceus*

*Skeletons.*—USNM 54814.

*Petaurista philippinensis grandis*

*Skeletons.*—USNM 183142, 307073, 314973.
*X-rays.*—USNM 358338, 358339, 358343, 358344, 358345, 358347.

*Petaurista philippinensis lylei*

*Skeletons.*—USNM 256914, 257844, 258016, 258017.

*Petaurista philippinensis yunanensis*

*Skeletons.*—USNM 43183, 58221.

*Pteromys momonga*

*Skeletons.*—USNM 5911, 9170, 10639.

*Trogopterus xanthipes*

*Skeletons.*—USNM 268872.

## APPENDIX II

*Body size in Glaucomys sabrinus.*—Body size in the northern flying squirrel varies geographically, but it is poorly documented. Therefore we summarize our knowledge of it here. The smallest *Glaucomys sabrinus* are in the eastern United States (*G. s. macrotis*, *G. s. coloratus*, and *G. s. fuscus*) and the largest animals are in northern Idaho and western Montana (*G. s. latipes*). Total length of skull averages from 36.6 mm (*G. s. fuscus*) to 42.9 mm (*G. s. latipes*), a difference of approximately 17%. Body mass for one of the smallest subspecies, *G. s. coloratus*, averages 110 g, varying seasonally from 107 g to 113 g in males, and from 109 g to 111 g in females (Weigl et al. 1999). Body mass for a larger subspecies, the Prince of Wales flying squirrel (*G. s. griseifrons*), averages 125 g: adult males average 132 g in the spring and 122 g in the autumn, whereas adult females average 125 g and 123 g, respectively (Smith and Nichols 2003). In western Oregon, flying squirrels (*G. s. oregonensis*) average 143 g in the winter and 127 g during the spring and summer (Witt 1991) for a grand average of 131 g. In the Coast Range of Oregon, Villa et al. (1999) obtained similar weights—the squirrels averaged 132.4 g; but in the Puget Trough of Washington, animals averaged 141.8 g, with males varying from 132.2 g in the spring to 140.8 g in the fall and females varying from 152.8 g in the spring to 146.5 g in the autumn. This geographic and seasonal variation of approximately 30% in mass corresponds with a skull length difference of 6.5% and length differences in trunk and long bones of 7–11% (Tables 1 and 3). Individuals of the largest subspecies of *G. sabrinus* probably average in excess of 160 g.