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BODY PROPORTIONS AND GLIDING ADAPTATIONS OF FLYING SQUIRRELS (PETAURISTINAE)

RICHARD W. THORINGTON, JR., AND LAWRENCE R. HEANEY

ABSTRACT.—Flying squirrels range in length of head and body from less than 90 mm to more than 400 mm. Large flying squirrels are more slender than tree squirrels or small flying squirrels. They have proportionately longer tails than small flying squirrels, but large tree squirrels have the longest tails of all, both absolutely and proportionately. Relative limb lengths decrease with size among flying and tree squirrels, but the ratio of forelimb to hindlimb length is generally higher for flying squirrels than for tree squirrels. The styliiform cartilage adds to the area of the patagium, but it is isometric with respect to size. Weight varies by a factor of almost 64 and the area of the patagium by a factor of almost 16, with little divergence from the expected isometric relationship. Therefore “wing loading” varies almost by a factor of four and is estimated to be as low as 30 Newtons/square meter (N/m^2) in small petauristines and as great as 110 N/m^2 in large ones.

Hang gliding seems to provide a good analogue for the gliding of flying squirrels, although the squirrels have lower aspect ratios (1.0 to 2.2) and lower glide ratios (less than 3) than do most hang gliders. From this analogy it seems probable that the heavier “wing loading” of large flying squirrels does not affect the glide ratio (horizontal distance/vertical drop) but that the larger flying squirrels must “fly” faster to maximize their glide ratio. It is also probable that small flying squirrels with lower “wing loadings” are more maneuverable, but large flying squirrels with heavier loadings are less affected by air turbulence.

Members of the Sciuridae are found on most vegetated portions of the earth's surface and have evolved into a wide variety of niches. One group, the flying squirrels, subfamily Petauristinae, has evolved into the unusual niche of nocturnal gliders. Only three other mammalian families—the Anomaluridae, Cynocephalidae, and Phalangeridae—have exploited this niche, and each is restricted to a single zoogeographic subregion, unlike the flying squirrels, which occur throughout most forested regions of the Palearctic, Oriental, and Nearctic regions.

We have studied the body proportions of a variety of species of flying squirrels. We first compared these with the body proportions of tree squirrels, in an attempt to gain a perspective on the basic adaptation of the Petauristinae for gliding. Second, we compared large flying squirrels with small ones. Among geometrically similar animals, weight should increase as the cube of a linear measurement, whereas the area of the patagium should increase as the square. Thus large flying squirrels should have patagia that are more heavily loaded than those of small flying squirrels, and this should affect their ability to glide. We compared the body proportions of large and small petauristines to see if there were ways in which large flying squirrels compensate for this allometric problem. We then used hang gliding as an analogue and attempted to determine what effect the allometric differences have on the gliding of flying squirrels.

MATERIAL AND METHODS

Sketetal measurements are based on most of the sciurid postcranial skeletons in the following museums: American Museum of Natural History, British Museum (Natural History), Field Museum of Natural History, Delaware Museum of Natural History, Bell Museum of Natural History, and U.S. National Museum of Natural History (USNM). Measurements were taken to the nearest 0.1 mm with dial calipers by both authors. Interobserver variance was much less than the left-right variance of the specimens. Lengths of the long bones are the same measurements described in Thorington (1972). All are greatest lengths, with the exception of the femur, which was mea-

sured from the head to the medial condyle. The vertebral lengths were measured ventrally on articulated skeletons.

Estimates of the ventral surface areas of flying squirrels were made from study skins in the USNM. Measurements were taken only on specimens that appeared to have the patagium extended. Different methods of preparation required different methods for estimating the areas, but generally it was possible to estimate the average width and length of the patagium. The areas listed are the products of these two figures. Thus they include the areas of the body and of the limbs. The area of the tail was estimated similarly. Direct measurements of area were obtained from tracings of a few fluid-preserved specimens which were soft enough to stretch out to natural positions and from tracings of freshly killed *Eoglaucomys* and *Petaurista* made by W. L. Abbott in 1891 in Kashmir.

The external measurements of most of the Southeast Asian squirrels are from collections in the USNM; most were collected by Illar Muul. This provided a uniformity of measurement not available in comparisons between collections of different investigators. Because the length of head and body (HB) was obtained as one measurement and the tail length as another, these two sets of data are independent of one another. They are not independent when length of head and body is obtained by subtracting tail length from total length. Although the lengths of head and body are similar when measured according to the two methods, they are not the same. Thus we avoided comparisons of samples that had been measured differently. Identifications of the specimens are those made by Muul.

We used ratios extensively in this paper. The use of ratios has been debated recently by Atchley et al. (1976), Hills (1978), Dodson (1978), Albrecht (1978), and Atchley and Anderson (1978). Some of the arguments are sufficiently obfuscating and intimidating to lead biologists to the conclusion that it is invalid statistically or at least unwise to use ratios under any circumstances. We disagree and would point to aerodynamics, which is sometimes called "the science of coefficients and ratios." The main points made by Atchley et al. (1976) and Atchley and Anderson (1978) are irrelevant to our study, because we did not study the correlations between ratios and we did not use ratios in multivariate analyses. The main question which may be raised is whether the ratios are normally distributed. This question was answered by examining the skewness and kurtosis of 45 representative ratios. One ratio was slightly skewed ($P < 0.05$) and none was significantly platykurtotic or leptokurtotic. None of our samples was large enough for a strong test of normality, but clearly the ratios did not differ from normal more than expected on the basis of chance. Accordingly, we submit that it is valid to use these ratios in interspecific comparisons, as we have done.

In this paper we have used the standard dimensions of physics, distinguishing between mass (in kg or g) and weight (in Newtons). This is essential in aerodynamics.

RESULTS

Body length, mass, and tail length.—The body lengths, masses, and tail lengths of 14 species of flying squirrels and 13 species of tree squirrels are shown in Tables 1 and 2. We hypothesized that flying squirrels would be more gracile than tree squirrels, because of selection for reduced patagial loading. In Fig. 1, a log-log plot of length of head and body versus mass shows that the regression lines are similar for tree and flying squirrels but that they diverge at larger body sizes. Small tree squirrels and flying squirrels are equally robust, but large tree squirrels are slightly more robust than large flying squirrels. This can be seen in the ponderal ratios as well. As shown in Table 3, this ratio is significantly higher in large tree squirrels than in large flying squirrels ($P < 0.01$). Thus for our sample, the hypothesis that flying squirrels should be more slender than tree squirrels is correct for large squirrels but not for small ones.

We also tested the hypothesis that large flying squirrels are more gracile than small flying squirrels. The regression equation for flying squirrels, shown in Fig. 1, is $\log \text{mass (g)} = 2.79 \log \text{length (mm)} - 4.13$. Thus mass increases at slightly less than the cube of the length of head and body. Correspondingly, the ponderal indices of large flying squirrels are less than those of small flying squirrels ($P < 0.05$) as shown in Table 3. This is not true of all squirrels as shown by the regression equation for tree

TABLE 1.—Length of head and body (mm), tail (mm), relative tail length, mass (g), and ponderal ratio ($\bar{X} \pm SD$) of flying squirrels.

Species	N	Length of head + body	Tail length	Tail/HB	Mass	Mass ³ /HB
<i>Petaurillus kintlochii</i>	4	90 ± 5	88 ± 7	0.97 ± 0.03	24 ± 7	0.0315 ± 0.0012
<i>Petinomys vordemanni</i>	26	112 ± 5	103 ± 6	0.92 ± 0.04	35 ± 5	0.0293 ± 0.0015
<i>Petinomys setosus</i>	30	116 ± 6	104 ± 4	0.90 ± 0.05	44 ± 5	0.0302 ± 0.0017
<i>Hylomys playurus</i>	15	118 ± 5	93 ± 6	0.79 ± 0.04	40 ± 5	0.0289 ± 0.0010
<i>Glaucomys volans</i>	43	130 ± 8	101 ± 7	0.78 ± 0.06	70 ± 13	0.0316 ± 0.0021
<i>Hylomys platyurus</i>	64	149 ± 5	129 ± 7	0.86 ± 0.05	83 ± 16	0.0292 ± 0.0018
<i>Glaucomys sabrinus</i>	14	169 ± 11	134 ± 11	0.81 ± 0.04	130 ± 24	0.0304 ± 0.0015
<i>Petinomys genibarbis</i>	2	178	188	1.06	108	0.0268
<i>Iomys horsfieldii</i>	46	180 ± 5	180 ± 10	1.01 ± 0.05	150 ± 26	0.0294 ± 0.0017
<i>Pteromyscus pulverulentus</i>	48	229 ± 12	217 ± 10	0.95 ± 0.06	236 ± 47	0.0269 ± 0.0016
<i>Petaurista elegans</i>	10	356 ± 10	381 ± 13	1.07 ± 0.04	1,169 ± 93	0.0298 ± 0.0013
<i>Aeromys tephromelas</i>	14	394 ± 20	458 ± 22	1.16 ± 0.07	1,189 ± 149	0.0269 ± 0.0010
<i>Petaurista alborufus</i>	18	410 ± 23	488 ± 28	1.11 ± 0.11	1,507 ± 192	0.0282 ± 0.0022
<i>Petaurista petaurista</i>	22	412 ± 17	475 ± 35	1.15 ± 0.09	1,539 ± 250	0.0280 ± 0.0014

squirrels [$\log \text{mass (g)} = 2.99 \log \text{length (mm)} - 4.54$] and the slightly higher ponderal indices of large tree squirrels versus small tree squirrels ($0.10 > P > 0.05$).

Because the tail seems to be important for balancing and steering a gliding animal, we hypothesized that the relative tail lengths of flying squirrels would be greater than those of tree squirrels. The data in Tables 1 and 2 show that this hypothesis is too simplistic. The regression lines cross because small tree squirrels tend to have shorter tails than small flying squirrels, but big tree squirrels have longer tails than big flying squirrels. This last fact predominantly reflects the very long tails of the giant tree squirrels (*Ratufa*). The relative tail lengths of *R. affinis* and *R. bicolor* exceed those of any flying squirrels and of any other tree squirrels. Thus our sample of tree squirrels exhibits a positive allometry of tail length (T) to length of head and body (HB), $\log (T) = 1.41 \log (HB) - 0.98$ ($r = 0.97$).

Among flying squirrels, we hypothesized that large animals would have more of a steering problem than small ones and therefore would have relatively, as well as absolutely, longer tails. Our data support this hypothesis. The largest flying squirrels have the longest tails relative to body length. The allometry is described by the regression, $\log (T) = 1.17 \log (HB) - 3.88$ ($r = 0.99$). However, the tails of small flying squirrels tend to be distichous, whereas those of large flying squirrels are not. Thus, tail length might be correlated with hair pattern as much as with size. Therefore we examined the pattern of variation within genera as well, for hair pattern does not vary within genera. Within the genera *Petinomys*, *Hylomys*, *Glaucomys*, and *Petaurista*,

TABLE 2.—Length of head and body (mm), tail (mm), relative tail length, mass (g), and ponderal ratio ($\bar{X} \pm SD$) of adult non-volant squirrels.

Species	N	Length of head + body	Tail length	Tail/HB	Mass	Mass ³ /HB
<i>Tamias maccllellandi</i>	4	112 ± 2	104 ± 6	0.93 ± 0.05	46 ± 1	0.0323 ± 0.0005
<i>Sundasciurus lowii</i> (Selangor)	8	127 ± 4	87 ± 9	0.68 ± 0.06	63 ± 9	0.0312 ± 0.0011
<i>Sundasciurus tenuis</i>	44	135 ± 6	115 ± 5	0.85 ± 0.04	74 ± 10	0.0310 ± 0.0016
<i>Sundasciurus lowii</i> (Sabah)	15	149 ± 7	94 ± 6	0.64 ± 0.06	93 ± 9	0.0305 ± 0.0011
<i>Sundasciurus brookei</i>	2	165	133	0.81	113	0.0292
<i>Callosciurus nigrovittatus</i>	44	197 ± 9	179 ± 9	0.90 ± 0.06	209 ± 28	0.0300 ± 0.0014
<i>Dremomys rufigenis</i>	12	201 ± 9	160 ± 28	0.80 ± 0.07	201 ± 15	0.0292 ± 0.0013
<i>Callosciurus notatus</i>	42	206 ± 8	190 ± 16	0.93 ± 0.08	223 ± 24	0.0295 ± 0.0010
<i>Callosciurus flavimanus</i>	3	213	194	0.91	245	0.0294
<i>Callosciurus caniceps</i>	29	218 ± 13	198 ± 11	0.92 ± 0.06	274 ± 38	0.0299 ± 0.0016
<i>Sundasciurus hippurus</i>	22	244 ± 12	262 ± 13	1.08 ± 0.09	439 ± 66	0.0310 ± 0.0011
<i>Callosciurus prevostii</i>	84	247 ± 11	243 ± 13	0.99 ± 0.05	440 ± 57	0.0307 ± 0.0012
<i>Ratufa affinis</i>	37	344 ± 18	420 ± 20	1.23 ± 0.09	1287 ± 181	0.0315 ± 0.0023
<i>Ratufa bicolor</i>	47	366 ± 16	432 ± 17	1.20 ± 0.07	1546 ± 175	0.0314 ± 0.0012

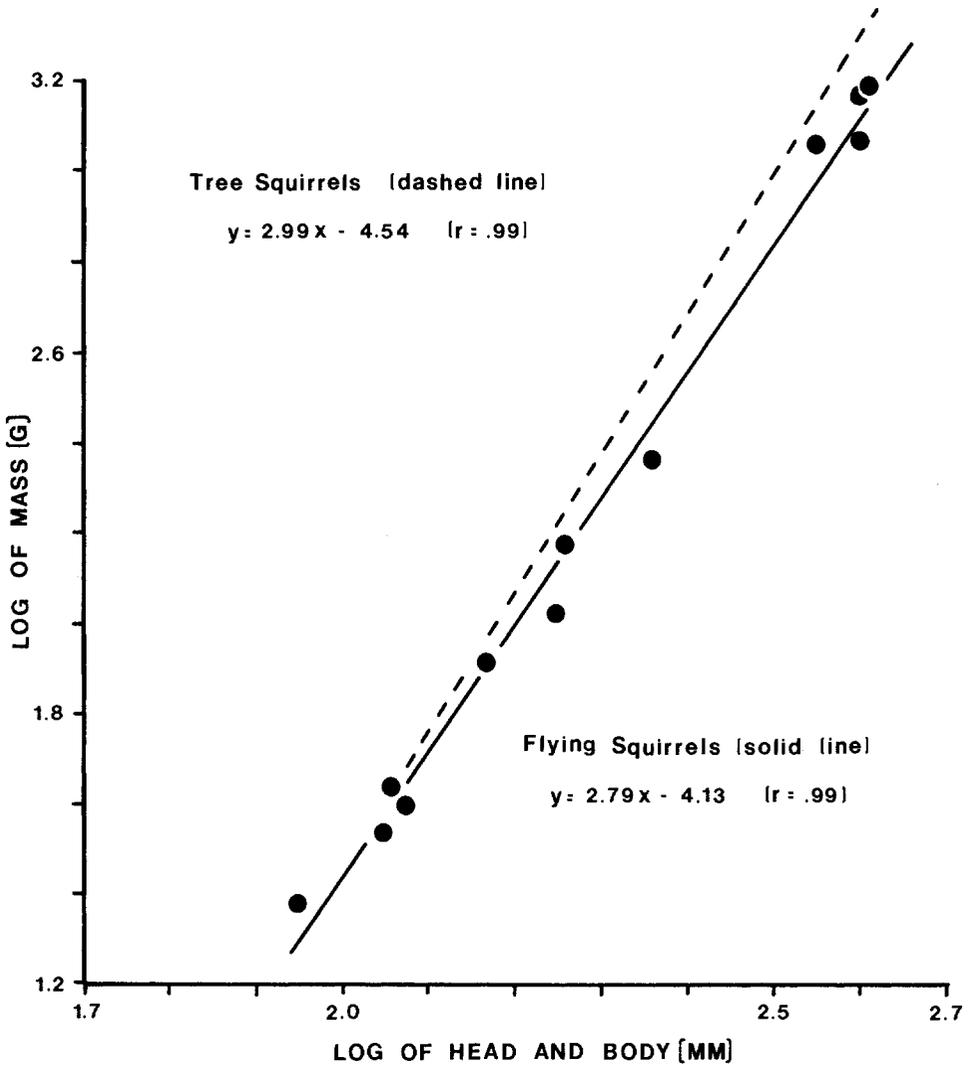


FIG. 1.—Relationship between mass and length of head and body in tree squirrels and flying squirrels. Points are plotted for flying squirrels only.

the largest species has the largest ratio of tail length to body length. Accordingly, we think there is a general trend within flying squirrels for relative tail length to increase with body size.

Limb lengths and proportions.—It is thought that flying squirrels have longer limbs than tree squirrels of the same size among North American squirrels (Peterka, 1936; Bryant, 1945), and we hypothesized it would be universally true because of selection for a large gliding membrane among flying squirrels. Figs. 2 and 3 summarize our data in Tables 4 and 5. They show that the relative limb lengths of flying squirrels are generally greater than those of tree squirrels but they cast doubt on the universality of the trend. *Microsciurus* and *Glaucomys* are the smallest animals graphed and their relative limb lengths are similar. Also our data show that there is little difference in the relative lengths of hind limbs of tree and flying squirrels, except for the giant tree squirrels, *Ratufa*, which have relatively short hind limbs.

TABLE 3.—Averages (\pm SE) of ponderal ratios ($\text{mass}^{.33}/\text{HB}$) of tree squirrels and flying squirrels.

Size	No. species*	Tree squirrels	No. Species*	Flying squirrels
Small	6	0.0302 \pm 0.0003	6	0.0299 \pm 0.0010
Large	5	0.0309 \pm 0.0003	6	0.0282 \pm 0.0005

* For all species, $n \geq 8$.

We also hypothesized that large flying squirrels would have relatively longer limbs than small ones in order to compensate for the allometric relationship between weight and area of patagium. This hypothesis is clearly false. Small flying squirrels have the highest ratios of limb length to trunk length, as may be seen in Figs. 2 and 3.

We knew from preliminary investigations that *Glaucomys* had relatively long distal elements in the limbs and we wondered if this was characteristic of all flying squirrels. The data in Tables 6 and 7 clearly show that it is true for the forelimb: the radius is long relative to humerus length in all flying squirrels and shorter in all tree squirrels. Among flying squirrels the ratio is inversely proportional to size, as it also appears to be among tree squirrels. There does not appear to be any difference between flying squirrels and tree squirrels in the length of the tibia relative to that of the femur. As in the forelimb, there is an inverse proportionality of this ratio to size in flying squirrels. The ratio of humerus length to femur length does not differ systematically between flying squirrels and tree squirrels, nor is there a regular pattern of change with size in either. The radius is long relative to the tibia in flying squirrels, as should be expected from the preceding relationship.

We suspected that the relative length of forelimb to hind limb might be important in flying squirrels because it would affect the shape of the patagium. Because flying squirrels glide with their knee and elbow joints almost fully extended, we have used the sums of length of long bones as an estimate of limb lengths. The data in Table 6 shows that summed lengths of radius and humerus average slightly more than 80% of the summed lengths of tibia and femur in flying squirrels, and less than 75% in tree squirrels (Table 7). All flying squirrels we have measured, except *Eoglaucmys*, have a higher intermembral ratio than any species of tree squirrel.

The styliform cartilage and uropatagium.—The preceding hypotheses about limb lengths ignored the styliform cartilage. Because the patagium is supported from the styliform cartilage at the wrist, it is possible for squirrels to evolve a wider membrane by growing a longer cartilage, independent of the length of the bones of the forelimb. We hypothesized that this was not an important factor. To test this, we measured the length of the cartilage (C) on one specimen each of 15 species of flying squirrels and regressed the data against the length of head and body (HB). This plot appears quite linear. The best fit of a power equation yields an allometric coefficient of 1.08, which is not significantly different from isometry. A linear equation ($C = -7.35 + 0.25 \text{ HB}$) explains only 4% less of the variance, so we concluded that there was no disproportionate increase in the length of the styliform cartilage of large flying squirrels compared with small ones. In another test of the hypothesis, we measured the styliform cartilages of 10 specimens each of seven species, ranging in size from *Petaurillus kinlochii* to *Aeromys*. The allometry coefficient was 1.01, again suggesting isometry.

Johnson-Murray (1977) found that the propatagia and plagiopatagia were equally well developed on small and large flying squirrels, and we concur. However, as she pointed out, there is a significant difference in the size of the uropatagium of large and small flying squirrels. On small flying squirrels the uropatagium is virtually nonexistent and it certainly does not contribute significantly to the area of the gliding membrane. In the large flying squirrels *Petaurista*, *Aeromys*, and *Aeretes*, there is a

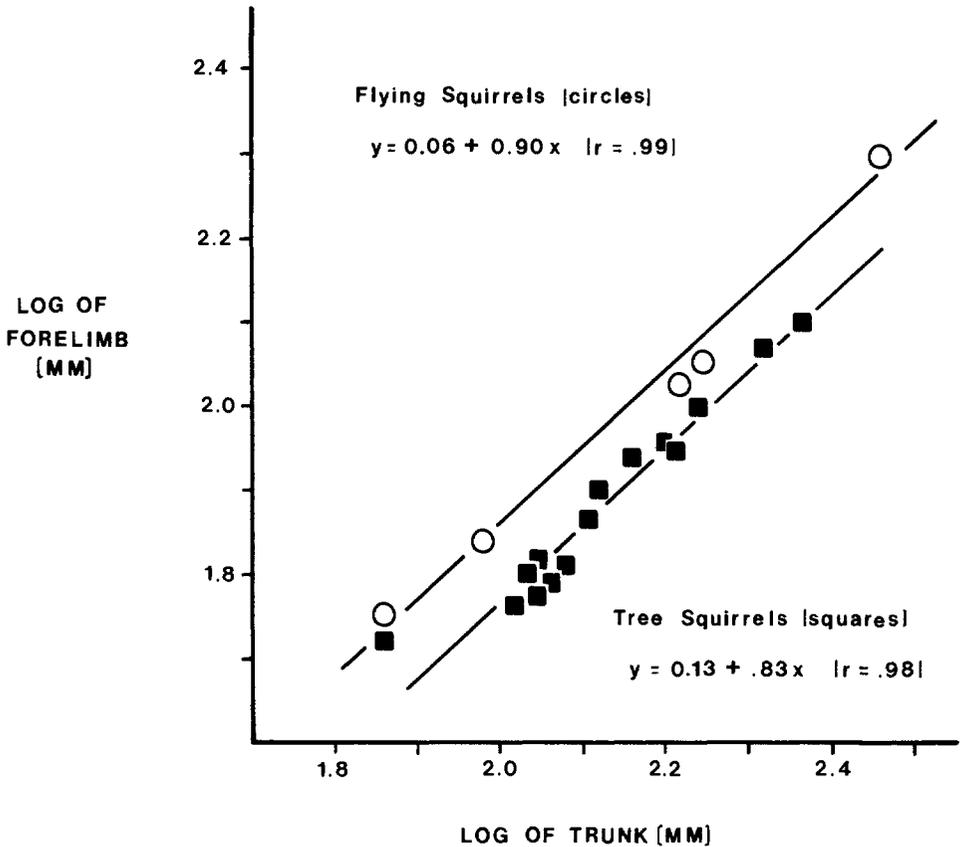


FIG. 2.—Relationship between lengths of forelimb and trunk in tree squirrels and flying squirrels.

significant uropatagium extending from the knee to the tail. This is one way in which the large flying squirrels seem to compensate for the increased loading of the gliding membrane. We attempted to quantify the increase in area, although we could not obtain very accurate measurements on museum skins.

The largest uropatagium is found on *Aeromys*, and on three specimens we estimated its area to be approximately 100 cm² of the total 1,600 cm² of the ventral surface of the body. The net contribution is somewhat less because our measurement of the area of the uropatagium includes the tail. Thus we estimated that *Aeromys* gains approximately 5% in patagial area by having a uropatagium. In *Petaurista* and *Aeretes* the percentage increase appears to be less.

TABLE 4.—Trunk and relative limb lengths of adult flying squirrels ($\bar{X} \pm SD$).

Species	N	Trunk ^a (mm)	Forelimb ^b /trunk	Hindlimb ^c /trunk
<i>Glaucomys volans</i>	19	72.7 ± 4.1	0.77 ± 0.03	0.91 ± 0.03
<i>Glaucomys sabrinus</i>	8	95.4 ± 3.5	0.72 ± 0.02	0.88 ± 0.03
<i>Eoglaucomys fimbriatus</i>	3	170.6	0.63	0.84
<i>Hylomys nigripes</i>	5	175.5 ± 2.4	0.65	0.80
<i>Petaurista petaurista</i>	11	286 ± 32	0.66 ± 0.04	0.83 ± 0.03

^a Trunk is defined as the summed lengths of the thoracic, lumbar, and sacral vertebrae. Only adult animals were included.

^b Forelimb length is humerus + radius.

^c Hindlimb length is femur + tibia.

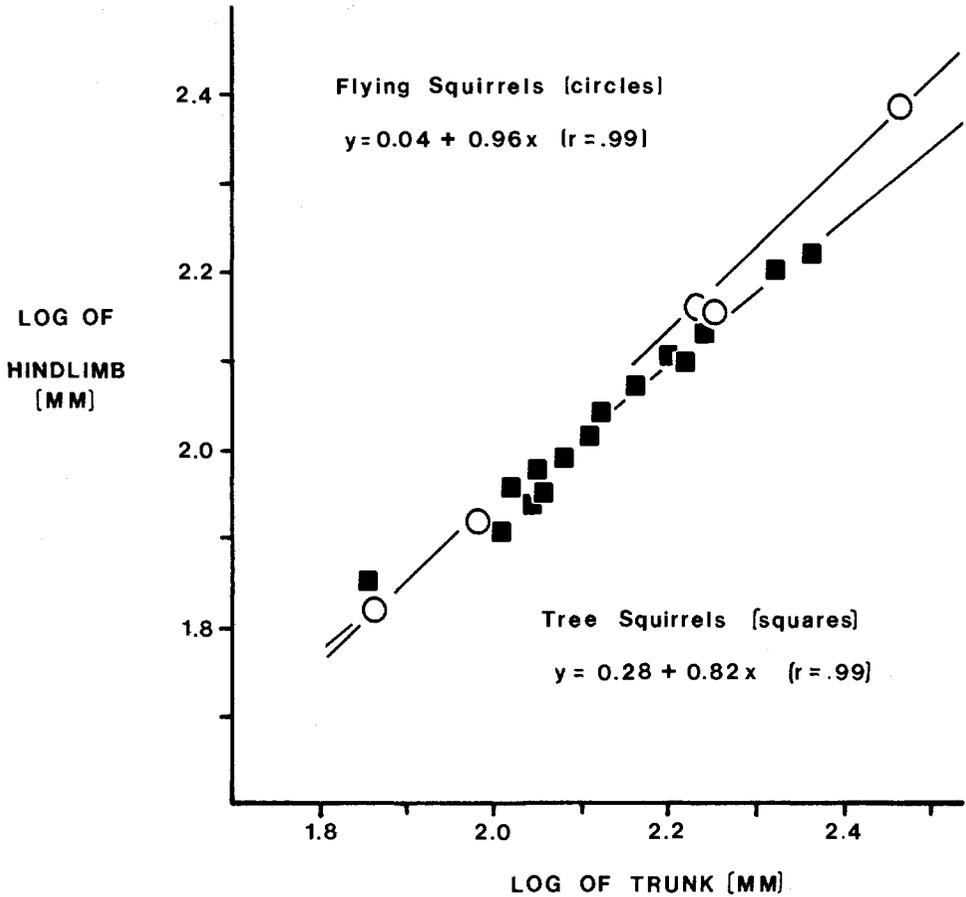


FIG. 3.—Relationship between lengths of hindlimb and trunk in tree squirrels and flying squirrels.

TABLE 5.—Trunk and relative limb lengths of tree squirrels ($\bar{X} \pm SD$).

Species	N	Trunk length (mm)	Forelimb/trunk	Hindlimb/trunk
<i>Microsciurus alfari</i>	2	73	0.73	0.96
<i>Tamiasciurus hudsonicus</i>	13	105 ± 5	0.57 ± 0.02	0.78 ± 0.03
<i>Sundasciurus steeri</i>	2	110	0.58	0.82
<i>Dremomys pernyi</i>	2	111	0.59	0.79
<i>Sciurus deppei</i>	5	111 ± 5	0.60 ± 0.03	0.85 ± 0.03
<i>Callosciurus notatus</i>	2	112	0.59	0.81
<i>Callosciurus flavimanus</i>	2	120	0.56	0.81
<i>Callosciurus erythraeus</i>	3	128	0.59	0.81
<i>Callosciurus prevostii</i>	5	131 ± 8	0.61 ± 0.03	0.84 ± 0.04
<i>Sciurus carolinensis</i>	43	145 ± 0.92	0.58 ± 0.003	0.82 ± 0.004
<i>Sciurus aberti</i>	3	159	0.56	0.79
<i>Protoxerus stangeri</i>	2	164	0.54	0.77
<i>Sciurus niger</i>	6	174 ± 11	0.57 ± 0.02	0.79 ± 0.03
<i>Ratufa affinis</i>	2	207	0.57	0.77
<i>Ratufa bicolor</i>	4	227 ± 9	0.56 ± 0.01	0.73 ± 0.02

TABLE 6.—Limb* proportions of flying squirrels ($\bar{X} \pm SD$).

Species	N	Ra/Hu	Ti/Fe	Hu/Fe	Ra/Ti	Ra + Hu/ Ti + Fe
<i>Glaucomys volans</i>	26	1.13 \pm 0.02	1.15 \pm 0.02	0.85 \pm 0.01	0.84 \pm 0.01	0.85 \pm 0.01
<i>Glaucomys sabrinus</i>	10	1.10 \pm 0.02	1.16 \pm 0.02	0.84 \pm 0.01	0.80 \pm 0.02	0.82 \pm 0.01
<i>Hylapetes electilis</i>	1	1.07	1.13	0.85	0.80	0.82
<i>Eoglaucomys fimbriatus</i>	3	1.05	1.09	0.77	0.74	0.75
<i>Hylapetes nigripes</i>	8	1.09 \pm 0.02	1.12 \pm 0.02	0.81 \pm 0.02	0.80 \pm 0.01	0.81 \pm 0.01
<i>Trogopterus horsfieldi</i>	1	1.03	1.05	0.79	0.78	0.79
<i>Aeromys tephromelas</i>	2	1.02	1.02	0.82	0.82	0.82
<i>Petaurista petaurista</i>	9	0.99 \pm 0.02	1.03 \pm 0.02	0.82 \pm 0.03	0.78 \pm 0.02	0.80 \pm 0.02

* Ra = radius; Hu = humerus; Ti = tibia; Fe = femur.

Estimates of patagium loading and aspect ratio.—We have measured museum skins of flying squirrels in order to obtain direct estimates of the area of the ventral surface of the body. These estimates include the ventral surface of the abdomen and limbs, as well as the patagium itself. This is “gross wing area,” generally used for reference in aerodynamics (Clancy, 1975:72). The measurements were taken only on the few skins that appeared to allow reasonable estimates of the dimensions of living squirrels. Most museum specimens are not prepared for this purpose.

As shown in Table 8, the smallest species, *Petaurillus kinlochii*, was estimated to have a loading of 40 N/m². The *Petaurillus* in this sample are rather heavy for their length, so the small *Petinomys*, with a loading of 30 N/m² may be more typical for small flying squirrels, and we would not be surprised to find small flying squirrels with a loading of 25 N/m². The largest flying squirrels in the USNM collections are subspecies of *Petaurista petaurista*, which seem to have ventral surfaces of 1,600 to 1,800 cm². Their masses were not recorded, but they probably approximated 1.5 to 2.0 kg, and thus they probably had loadings of 100 N/m² or more, like the specimens of *P. elegans* that we measured. Pregnant females and heavy individuals might be loaded as heavily as 125 N/m². Other loadings within this range were obtained from tracings of whole animals (Table 9).

In small flying squirrels, it is apparent that the area of the ventral surface of the tail is a significant percentage of the area of the gliding surface. The distichous arrangement of the hairs increases the area, and photographs of *Glaucomys* in flight show that the tail retains its shape. The relative area of the tail is less in the large flying squirrels, because the tail is relatively narrower, but the effect on the aerodynamics

TABLE 7.—Limb* proportions of tree squirrels ($\bar{X} \pm SD$).

Species	N	Ra/Hu	Ti/Fe	Hu/Fe	Ra/Ti	Ra + Hu/ Ti + Fe
<i>Microsciurus alfaroi</i>	7	0.98 \pm 0.02	1.18 \pm 0.01	0.85 \pm 0.01	0.70 \pm 0.01	0.77 \pm 0.01
<i>Tamiasciurus hudsonicus</i>	34	0.92 \pm 0.02	1.13 \pm 0.02	0.81 \pm 0.01	0.66 \pm 0.01	0.73 \pm 0.01
<i>Sundasciurus steeri</i>	33	0.94	1.06	0.77	0.68	0.72
<i>Dremomys pernyi</i>	4	0.94 \pm 0.04	1.14 \pm 0.01	0.80 \pm 0.02	0.65 \pm 0.01	0.72 \pm 0.02
<i>Sciurus deppei</i>	8	0.95 \pm 0.01	1.12 \pm 0.01	0.79 \pm 0.01	0.67 \pm 0.01	0.72 \pm 0.01
<i>Callosciurus notatus</i>	3	0.92	1.07	0.79	0.68	0.73
<i>Sundasciurus hoogstraali</i>	2	0.93	1.08	0.77	0.66	0.72
<i>Sundasciurus hippurus</i>	2	0.90	1.07	0.74	0.62	0.68
<i>Callosciurus erythraeus</i>	8	0.94 \pm 0.02	1.09 \pm 0.01	0.78 \pm 0.02	0.68 \pm 0.01	0.73 \pm 0.01
<i>Callosciurus prevostii</i>	5	0.90 \pm 0.01	1.06 \pm 0.01	0.81 \pm 0.01	0.69 \pm 0.01	0.75 \pm 0.01
<i>Protoxerus aubinnii</i>	2	0.91	1.12	0.80	0.66	0.72
<i>Sciurus carolinensis</i>	43	0.93 \pm 0.02	1.13 \pm 0.02	0.77 \pm 0.01	0.66 \pm 0.01	0.71 \pm 0.01
<i>Sciurus aberti</i>	6	0.95 \pm 0.02	1.12 \pm 0.02	0.78 \pm 0.02	0.66 \pm 0.01	0.72 \pm 0.01
<i>Protoxerus stangeri</i>	2	0.85	1.07	0.78	0.62	0.70
<i>Sciurus niger</i>	19	0.94 \pm 0.02	1.12 \pm 0.02	0.79 \pm 0.02	0.66 \pm 0.02	0.72 \pm 0.01
<i>Ratufa indica</i>	2	0.86	1.04	0.82	0.67	0.74
<i>Ratufa affinis</i>	2	0.84	1.01	0.81	0.68	0.74
<i>Ratufa bicolor</i>	4	0.83	0.98 \pm 0.02	0.82 \pm 0.01	0.69 \pm 0.01	0.76 \pm 0.01

* Ra = radius; Hu = humerus; Ti = tibia; Fe = femur.

TABLE 8.—Estimates of gliding surface area, weight, and loading for flying squirrels, based on museum skins. Surface area does not include head or tail areas.

Species	N	Area (cm ²)	Mass (g)	Loading (N/m ²)
<i>Petaurillus kinlochii</i>	3	55	20	40
<i>Petinomys vordemanni</i>	5	114	36	30
<i>Petinomys setosus</i>	5	92	39	40
<i>Hylopetes platyurus</i>	2	108	41	40
<i>Hylopetes spadiceus</i>	3	134	63	50
<i>Glaucomys volans</i>	1	150	70	50
<i>Petinomys genibarbis</i>	2	215	108	50
<i>Glaucomys sabrinus</i>	1	280	140	50
<i>Pteromyscus pulverulentus</i>	3	630	266	40
<i>Petaurista elegans</i>	4	850	920	110
<i>Aeromys tephromelas</i>	2	1,600	1,300	80

of gliding must be far from trivial. The area of the tail of *Petaurillus* is approximately 10 cm², or almost 20% of the rest of the ventral surface. The tails of some *Glaucomys sabrinus*, particularly those of the subspecies *alpinus* and *bangsi*, are particularly broad and have an area of 80 to 100 cm², which is 20 to 30% of the size of the ventral gliding surface. The tails of the larger *Pteromyscus* average 100 cm², which is 15% of the ventral area. The tails of the largest *Petaurista* and *Aeromys* have ventral surfaces of approximately 200 cm² beyond the uropatagium. Although the tail is not dorsoventrally flattened, it still adds 10 to 15% to the ventral area of the squirrel.

We obtained direct estimates of the area of the patagium from outline tracings of six flying squirrels and one photograph (Walker, 1947). We calculated the aspect ratios (wing span²/area) for these, which are shown in Table 9. These values ranged from approximately 1.0 to 2.2.

DISCUSSION

Flying squirrels evolved from non-glissant ancestors, but it is not clear whether the gliding adaptation arose only once. McKenna (1962) divided the subfamily into five groups and reported no evidence that would lead one to believe the group was polyphyletic. Black (1963:126) suggested that flying squirrels are diphyletic with four genera closely related to *Sciurus* and others derived from tree squirrels of the Callosciurini. Mein (1970) divided flying squirrels into three groups, and ascribed Miocene fossils to each. Thus he recognized three independent lineages in the early Miocene, but instead of arguing for polyphyletic origins from tree squirrels, he suggested that flying squirrels evolved from the Prosciurinae independent of the origin of tree squirrels from the Paramyinae. Based on immunological data, Hight et al.

TABLE 9.—Aspect ratios and "wing loadings" of flying squirrels, based on tracings of whole animals, tail areas excluded.

USNM No.	Taxon	Area (cm ²)	Aspect ratio	Loading (N/m ²)
Photo	<i>Glaucomys volans</i>		1.48	
194051	<i>G. sabrinus</i>	182	1.24	
501690	<i>Hylopetes</i> sp.	165	2.20	
20125	<i>Eoglaucomys fimbriatus</i>	687	1.04	81
20126	<i>P. petaurista albiventer</i>	1193	1.14	93
20130	<i>P. petaurista albiventer</i>	1387	1.34	80
334349	<i>P. petaurista grandis</i>	1069	1.42	104

(1974) suggested that *Iomys* is divergent from the other flying squirrels, but that all the other genera sampled form a monophyletic group and are most closely allied among tree squirrels with *Sciurus*. Thus there are currently at least four different hypotheses about the origin and evolution of flying squirrels. Accordingly, it is not clear whether this paper is a study of parallelism, convergence, or divergence in morphology.

We have compared the body proportions of flying squirrels with those of tree squirrels, because we think the morphology of tree squirrels is primitive and the morphology of flying squirrels is derived. This hypothesis is based on two arguments. First, the earliest known sciurid, from the White River Formation of the Oligocene, has the body proportions of Recent tree squirrels (Emry and Thorington, pers. obs.). Second, it seems most likely that patagia would have evolved among arboreal squirrels, probably among active forms which regularly leaped from tree to tree.

Whether or not the Petauristinae is polyphyletic, all flying squirrels are similar in postcranial anatomy and have evolved adaptations to the same locomotor problems. Only one significant change in body proportions seems to accompany the transition from small tree squirrel to small flying squirrel. This is the elongation of the antebrachium. It results in the higher ratio of lengths of radius to humerus and in the relatively longer forelimb, compared with length of trunk or hind limb, when flying squirrels are compared with tree squirrels. These changes probably reflect some shape factors which are aerodynamically important. Photographs and tracings of flying squirrels show that the patagium is always wider in front than behind.

Flying squirrels do not scale with size the same way as tree squirrels, but in view of the allometric relationship between weight and the area of the patagium, it is perhaps surprising that scaling is so similar. Flying squirrels range in size (length of head and body) from less than 90 to more than 400 mm. An animal that is four times the length of another is expected to weigh approximately 64 times as much but to have a patagium only 16 times as large. If geometrically similar, the largest flying squirrels should have patagia that are loaded four times as heavily as those of the smallest flying squirrels. This should have a significant effect on their gliding abilities. There are several ways in which flying squirrels could compensate for allometry. First, large flying squirrels could be relatively thinner than small ones, or at least lighter than expected on the basis of their length. As shown in Tables 1 and 3, this is so, and it is a way in which they scale differently than tree squirrels. The large flying squirrels are proportionately 16% lighter than the small ones. Second, they could increase the area of the patagium disproportionately to the square of trunk length, as by developing relatively longer limbs. This they do not do (Table 4), perhaps because it would compromise their climbing ability, or perhaps for aerodynamic reasons. Instead, the limbs of larger flying squirrels are relatively shorter, as in tree squirrels, and the styliiform cartilage is not lengthened to compensate. Therefore the area of the patagium is approximately 10% less than predicted by isometry. Third, large flying squirrels could develop assessorily gliding membranes. *Petaurista*, *Aeromys*, and *Aeretes* have uropatagia that increase the area up to 5%. Summing these three factors, we expect large flying squirrels to have a patagial loading of approximately 90% that predicted by isometry; still, this amounts to a loading 360% that of small flying squirrels. Our measurements (Tables 8 and 9) seem to corroborate this and to demonstrate that large flying squirrels have a patagium loading three to four times that of the small ones.

In order to predict how size and patagial loading will affect the gliding of flying squirrels, we have chosen hang gliders as a reasonable analogue (Markowski, 1977; Welch and Welch, 1979). There are Rogallo-wing hang gliders with aspect ratios and recommended wing loadings similar to those of flying squirrels, i.e., an aspect ratio

of 1.5 and a recommended wing loading of 1 pound/ft² (=50 N/m²). Such a glider provides a lift to drag ratio of approximately 3 and therefore has a maximal glide ratio (horizontal distance/vertical drop) of 3. This too is similar to the performance of flying squirrels. As described below, most field estimates are in approximate agreement with a maximal glide ratio of 3—a 300-foot glide for a 100-ft drop.

For a hang glider, and presumably for flying squirrels, wing loading per se does not affect the ratio of lift to drag, and hence it has no effect on the glide ratio (Markowski, 1977:283). It does affect the speed at which a glider must travel if it is to maximize the glide ratio. Because the speed is proportional to the square root of wing loading, a flying squirrel with a patagium loading four times that of another presumably must glide twice as fast to maximize the distance of its glide. This proportionality will be mitigated a bit because large flying squirrels glide at higher Reynolds numbers than small ones and this will reduce drag slightly. The optimal gliding speed is proportional to the fourth root of the inverse of the coefficient of drag at zero lift, so wing loading should be the dominant factor. For hang gliders, a wing loading of 50 N/m² is recommended for all-around performance. At lower wing loadings, the glider is too vulnerable to gusts of wind and air turbulence; it does not “penetrate” the air well. At higher wing loadings, the pilot must fly faster to maximize his glide ratio, and this leaves less time to react and steer. It is striking that the patagium loading of most flying squirrels is close to that recommended for hang gliding. Judging from the analogy, we suggest that the most lightly loaded flying squirrels are best adapted to gliding in forested areas where there is little turbulence and where slow flight speed and high maneuverability are important. A flying squirrel with a more heavily loaded patagium may be better adapted to more open areas, where air turbulence is more of a problem and maneuverability is less of one.

The aspect ratio directly affects the lift/drag ratio. For a Rogallo conical wing, changing the aspect ratio from 1 to 2 changes the lift/drag ratio from 3 to 4, approximately, and therefore changes the optimal glide ratio from 3 to 4 (Markowski, 1977:284). Accordingly, it would seem desirable that flying squirrels have long forelimbs for support of a wide patagium. As demonstrated, they do have long forelimbs relative to those of tree squirrels, but flying squirrels have very low aspect ratios compared to bats, as discussed below, and to birds. Our data are not adequate to illustrate how the aspect ratio varies among flying squirrels, but the measurements of the lengths of forelimbs suggest that the aspect ratios of small flying squirrels average higher than those of large flying squirrels. The uropatagium of large flying squirrels must also reduce the aspect ratio, which seems anomalous. Curiously, *Eoglaucomys* probably has the lowest aspect ratio of any flying squirrel (Table 9). This seemed remarkable to us for a species that lives at 3,000 m elevation, where the air is much less dense and provides less lift than near sea level where most flying squirrels occur.

These morphological features that reduce aspect ratio all occur among flying squirrels that probably must glide fast for aerodynamic reasons, i.e., because of their heavy wing loading or because they live at high elevations. Tests with rectangular airfoils of low aspect ratio provide a tentative explanation. Zimmerman (1932) found that airfoils with aspect ratios near 1.0 do not stall until a high attack angle is reached. Maximum lift coefficients and maximum resultant force coefficients increased as aspect ratio decreased in the range from 3 to 1. He argued that this would affect landing characteristics favorably by reducing landing speed. He also demonstrated that low aspect wings have moment characteristics more favorable to stability. Accordingly, it seems likely that flying squirrels with low aspect ratios are gaining stability and lowering landing speeds at the cost of reducing their glide ratios slightly.

Zimmerman's (1932) study also demonstrated that the tip shape of the wing greatly affects airfoil characteristics at low aspect ratios. Semicircular tips were much superior

to rectangular tips. We have been unable to treat this factor in flying squirrels thus far, because tip shape (as well as the sweepback angle of the "wing") appears to be under dynamic control (see illustrations in Walker, 1947 and 1975; Rue, 1967; Hoffmeister and Mohr, 1972; and Welch and Welch, 1979). The muscle humerodorsalis I (Johnson-Murray, 1977) appears to be oriented so as to give flying squirrels voluntary control over the shape of the wing tip.

Flying squirrels have higher "wing loadings" than do bats. According to Smith and Starrett (1979) most bats have wing loadings between 10 and 20 N/m², whereas those of flying squirrels range from 30 to 110 N/m². The difference is actually greater than this indicates because our calculations for flying squirrels are based on gross wing areas, whereas those of Smith and Starrett (1979) are based on net wing areas. Also, bats have higher aspect ratios than do flying squirrels. All genera of bats studied by Smith and Starrett (1979) have aspect ratios greater than 5, and molossids have an average aspect ratio of 7.5. We judge that few flying squirrels have aspect ratios higher than 2.0. The aspect ratios of the plagiopatagia of bats are much closer to the total aspect ratios of flying squirrels. Thus, the higher total ratios of bats are due primarily to the incorporation of the digits into their wings.

Another factor that affects gliding efficiency is billowing. Hang gliders are generally designed with 3° to 4° of billow. The less billow, the better the glide ratio can be, and hang gliders with 1° of billow have been flown. However, they are dangerous because they sideslip easily. As billowing is increased, the lift and drag coefficients are increased and air speed can be decreased, but at the cost of a decreasing glide ratio. Photographs suggest that flying squirrels can control the amount of billow in their patagia (Hoffmeister and Mohr, 1972:fig. 84). The alignment of the muscles humerodorsalis I and III (Johnson-Murray, 1977) would permit their use as battens to reduce billow, and by reducing billow the squirrels should be able to lengthen the glide. By increasing billow they can probably reduce air speed and glide ratio (Lawrence, 1974:45).

The performance of flying squirrels has been variously estimated in the wild. Sumner and Dixon (1953:396–397) described a glide of *Glaucomys sabrinus* that covered 125 feet with a glide ratio of 2. We have observed *Glaucomys volans* in Maryland and have estimated a glide ratio between 2 and 3. Walker (1975) cited a 50-m glide with an 18-m drop: a glide ratio of 2.8. In Japan we observed *Petaurista leucogenys* gliding between tall *Cryptomeria* trees at approximately a 45° angle, which is a glide ratio of 1.0. Similarly, Peter S. Rodman (pers. comm.) observed *Petaurista petaurista* in the Kutai Nature Reserve, East Kalimantan, Indonesia, gliding approximately 150 m with an equal drop. Davis (1962) reported a *Petaurista* in Sabah, Borneo, gliding 100 m with a corresponding drop of perhaps 35 m, which is a glide ratio of almost 3. Illar Muul (pers. comm.) has seen *Petaurista* glide 300 m from a limestone bluff to the tops of fruit trees while dropping approximately 125 m, which is a glide ratio of 2.4 (Muul also estimated the longest glide he has seen to be 400 m). From these estimates, we hypothesize that the maximal glide ratio of flying squirrels is on the order of 3, and that the ratio does not differ greatly from small to large squirrels. The initial part of the glide is steep and probably represents the period of time when the squirrel is reaching optimal velocity for gliding. Having reached this velocity, the squirrel is able to flatten out its glide to maximize the horizontal distance covered. At the end of the flight, it increases the angle of attack, which may cause it to swoop upwards before landing. There are varying reports about how hard flying squirrels land, but velocity at impact is probably under voluntary control. From our observations and readings we suspect that they can go into a "mush" or semistall for a hard but fast landing; they can reduce air speed by swooping upward at the end of a flight for a soft precise landing; or they can execute a parachute landing in emergencies. Pho-

tographs of landings may be found in Walker (1947:662–666), Doutt et al. (1966:127), Rue (1967:90), and Lawrence (1974:45).

We have found only one estimate of the speed of a glide. This is Walker's (1975) estimate of 22 m in 12 s (4.1 mph.) for *Glaucomys volans*. This seems slow and needs to be verified, because it implies a coefficient of lift of approximately 20. If we assume that the coefficient of lift is 1.0, a more reasonable value, then a *G. volans* of average size must glide at a speed of 8.4 m/s (19 mph.) to maintain a glide ratio of 3:1 or at 8.2 m/sec (18 mph) for a glide ratio of 2:1. If the maximum coefficient of lift were 2.0, the speeds would be 30% less.

CONCLUSIONS

Flying squirrels present little variation in linear proportions over a size range that leads to a four-fold difference in wing loadings. Large flying squirrels do not have relatively longer limbs to increase wing area and thus decrease wing loading. The major aerodynamic implication of the heavier wing loadings of large flying squirrels is that they must glide faster than small squirrels with lower wing loadings. We interpret some of the morphological specializations of large flying squirrels, such as the short forelimbs of *Eoglaucmys* and the uropatagium of *Petaurista* and *Aeromys*, as aerodynamic adaptations that lead to better landing characteristics, mostly by reducing landing speed. These specializations may reflect compromises between conflicting selective forces for increasing glide ratios and for maintaining safe gliding and landing speeds.

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