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Virginia Hayssen
Smith College, vhayssen@smith.edu

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PATTERNS OF BODY AND TAIL LENGTH AND BODY MASS IN SCIURIDAE

Virginia Hayssen*

Department of Biological Sciences, Smith College, Northampton, MA 01063, USA

For squirrels, physical size varies with ancestry, locomotion, and sex. Body length has little variation associated with subfamilies or tribes but varies significantly among genera within tribes. Thus, patterns in body size among genera represent more recent evolutionary pressures. Flying squirrels weigh less than similarly sized tree or ground squirrels but ecological profile and ancestry are confounded for flying squirrels. Tail length has clear relationships with ecological profile in squirrels. Tail length is shorter in ground squirrels, longer in tree squirrels, and longest in flying squirrels. In addition, in arboreal squirrels, females have longer tails, relative to body length, than those of males. This latter result suggests that reproductive constraints can influence external features of morphology.

Key words: allometry, body size, flying squirrels, gliding locomotion, ground squirrels, tail length, tree squirrels

The family Sciuridae is a monophyletic lineage of 278 species with 3 distinct ecological profiles and 8 phylogenetic groupings (Thorington and Hoffmann 2005). Squirrels inhabit diverse biomes from arid deserts, through temperate and tropical forests, to arctic and alpine habitats and range from equatorial regions to arctic tundra in North America, South America, Africa, and Eurasia. Adult squirrels range from 70 to 600 mm in head and body length and from 15 to 8,000 g in body mass.

Squirrels can be sorted into 3 ecological–energetic profiles related to locomotion and location of nest site (Thorington and Ferrell 2006). Ground squirrels are diurnal, nest in burrows, reproduce in burrows, forage on the ground, and have few adaptations for arboreal locomotion. Tree squirrels are diurnal, nest in trees, reproduce in trees, often forage in trees, and have strong adaptations for arboreal locomotion. Flying squirrels are nocturnal, nest in trees, reproduce in trees, often forage in trees, and are most adapted for arboreal and gliding locomotion. Thus, locomotion and predation risk differ among the 3 groups, but the 2 arboreal groups, tree and flying squirrels, have more similar ecological profiles.

Weight reduction is a common adaptation in volant vertebrates (birds and bats), such that the less an animal weighs the farther it can glide for a given wing area. If similar constraints influence squirrel locomotion, ground squirrels should be heavier at a given body length with the shortest tails compared to tree and flying squirrels, which should have the lightest bodies at a given body length with the longest tails (Scheibe et al. 1990; Scheibe and Robins 1998; Thorington and Heaney 1981).

If phylogeny constrains body size then different taxa should have distinctive body-size profiles representing the ancestral phenotype of the clade. If natural selection operates on body size then within-clade variation will be greater than between-clade variation. Phylogenetic constraints could be evident at different taxonomic levels. For instance, subfamilies and tribes could sort into distinct size categories or genera within higher taxa could have distinct body-size profiles.

Reproduction also could influence body size because the additional mass that a female carries during gestation and when transporting young has clear aerodynamic and energetic consequences for females but not for males (Hayssen and Kunz 1996), particularly for flying squirrels. To test this hypothesis, sex differences in tail length relative to body length can be compared across ground, tree, and flying squirrels. If tails have a function in locomotion, for instance as rudders or for balance, females and males should differ in tail length. Tail lengths also may differ because of sexual selection or allometry. If flying squirrels have a consistent pattern of body and tail size that is related to locomotion and differs from that of tree or ground squirrels, then this pattern should be similar to that of nonsciurid, mammalian gliders (e.g., Dermoptera, petaurid marsupials, and anomalurid rodents—Scheibe and Robins 1998).

Overall, the primary goal of this paper is to assess patterns in body size and tail length related to ecological profile, phylogeny, and sex across the entire family Sciuridae as well as within each subfamily or tribe with >1 genus. Additional

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* *Correspondent: vhayssen@email.smith.edu*

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goals include comparing body length measured as total length minus tail length (American method) with body length measured directly (European method), and providing equations to estimate body mass from head–body length in sciurids.

MATERIALS AND METHODS

Physical size.—Physical data were found for 99% ($n = 275$) of the 278 species of Sciuridae listed in the 3rd edition of *Mammal Species of the World: A Taxonomic and Geographic Reference* (Wilson and Reeder 2005). The number of species for each measurement category is as follows: females: body mass: 173 species, head–body length: 258 species, tail length: 257 species; adults: body mass: 190 species, head–body length: 260 species, tail length: 236 species; males: body mass: 163 species, head–body length: 254 species, tail length: 250 species. No data were available for 3 species: *Petinomys sagitta*, *Spermophilus pallidicauda*, and *Spermophilus ralli*. *Petinomys sagitta* is probably a synonym of *Petinomys genibarbis* (Thorington and Hoffmann 2005). The 2 *Spermophilus* were recently separated from other species for which data exist: *Spermophilus pallicauda* from *Spermophilus major* or *Spermophilus erythrogenys* and *Spermophilus ralli* from *Spermophilus relictus* (Harrison et al. 2003; Thorington and Hoffmann 2005).

The data on body mass, head–body length, and tail length (Appendix I) were obtained from the literature (including data on individual squirrels from Ognev [1963 {1947}]), from field notes (B. Patterson for *Tamias rufus*), from sources in Hayssen et al. (1993), and from 4,614 sciurids at the following museums: British Museum of Natural History, London, United Kingdom; Delaware Museum of Natural History, Wilmington, Delaware; Field Museum of Natural History, Chicago, Illinois; Milwaukee Public Museum, Milwaukee, Wisconsin; Museum of Comparative Zoology, University of California–Berkeley, Berkeley, California; Museum of Vertebrate Zoology, Michigan State University, Lansing, Michigan; Museum of Zoology, University of Michigan, Ann Arbor, Michigan; and United States National Museum, Smithsonian Institution, Washington, D.C.

Data were compiled separately for males, females, or adults of unknown sex. Most specimen tags provide information on sex but many regional accounts only give data for adults of unspecified sex. Thus, the data sets for males and females are based more closely on individual specimens, whereas data for adults of unknown sex include unspecified range data with more rounding error and with unclear sample sizes.

If only total length was given on a specimen tag (American convention), head–body length was calculated from total length by subtracting tail length. The terms head–body length and body length are used synonymously in this manuscript.

Tail length is not consistently measured by mammalogists and sometimes includes the hair at the tip of the tail and sometimes only includes the vertebrae. This difference adds to measurement error and, thus, increases variation. Measurements of tails with or without the hair tuft are not known to be correlated with the variables examined here (body mass, body size, ecological niche, or phylogeny) and, thus, this difference should not influence the direction of the results. However, the increase in variation will make a significant result more difficult to find.

American versus European measures of body length.—Differences in measures of tail length alter the calculation of head–body length from total length. Thus, body length measured as total length minus tail length may differ from body length measured directly as head–body length. I tested to see if this difference was significant by comparing the 2 measures in subspecies for which I had data measured directly as head–body length as well as data for body length when calculated from total and tail length. I only used taxa for which I had at least 4 specimens for each measure. I checked to make sure that similar geographic regions were represented by both measures. Twenty-three taxa with a total 496 specimens conformed to these criteria.

Analysis was by general linear models (GLM). Either total length or head–body length could be used as the response variable. I chose head–body length. Thus, head–body length was calculated for specimens measured using American conventions and taken directly from the tag of specimens measured using European conventions. I examined both head–body length and the $\log_{10}$ of body length. The explanatory variables were measure (European or American), taxon, and sex.

Indices of tail versus head and body length.—For each species, the proportion of tail length relative to head–body length was calculated as the average tail length divided by the average head–body length (tail length/head–body length). This was done separately for females, males, and samples in which sex was not distinguished. To assess how much larger the tails of females were relative to body length compared with those of males, the proportionality index for females was divided by that for males (female (tail length/body length)/male (tail length/body length)). If males and females do not differ this index will be 1, thus, a 1-sample *t*-test will test the hypothesis.

Ecological classification.—Flying, tree, and ground squirrels are grades, as opposed to clades, of squirrels. Flying squirrels have gliding membranes between their limbs and their bodies. Flying squirrels are the only group of squirrels that is both a grade and a clade. Tree and ground squirrels were classified according to the location of the nest in which young are most often born and raised. Species with fossorial nests were classified as ground squirrels. Species with arboreal nests were classified as tree squirrels. For species without reproductive data, classifications were made according to ecological and behavioral descriptions of the diet, location, and activity of animals within the species. Ground squirrels occur in Callosciurinae, Sciurinae (Sciurini), and Xerinae (all tribes), whereas tree squirrels occur in Callosciurinae, Ratufinae, Sciurillinae, Sciurinae (Sciurini), and Xerinae (Protoxerini). I use the term ecological profile to refer to the ecological classification of sciurids as ground, tree, or flying squirrels.

Phylogeny.—No species-level phylogeny of the family Sciuridae has consensus. The taxonomy used here follows Thorington and Hoffmann (2005). The following papers were used for particular groups: Heaney (1979—*Sundasciurus*), Hoffman et al. (in litt.—ground squirrels), Moore (1959—Sciurinae),

TABLE 1.—Sex-specific equations for predicting body mass (log10 g) from head–body length ($\log_{10}$ mm) for subfamilies and tribes with 3 or more genera: $\log_{10}$ mass = intercept + slope ($\log_{10}$ head–body length). Sex is female (f), male (m), or unknown (u). *n* is number of species. All equations except for Xerini are statistically significant at $P < 0.0005$. Equations for Xerini are not significant for males or females individually but are significant at $P = 0.01$ for adults of unknown sex. The overall equation ($n = 232$; $R^2 = 97.2\%$, $F = 3{,}962.2$, $d.f. = 2, 231$, $P < 0.0005$) for predicting body mass from body length (hb) in any squirrel is: $\log_{10} \text{mass} = -4.30 + 2.91(\log_{10} \text{hb}) - 0.07(\text{Peteromyini})$. In this equation, the Pteromyini term is coded 1 if the animal is a flying squirrel and 0 if it is not.

Taxon	Sex	*n*	Intercept (*SE*)	Slope (*SE*)	R^2 (%)
Callosciurinae					
All body lengths	f	37	−3.68 (0.21)	2.63 (0.10)	96
	m	31	−4.14 (0.20)	2.83 (0.09)	97
	u	40	−3.74 (0.24)	2.64 (0.11)	94
100−250 mm only	f	33	−3.85 (0.33)	2.71 (0.14)	91
	m	27	−3.91 (0.29)	2.73 (0.13)	95
	u	37	−3.73 (0.37)	2.65 (0.16)	88
Sciurinae					
Pteromyini, all body lengths	f	19	−4.28 (0.19)	2.86 (0.08)	99
	m	19	−4.24 (0.21)	2.84 (0.09)	98
	u	24	−3.84 (0.21)	2.68 (0.09)	98
Sciurini, all body lengths	f	26	−4.02 (0.27)	2.80 (0.11)	96
	m	25	−3.44 (0.38)	2.54 (0.16)	91
	u	25	−4.22 (0.39)	2.88 (0.16)	92
Xerinae					
Marmotini, all body lengths	f	64	−4.73 (0.13)	3.10 (0.06)	98
	m	58	−4.66 (0.19)	3.07 (0.08)	96
	u	62	−4.59 (0.18)	3.05 (0.08)	96
Protoxerini, all body lengths	f	16	−4.06 (0.51)	2.81 (0.22)	92
	m	18	−4.13 (0.47)	2.83 (0.21)	92
	u	27	−3.69 (0.29)	2.63 (0.13)	94
Xerini, all body lengths	f	5	−3.46 (2.44)	2.58 (1.04)	57
	m	5	−0.93 (2.65)	1.50 (1.11)	17
	u	5	−4.03 (1.30)	2.82 (0.55)	86

and Thorington et al. (2002—Pteromyini). *Spermophilus* is paraphyletic (Harrison et al. 2003), but the nomenclature for various clades has not solidified. Here, the genus is treated as an intact unit, but where relevant I point out patterns among clades in *Spermophilus*. Analysis was across the following 8 taxa: Callosciurinae (14 genera, 64 species), Ratufinae (1 genus, 4 species), Sciurillinae (1 genus, 1 species), Sciurinae: Pteromyini (15 genera, 44 species), Sciurinae: Sciurini (5 genera, 37 species), Xerinae: Marmotini (6 genera, 92 species), Xerinae: Protoxerini (6 genera, 92 species), and Xerinae: Xerini (3 genera, 6 species). For taxa with >1 genus, I present patterns of body mass, body length, and tail length across genera.

Statistical analyses.—Common-log transformations were performed to improve symmetry of distributions across species (Hoaglin et al. 1983). Some extreme outliers were not used but no more than 3% of the data was removed from a given analysis. The "Results" section lists any species excluded from an analysis. Sample sizes are numbers of species.

Both traditional statistical models and phylogenetic independent contrasts (PIC) were used. Traditional statistical treatment was by a variety of general linear models (GLM) using Minitab, version 15.1 (Minitab Inc., State College, Pennsylvania). The models included analysis of variance (ANOVA), least-squares regression, multiple regression, or analysis of covariance as appropriate (Hayssen and Lacy 1985; Snedecor and Cochran 1980). Phylogeny was assessed either by ANOVA with the 8 subfamilies or tribes as levels or using $n - 1$ taxa as independent explanatory variables, with Marmotini as the normative taxon (these 2 analyses yield the same sums of squares but provide different output in Minitab). Ecological profile was assessed by ANOVA with the 3 profiles as levels. When both ecological profile and phylogeny were in a model, *F*-tests are provided for each variate. Type III sums of squares or stepwise multiple regressions were used to assess significance of individual tribes or subfamilies ($\alpha = 0.05$). *P*-values are those associated with the entire model unless otherwise noted. Student's *t*-tests were used when a categorical independent variable had only 2 possibilities (e.g., male or female; ground or tree).

For continuous bivariate comparisons (body mass versus head–body length and tail length versus head–body length), PIC were performed with Mesquite (Maddison and Maddison 2007) and PDAP (Milford et al. 2003) using the generic phylogeny in Mercer and Roth (2003) supplemented by species information from Harrison et al. (2003), Herron et al. (2004), Piaggio and Spicer (2001), Steppan et al. (2004), Thorington and Hoffmann (2005), and *Mammalian Species* accounts. Branch lengths were assigned by the method of Pagel (1992). Results for these analyses are preceded by the label "PIC."

Predicting body mass from body length.—For many allometric analyses, body mass rather than body length is the appropriate measure of size. Unfortunately, body mass is not as readily available as body length. For squirrels, body mass has not been recorded for 40 species.

The data set compiled here is uniquely suited to deriving predictive equations for body mass from body length in squirrels. To generate a single overall predictive equation, one could use either data for females or males or both. I chose to use data from females preferentially for both mass and length because the energetic demands of life as a squirrel are more strongly focused on females. Body-mass data were available for 238 species. Most body-length and body-mass data were from females ($n = 172$ species). If data from females were not available, I used data on adults of unknown sex ($n = 63$ species). Finally, if neither measure was available, I used data for males ($n = 2$ species). For *Spermophilus townsendii*, mixed-sex, body-length data were used with a mass from females and, for *Petinomys crinitus*, body-length data from males were used with a mixed-sex mass. Common-log transformations were used for both length and mass. For the final predictive equation, outliers were excluded and significant phylogenetic effects (as determined by stepwise multiple regression) were included. I also calculated and provide equations using only males or only females as well as equations for individual taxa (Table 1).

RESULTS

Use of either American or European conventions did not differ statistically for estimating body length. GLM using either body length or the common log of body length as the response variable and measure (head–body or total), taxa (23–24 species; with or without a possible outlier, *Spermophilus franklinii*), and sex as explanatory variables indicated that how body length was evaluated (as head–body length or calculated from total and tail length; $n = 511$ specimens) was not significant in any model ($F = 0.08$–1.88, *d.f.* $= 1, 482$–$1, 508$, $P = 0.17$–0.78); sex was never significant ($F = 0.29$–0.56, *d.f.* $= 1, 482$–$1, 495$, $P = 0.46$–0.59), and taxa was always significant ($F = 232.59$–450.88, *d.f.* $= 22, 482$–$23, 508$, $P < 0.0005$). Thus, body length does not differ significantly when measured either directly (European method) or estimated from total and tail length (American method) and the 2 measures were pooled for subsequent analysis.

Because body mass is tightly correlated with body length in squirrels (Table 1), body length can be used to predict body mass. Five species had exceptionally high mass relative to size (*Exilisciurus exilis*, *Callosciurus orestes*, *Spermophilus undulatus*, *Marmota baibacina*, and *Marmota sibirica*) and 1 species had an exceptionally low mass (*Petaurista xanthotis*). Phylogenetically, the Pteromyini differ significantly ($t = -4.04$ to -5.02, *d.f.* $= 158$–169, $P < 0.0005$) from this allometric relationship and have lower body mass for their size. No other tribe has a statistically different allometric relationship between head–body length and body mass ($t = -0.15$–1.4, *d.f.* $= 158$–169, $P = 0.16$–0.96). Equations using data only for females ($n = 172$; $\log_{10}$ mass $= -4.39 + 2.96(\log_{10}$ female head–body length$) - 0.104($Peteromyini$)$; $R^2 = 97.2\%$, $F = 2932.21$, *d.f.* $= 2, 171$, $P < 0.0005$) or males ($n = 161$; $\log_{10}$ mass $= -4.39 + 2.94(\log_{10}$ male head–body length$) - 0.089($Peteromyini$) + 0.034($Marmotini$)$; $R^2 = 96.1\%$, $F = 1{,}282.26$, *d.f.* $= 3, 160$, $P < 0.0005$) are similar. A Marmotini term is included in the equation for males although it was not quite significant at $P = 0.053$ ($F = 1.95$, *d.f.* $= 1, 157$). Sex-specific equations for individual subfamilies or tribes are provided in Table 1. All equations except for Xerini are statistically significant at $P < 0.0005$ ($F = 161.82$–$3, 049.67$, *d.f.* $= 1, 15$–$1, 63$). Equations for Xerini are not significant for males or females individually ($F = 1.81$–6.23, *d.f.* $= 1, 4$, $P = 0.088$–0.271) but are significant at $P = 0.014$ for adults of unknown sex ($F = 26.40$, *d.f.* $= 1, 4$).

Effects of Sex, Phylogeny, and Ecological Profile on Physical Size Within Sciuridae

Head–body length.—Median head–body length for most squirrel taxa is ~200 mm (using data for females: Callosciurinae, $n = 58$, 184 mm; Sciurinae: Pteromyini, $n = 37$, 231 mm; Sciurinae: Sciurini, $n = 35$, 234 mm; Xerinae: Marmotini, $n = 88$, 188 mm; Xerinae: Protoxerini, $n = 29$, 204 mm; Xerinae: Xerini, $n = 6$, 238 mm). Only the giant tree squirrels of Asia (*Ratufa*) and the dwarf tree squirrel of the Amazon (*Sciurillus*) differ; Ratufinae and Sciurillinae also are the least diverse and oldest taxa within Sciuridae.

Phylogenetic differences. About 12% of the variation in head–body length ($\log_{10}$ mm) is related to phylogeny (ANOVA: females, $n = 258$, $F = 5.09$, *d.f.* $= 7, 257$, $P < 0.0005$, $R^2 = 12.5\%$; adults, $n = 260$, $F = 4.86$, *d.f.* $= 7, 259$, $P < 0.0005$, $R^2 = 11.9\%$; males, $n = 254$, $F = 4.80$, *d.f.* $= 7, 253$, $P < 0.0005$, $R^2 = 12.0\%$). The dwarf squirrel *Sciurillus* and the giant squirrels *Ratufa* are distinctive with respect to body size and these taxa influence the ANOVA. Without Sciurillinae and Ratufinae, ~8% of the variation in head–body length is correlated with phylogeny (ANOVA: females, $n = 253$, $F = 4.58$, *d.f.* $= 5, 252$, $P = 0.001$, $R^2 = 8.5\%$; adults, $n = 255$, $F = 4.16$, *d.f.* $= 5, 254$, $P = 0.001$, $R^2 = 7.7\%$; males, $n = 249$, $F = 4.38$, *d.f.* $= 5, 248$, $P = 0.001$, $R^2 = 8.3\%$).

Ecological differences. Head–body length ($\log_{10}$ mm) has little relation to ecological profile (ANOVA: females: $n = 258$, $F = 4.50$, *d.f.* $= 2, 257$, $P = 0.012$, $R^2 = 3.4\%$; adults: $n = 260$, $F = 3.88$, *d.f.* $= 2, 259$, $P = 0.022$, $R^2 = 2.9\%$; males: $n = 254$, $F = 4.07$, *d.f.* $= 2, 253$, $P = 0.018$, $R^2 = 3.1\%$).

Sex differences. Head–body length ($\log_{10}$ mm) does not differ between females ($n = 258$) and males ($n = 254$) in squirrels ($t = 0.03$, *d.f.* $= 509$, $P = 0.972$). The female : male body length ratio is 0.993 for 104 ground squirrels, 0.995 for 108 tree squirrels, and 1.018 for 32 flying squirrels. For individual taxa the ratios (female : male) are: Ratufinae 1.023; Sciurillinae 1.001; Sciurinae: Sciurini 0.989; Pteromyini 1.018; Callosciurinae 0.998; Xerinae: Xerini 0.940; Protoxerini 1.001; Marmotini 0.993. Despite these trends, ratios do not differ across ecological profiles (ANOVA: $n = 244$, $F = 2.16$, *d.f.* $= 2, 243$, $P = 0.118$, $R^2 = 1.8\%$), or taxa (ANOVA: $n = 244$, $F = 1.53$, *d.f.* $= 7, 243$, $P = 0.158$, $R^2 = 4.3\%$).

Tail length.—Unlike head–body length, median tail-length varies widely across squirrel taxa (using females: Callosciurinae, $n = 57$, 139 mm; Ratufinae, $n = 4$, 423 mm; Sciurillinae, $n = 1$, 102 mm; Sciurinae: Pteromyini, $n = 37$, 226 mm; Sciurinae: Sciurini, $n = 35$, 208 mm; Xerinae: Marmotini, $n = 88$, 91 mm; Xerinae: Protoxerini, $n = 29$, 184 mm; Xerinae: Xerini, $n = 6$, 197 mm).

Phylogenetic differences. Tail length is strongly correlated with phylogeny (ANOVA: females, $n = 257$, $F = 28.71$, *d.f.* $= 7, 256$, $P < 0.0005$, $R^2 = 44.7\%$; adults: $n = 236$, $F = 23.09$, *d.f.* $= 7, 235$, $P < 0.0005$, $R^2 = 41.5\%$; males, $n = 250$, $F = 26.22$, *d.f.* $= 7, 249$, $P < 0.0005$, $R^2 = 43.1\%$).

Ecological differences. Flying squirrels have the longest tails, tails of tree squirrels are intermediate in length, and ground squirrels have the shortest tails (ANOVA: females, $n = 257$, $F = 60.64$, *d.f.* $= 2, 256$, $P < 0.0005$, $R^2 = 32.3\%$; adults: $n = 236$, $F = 46.50$, *d.f.* $= 2, 235$, $P < 0.0005$, $R^2 = 28.5\%$; males, $n = 250$, $F = 53.21$, *d.f.* $= 2, 249$, $P < 0.0005$, $R^2 = 30.1\%$).

Sex differences. Tail length ($\log_{10}$ mm) does not differ between females ($n = 257$) and males ($n = 250$) across all squirrels ($t = 0.02$, *d.f.* $= 504$, $P = 0.983$). However, female flying squirrels have tails that are 5.7% longer than those of males, female tree squirrels have tails that are 1.8% longer than those of males, but female ground squirrels have tails that are 0.3% shorter than those of males (ANOVA: $n = 241$, $F = 8.14$, *d.f.* $= 2, 240$, $P < 0.0005$, $R^2 = 6.4\%$). Phylogenetic effects also are present (ANOVA: $n = 241$, $F = 2.96$, $d.f. = 7, 240$, $P = 0.005$, $R^2 = 8.2\%$): female Pteromyini have tails 5.7% longer than males and female Xerini have tails 1.9% shorter than those of males. For other taxa, tails of females relative to those males are 0.6% longer in Callosciurinae, 1.1% longer in Ratufinae, 5.8% longer in Sciurillinae, 3.8% longer in Sciurini, 1.3% longer in Protoxerini, and 0.4% shorter in Marmotini.

Tail length relative to head–body length.—Tail length is positively correlated with head–body length (regression: females, $n = 257$, $F = 121.88$, $d.f. = 1, 256$, $P < 0.0005$, $R^2 = 32.3\%$; adults, $n = 236$, $F = 120.59$, $d.f. = 1, 235$, $P < 0.0005$, $R^2 = 34.0\%$; males, $n = 249$, $F = 111.37$, $d.f. = 1, 248$, $P < 0.0005$, $R^2 = 31.1\%$; PIC: females, $F = 228.9$, $d.f. = 255$, $P < 0.0005$, $R^2 = 47.3\%$; adults, $F = 151.2$, $d.f. = 234$, $P < 0.0005$, $R^2 = 39.2\%$; males, $F = 239.3$, $d.f. = 247$, $P < 0.0005$, $R^2 = 49.7\%$). Phylogeny accounts for an additional 35–39% of the variation in tail length relative to head–body length (females, $F_{\text{partial}} = 44.73$, $d.f. = 7, 248$, $P < 0.0005$, $R^2 = 37.9\%$; adults, $F_{\text{partial}} = 35.90$, $d.f. = 7, 227$, $P < 0.0005$, $R^2 = 34.7\%$; males, $F_{\text{partial}} = 44.09$, $d.f. = 7, 247$, $P < 0.0005$, $R^2 = 38.8\%$).

Phylogenetic comparisons. Ratufinae have longer tails relative to body length and Marmotini have shorter tails relative to body length than all other squirrel taxa ($P < 0.05$). Ratufinae have longer tails than all other taxa; the differences are significant (data for females: $t = -1.97$ to 6.81, $d.f. = 248$, $P < 0.005$–0.050) except for Sciurillinae ($t = -1.32$, $d.f. = 248$, $P = 0.188$) and Pteromyini ($t = -1.76$, $d.f. = 248$, $P = 0.079$). Using data for females, tail length as a percent of body length across taxa, from longest to shortest, is: Ratufinae, 120% ($n = 4$); Xerinae: Protoxerini, 101% ($n = 29$); Sciurillinae, 98% ($n = 1$); Sciurinae: Pteromyini, 96% ($n = 37$); Sciurinae: Sciurini, 89% ($n = 35$); Callosciurinae, 83% ($n = 57$); Xerinae: Xerini, 79% ($n = 6$); and Xerinae: Marmotini, 45% ($n = 88$).

Ecological comparisons. Ground squirrels have significantly shorter tails relative to body length than either tree or flying squirrels, which have tails of similar length (ANOVA: females: $n = 257$, $F = 149.33$, $d.f. = 2, 256$, $P < 0.0005$, $R^2 = 54.0\%$; adults: $n = 236$, $F = 94.75$, $d.f. = 2, 235$, $P < 0.0005$, $R^2 = 44.8\%$; males: $n = 249$, $F = 136.94$, $d.f. = 2, 248$, $P < 0.0005$, $R^2 = 52.7\%$). Thus, the difference in absolute tail length between tree and flying squirrels is not apparent when tail length is considered relative to body length, but ground squirrels have shorter tails with both measures.

Sex differences. The ratio of tail to body length for females divided by the same ratio for males should equal 1 if females and males have the same tail length relative to head–body length. For 240 species, this ratio of ratios is 1.02 and the 95% confidence interval is 1.01–1.03. Thus, females have slightly longer tails than males for squirrels overall.

Body mass.—Like head–body length, but unlike tail length, body mass is similar across most groups but varies greatly within a group (median and range in grams for females: Callosciurinae, $n = 37$, 175, 17–673; Sciurinae: Pteromyini, $n = 19$, 210, 28–1,800; Sciurinae: Sciurini, $n = 26$, 406, 81–1,308; Xerinae: Marmotini, $n = 65$, 183, 46–5,000; Xerinae: Protoxerini, $n = 16$, 280, 40–761; Xerinae: Xerini, $n = 5$, 548, 217–742). As with head–body length, the large Ratufinae ($n = 4$, 1496, 1,237–1,808) and small Sciurillinae ($n = 1$, 38) are distinct.

Phylogenetic differences. Differences in body mass across taxonomic groups are slight but significant (ANOVA: females: $n = 173$, $F = 3.59$, $d.f. = 7, 172$, $P = 0.001$, $R^2 = 13.2\%$; adults: $n = 190$, $F = 2.99$, $d.f. = 7, 189$, $P = 0.005$, $R^2 = 10.3\%$; males: $n = 163$, $F = 3.60$, $d.f. = 7, 162$, $P = 0.001$, $R^2 = 14.0\%$). Two taxa contribute heavily to the results: Ratufinae with 4 large species and Sciurillinae with 1 dwarf species. Without these taxa the significance of phylogeny is reduced (ANOVA: females: $n = 168$; $F = 2.27$, $d.f. = 5, 167$, $P = 0.050$, $R^2 = 6.6\%$; adults: $n = 186$; $F = 2.35$, $d.f. = 5, 185$, $P = 0.043$, $R^2 = 6.1\%$; males: $n = 158$; $F = 2.54$, $d.f. = 5, 157$, $P = 0.031$, $R^2 = 7.7\%$).

Body mass is strongly and positively correlated with body length (PIC: females: $n = 172$, $F = 922.19$, $d.f. = 170$, $P < 0.0005$, $R^2 = 84.4\%$; adults: $n = 187$, $F = 110.03$, $d.f. = 185$, $P < 0.0005$, $R^2 = 76.7\%$; males: $n = 161$, $F = 503.20$, $d.f. = 159$, $P = < 0.0005$, $R^2 = 76.0\%$). Stepwise multiple regression indicates that relative to body size, Pteromyini (flying squirrels) are lighter than other squirrels ($P < 0.0005$) for females ($t = -5.02$, $d.f. = 169$), adults ($t = -3.59$, $d.f. = 184$), and males ($t = -4.04$, $d.f. = 158$) and Marmotini may be heavier than other squirrels (females: $t = 0.60$, $d.f. = 168$, $P = 0.549$; adults: $t = 2.15$, $d.f. = 183$, $P = 0.033$; males: $t = 1.95$, $d.f. = 157$, $P = 0.053$).

Ecological differences. Tree, ground, and flying squirrels do not differ in absolute body mass (ANOVA: females: $n = 173$, $F = 0.27$, $d.f. = 2, 172$, $P = 0.764$, $R^2 = 0.3\%$; adults: $n = 190$; $F = 2.02$, $d.f. = 2, 189$, $P = 0.136$, $R^2 = 2.1\%$; males: $n = 163$; $F = 1.35$, $d.f. = 2, 162$, $P = 0.262$, $R^2 = 1.7\%$). Stepwise multiple regression indicates that tree and ground squirrels exhibit the same allometric relationship of mass with size but flying squirrels (= Pteromyini) have smaller body mass for comparable body size (females: $t = -5.02$, $d.f. = 169$, $P < 0.0005$, adults: $t = -3.59$, $d.f. = 184$, $P < 0.0005$; males: $t = -4.04$, $d.f. = 158$, $P < 0.0005$).

Sex differences. The log of body mass does not differ between females ($n = 173$) and males ($n = 163$) across all squirrels ($t = -0.03$, $d.f. = 332$, $P = 0.980$). The proportion of female to male mass (female mass/male mass) can be used to compare sexual dimorphism across ecological or taxonomic groups. Overall, after removing 2 outliers (*Petinomys genibarbis* and *Spermophilus annulatus*), phylogenetic influences are small (ANOVA: $n = 150$, $F = 2.33$, $d.f. = 7, 149$, $P = 0.028$, $R^2 = 10.3\%$) with only Marmotini having a significant dimorphism ($t = -3.53$, $d.f. = 148$, $P = 0.001$; males 6% larger than females). Ecological effects are even smaller (ANOVA: $n = 150$, $F = 3.85$, $d.f. = 2, 149$, $P = 0.023$, $R^2 = 5.0\%$) with ground squirrels having a significant dimorphism ($t = -2.71$, $d.f. = 148$, $P = 0.007$; males 4% larger than females). The female : male ratios for ecological profiles are: ground 0.96; tree 1.02; flying 1.05; whereas those for phylogenetic taxa are Ratufinae 1.06; Sciurillinae 0.90; Sciurinae: Sciurini 1.02; Pteromyini 1.05; Callosciurinae 1.02; Xerinae: Xerini 0.98; Protoxerini 1.08; Marmotini 0.94.

Effects of Sex, Phylogeny, and Ecological Profile on Physical Size Across Genera Within Subfamilies and Tribes

Callosciurinae.—Most of the 14 genera (64 species) are 100–250 mm in body length. *Exilisciurus* and *Nannosciurus* are small (<100 mm), whereas *Rubrisciurus* is large (>250 mm). These generic differences are significant (ANOVA: females: $n = 58$, $F = 13.47$, $d.f. = 12, 57$, $P < 0.0005$, $R^2 = 78.2\%$; adults: $n = 59$, $F = 16.88$, $d.f. = 12, 58$, $P < 0.0005$, $R^2 = 81.5\%$; males: $n = 59$, $F = 12.38$, $d.f. = 13, 58$, $P < 0.0005$, $R^2 = 78.1\%$). Most callosciurines ($n = 55$ species) are tree squirrels (*Callosciurus*, *Dremomys*, *Exilisciurus*, *Funambulus*, *Prosciurillus*, *Sundasciurus*, and *Tamiops*), but 9 species are ground squirrels (*Hyosciurus*, *Lariscus*, *Menetes*, *Nannosciurus*, and *Rhinosciurus*). Body length does not differ between tree and ground squirrels because both groups are highly variable in size (body length: females: $n = 9$ ground, 49 tree, $t = 0.82$, $d.f. = 10$, $P = 0.43$; adults: $n = 8$ ground, 51 tree, $t = 0.25$, $d.f. = 8$, $P = 0.81$; males: $n = 8$ ground, 51 tree, $t = 0.75$, $d.f. = 8$, $P = 0.48$).

Examination of body-mass data of specimens of unknown sex suggests that tree squirrels are lighter than ground squirrels ($P = 0.013$) but these data do not include the small ground squirrel *Nannosciurus*. Data on *Nannosciurus* are present in the data sets for males and females and these data sets do not support a difference in body mass between ground and tree squirrels (mass: females: $n = 6$ ground, 31 tree, $t = -0.04$, $d.f. = 6$, $P = 0.97$; adults: $n = 6$ ground, 34 tree, $t = 2.64$, $d.f. = 28$, $P = 0.013$; males: $n = 5$ ground, 26 tree, $t = -0.23$, $d.f. = 4$, $P = 0.83$). Sex differences are not apparent in body length or mass (body length: $n = 58$ females, 59 males, $t = 0.01$, $d.f. = 114$, $P = 0.99$; mass: $n = 37$ females, 31 males, $t = 0.14$, $d.f. = 60$, $P = 0.89$).

Body mass and body length are tightly correlated (regression: females: $n = 37$, $F = 756.60$, $d.f. = 1, 36$, $P < 0.0005$, $R^2 = 95.6\%$; adults: $n = 40$, $F = 598.06$, $d.f. = 1, 39$, $P < 0.0005$, $R^2 = 94.0\%$; males: $n = 31$, $F = 1{,}020.03$, $d.f. = 1, 30$, $P < 0.0005$, $R^2 = 97.2\%$; Fig. 1A). No additional taxonomic (GLM: females: $n = 37$, $F = 0.48$, $d.f. = 12, 36$, $P_{\text{genus}} = 0.90$, $R^2 = 0.9\%$; adults: $n = 40$, $F = 1.08$, $d.f. = 10, 39$, $P_{\text{genus}} = 0.41$, $R^2 = 1.7\%$; males: $n = 31$, $F = 1.12$, $d.f. = 12, 30$, $P_{\text{genus}} = 0.40$, $R^2 = 1.2\%$) or sex differences (mass: $t = 0.14$, $d.f. = 60$, $P = 0.89$; body length: $t = 0.01$, $d.f. = 114$, $P = 0.99$) are evident. Removing the smallest and largest genera decreases the tightness of the relationships by 2–6% and makes the slopes and intercepts for males and females more similar (regression: females: $n = 33$, $F = 336.27$, $d.f. = 1, 32$, $P < 0.0005$, $R^2 = 91.6\%$; adults: $n = 37$, $F = 263.30$, $d.f. = 1, 36$, $P < 0.0005$, $R^2 = 88.3\%$; males: $n = 27$, $F = 445.60$, $d.f. = 1, 26$, $P < 0.0005$, $R^2 = 94.7\%$; Table 1). *Nannosciurus* is a small ground squirrel, lighter in mass than callosciurid tree squirrels of similar size, but larger ground squirrels are not lighter for their size. Thus, relative body masses of ground and tree squirrels generally do not differ (females: $n = 37$, $F = 0.16$, $d.f. = 1, 36$, $P_{\text{ground tree}} = 0.69$, $R^2 = 0.0\%$; adults: $n = 40$, $F = 0.01$, $d.f. = 1, 39$, $P_{\text{ground tree}} = 0.94$, $R^2 = 0.0$; males: $n = 31$, $F = 4.51$, $d.f. = 1, 30$, $P_{\text{ground tree}} = 0.043$, $R^2 = 0.4\%$).

Tail length is generally shorter than body length in callosciurids and generally differs between ground and tree squirrels. No sex differences are evident ($n = 57$ females, 60 males, $t = -0.19$, $d.f. = 114$, $P = 0.85$). In callosciurids, ground squirrels have shorter tails than tree squirrels (females: $n = 9$ ground, 48 tree, $t = -4.2$, $d.f. = 18$, $P = 0.001$; males: $n = 8$ ground, 51 tree, $t = -3.6$, $d.f. = 12$, $P = 0.003$) primarily because *Hyosciurus*, *Lariscus*, and *Rhinosciurus* are all ground squirrels. Two other genera of callosciurid ground squirrels, *Menetes* (tails ~75% of body length) and *Nannosciurus* (tails ~83% of body length), do not have short tails.

Sciurinae: Pteromyini.—Body lengths of the 15 genera (44 species) of flying squirrels (pteromyines) range from 70 to 500 mm and form roughly 3 size-groups: 75–90 mm, 150–250 mm, and >270 mm. Taxonomic differences are highly significant (ANOVA; females: $n = 37$, $F = 6.34$, $d.f. = 13, 36$, $P < 0.0005$, $R^2 = 78.2\%$; adults: $n = 37$, $F = 8.07$, $d.f. = 14, 38$, $P < 0.0005$, $R^2 = 82.5\%$; males: $n = 35$, $F = 5.90$, $d.f. = 11, 34$, $P < 0.0005$, $R^2 = 73.8\%$). No sex differences are apparent in body length ($n = 37$ females, 35 males, $t = 0.19$, $d.f. = 69$, $P = 0.85$) or mass ($n = 19$ females, 19 males, $t = 0.55$, $d.f. = 35$, $P = 0.59$).

Body mass–length correlations are extremely tight (regression: females: $n = 19$, $F = 1{,}201.08$, $d.f. = 1, 18$, $P < 0.0005$, $R^2 = 98.6\%$; adults: $n = 24$, $F = 895.70$, $d.f. = 1, 23$, $P < 0.0005$, $R^2 = 97.6\%$; males: $n = 19$, $F = 972.98$, $d.f. = 1, 18$, $P < 0.0005$, $R^2 = 98.3\%$; Fig. 1B) and little variation exists among genera (GLM: females: $n = 19$, $F = 1.27$, $d.f. = 8, 18$, $P_{\text{genus}} = 0.36$, $R^2 = 0.7\%$; adults: $n = 24$, $F = 0.41$, $d.f. = 8, 23$, $P_{\text{genus}} = 0.90$, $R^2 = 0.4\%$; males: $n = 19$, $F = 1.02$, $d.f. = 10, 18$, $P_{\text{genus}} = 0.50$, $R^2 = 1.0\%$). In any event, with so few species per genus and such tight correlations with body length, differences would be difficult to detect. Equations for males and females are nearly identical (Table 1) and that for specimens of unknown sex does not differ significantly from them.

Tail lengths in flying squirrels range from 70% to 120% of body length. *Glaucomys* and *Pteromys* consistently have the shortest tails (70–80% of body length), whereas the longest tails are in *Aeromys* (113–118%). Sex differences are apparent. Tail lengths are >95% of body length in 8 genera for females but in only 4 genera for males. In addition, regression lines of tail to body length versus body length for females and males have nearly identical slopes (0.375 versus 0.379) but the intercept for males is two-thirds that of females (0.066 versus 0.096). However, the variability is large for both. The ratio of tail to body length for females divided by the same ratio for males should equal 1 if females and males have the same tail length relative to head–body length. For 31 pteromyines, this ratio of ratios is 1.04 (1-sample $t = 2.07$, $P = 0.047$). Overall, tails of females are 5.7% longer than those of males ($n = 31$; $t = 3.8$ for ratio of female to male tails, $P = 0.0001$) and tail length of females relative to body size is 4% greater than that for males.

Sciurinae: Sciurini.—Of the 37 species in the tribe, 76% (28 species) are in the genus *Sciurus*. Most species are 160–300

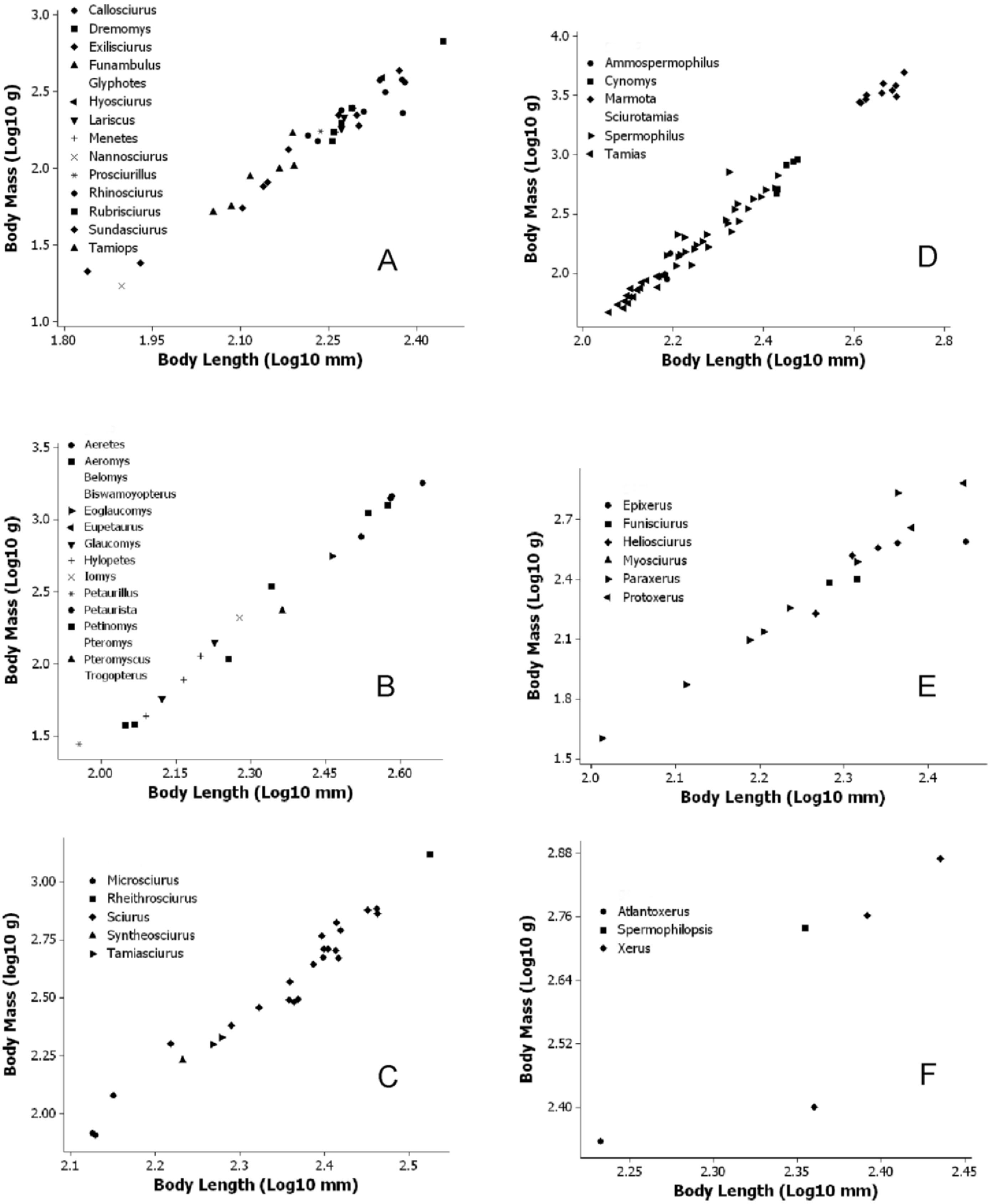

FIG. 1.—Body mass (in $\log_{10}$ g) versus head–body length (in $\log_{10}$ mm) for female sciurids in subfamilies or tribes with >1 genus. Data for males and adults of unknown sex are similar. All genera are listed, even those without data (indicated by no symbol before name in figure). A) Callosciurinae; B) Sciurinae: Pteromyini; C) Sciurinae: Sciurini; D) Xerinae: Marmotini; E) Xerinae: Protoxerini; and F) Xerinae: Xerini.

mm. Genus-level differences are significant (ANOVA: females: $n = 35$, $F = 12.38$, $d.f. = 4, 34$, $P < 0.0005$, $R^2 = 62.3\%$; adults: $n = 37$, $F = 10.10$, $d.f. = 4, 36$, $P < 0.0005$, $R^2 = 55.8\%$; males: $n = 34$, $F = 12.86$, $d.f. = 4, 33$, $P < 0.0005$, $R^2 = 63.9\%$). Sex differences in body length ($n = 35$ females, 34 males, $t = 0.10$, $d.f. = 66$, $P = 0.92$) or mass ($n = 26$ females, 25 males, $t = 0.15$, $d.f. = 48$, $P = 0.88$) are not evident.

Body mass and body length are tightly correlated (regression: females: $n = 26$, $F = 609.29$, $d.f. = 1, 25$, $P < 0.0005$, $R^2 = 96.2\%$; adults: $n = 25$, $F = 291.96$, $d.f. = 1, 24$, $P < 0.0005$, $R^2 = 92.7\%$; males: $n = 25$, $F = 249.81$, $d.f. = 1, 24$, $P < 0.0005$, $R^2 = 91.6\%$; Fig. 1C) with no taxonomic differences (GLM: females: $n = 26$, $F = 0.51$, $d.f. = 4, 25$, $P_{\text{genus}} = 0.73$, $R^2 = 0.4\%$; adults: $n = 25$; $F = 0.17$, $d.f. = 3, 24$, $P_{\text{genus}} = 0.92$, $R^2 = 0.2\%$; males: $n = 25$, $F = 0.15$, $d.f. = 4, 24$, $P_{\text{genus}} = 0.96$, $R^2 = 0.3\%$). The correlations of mass with length are less than for flying squirrels and slightly less than for callosciurines.

Tail length relative to body length is similar across genera (ANOVA: females: $n = 35$, $F = 2.21$, $d.f. = 4, 34$, $P = 0.091$, $R^2 = 22.8\%$; adults: $n = 36$, $F = 6.57$, $d.f. = 4, 35$, $P = 0.001$, $R^2 = 45.9\%$; males: $n = 34$, $F = 1.83$, $d.f. = 4, 33$, $P = 0.150$, $R^2 = 20.2\%$). *Tamiasciurus* has a shorter tail (65–70% of body length) than other sciurines (tail length is 85–95% of body length). The only ground squirrel, *Rheithrosciurus* has a tail 88–93% of its body length; thus, tree and ground squirrels do not differ in tail length. Females have slightly longer tails relative to body length (92% versus 88%; 1-sample *t*-test of female tail-to-body ratio over male tail-to-body ratio = 1, $n = 33$, $t = 2.34$, $P = 0.026$).

Xerinae: Marmotini.—Marmotines (all ground squirrels) range from roughly 100 to 600 mm in body length. The 6 genera form a graded series from smallest to largest as follows: *Tamias, Ammospermophilus, Spermophilus, Sciurotamias, Cynomys*, and *Marmota*. This phylogenetic effect is significant (ANOVA: females: $n = 88$, $F = 184.84$, $d.f. = 5, 87$, $P < 0.0005$, $R^2 = 91.8\%$; adults: $n = 85$, $F = 102.36$, $d.f. = 5, 84$, $P < 0.0005$, $R^2 = 86.6\%$; males: $n = 85$, $F = 165.14$, $d.f. = 5, 84$, $P < 0.0005$, $R^2 = 91.3\%$). Sex differences are not apparent ($n = 88$ females, 85 males, $t = -0.16$, $d.f. = 169$, $P = 0.87$).

Body mass is tightly correlated with body length (regression: females: $n = 64$, $F = 3{,}049.67$, $d.f. = 1, 63$, $P < 0.0005$, $R^2 = 98.0\%$; adults: $n = 62$, $F = 1{,}538.70$, $d.f. = 1, 61$, $P < 0.0005$, $R^2 = 96.2\%$; males: $n = 58$, $F = 1{,}401.21$, $d.f. = 1, 57$, $P < 0.0005$, $R^2 = 96.2\%$; Fig. 1D). Sex differences in this relationship are not evident (Table 1). Taxonomic effects are variable. For females, no taxonomic differences exist (GLM: $n = 64$, $F = 1.11$, $d.f. = 4, 63$, $P_{\text{genus}} = 0.36$, $R^2 = 0.4\%$). For males, phylogeny has a small effect (GLM: $n = 58$, $F = 3.09$, $d.f. = 4, 57$, $P_{\text{genus}} = 0.024$, $R^2 = 0.7\%$), because the data for males of the genus *Marmota* are less variable than those for females and adults of unknown sex. For adults of unknown sex, phylogeny has a significant effect (GLM: $n = 62$, $F = 9.58$, $d.f. = 4, 56$, $P < 0.0005$, $R^2 = 1.5\%$). These data include *Sciurotamias*, a genus not present in the data for males and females. *Sciurotamias* also has a distinctly lighter body mass for its body size so its inclusion in the data set generates the statistical significance.

Tail length is roughly 20–75% of body length in marmotines and is positively correlated with it (regression: females: $n = 88$, $F = 17.61$, $d.f. = 1, 87$, $P < 0.0005$, $R^2 = 17.0\%$; adults: $n = 81$, $F = 13.00$, $d.f. = 1, 80$, $P = 0.001$, $R^2 = 14.1\%$; males: $n = 82$, $F = 22.77$, $d.f. = 1, 81$, $P < 0.0005$, $R^2 = 22.2\%$). Sex differences are not evident (1-sample *t*-test of tail-to-body ratio of females over tail-to-body ratio of males = 1, $n = 81$, $t = 0.38$, $P = 0.71$) but genus differences are significant (GLM: females: $n = 88$, $F = 11.50$, $d.f. = 5, 87$, $P_{\text{genus}} < 0.0005$, $R^2 = 34.5\%$; adults: $n = 81$, $F = 7.69$, $d.f. = 5, 80$, $P_{\text{genus}} < 0.0005$, $R^2 = 29.4\%$; males: $n = 82$, $F = 9.28$, $d.f. = 5, 81$, $P_{\text{genus}} < 0.0005$, $R^2 = 29.8\%$). *Sciurotamias* and *Tamias* have the longest tails relative to body length with tails about 70–74% of head–body length, whereas *Cynomys* and *Marmota* have the shortest tails at 22% and 34%, respectively. Tails of *Ammospermophilus* at 48% of head–body length are intermediate. For *Spermophilus*, tail length is highly variable from 17% to 95% of head–body length. In fact, variation in absolute tail length in *Spermophilus* is much greater than that for other genera. The variation in *Spermophilus* may be related to the probable paraphyly of the genus (Harrison et al. 2003). In fact, the variation sorts well using the 5 lettered clades of Harrison et al. (2003). Relative to body length, 2 clades have short tails (20–40%, clades D and E), 2 clades have intermediate tails (40–80%, clades B and F), and 1 clade has longer tails (~90%, clade A).

Xerinae: *Protoxerini*.—Most of the 6 genera (30 species) of protoxerines are 100–300 mm. *Myosciurus* is small (70–75 mm). *Epixerus* and *Protoxerus* are the largest (>250 mm). Body-length differences among genera are highly significant (ANOVA: females: $n = 29$, $F = 7.47$, $d.f. = 5, 28$, $P < 0.0005$, $R^2 = 61.9\%$; adults: $n = 30$, $F = 8.80$, $d.f. = 5, 29$, $P < 0.0005$, $R^2 = 64.7\%$; males: $n = 30$, $F = 10.04$, $d.f. = 5, 29$, $P < 0.0005$, $R^2 = 67.7\%$) when *Myosciurus* is included. Without *Myosciurus*, the relationships of phylogeny with body length are reduced (ANOVA: females: $n = 28$, $F = 3.47$, $d.f. = 4, 27$, $P = 0.023$, $R^2 = 37.6\%$; adults: $n = 29$, $F = 4.23$, $d.f. = 4, 28$, $P = 0.10$, $R^2 = 41.3\%$; males: $n = 30$, $F = 4.66$, $d.f. = 4, 28$, $P = 0.006$, $R^2 = 43.7\%$). Most protoxerines are tree squirrels but *Epixerus* is a ground squirrel, as are 5 of 8 species of *Funisciurus*. Body length and mass do not differ between tree or ground squirrels in this tribe ($n = 16$–30, $t = 0.68$–1.25, $d.f. = 3$–13, $P = 0.236$–0.509), nor are sex differences apparent ($t = -0.07$–0.06, $P = 0.94$–0.95, $d.f. = 31$–54).

For protoxerines, body mass and body length are tightly correlated (regression: females: $n = 16$, $F = 161.82$, $d.f. = 1, 15$, $P < 0.0005$, $R^2 = 92.0\%$; adults: $n = 27$, $F = 430.42$, $d.f. = 1, 26$, $P < 0.0005$, $R^2 = 94.5\%$; males: $n = 18$, $F = 188.27$, $d.f. = 1, 17$, $P < 0.0005$, $R^2 = 92.2\%$; Fig. 1E) with no sex (Table 1) and minimal taxonomic differences (GLM: females: $n = 16$, $F = 5.49$, $d.f. = 4, 15$, $P_{\text{genus}} = 0.013$, $R^2 = 5.5\%$; adults: $n = 27$, $F = 1.32$, $d.f. = 5, 26$, $P_{\text{genus}} < 0.29$, $R^2 = 1.36\%$; males: $n = 18$, $F = 0.31$, $d.f. = 4, 17$, $P_{\text{genus}} = 0.86$, $R^2 = 0.7\%$). A single, female, body mass for *Epixerus* of 388 g appears to be low given that body masses for males and animals of unknown sex range from 460 to 710 g. If the mass for females is correct, then female *Epixerus* are smaller for their body length than other Protoxerini. Also, 2 of 3 models (GLM: females, $n = 11$, $F = 3.90$, $d.f. = 1, 10$, $P = 0.08$, $R^2 = 1.50\%$; adults, $n = 14$, $F = 5.14$, $d.f. = 1, 13$, $P = 0.04$, $R^2 = 3.61\%$; males, $n = 13$, $F = 0.95$, $d.f. = 1, 12$, $P = 0.4$, $R^2 = 0.89\%$) suggest that *Paraxerus* is generally heavier for its body length than is *Heliosciurus*, with much overlap among species of the 2 genera.

With respect to tail length, *Myosciurus* is distinctive. *Myosciurus* has a shorter tail (~70% of body length) than most protoxerines (tail length is 85–120% of body length).

Protoxerini is a mix of 6 ground and 23 tree squirrel species. Relative to body length, the ground squirrels generally have shorter tails than the tree squirrels (females: $t = -3.07$, $d.f. = 8$, $P = 0.015$; adults: $t = -2.15$, $d.f. = 10$, $P = 0.057$; males: $t = -1.86$, $d.f. = 6$, $P = 0.11$). If *Myosciurus* is excluded (a tree squirrel with a short tail) the significance is stronger (female: $t = -3.47$, $d.f. = 7$, $P = 0.010$; adults: $t = -2.37$, $d.f. = 9$, $P = 0.042$; males: $t = -2.04$, $d.f. = 6$, $P = 0.088$). Five of the 6 ground squirrels are in *Funisciurus*, a genus with generally shorter tails than other protoxerines and a genus with both tree and ground squirrel species. Within *Funisciurus*, the 5 ground squirrels have shorter tails than the 4 tree squirrels (82–86% versus 92–96% of body length), and this difference is significant for females (females: $t = -2.49$, $d.f. = 6$, $P = 0.047$; adults: $t = -1.75$, $d.f. = 5$, $P = 0.14$; males: $t = -0.91$, $d.f. = 4$, $P = 0.41$). The 6th ground squirrel is the large *Epixerus*, which does not have a short tail.

Sex differences in tail length associated with locomotion are demonstrable. Relative to body length, female protoxerine tree squirrels have tails 2.7% longer than males (1-sample *t*-test of tail-to-body ratio of females over tail-to-body ratio of males = 1, $n = 23$, $t = 2.29$, $P = 0.032$), whereas female protoxerine ground squirrels have tails 2% shorter than those of males (1-sample *t*-test of tail-to-body ratio of females over tail-to-body ratio of males = 1, $n = 6$, $t = -0.42$, $P = 0.69$).

Xerinae: Xerini.—Six species in 3 genera constitute the Xerini. Body length is 170–270 mm in a graded series from *Atlantoxerus*, the smallest, to *Spermophilopsis* and *Xerus*, which are more similar in size. Phylogeny accounts for 81–92% of the variation in body length (ANOVA: females: $n = 6$, $F = 11.25$, $d.f. = 2, 5$, $P = 0.040$, $R^2 = 88.2\%$; adults: $n = 5$, $F = 13.33$, $d.f. = 1, 4$, $P = 0.035$, $R^2 = 81.6\%$; males: $n = 6$, $F = 17.64$, $d.f. = 2, 5$, $P = 0.022$, $R^2 = 92.2\%$). The sexes do not differ in body size ($n = 6$ females, 6 males, $t = -0.65$, $d.f. = 9$, $P = 0.53$). All Xerini are ground squirrels.

Body mass is not related to body length or genus (GLM: females: $n = 5$, body length; $F = 5.73$, $d.f. = 1, 4$, $P = 0.25$, $R^2 = 67.5\%$, genus: $F = 1.54$, $d.f. = 2, 4$, $P = 0.49$, $R^2 = 24.6\%$; adults: $n = 5$, body length: $F = 4.45$, $d.f. = 1, 4$, $P = 0.17$, $R^2 = 89.8\%$, genus: $F = 0.09$, $d.f. = 1, 4$, $P = 0.79$, $R^2 = 0.4\%$; males: $n = 5$, body length: $F = 0.03$, $d.f. = 1, 4$, $P = 0.89$, $R^2 = 37.6\%$, genus: $F = 0.42$, $d.f. = 2, 4$, $P = 0.74$, $R^2 = 28.4\%$; Fig. 1F). Vagaries of the small data set are influential. Data for males and females include *Spermophilopsis* but lack one of the *Xerus*. In contrast, data for adults of unknown sex do not include *Spermophilopsis* but do include all 4 *Xerus*.

Tail length varies by genus and by sex in Xerini. Tail length relative to body length is similar for *Atlantoxerus* and *Xerus* (75–80%) but is much shorter in *Spermophilopsis* (25–30%) and these generic effects are significant (ANOVA: female tail-to-body ratio: $n = 6$, $F = 20.48$, $d.f. = 2, 5$, $P = 0.018$, $R^2 = 93.2\%$; adults: data only for *Xerus*; male tail-to-body ratio: $n = 6$, $F = 9.47$, $d.f. = 2, 5$, $P = 0.051$, $R^2 = 86.3\%$). Relative to body length, females have tails that are 14% longer (*Spermophilopsis*), 4% longer (*Xerus*), or 2% shorter (*Atlantoxerus*) than those of males (1-sample *t*-test of tail-to-body ratio of females over tail-to-body ratio of males = 1, $n = 6$, $t = 1.5$, $P = 0.19$).

DISCUSSION

For squirrels, physical size varies with major selective factors (phylogeny, reproduction, and ecological profile). Some patterns are constant across phylogenetic levels, for example, arboreal squirrels have longer tails than ground squirrels, whereas some patterns change depending on the level of analysis. Finally, some patterns are clear and demonstrable but the particular selective factors cannot be isolated. Flying squirrels have longer tails and smaller body mass than other squirrels, and female flying squirrels have longer tails than males. However, ancestry and ecological profile are confounded for flying squirrels.

Body size: patterns and consequences.—Body length and mass in squirrels have little relation to phylogeny (above the level of genus), ecological profile, or sex. A major exception is body mass in flying squirrels. Flying squirrels weigh significantly less than similarly sized tree or ground squirrels. Apparently, weight reduction for improved locomotory performance when gliding has been a strong selective pressure on flying squirrels.

Phylogenetic effects are minor because many subfamilies and tribes within subfamilies have multiple genera and these genera range widely in body size. Thus, at the subfamily or tribe level, most phylogenetic effects on body size occur in specialized taxa: the large tree squirrels in the subfamily Ratufinae and the small tree squirrels in the subfamily Sciurillinae.

Although body size is not related to phylogeny at the subfamily or tribe level, within tribes phylogeny has a highly significant relationship with body size. Thus, subfamilies and tribes span a range of body sizes, but genera within tribes or subfamilies often segregate into distinct size classes. This suggests that the early divergence of squirrels was into broad locomotory modes, habitat biomes, or geographic regions. Squirrels diverged as they adapted their physiology to these broad categories, eventually leading to subfamily and tribal divisions. Subsequently, differentiation occurred by body size, resulting in genus-level distinctions. Thus, adaptations of squirrels were initially into broad ecological niches and then these niches were partitioned by body size.

Tail length: patterns and consequences.—Unlike body size, tail length in squirrels is influenced by phylogeny, ecological profile, and sex. In general, more-arboreal squirrels have longer tails, and, in arboreal squirrels, females have longer tails than males (in some ground squirrels females may have shorter tails than males). These results hold at different phylogenetic levels: family, tribe, and genus.

Flying squirrels (Pteromyini) have the longest tails, whereas ground squirrels (Marmotini) have the shortest tails. In addition, females have longer tails relative to body length and this difference is greatest in flying squirrels and smallest in ground squirrels. This sex-by-locomotor interaction is apparent across tribes (e.g., Marmotini or Xerini versus Pteromyini or Sciurini), across genera within tribes (e.g., ground versus tree squirrels in Protoxerini, but not Callosciurinae), and across species within a genus (e.g., *Funisciurus*).

Tail length presumably influences a squirrel's life (Thorington 1966). Tails function in communication with predators (Hersek and Owings 1993; Rundus et al. 2007), but tails could also be a potential hazard with respect to predation. Not only do they give a predator a handle with which to capture a squirrel (as evidenced by the evolution of tail autotomy in diverse rodents, including sciurids—Shargal et al. 1999), but if a squirrel raises its tail when running, the increased drag will slow it down. The short tails of marmotines are long enough to brace the animal when upright during surveillance for predators but not so long as to reduce running speed when dashing to a burrow for safety. In tunnels, long tails could be an inconvenience and short tails could be used as sensory organs. Long tails could have thermoregulatory functions as parasols or nose warmers (Muchlinski and Shump 1979).

Predator escape by arboreal squirrels is often by climbing and leaping and less often by running on the ground. Influences of morphology on gliding and leaping are multiple and complicated (Stafford et al. 2002; Thorington and Heaney 1981, and references therein). Tail length and wing-loading (body mass divided by wing area) are undoubtedly important. Flying squirrels have a lower body mass and longer tails relative to body length than other squirrels. This will lower their "wing"-loading and improve the aerodynamic performance of their glides.

Tails are important in the 3-dimensional locomotion of tree and flying squirrels. Tails contribute to maneuverability and help stabilize yaw, pitch, and roll. A longer tail increases drag but improves gliding performance and balance. Thus, longer tails will enhance predator escape in arboreal squirrels and the longer tails of females will allow better maneuverability when carrying young either in utero or during lactation.

Gliding and climbing in females is influenced by gestation. A pregnant tree or flying squirrel will have increased "wing"-loading as well as a shift in center of gravity. These will alter her gliding performance (maneuverability, rate of descent, and speed) and her balance. In addition, the costs of a crash landing or a fall may include injury or death to developing embryos and fetuses. Thus, females have greater need for increased maneuverability, better balance, and, hence, longer tails. The longer tails of female tree and flying squirrels may assist with steering and stabilization. These longer tails also demonstrate differential selection on males and females for a locomotor trait and confirm a similar finding for mammalian gliders as a group (Scheibe and Robins 1998).

Comparisons of body size across genera.—Although phylogenetic influences on body size are not evident across subfamilies and tribes, phylogenetic effects are clear at lower taxonomic levels, that is, across genera within tribes. Two basic body-size patterns emerge. In 1, genera are arranged in a graded series. Sciurini and Marmotini fall into this pattern. In the 2nd, most genera are relatively homogenous in size with few small or large species. Pteromyini, Protoxerini, and Xerini conform to this pattern because they are top heavy with roughly equal numbers of medium to large genera and only 1 small genus. Being a small squirrel in these 3 groups is unusual. Callosciurinae best fits the clumped pattern, because body size in the many genera of callosciurids is relatively homogeneous with few very large or very small genera.

These patterns do not coincide with subfamily divisions. Sciurini and Pteromyini are both in Sciurinae, but Sciurini has the graded pattern and Pteromyini the clumped pattern. Similarly, Marmotini, Protoxerini, and Xerini are in Xerinae, but Marmotini has a graded pattern and the other 2 a clumped pattern. Thus, differentiation into different body-size classes occured after the subfamily–tribe split.

For nearly all groups, the relationship of body mass to body length is very tight and has little variation across genera. Xerini is the exception but also has the smallest number of genera for comparisons. The tight correlation between body mass and body length means that the predictive equations in Table 1 formulated at the subfamily or tribe level can be used for all genera within the tribe. Thus, one does not need a predictive equation for each genus.

Two groups, Callosciurinae and Protoxerini, have both tree and ground squirrel species and thus allow investigation of the effect of ecological profile within a subfamily or tribe. In both groups, tail length is generally shorter in the ground squirrels. Selection either favors a shorter tail in squirrels nesting underground or a longer tail in arboreal forms. Given the phylogenetically basal position of *Sciurillus* and *Ratufa* (Mercer and Roth 2003), longer tails are probably plesiomorphic and shorter tails are a derived condition.

Overview of size and tail length in squirrels.—Squirrels are a monophyletic lineage that has radiated broadly into diverse ecological and geographic areas. Changes in physical size accompanied this radiation but body size is not related to latitude in squirrels (V. Hayssen, in litt.). Thus, changes in physical size reflect more subtle biotic and abiotic selection pressures.

Phylogenetic influences on physical size are at the level of genus rather than higher taxonomic levels. This suggests that body-size differentiation occurred more recently than the traits that distinguish subfamilies and tribes.

Finally, division of sciurids into ground, tree, or flying squirrels has a size component, especially in tail length. With respect to body mass, flying squirrels are lighter for their size than other squirrels, reflecting the influence of gliding locomotion. Tail length has clear relationships with ecological profile in squirrels. Tail length is shorter in ground squirrels, longer in tree squirrels, and longest in flying squirrels. In addition, in arboreal squirrels, females have longer tails relative to body length than do males. This latter result demonstrates differential selection on males and females for a trait associated with locomotion.

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APPENDIX I

Physical size data averaged by sex (adult = sex unknown): head-body length in millimeters (body), tail length in millimeters (tail), and body mass in grams (mass). Mass for *Marmota camtschatica* was added in proof and not used in analysis.

	Female			Male			Adult			
Species	Body	Tail	Mass	Body	Tail	Mass	Body	Tail	Mass	References[a]
Sciurillinae										
Sciurillus pusillus	104.1	102.5	38.5	103.3	96.9	43.0	103.0	115.7	39.0	1, 2, 3, 4, 5, 6
Ratufinae										
Ratufa affinis	342.2	425.6	1236.9	335.2	409.3	1064.4	337.6	411.1	1120.7	1, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19
Ratufa bicolor	365.4	463.1	1807.5	362.2	447.3	1678.3	366.8	456.7	1442.0	1, 11, 16, 17, 19, 20, 21, 22
Ratufa indica	369.0	421.8	1391.7	350.4	421.2	1382.0	423.3	368.3	1550.6	1, 19, 23
Ratufa macroura	338.1	350.3	1600.0	335.3	360.5	1610.0	362.0			1, 7, 19, 23, 24
Callosciurinae										
Callosciurus adamsi	170.3	148.7	150.0	157.0	158.0		167.3	159.5	134.5	1, 10, 12, 14, 25
Callosciurus albescens	164.0	160.5	163.0	163.3	143.5	151.7	187.0	150.0		21, 26
Callosciurus baluensis	244.0	251.0		242.5	247.5		231.7	236.7	370.5	1, 14, 22
Callosciurus caniceps	222.3	219.4	312.9	215.5	242.5	316.4	215.9	230.4	266.9	1, 16, 17, 18, 23, 25, 27, 28, 29, 30
Callosciurus erythraeus	217.4	216.6	375.1	227.0	205.3	359.2	209.3	176.9	286.5	1, 17, 18, 22, 23, 25, 31, 32, 33, 34, 35, 36, 37, 38, 39
Callosciurus finlaysonii	191.8	172.8		190.1	173.4		212.1	222.0	278.0	1, 15, 17, 23, 25, 40
Callosciurus inornatus	203.0	204.8		191.0	210.8		225.0		325.0	1, 25, 41
Callosciurus melanogaster	212.0	180.6		209.3	179.6		213.0	176.0	292.3	1, 7, 25, 41, 42, 43, 44
Callosciurus nigrovittatus	186.9	165.5	239.4	184.3	159.2	202.8	199.0	182.5	218.6	1, 16, 17, 18, 21, 26, 28, 29, 30, 40
Callosciurus notatus	237.8	175.0	227.9	233.6	186.5	233.9	201.7	183.4	219.4	1, 8, 9, 10, 12, 13, 14, 16, 17, 18, 21, 25, 26, 28, 29, 30, 40, 45, 46, 47
Callosciurus orestes	154.0	139.8		148.0	157.5		153.1	154.2	278.0	1, 14, 25, 26, 41, 48, 49
Callosciurus phayrei	237.1	249.0	377.4	231.5	246.8	375.6	215.0	200.0	258.9	1, 23, 25, 27, 41
Callosciurus prevostii	239.7	233.3	361.9	238.9	233.0	353.7	241.4	234.7	403.2	1, 7, 8, 10, 12, 13, 14, 16, 17, 18, 21, 22, 25, 29, 40, 45, 50
Callosciurus pygerythrus	189.2	175.1		187.5	168.5		203.2	150.0	252.0	1, 23, 25, 27, 41
Callosciurus quinquestriatus				226.5	202.0		230.4	181.0		22, 23, 25, 37
Dremomys everetti	166.3	99.1		155.9	98.3		175.0	111.0	130.0	1, 14
Dremomys gularis							216.0	168.0		36
Dremomys lokriah	181.3	136.2	172.5	180.4	131.9	180.2	194.1	125.0		1, 7, 19, 23, 39
Dremomys pernyi	180.3	138.8	150.9	186.0	142.5	173.0	196.0	155.5	180.0	1, 37, 38, 51
Dremomys pyrrhomerus	194.5	148.7	245.0	207.5	146.1		198.8	151.5		1, 22, 37
Dremomys rufigenis	187.1	149.4	198.3	191.3	144.9	190.4	199.6	159.3	240.0	1, 7, 17, 18, 23
Exilisciurus concinnus	87.0	68.0		87.4	62.0		85.9	65.5	28.1	1, 25, 52, 53
Exilisciurus exilis	69.1	52.8	21.3	71.7	49.0	17.0	73.0	51.3	16.5	1, 7, 8, 10, 12, 13, 14, 52
Exilisciurus whiteheadi	84.9	65.3	24.0	86.5	63.2	21.1	88.0	69.0	22.1	1, 14, 52, 54
Funambulus layardi	154.5		168.0	144.0	158.0		146.1	177.8		1, 7, 24
Funambulus palmarum	146.6	157.7	99.2	149.3	147.7	117.5	146.1			1, 7, 19, 23, 24
Funambulus pennantii	155.0	134.6	102.9	134.4	130.0	95.2				1, 7, 55
Funambulus sublineatus	110.3	112.8		117.5	109.7		127.0			1, 23, 24
Funambulus tristriatus	158.6	139.0		159.8	143.4		190.5		139.0	1, 19, 23
Glyphotes simus				114.9	97.3		119.5	100.6		1, 14, 25
Hyosciurus heinrichi	224.3	98.8		214.8	98.9		219.8	95.0	296.0	1, 22, 25
Hyosciurus ileile	219.7	121.2	390.8	233.9	116.3	398.3	222.5		315.0	1, 22, 25
Lariscus hosei	189.0	86.0	215.0				181.0	126.0		1, 11, 14
Lariscus insignis	187.1	104.3	182.1	194.3	100.6	174.9	182.5	109.0	175.0	1, 8, 14, 17, 18, 28, 40
Lariscus niobe	194.6	85.6		189.8	90.4					1
Lariscus obscurus	202.0	86.4		201.7	88.1		187.0	86.0	242.0	1, 40, 43
Menetes berdmorei	182.7	132.9	172.0	181.6	138.2	176.0	180.9	140.0	190.0	1, 17, 23, 56
Nannosciurus melanotis	79.0	70.5	17.0	79.6	62.1	12.0	74.0	65.5		1, 14, 25
Prosciurillus abstrusus	131.0	107.5		132.6	110.4		134.0		79.2	1, 22, 25
Prosciurillus leucomus	172.1	155.4	175.0	171.4	155.7	171.8	159.4	160.0	128.0	1, 22, 25
Prosciurillus murinus	118.9	99.1		119.2	96.8		130.0		72.9	1, 25, 57
Prosciurillus rosenbergii							190.0	212.5		58
Prosciurillus weberi							160.0			25

APPENDIX I.—Continued.

Species	Female			Male			Adult			References[a]
	Body	Tail	Mass	Body	Tail	Mass	Body	Tail	Mass	
Rhinosciurus laticaudatus	203.9	119.4	232.5	212.0	117.7	241.7	208.8	134.3	198.0	1, 10, 14, 17, 18, 40, 47
Rubrisciurus rubriventer	279.1	231.4	673.3	281.7	225.8	703.2				1, 40
Sundasciurus brookei	151.9	122.1	132.5	153.9	112.7	124.0	168.8	136.0	114.3	1, 8, 14, 59
Sundasciurus davensis				198.0	182.0					60
Sundasciurus fraterculus	116.3	78.6		119.1	75.1					1, 44
Sundasciurus hippurus	234.9	246.6	432.7	247.4	234.9	429.9	235.2	230.5	363.0	1, 8, 10, 12, 13, 14, 16, 17, 18, 59, 61
Sundasciurus hoogstraali	202.0	165.4		203.5	160.5		204.8	176.0		1, 59
Sundasciurus jentinki	126.6	112.6	55.0	130.6	125.2	60.0	131.1	118.1		1, 8, 14, 59
Sundasciurus juvencus	195.5	155.1	245.3	200.9	171.8	283.9	204.6	165.3	259.0	1, 59
Sundasciurus lowii	137.5	88.8	76.4	143.9	92.9	78.7	130.2	82.7	83.5	1, 10, 12, 17, 18, 21, 25, 29, 43, 45, 59
Sundasciurus mindanensis	200.5	191.1		203.3	191.0		193.7	171.6	285.0	1, 53, 59
Sundasciurus moellendorffi	200.0	190.0	190.0		218.0		207.0	190.0		1, 25, 59
Sundasciurus philippinensis	193.7	192.1		193.0	172.0		191.7	219.0	244.0	1, 25, 54
Sundasciurus rabori	163.0	135.0		182.8	139.8		174.5		163.0	1, 25, 59
Sundasciurus samarensis	185.0	158.5	222.0	190.6	160.8	243.0	188.5	165.5		1, 59
Sundasciurus steerii	198.8	155.8	222.5	200.5	161.2	257.1	206.5	160.3		1, 25, 59
Sundasciurus tenuis	139.8	114.8	81.4	140.7	113.4	85.2	138.9	114.1	76.8	1, 14, 16, 17, 18, 21, 25, 29, 30, 59
Tamiops mcclellandii	112.9	108.8	51.8	113.8	108.3	49.4	107.6	102.2	39.0	1, 7, 17, 18, 23, 25, 37
Tamiops maritimus	121.2	101.8	56.5	119.5	101.1	54.5	122.9	100.1		1, 22, 25, 36, 37
Tamiops rodolphii	117.7	107.9		117.4	111.1		119.5	122.0	56.0	1, 17, 25, 62
Tamiops swinhoei	130.7	101.2	87.9	131.4	99.7		132.6	96.6	78.0	1, 25, 36, 37, 38
Sciurinae: Pteromyini										
Aeretes melanopterus	350.0	310.0					305.0	336.5		1, 25, 37, 38
Aeromys tephromelas	375.4	443.5	1253.8	385.0	395.0	1068.0	384.4	466.7	1092.7	1, 14, 17, 18, 25
Aeromys thomasi	343.3	410.0	1117.0	300.0	370.0		363.3	380.0	1423.3	1, 10, 12, 14
Belomys pearsonii	190.9	169.3		189.2	161.0	155.9	214.5	135.8		1, 17, 23, 25, 26, 37, 38
Biswamoyopterus biswasi							405.0			25
Eoglaucomys fimbriatus	290.2	290.1	560.1	288.5	289.0	733.6	271.0			1, 7, 23, 25
Eupetaurus cinereus	419.1	381.0					499.7	406.4		1, 23, 25
Glaucomys sabrinus	168.9	129.4	141.3	158.8	135.4	141.9	159.0	133.5	120.8	1, 7, 63, 64
Glaucomys volans	132.5	103.0	57.6	131.1	103.1	53.2	134.0	100.3	70.0	1, 22, 63, 65, 66, 67
Hylopetes alboniger	223.6	202.5		214.5	196.1	269.3	214.6	187.7	240.0	1, 17, 19, 23, 25, 37
Hylopetes bartelsi				197.0			139.0			25
Hylopetes lepidus	122.9	123.3	43.3	115.1	91.5	38.8	127.1	102.3		1, 14, 17, 18, 23, 49, 68
Hylopetes nigripes	283.2	313.9		264.1	314.6		270.0		534.0	1, 25
Hylopetes phayrei	158.3	143.7	113.4	162.3	146.7		170.8	143.4	171.0	1, 15, 17, 22, 25, 37, 61
Hylopetes platyurus	130.0	100.0								1, 69
Hylopetes sipora							140.0		89.2	25
Hylopetes spadiceus	146.4	129.1	78.0	142.0	118.1	70.9	147.9	125.8	75.9	1, 14, 18, 19, 23, 25, 49
Hylopetes winstoni				142.0	143.0		142.0			25, 57
Iomys horsfieldii	189.6	179.6	209.8	192.0	178.5	153.9	191.8	176.5	165.3	1, 14, 18, 49, 70
Iomys sipora	179.5	179.5		196.0	175.0					1
Petaurillus emiliae							70.0	64.5	13.5	14
Petaurillus hosei	87.0	98.0					83.0	88.8	21.1	14, 25, 70
Petaurillus kinlochii	90.0	83.0	28.0	88.0		19.8				1, 18
Petaurista alborufus	383.5	474.3	1454.3	421.2	433.3	1529.0	496.0	438.0		1, 17, 38
Petaurista elegans	332.8	363.3	759.8	330.3	355.0	948.0	346.7	366.4	1040.0	1, 14, 17, 18, 23, 37
Petaurista leucogenys	465.5	314.8		367.8	363.3		375.0	345.0	1178.9	1, 7, 71, 72
Petaurista magnificus	442.5	497.5	1800.0	382.3	451.7		413.2	480.0		1, 23, 25, 73
Petaurista nobilis	427.0	522.9		417.8	468.3		490.0	460.0	2710.0	25, 39, 73
Petaurista petaurista	380.3	493.3	1405.3	381.2	432.2	1264.3	378.9	459.1	2004.0	1, 7, 12, 14, 17, 18, 19, 21, 22, 23, 57, 68, 74, 75, 76
Petaurista philippensis	457.2	536.7		457.7	474.0		463.2	538.1	2268.0	1, 19, 22, 23, 24, 25, 36, 37
Petaurista xanthotis	353.0	340.0		407.7	341.7		440.5	379.1	965.0	1, 25, 37, 38
Petinomys crinitus				310.0	260.0				1130.0	77
Petinomys fuscocapillus	319.7	287.1					337.1	250.0	712.0	1, 23, 24, 25
Petinomys genibarbis	179.8	192.5	108.8	157.3	172.5	69.5	175.9	171.4		1, 14, 18, 25, 78
Petinomys hageni	220.0	215.3	345.9	260.8	224.0	358.6	253.3	238.3	388.0	1, 14, 21, 25

APPENDIX I.—Continued.

	Female			Male			Adult			
Species	Body	Tail	Mass	Body	Tail	Mass	Body	Tail	Mass	References[a]
Petinomys lugens	258.3	225.8		250.0	215.0		250.0	222.5	433.0	1, 25, 44
Petinomys mindanensis	341.5	388.3		323.8	348.4		289.3	295.8		1, 53, 54, 79, 80
Petinomys sagitta										No data
Petinomys setosus	116.7	106.2	38.2	113.4	94.1	41.3	118.9	107.1		1, 10, 14, 17, 18, 22, 25, 78, 81
Petinomys vordermanni	111.8	103.7	37.8	110.5	98.6	35.0	105.4	103.9		1, 14, 18, 25, 68, 78, 81, 82
Pteromys momonga	162.8	140.5		154.0	136.0		170.0	120.0	151.8	1, 71, 72, 83
Pteromys volans	160.8	111.7		157.1	112.9	137.5	168.7	113.9	131.3	1, 37, 71, 84, 85
Pteromyscus pulverulentus	230.8	230.5	235.0	223.4	222.6	253.9	250.3	214.0	268.5	1, 14, 18
Trogopterus xanthipes	309.9	298.7		330.0	270.0		300.0			1, 25, 37
Sciurinae: Sciurini										
Microsciurus alfari	134.7	106.8	81.2	133.1	111.8	83.2	142.3	106.8	87.5	1, 4, 5, 6, 22, 67, 86
Microsciurus flaviventer	133.5	109.9	82.6	136.3	110.0	98.0	138.7	121.6	93.0	1, 4, 5, 6, 22, 87
Microsciurus mimulus	141.3	115.7	120.0	146.9	112.0		142.0	113.0	120.0	1, 4, 5, 86
Microsciurus santanderensis	146.0	145.0		133.0	139.0		149.9	142.6		4, 88, 89
Rheithrosciurus macrotis	334.2	294.7	1308.1	349.8	315.7	893.0	343.5	320.5	1225.0	1, 8, 12, 14
Sciurus aberti	262.3	221.7	618.6	274.0	208.0	593.8	269.5	242.3	601.5	7, 22, 63, 67, 90, 91
Sciurus aestuans	165.1	179.2	200.0	178.0	168.6	165.0	202.8	182.7	180.3	1, 4, 5, 6, 92
Sciurus alleni	250.3	208.0	473.0	267.1	169.6	446.7	254.0	217.0		1, 7, 67
Sciurus anomalus	228.1	148.8	310.0	215.1	152.8	345.0	200.0	150.0	335.3	1, 85, 93, 94
Sciurus arizonensis	259.1	254.5	667.0	248.2	245.8	736.0	250.2	253.8	655.0	1, 22, 63, 67
Sciurus aureogaster	258.9	255.7	505.4	264.1	248.0	497.3	260.7	253.8	562.3	1, 6, 7, 22, 67, 95
Sciurus carolinensis	253.5	215.5	512.7	260.0	204.4	430.8	270.0	212.7	356.7	1, 7, 85, 86, 96, 97, 98, 99
Sciurus colliaei	243.4	260.4	440.8	248.6	243.2	335.2	266.1	274.1		1, 67, 95
Sciurus deppei	210.2	169.4	287.3	207.2	176.0	268.3	197.4	181.7	203.3	1, 6, 7, 22, 67, 86, 100
Sciurus flammifer	285.0	313.0					274.0	310.3		5, 101
Sciurus gilvigularis				166.0	167.0		169.2	173.5		4, 5
Sciurus granatensis	233.6	205.1	311.7	232.9	208.6	300.0	226.9	210.9	380.0	1, 4, 5, 6, 16, 22, 67, 86, 87, 102, 103, 104
Sciurus griseus	289.8	257.9	727.5	233.0	204.5		292.0	273.0	813.0	1, 63, 64, 67
Sciurus ignitus	184.8	191.9		191.0	190.8		181.9	174.3	221.5	1, 5, 6, 105
Sciurus igniventris	271.7	280.0		267.1	271.6		271.1	255.2	700.0	1, 4, 5, 22, 103
Sciurus lis	194.5	153.9		190.0	152.3	176.0	196.7	160.0	237.0	1, 71, 83, 106
Sciurus nayaritensis	282.2	276.5	756.2	300.0	280.0	684.0	290.8	271.0		1, 22, 63, 67
Sciurus niger	289.7	246.7	764.3	295.1	232.5	767.5	280.7	251.9		1, 7, 63, 67, 96, 107, 108, 109
Sciurus oculatus	249.0	248.0	582.0	308.3	215.0	553.0	275.0	257.0	600.0	1, 67
Sciurus pucheranii	160.1	154.4		165.1	171.5		157.1	147.9	100.0	1, 4, 5, 22, 103
Sciurus pyrrhinus	238.5	254.8		229.3	242.0		253.3	208.0		1, 5, 6
Sciurus richmondi	194.8	168.6	239.3	197.8	166.6	249.7	191.3	164.0	251.5	6, 7, 110
Sciurus sanborni	175.0	170.0					163.5			6, 111
Sciurus spadiceus	250.6	263.0	513.3	248.5	245.1	598.0	246.4	243.7	625.0	1, 4, 5, 6, 22, 103
Sciurus stramineus	250.3	292.1		251.3	275.4		256.7	310.0		1, 5, 6, 22
Sciurus variegatoides	260.6	278.7	468.8	255.9	262.8	536.9	263.5	268.9	576.8	1, 4, 6, 67, 86, 95, 112
Sciurus vulgaris	228.5	177.0	371.0	226.3	175.3	414.8	224.2	178.9	350.0	1, 7, 37, 38, 71, 85
Sciurus yucatanensis	231.0	218.5	302.4	237.7	230.8	454.3	237.9	242.0	451.8	1, 6, 22, 67, 95, 100
Syntheosciurus brochus	170.5	143.0	170.0	162.4	147.5	143.3	163.5	135.0		1, 4, 6, 22, 67, 86, 113
Tamiasciurus douglasii	185.0	145.0	199.3	181.0	119.0	206.9	189.7	126.3	242.5	1, 7, 63, 64, 114, 115
Tamiasciurus hudsonicus	189.7	123.6	213.0	187.0	123.7	194.0	186.6	123.4	195.0	1, 7, 22, 63, 114, 115, 116, 117, 118, 119
Tamiasciurus mearnsi							201.3	120.5		67, 120
Xerinae: Marmotini										
Ammospermophilus harrisii	151.8	74.9	98.3	155.4	74.3	116.0	161.0	86.7	122.0	1, 22, 63, 67
Ammospermophilus insularis	137.2	73.7		143.3	72.6					1
Ammospermophilus interpres	147.7	76.1	93.1	146.3	73.1	95.8	149.0	77.0	110.0	1, 7, 58, 63
Ammospermophilus leucurus	153.6	57.1	89.8	153.2	59.8	94.9	152.0	59.0	90.1	1, 7, 22, 63, 67, 121, 122, 123, 124
Ammospermophilus nelsoni	156.2	70.0	148.2	162.8	71.1	186.3	166.0		155.0	1, 7, 63, 121
Cynomys gunnisoni	269.1	54.0	470.2	285.4	55.5	814.4	291.0	69.0		1, 7, 63, 67, 125, 126
Cynomys leucurus	298.9	54.0	923.5	311.3	55.7	1118.8	298.5	86.0		7, 63, 67, 126, 127
Cynomys ludovicianus	292.2	76.3	881.3	298.8	84.9	849.0	295.1			1, 22, 63, 126, 127
Cynomys mexicanus	282.0	82.8	820.5	314.0	102.0		312.0	107.0		1, 7, 67, 126

APPENDIX I.—Continued.

Species	Female			Male			Adult			References[a]
	Body	Tail	Mass	Body	Tail	Mass	Body	Tail	Mass	
Cynomys parvidens	269.5	51.7	516.0	294.1	44.2	636.0	300.0	40.0		22, 63, 126
Marmota baibacina	538.4	159.3		508.8	150.0		474.3	138.2	7850.0	1, 7, 38
Marmota bobak	493.5	120.7	3875.0	510.9	122.7	4033.0	508.0		5050.0	1, 7, 128, 129
Marmota broweri	425.0	154.0	3180.0	551.2	176.8	3630.0	425.0			1, 63
Marmota caligata	484.8	199.0	3515.3	493.6	207.6		527.5	210.0	5500.0	1, 63, 130
Marmota camtschatica	508.0	177.8		539.8	152.4	3824.0	567.3	165.1		1, 131
Marmota caudata	513.7	234.5	5000.0	428.3	199.0	3978.0	524.1	182.0	4506.7	1, 37, 38, 132
Marmota flaviventris	409.7	164.7	2791.7	438.1	183.5	3909.3	417.0	165.0	2570.0	7, 63, 64, 130
Marmota himalayana	549.9	151.1		608.3	154.3		595.3	125.0	6000.0	1, 23, 37, 38
Marmota marmota	459.5	138.8	3324.0	438.4	165.0	4303.3	495.0	175.0		1, 7, 85
Marmota menzbieri	423.3	93.0	2966.0	438.5	96.6	3064.0				133, 134
Marmota monax	412.2	137.4	2754.4	407.4	130.4	2854.5	420.0	125.0	3500.0	1, 7, 63, 130
Marmota olympus	494.0	186.0	3120.0	521.0	219.0	3837.5	509.0	223.5	6000.0	63, 130, 135, 136
Marmota sibirica	392.9	145.7		410.4	142.1				8000.0	1, 7
Marmota vancouverensis	461.9	195.6	4000.0	475.0	220.0	4500.0	468.0	200.0	4750.0	1, 63, 130, 137, 138
Sciurotamias davidianus	204.0	142.9		212.3	140.7		261.8	140.2	260.0	1, 22, 37, 38
Sciurotamias forresti	224.0	160.0					233.1	154.0		1, 37
Spermophilus adocetus	168.3	131.9		175.5	150.2		194.0	156.0		1, 67
Spermophilus alashanicus				222.7	68.3		199.4	71.6		1, 37, 139
Spermophilus annulatus	219.3	207.6	386.3	221.2	215.2	260.0	209.5	208.0		1, 67
Spermophilus armatus	216.7	69.2	347.3	223.5	71.8	394.9	225.0	65.0	344.6	1, 7, 63, 124, 140
Spermophilus atricapillus	231.2	196.5	350.0	237.8	192.6	505.0	300.0	235.0		1, 67
Spermophilus beecheyi	254.3	171.0	508.5	273.2	181.7	621.3	246.9	179.0	599.5	7, 63, 64, 67, 121, 141, 142
Spermophilus beldingi	208.6	63.1	265.2	204.7	64.9	228.6	197.5	67.3	287.4	7, 63, 64, 121, 124
Spermophilus brevicauda	197.0	42.0					284.5	50.8		143, 144
Spermophilus brunneus	173.6	54.7	116.8	183.4	55.1		179.0	54.0	205.0	1, 63, 145
Spermophilus canus	160.2	40.8		153.3	38.4		171.1	36.3	154.0	1, 63, 146, 147
Spermophilus citellus	167.6	50.6	202.3	146.3	59.5	255.7	205.0	65.0	290.0	1, 85, 148
Spermophilus columbianus	247.8	84.3	441.4	258.0	101.3	490.1	269.5	98.0	576.0	1, 7, 22, 63, 149, 150, 151, 152, 153, 154, 155
Spermophilus dauricus	190.2	55.3		191.4	63.2		196.1	59.1	223.8	1, 37, 38, 156, 157
Spermophilus elegans	206.7	73.1	284.3	204.8	72.7	329.9	216.0	73.5	311.0	1, 7, 63, 158, 159, 160
Spermophilus erythrogenys	192.8	46.1		187.8	41.3	335.0	215.1	46.5	355.0	1, 7, 37, 38
Spermophilus franklinii	237.9	128.1	424.9	232.4	127.7	461.2	235.0	136.0	607.0	1, 7, 63, 161
Spermophilus fulvus	224.0	71.4		284.3	85.4	290.0	323.0	102.0	596.0	1
Spermophilus lateralis	176.5	83.4	159.7	180.0	87.2	178.0	174.0	88.0	245.7	1, 7, 22, 63, 64, 121, 149, 162, 163, 164, 165, 166
Spermophilus madrensis	168.0	65.0	152.0	169.0	64.0	151.0	175.0	58.0		1, 67
Spermophilus major	260.4	81.0		268.7	83.7		281.0	87.7		1
Spermophilus mexicanus	189.2	122.9	167.2	197.3	119.8	223.4	167.4	122.6	233.5	1, 7, 63, 67, 167
Spermophilus mohavensis	162.0	65.0	213.0			104.0	161.4	62.5	185.0	1, 7, 63, 121
Spermophilus mollis	160.9	45.6	115.3	173.3	42.8	118.8	167.0	49.2	165.0	1, 63, 64, 121, 124, 145, 146, 147, 168, 169
Spermophilus musicus	229.5	49.9		220.6	45.0					1
Spermophilus pallidicauda										No data
Spermophilus parryii	266.1	109.8	524.3	257.1	87.7	755.2	298.5	115.0	673.0	1, 7, 22, 63, 149, 170
Spermophilus perotensis	178.0	80.0	174.0				185.0	68.0		1, 67
Spermophilus pygmaeus	200.6	36.7		205.7	35.1		201.6	37.8	235.2	1, 7, 22
Spermophilus ralli										No data
Spermophilus relictus	236.0	62.0		239.9	72.1		242.4	72.0		1
Spermophilus richardsonii	221.0	70.0	273.4	231.6	75.0	398.5				1, 7, 63, 149, 171
Spermophilus saturatus	187.5	95.5	212.3	197.8	110.0	237.1	194.1	110.8	250.0	1, 7, 63, 172, 173, 174
Spermophilus spilosoma	162.3	74.4	137.3	167.3	66.5	128.0	157.2	74.2	133.9	1, 63, 67, 124
Spermophilus suslicus	212.7	47.6	224.0	179.9	45.5	212.3	209.0	40.3		1, 85
Spermophilus tereticaudus	152.6	90.3	142.1	151.4	92.1	124.4	148.3	87.7	142.3	7, 63, 67, 121, 124
Spermophilus townsendii			183.3			249.5	166.0	46.0		7, 63, 175
Spermophilus tridecemlineatus	164.0	82.7	142.8	164.3	86.8	156.8	168.0	82.0	187.5	1, 7, 22, 63, 149
Spermophilus undulatus	210.0	106.8	718.1	242.7	116.8	877.2	236.3	110.0	415.0	1, 7, 37, 38, 176
Spermophilus variegatus	270.1	207.3	672.6	282.3	205.1	733.7	295.5	207.5	662.5	1, 7, 22, 63, 67, 121
Spermophilus washingtoni	183.9	37.5	186.5	167.3	39.6	186.5	166.5	48.5	210.0	1, 7, 63, 145
Spermophilus xanthoprymnus	254.0	50.8		213.0	51.0		266.7	44.5	311.0	1, 177
Tamias alpinus	106.4	75.5		104.6	69.5		105.3	78.5	35.8	1, 7, 63, 64, 166, 178, 179

APPENDIX I.—Continued.

	Female			Male			Adult			
Species	Body	Tail	Mass	Body	Tail	Mass	Body	Tail	Mass	References[a]
Tamias amoenus	123.2	90.3	50.6	119.3	86.5	58.3	119.3	95.5	43.0	1, 7, 22, 63, 64, 166, 178, 179, 180
Tamias bulleri	134.0	91.5	74.9	131.9	84.6	66.1	130.4	104.8		1, 7, 22, 67, 178, 179
Tamias canipes	131.6	107.8		128.7	98.4		128.9	100.0	70.0	1, 63, 178, 179
Tamias cinereicollis	132.2	88.9	72.0	128.2			124.4	98.9	62.5	1, 63, 178, 179
Tamias dorsalis	127.6	104.5	74.4	123.5	94.3	64.7	125.6	105.0		7, 22, 63, 67, 178, 179, 181, 182, 183
Tamias durangae	135.0	98.4	83.8	135.0			227.7	102.2		22, 67, 178, 179, 184
Tamias merriami	135.3	112.4		131.6	106.4	68.0	133.4	116.1	71.3	1, 7, 22, 63, 64, 67, 166, 178, 179, 185
Tamias minimus	114.2	82.4	46.4	109.3	80.3	43.7	106.0	84.9	50.5	1, 7, 22, 63, 64, 166, 178, 182, 186
Tamias obscurus	128.3	117.0		125.3			124.1	103.3	69.0	63, 67, 178, 179
Tamias ochrogenys	152.5	115.1	94.1	147.8	109.0	72.7	148.7	113.8	94.1	63, 166, 179, 182, 187, 188
Tamias palmeri	126.1	80.3	55.2	126.6	98.0	52.4	125.5	94.0	59.7	1, 63, 166, 179, 182, 187, 189
Tamias panamintinus	119.6	87.1	54.1	117.1	89.1		107.2	91.7	53.2	1, 63, 166, 178, 179, 183
Tamias quadrimaculatus	138.2	94.5	87.4	135.8	95.4	78.1	135.6	102.6	82.8	1, 63, 64, 166, 178, 179
Tamias quadrivittatus	129.4	93.7	63.0	123.4	89.0		124.6	98.0	61.5	1, 63, 64, 166, 178, 179
Tamias ruficaudus	127.2	102.9	63.2	121.8	98.3	57.1	125.3	109.1	67.3	1, 7, 63, 178, 179, 190
Tamias rufus	123.8	95.4	57.6	120.2	91.3	53.3	124.0	87.0	57.0	63, 191
Tamias senex	147.5	107.3	94.0	146.3	103.7	86.0	142.6	102.9	89.7	1, 63, 64, 166, 179, 187, 188, 192
Tamias sibiricus	150.5	108.2	96.2	149.3	106.5	93.4	147.5	116.2	99.5	1, 22, 37, 38, 71, 83, 85, 178, 193
Tamias siskiyou	146.7	107.2		144.5	105.0		144.4	105.2	75.0	63, 166, 179, 187, 192
Tamias sonomae	138.3	106.6		134.3	106.4		133.2	111.6	70.0	1, 65, 169, 181, 182
Tamias speciosus	127.1	88.5	62.7	122.2	86.8	56.8	124.4	94.8	59.2	1, 22, 63, 64, 166, 178, 179
Tamias striatus	145.9	95.0	93.9	148.6	87.7	101.0	150.0	93.2	242.1	1, 7, 22, 63, 178, 194, 195, 196, 197, 198, 199
Tamias townsendii	146.3	115.9	76.1	141.8	110.5	70.3	139.0	110.9	104.0	1, 7, 63, 178, 187
Tamias umbrinus	125.4	97.7	64.6	121.2	94.4	56.0	125.7	96.9	40.8	1, 22, 63, 166, 178, 179
Xerinae: Protoxerini										
Epixerus ebii	278.3	284.3	388.0	288.3	277.0	652.0	280.7	290.0	577.4	1, 7, 200, 201, 202
Funisciurus anerythrus	172.0	167.5		176.7	166.3		192.3	165.0	217.8	22, 200, 201, 202, 203
Funisciurus bayonii	250.5	199.0		184.2	201.1		177.5	150.0	135.0	1, 200
Funisciurus carruthersi	224.0	191.7		208.7	189.9		229.0	192.5	268.0	1, 204
Funisciurus congicus	160.5	162.4		173.6	160.6		150.5	165.0	111.2	1, 7, 200, 201
Funisciurus isabella	165.3	161.3		161.3	148.8		162.8	155.0	107.1	1, 7, 200, 201, 202
Funisciurus lemniscatus	167.6	135.8		170.7	135.4		169.3	160.0	140.9	1, 200, 201, 202
Funisciurus leucogenys	206.7	147.2	251.9	204.4	148.8	271.4	192.5	165.0	250.0	1, 200
Funisciurus pyrropus	191.6	150.9	240.3	193.1	145.3	225.0	204.4	150.0	265.6	1, 7, 201, 202, 204
Funisciurus substriatus	161.0	155.0		165.0	155.0		180.8	170.0	186.1	1, 200, 201, 202
Heliosciurus gambianus	204.0	230.3	328.6	217.7	239.9	245.0	200.6	201.5	212.9	1, 7, 201, 204, 205
Heliosciurus mutabilis	231.0	274.0	382.5	225.7	235.2	332.9	240.0	185.0	290.0	1, 200
Heliosciurus punctatus	184.8	207.0	168.6	182.3	201.4	165.9	190.0		174.3	1, 201
Heliosciurus rufobrachium	219.1	240.1	360.6	228.4	245.8	379.8	232.0	235.8	351.7	1, 7, 22, 201, 202, 204, 205
Heliosciurus ruwenzorii	209.0	249.3		224.5	252.6	305.0	227.3	274.0	291.0	1, 204, 205
Heliosciurus undulatus	235.3	270.0		241.1	261.9		232.2	277.4	315.0	1, 200, 205, 206
Myosciurus pumilio	74.8	50.0		72.1	55.3		71.8	55.0	16.1	1, 200, 201, 202, 207, 208
Paraxerus alexandri	102.9	110.4	40.2	106.4	103.3	45.0	105.0	127.0	54.5	1, 204
Paraxerus boehmi	129.6	146.0	74.8	129.8	138.1	60.0	124.6	135.6	70.5	1, 204
Paraxerus cepapi	171.7	169.1	180.2	177.3	169.4	186.0	184.4	174.3	220.2	1, 7, 201, 204, 209, 210
Paraxerus cooperi				200.0	190.0		195.0	190.0	250.0	1, 200
Paraxerus flavovittis	170.6	163.0		167.8	157.4		179.0	158.0		1, 204
Paraxerus lucifer	230.8	197.2	680.4	228.7	198.0	680.4	243.8	197.5	685.0	1, 204
Paraxerus ochraceus	160.1	166.1	137.5	164.7	164.4	124.8	160.5	158.5	93.0	1, 204, 205, 211
Paraxerus palliatus	206.9	201.4	307.4	212.2	206.8	312.0	205.9	196.7	308.5	1, 7, 204, 205, 210, 212
Paraxerus poensis	154.2	159.1	125.0	155.0	166.1	114.5	156.8	160.0	103.6	1, 7, 200, 201, 202
Paraxerus vexillarius	226.6	183.7		228.1	180.5	243.0	238.5	200.0		1, 204
Paraxerus vincenti	208.0	213.5		214.7	206.0		212.0	209.0		1, 212
Protoxerus aubinnii	240.0	304.4	454.3	239.7	300.7	415.0	255.0	300.0	525.0	1, 200, 201
Protoxerus stangeri	276.7	298.6	760.8	279.5	300.1	538.3	304.6	307.5	658.4	1, 7, 201, 202, 204, 205

Appendix I.—Continued.

Species	Female			Male			Adult			References[a]
	Body	Tail	Mass	Body	Tail	Mass	Body	Tail	Mass	
Xerinae: Xerini										
Atlantoxerus getulus	170.8	129.3	217.2	177.0	136.5	232.8	189.1		251.0	1, 201
Spermophilopsis leptodactylus	226.4	70.5	548.3	239.7	65.4	620.0				1, 7
Xerus erythropus	272.4	211.7	741.7	287.9	216.8	559.8	260.8	225.5	519.8	1, 7, 200, 201, 204, 205, 213
Xerus inauris	246.4	211.7	579.7	247.4	214.5	618.3	247.6	209.3	610.0	1, 7, 200, 201, 214, 215, 216
Xerus princeps	248.6	234.3		265.8	252.8		260.5	247.3	665.2	1, 200, 215, 216
Xerus rutilus	229.1	182.6	252.0	268.1	187.8	306.7	226.2	202.5	368.8	1, 7, 200, 201, 204, 205

[a] 1, this study; 2, Olalla 1935; 3, Anthony and Tate 1935; 4, Eisenberg 1989; 5, Allen 1915; 6, Emmons 1990; 7, Hayssen, et al. 1993; 8, Banks 1931; 9, Banks 1978; 10, Chasen and Kloss 1931; 11, Robinson and Kloss 1911; 12, Davis 1962; 13, Lyon 1908; 14, Payne et al. 1985; 15, Allen and Coolidge 1940; 16, Payne 1979; 17, Lekagul and McNeely 1977; 18, Medway 1969; 19, Agrawal and Chakraborty 1979; 20, Largen 1985; 21, Miller 1942; 22, Goodwin 1953; 23, Blanford 1888; 24, Phillips 1928; 25, Corbet and Hill 1992; 26, Bonhote 1901d; 27, Bonhote 1901c; 28, Saiful et al. 2001; 29, Lee 1997; 30, Rudd 1965; 31, Dao 1966; 32, Tamura 1999; 33, Robinson and Wroughton 1917; 34, Yo et al. 1992; 35, Tamura and Terauchi 1994; 36, Osgood 1932; 37, Allen 1940; 38, Helin et al. 1999; 39, Saha 1977; 40, Kloss 1915; 41, Silva and Downing 1995; 42, Bonhote 1901a; 43, Whitten 1981; 44, Jenkins and Hill 1982; 45, Nor 1996; 46, Hafidzi 1998; 47, Lee and Goh 2000; 48, Trainer 1985; 49, Chasen 1940; 50, Bonhote 1901b; 51, Dao 1969; 52, Heaney 1985; 53, Heaney and Rabor 1982; 54, Rabor 1977; 55, Purohit and Ghosh 1965; 56, Rabinowitz 1990; 57, Sody 1949; 58, Jentink 1879; 59, Heaney 1979; 60, Sanborn 1952; 61, Dao and Cao 1990; 62, Jones 1974; 63, Wilson and Ruff 1999; 64, Grinnell and Storer 1924; 65, Goodwin 1961; 66, Wood and Tessier 1974; 67, Elliot 1904; 68, Medway 1965; 69, Jentink 1890; 70, Thomas 1900; 71, Kawamichi 1996b; 72, Ando and Shiraishi 1984; 73, Ghose and Saha 1981; 74, Lee et al. 1993; 75, Lee et al. 1992; 76, Kloss 1916; 77, Hollister 1911; 78, Muul and Liat 1971; 79, Rabor 1939; 80, Sanborn 1953; 81, Abdullah and Ahmad 1998; 82, Muul 1980; 83, Ando and Shiraishi 1991; 84, Won 1968; 85, Macdonald and Barrett 1993; 86, Goodwin 1946; 87, Thomas 1901a; 88, Borrero-H. and Hernandez-C. 1957; 89, Hernandez-Camacho 1960; 90, Mruphy and Linhart 1999; 91, Keith 1965; 92, Thomas 1901b; 93, Ozkurt et al. 1999; 94, Hecht-Markou 1994; 95, Musser 1968; 96, Brown and Yeager 1945; 97, Robinson and Cowan 1954; 98, Uhlig 1955; 99, Thoma and Marshall 1960; 100, Reid 2001; 101, Thomas 1904; 102, Mondolfi and Boher 1984; 103, Allen 1914; 104, Hershkovitz 1947; 105, Redford and Eisenberg 1992; 106, Kanamori and Ando 1974; 107, Packard 1956; 108, Nixon et al. 1991; 109, Lowery and Davis 1942; 110, Jones and Genoways 1971; 111, Osgood 1944; 112, Harris 1930; 113, Heaney and Hoffmann 1978; 114, Smith 1968; 115, Smith 1981; 116, Layne 1954; 117, Howell 1936; 118, Klenner and Krebs 1991; 119, Davis 1969; 120, Lindsay 1981; 121, Grinnell and Dixon 1918; 122, Bartholomew and Hudson 1959; 123, Kenagy and Bartholomew 1985; 124, Hudson and Deavers 1973; 125, Hoogland 1998; 126, Hollister 1916; 127, Tileston et al. 1966; 128, Beskrovnyi 1970; 129, Nicht et al. 1971; 130, Howell 1915; 131, Armitage and Blumstein 2002; 132, Blumstein 1997; 133, Yanushko 1951; 134, Kashkarov 1925; 135, Armitage 1981; 136, Edelman 2003; 137, Nagorsen 1987; 138, Heard 1977; 139, Bucher 1888; 140, Millesi et al. 1999; 141, Fitch 1948; 142, Tomich 1962; 143, Thomas 1912; 144, Brandt 1843; 145, Yensen 1991; 146, Merriam 1913; 147, Rickart 1989; 148, Huber et al. 1999; 149, Iwaniuk 2001; 150, Boag and Murie 1981; 151, Dobson and Kjelgaard 1985; 152, Moore 1937; 153, Hare and Murie 1992; 154, Festa-Bianchet and King 1991; 155, Neuhaus 2000; 156, Wang et al. 1992; 157, Song and Zeng 1991; 158, Clark 1970; 159, Zegers and Williams 1977; 160, Stanton et al. 1994; 161, Haberman and Fleharty 1971; 162, Hatt 1927; 163, Skryja and Clark 1970; 164, Bronson 1979; 165, Phillips 1981; 166, Johnson 1943; 167, Edwards 1946; 168, Rickart 1988; 169, Davis 1939; 170, McLean and Towns 1981; 171, Dobson and Michener 1995; 172, Kenagy et al. 1989; 173, Trombulak 1988; 174, Kenagy et al. 1990; 175, Van Horne et al. 1997; 176, Mayer and Roche 1954; 177, Yiğit et al. 2000; 178, Levenson 1990; 179, Howell 1929; 180, Schulte-Hostedde and Millar 2000; 181, Dunford 1974; 182, Merriam 1897; 183, Burt 1931; 184, Best et al 1993; 185, Wunder 1970; 186, Willems and Armitage 1975; 187, Sutton 1987; 188, Sutton and Nadler 1974; 189, Gannon and Stanley 1991; 190, Soper 1973; 191, Patterson, B. (in litt., field notes, 1981); 192, Sutton and Patterson 2000; 193, Kawamichi 1996a; 194, Bowers and Carr 1992; 195, Svendsen and White 1997; 196, Hooper 1942; 197, Yerger 1955; 198, Panuska and Wade 1957; 199, Clulow et al. 1969; 200, Kingdon 1997; 201, Roth and Thorington 1982; 202, Emmons 1980; 203, Poche 1975; 204, Kingdon 1974; 205, Hollister 1919; 206, Grubb 1982; 207, Jones and Setzer 1970; 208, Gharaibeh and Jones 1996; 209, Viljoen 1975; 210, Viljoen 1983; 211, Canova and Fasola 2000; 212, Viljoen 1989; 213, Linn and Key 1996; 214, Waterman 1996; 215, Herzig-Straschil and Herzig 1989; 216, Haim et al. 1987.

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