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### FACTORS INFLUENCING MORPHOLOGICAL EVOLUTION OF THE LIMES IN FOSSORIAL MAMMALS (SCIURIDAE AND SORICIDAE)

By

Donald Louis Swiderski, Jr.

A DISSERTATION

## Submitted to Michigan State University in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

Department of Zoology

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### ABSTRACT

### FACTORS INFLUENCING MORPHOLOGICAL EVOLUTION OF THE LIMBS IN FOSSORIAL MAMMALS (SCIURIDAE AND SORICIDAE)

By

Donald Louis Swiderski, Jr.

Morphological evolution may be driven by selection acting on ability to function, but intrinsic traits of organisms may influence the response to selection. This dissertation examines the influences of three intrinsic traits (size, complexity and integration) on the evolution of limb morphology in fossorial (burrowing) mammals. Selection for digging ability should reduce the mobility of limb joints and increase attachment surfaces for muscles used during digging.

Qualitative differences in joint surface morphology were compared to expected directions of change inferred from the phylogenetic history of fossoriality. Deviations from expectation were compared to the distributions of size, complexity and integration to determine whether these traits had influenced either the rate or direction of morphological evolution. Quantitative morphometric methods were used in a similar analysis of scapular evolution. The morphometric approach permitted rigorous tests on the scapulae that could not be performed on the joints.

The analysis of joints found that changes consistent with increasing fossoriality are only slightly more numerous than conflicting changes. Size did not influence either the direction or rate of morphological evolution. Integration may be associated with differences in the rate of between joints in the same limb. Neither integration nor complexity were associated with changes in the direction of morphological evolution. Similarly, the analysis of the scapulae found several changes consistent

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with increasing fossoriality, but did not find a continuous series of consistent changes. There is no evidence that size or integration account for the lack of a persistent long-term trend.

These results indicate that function may predict a general direction of morphological change, but not changes in specific parts or differences between specific pairs of taxa. Also, there is no compelling evidence that restrictions imposed by size, complexity or integration account for deviations from the expected pattern of long-term morphological evolution. These three traits may still have influenced short-term patterns that could not be resolved in this dissertation. Variation in these patterns may account for the lack of a long-term trend, but other factors not examined in this dissertation may also have affected morphological evolution in these taxa.

#### ACKNOWLEDGEMENTS

I would like to thank my guidance committee (Dr. D. O. Straney, Dr. R. L. Anstey, Dr. G. Bush, Dr. A. C. Carmichael, and Dr. D. Hall) for their patience and their thoughtful suggestions. I am grateful to the following curators for loans of their specimens: Dr. A. C. Carmichael, The Museum, Michigan State University; Dr. P. Myers, Museum of Zoology, University of Michigan; and Dr. B. Patterson, Field Museum of Natural History. Dr. D. Erwin generously permitted my use of his digitizing equipment. I would also like to thank Dr. F. L. Bookstein, Center for Human Growth and Development, University of Michigan, for his time in consultation on the use of his methods and the interpretation of their results. Finally, I would like to acknowledge my wife, Miriam Zelditch for her patience, encouragement and suggestions.

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### INTRODUCTION

Evolutionary morphologists generally agree that several factors may determine the rate or direction of morphological change (Bell 1987, Cohan et al. 1989, Dullemeijer 1974, Fortelius 1985, Rensch 1959, Seilacher 1984). Among these factors are causal mechanisms that act on genotype frequencies to produce phenotypic differences between generations, including selection (Bock 1980, Cracraft 1981, Gans 1974, Simpson 1944, Van Valen 1971) and genetic drift (Bryant and Meffert 1988, Wright 1931). These causal mechanisms produce morphological evolution by determining the representation of heritable phenotypic traits in successive generations. Another set of factors are organismal properties (e.g., complexity and symmetry) which do not directly cause genetic change but may influence the phenotypic response to selection and drift (Dullemeijer 1974, Lauder 1981, Vermeij 1973). Both kinds of factors may be important determinants of morphological evolution.

There is some argument over whether development is a causal or non-causal factor in morphological evolution. Several authors (Bell 1987, Gould 1966, 1977, Livezy 1989, McNamara 1978) have stressed the role of developmental mechanisms in guiding morphological evolution. Some authors have suggested that development directly causes evolutionary change:

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"If development constrains and channels variation and imposes discontinuities in variation as well, then it is an evolutionary force in its own right and not just a contributor to the random pool of small scale variation that makes natural selection the only force of evolutionary change." (Gould 1982).

Although developmental mechanisms do cause morphological change during ontogeny, and may mold the patterns of morphological variation exposed to selection, developmental mechanisms do not directly cause genetic evolution. Because development does not act on genotype distributions, it cannot be a proximal causal factor in morphological evolution. However, the ontogenetic changes which are caused by development may influence the phenotypic expression of genetic change. Thus, developmental mechanisms can be treated as factors which may influence morphological responses to selection and drift.

The large number of factors that could direct morphological evolution suggests that no one cause or property is likely to be a complete explanation of morphological divergence between species. Potentially, each cause and each property may explain a portion of the divergence in any particular case. Therefore, a complete explanation of morphological change must incorporate all of the factors which may be involved. Unfortunately, it is not practical to include all mechanisms and all properties in a single project. The usual approach is to focus on a few of the potential factors and hope that the remaining factors will be addressed by later studies. Despite this hope, most studies have concentrated on the mechanisms which are purported to cause morphological evolution. This dissertation focusses on factors which have received considerably less attention: the intrinsic properties of organisms.

• are til integ: proper iesa i 1994) inte: norid Iner: Tae. With caré ₹£e ofte 13 <u>a</u>: 1 S', ż ż t The intrinsic properties that will be examined in this dissertation are three general characteristics of multi-element systems: complexity, integration and size. Unfortunately, clear definitions of these properties are hard to find. Morphometric studies (Bradley et al. 1989, Lessa and Thaeler 1989, Livezy 1989, Radinsky 1985, Saunders and Swan 1984) and experimental functional studies (Bramble 1989, Liem 1973, Lombard and Wake 1977, Roth and Wake 1985, Sanford and Lauder 1989) provide ample demonstration of coordinated variation and evolution among morphological traits. Some studies have tried to infer which properties underlie the observed patterns of coordination (Gould 1984, Lessa and Thaeler 1989, Wake et al. 1983), but such studies are hard to pursue without definitions of the properties. The definitions of size, complexity and integration will be examined in the following sections. The definition of shape will also be examined, because size and shape are often represented as two complimentary components of morphology.

### SIZE AND SHAPE

Traditionally, size is defined as magnitude or scale (Fortelius 1985, Thompson 1917). This is a conceptually simple definition of size and a "dimensionless" definition of shape follows naturally; however, these definitions can be difficult to apply. This definition of size suggest that morphology be analyzed in a fashion analogous to the decomposition of a vector into magnitude and direction. However, the definition does not provide clues for how morphology should be measured to permit such a decomposition.

A common approach to separating size and shape is based on estimation of covariances during growth among log-transformed distance measurements (Huxley 1932, Thompson 1917, Wright 1932). This approach utilizes principal components analysis, a statistical procedure that resolves multivariate variation into distinct, independent axes of variation (Reyment et al. 1984). Typical results of principal components analysis indicate that most variation in a population can be summarized by a single vector with which all measurements have high positive correlations (Reyment et al. 1984). This vector, the first principal component, represents Wright's (1932) general size factor, and reflects the joint responses of all measured traits to the factors affecting growth (Bookstein et al. 1985, Riska 1985). Unfortunately, the covariances of different traits with the first principal component vary, indicating variation in proportion or shape among individuals. Only when all responses to "size" are the same will the first principal component be strictly independent of shape. Variation in the coefficients on the first principal component indicates allometry, covariance of size and shape during growth (Mosimann and James 1979). Thus, principal components analysis is a method for separating growth-dependent (allometric) and growth independent shape variation, but it is not a method for separating size and shape variation.

Principal components analysis confounds size and shape because the variation of all measurements of all individuals is summarized by a small number of axes. In an alternative multivariate approach, the measurements of each individual are treated as vectors in multidimensional space (Mosimann and James 1979). The multidimensional

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resultant vector, composed of all the measurements on an individual, is partitioned into two components: a direction (shape) and a scalar (size). In this approach, size and shape are described with reference to the multivariate origin (all measurements = 0); although size and shape differences still can be described in terms of relative deviations from the mean. A similar approach has been developed by Bookstein (in press). In this approach, shape is represented by locations of points on a form, equivalent to directions to the point from a center, and size is measured by the summed absolute distances of all points from the center. The methods developed by Bookstein (in press) and Mosimann and James (1979) describe size without reference to shape, permitting size comparisons of different shapes. Both treat size and shape independently, permitting explicit tests for covariance between size and shape, and both preserve the traditional contrast between magnitude and direction.

The measurements of size proposed by Bookstein (in press) and Mosimann and James (1979) both imply that single measures of size (e.g., weight) generally are not appropriate. However, under certain circumstances, a single size measure may be justified. The following examples represent two different justifications for using weight as a size measure. In an analysis of joint surfaces (Swartz 1989), selection is hypothesized to sort morphologies of joints according to their ability to perform the weight-bearing function. In an analysis of antler and head weight (Gould 1974), selection is hypothesized to act on antler and head morphologies to minimize the load on the neck. Both examples are analyses of narrowly defined mechanical problems. Only for specific

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mechanical problems like these, is a particular single size measure appropriate.

### INTEGRATION AND COMPLEXITY

Complexity and integration refer to closely related morphological properties. There does not appear to be a consensus in the literature regarding the precise relationship between these two properties. In fact, some authors treat the two as if they were not distinct properties but converses of a single property (Simon 1962, Wicken 1979). If complexity and integration are carefully defined, however, the two properties can be distinguished.

The most commonly used measurement of complexity is the number of parts (Rensch 1959, Riedl 1978, Schopf et al. 1975). Unfortunately, the definition of "part" is unclear (Saunders and Ho 1981). At a superficial level, parts are nothing more than components of a larger whole. However, the key trait that distinguishes parts of a whole from members of a set is that parts are connected to each other. The connections are important intrinsic properties of complex structures; they are the interactions or relationships that knit the parts into a whole. In contrast, members of a set are related only by definition.

While the preceding paragraph provides a description of "part" rather than an explicit definition, it does suggest a procedure by which parts can be recognized. Because parts are connected, they will covary; because parts are separate, they will also have some unique, independent variation, as well. A covariance of zero would indicate no connection, demonstrating that the supposed parts represent different wholes; a

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covariance of one would demonstrate that the supposed parts represent arbitrary samples of an elementary structure. Thus, factor analysis or a similar procedure could be used to infer parts and wholes from patterns of variation and covariation.

The definition of "part" is only one problem produced by equating complexity with reducibility. Another problem is that parts often are connected hierarchically: they are organized into subunits such that entities treated as elementary at one level of analysis may be treated as composites at a lower level (e.g., atoms and protons are both parts of molecules). This observation of hierarchical structure should not be treated as an indication that "part" and "simple" are arbitrary, as Saunders and Ho (1981) suggest; connections and parts are not less real just because they cannot be perceived in every analysis. The observation does suggest that numbering parts is a naive way to measure complexity because parts are not connected one-to-one. Enumeration of connections also is inappropriate, because the same number of connections can be organized in different patterns. Moreover, it is the pattern of connections which determines which groups of parts will covary. Thus, complexity should be defined as the organization of connections among parts. This organization can be used to derive some measure of complexity which takes into account both the number of parts and the number of covarying groups of parts.

The observation that connection and covariation are important properties of complex structures and their parts reflects the close relationship between complexity and integration. In fact, Olson's (1953) observation that functionally related parts covary was the foundation of

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the biological study of integration. Olson and Miller (1958) subsequently developed the thesis that correlated evolution of functionally related structures should be an expected consequence of what they called "morphological integration". They described morphological integration as the interdependency of morphological traits. The heart of morphological integration is the recognition that parts of organisms are not independent, but are connected and interact during growth and development or performance of a function. The observation that parts are interdependent can be traced to Cuvier, in the early 19th century (Russell 1916).

There is some disagreement whether integration is the interaction of the parts or the covariation which results from the interaction. Resolution of this argument is crucial for any coherent discussion of the evolutionary role of integration. If integration is defined as covariance, then phenotypic integration may bear no relationship to evolutionary correlation; as quantitive geneticists point out only genetic covariances can directly determine evolutionary correlation (Atchley et al. 1981, Lande 1986, Leamy 1977). However, Cheverud (1988) demonstrated that incongruence between genetic and phenotypic covariances may indicate a poor estimate of the genetic covariances. In addition, several authors (Burger 1986, Charlesworth et al. 1982, Cheverud 1982, Learny 1977, Schmaulhausen 1949, Simpson 1944) have argued that selection on functional interactions may produce and maintain both genetic and phenotypic covariances. The practical resolution appears to be identification of morphological integration with phenotypic covariance and distinguishing the causes of phenotypic covariance as sources of

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The go complexity, Selection e expected to Torphology. integration. This resolution interprets morphological integration as a consequence of underlying causal factors (reference to these factors as functional or developmental integration is apt to be confusing and should be abandoned). These factors influence evolutionary trajectories only through their role as translators of genetic variation into phenotypic variation and covariation.

An approach similar to the resolution proposed above was developed by van der Klaauw (1945, 1948-1952) and Dullemeijer (1958, 1974). They recognize a large set of potential interactions between parts which might contribute to phenotypic covariance and coordinated evolution of parts. This approach is quite flexible: Moss and coworkers (Moss 1962, Moss and Saletijn 1969, Moss and Young 1960) analyzed the evolutionary consequences of the physical proximity of organ systems in the head; several other workers have analyzed the evolutionary consequences of changes to the mechanical connections of parts involved in a single function (Emerson 1988, Gans 1974, Liem 1973, Lombard and Wake 1977, Sanford and Lauder 1989). All these studies, like Olson and Miller (1958) exploit the distinction between the interactions of parts and the associated patterns of coordinated phenotypic change.

### OBJECTIVES

The goal of this dissertation is to examine the relationships of complexity, integration and size to the evolution of limb morphology. Selection for locomotor ability (e.g., running, digging or climbing) is expected to be one to the driving forces motivating changes in limb morphology. Other causal factors, including other selection pressures,

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may account for some of the changes in these structures, but because this dissertation focusses on the intrinsic properties, only one selection pressure is included. Patterns of functional change are inferred from comparative natural history data, interpreted in the context of current phylogenetic hypotheses. Published accounts of the mechanics of mammalian running, climbing and digging are used to predict general patterns of shape change. The particular objectives are to determine: a) whether morphological differences between species are consistent with functional divergence, and b) whether size, complexity and integration are associated with deviation of morphological evolution from the pattern of function divergence.

This dissertation examines morphological change in two clades of functionally diverse mammals: Sciuridae (squirrels), and Soricidae (shrews). In both groups, derived species of some lineages are distinguished by nesting in burrows which they excavate. All species of both lineages forage above-ground. Traditionally, animals that dig nesting burrows and forage above-ground are termed semi-fossorial to distinguish them from fossorial animals that dig foraging tunnels as well as nesting burrows. This usage of fossorial and semi-fossorial implies that semi-fossorial animals are on an evolutionary trajectory toward the completely subterranean habits of fossorial animals. However, semifossoriality does not always lead to subterranean habits, but may be a stable ecological strategy in its own right. For example, rodents of the family Heteromyidae apparently have been semi-fossorial since the Miocene, and one subfamily of heteromyids (Dipodomyinae) has remained semi-fossorial while evolving a specialized mode of terrestrial

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locamotion (Wood 1935). Hildebrand (1985) points out that the distinction between fossorial and semi-fossorial habits fosters confusion because fossorial is also used as more general term referring to all animals that dig. This usage is consistent with usage of the term fossoriality to refer to a general propensity to dig. Hildebrand suggest that fossorial be used to refer to all animals that dig burrows, that subterranean be used to indicate a specialized subgroup of fossorial animals, and that semi-fossorial be dropped. In this dissertation, I will be following Hildebrand's suggestion, and using fossorial to distinguish those species that dig tunnels from those that do not.

The sciurid lineage included in this study exhibits a general shift from arboreal tree squirrels to fossorial ground squirrels and prairie dogs. Mechanical differences between grasping and digging suggest that the joint surfaces of the limbs of ground squirrels may have diverged from tree squirrels. The mechanical differences may also be reflected in the shape of the scapula, where many shoulder muscles are attached. Another reason for expecting morphological divergence in this group is the high energetic cost of digging, which may be associated with strong selection pressures (Andersen 1988, Vleck 1979, 1981). Continuing interest in the social organization of squirrels has provided a large base of ecological and natural history data, including good documentation of the fossoriality and arboreality of many species. This, in combination with a well established phylogeny, provides a good opportunity to analyze the morphological response to a single direction of functional change.
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The Soricidae included in this study exhibit convergent transitions from terrestrial to fossorial habits. The transition from terrestrial to fossorial may be less extreme than the transition from arboreal to fossorial, but the small size and elevated metabolic rate of shrews may amplify selection pressures favoring traits that reduce energetic costs (Buckner 1964, Genoud 1988, Vogel 1976). Thus, burrowing shrews may exhibit many of the fossorial specializations found in ground squirrels. However, because shrew scapulae differ markedly from most other mammals, and because shrews lack arboreal specializations of the hindlimb found in squirrels, only shrew wrists are included in this study.

The fossorial shrews and squirrels that will be examined in this study exhibit several characteristics typical of other groups of fossorial mammals (e.g., moles and pocket gophers). These traits include: reduced external ears and tail, narrow elongate body form, broad flat claws, short limbs (Hildebrand 1985). These external features are not modified in fossorial shrews and squirrels to the extent found in moles and pocket gophers, but still provide evidence that shrew and squirrel morphology is being modified in response to increasing fossoriality. Thus, the external characteristics of fossorial shrews and squirrels support the expectation that the articulation surfaces of the joints, and the muscle attachment areas of the sciurid scapula, will be also be modified in fossorial species.

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This chapter reviews the phylogenies and natural histories of the taxa examined during this study. For both families, phylogenetic reconstructions are based primarily on biochemical and chromosomal studies; therefore, morphological and functional evolution can be analyzed without circularity. Some studies of cranial and dental morphology are also discussed, especially where relevant molecular analyses have not been performed. Cranial and dental traits are not completely independent of limb function, but the evolution of the head and limbs is usually separable enough to avoid circularity. Natural history data from the literature provides evidence of functional differences among taxa. These data include nest sites, diet and foraging sites, overwintering strategies (e.g. hoarding and hibernation) and predator avoidance behaviors. The functional differences, in combination with the phylogenetic relationships, are the empirical foundations for hypotheses of expected patterns of morphological evolution.

## SCIURIDAE

The phylogenetic relationships of the sciurids examined in this dissertation are shown in Figure 1. This study focusses on four genera of terrestrial sciurids: <u>Tamias</u> (chipmunks), <u>Marmota</u> (woodchucks), <u>Spermophilus</u> (ground squirrels) and <u>Cynomys</u> (prairie dogs). A fifth genus, <u>Annospermophilus</u> (antelope ground squirrels), is also considered a member of the same group, but was omitted from this study because their





Figure 1. Phylogenetic relationships of Sciuridae

phylogenetic and ecological relationships are poorly known. Several morphological and electrophoretic analyses indicate that the five genera constitute a monophyletic group (Black 1963, Bryant 1945, Ellis and Maxson 1980, Hafner 1984, Hight et al. 1974).

No formal taxonomic designation is available for this group of terrestrial sciurids. Simpson (1945) classified the group as a tribe, Marmotini, within the subfamily Sciurinae (which includes all sciurids but flying squirrels). Because chipmunks have many cranial and dental traits which are intermediate between ground squirrels and tree squirrels, Black (1963) removed chipmunks from Marmotini and raised them to equivalent rank as the tribe Tamiini. In the most recent analysis of the phylogeny of this group, Hafner (1984) accepted Black's classification with only minor amendments. Hafner's classification will be used in this dissertation, but it does not include a convenient term for Tamiini + Marmotini. As a group, Tamiini + Marmotini has a Holarctic distribution (Black 1963, Hafner 1984). Therefore, Tamiini + Marmotini will be referred to in this dissertation a "northern ground squirrels".

Other terrestrial or fossorial squirrels are known from Africa and southern Asia (Black 1972, Emry and Thorington 1984). Black (1972) argued that paleogeographic distributions suggest a possible relationship between some African ground squirrels and the northern ground squirrels. However, Moore (1959) had previously demonstrated that morphological traits shared by the two groups are common among most members of the family Sciuridae. No biochemical or chromosomal studies including both northern and southern ground squirrels have been performed, but Nadler and Hoffman (1970) show that the karyotype of Spermophilopsis, a close

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relative of the southern ground squirrels, is close to the primitive karyotype of the Sciuridae. This suggests that any karyotypic traits shared by northern and southern ground squirrels also may be primitive. More data are needed, but those available do not support a close relationship between northern and southern ground squirrels.

There is consensus in the literature that the northern ground squirrels are derived from tree squirrels (Bryant 1945, Ellis and Maxson 1980, Emry and Thorington 1982, 1984, Hafner 1984, Moore 1959). The main alternative view is promoted by Black (1963, 1972), who has argued that the presence of both groups in the late Oligocene of Europe suggests an intermediate, chipmunk-like, common ancestor earlier in the Oligocene. Black's argument is based on an assumption of gradual divergence of both groups from their common ancestor and an apparent lack of any sciurids before latest Oligocene. However, early to middle Oligocene tree squirrel fossils were discovered in Europe and North America during the 1970's (Emry and Thorington 1982, 1984, Vianey-Liaud 1985). These fossils bear close affinity to the tribe Sciurini, which includes the extant genera Sciurus and Tamiasciurus. In fact, only minor morphological differences distinguish these fossils from Sciurus. No other squirrels are known before the late Oligocene, and chipmunks have not been reported before early Miocene (Hafner 1984). These fossil records correspond well with times since divergence inferred from immunological distances (Ellis and Maxson 1979, 1980, Hight et al. 1974). In addition, chromosomal studies indicate that Sciurus has a primitive karyotype and that karyotypic divergences of northern ground squirrels from tree squirrels are consistent with their immunological distances

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(Nadler 1966, Nadler and Hoffmann 1970). Thus, the available data suggest that the northern ground squirrels are derived from the much more conservative tree squirrels of the tribe Sciurini.

In this dissertation, Sciurini are represented by four species of Sciurus and also by Tamiasciurus hudsonicus. Ecologically and morphologically, all five species of tree squirrels are very similar, differing primarily in body size (Moore 1959, Musser 1968). This uniformity appears to be the general case in Sciurini; the principal exceptions are associated with extreme dwarfism in some South America taxa (Hershkovitz 1969, Moore 1959, Wells and Giacalone 1985). Bacular morphology does distinguish Tamiasciurus from Sciurus (Moore 1959), and S. deppei from the other Sciurus species in this dissertation (Nitikman 1985). The karyotype of Tamiasciurus is also distinct from Sciurus (Nadler and Sutton 1967), but the immunological distance between these genera is no greater than the distances between Sciurus species (Ellis and Maxson 1980). The same studies show that S. carolinensis and S. niger have identical karyotypes and diverged less than 4 million years ago. No immunological or karyotypic data are available for S. aureogaster and S. deppei; their positions in Figure 1 are inferred from morphology, alone.

The first branch point in the phylogeny of the northern ground squirrels is the divergence of Tamiini and Marmotini (Ellis and Maxson 1980, Hafner 1984, Hight et al. 1974). The traditional classification of Tamiini recognizes three groups <u>Tamias striatus</u>, <u>Eutamias</u> (<u>Eutamias</u>) <u>sibiricus</u>, and <u>Eutamias</u> (<u>Neotamias</u>) (White 1953). However, more recent studies conflict with that classification. Immunological distances

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between the three subgenera are nearly equal (Ellis and Maxson 1979, 1980). Chromosomal studies show that the karyotype of <u>E</u>. <u>sibiricus</u> is unique (Nadler et al. 1969, 1977). Cladistic analyses demonstrate that some species of <u>Neotamias</u> possess uniquely derived biochemical or morphological traits (Levenson et al. 1985). None of these studies find any derived traits shared by <u>E</u>. <u>sibiricus</u> and <u>E</u>. (<u>Neotamias</u>). Accordingly, Nadler et al. (1977) and Levenson et al. (1985) argue that chipmunks should be classified as a single genus, <u>Tamias</u>, as originally proposed by Illiger in 1811. The phylogenetic relationships of the chipmunk species shown in Figure 1 is based primarily on Levenson et al. (1985). <u>T</u>. <u>bulleri</u> and <u>T</u>. <u>rufus</u> were not analyzed in that study; their phylogenetic positions are inferred from Callahan (1980) and Hoffmeister and Ellis (1979).

The next major branch in Figure 1 separates <u>Marmota</u> from <u>Spermophilus</u> and <u>Cynomys</u>. Fossil records and morphology of extant species indicate that <u>Marmota</u> are more closely related to <u>Spermophilus</u> than to <u>Tamias</u> (Bryant 1945, Black 1963). Extant species of <u>Marmota</u> are morphologically and ecologically similar to one another (Bryant 1945, Jones et al. 1983). Karyotypic studies indicate that the two species in Figure 1 represent the most primitive (<u>M. monax</u>) and most derived (<u>M. flaviventris</u>) members of the genus (Hoffmann and Nadler 1968).

<u>Spermophilus</u> includes more species and greater morphological diversity than any other genus of northern ground squirrels. <u>Spermophilus</u> is divided into at least six subgenera, four of which are represented in Figure 1. Karyotypes and immunological distances indicate that the subgenera <u>Otospermophilus</u> (<u>S. variegatus</u>) and <u>Callospermophilus</u>

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(<u>S. lateralis</u>) are the most primitive, least divergent from <u>Sciurus</u> (Gerber and Birney 1968, Nadler 1966). <u>Otospermophilus</u> also has the least divergent morphology (Bryant 1945), and the oldest <u>Spermophilus</u> fossils are referred to this subgenus (Black 1963). The most divergent species are found in the subgenera <u>Spermophilus</u> (<u>S. columbianus</u> and <u>S. richardsonii</u>) and <u>Ictidomys</u> (<u>S. spilosoma</u> and <u>S. tridecemlineatus</u>) (Black 1963, Bryant 1945, Nadler 1966). The subgenera <u>Spermophilus</u> and <u>Ictidomys</u> also include species that are only slightly more divergent than <u>Otospermophilus</u>. The less modified species share several traits which indicate that <u>Ictidomys</u> and <u>Spermophilus</u> are more closely related to each other than either is to another subgenus (Black 1963, Bryant 1945, Nadler 1966). Immunological distances show that <u>Otospermophilus</u> and <u>Callospermophilus</u> are as closely related as <u>Spermophilus</u> and <u>Ictidomys</u> (Gerber and Birney 1968).

<u>Cynomys</u> is the most derived genus of the northern ground squirrels (Black 1963, Bryant 1945, Nadler and Harris 1967, Nadler et al. 1971). The least modified prairie dog, <u>C</u>. <u>qumnisoni</u>, is morphologically and ecologically similar to derived species of the subgenus <u>Spermophilus</u> (Black 1963, Bryant 1945). The karyotype of <u>C</u>. <u>qunnisoni</u> shows affinities to species in three subgenera of <u>Spermophilus</u>: <u>Poliocitellus</u>, and primitive members of <u>Spermophilus</u> and <u>Ictidomys</u> (Nadler 1966, Nadler et al. 1971). Because these four karyotypes are very similar, the relationship of <u>Cynomys</u> to the subgenera of <u>Spermophilus</u> remains unresolved.

Ten natural history traits were used to determine the ecological divergence of northern ground squirrels from tree squirrels (Table 1).

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Table 1. Fossoriality of sciurids.

Key to symbols: a) burrow, b) complex burrow, c) multiple burrows
d) year-round burrow use, e) adult migration, f) hibernation,
g) hoarding, h) subterranean items in diet, i) foraging only on the
ground, m) coloniality, x) trait present, \*) trait varies among
individuals.

Single number scores are determined by counting the number of traits a-i that are present and subtracting m, if it is present. For scores spanning a range of values, the lower value is the fossoriality of an individual lacking all variable traits (x's only), the upper value is the fossoriality of an individual possessing all variable traits (x's + \*'s).

References: 1) Broadbanks 1974, 2) Elliot 1978, 3) Ferron and Ouellett 1989, 4) Garrett and Franklin 1988, 5) Jones et al. 1983, 6) Lechleitner 1969, 7) Merriam 1971, 8) Michener and Koeppl 1985, 9) Oaks et al. 1987, 10) Pizzimenti and Hoffmann 1973, 11) Rayor et al. 1987, 12) Streubel and Fitzgerald 1978a, 13) Streubel and Fitzgerald 1978b, 14) Svendson 1974, 15) Svendson 1976, 16) Tevis 1952, 17) Tevis 1953, 18) Tevis 1955, 19) Tileston and Lechleitner 1966, 20) Wiggett et al. 1989, 21) Woods 1980

Table 1. Fos

Species

Tamas stria

T. bulleri

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Table 1. Fossoriality of sciurids

Species	Traits	Score	References
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Tamias striatus	x x x * x x	5-6	2, 5, 21
T. bulleri	x x * x	3-4	6
T. amoenus	x x x x	4	1, 16, 17, 18, 21
T. rufus	* * * * *	5	6
T. ruficaudus	x * x x	3-4	1, 21
T. minimus	x x * * x	3-5	1, 5, 6, 21
Marmota monax	x x x * x x	5-6	3, 5, 7
M. flaviventris	x * x * x × x x	3-5	5, 6, 14, 15, 21
Spermophilus variegatus	x * * * * x	2-6	6, 9
S. lateralis	x x x x x x	5	6, 16, 17, 18, 21
S. richardsonii	<b>x x x * x x</b> x	6-7	5, 8, 21
S. columbianus	**** ****	7	20, 21
S. spilosoma	x x x * x x	5-6	6, 12
S. tridecemlineatus	* * * * * * * * *	8	5, 6, 13, 21
Cynamys gunnisani	x x * x	3-4	6, 10, 11, 19
C. ludovicianus	<b>x x x x x x</b>	4	4, 5, 6, 19, 21

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These traits estimate the amount of digging done by an individual animal, and may reflect selection pressures to increase digging ability. The number of traits exhibited by a species (listed as "score" in Table 1) ranks that species according to the amount of time spent digging, and is independent of the purpose of the digging. This summary representation of fossoriality is important because morphology is expected to evolve in response to the amount of digging, not the purpose of digging.

Nine of the traits in Table 1 can be grouped into three general categories: 1) size of the burrow or burrow-system (a, b and c), 2) burrow use (d - g), and 3) foraging behavior (h and i). The first two categories include direct indicators of the amount of time an animal spend on digging to provide itself with an adequate burrow system. Trait h, foraging on subterranean items, also is a direct indicator of digging time, digging time spent on foraging. Trait i, foraging restricted to the ground, is an indirect indicator of selection on digging ability; animals with this trait are more dependent on burrows than on trees to escape predators. The tenth trait (m) is coloniality. This trait has a negative score because: 1) digging may be a cooperative activity in a colonial species (Tileston and Lechleitner 1966), and 2) juveniles either inherit the maternal burrow or occupy vacant burrows in the colony to which they immigrate (Garrett and Franklin 1988, Wiggett et al. 1989). Thus, individuals in a colonial species do relatively less digging than individuals in a solitary species with otherwise similar life-history traits. Only three species in Table 1 are colonial: M. flaviventris (Svendson 1974), S. columbianus (Wiggett et al. 1989) and

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<u>C. ludovicianus</u> (Garrett and Franklin 1988, Pizzimenti and Hoffmann 1973).

Tree squirrel life-histories are used as the base-line for the rating scheme. The tree squirrels in this study have similar lifehistories (Lechleitner 1969, Musser 1968, Nixon et al. 1968) and were assigned a rating of zero. Tree squirrels are solitary and active throughout the year. They nest in trees, and forage primarily on tree products (fruit, nuts, seeds, new shoots). Tree squirrels will forage on the ground, but prefer to forage in the trees (Lechleitner 1969, Nixon et al. 1968). Ground foraging generally focusses on wind-falls but items that are not derived from trees (grasses, grains, mushrooms) may also be included in the diet. Digging by tree squirrels is rather limited, most digging is associated with hiding and recovering hoarded nuts. The caches are rarely deeper than 8 cm., and are usually located in loose soil (Lechleitner 1969).

All species listed in Table 1 live in burrows for at least part of the year (Broadbanks 1974, Jones et al. 1983, Lechleitner 1969, Pizzimenti and Hoffmann 1973, Wiggett et al. 1989). Most <u>Tamias</u> and some species of <u>Marmota</u>, <u>Spermophilus</u> and <u>Cynomys</u> have relatively simple burrows: two or three entrances connecting to a tunnel which leads to a nest chamber. The more complex burrows used by other species may have six or more openings, refuse chambers, storage chambers and a nest chamber; all connected by a network of tunnels. A few species maintain not only a complex home burrow, but also several simpler burrows which serve as temporary shelters when the animals are threatened by storms or

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predators (Ferron and Ouellet 1989, Streubel and Fitzgerald 1978b, Woods 1980).

Most species in Table 1 use a burrow all year. The exceptions are <u>S. variegatus</u> and some species of <u>Tamias</u>. These animals occupy burrows only in the winter and move to a tree nest in the summer (Broadbanks 1974, Oaks et al. 1987). This move might seem to imply more digging for these species because a new burrow usually must be dug to replace the abandoned one. However, some temporary winter burrows are simple; and residents of permanent burrows tend to remodel the burrow on a regular basis (Elliot 1978, Pizzimenti and Hoffmann 1973, Tileston and Lechleitner 1966). Consequently, excavating a new winter burrow. Also, nesting in a tree may reflect greater reliance on climbing ability when foraging or escaping from predators, which implies weaker selection pressures on digging ability.

Species that use burrows during the entire year tend to be sedentary, residing in the same burrow for the entire adult life-span. Migration of adults usually occurs only under conditions of high environmental stress due to high population density or resource depletion; but, in four species, adult migration is relatively common under less stressful conditions. These movements are important because they increase the number of burrows dug during an animal's life-span. Adult migration is most frequent in <u>M. monax</u>. This species commonly has summer dens in open fields and winter dens in more sheltered, wooded areas; and the sites chosen for these dens routinely varies from year to year (Ferron and Ouellet 1989, Merriam 1971). <u>M. flaviventris</u> exhibits

. ess site <u>S. 73</u> et al :: :: bit : spect peri <u>.</u> 3eog Rate: Hiter: ومفا fliz stric care Lech ÷.e. 9007 ::::: <u>act:</u> a: a: - -----:: **T**  less frequent seasonal shifts and is more likely to return to the same site in subsequent years (Svendson 1976). Some individuals of <u>S. variegatus</u> also undertake seasonal migrations between habitats (Oaks et al. 1987). Adult migration in <u>S. richardsonii</u> is not well understood; it is more frequent than would be predicted from environmental stress, but does not match the seasonal migration patterns exhibited by other species (Michener and Koeppl 1985).

All <u>Spermophilus</u> and <u>Marmota</u>, and most <u>Tamias</u> hibernate. However, periodic arousal is common in hibernating <u>Tamias</u>, and some species of <u>Tamias</u> and <u>Spermophilus</u> do not hibernate in the southern parts of their geographic ranges (Jones et al. 1983, Oaks et al. 1987, Streubel and Fitzgerald 1978a). <u>C. ludovicianus</u> do not hibernate; but it is unclear whether <u>C. gunnisoni</u> hibernate (Pizzimenti and Hoffmann 1973). Laboratory studies of <u>C. gunnisoni</u> have demonstrated depression and fluctuation of body temperature indicative of torpor; however, these studies and field observations indicate unusually frequent arousal compared to known hibernators (Rayor et al. 1987, Tileston and Lechleitner 1966).

All species in Table 1 rely on accumulated body fat for a portion of their winter energy requirements. <u>Marmota</u> and most <u>Spermophilus</u> accumulate enough fat that they do not require other energy sources during the winter (Jones et al. 1983, Lechleitner 1969). <u>Cynomys</u> are active during the winter and are able to supplement fat reserves with available forage (Tileston and Lechleitner 1966). <u>Tamias</u>, because of their small size and relatively smaller fat reserves, periodically rouse from hibernation to feed on hoarded nuts and seeds (Elliot 1978, Jones et

al. 1983, Spermoniti growth 15 iechiet in modie to nuts and The although generall 1978, <u>Mi</u> species to tree inverteb פיידברים al though and Ouel Spermer: diet as sibterra Several <u>s. tride</u> in its c least de <sup>forage</sup> : et al. : al. 1983, Lechleitner 1969, Tevis 1955). In <u>Tamias</u> and many <u>Spermophilus</u>, hoarded supplies are important in early spring, when new growth is still rather sparse (Elliot 1978, Jones et al. 1983, Lechleitner 1969). Some of these species also rely on stored supplies in middle to late summer, after growth has slowed but before most fruits, nuts and seeds have ripened.

The diets of most Tamias differ little from tree squirrel diets; although Tamias are more likely to eat leafy parts of plants, and generally favor grasses, forbs (herbs) and bushes over trees (Elliot 1978, Musser 1968, Nixon et al. 1968, Tevis 1952, 1953). Several Tamias species also supplement their diets with subterranean foods inaccessible to tree squirrels: root stocks, tubers, corms, fungi and fossorial invertebrates (Elliot 1978, Tevis 1952, 1953). In contrast, Marmota and Cynomys are grazers, dependent on grasses, forbs and their seeds; although C. ludovicianus does include roots in its winter diet (Ferron and Ouellet 1989, Tileston and Lechleitner 1966, Svendson 1974). Spermophilus are also grazers, but none are as strictly limited to this diet as Marmota and Cynomys. Most Spermophilus regularly include subterranean plant parts and fungi (Jones et al. 1983, Lechleitner 1969). Several species also prey on invertebrates and small vertebrates, but S. tridecemlineatus is the only species that routinely includes animals in its diet (Streubel and Fitzgerald 1978b). The Spermophilus species least dependent on grazing are the more primitive taxa which frequently forage in bushes and trees; these taxa have diets similar to Tamias (Oaks et al. 1987, Tevis 1952, 1953).

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The natural history data available for squirrels permit a relatively detailed analysis of functional evolution in this group. The traits in Table 1 were mapped onto the phylogeny shown in Figure 1, using a procedure developed by Farris (1970). This method is designed to find the most parsimonious hypothesis of character evolution, the hypothesis that requires the fewest character state transformations. In this approach, traits shared by all taxa above a branch point (node) are inferred to be present in the hypothetical common ancestor represented by that node. The latest such traits could have evolved is during the period represented by the segment immediately below the node. If the trait varies above the node, the hypothetical ancestor is assigned the character state that implies the fewest transformations above the node. If more than one solution is possible, the character state assignment is based on the most parsimonious solution for the next most inclusive set of taxa, the descendants of the hypothetical ancestor represented by the immediately preceding node. In the analysis of sciurid fossoriality, the behavioral traits listed in Table 1 were used rather than scores because scores may represent different combinations of traits.

Only one trait in Table 1, use of a burrow (a), is neither convergent nor reversed. This trait is shared by all of the northern ground squirrels and is interpreted to be a primitive characteristic of this lineage. Most of the behavioral traits have undergone multiple transformations, but have only one most parsimonious solution. Two traits have more than one equivalent most parsimonious solution: hoarding (g) and foraging only on the ground (h). There are eight combinations of solutions for g and h; and therefore, eight alternative

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The two most different interpretations are shown in Figures 2 and 3. Figure 2 shows the interpretation with the least fossorial ancestors; Figure 3, the interpretation with the most fossorial ancestors. Both trees indicate moderate early divergence from tree squirrels by the common ancestor of Tamiini and Marmotini, including acquisition of a permanent burrow (a, d) and hibernation (f). Four traits have widely scattered distributions suggesting each has arisen several times since the divergence of the terminal taxa: multiple burrows (c), adult migration (e), subterranean items in the diet (i), and coloniality (m). Consequently, both trees suggest that most evolution of fossoriality has occurred independently, since the divergence of the terminal taxa. These trees also suggest that the evolutionary trend in Tamias is toward greater flexibility, rather than a commitment to either fossoriality or arboreality; a similar transition is seen in S. variegatus. There may also be behavioral flexibility in M. flaviventris, but this probably reflects variable social organization rather than fluctuation between fossorial and arboreal habits.

The least fossorial ancestors interpretation (Figure 2) adds little to the common pattern just outlined. Hoarding (g) and foraging only on the ground (h) characterize genera or subgenera, so there are small increases in fossoriality as the Marmotini diversify. The only place where fossoriality increases along the basal lineage is the segment leading to the common ancestor of prairie dogs and derived ground squirrels. In Figure 3, the most fossorial ancestors interpretation,



Figure 2. Phylogeny of sciurid natural history traits, I. Symbols for traits as in Table 1. (-) indicates loss of a trait. (+/-) indicates transition to variable trait.

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Figure 3. Phylogeny of sciurid natural history traits, II. Symbols for traits as in Table 1. (-) indicates loss of a trait. (+/-) indicates transition to variable trait.
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The two most extreme interpretations of functional evolution are only slightly different, which permits formulation of a general hypothesis of morphological evolution. If morphological evolution is determined by increasing fossoriality, the phylogenetic distribution of morphological changes can be predicted from Figures 2 and 3. Both figures indicate that most morphological changes should be convergent, occurring independently during the divergence of each individual species. There should also a relatively large number of changes during the divergence of the northern ground squirrel lineage from tree squirrels. A few traits may distinguish groups at intermediate taxonomic levels, but the relative numbers of changes characterizing intermediate groups are difficult to predict.

## SORICIDAE

Based on morphology, physiology and geographic distribution, extant shrews are divided into two subfamilies: Soricinae and Crocidurinae (George 1986, Repenning 1967). Because the Soricinae have a Holarctic distribution, they have been studied more extensively than the more southern Crocidurinae. Consequently, the phylogenetic and ecological relationships of the Soricinae are better known, although many species are still poorly understood. Because the Soricinae are better known, most of the shrew species in this dissertation are from that subfamily;

the C <u>....</u> show 1988 m 222. cf 199 77 5 2 D C the Crocidurinae are represented by <u>Crocidura horsfieldi</u> and <u>Suncus</u> <u>murinus</u>.

The phylogenetic relationships of the shrews used in this study are shown in Figure 4. Relationships among genera and within <u>Sorex</u> are based primarily on cladistic analysis of electrophoretic studies (George 1986, 1988). Relationships among <u>Cryptotis</u> species are inferred from morphometric and dental traits (Choate 1970). Although there is considerable argument about the shrew phylogeny, the relative positions of the species shown in Figure 4 appears to be stable (Catzeflis et al. 1982, Frykman and Simonsen 1984, George 1988, van Zyll de Jong 1982).

The primitive characteristics of shrews, the traits shared by their most recent common ancestor, cannot be inferred readily. Shrews are smaller than most mammals, and have more delicate skeletons. As a result, the fossil record for shrews is poorer than the record for most mammals; postcranial elements are especially rare (Repenning 1967). Consequently, the primitive locomotor habits of Soricidae cannot be inferred from fossils. Because of their cryptic habits, the natural history data on shrews are sparse and poorly corroborated, and some extant shrews are only slightly better know than fossil species (Choate 1970, Hutterer 1985). This limited amount of natural history data cannot resolve degrees of fossoriality. Therefore, in this dissertation, shrews are only divided into fossorial and terrestrial groups.

External morphology and available behavioral observations indicate that most shrews are terrestrial, foraging primarily on the surface or just below the leaf litter (Hutterer 1985). This majority indicates that the primitive common ancestor of shrews probably also was terrestrial.

Figure 4 fossoria



Figure 4. Phylogenetic relationships of Soricidae. f) indicates fossorial lineages.

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However, the determination that the primitive habit was terrestrial does not lead immediately to a model or description of the primitive morphology. There are a variety of foraging strategies among terrestrial shrews, and terrestrial shrews are found in many different habitats (Buckner 1966, Genoud 1988, Larochelle and Baron 1989, Sharma 1958). Variation in limb length and external hand morphology (Hutterer 1985) indicates at least the possibility of shape variation in the limb skeleton, as well. Given the large amount of variation present, one species cannot be chosen as the most likely representative of the primitive morphology. Therefore, several species of terrestrial shrews were used in this study, including two representatives of the Crocidurinae.

The analysis of shrews, like the analysis of squirrels, focusses on the divergence of fossorial species. Several genera are thought to include fossorial species, but only <u>Blarina</u> and <u>Cryptotis</u> appear to constitute an extended lineage of fossorial species: the tribe Blarinini. Field observations confirm that <u>Blarina brevicauda</u> and <u>Cryptotis parva</u> nest below the surface and dig their own tunnels, although both will take advantage of abandoned mole and chipmunk tunnels (George et al. 1986, Merritt 1986, Whitaker 1974). The other two species of <u>Cryptotis</u> in this dissertation seldom have been observed alive, but their morphological similarity to <u>B</u>. <u>brevicauda</u> indicates that they also are probably fossorial (Choate 1970). Two species of <u>Sorex</u> also are inferred to be fossorial: <u>S</u>. <u>fumeus</u> nests underground and is most frequently found underground (Hamilton 1940) and <u>S</u>. <u>araneus</u> feeds primarily on fossorial prey (Butterfield et al. 1981, Pernetta 1976). Because Blarinini,

<u>S. fumeus</u> and <u>S. araneus</u> are distantly related, and phylogenetically intermediate taxa are not fossorial, the fossoriality of these three taxa is probably convergent. Therefore, the three groups are expected to have independently derived modifications of wrist joint morphology.

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# GENERAL ANATOMY

This chapter reviews the anatomical structures examined during this dissertation. The description of the wrist includes both squirrels and shrews; descriptions of other joints and the scapula address only squirrels because these structures were not analyzed in shrews. Each description is deliberately broad, encompassing the range of variation in the taxa studied. The descriptions of joints primarily address arrangements of bones and shapes of articulating surfaces. Some characteristics of ligaments and muscles that are important for understanding joint mobility also are included, but ligaments and muscles generally are not treated in detail. The description of the scapula includes both the shape of the bone and general information about the positions and functions of muscles attached to the scapula.

## WRIST

In squirrels, eight bones articulate between the radius and ulna and the metacarpals. Seven of these bones, the carpal bones, are arranged in two rows (Figure 5a); the eighth is a sesamoid bone, the pisiform, which articulates with the ventral surfaces of the triquetrum and ulna. Another sesamoid bone, the falciform, articulates only with the ventral surface of the scapholunar. Because the falciform articulates only with the scapholunar, it is not part of the chain of articulations connecting the forearm and hand.



A) Sciur

<sup>Figure</sup> 5 figures







Figure 5. Arrangement of wrist bones in squirrels and shrews. Both figures are left wrists in dorsal view.

triq into and proj lıga uina cen: S1.7 e!!; The for bet Pro Sca cra POS inte Tec 5:17 1 : Prox tidg ъc. The proximal row of carpal bones includes the scapholunar and the triquetrum. The scapholunar has a convex, ellipsoidal surface that fits into an ellipsoidal cup at the distal end of the radius. The triquetrum and pisiform form a small socket which receives the narrow distal projection of the ulna. The osseous socket is open laterally, but a ligamentous band completes the socket. The shapes of the socket and ulnar tip are more variable than the radius and scapholunar surfaces.

The distal row of carpal bones includes the trapezium, trapezoid, centrale, capitate and hamate. All distal carpals except the hamate have simple, nearly flat proximal surfaces that combine to form a continuous ellipsoidal surface articulating with the distal scapholunar surface. The medial portion of the hamate may contribute to the combined surface formed by the other distal carpals, but most of the hamate occupies a gap between the ventral margins of the triquetrum and scapholunar. A lateral process on the hamate follows the dorsal edge of the triquetrum. The scapholunar and several of the distal carpals have ventral processes that cross the intracarpal joint. These processes combine with the hamates position between the scapholunar and triquetrum to produce an interdigitation of the proximal and distal carpals.

There are five metacarpals in squirrels. Metacarpal 1, at the medial end of the series, is rudimentary and articulates with the medial surface of the trapezium. Articulating with the distal end of metacarpal 1 is a rudimentary digit that is functional only in prairie dogs. The proximal surfaces of metacarpals 2-5 form a series of dorso-ventral ridges and grooves. This morphology is formed by both the shapes of the individual surfaces and the relative positions of the metacarpals. The

÷ 51 **;**: W. ċ 0 De ģ; Ņ s .71 2 . ċ . 3 2 distal carpals articulating with metacarpals 2 and 3 have relatively simple distal surfaces that correspond to small parts of the ridge and groove complex. The trapezium also has a ledge along its dorsal margin which extend distally over the dorso-medial surface of metacarpal 2. The distal surface of the hamate is more complex than the surfaces of the other distal carpals because the hamate articulates with several metacarpals: 5, 4, and part of 3. The lateral portion of the ridge and groove complex is more rounded and has less relief than the medial portion.

Shrews have the same basic arrangement of wrist bones as squirrels (Figure 5b). The most important difference is that the first digit of shrews is functional and metacarpal 1 is about the same size as metacarpal 5; the orientation of metacarpal 1 in shrews is also roughly parallel to the other metacarpals. The trapezium, which articulates with metacarpal 1. is also more similar in shape and position to the other distal carpals; having a block-like shape and a position between metacarpal 1 and the scapholunar rather than between metacarpals 1 and 2. Another important modification in some shrews is fusion of the proximal carpals. Most shrews, like squirrels, have a scapholunar formed by fusion of the scaphoid and lunate. In some shrews the scaphoid and lunate remain separate. In other shrews the scaphoid, lunate and triquetrum all fuse into a single element. Shrews lack an independent centrale; the shape of the scaphoid and the position of the centrale in other mammals suggests that the centrale is fused to the scaphoid (Yalden 1966, 1972). Shrews also lack a falciform. All of these differences are relatively minor; none of them change the overall organization of the

wist. the wr joints arrang fancti net d er:vel adjac relat toge te <u>di s</u> at i ŤΞ. car ca 1 (d 20 i <u>د</u> wrist. The similarities are more profound and allow comparisons between the wrists of shrews and squirrels.

The organization of the wrist suggests that it functions as three joints: carpal-antebrachial, intracarpal and carpal-metacarpal. The arrangements of ligaments and muscles also indicate that the wrist may function as three joints. In shrews, individual ligaments generally are not differentiated. Instead, there appears to be a ligamentous sheath enveloping the entire wrist and additional ligamentous bands between adjacent bones in each row. The bands within rows permit little or no relative movement of bones in that row. The metacarpals are also bound together, as are the radius and ulna. Consequently, the only movement in the wrist is between rows. In squirrels, individual ligaments do differentiate, but the bones in each row remain tightly bound, especially at the ventral edges. This organization of the wrist into three functional joints appears to be common among mammals (Yalden 1970, 1972).

The muscles do not reflect the three divisions of the wrist as completely as do the ligaments. Muscles either insert on the proximal carpals (or the sesamoids articulating with the carpals) or extend beyond the carpal-metacarpal joint to insert on the metacarpals or phalanges (digits). No muscles insert on the distal carpals.

## ELBOW

The elbow is formed by the humerus, radius and ulna (Figure 6). In sciurids, the articular surface of the humerus can be divided into two distinct regions: a rounded groove (trochlea) that articulates with the ulna, and an ellipsoid ball (capitulum) that articulates with the radius.



Figure 6. Articular surfaces of the left elbow of <u>S</u>. <u>carolinensis</u>, in cranial view. Humerus is separated to show the surface of the ulna. Articular surfaces are stippled.

The corresponding surfaces are the saddle-shaped trochlear notch on the dorsal surface of the ulna, and a shallow cup on the head of the radius. Ligaments connecting these three bones prevent dislocation of the elbow by tensile forces that might be incurred when hanging vertically or digging. These ligaments do not limit the range of motion at the elbow; apparently, movement is restricted by the shapes of the bones and the amount of muscle surrounding the joint.

#### KNEE

The knee is formed by the femur and tibia (Figure 7). The sciurid femur has two nearly cylindrical condyles which articulate with shallow concave pads on the tibia. Articular surfaces on the femur and tibia have nearly complimentary curvatures in caudal view (Figure 7a), but in lateral view (Figure 7b) the shapes clearly are not complimentary. In life, two crescentic cartilages are present between the two bones. The cartilages open toward the fossae between the paired condyles of the two bones, and ligaments connect the horns of the crescents to the fossa of the tibia. The femur and tibia are in direct contact at the open centers of the cartilages. These cartilages provide complimentary surfaces for the femur and tibia, and may absorb some of the stress loading on the ends of the bones. The cartilages and the ligaments attached to them probably also help keep the femur in place on the tibia, but apparently do not interfere with the range of motion at this joint. Additional ligaments between fossae, and connecting medial or lateral edges prevent disarticulation of the knee by tensile or shear forces. The volume of muscle around the knee also limits the range of motion.



Figure 7. Articular surfaces of the right knee of <u>S</u>. <u>carolinensis</u>. Both views are shown with the knee flexed in a typical standing posture. Articular surfaces are stippled.



Figure 8. Arrangement of ankle bones in <u>S</u>. <u>niger</u>. Tibia and fibula are shown folded back to expose articular surfaces and the relative positions of the astragalus and calcaneus.

С

#### ANKLE

Sciurids have seven tarsal bones between the tibia and fibula and the metatarsals (Figure 8). Unlike the carpal bones of the wrist, the tarsal bones do not form distinct rows. The astragalus articulates dorsally with the tibia and fibula, ventrally with the calcaneus, and distally with the navicular. The calcaneus articulates distally with the cuboid. The cuboid articulates directly with metatarsals 4 and 5, but the navicular is connected to metatarsals 1-3 through the cuneiforms.

The arrangement of both muscles and ligaments reflect the overlapping arrangement of the bones. Muscles acting across the ankle either insert on the calcaneus, or extend beyond the midtarsal joint. Ligaments bind the tibia and fibula, preventing movement between these two bones. Because the fibula is much smaller than the tibia, the distal end of the fibula functions as the lateral wall of the tibial socket. Ligaments also bind cuboid, navicular, cuneiforms and metatarsals. Relative movement of these bones appears to be limited to some flattening of the arch and possibly some fanning of the metatarsals. Ligaments extend from the tibia and fibula to both the astragalus and calcaneus. Additional ligaments connect the calcaneus and astragalus to each other. The ligaments among these four bones prevent dislocation, but the ranges of motion of calcaneus and astragalus are limited primarily by the shapes of the bones. There are no ligaments between the astragalus and the distal tarsals; but the calcaneus is connected to both the cuboid and the navicular. These ligaments play an important role in limiting movement of the distal tarsals relative to the calcaneus.

mor ini Sza :::: tte i. <u>i</u>e je: the in. Se ÷ <u>k:</u> Ŀ ay: 51 **.**.... ಂದ SIZ Ľ.e Despite the overlapping arrangement of bones, the distinct morphologies and orientations of the mobile articulation surfaces indicate that the ankle functions as three joints (Lewis 1980a, 1980b, Szalay 1985). The first joint is the upper ankle joint, formed by the trochlear surface of the astragalus and a saddle-shaped socket on the tibia. The second joint is the lower ankle joint, formed by trough on the ventral surface of the astragalus and an elevated, sloping surface on the calcaneus. A second flat area on the calcaneus provides support for the medial side of the astragalus. The third joint is the midtarsal joint, formed by the distal surfaces of the astragalus and calcaneus and the proximal surfaces of the navicular and cuboid. These surfaces vary in shape from spherical to ellipsoidal.

#### SCAPULA

The main portion of the scapula is a nearly flat, triangular to semicircular blade (Figure 9). The lateral surface of the blade is divided into two fossae by a dorso-ventral ridge, the spine (Figure 9a). At its caudal edge, the blade turns laterally to form an axillary ridge. In some taxa, the blade extends caudally beyond the dorsal end of the axillary ridge, forming the teres fossa. The ventral end of the spine supports a broad, caudally directed, triangular metacromion process and a narrower, cranioventrally directed acromion process, which articulates with the clavicle. In sciurids, the metacromion and acromion are continuous, but they are more distinct in other mammals. The medial surface of the scapula, the subscapular fossa, is partially divided by the subscapular ridge (Figure 9b). The ventral expansion of the scapula



Figure 9. Scapular morphology of <u>S</u>. <u>carolinensis</u>.

C é has an ovoid socket, which articulates with the humerus. A small coracoid process arises near the socket and extends caudomedially.

All of the muscles attaching to the scapula have several functional roles; the functions described below are the primary roles these muscles play during locomotion and digging. These functions are likely to be the focus of selection on digging ability, and also represent the main sources of stresses loading on the scapula. Thus, the functions described below are expected to be the primary factors driving evolution of the scapula.

Muscles attaching to the scapula can be divided into three functional groups. The first group are muscles attaching the scapula to the trunk; including the rhomboideus, trapezius and serratus muscle groups. These muscles attach along the dorsal margin of the scapula and along the spine. The primary functions of these muscles may be to stabilize the scapula and to transmit ground reaction forces to the trunk, but they may also shift the scapula to provide a better mechanical position for muscles acting across the shoulder (Badoux 1974, Hildebrand 1985, Jenkins 1974). The second group of muscles extend from the scapula to the humerus. This group includes three sets of muscles: 1) the fan-shaped supraspinatus, infraspinatus and subscapularis, named after the fossae they occupy; 2) the deltoid muscles occupying the acromion and metacromion; and 3) the teres muscles occupying the teres fossa and axillary ridge. Muscles anterior to the spine pull the limb forward for the next step, muscles posterior to the spine pull the limb back during the propulsive phase of the step (Roberts 1974). These roles are essentially the same during digging; dirt is moved instead of the animal

(Hildebrand 1985, Lehman 1963). Because the limb is partially flexed (folded) in the normal posture of small mammals, muscles anterior to the spine also play an important role in weight-bearing (Jenkins 1974, Roberts 1974); this load is especially large when climbing head-first down a tree trunk (Taylor 1974). The third group of muscles primarily act across the elbow. The main portions of these muscles are found distal to the shoulder joint, but some divisions attach to the coracoid and axillary ridge near the articular surface.

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In both shrews and squirrels, phylogenetic distributions of natural history traits indicate evolutionary transitions toward more fossorial behavior in some lineages. Increasing fossoriality is expected to drive morphological evolution because digging requires extremely large forces (Hildebrand 1985) which are energetically expensive to generate (Vleck 1979). Morphological transformations commonly associated with fossoriality include increases in muscle mass and bone thickness to generate and transmit the forces required for digging, and decreased bone length and shifts in muscles attachment sites to improve leverage and reduce the cost of digging (Hildebrand 1985, Lehman 1963, Taylor 1978). The primary goal of the study presented in this chapter is to determine whether the articulation surfaces of limb joints also are modified during the evolution of fossoriality.

The shapes of articulation surfaces are expected to evolve with function because articulation surfaces directly determine the directions in which movement can occur. For example, spherical surfaces will have the greatest directional freedom, permitting rotation as well as bending in any direction, but tongue-in-groove arrangements (spline, trochlea) prevent rotation and only permit bending in the direction of the matched ridge and groove. Thus, the shapes of articulation surfaces set limits on the movement of distal limb segments.

Studies on primates and carnivores have demonstrated that the joints of arboreal species usually permit greater directional freedom of movement than the joints of their terrestrial relatives. The relative

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Demonstration that changes in articulation surfaces are causally linked to the evolution of fossoriality requires more than comparison of morphologies across levels of fossoriality. The functional and morphological transformations must be considered in their phylogenetic context. Because lineages evolve independently, taxa cannot be treated as samples drawn from the same distribution (Felsenstein 1985). Instead, patterns of functional and morphological transformation must be inferred

from phylogenetic relationship (Felsenstein 1985, Lauder 1981). Then, hypotheses of form-function relationships can be tested by analyzing the congruence of functional and morphological transitions (Schaefer and Lauder 1986).

The secondary goal of this study is to determine whether size, complexity or integration are responsible for deviations of morphological evolution from the pattern predicted by the evolution of function. Body size may be linked to the rate of morphological evolution by metabolic rate. Small size is generally associated with elevated metabolic rate; the metabolic rates of shrews are especially high (Buckner 1964, Genoud 1988, Vogel 1976). High metabolic rate is expected to amplify selection pressures to reduce energetic costs (Genoud 1988). Therefore, within both shrews and sciurids, small species should have more changes than large species at the same level of fossoriality. The elevated selection pressure associated with small size could also lower the frequency of morphological changes that are not consistent with increased fossoriality. The stronger energetic constraint may lower the tolerance for morphological changes that do not contribute to digging ability.

The affects on morphological evolution of integration and complexity are each dependent on the other. Complex unintegrated structures are expected to have large numbers of changes because each part may have several alternate states and the realized state of one part is independent of the state of another part (Vermeij 1973). Simpler unintegrated structures should have fewer changes because there are fewer potential combinations of changes. For joints of equivalent complexity, integration should influence both the rate and direction of morphological
change. Integration may be linked to the rate of morphological evolution because changes to the integrated structures must be coordinated (Emerson 1988, Lauder 1981, Vermeij 1973). In effect, selection acts on the parts of an integrated structure as though they comprise a single unit. The requirement for coordinated change is expected to limit the rate of change unless a similar pattern of genetic or developmental integration organizes the response to selection (Burger 1986, Vermeij 1973, Wagner 1988). Integration may also bias the distribution of morphological change by inhibiting some types of changes more than others (Burger 1986, Emerson 1988, Wagner 1988). Thus, integration may also affect the frequency of morphological changes that are not consistent with increased fossoriality. Among integrated joints, complexity is expected to increase the inhibitory effects of integration: if more bones are integrated, more simultaneous changes will be required (Emerson 1988, Lauder 1981, Vermeij 1973). Thus, complex joints will have more changes than simple joints only if the complex joints are not integrated. If the complex joints are integrated, they will have fewer changes than simple joints.

## METHODS

Anatomical differences were described from dry skeletal preparations and fluid preserved specimens. Camera-lucida drawings of articulated skeletons were compared to determine differences in the number and arrangement of bones. Camera-lucida drawings of articulation surfaces were prepared after dissection. These drawings provided the basis for qualitative comparisons of joint surfaces.

Fresh-caught representatives of selected taxa also were included to determine whether observed structural differences affect the mobility of joints. Manipulation of fresh-caught specimens during dissection also provided data on the influence of soft tissues on the mobility of joints. Limits on movement remaining after soft tissues were removed are attributed to the articulation surfaces.

This study includes all of the shrew species shown in Figure 4 and most of the squirrel species shown in Figure 1. The species not available for this analysis are: <u>S. aureogaster</u>, <u>S. deppei</u>, <u>T. rufus</u>, <u>S. variegatus</u>, and <u>S. richardsonii</u>. Because systematic collections of mammals emphasize variation of skulls and skins, limb skeletons, especially distal elements, are not preserved for most specimens. Consequently, fewer than six individuals were available for most species. Sample sizes for each species are given in Appendix A.

Morphological traits were mapped onto the phylogenies shown in Figures 1 and 4, following the same procedure used for the natural history traits. The procedure used was developed by Farris (1970) to find the most parsimonious hypothesis of character evolution, the hypothesis that requires the fewest character state transformations.

Two tests were used to evaluate the hypothesis that morphological transformations are determined by functional transitions. One test was simply to compare the observed morphological changes to the predicted morphological changes inferred from the functional transitions. The second test was Spearman's rank order correlation coefficient (r.). For this test, cases are ranked according to their scores on two different variables. Ties are given the median rank (three cases tied for second

all would be ranked third). The value of  $r_{p}$  is based on the sum of squared differences between the ranks and the number of cases, and the significance of  $r_{p}$  can determined from standard statistical tables (Snedecor and Cochran, 1967). This test was used to determine whether the number of morphological differences between taxa could be predicted from the number of functional differences.

The use of rank order correlation is necessary because numbers of changes, morphological or functional, are not continuous measured variables. Also, there is no <u>a priori</u> reason that they should be normally distributed (Felsenstein 1985). The fossoriality scores of sciurids clearly are not normally distributed (Table 2). Therefore, statistical tests that require normal distributions of variables are not valid. Rank order correlation is used it does not require normal distributions.

Rank order was also used to examine the influences of size, integration and complexity on the rate and direction of morphological evolution. The preferred approach to inferring integration and complexity is to identify patterns of covariation within species. This approach cannot be used with the sample sizes available for this dissertation. Adequate sample sizes, especially for the distal limb joints, are unlikely to be available for any mammals that are not routinely maintained in lab colonies. For this dissertation, integration is inferred from the complementarity of the articulation surfaces and coordination of changes to both sides of the joint. Complexity is inferred from the arrangement of bones, particularly, which bones articulate at a joint. A seven bone joint (the intracarpal joint of the

Table 2.Sciurid species ranked by behavioral divergence from treesquirrels.Fossoriality scores are taken from Table 1.

Fossoriality	Rank
Score	

<u>S. tridecemlineatus</u>	8	1
<u>S. columbianus</u>	7	2
<u>S. spilosoma</u>	5-6	4
M. monax	5-6	4
<u>T</u> . <u>striatus</u>	5-6	4
<u>S. lateralis</u>	5	6
<u>C. ludovicianus</u>	4	8.5
<u>M. flaviventris</u>	3-5	8.5
T. minimus	3-5	8.5
T. amoenus	4	8.5
<u>C. gunnisoni</u>	3-4	12
<u>T. bulleri</u>	3-4	12
T. <u>ruficaudus</u>	3-4	12

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wrist) is more complex than a two bone joint (the knee). To analyze the influences of complexity and integration, joints were classified as integrated or unintegrated and ranked by complexity, the number of morphological changes, and the proportion of changes consistent with the expected direction of morphological change. Neither complementarity of articulation surfaces, nor the arrangement of bones vary in squirrels, therefore, the effects of complexity and integration on sciurid evolution will only be evident in comparisons between joints. The effect of size was examined by ranking taxa by body weight, number of morphological changes, and the proportion of changes consistent with functional predictions.

## DESCRIPTIONS OF MORPHOLOGICAL CHANGES

## Soricidae

Shrew wrists exhibit only two transformations, and these only occur in the Blarinini. Blarinini are the only shrews in this study with fusion of all of the proximal carpals (Figure 10). However, this change may have little functional significance because ligaments prevent independent movement of the proximal carpals of other shrews. The second transition is from a distinctly ellipsoidal scapholunar surface to a nearly spherical surface (Figures 11a and 11b). This change is accompanied by the addition of shelf in the socket of the radius (Figures 11c and 11d). This change also has no effect on wrist mobility; the articulation surfaces of the ulna, triquetrum and pisiform limit movement to flexion and extension in all shrews. There is some variation in the curvature of the ulnar styloid and its socket, but they retain the same

Fig



Figure 10. Left wrist of <u>Blaring</u> in dorsal view.



Figure II. Antebrachial-carpal joint changes in shrews. A and C are <u>§. cinereus</u>; B and D are <u>B. brevicauda</u>. P-pisiform, R-radius, S-scapholunar, T-triquetrum, U-ulna, d-dome, sh-shelf, so-socket. Ventral is up in A and B; right in C and D. All four are from the left manus.

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Figure 12. Distal wrist joints of shrews. A) intracarpal; proximal carpals folded under distal carpals. B) carpal-metacarpal; distal carpals folded under metacarpals. S-scapholunar, T-triquetrum, g-groove, r-ridge.

basic shape in all shrews. The intracarpal and carpal-metacarpal joints of shrews exhibit some variation in relief, but are characterized by dorso-ventral grooves that limit mobility to flexion and extension in all species (Figure 12).

The morphological changes in the wrists of blarinine shrews have little if any functional significance. Fusion of the proximal carpals functions as reinforcement of ligaments that prevent relative movement among these bones in other shrews. Modification of the articular surfaces between the radius and scapholunar reduces the ability of these surfaces to prevent rotation at the antebrachial-carpal joint; but the surfaces of the ulna, triquetrum and pisiform retain morphologies that prevent rotation. Consequently, the changes in the radius and scapholunar do not appear to have any affect on wrist mobility; mobility is still restricted by the ulna and triquetrum. Thus, neither change in wrist morphology represents a modification of wrist mobility; these changes only represent reduction of the number of structures preventing deviations of the digging stroke. These changes may simply represent changes in safety factors.

## <u>Sciuridae</u>

Knee morphology varies little among tree squirrels. The variation is generally limited to the outlines of the tibial condyles and the heights of their interior ridges. The ranges of variation in <u>Sciurus</u> species overlap, so they cannot be discriminated by knee morphology. All knee articulation surfaces of <u>Tamiasciurus</u> have relatively greater curvature than those of <u>Sciurus</u>, allowing the two genera to be

discriminated. Greater curvature is also found in <u>Tamias</u>, while flatter surfaces are found in <u>Marmota</u>, <u>Cynomys</u> and <u>S</u>. <u>columbianus</u>.

A much more distinctive transformation involves the asymmetry between medial and lateral femoral condyles (Figure 13). In tree squirrels, the lateral condyle is slightly lower than the medial condyle. This asymmetry is greater in <u>Tamiasciurus</u> than in <u>Sciurus</u>. In Marmotini and Tamiini, the asymmetry is reversed; the medial condyle is lower than the lateral condyle. The reversed asymmetry is greatly exaggerated in <u>C. gunnisoni</u>. Because the heights of the tibial condyles are not altered (Figure 14), the effect of the femoral transformation is that the tibia angles laterally in Marmotini and Tamiini relative to its orientation in Sciurini. The knee articulation surfaces of some marmotines are at a slight angle to each other, which may be a response to the displacement of the tibia.

The ankle of the largest tree squirrel in this study, <u>S</u>. <u>niger</u>, differs from the ankle of other tree squirrels in the orientation of the lateral surface of the lower ankle joint (Figures 15a and 15b). Consequently, the astragalus is tilted and rotated in <u>S</u>. <u>niger</u>, relative to other tree squirrels (Figures 15c and 15d). The new position of the astragalus in <u>S</u>. <u>niger</u> produces a larger angle between the tibia and the sole of the foot. The larger angle may permit easier accommodation of the sole of the foot to the side of branch. The angle may also help resist shear stress tending to force the astragalus laterally when gripping the side of a branch. In the new position, a higher proportion of the load transmitted through the tibia and astragalus resolves normal to the lateral articulation surface of the calcaneus.



Figure 13. Distal ends of sciurid femora. a) <u>S. niger</u>, b) <u>I. hudsonicus</u>, c) <u>I. striatus</u>, d) <u>S. columbianus</u>, e) <u>S. lateralis</u>, f) <u>S. tridecemlineatus</u>, g) <u>C. gunnisoni</u>. All drawings are right femora.



Figure 14. Proximal ends of sciurid right tibiae, in caudal view. a) <u>S. niger</u>, b) <u>I. hudsonicus</u>, c) <u>I. striatus</u>, d) <u>S. columbianus</u>, e) <u>S. lateralis</u>, f) <u>S. tridecemlineatus</u>, g) <u>C. ludovicianus</u>.

Figure 15. Lower ankle joint orientation. a) calcaneus, <u>S. niger;</u>
b) calcaneus, <u>S. carolinensis;</u> c) calcaneus and astragalus, <u>S. niger;</u>
d) calcaneus and astragalus, <u>S. carolinesis;</u> e) calcaneus and astragalus, <u>T. striatus;</u> f) calcaneus and astragalus, <u>S. columbianus</u>. All scales are 1 mm.





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Figure 15. Lower ankle joint orientation

A similar, smaller change of the lower ankle joint is characteristic of Marmotini and Tamiini (Figures 15e and 15f). In these fossorial animals, the change may be a response to the wider, lower stance used for locomotion through tunnels. This stance would increase the shear component of the weight transmitted to the calcaneus, and the reoriented articulation surface would reduce the shear component at the joint.

Another change in the ankle which resist larger shear forces experience by fossorial sciurids is enlargement of the distal end of the fibula (Figure 16). The fibula resists forces tending to pull the lower leg medially across the foot. Such forces may be induced during digging if the lower leg is rotated at the knee to point the toes out, placing the foot oblique to the body axis. This may be a typical digging posture because the foot will be oblique to the direction of reaction forces pulling the digging animal forward. The oblique foot posture will improve traction, but would also induce the medial shear just described.

The articulation surfaces of the upper ankle joint are flatter in Marmotini and Tamiini than they are in Sciurini. This transformation reduces the possible angular displacement of the astragalus relative to the tibia. Reduction of the range of movement at this joint may reflect smaller variation in the orientation of support surfaces for non-arboreal species.

One other transformation of the foot morphology may also influence the mobility of ankle joints; although it is not a modification of the articulation surfaces. The metatarsals of tree squirrels form a mediolateral arch in which metatarsal 5 is rotated 60 to 70 relative to metatarsal 2 (Figure 17). A higher arch, with a larger angle, is present





I. <u>striatus</u>



Figure 16. Distal ends of left tibiae and fibulae

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in Tamiini and most Marmotini. Increasing the arch could increase rotation and reduce flexion and extension at the midtarsal joint; however, an extensive network of thick ligaments among these bones immobilizes this region of the foot. A more likely explanation is that the curvature of the foot provides an edge which improves traction in the digging stance described earlier. The only sciurid with a flatter arch than tree squirrels is <u>M</u>. <u>flaviventris</u>. The flat arch of this rather large squirrel provides greater width and surface area of the sole, for better traction climbing on rocks. <u>M</u>. <u>monax</u>, which lives in less rocky terrain, has the primitive arch height.

The elbows of Marmotini and Tamiini are modified on both the ulnar and the radial sides of the joint. The head of the radius is more ellipsoidal in most of the northern ground squirrels (Figure 18). Eccentricity of the ellipse is especially large in <u>Marmota</u> and <u>Cynomys</u>. There are corresponding increases in the eccentricity of the capitulum of the humerus, which articulates with the radius. In addition, the proximally directed process on the dorsal rim of the radial head is also enlarged. These modifications limit rotation of the radius, but may allow adduction and abduction of the forearm (deflection toward and away from the ventral midline, which can only occur if both the humero-ulnar and the humero-radial articulations permit these movements). Of the northern ground squirrels included in this analysis, only <u>S</u>. <u>lateralis</u> has relatively round humero-radial articulations similar to those of tree squirrels.

The trochlear notch of the ulna is also modified in most Marmotini and Tamiini; only <u>T</u>. striatus and <u>S</u>. lateralis retain morphologies



Figure 17. Mediolateral arch of the left metatarsals

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Figure 18. Proximal radial articulation surfaces. a) <u>S. carolinensis</u>,
b) <u>I. striatus</u>, c) <u>I. amoenus</u>, d) <u>M. monax</u>, e) <u>S. lateralis</u>, f) <u>S. columbianus</u>,
g) <u>S. tridecemlineatus</u>, h) <u>C. ludovicianus</u>. All figures are right radii; all scales=1 mm.

similar to the Sciurini (Figure 19). The pattern of change varies among northern ground squirrels. The entire trochlear notch is narrower with steeper slopes in <u>Neotamias</u> (Figure 19c) and <u>Marmota</u>. In derived <u>Spermophilus</u>, there is an initial change in which only the proximal slope of the trochlear notch becomes steeper (Figure 19e). The distal slope is modified later, and independently, in <u>Ictidomys</u> (Figure 19f) and <u>C. gunnisoni</u>. In all taxa the modifications of the trochlear notch are accompanied by changes making the trochlea of the humerus narrower and deeper. These changes at the humero-ulnar joint limit adduction and abduction of the forearm as well as limit rotation of the ulna. The partial changes, involving only the proximal side of the joint in <u>S. columbianus</u> and <u>C. ludovicianus</u>, are most effective when the forearm is fully extended. The complete transformation found in other taxa limits adduction, abduction and rotation in all forearm positions.

The wrist has undergone many more transformations than the other joints during the evolution of Marmotini and Tamiini. In fact, each of the divisions of the wrist has more changes than any of the other joints. Although many of the changes restrict wrist movement, several appear to have no affect on joint mobility. In the antebrachial-carpal joint, there are transformations of the articulation surfaces of all four bones (Figure 20). The ulnar styloid is conical in both <u>Sciurus</u> and <u>Tamiasciurus</u>; however, the sides of the cone are more rounded in <u>Tamiasciurus</u>. In both genera there is variation in the width of the cone, but the species cannot be readily discriminated by this trait. <u>Tamias</u> can be distinguished from the tree squirrels by its ovoid ulnar styloid. The ulnar styloid is ellipsoidal in the ground squirrels





Figure 20. Antebrachial-carpal joints of sciurids. A) <u>S</u>. <u>carolinensis</u>, left radius and ulna, right proximal carpals; B) <u>T</u>. <u>striatus</u>, right radius and ulna; C) <u>S</u>. <u>columbianus</u>, right radius and ulna, left proximal carpals; D) <u>S</u>. <u>tridecemlineatus</u>, right radius and ulna, left proximal carpals; E) <u>C</u>. <u>ludovicianus</u>, right radius and ulna, left proximal carpals.





<u>S. columbianus</u> and <u>S. spilosoma</u>. In the other marmotines, this structure is a blunt, rounded triangle; it is almost completely round in <u>Marmota</u> and <u>Cynomys</u>.

The corresponding socket on the triquetrum does not vary as much as the ulnar styloid. In general, the socket varies only in size, accommodating to size of the styloid. The socket does not appear to respond to variations in the shape of the styloid. However, the socket shifts to a more lateral position in the Marmotini, and is also oriented to face more laterally than in the other sciurids. The lateral shift of the socket may limit abduction and adduction.

The socket on the distal end of the radius is nearly round in the Sciurini, although there is some variation in its eccentricity. The surface of the scapholunar is also slightly ellipsoidal in Sciurini, but more distinctly ellipsoidal in Tamiini and Marmotini. The distal articular surface of the radius is more variable than the proximal scapholunar surface, which remains consistently ellipsoidal. The outline of the radial surface is ovoid in Tamias. This socket is nearly rectangular in Marmota, Cynomys, S. columbianus and S. spilosoma; but differences in the outlines indicate that these four taxa have converged on the rectangular outline. Many of the sciurids develop elevated ridges on the rims of the radial socket. In Tamiasciurus, presence of the dorsal and ventral rims varies between individuals. The presence or absence of the ridges is fixed in most Tamiini and Marmotini. Most species in these tribes have both ridges, but S. columbianus and S. spilosoma lack dorsal ridges while T. amoenus and S. spilosoma lack ventral ridges. Medial ridges are found in all <u>Tamias</u> and <u>S. spilosoma</u>.

This distribution of ridges suggests that dorsal and ventral ridges may be primitive to both Tamiini and Marmotini, and subsequently lost by some taxa; while medial ridges are primitive to Tamiini and convergent in <u>S. spilosoma</u>. All Marmotini and two chipmunks (<u>T. striatus</u> and <u>T. minimus</u>) have relatively large radial styloids. The large styloids probably are primitive in Marmotini and convergent in the two chipmunks.

The changes in the antebrachial-carpal joint are difficult to interpret because potential movement of the radius must also be considered. Rounding of the ulnar styloid increases the potential for the proximal carpals to rotate, pivoting on the ulnar styloid. The ellipsoidal or rectangular radial surfaces tend to reduce rotation of the distal carpals relative to the radius. If the radius rotates around the ulna, fixing the proximal carpals against the radius only insures that the carpals rotate with the radius. However, in most members of the northern ground squirrel lineage, the radius is relatively immobile. Consequently, the transformations of distal ulnar and radial articulation surface shapes may reflect a shift in the location at which proximal carpal rotation is controlled, possibly motivated by increasing size of the radius relative to the ulna. The hypothesis that there has been a shift in the location at which rotation is controlled is supported by the development of dorsal and ventral ridges bounding the radial socket: addition of the ridges increases the surface area blocking rotation, which is consistent with the shift to a larger bone having greater articulation surface area. The ridges may also resist dorso-ventral shear across the joint surface. The changes in ulnar styloid position and radial styloid size increase resistance to medio-lateral shear and

also inhibit adduction and abduction. Thus, the overall trend at the antebrachial-carpal joint appears to be that mobility is increasingly restricted to flexion and extension.

One of the changes in the distal carpals affects both the intracarpal and carpal-metacarpal joints. This change is an increase in the width of the hamate, which characterizes marmotines and tamiines. Because of its increased width, the hamate and scapholunar articulate over a broader area and part of the hamate lies directly between the scapholunar and metacarpal 3 (Figure 21). The overlap of these three bones may reduce shear between medial and lateral sides of the wrist.

The width of the centrale is also increased in all of the northern ground squirrels. However, there are several different configurations of the centrale and adjacent distal carpals, indicating that expansion of the centrale may be convergent (Figure 22). All Tamiini have a rectangular centrale that completely separates the capitate from the scapholunar. The centrales of the Marmotini only partially intrude between the capitate and scapholunar, but also extend between the ventral trapezoid and scapholunar. In <u>Cynomys</u>, the capitate and scapholunar have an unusually broad area of contact for this tribe, and the trapezoid is almost completely separated from the scapholunar. The outline of the centrale also varies. In Sciurini it is a narrow rectangle. In Tamiini, the scapholunar is a much broader rectangle. The scapholunar is round in all Marmotini except <u>S</u>. <u>lateralis</u>, in which it forms a wedge tapering ventrally.

The proximal face of the centrale also has a small knob which fits into a pit on the surface of the centrale. There are also several



Figure 21. Left wrist of <u>T. striatus</u> in dorsal view.



Figure 22. Proximal surfaces of distal carpals. tz trapezium; td, trapezoid; ce, centrale; ca, capitate; h, hamate. All figures are from the right side; all scales are 1mm.

ligaments that connect the distal carpals to the scapholunar pit. In most sciurids, the knob and pit are symmetrical, but in <u>Tamias</u> there is a transition towards relatively shallow slopes on the lateral sides of these features. There is also some variation in the sizes of these structures, but only in <u>Marmota</u> and <u>Cynomys</u> are the sizes distinctly different from other taxa: smaller in <u>Marmota</u> and larger in <u>Cynomys</u>.

The variations of the knob and pit are rather unimportant because these features are only one part of the interdigitations that limit movement at the intracarpal joint to flexion and extension. The changes in the pit and knob may weaken or strengthen overall resistance to other movements, but manipulations of the bones suggest that the other structures may be sufficient. There are two other changes in the interdigitation at the intracarpal joint: 1) addition of a new interdigitating process on the ventral surface of the marmotine scapholunar (this process is subsequently reduced in size in <u>S. tridecemlineatus</u> and <u>Cynomys</u>), and 2) ventral extension of the triquetrum lateral to the hamate in <u>Spermophilus</u> and <u>Cynomys</u>.

The carpal-metacarpal joint has undergone fewer changes than other parts of the wrist. The changes are found only in <u>Tamias</u> and <u>Marmota</u>. The most striking change involves metacarpal 2 and the distal carpals articulating with it. In most other sciurids, the ridges on metacarpal 2 are expanded at their dorsal and ventral ends (Figure 23). These expansions are enveloped by the distal carpals, particularly the trapezium and capitate. Consequently, metacarpal 2, and the other three metacarpals attached to it, are immobilized by the distal carpals. The ridges and grooves are straightened in <u>Tamias</u>, apparently permitting



Figure 23. Proximal surfaces of metacarpals.
extension of the metacarpals. A transverse ridge, present in all sciurids, prevents flexion. Straightening of metacarpal 2 also occurs to a lesser degree in <u>Marmota</u>. Metacarpal 3 is also modified in <u>Tamias</u>, losing the central groove and acquiring an s-shaped profile. The profile is relatively flat in most <u>Tamias</u>, with a more distinct proximal process at the ventral margin than is found in <u>T. striatus</u>. These surfaces also permit extension but not flexion. Metacarpal 3 of <u>Marmota</u> also acquires a profile similar to that found in most <u>Tamias</u>, but retains the central groove. Loss of central groove also occurs in metacarpal 4 of <u>Tamias</u>, but this metacarpal remains smoothly convex and does not acquire and s-shaped profile.

The last changes in the wrist are modifications of the mediolateral arch of the metacarpals. <u>Tamiasciurus</u>, <u>Tamias</u> and some <u>Spermophilus</u> have similar degrees of arching. The arch is flatter in <u>Sciurus</u> and higher in <u>Marmota</u>, <u>Ictidomys</u> and <u>Cynomys</u>. Flattening of the arch in <u>Sciurus</u> probably increases gripping ability as does flattening of the metatarsal arch. Increasing the arch may focus digging forces on a smaller area of ground and reduce the amount of work required for digging.

# COMPARISON OF MORPHOLOGICAL AND FUNCTIONAL EVOLUTION

Only two transformations were observed in shrews. These changes were only observed in some of the fossorial species, and have little or no affect on digging ability. Because there are so few changes in shrew wrists, a more detailed analysis of the relationship between morphological and functional evolution in shrews is not possible. Consequently, this section, and the following section which considers

some of the factors influencing that relationship, will only investigate the evolution of sciurid joints.

The transformations of sciurid joints are summarized in Table 3. For convenience, the transformations are grouped into five categories according to the functional mechanisms by which they affect digging ability. Most of the transformations are consistent with increased fossoriality.

In the first category on Table 3 are transformations that appear to be associated with changes in posture. Most of the transformations in this category contribute to lower carriage of the body. Lower carriage permits fossorial animals to dig relatively smaller tunnels which require less work. All of the postural changes involve hindlimb joints; two are common to all members of the northern ground squirrel lineage.

Approximately one fourth of the transformations alter the range of motion (Table 3). A decrease in the range of motion is consistent with increased fossoriality because fossorial animals face less variation in the orientation of support surfaces. More importantly, reduction of the range of motion eliminates extreme positions where muscles are oblique to the bones on which they insert and are inefficient at producing movement. Two types of transformation reduce the range of movement: flattening the articulation surface (resulting in a longer radius and smaller angle of rotation) and extending the margins of the socket to enclose more of the articulating bone (reducing the angle of rotation, only). Flattening tends to occur in the hindlimb joints; enclosure, in the antebrachial-Carpal joint. Several reductions of the range of joint movement occurred early in northern ground squirrel evolution, during divergence of genera,

Table 3. Summary of modifications of sciurid joints.

Character description Joint Taxa Effect Changes in posture (orientation of articular surfaces) reverse femoral condyle asymmetry B K + NGS в' exaggerate reversed asymmetry K + SPT, CYG C tilt astragalo-calcaneus joint A + NGS. (SCN) Changes in range of motion A increase curvature of knee surfaces K -TA, (TSH) A' decrease curvature of knee surfaces K + MA, CY, SPC E decrease curvature of upper ankle joint A + NGS raise dorsal rim of distal radial socket W + NGS, (TSH, var.) L loss of raised dorsal rim -L W -SPC, SPS raise ventral rim of distal radial socket Μ W + NGS, (TSH, var.) -M loss of raised ventral rim W -TAA. SPS Ν raise medial rim of distal radial socket W + TA, SPS Х increase curvature of metacarpal 3 W -TAS Changes in possible directions of movement G more ellipsoidal humero-radial surfaces E + NGS -G SPL less ellipsoidal humero-radial surfaces E -G' further increase of G E + MA, CY, IC narrow posterior trochlea and notch H E + NE, MA, dSP, CY H' narrow anterior trochlea and notch E + NE, IC, CYG I more rounded ulnar styloid W -TA, MA, CY, SPL, SPT, (TSH) Т! more ellipsoidal ulnar styloid W + SPC, SPS K distal radial socket more ovoid W -TA K' distal radial socket more rectangular W + MA, CY, SPC, SPS V straighten metacarpal 2 ridges W -TA, MA W eliminate groove on metacarpal 3 W -TA Y eliminate groove on metacarpal 4 W -TA Key to Table 3: Joints: A, ankle; E, elbow; K, knee; W, wrist Effect: (+), consistent with increasing fossoriality; (-), conflicting with increasing fossoriality. Taxa: CY, Cynomys; CYG, C. gunnisoni; IC, Ictidomys; MA, Marmota; MAF, M. <u>flaviventris</u>; MTI, Marmotini; NE, <u>Neotamias</u>; NGS, northern ground squirrels; SC, Sciurus; SCN, S. niger; SP, Spermophilus; dSP, derived Spermophilus; SPC, S. columbianus; SPL, S. lateralis; SPS, S. spilosoma; SPT, S. tridecemlineatus; TA, Tamias; TAA, T. amoenus; TAM, T. minimus; TAS, T. striatus; TSH, Tamiasciurus hudsonicus; var., variable; (), tree Squirrels.

Table 3 (cont'd.).

Changes in bracing mechanisms (S, shear resistance; L, locking mechanism)

D	enlarged fibula	A	+S	NGS			
J	lateral triquetrum socket	W	+S	MTI			
L*	raise dorsal rim of distal radial socket	W	+S	NGS	(TSF	i, var.	)
-L*	loss of raised dorsal rim	W	-S	SPC	SPS	•	Ī
M*	raise ventral rim of distal radial socket	W	+S	NGS	(TSE	i, var.	)
-M*	loss of raised ventral rim	W	-S	TAA	SPS		í
N*	raise medial rim of distal radial socket	W	+S	TA,	SPS		
0	larger radial styloid	W	+S	MTI	TAS	, TAM	
Ρ	wider hamate	W	+S	NGS			
Q	centrale remains rectangular,						
~	expanded laterally	W	+S	TA			
0'	centrale wedge-shaped,						
~	expanded medially and laterally	W	+S	SPL			
0''	centrale rounded, expanded medially						
-	and laterally	W	+S	MA,	SPC,	IC	
0''	centrale rounded, expanded medially	W	+S	CY			
Ŕ	asymmetric centrale knob / scapholunar pit	W	-L	NE			
S	larger centrale knob / scapholunar pit	W	+L	CY			
s'	smaller centrale knob / scapholunar pit	W	-L	MA			
Ţ	new distal scapholunar process	W	+L	MTT			
- T	reduce size of new process	W	-T.	CY.	SPT		
ū	extend ventral process of triguetrum	W	+T.	SP.	CY		
Ŭ	chedia valitai process or triquetran			υ,	~		
Arch	25						
F	higher metatarsal arch	A	+	TA,	dSP,	CY	

F'	flatter metatarsal arch	A	-	MAF	
Z	flatter metacarpal arch	W	-	(SC)	
Z'	higher metacarpal arch	W	+	MA, CY,	IC

\* character described previously; has more than one functional role

at the latest. Changes that are not consistent with increasing fossoriality, increasing rather than decreasing the range of motion, are most common in <u>Tamias</u>.

Another quarter of the transformations alter the number of directions in which a distal limb element can move (Table 3). Reduction of directional freedom of movement is consistent with increased fossoriality primarily because the reduction limits deflection of the digging stroke by obstructions. This type of transformation occurs only in the forelimb, the primary digging tool; this is the only type of transformation occurring at the elbow. Except for one reversal in <u>S</u>. <u>lateralis</u>, all elbow changes are consistent with increased fossoriality. Both <u>S</u>. <u>lateralis</u> and <u>T</u>. <u>striatus</u>, are distinguished from other northern ground squirrels by their relatively primitive elbow morphology. Again, transformations that appear to reduce digging ability are more common in <u>Tamias</u> than in other northern ground squirrel genera.

Almost half of the transformations alter bracing mechanisms: projections which cross a joint (Table 3). Some of the projections fit into a socket on the opposing bone, others are elements in a set of interdigitating processes, and a few lie adjacent to an external surface on the opposing bone. Many of these projections resist shear stress across the articulation surface. The rims of the distal radial socket act in this capacity as well as limiting the range of motion. Increasing the size of a bracing projection, or shifting one to a more external position, would enable it to resist the larger forces that fossorial animals are expected to experience. Modifications of individual elements

in interlocking mechanisms are unlikely to change the freedom of movement because other elements in these redundant complexes are sufficient to impose the original restriction. However, single changes cannot be ignored because they may alter the maximum stress the complex can resist. In addition, the accumulation of several individual changes in the evolutionary history of a lineage may precipitate dramatic changes in freedom of movement. Two transformations of bone size are tentatively included among the shear bracing mechanisms: increases in hamate and centrale widths. These changes increase the overlapping of wrist bones, which may resist proximo-distal shear across rows, although fusion of these bones might be more effective. Almost all transformations of bracing mechanisms occur in the wrist. Most changes of single projections increase resistance to shear, but half of the changes in locking mechanism elements decrease shear resistance. There does not appear to be a clear taxonomic pattern to the distribution of increased and decreased shear resistance.

The last set of transformations listed in Table 3 are modifications of the transverse arches of the metatarsals and metacarpals. Increasing the curvature of the arches bring the claws closer together, focussing muscle-generated forces on a narrower area. Thus, increasing the metacarpal arch improves an animal's ability to break up the soil. The function served by increasing the metatarsal arch is less clear because only the forelimbs are used for digging; hindlimbs are used to brace the animal while digging and to kick loose dirt away from the work area. However, a higher metatarsal arch may provide an edge in the foot, giving

the animal better traction for bracing. Flattening the arches increases surface area and provides better grip for climbing.

The phylogenetic pattern of morphological transformations is shown in Figure 24. This figure indicates that the initial transition from tree squirrels to northern ground squirrels is characterized by a relatively large number of changes compared to most other transitions within the northern ground squirrels. Behavioral changes that occurred during the initial transition from tree squirrels are the acquisition of permanent burrows, hibernation, and possibly hoarding (Figures 2 and 3). All four joints are modified during this transition. The changes in the hindlimb are almost exclusively modifications for a wider digging stance. The wrist modifications are functionally more diverse, improving bracing and limiting range of motion, but most of them occur at the antebrachialcarpal joint. The elbow is the only joint where there is restriction of the direction of movement. These early morphological transformations appear to be responses to the large forces required for digging, but do not contribute much to directing those forces (there is little restriction of the path of the digging stroke).

Divergence of <u>Tamias</u> from the early northern ground squirrels may not have involved any behavioral change (possibly the acquisition of hoarding occurred in this interval). Despite the lack of behavioral evolution, the morphological divergence of <u>Tamias</u> is characterized by several modifications of the wrist, most of them detrimental to digging ability. There is also one change in the knee, increasing curvature producing a greater range of motion, which is also detrimental to digging ability. The wrist changes are primarily located at the



Figure 24. Phylogenetic distribution of changes in fossorial sciurid joints. Character codes as in Table 3. x indicates changes conflicting with the direction of behavioral evolution.

antebrachial-carpal joint; but there is some transformation of the carpal-metacarpal joint. Changes at the carpal-metacarpal joint appear to be restricted to <u>Tamias</u> and <u>Marmota</u>. In <u>Tamias</u>, most modifications in both wrist joints increase the directional freedom of movement. Evidently, morphological evolution during the divergence of <u>Tamias</u> is distinguished by a large increase in wrist mobility indicative of a decrease in digging ability, despite the lack of behavioral evolution.

Morphological diversification of the species within <u>Tamias</u> does appear to be consistent with the evolution of function. Figures 2 and 3 indicate little behavioral diversification among chipmunks, the main changes appear to be behavioral flexibility in both hibernation and nesting in trees. Figure 24 indicates a corresponding lack of morphological change. The most notable morphological transformation occurs during divergence of <u>Neotamias</u>. The transformation is an increase in the curvature of the humero-ulnar portion of the elbow, which restricts the direction of movement to a single plane. This particular change conflicts with the behavioral data because no increase of fossoriality was indicated for <u>Neotamias</u>. In addition, the only chipmunk with a notable increase in fossoriality, <u>T</u>. <u>striatus</u>, is conspicuous for its lack of change at the humero-ulnar joint.

In the basal lineage of the Marmotini, from the divergence of <u>Tamias</u> to the divergence of <u>Cynomys</u>, the accumulated morphological changes are almost as numerous as in the initial divergence of northern ground squirrels from tree squirrels. The changes along the marmotine baseline appear to be a partial continuation of the early divergence from tree squirrels: there are additional increases in both wrist bracing and

elbow restriction, but there is no further modification of the hindlimb. The morphological changes in the basal lineage are consistent with a general trend of increasing fossoriality, but outstrip the few behavioral changes occurring over this interval (increased burrow complexity and foraging restricted to the ground). The distribution of morphological changes also indicate that a substantial proportion of them may have occurred before <u>Marmota</u> diverged.

<u>Marmota</u> appears to have undergone a large amount of morphological change during its divergence from the basal lineage. However, the net improvement in digging ability is somewhat smaller because 1/3 of the changes are not consistent with increased fossoriality. For example, the ulnar styloid is rounder but the distal radial socket is more rectangular; consequently, wrist mobility is unchanged. Only at the knee and elbow is there evidence of a definite decrease in joint mobility. Thus, there is a net morphological change consistent with predictions of improved digging ability, but the effective improvement is limited to the knee and elbow. Relatively little morphological change occurred during the divergences of <u>M. monax</u> and <u>M. flaviventris</u> from their most recent common ancestor. The distribution of morphological changes may indicate that the behavioral changes occurring in <u>Marmota</u>, adult migration and use of multiple burrows, may be shared primitive traits of the genus, not convergent derived traits of M. monax and M. flaviventris.

The behavioral data indicate that the most primitive ground squirrel in this study, <u>S</u>. <u>lateralis</u>, has undergone one change indicating an increase in fossoriality, the addition of subterranean items in the diet. However, in the interpretation of behavioral evolution assuming the most

fossorial ancestor possible, the addition of this trait may be balanced by a return to foraging in trees. The morphological changes exhibited by <u>S. lateralis</u> include a reversal of earlier modifications of the elbow, and appear to suggest a slight decrease in digging ability. Thus, the morphological changes are more consistent with the second interpretation of behavioral evolution.

After divergence from their most recent common ancestor, S. columbianus and S. tridecemlineatus appear to have undergone parallel behavioral transformations: both acquired multiple burrows and added subterranean items to their diets (Figures 2 and 3). These traits are not found in S. spilosoma, the closest relative of S. tridecemlineatus in this study. A similar pattern of morphological evolution might be expected: S. columbianus and S. tridecemlineatus undergo parallel transformations of articulation surfaces while S. spilosoma remains relatively unchanged. The phylogenetic distribution of morphological changes indicate that S. spilosoma and S. tridecemlineatus share restrictions of elbow mobility and an increase in wrist bracing, which are all consistent with increasing fossoriality. After these species diverge, a few changes in the wrist increase mobility and decrease bracing in <u>S</u>. tridecemlineatus, effectively reversing the immediately preceding changes, and conflicting with the further increase of fossoriality in this species. S. spilosoma and S. columbianus both exhibit changes consistent with increased fossoriality, including parallel changes restricting mobility at the antebrachial-carpal joint and the knee. Thus, the subgenus Ictidomys (represented by S. spilosoma and <u>S. tridecemlineatus</u>) and the species <u>S. spilosoma</u> appear to have

undergone more morphological changes consistent with increased digging ability than could be predicted from the amounts of digging indicated by the behavioral traits. Only in <u>S</u>. <u>columbianus</u> do there appear to be matched increases in both the amount of digging and digging ability.

<u>Cynomys</u> is the only taxon in this study in which a reduction of digging ability is expected. This reduction is due to losses of hibernation and hoarding, and in <u>C</u>. <u>ludovicianus</u>, acquisition of coloniality. The observed morphological changes increase wrist bracing and decrease knee and elbow mobility. These changes suggest a substantial increase of digging ability in <u>Cynomys</u>. Thus, this genus, like <u>Tamias</u>, exhibits a morphological transition apparently at odds with its behavioral transition. The results for <u>Tamias</u> and <u>Cynomys</u> differ in the direction of the expected change.

The preceding narrative comparison of the patterns of behavioral and morphological evolution indicates that the directions of morphological change generally are consistent with the hypothesis that function drives morphological evolution. However, there does not seem to be a close correspondence between the relative numbers of morphological and behavioral changes. Table 4 illustrates the discrepancies between behavioral and morphological divergences of northern ground squirrel species from tree squirrels. Behavioral ranks are based on fossoriality scores from Table 1. Morphological ranks are based on the net number of morphological changes on Figure 24 that are consistent with increasing fossoriality (# consistent - # inconsistent). In a comparison of two rankings of 13 species,  $r_s$  must be greater than .532 to be judged significant (p<0.05). The value of  $r_s$  for the morphology and

Table 4. Sciurid species ranked by morphological and behavioral divergence from tree squirrels. 1 indicates species most divergent from tree squirrels.

		Morphology	Fossoriality
<u>c</u> .	gunnisoni	1	12
<u>c</u> .	ludovicianus	2	8.5
<u>s</u> .	tridecemlineatus	3.5	1
<u>s</u> .	<u>spilosoma</u>	3.5	4
<u>s</u> .	<u>columbianus</u>	5	2
<u>₩</u> .	monax	6	4
<u>M</u> .	<u>flaviventris</u>	7	8.5
<u>s</u> .	<u>lateralis</u>	8	6
<u>T</u> .	minimus	9	8.5
<u>T</u> .	bulleri	10.5	12
<u>T</u> .	ruficaudus	10.5	12
Ţ.	<u>striatus</u>	12.5	4
<u>T</u> .	amoenus	12.5	8.5

 $r_s = .225, p > 0.05$ 

fossoriality ranks in Table 4 is far below this level, indicating that there is no relationship between the amount of behavioral deviation from tree squirrels and the amount of morphological deviation. An alternative test of the relationship between the rates of morphological and behavioral evolution is a comparison of the rank order correlations of the segments between phylogenetic branch points. Ranks of segments are determined by the net numbers of morphological and behavioral changes consistent with increasing fossoriality inferred to occur in each segment. Two different tests were performed, one with each of the alternative phylogenies of the behavioral traits. r<sub>s</sub> was less than .15 for both tests, far below the value of .4 required to be judged statistically significant. Thus, this test also indicates that there is no relationship between the evolutionary rates of joint surface morphology and the evolutionary rates of the behavioral traits associated with fossoriality.

### TRAITS INFLUENCING MORPHOLOGICAL EVOLUTION

Size is one trait expected to influence the pattern of morphological evolution. For this study, size is measured by body weight, specifically, the ranges of weights encompassed by all specimens in this dissertation for which weights were recorded by the original collectors. This includes specimens used only in the analysis of scapular morphology. The expanded sample of individuals used in the study of joints and the study of scapulae provides a more accurate estimate of the real weight ranges represented by the species that were analyzed.

Table 4 shows that morphological evolution is not just a response to the evolution of function. However, the influence of size on morphological evolution cannot be inferred from Table 4 because the morphology ranks are based on all changes accumulated since the fossorial lineage diverged from the tree squirrel lineage. The fossil record indicates that size changes are primarily associated with the divergences of Tamias, Marmota and Cynomys from the basal lineage: Tamias became smaller; Marmota and Cynomys became larger (Black 1963, Bryant 1945). There was relatively little size evolution within the basal lineage or in Spermophilus. Extant Spermophilus cover nearly the same weight range as extant Sciurus (123-1034 g. and 139-904 g., respectively). Morphological changes in the joints of each Tamias, Marmota and Cynomys occur primarily during the divergence of each genus from the most recent common ancestor that genus shares with Spermophilus (Figure 24). There is little diversification among species within Tamias, Marmota or Cynomys. Therefore, a better analysis of the influence of size might be a comparison among genera, using all changes in Tamias, Marmota and Cynomys since their divergences from the basal lineage (Table 5). In Table 5, the numbers of changes in Spermophilus include changes to the basal lineage between the divergences of <u>Marmota</u> and <u>Cynomys</u>.

Table 5 shows that there is little correspondence between rank by weight (RWT) and rank by number of morphological changes (R#). The two heaviest genera have the same number of changes; the numbers of changes in the two lightest genera are in reverse order of their weights. There is even less correspondence between RWT and rank by percent of changes consistent with behavioral evolution (R%C). R%C is extremely low for

Table 5. Sciurid genera ranked by body weight and morphological change.

	WT	#	#C	%C	RWT	R#	R%C
<u>Tamias</u>	36-116	15	7	47	l	2	3
Spermophilus	123-630	23	16	70	2	l	l
Cynomys	750-935	10	1	10	3	3.5	4
Marmota	2160-3402	10	6	60	4	3.5	2

Key to Columns: WT, weight range; #, number of changes; #C, number of changes consistent with behavioral evolution; %C, percent of changes consistent with behavioral evolution; RWT, rank by WT; R#, rank by #; R%C, rank by %C.

<u>Cynomys</u>. This genus has several morphological changes that improve digging ability, but the behavioral traits indicate decreasing fossoriality. Reversal of behavioral evolution may bring about lowered selection pressure on the digging ability of <u>Cynomys</u>, which could account for the low R%C of this genus. R%C is also low for <u>Tamias</u>, conflicting with the expected influence of size in these small animals. <u>Tamias</u> does not appear to have undergone reversal of its behavioral evolution, as has <u>Cynomys</u>; instead, <u>Tamias</u> has several changes at the carpal-metacarpal joint which are incompatible with increasing fossoriality. Some change in the way the hand is used may have resulted in a series of unpredicted morphological changes at this joint.

The values of  $r_s$  were not calculated for Table 5 because rank order correlations cannot be significant if there are fewer than five cases. In fact, with five cases, the significance level of a perfect rank order correlation ( $r_s$ =1) is only 0.05. Therefore, the comparisons in Table 5 could never conclusively demonstrate an association between size and morphological evolution. Table 5 does suggest that there is probably no association, however. The summed squared differences between ranks for the comparison of RWT to either R# or R%C would only be significant if there were at least seven cases. That would require either that there be no differences between ranks for the three cases which might be added to the four already in Table 5, or that the average difference between ranks be considerably smaller (0.1 rather than 0.75 in Table 5).

In Table 6, the joints are listed in order of the expected ranks (ER#), based on inferred integration and complexity. The numbers of changes (#) and the percent of morphological changes consistent with

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Table 6.	Joints	ranked	by	integration	and	complexity	vs.	morphological	
	change	•							

	I	В	#	#C	%C	ER#	OR#	R%C	RB
Antebrachial-carpal	-	5	24	10	43	1	1	6	5
Knee	-	2	7	4	5 <b>7</b>	2	4	4	1.5
Lower Ankle Joint	+	2	1	1	100	3	7	1.5	1.5
Upper Ankle Joint	+	3	2	2	100	4.5	6	1.5	3.5
Elbow	+	3	11	8	73	4.5	3	3	3.5
Intracarpal	÷	7	15	8	53	6	2	5	6
Carpal-metacarpal	+	9	5	0	0	7	5	7	7

Key to columns: I, integration; +, present; -, absent; B, number of bones; ER#, expected rank by number of morphological changes; OR#, observed rank by number of morphological changes; RB, rank by increasing number of bones; all others are the same as in Table 5. behavioral evolution (%C) include all morphological changes occurring during the evolution of northern ground squirrels. Changes that improve digging ability in <u>Cynomys</u> are counted as inconsistent because fossoriality decreases in that genus. The antebrachial-carpal joint is expected to have the most changes because it is the unintegrated joint with the largest number of bones. The carpal-metacarpal joint is expected to have the fewest changes because it is the integrated joint with the largest number of bones. The antebrachial-carpal joint does have the largest number of bones. The antebrachial-carpal joint does have the largest number of changes, but two integrated forelimb joints have more changes than the unintegrated knee. Among the integrated joints, all of the forelimb joints have more changes than the simpler ankle joints. Thus, the observed ranks (OR#) are inconsistent with the expected ranks (ER#);  $r_s=0.276$ , well below the value of 0.750 required to be judged statistically significant at the 0.05 level.

The percent of morphological changes consistent with behavioral evolution (%C) was expected to be higher for integrated joints than for unintegrated joints. In reality, %C for both unintegrated joints is higher than %C for the integrated carpal-metacarpal joint, and %C is higher for the unintegrated knee than for either integrated wrist joint. Thus, %C does not have a clear association with the presence or absence of integration. Interestingly, R%C seems to be nearly the inverse of OR#, and is very similar to rank by number of bones (RB, where 1 indicates the joint with fewest bones). R%C deviates sufficiently from the inverse of OR# that this relationship cannot be considered statistically significant ( $r_s = -0.420$ , p>0.05). However, R%C is close enough to RB to be judged significant ( $r_s = 0.777$ , p<0.05), indicating that

joints with large numbers of bones tend to have a larger proportion of morphological changes that are incompatible with behavioral evolution.

There is some indication that differences between forelimb and hindlimb may account for the failure to find clear associations between morphological evolution and complexity or integration. In each limb, the unintegrated joint has more changes than the integrated joints in the same limb, and the unintegrated joint usually has a lower %C than the integrated joints. Unfortunately, the hindlimb joints tend to have fewer changes than forelimb joints, and the changes in the hindlimb are more likely to be consistent with behavioral evolution. Consequently, ER# and OR# are often quite different. The difference in numbers of changes between forelimb and hindlimb might indicate higher intensity of selection on forelimbs, which do the digging, than on the hindlimbs, which brace the body against reaction forces, but the higher %C for hindlimbs suggests that they are under more intense selection.

### DISCUSSION

Based on the morphological characteristics of specialized burrowers, especially moles, fossorial sciurids were expected to have joints that restrict mobility and resist shear. In moles, joints commonly have ridges and grooves or narrow, elliptical articulation surfaces that limit movement to a single plane, and interlocking mechanisms capable of bearing shear stress (Yalden 1966). Fossorial sciurids were expected to deviate from tree squirrels by accumulation of these traits. Highly fossorial sciurids were expected to have more of these traits than less fossorial sciurids.

Most of the observed transformations in fossorial sciurids were consistent with the expected direction of change, reducing freedom of movement and increasing resistance to shear, but nearly half of the changes conflicted with these predictions. More than half of all changes are convergent, including most of the changes that conflict with the expected direction of change. Evolution of the basal lineage consistently showed the expected changes, but deviation of contemporary genera from the basal lineage tends to be characterized by a combination of expected and conflicting changes. Few of the conflicting changes are reversals that eliminate advantages conferred by earlier transformation. More often, a change to one part of a joint that strengthens it or reduces its mobility, is either coupled with or followed by a change to another part of the joint that weakens it or removes a restriction on its mobility. Consequently, the net effect is little or no improvement in digging ability.

Species within <u>Tamias</u>, and the two species of <u>Marmota</u>, show little or no independent changes. Both genera appear to have been highly conservative after their initial divergences from the basal ground squirrel lineage. Compared to <u>Tamias</u> and <u>Marmota</u>, <u>Spermophilus</u> species have fewer shared changes since their divergence from the basal lineage, and there is more differentiation within <u>Spermophilus</u>. Despite these differences, all three groups show similar combinations of improvements and reductions of digging ability. The temporal pattern of morphological evolution in <u>Cynomys</u> is similar to the patterns in <u>Tamias</u> and <u>Marmota</u>: most of the change occurs during divergence from the common ancestor shared with <u>Spermophilus</u>, not during diversification within <u>Cynomys</u>. The

main distinction between morphological evolution in <u>Cynomys</u> and morphological evolution in the other genera is that most changes that occur during the evolution of <u>Cynomys</u> enhance digging ability, despite behavioral evidence that <u>Cynomys</u> has become less fossorial.

The enhancement of digging ability in the less fossorial <u>Cynomys</u> indicates that substantial net improvement in digging ability is possible in sciurids. Yet, the progressive trend toward increasing fossoriality does not lead to net improvement of digging ability in most of the sciurids examined in this dissertation. There is no general trend toward a more mole-like morphology. Rather, changes that improve digging ability are counterbalanced by changes that reduce digging ability.

The results of the analysis of sciurid joints are as perplexing as the results of the analysis of shrew wrists. The wrist joints of all shrews have the traits that fossorial sciurids were expected to acquire. Regardless of fossoriality, all shrews retain structures that limit mobility and resist shear. The contrast between observed and expected patterns of morphological evolution in non-fossorial shrews is even more dramatic than the contrast between observed and expected change in <u>Cynomys</u>. <u>Cynomys</u> remained fossorial, so retention of traits that enhance digging ability should be expected; the presence of additional enhancements may simply reflect a mistaken estimate of the importance of digging ability in this genus. Retention of similar traits in non-fossorial shrews might be explained by function if functions other than digging can be shown to impose demands on joint morphology similar to the demands imposed by digging. In other words, the proposed alternative function must also require joints to bear large loads, and

restrict directions of movement. Similar demands may be found in especially large animals (Leinders 1979, Leinders and Sondaar 1974, Swartz 1989), or in specialized runners and jumpers where the ability to bear the impact of landing outweighs the importance of joint mobility for turning (Biewener et al. 1988, Leinders 1979, Leinders and Sondaar 1974). There is some evidence from shrew behavior and ecology that the loads borne by shrew wrists are large relative to the demands for maneuverability (Hutterer 1985). Most shrews appear to be ambush predators, tackling prey after a short sprint. Also, shrew prey are often large relative to shrew body size. Finally, shrews are generalized predators, not dependent on any one type of prey. Thus, there may be relatively little demand on maneuverability, especially in contrast to the demands imposed by tackling relatively large prey.

Some of the discrepancies between patterns of functional change and patterns of morphological change in sciurids may be due to inaccuracy of the estimated functional change. Eurrow size and usage may not be good estimators of the amount of time and energy spent digging. Even if time and energetic cost of digging were accurately and directly measured, they would predict morphological change only if selection were acting on the time or cost of digging. At present, selection on digging ability can only be inferred from demonstrations that the burrow systems of pocket gophers (Andersen 1988, Vleck 1981) and mole rats (Jarvis and Sale 1971) are consistent with predictions of optimal foraging theory. Pocket gophers and mole rats feed almost exclusively on items uncovered while digging tunnels, consequently their tunnels record their foraging search pattern. This model does not fit the behavioral ecology of fossorial

sciurids which feed at the surface and only use their tunnels as refugia (Elliot 1978, Jones et al. 1983, Tevis 1955, Tileston and Lechleitner 1966). Tunnel location may reflect favored foraging sites, but it does not reflect a search pattern. Consequently, burrow costs and benefits to ground squirrels are not as intimately linked as the costs and benefits to pocket gophers. Thus, even if the costs of digging were known, they might not predict morphological change in sciurids.

Several hypotheses proposing that intrinsic properties influence the rate or direction of morphological evolution were tested and rejected. The tests employed are fairly weak, and more detailed measurement of both behavior and morphology may reveal patterns of association between behavioral and morphological evolution that could not be found in this study. Even so, the results of my analysis indicate that the hypothesized influences of size, complexity and integration must be much more subtle than previous studies of this type have indicated (cf. Emerson 1988, Liem 1973, Vermeij 1971). More importantly, the observed deviations of morphological evolution from the expected pattern cannot be attributed to a general inhibition of morphological evolution that is imposed by some set of intrinsic constraints: there are numerous morphological changes in the expected direction. What the present study cannot explain are concurrent changes in the opposite direction.

The results of my studies on the evolution of joint surface morphology suggest a hypothesis that could be tested by analysis of responses to selection. Earlier in this discussion I argued that shrews may have retained fossorial characteristics because selection pressures to maintain load bearing ability are greater than the selection pressures

to improve maneuverability. Fossorial sciurids may be under more balanced selection pressures for load bearing ability and maneuverability. The specific hypothesis is that fossorial sciurids face selection for both digging ability and running ability. Both abilities are critical for first year survival: running, to avoid predators; digging, to establish an adequate home burrow after dispersal. Annual mortalities are often guite high, and both predation and winter weather account for large proportions of the losses (Armitage 1981, Armitage and Downhower 1974, Michener and Michener 1977). Because both predation and winter weather are important causes of mortality, an individual's success is likely to be a function of both running and digging ability (a good runner may not survive the winter if it cannot dig an adequate burrow, and a good digger may not get a chance to dig a burrow if it cannot escape predators). If running and digging abilities are not equally balanced in each individual, the population can improve either ability, and may show improvement in both (cf. Charlesworth and Rouhani 1988, Felsenstein 1979, Lande and Arnold 1983, Via and Lande 1985). Counterbalanced changes like those observed in fossorial sciurids could accumulate if the competing selection pressures are not acting simultaneously on each individual, so that some individuals survive by virtue of their digging ability while others survive by virtue of their running ability. However, these conditions could also lead to a polymorphic population in which some individuals are specialized for burrowing and others for running. This model could be tested either by measuring selection on running and digging ability, or by measuring

selection on morphological traits demonstrably correlated with these abilities.

An alternative model depends on long-term variation in the adaptive values of traits (Felsenstein 1988, Riska 1989). Under this model, selection during one generation may favor improved digging ability and selection during the next generation may favor improved running ability (e.g., if intense predation and severe winters do not occur the same year). Extreme modifications that improve one ability at the expense of the other will be eliminated when the direction of selection is reversed, but over time there could be an alternating series of less drastic improvements. This alternation could not be tracked in the present study, but it might be detected in a more complete taxonomic sample or in stratigraphic sequence. Studies of selection in extant populations may also demonstrate variation in the relative intensities of the two selection pressures over time or between populations.

The proposals presented in the two preceding pages represent an approach to the study of morphological evolution guite different from the one I employed in the study of joints. My approach, gualitative comparison of morphological differences in phylogenetic context, revealed a complex pattern of counterbalanced morphological transformations. The results conflict with the rather simple predictive models I used, models typical of studies attempting to infer patterns of morphological evolution under selection. The counterbalanced transformations found in sciurids demonstrate that the evolution of joints surfaces is not adequately represented by a model predicting selection for one function inhibited by intrinsic constraints. Instead, selection may have been

acting on two functions, possibly more. Thus, the morphological comparisons provide justification and guidance for careful examination of potentially complex selection regimes.

# EVOLUTION OF THE SCAPULA

Although the scapula is a single bone, it can be divided into several morphologically distinctive regions (fossae, ridges, projections). Many of these regions serve as attachment sites for single muscles or for groups of muscles with similar functions. Thus, the scapula can be treated analytically as though it were composed of several independent parts. This treatment allows a study of the effects of size, complexity and integration on morphological evolution, the results of which can be compared to the study of joints in the preceding chapter. In addition, scapulae are available in larger numbers than complete sets of wrist or ankle bones. The larger samples of scapulae permit more refined, quantitative analyses which were not possible for the joints.

Previous analyses of scapular evolution demonstrate some general patterns which also may be found in the Sciuridae. Taylor (1974) and Lehman (1963) both demonstrate qualitative modification of the scapula during evolutionary shifts in forearm function. Taylor showed that the anterior portion of the scapula is wider in arboreal viverrid carnivores than in unspecialized generalists. The anterior scapula is an insertion area for protractors which advance the forelimb and, during head-down descent, support body weight. Lehman demonstrated that two families of non-sciurid rodents exhibited parallel transformations of the scapula associated with increasing fossoriality. Both families exhibit dramatic expansions of the posterior region of the scapula, where forelimb retractor muscles insert. Lehman and Taylor suggest that scapular shape

is modified in response to selection on muscle function, and illustrate coordinated changes in scapular shape, muscle mass and muscle position.

Similar results were obtained in a quantitative study by Oxnard (1968). Oxnard used canonical variates analysis to identify traits which discriminate between functional groups. Most of Oxnard's measurements pertain to insertion areas of two muscles. This focus was motivated by the hypothesis that changes in muscle position and patterns of muscle activity evolved to minimize, or at least balance, stresses loading on the scapula. The canonical variates analysis showed common patterns of change in different mammalian orders undergoing the same functional transition.

Roberts (1974) demonstrated that muscle positions do not simply balance the stresses in the scapula, but also direct the stresses to parallel the ridges in the scapular blade. Thus, the ridges act as support beams in addition to increasing muscle attachment area. The spine is especially important in this role. Roberts confirmed that protractor insertion area tends to increase during the transition from terrestrial to arboreal habit, but that increases in this area cannot resolve fine differences in locomotor behavior. In analyses of ridge number and orientation, Roberts showed that these traits also vary in response to body size and locomotor function. By including both muscle attachment area and ridge morphology in the description of scapula morphology, Roberts was able to discriminate between taxa that have relatively small differences in locomotor function.

The studies cited above describe transformations of the scapula that may also have occurred during the evolution of the Sciuridae. The

primary transformation in fossorial sciurids should be expansion of the posterior regions of the scapula, increasing the area and improving the position of retractors. These muscles are important for both climbing and digging, but must generate much greater forces for digging. A secondary transformation should be narrowing of the anterior muscle attachment areas and of the angle between the spine and a ridge found in this area. (There is no ridge in the posterior attachment area of most sciurids.) The anterior of the scapula should be relatively wider in arboreal animals than in non-arboreal mammals, providing support for muscles which resist gravity during the head-down descent of climbers. In addition, the angle between the spine and the anterior ridge should be wider in arboreal animals to bear the relatively large stress loaded on this broadened region of the scapula. In sciurids, the amount of climbing decreases as fossoriality increases, so there should be a decrease in the size of the anterior attachment area and the angle between the spine and the anterior ridge. This transformation may be less dramatic than the increase of the posterior area because selection may not be acting directly to reduce anterior muscles and scapular bone. Reduction of these tissues does not improve digging ability directly, but may reduce the metabolic cost of maintaining the tissues as their functions become less important. Overall, the anterior of the scapula is expected to be reduced and the posterior enlarged as fossoriality increases during the evolution of sciurids.

Arboreal and fossorial animals should show different allometric trends. In both groups, body weight increases the gravitational force loading on the forelimb and scapula. However, the significance of the

gravitational load differs between climbers and diggers. The increased weight of large diggers can be transmitted to the ground to assist digging, reducing the force that must be supplied by muscle activity. Consequently, expansion of the posterior regions of the scapula should be less for large fossorial sciurids than for smaller species at a similar fossoriality level. In contrast, the increased weight of large climbers requires relatively larger muscles to produce to force needed to resist gravity (Cartmill 1985). Because large climbers need larger retractors for climbing up as well as larger protractors for climbing down, anterior and posterior fossae both should be larger in large climbers then in small climbers. As a result, the scapulae of large climbers may differ from those of small climbers in size but not shape. In addition, the posterior fossa of large tree squirrels may be intermediate in size between the posterior fossa of small tree squirrels and posterior fossa of fossorial sciurids. The anterior fossa of small tree squirrels may be intermediate in size between the anterior fossa of large tree squirrels and the anterior fossa of fossorial sciurids.

The studies cited above also indicate that the scapula may be poorly integrated. The scapula can be described as a collection of muscle attachment areas and struts. These structures may be integrated by their presence on a single bone, or sets of structure may be related by a common muscle function, such as retraction. However, the studies on other mammals suggest that each area and strut evolves independently. The results of these earlier studies may indicate that each skeletal structure is responding to a separate evolutionary influence, possibly because each structure is associated with a distinct muscle or muscle

group. There is also behavioral evidence that anterior and posterior regions of the scapula should evolve independently in sciurids: many of the less fossorial sciurids have retained arboreal foraging habits while acquiring fossorial sheltering habits. The less fossorial species are generally more primitive than highly fossorial species, suggesting that reduction of the anterior scapular region may have occurred later in sciurid evolution than enlargement of the posterior region.

#### METHODS

Five of the species presented in Figure 1 were excluded from this study because the available sample sizes were insufficient to estimate means: T. bulleri, both species of Marmota, and both species of Cynomys. Most of the remaining species are represented by 20 individuals; the exceptions are T. amoenus (n=18) and S. spilosoma (n=19). Samples were drawn from as many subspecies or geographic localities as possible, to broaden representation of intraspecific variation. This reduces the possibility that statistically significant differences between species are artifacts of sampling. All individuals used in this study are adults. Whenever possible, sexual maturity was recognized by fusion of cranial or pelvic sutures, or by eruption of all adult teeth. In a few instances, maturity could only be inferred from the size of the scapula relative to other members of the population. Sex was not considered during selection of individuals for this study. Sexual dimorphism accounts for less than 10% of the variation in head and body length of most chipmunks, and is not statistically significant in most populations of the chipmunk species used in this study (Levenson 1990). In ground

squirrels, sexual dimorphism in weight is generally exceeded by seasonal variation (Armitage 1981).

Scapular size and shape were recorded following protocols developed by Bookstein (Bookstein et al. 1985, Bookstein, in press, Tabachnick and Bookstein 1990). Scapular morphology was recorded as the positions of selected points (landmarks) in X-Y coordinate space. The landmarks used in this study are illustrated in Figure 25 and described in Table 7. The ends of the spine, landmarks 1 and 9, were designated as endpoints of a baseline and standardized at (0,0) and (1,0). This standardization removes the size component of morphology, representing shape as the positions of the landmarks in the standardized coordinate space (shape coordinates). Shape coordinates are positions and imply no relationship to other landmarks. In other words, coordinates do not convey distances between landmarks, although the distances between any pair of landmarks can be computed from the coordinates. Because shape coordinates are not distances, the set of shape coordinates for a suite of landmarks constitutes a representation of shape that is independent of size. This permits separate analysis of size and shape variation, and also accurate analysis of covariation between size and shape.

Scapular size is determined from the untransformed coordinates of the landmarks. The centroid of all the landmarks is located and the distances of all landmarks, including the endpoints of the baseline, are calculated (Figure 26). Centroid size is the square root of the sum of the squared distances. The sum of squared distances is analogous to an area, and like area, centroid size is independent of shape. Extended



Figure 25. Locations of landmarks.

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Table 7. Anatomical description of scapular landmarks

1	ventral end of spine
2	dorsal end of acromio-clavicular articulation
3	ventral end of acromio-clavicular articulation
4	flexure demarking boundary between acromion and metacromion
5	ventral end of caudal margin of metacromion
6	dorsal end of metacromion-spine intersection
7	caudal end of vertebral border (on teres fossa)
8	intersection of axillary ridge with vertebral border (caudo-dorsal
	corner of infraspinous fossa)
9	intersection of spine with vertebral border
	or, projection of spine to the vertebral border
10	projection of subscapular ridge to the vertebral border
11	dorsal end of anterior marginal ridge

12 transition between blade and articular process at the cranial edge



Figure 26. Graphic representation of centroid size.
geometric and algebraic proofs of the independence of centroid size and shape are presented in Bookstein (in press).

Scapular landmarks were recorded using a videodigitizer. The scapula is relatively flat, so distortion by "photographic flattening" is small. Distortion is most likely to affect the landmarks on the acromion and metacromion. Variation in the height of the acromion and metacromion may affect their apparent size and position relative to the blade; positions of landmarks on the acromion and metacromion will not be distorted with respect to each other.

The predicted shape changes described in the introduction of this chapter were translated into directions of displacement relative to the baseline for the ten landmarks not assigned to the baseline. The ends of the spine (landmarks 1 and 9) were chosen as the ends of the baseline because the expected changes (based on studies of other taxa) are widening or narrowing not lengthening or shortening. In addition, muscles anterior to the spine are protractors, muscles posterior to the spine are retractors. This segregation of functions by position relative to the spine also applies to the large fan-shaped muscles attaching to the scapula on both sides of the spine (e.g., trapezius): sections anterior to the spine are protractors, posterior segments are retractors.

Because landmarks 1 and 9 are standardized at coordinates (0,0) and (1,0), the dorsal-ventral axis is aligned with the X coordinate axis. Figure 27 illustrates reduction of a scapular shape to a constellation of landmarks in an arbitrary (digitizer) coordinate space and rotation of constellation into the standardized shape-coordinate space. In the shape-coordinate space used for this study, landmarks posterior to the









Figure 27. Translation of morphology in shape coordinates. A) scapula with landmarks; B) landmarks, alone; C) rotation of landmarks by standardization of baseline coordinates.

spine have positive values on the Y coordinate axis, and posterior displacement of a landmark is represented by a positive change in the value of its Y coordinate. Thus, the expected widening of the infraspinous fossa, which entails a posterior displacement of landmark 8, would be represented by larger values of coordinate 8Y.

Selection for digging ability is expected to influence morphology of the anterior scapula only indirectly. As fossoriality increases, arboreality and the functional importance of protractors decrease. Consequently, areas of muscle attachment surfaces located anterior to the spine may also decrease. Anterior landmarks will have smaller negative Y coordinate values as the sizes of the acromion (landmarks 2 and 3) and supraspinous fossa (10, 11 and 12) decrease.

Landmarks 10 and 11 may also be displaced along the X axis as the supraspinous fossa narrows. These landmarks represent intersections of ridges with the margin of the supraspinous fossa. As the fossa narrows, the ridges may rotate toward the spine (like struts of a folding fan), or they may simply shorten. How these ridges might be modified can be inferred from the fan-like fiber arrangement in the muscles attached to anterior of the scapula. Muscle fibers attached to the dorsal end of the scapula are nearly parallel to the spine, fibers attached near the ventral end are more oblique to the spine. Stresses loading on the scapula tend to be parallel to the spine near the dorsal end, and oblique to the spine near the ventral end. Thus, the subscapular ridge (10) may rotate in as the fan of muscle narrows, but anterior marginal ridge (11) may simply shorten, remaining oblique to bear the load imposed by the remaining oblique fibers. If a ridge rotates inward, without changing

length, the X coordinate the landmark at the end of the ridge will increase; if the ridge shortens without rotating, the X coordinate will decrease. Because the particular combination of rotation and shortening cannot be anticipated, the specific direction of displacement cannot be predicted for landmarks 10 and 11.

On the metacromion, landmark 5 is expected to move caudally to expand the area available for retractors inserting on the metacromion (deltoids), and ventrally to increase the angle between the deltoids and the humerus. Landmark 4, at the boundary between acromion and metacromion may stay near the dorso-ventral axis, but should move ventrally with landmark 5. Landmark 6 is expected to move dorsally to expand the area of the metacromion, but, like landmark 4, is expected to stay near the dorso-ventral axis. Posterior displacement of landmark 6 would indicate tilting of the spine in that direction, which would restrict the volume above the infraspinous fossa available for retractors attached to the fossa. Therefore, posterior displacement of landmark 6 would be detrimental to digging ability and is not expected to occur. Anterior tilting of the spine would reduce the angle between the humerus and the deltoids, reducing the mechanical efficiency of the these muscles, which would also be detrimental to digging ability. Consequently, landmark 6 is not expected to move along the cranio-caudal axis.

Expansion of the infraspinous fossa should result in caudal displacement of landmark 8. The X coordinate of landmark 8 is expected to be near 1.0; landmarks 8 and 9 are expected to be as far dorsal as possible to produce the largest area in the infraspinous fossa. Thus, 8X

is not expected to differ among fossorial sciurids. Because landmark 7 is posterior to 8, displacement of landmark 7 should reflect expansion of the infraspinous fossa, and the teres fossa on which 7 is located. Like 8X, 7X is expected to have a value near 1.0 and to exhibit little divergence within fossorial sciurids.

For each fossorial species, the amount of displacement at each landmark should reflect the level of fossoriality of that species. Consequently, in a plot of species means for the coordinates of a particular landmark, species should be arrayed along a straight line in the same order as their level of fossoriality. For example, a plot of landmark 8 should show increasing values of 8Y as fossoriality increases. Fossorial species are listed in rank order of increasing fossoriality in Table 8. All tree squirrels have rank 0.

Initial assessments of the influence of size on shape change can be made from the same coordinate plots used to determine the influence of fossoriality on shape change. Small fossorial species are expected to diverge from tree squirrels in the same direction as larger species, but farther than larger species of the same fossoriality rank.

Size will be measured by body weight, but because body weights are not available for all specimens used in this study, regressions cannot be performed to test for correlations between scapular size and body weight in all species. However, scapular size can be determined for all individuals examined, and there is a strong relationship between mean scapular size and mean body weight (Table 9). Not only is this relationship highly significant (p<0.001), the correlation coefficient  $(r^2)$  is quite high, indicating that most of the interspecific differences

Table 8. Fossoriality ranks of fossorial sciurids used in analyses of scapular morphology. Fossoriality levels are median values of the scores, based on behavioral traits, listed in Table 1.

	Species	Fossoriality level	rank
<u>T</u> .	ruficaudus	3.5	1
<u>T</u> .	amoenus	4	3
<u>T</u> .	<u>minimus</u>	4	3
<u>s</u> .	<u>variegatus</u>	4	3
<u>T</u> .	rufus	5	5.5
<u>s</u> .	<u>lateralis</u>	5	5.5
<u>T</u> .	<u>striatus</u>	5.5	7.5
<u>s</u> .	<u>spilosoma</u>	5.5	7.5
<u>s</u> .	richardsonii	7	9.5
<u>s</u> .	<u>columbianus</u>	7	9.5
<u>s</u> .	tridecemlineatus	8	11

Table 9. Correlation of mean body weight with scapular size.

:	species	sample size	mean body wt. (g)	cube root body wt.	mean centroid size
<u>T</u> .	<u>minimus</u>	9	40	3.420	2.120
<u>T</u> .	amoenus	13	50	3.684	2.160
<u>T</u> .	<u>ruficaudus</u>	18	59	3.893	2.262
<u>T</u> .	rufus	20	57	3.849	2.387
<u>T</u> .	<u>striatus</u>	12	92	4.514	2.774
<u>s</u> .	<u>spilosoma</u>	6	135	5.130	3.038
<u>s</u> .	<u>tridecemlineatus</u>	2	182	5.667	3.109
<u>T</u> .	hudsonicus	8	170	5.540	3.383
<u>s</u> .	lateralis	11	202	5.867	3.422
<u>s</u> .	<u>deppei</u>	17	274	6.495	3.950
<u>s</u> .	<u>richardsonii</u>	19	346	7.020	4.415
<u>s</u> .	<u>columbianus</u>	20	509	7.984	4.622
<u>s</u> .	aureogaster	5	577	8.325	4.668
<u>s</u> .	<u>carolinensis</u>	5	554	8.213	4.889
<u>s</u> .	variegatus	8	646	8.645	5.302
<u>s</u> .	niger	8	7 <del>9</del> 7	9.272	5.415

t of slope = 108.3, p<0.001 r<sup>2</sup> = 0.880

Sample size is the number of individuals used to estimate mean body weight. This sample is restricted to individuals used in the analysis of scapular morphology for which weights were reported by the original collectors. Mean centroid size is based on the total sample of scapulae for each species (n=18-20). in mean scapular size are explained by differences in mean body weight. Thus, mean scapular size is a fair substitute for the more poorly estimated mean body weight in tests of transspecific allometry. Because sample sizes for body weight are small in most species, the static allometry of scapular size and body weight among adults within each species often cannot be determined. However, the allometric relationship between scapular size and scapular shape can still be examined to test whether interspecific differences are consistent with intraspecific variation.

The analysis of allometry between scapular size and scapular shape must be performed using multiple regression. This method is necessary because each landmark is represented by two values, its X and Y shape coordinates. Allometric changes in a landmark's position must be determined by simultaneously regressing centroid size on both coordinates. In this type of analysis, centroid size is the dependent variable having its variation explained by covariation with the X and Y shape coordinates (Snedecor and Cochran, 1967). This is an inversion of the usual conceptual model in which size is the independent variable used to predict changes in shape, but is consistent traditional attempts to infer the simultaneous affect of size on several traits (eg., Atchley et al. 1981, Jolicoeur and Mosimann 1960, Livezy 1989). If the multiple regression does indicate a statistically significant relationship between centroid size and the shape coordinates (indicated by an F-test of the squared multiple correlation  $\mathbb{R}^2$ , Snedecor and Cochran, 1967), a pair of standard univariate regressions can be performed to determine the change in each coordinate as a function of centroid size. In other words,

multiple regression indicates whether an allometric relationship exists, univariate regression describes the allometric relationship.

## RESULTS

The posterior landmarks (5-8) are expected to be directly affected by selection for increasing fossoriality. These landmarks should undergo the largest displacements and permit the clearest discrimination of species by level of fossoriality. The mean locations of landmarks 5, 7 and 8 for all 16 species (including all five tree squirrel species) are shown in Figure 28. The plot for landmark 8 shows that the five tree squirrels can be discriminated from the fossorial species. The axis of discrimination is unexpected: tree squirrels tend to have larger values of 8X, rather than smaller values of 8Y. For most fossorial species, the mean of 8Y falls within the range of tree squirrel means. The fossorial species outside the tree squirrel range all have smaller values of 8Y. Thus, the infraspinous fossa of fossorial species is shorter and sometimes narrower than the fossa of tree squirrels, not wider as expected.

Among fossorial species, the position of landmark 8 bears little, if any, relationship to the level of fossoriality. The means of 8X and 8Y, and the fossoriality ranks of the fossorial species are listed in Table 10. Coordinate means are ranked by distance from the origin, reflecting relative length (8X) and width (8Y) of the infraspinous fossa. Ranks of both coordinates are expected to be correlated with fossorality rank (8Y was not expected to change, but changes that do occur should be related to fossoriality). Spearman rank order correlations ( $r_s$ ) of



Figure 28. Mean coordinates of landmarks 5, 7, and 8. Labels at mean coordinate positions indicate fossoriality rank of the species with that mean. Arrows on axes point dorsally (X) and caudally (Y).

Table 10. Fossorial species ranked by fossoriality and coordinates of landmarks 8 and 7.

Spe	ecies	Fossorialit	У				Coord	inates			
_		rank		8X		83	ľ	71	K	73	2
			mean	, 1	rank	mean,	rank	mean,	rank	mean,	rank
<u>T</u> .	ruficaudus	<u>s</u> 1	0.9	87	6	0.272	8	0.958	4.5	0.292	7.5
<u>T</u> .	amoenus	3	0.9	92	7	0.236	3	0.963	6	0.260	4
<u>T</u> .	minimus	3	0.9	82	2	0.257	5.5	0.958	4.5	0.274	5.5
<u>s</u> .	variegatus	<u>s</u> 3	0.9	98	10	0.163	1	0.969	7.5	0.174	1
<u>T</u> .	<u>rufus</u>	5.	5 0.9	86	5	0.287	9	0.951	l	0.300	9
<u>s</u> .	<u>lateralis</u>	5.	5 0.9	93	8	0.219	2	0.974	10	0.240	2
<u>T</u> .	<u>striatus</u>	7.	5 1.0	07	11	0.238	4	0.985	11	0.255	3
<u>s</u> .	<u>spilosoma</u>	7.	5 0.9	97	9	0.291	10	0.970	9	0.316	10
<u>s</u> .	<u>richardsor</u>	<u>nii</u> 9.	5 0.9	80	1	0.257	5.5	0.954	2	0.274	5.5
<u>s</u> .	<u>columbian</u> u	<u>15</u> 9.	5 0.9	85	4	0.264	7	0.956	3	0.292	7.5
<u>s</u> .	<u>tridecemli</u>	ineatus 11	0.9	84	3	0.299	11	0.969	7.5	0.319	11

rs		8X	8Y	7X	7Y
	fossoriality rank	-0.27	0.43	0.05	0.43

p>0.05 for all values of  $r_{s}$ .

coordinate means with fossoriality are -0.27 for 8X and 0.43 for 8Y; neither is significantly different from 0.0 (p>0.05).

The position of landmark 7 does not discriminate as well between tree squirrels and fossorial sciurids as does the position of landmark 8. Two ground squirrels cannot be distinguished from tree squirrels by either 7X or 7Y: <u>S. tridecemlineatus</u> and <u>S. spilosoma</u>, fossoriality ranks 11 and 7, respectively. Most other fossorial species can be discriminated from tree squirrels by low values of 7Y. Discrimination between fossorial species and tree squirrels was expected on the Y axis, but the direction of divergence is contrary to expectation: the teres fossa has become narrower rather than wider. Mean coordinates of landmark 7 in fossorial species are included in Table 10. As with landmark 8, neither the X nor the Y coordinate of landmark 7 is correlated with fossoriality.

The position of landmark 5 can be used to distinguish the three most fossorial ground squirrels (ranks 9 and 11) from tree squirrels, but the lower fossoriality levels are difficult to distinguish from either tree squirrels or the most fossorial ground squirrels. During the transition from tree squirrel to the most fossorial ground squirrels, the position of landmark 5 has moved ventrally and caudally. This shift is consistent with the expected movement of landmark 5. Most of the other fossorial sciurids also show displacement of landmark 5 in at least one of the expected directions. One chipmunk, <u>T. amoenus</u>, cannot be distinguished from tree squirrels; and in one ground squirrel, <u>S. variegatus</u>, landmark 5 is anterior of its position in tree squirrels. Neither 5X nor 5Y is significantly correlated with fossoriality (Table 11).

Table 11. Fossorial species ranked by fossoriality and coordinates of landmark 5.

Species		Fossoriality	Coordinates				
-		rank	51	K	5 <b>Y</b>		
			mean,	rank	mean,	rank	
<u>T</u> .	<u>ruficaudus</u>	1	-0.119	4	0.193	6	
<u>T</u> .	ampenus	3	-0.096	2	0.161	3	
<u>T</u> .	minimus	3	-0.111	3	0.174	4	
<u>s</u> .	<u>variegatus</u>	3	-0.120	5	0.127	1	
<u>T</u> .	rufus	5.5	-0.141	8	0.157	2	
<u>s</u> .	<u>lateralis</u>	5.5	-0.130	7	0.215	10	
<u>T</u> .	<u>striatus</u>	7.5	-0.090	1	0.207	8	
<u>s</u> .	<u>spilosoma</u>	7.5	-0.179	11	0.204	7	
<u>s</u> .	richardsoni	<u>i</u> 9.5	-0.145	9	0.187	5	
<u>s</u> .	<u>columbianus</u>	9.5	-0.125	6	0.230	11	
<u>s</u> .	tridecemline	eatus 11	-0.149	10	0.214	9	

r,		5X	5 <b>Y</b>
	fossoriality rank	0.59	0.58

p>0.05 for both values of  $r_s$ .

Although fossorial sciurids differ from tree squirrels in the expected direction, the amount of difference does not appear to be associated with the level of fossoriality.

Failure to find consistent trends in landmarks 5, 7 and 8 may be due to the relatively small differences in mean fossoriality between fossoriality ranks. For example, ranks 1 and 3 correspond to fossoriality levels of 3.5 and 4. Most species in these two ranks have overlapping ranges of intraspecific variation in fossoriality level. A similar situation exists for species in ranks 5.5 and 7.5 (levels 5 and 5.5). In Figure 29, mean coordinate positions are plotted as in Figure 28, and fossorial species are segregated into 3 groups: a) low, fossoriality levels 3.5 and 4; b) medium, levels 5 and 5.5; and c) high, levels 7 and 8. Polygons connect (or surround) the mean coordinate positions of all members of a given fossoriality group; polygons are also drawn for tree squirrels.

The polygons for mean positions of landmark 5 show discrimination of high and medium fossoriality groups from tree squirrels (Figure 29). The high and medium groups cannot be discriminated from each other. There also appears to be restriction of the range of diversity during the transition from medium to high fossoriality. However, this may be an artifact of sampling: the high fossoriality group includes fewer species than any other group. High and low fossoriality groups also appear to be distinct, but the ability to discriminate between them may be weaker than shown if a larger sample of the high fossoriality group proves to have greater diversity. The polygons for landmark 5 also indicate that the

Figure 29. Ranges of mean coordinates of landmarks 4, 5, 7, and 8 in fossoriality groups. Letter labels indicate fossoriality group: T and t) tree squirrel, L and 1) low fossoriality species, M and m) medium fossoriality species, H and h) high fossoriality species. Upper case letters indicate relatively large members of the group, lower case letters indicate relatively small members of the group. Arrows on axes point dorsally (X) and caudally (Y).



Figure 29. Ranges of mean coordinates of landmarks 4, 5, 7, and 8 in fossoriality groups.

low fossoriality group cannot be distinguished from tree squirrels, and are poorly discriminated from the medium fossoriality group.

Re-examination of landmark 7 reveals that the fossoriality groups are each arrayed along a unique axis of variation (Figure 29). All three axes of differentiation are at low angles to the Y axis of the coordinate grid. In contrast, the distribution of landmark 7 in tree squirrels does not exhibit a strong directional bias. Also, the three fossoriality groups cannot be distinguished from one another, and the high and medium fossoriality groups include species that cannot be discriminated from tree squirrels. The polygons for landmark 8 clarify the discrimination between tree squirrels and fossorial species by this landmark (Figure 29). There also is less overlap of fossoriality group ranges for landmark 8 than for landmark 7. In addition, the axes of within group distribution of landmark 8 positions may be nearly parallel.

Examination of positional changes in the remaining landmarks will begin by determining whether the low, medium and high fossoriality groups can be distinguished from each other and from tree squirrels. If these groups can be discriminated in this coarse-grained analysis, a more detailed analysis by rank order correlation across finer fossoriality differences would be justified.

The distribution of mean positions of landmark 4 is similar to the distribution of landmark 5 (Figure 29). The ranges of fossoriality groups are smaller for landmark 4, and most pairs of groups cannot be readily distinguished. The high fossoriality group can be distinguished from the low fossoriality group and from tree squirrels. However, the direction of change is primarily caudal, not ventral as expected. Caudal

displacement of landmark 4 could be detrimental to digging ability if it exceeds the caudal displacement of landmark 5, shortening the ventral margin of the metacromion. This negative effect depends on landmark 4 serving as a consistent indicator of the boundary between retractors on the metacromion and protractors on the acromion. Alternatively, landmark 4 may not represent a functional boundary, or caudal movement of landmark 4 may be associated with recruitment of protractors to act as retractors.

The remaining caudal landmark, 6, permits discrimination of fossorial sciurids from tree squirrels, but does not permit discrimination between the three fossoriality groups (Figure 30). Relative to its location in tree squirrels, landmark 6 is ventral in fossorial sciurids. This landmark was expected to move dorsally during the evolution of fossoriality. The position of landmark 6 has also moved caudally in all fossorial sciurids except <u>S</u>. <u>variegatus</u>. Ventral movement of landmark 6 shortens the dorso-ventral length of the metacromion, potentially reducing the area available for retractors inserting on the metacromion. However, the area of the metacromion may not be reduced if there is sufficient widening of the metacromion. The net effect of shortening and widening cannot be determined from this plot but will be evaluated when scapular outlines are considered later in this chapter.

Landmarks 10, 11 and 12, on the supraspinous fossa were expected to be only indirectly affected by increasing fossoriality. Therefore, it is not surprising that fossoriality levels are not readily discriminated by the positions of these landmarks (Figure 30). What is surprising is that for each of these landmarks, the low fossoriality group is the most



Figure 30. Ranges of mean coordinates of landmarks 6, 10, 11 and 12 in fossoriality groups. Labels as in Figure 29.

divergent from tree squirrels. The direction of divergence is caudal at all three landmarks, so all sciurids in the low fossoriality groups have relatively narrower supraspinous fossae than tree squirrels. The direction of divergence in the low fossoriality group is consistent with expectation; the progressively greater similarity to tree squirrels as fossoriality increases is not consistent.

Landmark 10 shifts dorsally, as well as caudally. If the subscapular ridge on which 10 is located, were only shortening, landmark 10 would move ventrally and caudally. The combination of dorsal and caudal movements indicates that the ridge is rotating toward the spine. Lengthening or shortening of the ridge associated with rotation cannot be determined from this plot, alone, but must be deferred until the analysis of outlines later in this chapter. The caudal shift of landmark 11 is associated with dorsal movement in some species and ventral movement in others. The anterior marginal ridge associated with landmark 11 may have undergone several different combinations of changes in orientation and length.

Like landmarks 10, 11 and 12, landmarks 2 and 3 were expected to be indirectly affected by increasing fossoriality. Accordingly, caudal shifts poorly discriminating between fossoriality groups were anticipated for landmarks 2 and 3. Both 2 and 3 do show caudal changes that distinguish fossorial species from tree squirrels, but the main direction of change within fossorial sciurids is ventral (Figure 31). Within each fossoriality group, ventral shifts tend to be associated with small caudal shifts, but between-group transitions are characterized by even smaller caudal displacement relative to ventral displacement. There may



Figure 31. Ranges of mean coordinates of landmarks 2 and 3 in fossoriality groups. Labels as in Figure 29.

even be some cranial displacement in the transition to high fossoriality species. Caudal displacement of landmark 2 usually is smaller than the caudal displacement of landmark 3. This suggests a reorientation of the surface between 2 and 3 which articulates with the clavicle. Ventral displacement of the acromion was expected to occur in large tree squirrels to improve the mechanical position of the protractors relative to the humerus. This displacement may be serving the same purpose for the relatively reduced protractors of fossorial sciurids.

The influence of size on morphological change was examined by dividing tree squirrels and each of the fossoriality groups into large and small size classes. These size classes only apply within groups: in a comparison of mean weights, the large, medium fossoriality sciurids (S. spilosoma, 135g., and S. lateralis, 202 g.) are closer to small tree squirrels (S. deppei, 274 g., and T. hudsonicus, 170 g.) than to large, high fossoriality sciurids (S. richardsonii, 346 g., and S. columbianus, 509 g.).

Within tree squirrels, landmarks 5, 7, 8, 10 and 11 have distributions in which the mean landmark positions of the two small tree squirrels are located near one edge of the distribution (Figures 29 and 30). However, regression of scapular size on landmark coordinates failed to find significant relationships in tree squirrels at any landmark (p>0.05). Thus, there is no transspecific allometry among these five tree squirrels. Morphological differences among the scapulae of these species are independent of size. Also, only landmark 12 in <u>S. aureogaster</u> exhibited allometry in analyses of adults within species. Consequently, differences between tree squirrels and fossorial sciurids

cannot be interpreted as extrapolations of transspecific allometry or adult static allometry within tree squirrels.

Small size in the low fossoriality groups is represented by three chipmunk species, large size is represented by <u>S</u>. <u>variegatus</u>, the largest ground squirrel in this analysis. Mean landmark positions for <u>S</u>. <u>variegatus</u> are often distant from the landmark positions for chipmunks. In fact, the plots of landmark positions frequently indicate that <u>S</u>. <u>variegatus</u> is morphologically distinct from all of the other species in this study. In contrast, the low fossoriality chipmunks are rarely distinguishable as a separate group, and often cannot be discriminated from tree squirrels. The difference between <u>S</u>. <u>variegatus</u> and the chipmunks is allometric in so far as both size and shape are different. However, the contrast between <u>S</u>. <u>variegatus</u> and the chipmunks is best regarded as an artifact of the analytic procedure: the morphology of <u>S</u>. <u>variegatus</u> is an anomaly among all fossorial sciurids, not just among low fossoriality species. Another low fossoriality ground squirrel might have presented a very different contrast.

The medium fossoriality group includes two chipmunks and two small ground squirrels. The ground squirrels constitute the large size class in this fossoriality group. The differences in positions of landmarks 2 and 3 between large and small members of this group appear to be consistent with the general trend of landmark displacement between fossoriality groups. However, the gap between large and small members of the medium fossoriality group are quite large. Consequently, the large members, medium fossoriality ground squirrels, are more similar to high fossoriality ground squirrels, and the small members, medium fossoriality

chipmunks, are more similar to low fossoriality chipmunks. These similarities suggest a phylogenetic contrast rather than an allometric one: the difference between medium fossoriality ground squirrels and chipmunks may be due to the separate phylogenetic histories of the two genera and are only coincidentally associated with a size contrast in this sample of four species. The plots of mean positions for landmarks 4, 5, 11 and 12 also suggest that the apparent size contrast may actually reflect phylogenetic divergence. The mean positions of landmark 10 may be a less distinct version of coincidental size and phylogenetic difference between medium fossoriality chipmunks and ground squirrels. The plots of landmarks 6, 7, and 8 have the large and small medium fossoriality sciurids arrayed in crossing patterns. These are the only landmarks that do not reflect the taxonomic affiliations of the medium fossoriality sciurids, but clearly, they also do not reflect allometric trends.

Possible allometries in the high fossoriality group could not be rigorously tested because there are only three species in this group. The plots of landmark means in these three species should be colinear with the small species, <u>S</u>. <u>tridecemlineatus</u>, most divergent from tree squirrels, in the expected direction. The largest of the three species, <u>S</u>. <u>columbianus</u> should be closest to tree squirrels. The intermediate sized species is <u>S</u>. <u>richardsonii</u>. Only the plots of landmarks 3, 6, 7, and 10 show the means of these species in a nearly linear array, but <u>S</u>. <u>richardsonii</u> does not occupy the intermediate position in any of the four plots. The mean positions of most of the remaining landmarks (4, 5, 8 and 11) indicate that <u>S</u>. <u>tridecemlineatus</u> differs from the other two

species in the expected direction. However, these four contrasts between <u>S. tridecemlineatus</u> and the other two species cannot be attributed definitively to allometry. <u>S. richardsonii</u> is also smaller than <u>S. columbianus</u>, so allometry cannot be a complete explanation of both divergences from S. columbianus.

Comparisons between size classes within fossoriality groups revealed some morphological differences that could be attributed to allometry, but most of the morphological differences may actually reflect phylogenetic divergence that is unrelated to the evolution of size. Morphological differences between tree squirrels, chipmanks and ground squirrels are illustrated in Figures 32, 33 and 34. These are the same plots of species means as in Figures 29, 30 and 31, but with taxonomic groups highlighted rather than functional groups. Most landmarks suggest that only two groups can be distinguished, but do not agree on which two groups: 6, 7, and 8 indicate that tree squirrels can be discriminated from ground squirrels + chipmunks; 12 discriminates chipmunks from tree squirrels + ground squirrels; 4 and 5 (if <u>S</u>. variegatus is excluded) discriminate ground squirrels from tree squirrels + chipmunks. The lack of agreement among these landmarks indicates that the divergences of ground squirrels and chipmunks from tree squirrels are characterized by changes in different combinations of landmarks. In addition, the mean positions of four landmarks (2, 3, 6, and 11) suggest that chipmunks and ground squirrels diverge from tree squirrels in different directions at each of these landmarks. Only landmarks 2 and 3 permit all three taxonomic groups to be distinguished, but the various patterns described



Figure 32. Ranges of mean coordinates of landmarks 4, 5, 7 and 8 in taxonomic groups. T) tree squirrels, C) chipmunks, G) ground squirrels.



Figure 33. Ranges of mean coordinates of landmarks 6, 10, 11 and 12 in taxonomic groups. Labels as in Figure 32.



Figure 34. Ranges of mean coordinates of landmarks 2 and 3 in taxonomic groups. Labels as in Figure 32.

above provide abundant evidence that scapular evolution has followed different paths in chipmunks and ground squirrels.

Within these taxonomic groups evidence of transspecific allometry was rare. The lack of transspecific or static adult allometry in tree squirrels was reported earlier in this chapter. There also was no transspecific or static adult allometry in chipmunks. Static adult allometry could not be found in ground squirrels, and only landmarks 2 and 5 exhibit transspecific allometry in ground squirrels: +2X, +5X, -5Yas size increases (p<0.05). These allometries are consistent with expectation, but the slopes (<0.03) and  $r^2$ 's (<0.3) are quite low, indicating that only small proportions of the changes in landmark positions are associated with the evolution of size.

The results of the preceding analyses of landmark displacements suggest that the landmark positions may be evolving independently. None of the plots of landmark positions in Figures 32, 33 and 34 can be made to fit any other plot by translation, rotation, inversion or rescaling. Thus, there is no common pattern of change shared by any subset of these landmarks. The lack of a consistent pattern of change and the effect of the individual landmark changes on scapular morphology can be most clearly shown by comparing scapular outlines. Figure 35 shows approximate scapular outlines drawn by connecting the mean coordinate positions of the landmarks. One outline represents the mean shape of all five tree squirrel species. The other two outlines are means of single species of chipmunks: T. <u>striatus</u> and T. <u>minimus</u>. These two chipmunks are often at different poles of the chipmunk distribution, and therefore



Figure 35. Mean scapular outlines of tree squirrels and chipmunks. T) mean of five tree squirrel species, S) <u>T</u>. striatus, M) <u>T</u>. minimus. Landmarks labelled by number.

represent a substantial portion of the range of scapular diversity in the genus <u>Tamias</u>.

The scapulae of T. minimus and T. striatus have undergone very different patterns of morphological divergence from the tree squirrel scapula. The acromion is shortened and narrowed in T. minimus; it is ventrally displaced in T. striatus. The narrowing in T. minimus is accomplished by ventral displacement of landmark 2 without a corresponding displacement of landmark 3. The ventral displacement of whole acromion in T. striatus appears to be a rotation of the acromion which straightens the angle at landmark 4. The two chipmunks have different displacements at landmarks 4 and 5 but the ventral edge of the metacromion is in the same position and orientation in both species. The only difference is that the length of this edge is greater in T. striatus. Caudal displacements of landmarks 5 and 6 are greater in <u>**T**</u>. <u>striatus</u> than in <u>**T**</u>. <u>minimus</u>, but there is greater ventral displacement of landmark 6 in <u>T. minimus</u>. The result is a large increase in metacromial area in T. striatus, and probably a net reduction of area in T. minimus. The position of the metacromion and the resulting muscle orientation appears to be equally efficient in both chipmunks. Thus, there appears to have been independent changes of area and position by independent modification of distinct regions of the metacromion.

The infraspinous fossa is narrowed and shortened in <u>T</u>. <u>minimus</u>, it is only narrowed in <u>T</u>. <u>striatus</u>. The difference may reflect pressure on <u>T</u>. <u>striatus</u> to maintain the primitive position of vertebral border of the fossa. There are roughly equivalent reductions of the teres fossa in both taxa, possibly indicating integration of landmarks 7 and 8. In the

supraspinous fossa, the primitive position of the vertebral border is maintained in both chipmunks, which could signal integration of the subscapular ridge and the vertebral border. If these two structures are integrated, rotation of the ridge would be accompanied by lengthening as the dorsal end of the ridge tracks the border. There is greater shortening of the vertebral border in T. minimus than in T. striatus. Substantial change of supraspinous width between landmarks 10 and 11 occurs only in T. minimus. Between landmarks 11 and 12, the fossa of both chipmunks is considerably narrower than in tree squirrels. Narrowing of the ventral portion of the fossa occurs by translation of the marginal ridge in T. striatus, and by rotation of the ridge in T. minimus. Thus, similar transformations of the supraspinous fossa apparently were accomplished by different combinations of independent local transformations in separate regions of the fossa. Also notable is the fact that the metacromion was more modified in  $\underline{T}$ . striatus than in T. minimus, while the supraspinous fossa was more modified in T. minimus. If both species are responding to pressure on digging ability, then they have had quite different responses to the same pressure.

Figure 36 shows the outline of the mean tree squirrel and outlines of three ground squirrels. <u>S. tridecemlineatus</u> and <u>S. richardsonii</u> are shown because they often represent opposite poles of the ground squirrel distribution. <u>S. variegatus</u> is included to illustrate its unique morphology. All three ground squirrels show straightening of the angle at landmark 4, and all three have more straightening than occurred in <u>T. striatus</u>. In <u>S. variegatus</u>, as in <u>T. striatus</u>, straightening of this angle involves rotation of the acromion with little change in the



Figure 36. Mean scapular outlines of tree squirrels and ground squirrels. T) mean of five tree squirrel species, V) <u>S</u>. <u>varieqatus</u>, R) <u>S</u>. <u>richardsonii</u>, L) <u>S</u>. <u>tridecemlineatus</u>. Landmarks labelled by number.

position of the metacromion. In <u>S. richardsonii</u> and <u>S. tridecemlineatus</u>, rotation of the acromion is accompanied by ventral displacement of landmark 5, rotating the ventral edge of the metacromion as well. Landmarks 2 and 3 have different relative caudal displacements in the three ground squirrels, producing different orientations of the acromioclavicular articulation between these landmarks. There is caudal widening of the metacromion in both S. tridecemlineatus and S. richardsonii, but it is produced by different combinations of displacements at landmarks 5 and 6. In <u>S</u>. tridecemlineatus there is relatively greater widening at 5 and shortening at 6, producing a reorientation and possible shortening of metacromial area in this species. This combination of changes may have resulted in a relatively greater metacromial area and a more mechanically efficient muscle orientation in <u>S</u>. <u>tridecemlineatus</u> than is present in <u>S</u>. <u>richardsonii</u>. The metacromion of S. variegatus is both shorter and narrower than the tree squirrel metacromion. These comparisons indicate that local regions of the acromion and metacromion can be modified independently.

The three ground squirrels have shorter infraspinous fossae than tree squirrels. The amount of shortening differs among the ground squirrels, but the vertebral border of the fossa is in approximately the same orientation in all three species, indicating that the width and length of the fossa may be integrated in ground squirrels. Narrowing of the teres fossa also appears to be positively associated with narrowing of the infraspinous fossa. The infraspinous fossa of <u>S</u>. <u>tridecemlineatus</u> is wider than the tree squirrel mean, but narrower than the means of some individual tree squirrel species.

The location of landmark 10 in <u>S</u>. <u>tridecemlineatus</u> differs only slightly from its location in tree squirrels. Dorsal movement of this landmark in <u>S</u>. <u>richardsonii</u> reflects both caudal rotation of the subscapular ridge and lengthening of the ridge associated with dorsal rotation of the anterior vertebral border. In <u>S</u>. <u>variegatus</u>, there is shortening and rotation of the ridge, and shortening and lowering of the vertebral border. Thus, the orientations of the subscapular ridge and anterior vertebral border are not integrated, nor are the anterior and posterior segments of the vertebral border.

Landmark 10 is not the only location on the supraspinous fossa where a ground squirrel exhibits little divergence from tree squirrels: landmark 12 exhibits only a small change in S. variegatus, both 11 and 12 have only small changes in <u>S</u>. <u>richardsonii</u>. The combined changes in locations of landmarks 10 and 11 in S. variegatus have resulted in substantial narrowing of the fossa. Local narrowing is roughly proportional to the primitive width in tree squirrels, effectively flattening the anterior marginal curve. The subscapular and anterior marginal ridges are both rotated toward spine, and the anterior marginal ridge is substantially shortened. In S. richardsonii, rotation and lengthening of the subscapular ridge results in a slight dorsal expansion of the supraspinous fossa. The small changes at landmarks 11 and 12 result in a small caudal translation of the marginal ridge without any rotation. This results in a slight narrowing of the middle and ventral portions of the supraspinous fossa in <u>S</u>. richardsonii. The narrowing appears to exceed the lengthening, so there is a very small reduction of the area of the fossa in this species. S. tridecemlineatus has an

unusual modification of the supraspinous fossa: the subscapular ridge is nearly unchanged but the anterior marginal ridge is rotated away from the spine and dramatically shortened. Thus, the dorsal region of the fossa is unchanged, the middle is substantially reduced, and the ventral region is considerably enlarged. The net effect is a narrower, almost rectangular fossa with only a slight reduction of area. These transformations in ground squirrels show that they, like chipmunks, each have unique morphological transformations of the scapula. In addition, there has been independent modification of most local regions of the scapula in both chipmunks and ground squirrels. Only landmarks 7 and 8 in ground squirrels have displacements suggestive of integration between scapular regions.

## DISCUSSION

Each of the functional groups of species used in this study has a distinctive scapular morphology. However, most of the morphological differences between groups are inconsistent with their differences in fossoriality. Widening of the metacromion is the only persistent transformation that is clearly consistent with increasing fossoriality. There are other shape transformations consistent with the transition from arboreality to low fossoriality but these changes are reversed in the transition from low fossoriality to high fossoriality. Other transformations are consistent with the transition from low fossoriality to high fossoriality, but are reversals of changes conflicting with the transition from arboreality to low fossoriality. In contrast, one of the most persistent transformations, the postero-ventral movement of the
acromio-clavicular articulation, has no obvious connection with digging ability. Based on these results, the evolution of digging cannot be a general explanation of scapular evolution in fossorial sciurids. These results do indicate that the scapula is evolving, but not in response to the mechanical demands of digging.

There is no indication that allometry has prevented scapular morphology from responding to the demands of digging. Transspecific allometry was rarely found, and the allometry that can be identified with any degree of certainty tends to be consistent with the changes expected to accompany increasing fossoriality. In addition, the allometries that were found did not prevent changes that conflict with increasing fossoriality, so the factors that are driving morphological evolution were capable of overriding any restrictions on change that might have been imposed by allometry. Other allometric trends may exist across ages or across small lineages within genera. Larger samples and better phylogenies will be necessary to test whether these allometries exist and whether they influence morphological evolution.

Analysis of the evolutionary changes in the locations of individual landmarks shows that the anatomically distinct regions of the scapula evolve independently. The only landmarks that appear to be integrated are 2 with 3 and 7 with 8. However, there may be more integration of the scapula than is represented by these results, either during development or within smaller taxonomic units. Zelditch and Carmichael (1989) have demonstrated that integration acting during restricted periods of development may have no effect on morphological evolution if selection acts during the unintegrated periods of development. Even if integration

persists throughout development, selection may act on the integrating factors (Burger 1986, Wagner 1988) and produce a pattern of morphological change that could not be predicted from any one pattern of integration. Again, sampling across ages and within narrower taxonomic ranges will be necessary to demonstrate that integration exists within these shorter periods.

The results of my study do not imply that there are no changes in the scapular region attributable to the evolution of fossoriality; only that the scapula, itself, is only weakly affected by digging. This may indicate that the musculature has responded to the functional shift in a way that did not require modification of the scapula. Goldstein (1977) has demonstrated that there is variation in the proportion of white and red muscle fibers in fossorial mammals producing variation in oxygen demand and energetic efficiency of muscle activity. Stalheim-Smith (1989) demonstrated that differences in muscle contraction can produce differences in output force without modification of muscle attachment area or position. Alternatively, the results of my study may simply reflect the fact that the largest retractors (pectoralis and latissimus dorsi) by-pass the scapula. Thus, the possibility exists that substantial changes in digging ability may be effected without corresponding modification of the scapula.

The possibility of independent response of the musculature to increasing fossoriality might explain a failure to find evolutionary changes in scapular morphology. However, my results indicate that the scapula is evolving, but that the pattern of evolution often is not consistent with increasing fossoriality. There also are different

patterns of scapular evolution in chipmunks and ground squirrels. Subsequent analyses must determine what alternative factors might act on scapular morphology, giving special consideration to those that discriminate between chipmunks and ground squirrels. One possibility is that chipmunks, tree squirrels and ground squirrels may each differ in the sequence of limb movements during climbing and digging. If so, different muscles could be acting during the power stroke, and different modifications of muscle attachment sites would be needed accommodate a increased load on whichever set of muscles has primary responsibility for generating the necessary force. Changing the sequence might also shift the load to larger muscles capable of generating the larger forces, thereby avoiding the need for a corresponding skeletal modification.

The comparisons of changes in mean landmark positions between landmarks, and the comparisons of scapular outlines, indicate that the scapula should be treated conceptually as a multielement system, despite being a single bone. Like the skull, the scapula plays a variety of functional roles and its evolution may be a compromise response to several independent functional demands. With this multiplicity of roles, it should not be surprising if future study uncovers a shifting pattern of integration and allometry and a variety of responses to seemingly simple functional transitions.

## SUMMARY AND RECOMMENDATIONS FOR FUTURE STUDY

The ability of an animal to function in its environment is expected to be one of the primary factors determining the course of morphological evolution. In this dissertation, I examined patterns of morphological evolution in two groups of fossorial (burrowing) mammals: Soricidae and Sciuridae. Burrowers are expected to have structures permitting them to exert and withstand large forces. The limb joints of fossorial animals are expected to have modifications which restrict freedom of movement at the joint, reducing the potential of obstructions (pebbles, roots) to deflect the digging stroke. These limitations on movement should reduce both wasted energy and the risk of injury (sprain, dislocation). On the scapula there should be changes in the sizes of muscle attachment areas. These changes should reflect the relative importance of muscles during digging: muscles directly contributing to the production of forces needed for digging should have increased attachment areas; muscles that do not contribute to digging ability should have reduced attachment areas. The amount of morphological change, in both scapula and joints, should reflect the relative importance of digging ability in the animal's ecology (level of fossoriality). As fossoriality increases, the morphological divergence from non-fossorial ancestors should also increase. Thus, the direction and amount of change in morphology are expected to reflect the direction and amount of change in fossoriality.

A variety of factors are expected to modify the morphological response to the evolution of function; integration, complexity and size

were examined in this dissertation. Integration, by requiring changes in multiple structures to be coordinated, may modify the direction of morphological change. The rate of morphological change may also be affected by integration. If integration unifies the responses of structures under different selection pressures, morphological change may be retarded, but if integration unifies the responses of structures under a common selection pressure, morphological change may be accelerated. Increasing complexity, by raising the number of structures that are coordinated by integration, is expected to amplify the influence of integration. Size is expected to modify only the rate of morphological change. Selection pressure to improve the digging ability of small animals should be more intense than selection pressures on larger animals, but size alone should not alter the way in which morphology is changed. Thus, size, complexity and integration were expected to account for at least some of the cases in which the amount or direction of morphological change differed from the morphological change predicted from the evolution of function.

In the wrist joints of the shrews (Soricidae) that were examined during this project, only a few morphological changes were found. These changes distinguish one lineage of fossorial shrews from non-fossorial shrews, but the changes were not found in all fossorial shrews. Thus, the morphological changes that were found reflect taxonomic differences not functional differences. The morphological differences among shrew wrists may be independent of fossoriality because all non-fossorial shrews have the types of morphological structures that fossorial species were expected to acquire. These structures probably were present in the most recent common ancestor of all shrews. The primitiveness of these structures may indicate that the common ancestor of shrews was fossorial; but if this were the case, the retention of these structures in non-fossorial species remains to be explained. Alternatively, the small size of shrews may require relatively stronger joints than are present in most other mammals. This would account for the lack of divergence between fossorial and non-fossorial shrews as well as the primitiveness of the structures fossorial shrews were expected to acquire.

The joints of fossorial sciurids underwent numerous morphological changes. Most of the changes are consistent with increasing fossoriality, but almost half of the changes are detrimental to digging ability. None of the joints exhibited a persistent, progressive series of changes consistent with increasing fossoriality. In the forelimb joints, many of the expected changes were associated with, or followed by, changes detrimental to digging ability. Hindlimb joints exhibited expected changes early in the divergence of fossorial species from tree squirrels, but exhibited little additional modification during subsequent diversification of the fossorial lineage. Thus, there is a slight tendency for the evolution of joints to follow the direction of change indicated by increasing fossoriality, but the amount of morphological change in not consistent with the amount of change in fossoriality.

Integration and complexity were hypothesized to account for the discrepancy between the evolution of morphology and the evolution of fossoriality. Because joints could only be classified as integrated or unintegrated, detailed examination of the influence of integration and complexity was not possible. In addition, the presence or absence of

integration at a particular joint did not differ between any of the species examined for this study, so analyses of the influence of integration and complexity were based on differences between joints rather than between taxa. Integration and complexity do appear to account for differences in evolutionary rate between joints within the forelimb or hindlimb, but do not account for differences in rate between the forelimb and hindlimb. Integration and complexity also do not appear to have influenced the direction of morphological change: the proportion of changes consistent with increasing fossoriality does not differ between integrated and unintegrated joints. Thus, there is no discernable link between the distribution of counterbalancing changes and the distributions of integration and complexity.

The influence of body size on the evolutionary patterns of small fossorial sciurids (chipmunks) and the larger ground squirrels cannot be determined from my analysis. In neither group are there enough differences between species to determine whether a similar pattern exists within either chipmunks or ground squirrels. Also, the pattern found in chipmunks is similar to the evolutionary pattern of the largest fossorial sciurids, woodchucks. If size is responsible for the evolutionary patterns of chipmunk and woodchuck joints, the affect of size would appear to be determined by deviation from an intermediate size within the size range of ground squirrels.

Like the analysis of sciurid joints, the analysis of sciurid scapulae revealed considerable morphological change. Changes consistent with increasing fossoriality appear to be less frequent in scapulae than in joints. Few parts of the scapula exhibited a consistent trend in any direction; those that did, exhibited changes that do not appear to be linked to digging ability. In addition, changes that are consistent with improving digging ability are counterbalanced by changes in other parts of the scapula that appear to reduce digging ability. Thus, in the scapula, as the joints, the amount of morphological change is not consistent with the amount of change in fossoriality.

A few parts of the scapula are integrated, as shown by coordinated patterns of change within each integrated complex. One integrated complex exhibits a consistent trend that is unrelated to digging ability. The other integrated complex exhibits wild fluctuation of both direction and amount of change as fossoriality increases. The erratic evolutionary behavior of the latter complex is consistent with the behavior of other parts of the scapula. Therefore, in the scapula as in the joints, deviation from expected improvements of digging ability cannot be attributed to inhibitions on morphological evolution imposed by integration.

The analysis of the influence of body size on scapula evolution also produced a result confirming the conclusion based on the coarser analysis performed on joints. Comparisons between species of similar fossoriality and different sizes found differences in scapular morphology only when the species were distantly related (represented different genera). Few of the differences found in these size comparisons were consistent with the expectation that the smaller species would have better digging ability. The association of these differences with taxonomic relationships provide further evidence that the observed morphological differences do not reflect an interaction between size and fossoriality. Instead, differences in scapular morphologies among sciurids, reflect phylogenetic relationships and are not associated with either size or fossoriality.

The results of this dissertation are contrary to several conventional models of morphological evolution. In sciurids, and possibly in shrews, morphological evolution failed to produce a consistent suite of structural changes in response to a history of persistent functional change. The functional transition cannot be dismissed as trivial; much of the animals' ecology depends on acquisition, modification and utilization of a burrow. The energetic costs of maintaining a burrow are high, and the penalties for inadequate energy investment on a burrow are steep. Under these circumstances, the expectation of substantial morphological change improving digging ability is reasonable.

The dissertation may have focussed on the wrong structures: there may be substantial, consistent modification of the proportions and muscle attachment surfaces of the long bones of the limbs (e.g., humerus, ulna, tibia). This possibility is readily investigated, but the result would not explain why the lack of consistent change in the scapula and joints. If the long bones also do not show a consistent pattern, an explanation is needed for fluctuating changes in the whole limb; if the long bones do show a consistent pattern, an explanation is needed for the difference in response between regions of the limb. Conventional explanations for lack of morphological change focus on the evolutionary roles of integration and allometry. Allometry and integration are rare in the scapula. Integration was evident in some but not all joints. In the scapula and joints, morphological differences reflect taxonomic affiliation more frequently than size or integration. These results suggest that neither allometry nor integration are as widespread as they are alleged to be (cf. Dullemeijer 1974, Moss and Young 1960, Olson and Miller 1958, Rieldl 1978). For most structures in the sciurid joints and scapulae, allometry and integration are not present, and therefore cannot be implicated in the failure of morphology to respond to the evolution of fossoriality. Lack of morphological change despite an important functional transition, and morphological change conflicting with a functional transition, are not dependent on limitations imposed by integration or allometry.

The results of this dissertation do not permit identification of the factor or factors that are responsible for the absence of consistent patterns of morphological change in the joints and scapulae of fossorial sciurids. However, the results do provide some clues which suggest lines of research that may uncover explanations for the patterns of morphological evolution described in this dissertation. Other clues are furnished by comparing the ecology of ground squirrels to the ecology of pocket gophers (on which the expectations of this dissertation are based), and by exploration of the functional interactions among skeletal structures in limbs.

One of the clues is the tendency of the scapulae and joints of fossorial sciurids to combine changes that improve digging ability with changes that reduce digging ability. The changes that reduce digging ability improve running ability. These changes usually are not reversals

of earlier transformations, but are modifications of primitive traits. Thus, the suite of apparently conflicting transformations may represent combined improvements in both running and digging abilities; both abilities appear to be important components of fitness. The contrasting demands of running and digging do not appear to impose a tradeoff in the conventional sense. Improvement of one ability may be tempered or inhibited by improvement of the other ability, but modifications favorable to both abilities do accumulate.

Running ability is one of the major functional differences between ground squirrels and pocket gophers. All fossorial sciurids forage above ground and must be able to run to the nearest hole to escape from predators. Pocket gophers forage from within their tunnels, which protect them from detection by predators. Thus, pocket gophers may have greater improvement of digging ability because their greater fossoriality serves to reduce selection on running ability.

The hypothesis of a tradeoff between running and digging ability can be tested in comparative studies of pocket gophers and the closely related kangaroo rats. Both groups are derived from pocket mice, semi-fossorial, semi-arboreal rodents ecologically similar to chipmunks. Fossoriality increases dramatically in the transition from pocket mouse to pocket gopher; there is little if any change of fossoriality in the transition from pocket mice to kangaroo rats. In both lineages the locomotor function of the forelimb is reduced: in pocket gophers, because subterranean habits have reduced selection for locomotor ability; in kangaroo rats, because bipedalism focuses selection for locomotor ability on the hindlimb. Neither group should have the counterbalanced changes observed in fossorial sciurids, at least not to the same degree (kangaroo rats and pocket gophers do use forelimbs for slow locomotion). A corroborating comparison could also be made within pocket gophers. Some pocket gophers employ their incisors as auxiliary digging tools. The use of teeth in digging may reduce the need for the forelimb to respond to selection for digging ability and permit the hand to respond more freely to selection on locomotor ability. The results may show that tooth-digging pocket gophers are better dispersers and are better able to escape those predators that do invade the burrow.

The study proposed in the previous paragraph may also explain the contrasting phylogenetic patterns of different sciurid groups. Differences between patterns of morphological evolution may represent different balances of the various forelimb functions. The different compromises would result in different amounts and combinations of morphological change for a given increase in fossoriality.

An alternative explanation for the contrasting patterns may be variation in allometry or integration. There appears to be little of either in chipmunk and ground squirrel limbs, but they may be evident in infrageneric lineages. If changes in allometry or integration characterize divergence of subgenera or species group, there may be no common patterns to characterize whole genera. Different allometries or patterns of integration may also account for the failure of morphological differences to match relatively simple models of functional divergence. Different characteristic trends in the evolution of integration and allometry may even account for the morphological divergence between ground squirrels and chipmunks without reference to functional

divergence. The search for diversity in patterns of allometry and integration should also be conducted within species (e.g., variation in allometric growth between individuals or populations, variation in integration across ontogeny or between populations). There are many taxonomic levels where variability of allometry or integration may be obscuring the common pattern that was expected to emerge from the analyses performed for this dissertation.

The last clue to be discussed here is the observation that when integration was found, it tended to unite structures found on different bones, not structures found on the same bone. In fact, the scapula was not expected to be integrated because few parts interact directly. Most parts of the scapula are only associated through functions shared by the separate muscles attaching each part. One of the two instances of scapular integration was at a joint where the two parts were codeterminants of the orientation of an articular surface. Similary, at the joints that were analyzed, there appeared to be integration between bones, but little within bones. Evidently, two structures on one bone may be more integrated with separate structures on other bones than with each other. Also, bones on opposite sides of a joint were more likely to be integrated than bones on the same side. These results suggest that future studies on integration in limbs should focus on structures bridging joints. Such studies would include analyses of the attachment sites of the muscles producing movement at the joint, and the attachment sites of the ligaments preventing disarticulation at the joint.

The analysis of integration between bones could be performed on limbs. The study would examine covariation among structures from

different bones within the limb. However, a project of this type would probably be limited by the small number of segments within a single limb. In addition, the results may be confounded by functional differentiation between limb segments. A study focussing on vertebral structures might permit a more robust assessment of the relative importance of within-bone and between-bone integration. One advantage offered by the vertebral column is the fact that it contains a much larger number of joints. The other advantage results from the pattern of functional differentiation along the vertebral column. The vertebral column can be divided into functional regions (cervical, thoracic, lumbar, etc.) Functional difference between regions are generally larger than functional differences pairs of vertebrae within regions. Sampling several pairs of vertebrae within each region and avoiding vertebrae in transitional zones between regions would allow the influence of functional on integration to be removed as a separate factor prior to any analysis of integration within and between serial structures.

The results of my dissertation do not permit definitive identification of the factors responsible for morphological evolution in shrews and squirrels. However, these results do demonstrate morphology has not responded to an important functional transition. In addition, allometry and integration either did not exist or did not exert any control over the long term pattern of morphological change. Based on these results, constraints imposed by allometry or integration should not automatically invoked to explain the absence of a coherent morphological response to the evolution of function.

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APPENDIX A

## APPENDIX A

## SAMPLE SIZES FOR JOINTS

	total	wrist	ankle	elbow	knee
Soricidae					
<u>Crocidura</u> <u>horsfieldi</u>	3	3			
<u>Suncus murinus</u>	2	2			
<u>Notiosorex</u> crawfordi	2	2			
Sorex arcticus	4	4			
<u>S. araneus</u>	1	1			
<u>S. cinereus</u>	8	8			
<u>S. fumeus</u>	3	3			
<u>Blarina</u> <u>brevicauda</u>	11	11			
<u>Cryptotis goodwini</u>	2	2			
<u>C. parva</u>	4	4			
<u>C. nigrescens</u>	2	2			
Sciuridae					
Tamiasciurus hudsonicus	<u>s</u> 5	5	5	5	5
<u>Sciurus carolinensis</u>	4	4	4	4	4
<u>S. niger</u>	3	3	3	3	3
<u>Tamias</u> <u>striatus</u>	8	8	5	8	7
<u>T. bulleri</u>	1	1	1	1	1
T. amoenus	4	1	4	4	4
<u>T. ruficaudus</u>	4	4	4	4	3
<u>T. minimus</u>	1	1	1	1	1

	total	wrist	ankle	elbow	knee
<u>Marmota monax</u>	3	3	3	3	3
<u>M. flaviventris</u>	3	3	3	3	3
Spermophilus lateralis	7	3	5	5	6
<u>S. columbianus</u>	5	5	5	5	5
<u>S. spilosoma</u>	9	3	9	5	6
<u>S. tridecemlineatus</u>	6	6	6	6	5
Cynamys gunnisoni	2	2	2	2	2
<u>C. ludovicianus</u>	3	3	3	3	3