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PHYLOGENETIC IMPLICATIONS OF COMPARATIVE PELAGE MORPHOLOGY IN APLDONTIDAE AND THE NEARCTIC SCIURIDAE, WITH OBSERVATIONS ON SEASONAL PELAGE VARIATION

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The family Sciuridae presents a taxonomic array of species well suited for comparative studies. The group is cosmopolitan in distribution, consisting of at least 49 genera and 262 species (McLaughlin, 1984). The Nearctic taxa afford a suitable sampling of this diversity (Hall, 1981).

The Nearctic Sciuridae commonly are thought to consist of three phyletic lines that are generally coincidental to differing ecological niches—ground squirrels (*Marmota*, *Cynomys*, *Ammospermophilus*, and *Spermophilus*) and chipmunks (*Tamias*), tree squirrels (*Sciurus* and *Tamiasciurus*), and flying squirrels (*Glaucomys*). The primary purpose of this study was to produce a sciurid phylogeny based on pelage morphology that can be compared to other phylogenies derived from paleontological evidence (Black, 1963), skeletal and dental morphology (Bryant, 1945), immunology (Hight *et al.*, 1974), and electrophoretic analysis (Hafner, 1984).

Previous investigators of mammalian pelage characters have addressed the descriptive microanatomy of individual hair shafts (Hausman, 1920, 1924, 1930; Short, 1978; Williams, 1938). Medullar organization and cuticular scale patterns have received the most attention. Such features have proven useful in construction of identification keys of hairs (Keogh, 1983; Mathiak, 1938; Mayer, 1952; Moore *et al.*, 1974), although

attempts to assess systematic relationships with these data have met with limited success (Benedict, 1957; Cole, 1924; Hess *et al.*, 1985; Homan and Genoways, 1978; Nason, 1948). However, many aspects of the pelage of wild mammals have been largely neglected (Ling, 1972). Detailed information regarding seasonal pelage variation and molt is surprisingly scarce for many species (Merritt, 1986; Stangl *et al.*, 1986), and the potential impact of seasonal variability of previously studied hair and pelage characters was not considered by many previous investigators. A secondary purpose of this investigation was, therefore, to characterize qualitative and quantitative aspects of seasonal pelage variation for the Sciuridae.

In this paper, we introduce a suite of pelage characters not traditionally utilized in systematic studies, taking into account any seasonal variability. Cross-sectional morphology of guard hair bodies and hair distribution patterns of both wool and guard hairs representing the eight Nearctic sciurid genera and the out-group *Aplodontia rufa* are presented. The systematic implications of these data are discussed.

MATERIALS AND METHODS

Taxa included in this study are restricted to Nearctic species that occur in the United States. All specimens examined were represented as museum study skins from the collections of Midwestern State University (MWSU) and Texas Tech University (TTU). Specimens demonstrating seasonal pelage extremes were available for most of the species.

As outlined below, hair distribution patterns and external morphology of guard hairs were assessed for the out-group taxon *Aplodontia rufa*, and for representative members of the sciurid genera *Glaucomys*, *Sciurus*, *Tamiasciurus*, *Tamias* (*sensu* Levenson *et al.*, 1985), *Marmota*, *Cynomys*, *Ammospermophilus*, and *Spermophilus*.

Pelage characterization.—Specimens were examined initially by combing through pelage and brushing hairs anteriorly with a needle probe under a dissecting microscope. In this way, hair distribution patterns could be discerned (singly distributed or gathered into tufts resulting from closely associated hair follicles), as well as distribution of any tufts (singly distributed or arranged into definite tracts).

Guard hair morphology.—Assessment of guard hair morphology was restricted to external form. From six to 10 guard hairs

were plucked from the midlateral line along the left flank of each specimen. Total length of each guard hair and maximum width across the body were measured with an ocular micrometer. Relative length and distinctiveness of subdivisions of each hair shaft were noted. Cross-sections were made with razor blades to examine cross-sectional configurations at midbody. Sectioned guard hairs of selected taxa were mounted on scanning electron microscope (SEM) specimen stubs using two-sided tape. The stubs were then coated with gold in a DC sputtering apparatus to 400 angstroms. The coated specimens were examined with an ISI SIII SEM.

Methods of analyses.—Phylogenetic relationships of sciurid genera were assessed following Hennig (1966). Pelage features were hypothesized as primitive or derived on the basis of out-group comparisons with *Aplodontia rufa*. Character states were then coded and ordered into polarity series, from primitive to most derived, and subsequently were cladistically analyzed to produce the most parsimonious phylogeny.

RESULTS

Pelages of all taxa were characterized by distinct tufts of hairs, composed of both wool and guard hairs. Wool hairs were usually the more abundant, and were consistently slender, oval to circular in cross-section, uniform in width, and wavy. One or more wool hairs are produced by each follicle or by closely associated follicles. These hairs were directed posteriorly, and became enmeshed to form the wool coat or underfur that is at least seasonally typical of all species examined.

Guard hairs were comparatively stout and usually associated with tufts of wool hairs. They were at least as long, but usually longer than the accompanying wool hairs. The guard hair shaft typically was divisible into three recognizable regions (Fig. 1A), the proportional and overall lengths of which usually varied seasonally (Table 1). Cross-sectional morphology of the shaft body was usually characteristic of a given genus, and did not appear to vary seasonally. Guard hairs either projected beyond the wool layer (Fig. 1B) or curved sharply posteriorly, providing a shingling effect to form a roof over the underfur (Fig. 1C). Both guard hair conditions were found in most taxa examined (Fig. 1D), and in such pelages projecting guard hairs usually are longer and stouter than the other guard hairs. In taxa for which

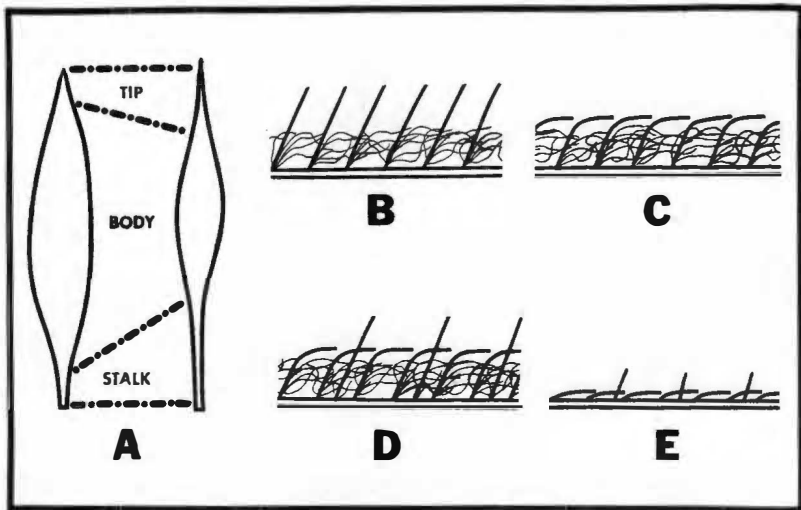


FIG. 1.—Schematic representation of guard hair and pelage configurations exhibited in members of Aplodontidae and Sciuridae: A, representation of subdivisions of guard hair shafts for (left) summer conditions as occurs in some *Spermophilus* and (right) the more typical guard hair (proportions exaggerated and not drawn to scale); B, wooly pelage with projecting guard hairs; C, wooly pelage with guard hairs contributing only to protective roof; D, wooly pelage consisting of guard hairs both projecting and contributing to protective roof; E, pelage typified by near absence of wool and guard hairs both projecting and providing a shingling effect.

the underfur is seasonally absent, roofing guard hairs lie flat against the body (Fig. 1E).

Cold-weather pelages differed primarily from those of warmer months by an increase in length and number of wool hairs (Table 2), and by elongation of guard hair stalks. Winter guard hairs typically tended to be narrower than warm-season counterparts. The increased density of hair tufts in cold-season pelages was evident in many taxa, but was not readily quantified.

Generic Accounts

Following are synoptic descriptions of guard hairs and degree of observed pelage variation, presented in the systematic order of Jones *et al.* (1986).

APLODONTIDAE

Genus *Aplodontia*

Negligible variation in seasonal pelages in *A. rufa*; undercoat of wool hairs always present; tufts singly and evenly distributed;

TABLE 1.—Arithmetic mean and range for guard hair measurements in aploidontid and sciurid rodents. Measurements are in millimeters. Sample sizes shown in parentheses (from left to right) for summer length, winter length, summer width, and winter width.

Taxa	Length of Guard Hairs		Width of Guard Hairs	
	Summer	Winter	Summer	Winter
<i>Aplodontia rufa</i> (7,6,8,5)	17.5	21.8	.084	.081
	15.9-20.7	18.1-24.1	.074-.096	.074-.093
<i>Tamias striatus</i> (8,6,5,6)	9.8	10.9	.074	.068
	8.9-11.1	10.0-11.7	.074-.074	.067-.074
<i>T. dorsalis</i> (6,6,7,7)	7.6	12.0	.047	.043
	6.4-8.7	10.4-14.8	.038-.053	.037-.052
<i>Marmota monax</i> (6,5,7,5)	33.0	27.7	.153	.137
	24.8-38.5	23.0-30.9	.144-.178	.113-.151
<i>M. flaviventris</i> (6,6,6,7)	29.9	24.2	.141	.160
	29.1-30.6	20.6-27.9	.125-.159	.151-.170
<i>Ammospermophilus leucurus</i> (9,7,8,8)	6.3	13.8	.131	.091
	4.7-8.7	8.5-18.5	.118-.144	.074-.111
<i>A. interpres</i> (7,7,8,8)	6.0	12.6	.127	.089
	5.6-7.4	11.5-14.8	.111-.144	.074-.104
<i>Spermophilus washingtoni</i> (5,0,5,0)	9.7	—	.075	—
	9.1-10.4		.074-.077	
<i>S. armatus</i> (5,0,5,0)	15.4	—	.078	—
	14.1-16.5		.074-.085	
<i>S. undulatus</i> (5,0,5,0)	18.5	—	.073	—
	15.9-20.0		.067-.077	
<i>S. tridecemlineatus</i> (8,8,7,6)	5.7	10.9	.111	.097
	4.8-6.7	8.5-14.8	.111-.130	.081-.104
<i>S. mexicanus</i> (6,7,6,8)	5.9	13.8	.132	.109
	5.0-6.5	12.2-16.5	.111-.148	.074-.141
<i>S. spilosoma</i> (8,5,6,7)	6.2	13.6	.108	.084
	6.0-7.0	11.5-17.0	.094-.121	.074-.107
<i>S. variegatus</i> (8,8,7,6)	16.1	16.3	.171	.147
	13.9-19.2	13.7-19.2	.144-.189	.130-.170
<i>S. tereticaudus</i> (6,7,6,8)	4.7	12.9	.153	.065
	4.6-5.3	9.3-15.7	.140-.158	.052-.074
<i>S. lateralis</i> (9,7,6,6)	9.0	12.1	.084	.078
	7.0-11.5	11.1-13.0	.074-.104	.074-.081
<i>Cynomys ludovicianus</i> (8,8,8,7)	13.6	26.6	.148	.109
	11.1-16.1	24.8-28.9	.144-.156	.100-.118
<i>Sciurus aberti</i> (7,8,7,9)	17.6	20.8	.083	.074
	11.1-20.7	15.4-25.5	.074-.093	.044-.140
<i>S. niger</i> (7,8,8,8)	10.1	22.2	.177	.097
	8.1-13.3	14.8-30.3	.089-.144	.081-.118
<i>Tamiasciurus hudsonicus</i> (8,6,7,7)	14.1	16.3	.100	.095
	11.1-15.5	10.4-20.7	.089-.111	.085-.104
<i>Glaucomys volans</i> (7,6,7,7)	10.9	15.9	.035	.037
	7.7-11.7	15.6-16.7	.030-.037	.033-.040
<i>G. sabrinus</i> (7,8,6,6)	19.4	19.0	.039	.040
	16.3-24.8	15.5-16.7	.037-.144	.033-.052

TABLE 2.—Composition of hair tufts in apodontid and sciurid rodents.

Taxa	Guard Hairs/Tuft		Wool Hairs/Tuft	
	Summer	Winter	Summer	Winter
<i>Aplodontia rufa</i>	0-1	0-1	8-12	7-10
<i>Tamias striatus</i>	1	1	6-9	8-10
<i>T. dorsalis</i>	1	1	6-8	6-9
<i>Marmota monax</i>	0-1/pr.	1-3/pr.	3-5	6-10
<i>M. flaviventris</i>	0-1/pr.	1-2/pr.	4-8	7-12
<i>Ammospermophilus leucurus</i>	1	1	1-3	3-6
<i>A. interpres</i>	1-2	1-2	1-3	3-5
<i>Spermophilus washingtoni</i>	1	—	4-6	—
<i>S. armatus</i>	1	—	3-4	—
<i>S. undulatus</i>	1	—	9-12	—
<i>S. tridecemlineatus</i>	1	1	0-1	3-6
<i>S. mexicanus</i>	1	1	0-1	3-6
<i>S. spilosoma</i>	1	1	0-1	3-6
<i>S. variegatus</i>	1	1	2-4	6-8
<i>S. tereticaudus</i>	1	1	0-1	4-6
<i>S. lateralis</i>	1	1	3-6	6-9
<i>Cynomys ludovicianus</i>	2-4	2-4	1-2	7-12
<i>Sciurus aberti</i>	1	1	5-7	6-9
<i>S. niger</i>	1	1	3-6	3-7
<i>Tamiasciurus hudsonicus</i>	1	1	7-8	8-14
<i>Glaucomyz volans</i>	1	1	3-4	4-8
<i>G. sabrinus</i>	1	1	4-6	4-8

guard hairs sparsely distributed, slightly oval to circular in cross-section (Fig. 2A), and projecting beyond undercoat. Presumably there is a single, although not obvious, molt.

SCIURIDAE

Wide range of variation in degree of seasonal pelage variation, usually most pronounced in those taxa that molt twice annually; bodies of guard hair on long slender stalks that penetrate through wool layer; some guard hairs longer and stouter than others for most taxa and project beyond the wool layer; most curve posteriorly to shield or roof the wool layer, at least to some extent. Some degree of dorsoventral compression occurs in at least some hairs for all taxa examined.

Genus *Tamias*

Minimal seasonal pelage variation was noted for *T. striatus* and *T. dorsalis*. Two annual molts are thought to occur. Undercoat of wool hairs always present; tufts singly and evenly distributed;

guard hairs in cross-section oval or elliptical proximally (Fig. 2B), becoming circular distally, as figured by Mathiak (1938); guard hair tips exceptionally long and slender; underfur effectively roofed by guard hairs.

Genus *Marmota*

Marked seasonal pelage variation noted for *M. monax* and especially *M. flaviventris* due to attrition and wear (that is, fraying of guard hairs, loss of wool hairs), because there is only a single annual molt; underfur of wool always present, becoming sparse in the summer pelage; summer guard hairs frayed; tufts occur in pairs that are singly and evenly distributed in *M. monax* and arranged in definite tracts in *M. flaviventris*; guard hairs strongly compressed dorsoventrally (Fig. 2G), and characterized by slight dorsal or ventral concavities or both, along much of the shaft as figured by Mathiak (1938); underfur incompletely roofed.

Genus *Ammospermophilus*

Extreme pelage dimorphism due to two annual molts in both *A. leucurus* and *A. interpres*; tufts singly and evenly distributed; guard hairs seasonally dimorphic, dorsoventrally compressed, and marked by a deep, marginally well-defined, dorsal trough along most of shaft (Fig. 2I). *Warm-weather pelage*: guard hairs typified by extremely short stalk; wool hairs sparse and about one-half length of guard hairs. *Cold-weather pelage*: woolly undercoat of numerous, elongated hairs; guard hairs typified by elongate stalk projecting through wool layer; underfur completely roofed.

Genus *Spermophilus*

Degree of variation in seasonal pelage differs among species examined but apparently is consistent within subgenera. Probably two annual molts occur in most species. Tufts are singly and evenly distributed. Guard hairs are dorsoventrally compressed and marked by a deep, marginally well-defined, dorsal trough (Figs. 2J-L) along most of the shaft.

Subgenus *Spermophilus*.—The species *S. washingtoni*, *S. armatus*, and *S. undulatus* are northern taxa of high latitudes or altitudes and have relatively short active seasons. The subgenus is characterized by notably thinner guard hairs than found elsewhere in the genus, and by perhaps two annual molts. Butterworth (1958) described two yearly molts for *S. undulatus*, the latter of which was the more gradual. David F. Balph

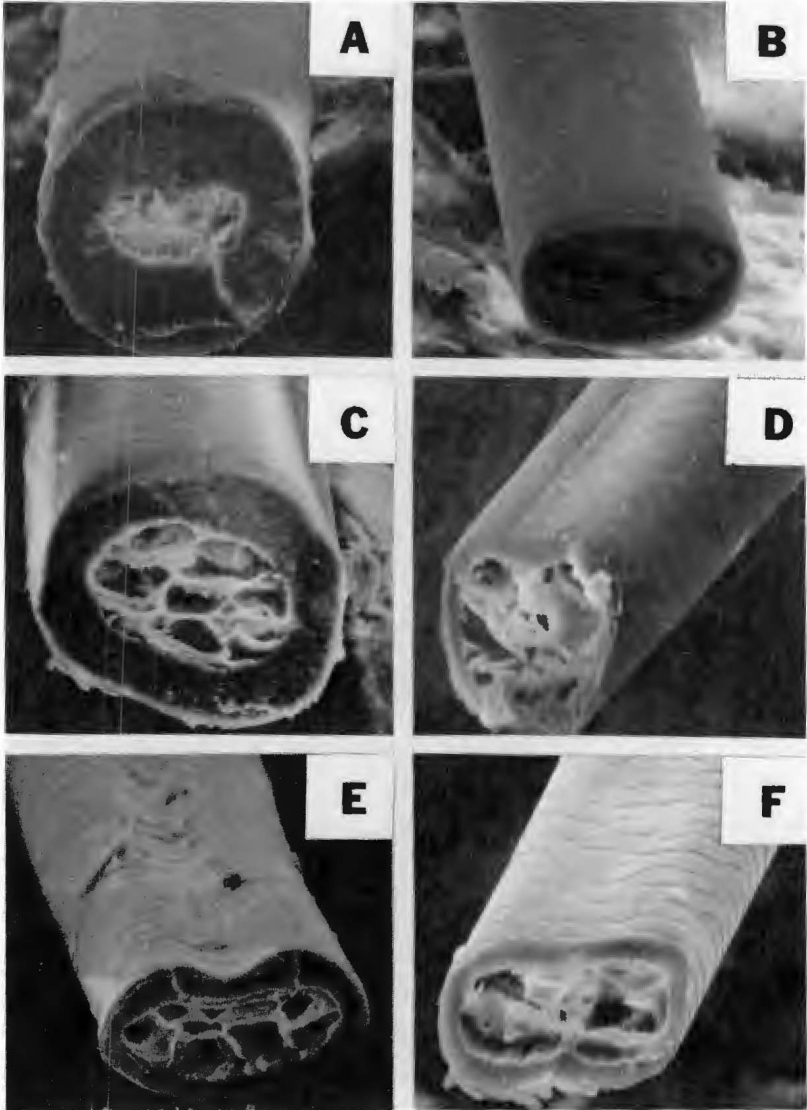


FIG. 2.—Scanning electron micrographs of cross-sectional configurations of mid-sections of guard hair bodies for select taxa: A, *Aplodontia rufa* (352x); B, *Tamias striatus* (445x); C, *Sciurus niger* (378x); D, *Sciurus aberti* (406x); E, *Tamiasciurus hudsonicus* (365x); F, *Glaucomys sabrinus* (693x).



FIG. 2 (continued).—G, *Marmota monax* (239x); H, *Cynomys ludovicianus* (347x); I, *Spermophilus tridecemlineatus* (522x); J, *Ammospermophilus leucurus* (342x); K, *Spermophilus variegatus* (177x); L, *Spermophilus lateralis* (261x).

(personal communication) related that the dyed pelages of emerging adults of *S. armatus* were soon replaced, necessitating remarking. These marks gradually disappeared at the end of the active season, the result of either a more gradual second molt (as in *S. undulatus*) or of wear. Specimens available to us did not allow determination of any seasonal dimorphism of pelage characters. Underfur of examined specimens of this subgenus is well developed, and in *S. undulatus* is incompletely roofed.

Subgenera *Ictidomys* and *Xerospermophilus*.—*Spermophilus tridecemlineatus*, *S. mexicanus*, and *S. spilosoma* of the subgenus *Ictidomys* and *S. (Xerospermophilus) tereticaudus* each molt twice annually, and exhibit the most extreme cases among the sciurids studied of seasonal pelage dimorphism. *Warm-weather pelage*: Wool hairs sparse and vestigial, occurring only as occasional sprigs at the base of some guard hairs; seasonal absence of underfur as reported for *S. spilosoma* (Williams, 1938) and *S. mexicanus* (Stangl *et al.*, 1986); guard hairs extremely short and stout and with short stalks; guard hair bodies lie flat against the integument, parallel to the body axis, providing a shingling effect. *Cold-weather pelage*: Notable elongation of guard hair stalks allows for roofing effect of underfur, which consists of numerous elongate wool hairs as in the cold-weather pelage of *Ammospermophilus*.

Subgenus *Otospermophilus*.—*Spermophilus variegatus* exhibited little seasonal variability in guard hairs, which may indicate a single annual molt. An undercoat of wool always was present, although sparse in warm-weather pelage.

Subgenus *Callospermophilus*.—*Spermophilus lateralis* exhibited the least observed variation in seasonal pelage and seasonal guard hair dimorphism of the genus, perhaps indicating a single annual molt. The dorsal guard hair troughing characteristic of the genus (and shared with *Ammospermophilus*) is not so pronounced in *S. lateralis* as in other members of the genus.

Genus *Cynomys*

Extreme seasonal pelage dimorphism in *C. ludovicianus* results from two annual molts. Tufts singly and evenly distributed; guard hairs dorsoventrally compressed, and possessed of broad, marginally well-defined, dorsal trough (Fig. 2H). *Warm-weather pelage*: Wool hairs sparse and vestigial, occurring only as occasional sprigs at the base of some guard hairs; guard hairs extremely short and stout with short stalks; guard hairs lie flat

against the integument, parallel to the body axis, providing a shingling effect. *Cold-weather pelage*: Elongation of guard hair stalk allows for roofing effect of underfur, which consists of numerous elongate wool hairs as found in *Ammospermophilus* and some *Spermophilus*; underfur completely roofed.

Genus *Sciurus*

Differences in degrees of seasonal pelage dimorphism were noted between *S. aberti* and *S. niger*. Undercoat of wool hairs always present; guard hairs of members of the genus, as figured by Mathiak (1938), Moore *et al.* (1974), and Short (1978), demonstrate a shallow dorsal groove along the narrow, elongate stalk; body typically circular in cross-section in stouter, spinelike guard hairs (Fig. 2C), but others have a shallow dorsal trough (Fig. 2D) and some dorsoventral compression; tufts singly and evenly distributed. Seasonal pelage variation was minimal in *S. aberti* for assessed characters, although the cold-weather pelage was noticeably plush. Moderate seasonal variation was noted in *S. niger*, due mostly to differences in length of guard hairs. A single annual molt is thought to characterize the genus, although Nash and Seaman (1977) cited two molts in *S. aberti*.

Genus *Tamiasciurus*

Pelage characters of *T. hudsonicus* are the same as in *Sciurus*, although troughing of some individual guard hairs was more pronounced (Fig. 2E). Variation in seasonal pelages is due to extremely abundant wool hairs that characterize cold-weather pelage. Two annual molts are reported for the genus.

Genus *Glaucomyx*

Undercoat of wool hairs always present; tufts single and arranged in tracts; guard hairs circular to elliptical in cross-section and extremely fine, with no readily defined body of the shaft; shallow dorsal concavity noted in some hairs (Fig. 2F); roofing complete. Seasonal variation was negligible for *Glaucomyx sabrinus*, more pronounced in *G. volans*. Two molts annually are thought to occur.

Coding of Pelage Characters

Pelage characters judged useful in phylogenetic analysis of the Nearctic Sciuridae are associations of hairs and guard hair morphology. These features were identified, coded, and ordered into polarity series as follows. The resulting matrix (Table 3) was

TABLE 3.—*Distribution of pelage character states of Aplodontia and Nearctic genera of Scuriidae. Taxa are coded as follows: A, Aplodontia; B, Sciurus; C, Tamiasciurus; D, Tamias; E, Marmota; F, Cynomys; G, Ammospermophilus; H, Spermophilus; I, Glaucomys. For explanation of character coding, see text.*

Character number	Taxa								
	A	B	C	D	E	F	G	H	I
1	0	1	1	1	1	1	1	1	1'
2	0	1	1	1'	1''	1''	1''	1''	1
3	0	1	1	0	0	1'	1''	1''	0
4	0	0	0	0	1	0	0	0	0
5	0	0	0	0	0	0	0	0	1
6	0	0	0	0	0	1	0	0	0

used to construct a hypothetical phylogeny (Fig. 4). Zero states correspond to the presumed primitive condition for each character. Numbered states designate conditions derived from that primitive condition. Increasingly derived conditions are designated, from primitive to most derived as follows: 0, 1, 1', 1''.

Character 1. Curvature of guard hairs to produce roofing of underfur: 0 = none, all guard hairs project beyond underfur; 1 = most guard hairs curved posteriorly, contributing to roofing effect; 1' = all guard hairs curved posteriorly, contributing to roofing effect.

Character 2. General midbody cross-section of guard hairs: 0 = circular cross-section for all guard hairs; 1 = some dorsoventral compression in most guard hairs, others circular in cross-section; 1' = elliptical cross-section for all hairs; 1'' = extreme dorsoventral compression, resulting in flattened cross-section.

Character 3. Troughing of dorsal surface of guard hairs: 0 = none; 1 = most guard hairs troughed, margins gently sloping and so not well defined; 1' = all guard hairs troughed, margins abrupt and well defined, trough broad; 1'' = as in 1', but trough narrow.

Character 4. Tuft association: 0 = tufts occur singly; 1 = tufts arranged in pairs.

Character 5. Tuft distribution: 0 = tufts evenly distributed; 1 = tufts aligned into linear tracts.

Character 6. Number of guard hairs per tuft: 0 = no more than one guard hair per tuft; 1 = more than one guard hair per tuft.

DISCUSSION

The pelage serves primarily as a thermoregulatory organ in most terrestrial mammals, although the first hairs of mammal-like reptiles or of the earliest mammals may have been tactile

structures (Ling, 1972). If this is true, such hairs logically would have projected away from the body to increase the sensory field, much as do vibrissae in extant mammals. From this situation of presumably single hairs arising from primordial follicles, it is hypothesized that a close association of two smaller follicles evolved ("primitive trio" of Ling, 1970, 1972; Lyne, 1966; Noback, 1951), corresponding to a central guard hair and two wool hairs, and initiating the development of the pelage as an insulative covering. The ease with which the pelage of *Aplodontia rufa* may be derived from the hypothetical primitive pelage is in agreement with primitive placement of the Aplodontidae (Hall, 1981; Romer, 1966; Vaughan, 1986; Walker, 1975).

Primitive Sciurid Pelage

Pelage characteristics of typical tree squirrels are least changed from the aplodontid condition, sharing the following pelage features that therefore, are, interpreted as primitive for the Sciuridae: 1) two distinct hair classes—guard and wool; 2) association of hairs into singly and evenly distributed tufts; 3) comprised minimally of a single guard hair and few to several wool hairs. A shared derived sciurid feature is the roofing of the underfur by guard hairs, made possible by the proliferation and curvature of guard hairs. The circular cross-section of guard hair bodies typical of *Aplodontia* (Fig. 2A) and of at least some of the guard hairs of tree squirrels (Fig. 2C) is considered the primitive configuration.

Troughing of guard hairs appears independently among such diverse families as the Heteromyidae (Homan and Genoways, 1978), Cricetidae (Short, 1978), Bovidae (Keogh, 1983), Leporidae (Moore *et al.*, 1974), the first-cited authors noting a probable convergence of troughing among the heteromyids. Convergent troughing similarly is judged to have occurred in the tree squirrels and ground squirrels. Troughs of the former group are distinctive in their gradually sloping margins and associations with circular (or nearly so) guard hairs (Fig. 2D-E). Those of the ground squirrels are marginally well-defined (Figs. 2H-L), and are associated with the flattened guard hairs characteristic of the clade.

Systematic Implications

The generally recognized trichotomy of Nearctic sciurids is readily definable by pelage features. When these data are

cladistically analyzed, the resulting hypothetical phylogeny (Fig. 4) is congruent in several respects with those (Fig. 3) proposed on the basis of fossil history (Black, 1963), morphology (Bryant, 1945), and biochemistry (Hafner, 1984; Hight *et al.*, 1974), although interrelationships of the three clades are obscure, and placement of the chipmunks with the ground squirrels is arguable (see discussion below).

Tree squirrels.—The view that the tree squirrel genera *Sciurus* and *Tamiasciurus* comprise the most primitive branch of the Nearctic sciurids (Black, 1963; Bryant, 1945; Emry and Thorington, 1984; Hafner, 1984) is supported by our pelage data, as these taxa essentially retain the primitive sciurid pelage. Based on skeletal morphology, Emry and Thorington (1984) remarked on the primitive nature of sciurids in general, and *Sciurus* in particular. Our data do not refute their designation of this group as “living fossils.”

Our data indicate that *Sciurus aberti* may represent a divergent taxon from the other tree squirrels. The trough is distinctly shallower than those of either *S. niger* or *Tamiasciurus*. Further evidence is the probability that *S. aberti* undergoes two annual molts.

Chipmunks.—*Tamias* is usually viewed as intermediate between the tree squirrels and more derived ground squirrels (Fig. 3), with closer affinities to the latter. Our placement of *Tamias* at the base of the ground squirrel clade is tentative, based solely on the elliptical cross-section of guard hairs. We interpret this condition as intermediate between the primitive, more rounded guard hairs of tree squirrels, and the flattened condition exhibited by ground squirrels. Chipmunk pelage is otherwise quite primitive.

Levenson *et al.* (1985) synonymized *Eutamias* with *Tamias*, an arrangement followed by many later workers (for example, Jones *et al.*, 1986). Although our data do not conflict with this placement, we note that the guard hairs of *T. striatus* appear proportionally larger than those of *T. (Eutamias) dorsalis* (Table 1). A more comprehensive assessment of chipmunk pelages may be warranted.

Ground squirrels.—The pelage of ground squirrels is highly derived, and is readily distinguished by extreme dorsoventral compression of the guard hair bodies. The polarity series of troughing within this clade is from no trough (*Marmota*) to broad trough (*Cynomys*) to narrow trough (*Ammospermophilus* and *Spermophilus*). The resulting sister-group relationship of the

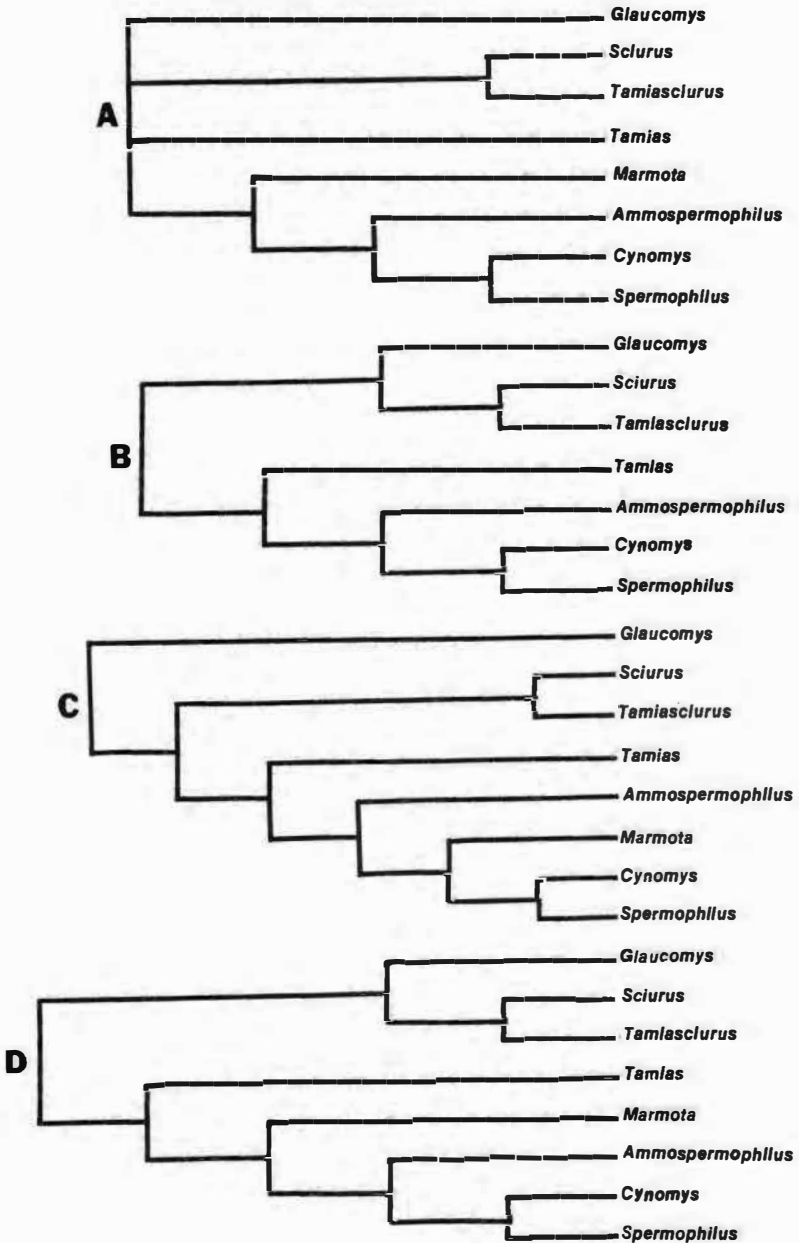


FIG. 3.—Hypothetical phylogenies of Nearctic Sciuridae, based on: A, morphology (Bryant, 1945); B, immunology (Hight *et al.*, 1974); C, electrophoresis (Hafner, 1984); and D, fossil history (Black, 1963).

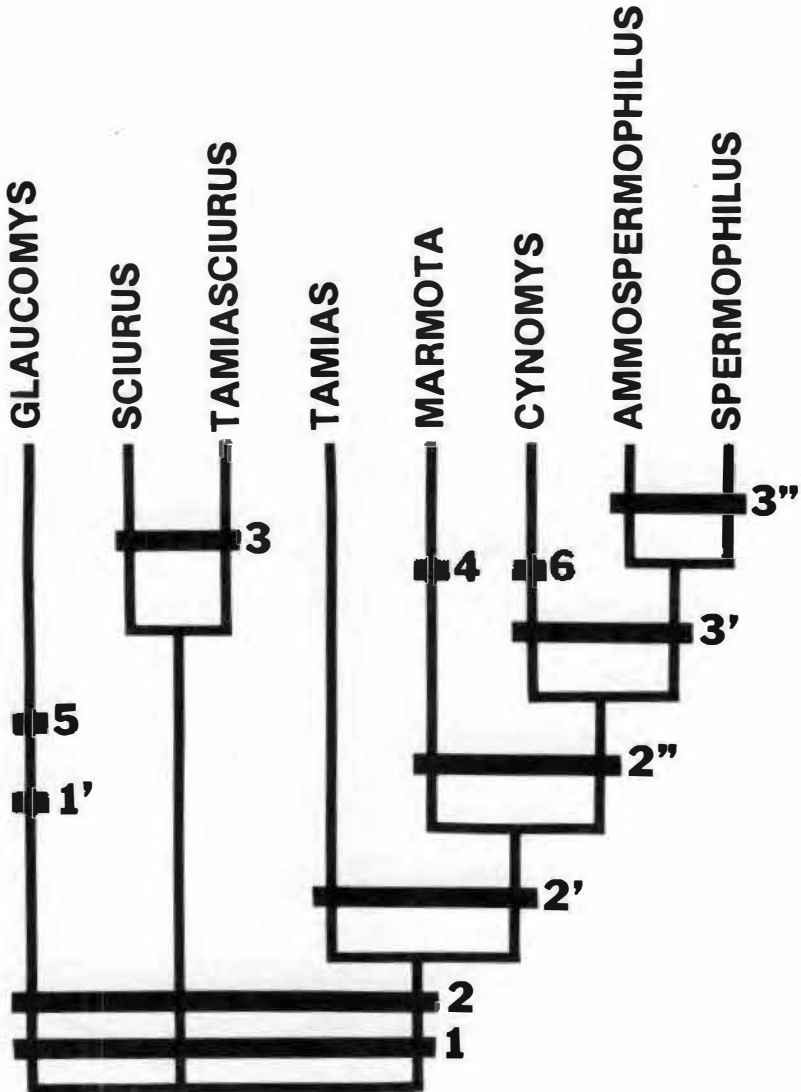


FIG. 4.—Arrangement of genera of Nearctic Scuriidae, derived from a cladistical analysis of select pelage characters. Derived character states include: 1, curvature of guard hairs; 2, midbody cross-section of guard hairs; 3, troughing of guard hairs; 4, association of hair tufts; 5, distribution of hair tufts; 6, number of guard hairs per tuft. See text for discussion.

latter two genera, based on pelage data, conflicts with previous systematic assessments. For example, *Ammospermophilus* has traditionally been viewed as a basal branch from the *Cynomys-Spermophilus* clade (Black, 1963; Bryant, 1945; Hight *et al.*, 1974) or even as basal to the *Marmota-Cynomys-Spermophilus* lineage (Hafner, 1984). Uniquely derived characters include pairing of tufts in *Marmota* (situated in tracts in *M. flaviventris*), and of more than a single guard hair per tuft in *Cynomys*.

Flying squirrels.—The highly derived pelages of *Glaucomys* present a dilemma, and our data do not offer any resolution as to their relationships with other squirrels. Other workers (Black, 1963; Hight *et al.*, 1974) supported, or at least inferred, a closer relationship to the tree squirrels than to other groups. No guard hairs project beyond the pelage as all appear to contribute to roofing of the wool layer. These hairs are fine, not regionally well-differentiated, and difficult to distinguish from wool hairs. The occurrence of the closely situated tufts into tracts, as exhibited by *Marmota flaviventris*, documents the convergence of this pattern of hair distribution.

Seasonal Pelage Variation

Considerable variation in the degree of seasonal pelage differentiation exists within the Sciuridae. The lack of detailed molting information for many species precludes incorporating such data into a systematic analysis at this time. However, we note a general trend from the more primitive pelages that are replaced but once annually and exhibit little seasonal change, to the situation of two annual molts shown by more derived taxa, which account for extreme dimorphism in seasonal pelages.

Taxa that undergo a single annual molt appear to exhibit negligible (*Aplodontia*) or minimal (*Sciurus niger* and some other squirrels) seasonal variation. Any seasonal pelage differentiation in such cases would necessarily result from loss, bleaching, or fraying of hairs, as is noted from the marmots in general, and *Marmota flaviventris* in particular. These large ground squirrels undergo a single molt, but through wear and hair attrition exhibit a markedly sparse summer pelt.

Two molts annually characterize *Glaucomys*, *Tamias*, and at least most of the ground squirrels. The apparently derived event of a second molt allows for the independent evolution of a second generation of hair follicles that accounts for the extreme seasonal

differentiation demonstrated by *Cynomys*, some *Spermophilus*, and *Ammospermophilus*, but little seasonal variation among the chipmunks.

We note that the guard hairs of cold-weather pelages typically are narrower at midbody than their warm-weather counterparts (Table 1). This is readily explained for those taxa that molt twice annually. However, this seasonal dimorphism also is noted for species known to molt but once a year. We are reluctant to speculate as to the cause of this circumstance.

Future Topics of Study

Carothers (1986, and references cited therein) noted that comparative studies revealing associations between morphological characters and common selective pressures can provide evidence for the adaptive value of those features. Ling (1970) has documented the correlation between flattening of guard hairs of carnivores from semiaquatic and marine habitats. Our study demonstrates a general association between flattened guard hairs and extreme seasonal pelage variation with a terrestrial existence. Any "performance advantage" (Carothers, 1986) of pelage characters has yet to be demonstrated, and is beyond the scope of this study. However, such data will be extremely useful in better understanding pelage biology, including documentation of any possible selective values of the pelage and its components beyond the widely recognized role of providing insulation.

Other topics deserving of study include a more comprehensive assessment of levels of pelage similarity among the species-rich subgenera of *Spermophilus* and *Sciurus*, and of Nearctic species with their Old World generic and ecological counterparts. Seasonal variation for such characters as cuticular scale and medullar patterns of hairs must be assessed for those taxa that undergo more than one annual molt. Additionally, the extent of geographic variation for any of the above pelage features has yet to be addressed.

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SPECIMENS EXAMINED

For species with two specimens listed, the first represents what is interpreted as having the warm-weather pelage and the second is representative of the cold-weather condition.

Aplodontia rufa.—MWSU 124, 15 August 1961 from Seattle, King Co., Washington; MWSU 12810, 15 January 1968 from Satsop, Greys Harbor Co., Washington. *Tamias striatus*.—MWSU 12835, 3 July 1975 from 7 mi. E Alton, Oregon Co., Missouri; MWSU 6786, 31 August 1968 from 12 mi. E Gladwin, Gladwin Co., Michigan. *T. dorsalis*.—MWSU 10107, 8 August 1972 from Bear Wallow, Santa Catalina Mountains, Pima Co., Arizona; MWSU 10108, 7 November 1965 from Bear Wallow, Santa Catalina Mountains, Pima Co., Arizona. *Marmota monax*.—MWSU 13340, 7 April 1979 from 7 mi. SW Harrison, Boone Co., Arkansas; TTU 17865, 5 September 1972 from Rice Creek, 3 mi. W Fridley, Anoka Co., Minnesota. *M. flaviventris*.—MWSU 3801, 13 August 1966 from 1.5 mi. N Wheeler Peak, Taos Co., New Mexico; MWSU 123, 30 May 1961 from 20 mi. W Creede, Mineral Co., Colorado. *Ammospermophilus leucurus*.—MWSU 12316, 19 August 1981 from 15 mi. NW Cisco, Grant Co., Utah; MWSU 2663, 14 March 1966 from 3 mi. E Dragerton, Carbon Co., Utah. *A. interpres*.—MWSU 10104, 23 July 1974 from 7 mi. E Bandera Mesa, Presidio Co., Texas; MWSU 8912, 19 February 1972 from 57 mi. E Redford, Presidio Co., Texas. *Spermophilus washingtoni*.—TTU 36302, 19 May 1972 from 11 mi. E Connell, Franklin Co., Washington. *S. armatus*.—TTU 36307, 11 June 1964 from 1 mi. E Kimball's Junction, Summit Co., Washington. *S. undulatus*.—TTU 6217, 28 July 1967 from Cape Thompson, Alaska. *S. tridecemlineatus*.—MWSU 140, 19 June 1953 from Wichita Falls, Wichita Co., Texas; MWSU 13241, 5 October 1985 from Wichita Falls, Wichita Co., Texas. *S. mexicanus*.—MWSU 6003, 12 April 1968 from 1 mi. S Seymour, Baylor Co., Texas; MWSU 9842, 17 July 1972 from 5 mi. NNW Comstock, Val Verde Co., Texas. *S. spilosoma*.—TTU 7518, 11 August 1968 from 19 mi. W Odessa, Ector Co., Texas; MWSU 12814, 19 October 1982 from 2 mi. S Lubbock, Lubbock Co., Texas. *S. variegatus*.—MWSU 178, 12 May 1963 from Llano River, 12 mi. W Junction, Kimble Co., Texas; MWSU 3600, 28 January 1967 from 10 mi. E Junction, Kimble Co., Texas. *S. tereticaudus*.—TTU 3706, 22 April 1967 from 1 mi. N Puerto Penasco, Sonora, Mexico; MWSU 13044, 16 March 1982 from Tuscon, Pima Co., Arizona. *S. lateralis*.—MWSU 6007, 27 July 1967 from 10 mi. S Red River, Taos Co., New Mexico; MWSU 5564, 10 September 1965 from 3 mi. E Red River, Taos Co., New Mexico. *Cynomys ludovicianus*.—MWSU 10627, 1 July 1967 from 25 mi. NE Childress, Childress Co., Texas; MWSU 9927, 19 January 1974 from 7 mi. W Holliday, Archer Co., Texas. *Sciurus aberti*.—MWSU 13283, 7 September 1985 from 5 mi. N South Fork, Rio Grande Co., Colorado; MWSU 12809, 15 October 1976 from Bear Wallow, Santa Catalina Mountains, Pima Co., Arizona. *S. niger*.—MWSU 10074, 8 May 1975 from Wichita Falls, Wichita Co., Texas; MWSU 10636, 3 February 1977 from Wichita Falls, Wichita Co., Texas. *Tamiasciurus hudsonicus*.—MWSU 1964, 2 October 1965 from Sheeps Crossing, White Mountains, Apache Co., Arizona; MWSU 6547, 11 November 1968 from Jackson Spring, Alpine, Apache Co., Arizona. *Glaucomys volans*.—MWSU 227, 28 April 1962 from 4 mi. S Dougherty, Murray Co., Oklahoma; MWSU 8240, 5 September 1968 from 12 mi. E Gladwin, Gladwin Co., Michigan. *G. sabrinus*.—MWSU 5985, 22 July 1967 from Elephant Back Mountain, Yellowstone National Park, Wyoming; MWSU 5873, 6 September 1967 from West Thumb, Yellowstone National Park, Wyoming.

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