

**POSTCRANIAL PROPORTIONS OF
MICROSCIURUS AND SCIURILLUS,
THE AMERICAN PYGMY TREE SQUIRRELS**

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RESUMEN. Las ardillas pigmeas americanas (*Microsciurus* y *Sciurillus*) difieren significativamente de *Sciurus* en sus proporciones corporales. Teniendo miembros relativamente mas largos, todas las ardillas pigmeas difieren de *Sciurus*, y se cree que la diferencia es una adaptacion para la vida arborea en ardillas de tamaño pequeño. Las ardillas pigmea son heterogeneas en la proporcion de sus huesos largos y de los segmentos vertebrales lumbares y toracicos, y no todos difieren de *Sciurus*. Se sugiere que estas características podrian estar correlacionadas con diferencias ecologicas y conductuales dentro de las ardillas pigmeas.

ABSTRACT. The American pygmy squirrels (*Microsciurus* and *Sciurillus*) differ significantly from *Sciurus* in body proportions. In having relatively longer limbs, all the pygmy squirrels differ from *Sciurus*, and the difference is presumed to be an adaptation for arboreality in small squirrels. The pygmy squirrels are heterogeneous in the proportions of their long bones and proportions of lumbar to thoracic vertebral segments, and not all differ from *Sciurus*. These features are postulated to correlate with ecological and behavioral differences among pygmy squirrels.

INTRODUCTION

The genus *Microsciurus* contains a small number of poorly known species of diminutive tree squirrels, which range from southern Nicaragua to southern Peru and western Brazil. The anatomy of the skull has been reported in a number of taxonomic papers, notably by Allen (1914, 1915), Anthony and Tate (1935), Hill (1959), and Moore (1959), and the baculum of several species has been described by Didier (1955) and Burt (1960). Unfortunately, *Microsciurus* was not included in Bryant's (1945) classical paper on the postcranial anatomy of North American squirrels. The limb proportions of *M. alfari* differ in several respects from those of North American *Sciurus* (Thorington and Heaney, 1981), although *Microsciurus* does not differ greatly from *Sciurus* in bacular morphology (Burt, 1960).

Sciurillus, the smallest and most divergent of the American tree squirrels, includes a single species, *S. pusillus*, which is known from scattered locations in the Guianas, and the

Brazilian and Peruvian Amazon. Thomas (1914) first allied *Sciurillus* with the pygmy squirrels of Africa and Asia on the basis of cranial similarities, but later (1915) grouped it with the other American tree squirrels on the basis of bacular morphology. This latter assignment was contested by Anthony and Tate (1935) but supported by Moore (1959) and Hill (1959). Because of these disagreements about the affinities of *Sciurillus*, its cranial morphology has been carefully studied, but there is little information on its postcranial anatomy.

The purpose of this study is to examine the postcranial skeletal anatomy of *Microsciurus* and *Sciurillus*, particularly the proportions of the appendicular skeleton, so that they can be compared with larger American tree squirrels and used to formulate or to test hypotheses about the influence of body size on body proportions of arboreal mammals.

MATERIALS AND METHODS

We studied skeletons of four species (*Microsciurus alfari* - 14; *M. mimulus* - 12; *M. flaviventer* - 15; and *Sciurillus pusillus* - 2) from the U.S. National Museum of Natural History, Louisiana State Museum, and the Museum of Comparative Zoology. Approximately two thirds of each sample were adult specimens with sutures of the long bones fused. Juveniles less than adult size were excluded from the analyses reported in Tables 1-4.

The vertebral measurements were taken ventrally on dried straightened backbones. The vertebral columns were straightened by soaking the specimens in water, inserting a straight wire into each column, and drying them in this position. The length of the cervical vertebrae was measured from the anterior end of the odontoid process of the axis to the posterior end of the centrum of C7. Measurements of thoracic vertebrae 1 through 10 and 1 through 12, thoracic vertebra 11 through lumbar vertebra 7, lumbar vertebrae 1 through 7, and sacral vertebrae 1 through 3 include the lengths of the centra of all the vertebrae in each segment. Independent measurements were made of the entire precaudal portion of the column, from the odontoid process of C2 to the posterior end of the sacral vertebrae, and of the trunk vertebrae, from T1 to S3.

The following limb measurements were taken: the greatest length of the humerus, from the head to the medial margin of the trochlea; the greatest length of the radius, from the medial edge of the head to the tip of the styloid process; the greatest medial length of the femur, from the head to the medial condyle; and the greatest length of the tibia, from the proximal articular surface to the tip of the medial malleolus. All specimens were measured by both authors using Fowler Max-Cal calipers. The data were recorded directly by a microcomputer, using a public-domain program (INCAL 1.2) developed by Joe Russo, Office of Information Resource Management, Smithsonian Institution. Measurements were retaken whenever the two authors disagreed by more than 0.10 mm. Interobserver differences accounted for only a few percent of the variance in the resulting data. Quantitative analyses were conducted with "Systat", a series of statistical programs developed for microcomputers. The skewness and kurtosis of ratios were examined: none departed significantly from normality. Therefore parametric statistics were used in the analyses.

RESULTS

The normal vertebral numbers for *Microsciurus* are 7 cervical, 12 thoracic, 7 lumbar, and 3 sacral. All specimens had 7 sternebrae, except one *M. flaviventer* which had sternebrae 5 and 6 fused. The transitional vertebra was always thoracic 10. All specimens had a total of 19 thoracic and lumbar vertebrae, but the number of rib-bearing vertebrae varied slightly. One of 7 *M. alfari* and one of 12 *M. mimulus* had 13 rib-bearing vertebrae. One *M. mimulus* had an extra rib on one side only. Of the *M. flaviventer*, 3 of the 15 specimens examined had an extra sacral vertebra, for a total of 4. Both specimens of *Sciurillus pusillus* had 7 cervical, 13 thoracic, 6 lumbar, and 3 sacral vertebrae. The transitional vertebra was thoracic 10, and there were 7 sternebrae. If the lumbar region is defined by the lumbar type of zygapophyses (Washburn and Buettner-Janusch, 1952), then the T10 - T11 articulation forms the transition from thoracic to lumbar regions in both *Microsciurus* and *Sciurillus*. If the thoracic region is defined by the presence of ribs, as is the usual convention, then the transition between the two regions lies at the T12 - L1 articulation in *Microsciurus* and at the T13 - L1 articulation in *Sciurillus*.

The measurements and proportions of the limb bones of *Microsciurus* demonstrate that *M. alfari* and *M. flaviventer* have a relatively longer radius than does *M. mimulus* (Tables 1 and 2). It is almost 100% of the length of the humerus in the former two species, contrasting with 95% in *M. mimulus*. The long radius of *M. alfari* and *M. flaviventer* is also reflected in the ratio of the lengths of the distal bones, radius and tibia. *M. mimulus* differs significantly ($p < .05$) from the other two species in this ratio. In addition, the humerus appears to be relatively shorter in *M. alfari* and *M. flaviventer* than in *M. mimulus*, as shown by the ratio of humerus to femur lengths, whereas the relative lengths of femur and tibia are virtually the same in all three species.

By either lumbar definition, the relative length of the region varies significantly among the three species of *Microsciurus*, with *M. alfari* differing the most from the other two species in having the shortest lumbar region (Tables 3 and 4). *M. flaviventer* is intermediate and *M. mimulus* has relatively the longest lumbar region.

The length of the forelimb is 66-69% of the trunk length and the hindlimb is 86-92% of trunk length in the three species of *Microsciurus*. *M. mimulus* has the shortest limbs and *M. alfari* has the longest.

In linear measurements, the one adult *Sciurillus* is approximately 80% the size of *Microsciurus mimulus*. In vertebral proportions and in the relative lengths of the limbs, it does not differ significantly from *Microsciurus flaviventer*. The relative lengths of the long bones differ from *Microsciurus* only in the shortness of the tibia, especially in comparison with the radius. Consequently, the intermembral ratio of *Sciurillus* is higher than that of *Microsciurus*.

DISCUSSION

Tree squirrels climb vertical trunks by reaching up and to the side with their forelimbs, obtaining a secure grip on the trunk, then pulling themselves up with their forelimbs while pushing upwards with their hindlegs (personal observations on several species of *Sciurus*). On rough bark, a squirrel has little problem gripping with its claws no matter how its forelimbs are placed, but *Sciurus* commonly places its forelegs 30-45 degrees from

the vertical. On smooth bark, this lateral positioning of the forelimbs around the trunk must be particularly important, so that the squirrel can apply force normal (perpendicular) to the trunk and drive its claws into the bark (Figure 1). This is analogous to the problem of friction grip, as analyzed by Cartmill (1974, 1985), except that the normal force (N in Figure 1) must be great enough to drive the claws into the bark of the tree and that the strength of this purchase on the bark must exceed the tangential force (T in Figure 1). Lateral positioning of the limbs is important for a small squirrel on a large trunk, because increasing the span will increase the normal component of the adductive force. The relative size of the normal and tangential components can be computed, if one knows the span of the squirrel and the radius of the tree. For a pygmy squirrel with a reach of 100 mm, the normal component would be approximately 20% of the adductive force on a bole with a quarter-meter radius and only 10% on a half-meter bole. The tangential components would be 98% and 99.5% respectively. Field observations are concordant with the hypothesis that increasing the span is important to a pygmy squirrel. Emmons (1975, 1979) noted an exaggerated lateral positioning of the limbs in the African pygmy squirrel, *Microsciurus*, and has observed the same type of posture in *Microsciurus flaviventer* and *Sciurillus pusillus* (personal communication). Heaney (personal communication) has noted the same thing for pygmy tree squirrels (*Exilisciurus*) in the Philippines. A squirrel descending head first down a trunk reverses its hind feet and grips the bark with its claws. Again, the more laterally the feet are positioned, the more force the squirrel can apply to drive the claws into the bark. *Sciurus carolinensis* can completely reverse its hind feet when hanging from a branch or descending on a flat vertical surface (Jenkins and McClearn, 1984: fig 7), but it seldom does this when descending a large tree trunk. Instead, it usually places its feet more laterally, gripping the trunk between them (personal observation). A small squirrel descending a big tree trunk should have more exaggerated problems than a larger squirrel and hence should exaggerate the lateral position of its limbs, as reported by Emmons (1975). Based on these analyses, we might expect small squirrels to prefer trunks of smaller diameter or trunks that are not smooth. This is not true for the species observed by Emmons. Alternatively, we might expect to find that pygmy squirrels have relatively longer limbs than do larger tree squirrels. We shall examine our data to test this last hypothesis.

Microsciurus and *Sciurillus* have relatively longer limbs than do *Sciurus*. The forelimb is estimated to be 75% of trunk length in *Sciurillus* and averages from 66 to 69% in three species of *Microsciurus*; whereas, in four species of *Sciurus* it averages from 56 to 60% (*S. niger*, *S. aberti*, *S. carolinensis*, and *S. deppei* -- Thorington and Heaney, 1981). The difference is less extreme in the hindlimb. The hindlimb averages 86 to 92% of trunk length in *Microsciurus*, 86% in *Sciurillus*, and 79 to 85% in *Sciurus*. There is a concomitant difference in the intermembral ratio: the forelimb is 81% the length of the hindlimb in *Sciurillus*, 76 to 77% in *Microsciurus*, and 71 to 72% in *Sciurus*. Thus our data fit the hypothesis that smaller tree squirrels have relatively longer limbs than larger ones. However, the hypothesis gave us no reason to expect that the forelimbs of small squirrels would be relatively more elongated than hind limbs. The opposite is true of almost all groups of primates (Jungers, 1985) -- the forelimb/hindlimb ratio increases with increasing body size except in cheirogaleids and lorises. A logical explanation for the normal trend in primates is provided by Cartmill (1974, 1985) and Jungers (1977, 1979, 1984, 1985). The opposite trend in squirrels and lorises is unexplained except as part of the more general

trend to move the center of gravity relatively closer to the support in larger animals (Jungers, 1985).

The hind limbs provide the main force in locomotion in squirrels, particularly when they are leaping or bounding. The problems of a leaping squirrel would appear to be a function of size also. The same gap between branches is a relatively larger leap for a smaller squirrel. This leads us to hypothesize that a smaller squirrel would be more specialized for leaping, which is accomplished in some mammals by elongation of the hind limbs with especial emphasis on the more distal elements of the leg (Howell, 1944: p. 208). Emmons argues that bounding is more important than leaping in tropical squirrels: that it is essential for a ground-foraging squirrel to return quickly to the safety of a tree. Since stride length and speed scale with body size (Calder, 1984), a smaller squirrel should be a slower squirrel unless it is more specialized for bounding. Thus Emmons' argument can lead to the same prediction, that smaller squirrels should have more elongate hind limbs. Our data for *Microsciurus* are consistent with these hypotheses, because the hindlimbs are both relatively longer than those of *Sciurus* and also the tibia is relatively longer than the femur (1.17 to 1.18 in *Microsciurus*, 1.12 to 1.13 in *Sciurus*). This is not true for *Sciurillus*, which has the same tibia/femur ratio as does *Sciurus*. Either *Sciurillus* contradicts our hypotheses or it is not as much of a leaper or bounder as is *Microsciurus*. We favor the latter explanation. In primates, the most common trend is for the tibia/femur ratio to decrease with increasing body size (Jungers, 1985), just as it does in the *Microsciurus* - *Sciurus* comparison. This is not true for the Callitrichidae: the sap-feeding pygmy marmoset has a lower crural index than does the lion tamarin, analogous to a *Sciurillus* - *Microsciurus* comparison.

Elongation of the radius relative to the humerus could have two explanations. First, it could reflect the use of the forelimb in leaping. Elongation of the radius should enable the squirrel to extend its forepaw more rapidly and thus increase its speed at take-off. We are not sure how seriously to treat this idea. A larger radius/humerus ratio is found in *Sciurillus* (1.01), *Microsciurus alfari* (1.00), and *M. flaviventer* (1.00), but not in *M. mimulus* (0.95) relative to *Sciurus* (0.93 to 0.95). Thus the greatest relative elongation is found in one species, *Sciurillus pusillus*, which we suspect is not an extraordinary jumper because it does not exhibit elongation of the tibia relative to the femur. Also *Microsciurus mimulus* resembles *Sciurus* in the relative lengths of the radius and humerus, whereas it differs from *Sciurus* in having a significantly larger ratio of tibia/femur. Because of this discordance between the brachial and crural ratios, we doubt that they reflect the same functional adaptations.

Second, relative elongation of the forearm could be an adaptation to vertical climbing. Muscles from the trunk insert almost to midshaft on the humerus of tree squirrels, thus the shoulder is not nearly as mobile in squirrels as in humans and other primates. Elongation of the forearm can provide more mobility and greater protraction of the forelimb than the same amount of elongation of the upper arm because of this reduced mobility of the humerus. Thus forearm elongation could merely be an efficient way to lengthen the arm and could be part of the same adaptation for expanding the grasp of a small squirrel climbing a large vertical trunk, as discussed before.

We are left with the question why *Microsciurus mimulus* does not exhibit this elongation of the forearm, whereas the other three species of pygmy squirrels do. We can think of several possible explanations for this. In Central America *M. mimulus* is found in "fog

forest" (Handley, 1966), in contrast to *M. alfari* which occurs mostly in lowland forest (Goodwin, 1946; Handley, 1966), as do *M. flaviventer* and *Sciurillus* in South America. Also *M. alfari* is commonly found in association with *Scheelia* palms (Enders, 1935) which must present a more extreme problem to a small tree squirrel because of their smooth branchless trunks. Thus it is possible that *Microsciurus mimulus* is less derived in forelimb proportions than *M. alfari* and the other pygmy squirrels because its habitat is different, e.g. fewer palms or smaller trees. Alternatively, there may be behavioral or niche differences between the species, with *M. mimulus* preferring a small-branch niche or with *M. alfari*, *M. flaviventer*, and *Sciurillus* spending more time clinging to vertical surfaces while involved in bark gleaning, sap feeding, or other such activities, as reported by Moynihan (1976, pp. 133-134) and Emmons (personal communication).

Among primates, forearm elongation is a more heterogeneous phenomenon than among squirrels. In Jungers (1985) study of 11 family and subfamily groups, there was no size-related change in three families, a relative decrease in forearm length with increasing body size in five families, and a relative increase in the three other groups. The pygmy marmoset - lion tamarin trend is opposite from the *Sciurillus* - *Sciurus* trend. Thus it is probable that there is no single explanation of relative forearm length among primates, as among squirrels.

Another morphological measure of jumping or bounding ability is provided by the measurements of the vertebral column. Flexion and extension of the vertebral column occurs mostly between vertebrae with the lumbar type of articulation. Greater flexion and extension increases the stride length and speed of bounding animals (Howell, 1944: p. 116). Since leaping involves extension of a flexed column, a longer lumbar segment of the vertebral column has been hypothesized to correlate with greater ability to leap (Erikson, 1963). Our data provide ratios of thoracic and lumbar segments of the vertebral column, in which the vertebrae are defined both by whether they are rib-bearing and by the type of articulation (Washburn and Buettner-Janusch, 1952). Unfortunately, there is only a single species of *Sciurus* (*S. carolinensis*) for which there are comparable data (Thorington, 1972). In this comparison, *M. mimulus* is much like *Sciurus*, whether the segments are defined by ribs (0.96 vs 0.97) or by the articulation of the zygapophyses (1.49 vs 1.48), and the ratios for *M. flaviventer*, *S. pusillus* and *M. alfari* are progressively less. This is an unanticipated result, because it suggests that *M. mimulus* is more specialized than *M. alfari* for jumping or bounding, whereas the relative length of the hind limb suggests the opposite. Comparing the lengths of all the segments of the vertebral column and the length of the hind limb, we confirmed that both factors are involved: in *M. alfari* the hind limb is longer and the lumbar region is shorter than in *M. mimulus* (Table 4). This implies that *M. alfari* leaps and bounds differently than *M. mimulus*, using the hind limb more and extension of the vertebral column less. This pattern of locomotion would be appropriate for a squirrel that leaps frequently from vertical surfaces. Because *M. mimulus* is like *Sciurus* in the relative lengths of the vertebral column, we suggest that it is primitive and that *M. alfari* is derived in this feature.

In summary, we conclude that the American pygmy squirrels differ in body proportions from the larger tree squirrels. Some of the differences, such as the relatively long limbs of the pygmy squirrels, are probably an adaptation for arboreality in small sciurids. Other traits, such as the relative elongation of the radius and the tibia or the reduction in length of the lumbar segment of the vertebral column, are not simply or consistently corre-

lated with the small size of pygmy squirrels, and hence the differences can not be attributed to size alone. It is probable that these reflect different ecological and behavioral adaptations among pygmy squirrels and between some of them and the larger tree squirrels: for example, a propensity for bark gleaning, clinging to vertical surfaces, leaping from vertical supports, or less terrestrial foraging.

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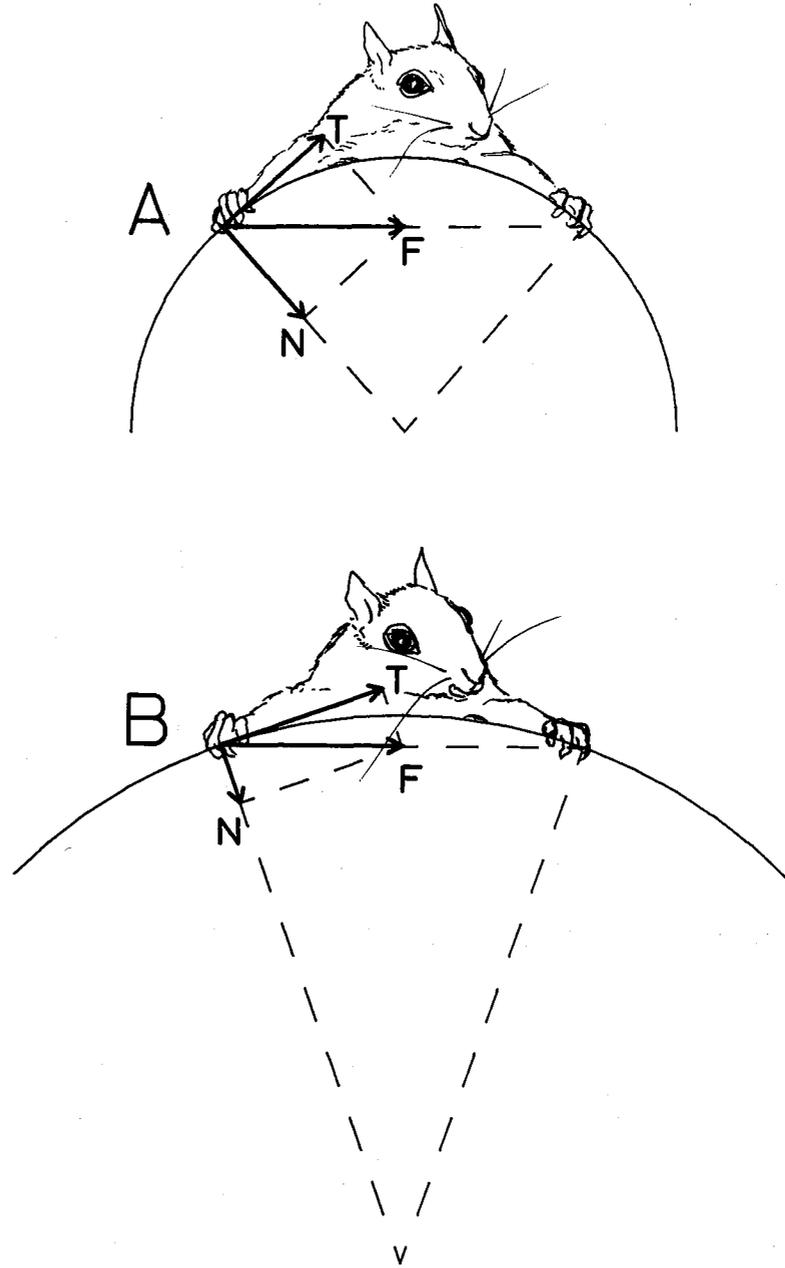


Figure 1. Vector diagrams of forces generated by a squirrel climbing a tree. The squirrel exerts adduction force (F) which may be resolved into a component (T), tangential to the surface and a component (N), normal (perpendicular) to the surface. Force N drives the claw into the tree, force T causes the claw to skid across the bark if the claw has not penetrated the surface or caught a rough spot. On a small trunk (A) component N is larger and T is smaller than on a larger trunk (B). Therefore the claw is less likely to dig in and more likely to skid on a larger trunk.

Table 1. Lengths of Long Bones of *Microsciurus* and *Sciurillus* (Means and Standard Deviations)

Species	Humerus	Radius	Femur	Tibia
<i>M. alfari</i>	26.12 ± .74	26.01 ± .60	31.20 ± .82	36.46 ± 1.10
<i>M. flaviventer</i>	28.40 ± 1.16	28.44 ± .77	33.76 ± 1.44	39.69 ± 1.54
<i>M. mimulus</i>	25.46 ± .41	24.20 ± .50	29.87 ± .52	35.05 ± .75
<i>S. pusillus</i>	20.6	20.7	24.0	26.9

Table 2. Ratios of Lengths of Long Bones of *Microsciurus* and *Sciurillus* (Means and Standard Deviations).

Species	Rad/Hum	Tib/Fem	Hum/Fem	Rad/Tib	(Hum+Rad) (Fem+Tib)
<i>M. alfari</i>	0.998 ±0.022	1.177 ±0.012	0.841 ±0.012	0.709 ±0.009	0.770 ±0.007
<i>M. flaviventer</i>	0.998 ±0.017	1.179 ±0.037	0.836 ±0.014	0.711 ±0.016	0.770 ±0.011
<i>M. mimulus</i>	0.953 ±0.012	1.170 ±0.017	0.850 ±0.017	0.693 ±0.008	0.764 ±0.012
ANOVA : F=	20.29	0.42	3.85	5.14	0.68
p=	<0.001	0.66	0.03	0.013	0.52
<i>S. pusillus</i>	1.01	1.12	0.86	0.77	0.81

Hum = Humerus; Rad = Radius; Fem = Femur; Tib = Tibia.

Table 3. Lengths of Vertebral Segments (Means and Standard Deviations)

Species	C2-7	T1-10	T1-12	T11-L7	L1-7	S1-3
<i>M. alfari</i>	13.06 ±0.50	26.59 ±1.37	33.27 ±1.78	37.13 ±2.07	30.54 ±1.67	10.66 ±0.51
<i>M. flaviventer</i>	13.84 ±0.46	28.68 ±1.65	36.21 ±2.18	41.62 ±2.88	34.07 ±2.36	11.73 ±0.55
<i>M. mimulus</i>	12.79 ±0.62	25.67 ±1.49	32.56 ±1.78	38.10 ±1.54	31.14 ±1.27	10.61 ±0.36
<i>S. pusillus</i>	9.9	19.7	24.5	27.9*	23.2*	7.9

C = Cervical; T = Thoracic; L = Lumbar; S = Sacral.

* The homologous vertebrae of *Sciurillus* were measured. By conventional definition these were T11-L6 and T13-L6.

Table 4. Relative Lengths of Lumbar Vertebrae and of Limbs (Means and Standard Deviations)

Species	Lumbar/Thoracic		Limbs/Trunk	
	$\frac{T11-L7}{T1-10}$	$\frac{L1-7}{T1-12}$	$\frac{Hum+Rad}{T1-S3}$	$\frac{Fem+Tib}{T1-S3}$
<i>M. alfari</i>	1.396 ±0.020	0.918 ±0.014	0.693 ±0.031	0.918 ±0.041
<i>M. flaviventer</i>	1.451 ±0.035	0.941 ±0.024	0.688 ±0.031	0.905 ±0.033
<i>M. mimulus</i>	1.486 ±0.040	0.957 ±0.026	0.660 ±0.023	0.862 ±0.028
ANOVA : F	14.82	6.42	3.26	7.11
p=	<0.001	0.005	0.059	0.004
<i>S. pusillus</i>	1.44	0.94	0.75	0.92

Table 5. Vertebral and limb lengths and proportions of *Sciurillus*.

Specimen	Hum	Rad	Fem	Tib	Rad/ Hum	Tib/ Fem	Hum/ Fem	Rad/ Tib
27994 juv	19.8	---	22.8	26.0	---	1.14	0.87	---
27995 ad	20.6	20.7	24.0	26.9	1.01	1.12	0.86	0.77

Specimen	C2-7	T1-10	T1-12	T11-L6	T13-L6	S1-3
27995 ad	9.9	19.7	24.5	27.9	23.2	7.9

Specimen	$\frac{(Hum+Rad)}{(Fem+Tib)}$	$\frac{T11-L6}{T1-10}$	$\frac{T13-L6}{T1-12}$	$\frac{Hum+Rad}{T1-S3}$	$\frac{Fem+Tib}{T1-S3}$
27995 ad	0.81	1.44	0.94	0.75	0.92

Table 4. Relative Lengths of Lumbar Vertebrae and of Limbs (Means and Standard Deviations)

Species	Lumbar/Thoracic		Limbs/Trunk	
	$\frac{T11-L7}{T1-10}$	$\frac{L1-7}{T1-12}$	$\frac{Hum+Rad}{T1-S3}$	$\frac{Fem+Tib}{T1-S3}$
<i>M. alfari</i>	1.396 ±0.020	0.918 ±0.014	0.693 ±0.031	0.918 ±0.041
<i>M. flaviventer</i>	1.451 ±0.035	0.941 ±0.024	0.688 ±0.031	0.905 ±0.033
<i>M. mimulus</i>	1.486 ±0.040	0.957 ±0.026	0.660 ±0.023	0.862 ±0.028
ANOVA : F	14.82	6.42	3.26	7.11
p=	<0.001	0.005	0.059	0.004
<i>S. pusillus</i>	1.44	0.94	0.75	0.92

Table 5. Vertebral and limb lengths and proportions of *Sciurillus*.

Specimen	Hum	Rad	Fem	Tib	Rad/ Hum	Tib/ Fem	Hum/ Fem	Rad/ Tib
27994 juv	19.8	---	22.8	26.0	---	1.14	0.87	---
27995 ad	20.6	20.7	24.0	26.9	1.01	1.12	0.86	0.77

Specimen	C2-7	T1-10	T1-12	T11-L6	T13-L6	S1-3
27995 ad	9.9	19.7	24.5	27.9	23.2	7.9

Specimen	$\frac{(Hum+Rad)}{(Fem+Tib)}$	$\frac{T11-L6}{T1-10}$	$\frac{T13-L6}{T1-12}$	$\frac{Hum+Rad}{T1-S3}$	$\frac{Fem+Tib}{T1-S3}$
27995 ad	0.81	1.44	0.94	0.75	0.92