Geographic Variation in Morphology and Allozymes Within Tree Squirrels, Sciurus Niger and S. Carolinensis, of the Lower Mississippi River Valley.

Nancy D. Moncrief
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Geographic variation in morphology and allozymes within tree squirrels, *Sciurus niger* and *S. carolinensis*, of the lower Mississippi River valley

Moncrief, Nancy D., Ph.D.
The Louisiana State University and Agricultural and Mechanical Col., 1987
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GEOGRAPHIC VARIATION IN MORPHOLOGY AND ALLOZYMES

WITHIN TREE SQUIRRELS, SCIURUS NIGER AND

S. CAROLINENSIS, OF THE LOWER MISSISSIPPI RIVER VALLEY

A Dissertation

Submitted to the Graduate Faculty of the Louisiana State University and Agricultural and Mechanical College in partial fulfillment of the requirements for the degree of Doctor of Philosophy in The Department of Zoology and Physiology

by Nancy D. Moncrief
B.S., Memphis State University, 1978
M.S., Fort Hays State University, 1981
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TABLE OF CONTENTS

ACKNOWLEDGEMENTS .................................................................11
LIST OF TABLES ........................................................................vi
LIST OF FIGURES ......................................................................vii
ABSTRACT...................................................................................ix

INTRODUCTION.............................................................................1
Importance of Geographic Variation to Evolutionary Theory ..........1
Analytical Techniques: Goals and Inferences.................................3
The Potential Role of the Mississippi River in Effecting and/or
Maintaining Differentiation among Populations .........................8
Previous Studies of Geographic Variation in Fox and Gray
Squirrels..................................................................................13
Objectives of This Study...........................................................15

MATERIALS AND METHODS.......................................................17
Sampling Design and Allocation of Specimens to A Priori Groups..17
Morphometric Analyses...............................................................18
Electrophoretic Analyses...........................................................23
RESULTS AND DISCUSSION ..................................................30

Sciurus niger..................................................30
Morphometric analyses..............................................30
Electrophoretic analyses............................................37

Sciurus carolinensis............................................45
Morphometric analyses..............................................45
Electrophoretic analyses............................................49

Changes in the Vegetation of Eastern North America During the Last 40,000 Years: Potential Effects on Evolution in Tree Squirrels of the Genus Sciurus............................................56

Recent Geologic and Physiographic History of the Lower Mississippi River Valley.............................................60

Patterns of Variation in Fox and Gray Squirrels: Potential Effects of the Mississippi River on Differentiation in Tree Squirrels............................................62

Conclusions..........................................................74

LITERATURE CITED ..........................................................76

TABLES ...........................................................................93

FIGURES .................................................................113

APPENDIX I ...............................................................140

APPENDIX II .............................................................149

CURRICULUM VITAE .....................................................152
<table>
<thead>
<tr>
<th>TABLE</th>
<th>PAGE</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 Samples of <em>Sciurus niger</em> used in morphometrics</td>
<td>93</td>
</tr>
<tr>
<td>2 Samples of <em>Sciurus carolinensis</em> used in morphometrics</td>
<td>94</td>
</tr>
<tr>
<td>3 Samples of <em>Sciurus niger</em> used in electrophoresis</td>
<td>95</td>
</tr>
<tr>
<td>4 Samples of <em>Sciurus carolinensis</em> used in electrophoresis</td>
<td>96</td>
</tr>
<tr>
<td>5 Means of morphological characters for <em>Sciurus niger</em></td>
<td>97</td>
</tr>
<tr>
<td>6 Morphological character correlations</td>
<td>98</td>
</tr>
<tr>
<td>7 Loadings of morphological characters for <em>Sciurus niger</em></td>
<td>99</td>
</tr>
<tr>
<td>8 Allelic frequencies, mean heterozygosity, expected number of heterozygotes, and percent polymorphism for <em>Sciurus niger</em></td>
<td>100</td>
</tr>
<tr>
<td>9 F-statistics for <em>Sciurus niger</em></td>
<td>101</td>
</tr>
<tr>
<td>10 List of alleles found in both species</td>
<td>102</td>
</tr>
<tr>
<td>11 Estimates of genetic distance for <em>Sciurus niger</em></td>
<td>103</td>
</tr>
<tr>
<td>12 Estimates of genetic distance between subspecies of <em>Sciurus niger</em></td>
<td>104</td>
</tr>
<tr>
<td>13 Estimates of genetic distance between riverbank samples of <em>Sciurus niger</em></td>
<td>105</td>
</tr>
<tr>
<td>14 Means of morphological characters for <em>Sciurus carolinensis</em></td>
<td>106</td>
</tr>
<tr>
<td>15 Loadings of morphological characters for <em>Sciurus carolinensis</em></td>
<td>107</td>
</tr>
</tbody>
</table>
16 Allelic frequencies, mean heterozygosity, expected number of heterozygotes, and percent polymorphism for Sciurus carolinensis..........................108
17 F-statistics for Sciurus carolinensis............................109
18 Estimates of genetic distance for Sciurus carolinensis........110
19 Estimates of genetic distance between subspecies of Sciurus carolinensis................................................111
20 Estimates of genetic distance between riverbank samples of Sciurus carolinensis..............................112

LIST OF FIGURES

FIGURE PAGE

1 Distribution of Sciurus niger subspecies..................113
2 Distribution of Sciurus carolinensis subspecies..........114
3 Location of Sciurus niger morphometric samples........115
4 Location of Sciurus carolinensis morphometric samples...116
5 Illustration of morphometric characters...................117
6 Location of Sciurus niger electrophoretic samples.......118
7 Location of Sciurus carolinensis electrophoretic samples119
8 UPGMA phenogram based on taxonomic distances for Sciurus niger.........................................................120
9 Plot of first two principal components for Sciurus niger121
10 Pie diagrams for MPI in Sciurus niger......................122
11 Pie diagrams for PGM-1 in *Sciurus niger*..........................123
12 Pie diagrams for ADA in *Sciurus niger*..........................124
13 Pie diagrams for NP in *Sciurus niger*..........................125
14 Pie diagrams for IDH-1 in *Sciurus niger*.......................126
15 UPGMA phenogram based on genetic distance estimates for *Sciurus niger*.........................................................127
16 Distance-Wagner tree based on genetic distance estimates for *Sciurus niger*.........................................................128
17 UPGMA phenogram based on taxonomic distances for *Sciurus carolinensis*.................................................................129
18 Plot of first two principal components for *Sciurus carolinensis*.................................................................130
19 Pie diagrams for ACN-1 in *Sciurus carolinensis*................131
20 Pie diagrams for 6PGD in *Sciurus carolinensis*...................132
21 Pie diagrams for PGM-1 in *Sciurus carolinensis*..................133
22 Pie diagrams for ADA in *Sciurus carolinensis*...................134
23 Pie diagrams for ACP in *Sciurus carolinensis*....................135
24 UPGMA phenogram based on genetic distance estimates for *Sciurus carolinensis*.................................................................136
25 Distance-Wagner tree based on genetic distance estimates for *Sciurus carolinensis*.................................................................137
26 Paleovegetation map of eastern North America for 18,000 years before present.................................................................138
27 Premodern and modern deltaic complexes of the Mississippi River.................................................................139
ABSTRACT

Geographic variation was studied in fox squirrels, *Sciurus niger*, and gray squirrels, *S. carolinensis*, by comparing patterns of differentiation within and between these two sympatric species. Patterns of variation were examined in light of the lower Mississippi River as a potential barrier to dispersal and gene flow in these squirrels. Differences within and between species were analyzed using morphologic (15 cranial and mandibular measurements) and allozymic (35 presumptive gene loci) characters. Geographic patterns of variation among populations were apparent in the morphology and allozymes of both species; patterns of differentiation in morphologic and allozymic characters are similar between species; however, morphologic variation is not congruent with allozymic variation within either species. Fox squirrels and gray squirrels each vary morphologically so that, within each species, individuals that inhabit the Mississippi River floodplain and delta region are smaller than animals from adjacent regions. This size variation may be a nongenetic response to environmental factors, or it may reflect regional differences in selective regimes, and thus may represent genetic variation among populations. Available data are insufficient to distinguish between these two causal
mechanisms. Allozymically, fox squirrels and gray squirrels exhibit similar patterns of differentiation; within each species, there are differences among eastern and western populations, as defined by their geographic location relative to the present Mississippi River channel. Thus, the Mississippi River and associated habitats may have been (and may still be) a barrier to gene flow in these species.

This study provides considerable evidence that the lower Mississippi River has influenced morphologic differentiation in fox and gray squirrels and that the river has impeded (and may still impede) gene flow in these species. The role of the river as a barrier to dispersal and gene flow may have resulted from direct effects; the Mississippi River may be a substantial physical barrier to tree squirrels. It is also highly likely that the river has affected dispersal and gene flow in tree squirrels indirectly due to environmental and vegetational shifts that occurred in the alluvial valley of the Mississippi River during the late Quaternary.
IMPORTANCE OF GEOGRAPHIC VARIATION TO EVOLUTIONARY THEORY

Patterns of geographic variation within species have long been of interest to evolutionary biologists because processes that effect differences among conspecific populations are assumed also to result in evolutionary divergence and speciation (Gould and Johnston, 1972; Mayr, 1963, 1970; Miller, 1956). In fact, Gould and Johnston (1972:457) assert that "the foundation of most evolutionary theory rests upon inferences drawn from geographic variation or upon the predictions made about it." Thus, it is commonly held that an understanding of patterns of variation in space and time is essential to the study of speciation (Gould and Johnston, 1972; Endler, 1977), and that the components and stability of spatial patterns of differentiation among conspecific populations should be investigated before these patterns are used to construct hypotheses of higher order processes (Chernoff, 1982; Sullivan, 1985). However, the view that transpecific evolution is an extension of events at or below the species level is not without challenge (Cracraft, 1983; Eldredge and Cracraft, 1980; Goldschmidt, 1940; Zink, 1986; Zink and Remsen, 1986). Part of the disagreement with this view results from different opinions regarding species definitions and
the relevance of the biological species concept (Mayr, 1963) to the study of geographic variation. Zink (1986), Zink and Remsen (1986), and others emphasize that the influence historical patterns exert on differentiation among populations is independent of considerations about reproductive isolation and speciation. Additionally, there is no consistent or predictable relationship between the level and quality of phenotypic and genotypic differentiation or between these types of differences and reproductive isolation (Ayala, 1982; Schnell and Selander, 1981; Wayne and O'Brien, 1986; Zink and Remsen, 1986).

Although they have questioned the relevancy of intraspecific variation to theories of transpecific evolutionary processes, Zink (1986) and Zink and Remsen (1986) concede that analysis of geographic variation might clarify the nature of phenotypic and genotypic change, which is itself an interesting topic for evolutionary study. Furthermore, because geographic variation is the result of both deterministic forces (e.g., differential selection in different environments) and stochastic processes (e.g., vicariant events and genetic drift), studies of geographic variation may shed light on the processes of adaptation and speciation. So at the least, intraspecific geographic variation can serve as a model to study both stochastic and adaptive mechanisms of change, the relative importance of which "remains the most important unsolved problem in our understanding of the mechanisms that bring about biological evolution" (Dobzhansky,
Traditionally, studies of geographic variation in vertebrates have focused on morphological characters in an attempt to classify animals for taxonomic assignment, thereby inferring genetic relationships. However, an individual's phenotype is determined not only by its genotype, but also to some extent by its external and developmental environment, in addition to the complex interaction between its genes and the environment. As a result, the mechanisms that produce phenotypic variation among individuals in different natural populations may be extremely complex and therefore very difficult, if not impossible, to understand. Geographic variation in phenotype is commonly interpreted as an adaptive response to local environmental differences, implying underlying genetic differences (Antonovics, 1971; Burnett, 1983; James, 1970; Johnston and Selander, 1971; Kennedy and Lindsay, 1984; Murphy, 1985; see also James, 1982). Morphological differences are often attributed to adaptation, even though phenotypic differences may also reflect non-genetic changes due to environmental influences (James, 1983; Bernays, 1986; Ralls and Harvey, 1985; Patton and Brylski, in litt.) or to changes in the timing of onset and offset of growth and the rate at which particular body regions
grow (Alberch et al., 1979; Riska, 1986; Creighton and Strauss, 1986). Thus, even if morphological traits are significantly heritable within populations, their expression among localities might be primarily influenced by environmental factors, so that morphological similarities or differences may not necessarily indicate underlying genetic similarities or differences (Gould and Johnston, 1972).

When no correlation is found between the external environment and patterns of geographic variation, factors unrelated to local environment (i.e., genetic components) often are proposed as determinants of phenotypic differentiation. This approach infers genetic similarity from morphological similarity and results in phylogenies based on morphological characters, even though these characters often are polygenic and may be greatly influenced by developmental constraints (Alberch, 1980; Alberch et al., 1979; Creighton and Strauss, 1986; Pengilly, 1984; Riska, 1986; Wayne, 1986). So, while evolutionary biologists have used morphological similarity as evidence of similar adaptive responses to local environments, systematists have used morphological similarity as evidence of genetic relatedness.

A more direct method of inferring phylogenetic relationships utilizes the technique of protein electrophoresis. With this procedure, the genotype of an individual can be determined for gene loci at which alleles are inherited in a simple Mendelian
fashion, circumventing problems of interpretation that are associated with polygenic traits and epistatic effects. In general, genetic differentiation increases as a function of time since populations last shared a common gene pool; therefore, within a given lineage, a certain number of electrophoretically detectable differences corresponds to a certain length of time during which the populations in question have been reproductively isolated. In addition, the majority of electrophoretically detectable traits in homeotherms seem to be effectively neutral with respect to natural selection (Barrowclough et al., 1985; Chakraborty et al., 1980; Kimura, 1983; Sarich, 1977). The apparent selective neutrality of electrophoretic traits lends them to studies that investigate the genetic structure of populations, levels and patterns of gene flow, and the pattern of evolutionary divergence among populations (Smith et al., 1982). Knowledge of each of these evolutionary phenomena is essential to interpreting patterns of geographic variation.

Studies that examine both morphologic and electrophoretic characters in a set of populations have at least two advantages over the traditional approach of examining only morphology. First, they can assess the relative contribution of adaptative and stochastic mechanisms in determining the pattern and extent of geographic variation among populations. Second, concordance in patterns of variation between these data sets allows inferences to be made regarding historical patterns of
environmental change that may account for the evolutionary
divergence of populations through space and time. Without
independent hypotheses of phylogenetic relationships, analyses of
morphology cannot distinguish between environmental and genetic
influences. In short, inclusion of phylogenetic information in
studies of geographic variation effectively reduces the number of
ad hoc interpretations necessary to explain patterns of
phenotypic relationships.

Considering the number of studies that have examined either
electrophoretic or morphologic variation among populations,
relatively few studies of geographic variation in terrestrial
vertebrates have examined phylogenetic information independent of
morphological characters (Handford and Nottebohm, 1976; Kennedy
and Lindsay, 1984; Larson and Highton, 1978; Smith and Patton,
1980; Smith, 1979; Straney and Patton, 1980; Sullivan, 1985;
Zink, 1986). Of these, Kennedy and Lindsay (1984) found
morphological variation in raccoons (*Procyon lotor*), which they
attributed to environmental influences and adaptation. They
could not compare morphological with electrophoretic patterns
because there were no obvious patterns in the very low levels of
genic variation they measured in raccoons. Similarly, Zink
(1986) found very little genetic differentiation among
populations of Fox Sparrows (*Passerella iliaca*), but he concluded
that patterns of morphological variation in this species are
d geometrically structured and are the result of local
environmental influences. In a study of chipmunks (*Tamias minimus*), Sullivan (1985) reported geographically related variation in allozymes and bacular morphology, but he determined that cranial morphology is extremely conservative and may reflect ecologic conditions that mask phyletic patterns. Similarly, Larson and Highton (1978) discovered striking allozymic variation among populations of salamanders (*Plethodon welleri* and *P. dorsalis*) that are virtually indistinguishable morphologically. Handford and Nottebohm (1976) also reported little or no morphologic differentiation among populations of Rufous-collared Sparrows, *Zonotrichia capensis*, which was not congruent with the allozymic differences they found among populations. Smith and Patton (1980) reported patterns of variation in both allozymic and morphologic traits in pocket gophers (*Thomomys bottae*), but they concluded that these patterns were not congruent. In contrast, investigations of geographic variation in the California mouse, *Peromyscus californicus*, (Smith, 1979) and in Goldman's pocket mouse, *Perognathus goldmani*, (Straney and Patton, 1980) revealed morphological variation that was strikingly concordant with geographically related patterns of differentiation as revealed by electrophoretic (Smith, 1979) and chromosomal (Straney and Patton, 1980) evidence.

It is apparent from this brief review of the literature on geographic variation that no clear consensus has emerged from studies that have compared patterns of variation in morphological
and biochemically detectable traits. Part of the difficulty in comparing morphologic and electrophoretic data may result from the statistical limitations inherent in detecting genetic differences among samples using morphological traits (which often have complex and poorly understood genetic bases) as opposed to using traits that have simpler and better understood mechanisms of inheritance, such as allozymes (Lewontin, 1984, 1986; Zink, 1986). Nonetheless, it is important that both types of data be included in studies of geographic variation because the relative influence of phylogeny versus environment on various character sets remains to be determined.

The Potential Role of the Mississippi River in Effecting and/or Maintaining Differentiation among Populations

Interruption of gene flow has long been assumed to be critical to the process of genetic differentiation among populations (Mayr, 1963; Slatkin, 1985b, 1987). However, in 1969, Ehrlich and Raven disputed the prominence of the role that gene flow plays in maintaining similarities among populations of a species. They concluded that in many species of animals and plants, similarity in selection pressure, not gene flow, is responsible for the lack of differentiation among populations. Ehrlich and Raven (1969) also suggested that gene flow is rarely
strong enough to unite local populations into a genetically homogeneous group, and they implied that interruption of gene flow does not necessarily result in divergence of populations.

Jackson and Pounds (1979) questioned Ehrlich and Raven’s conclusions as they pertained to vertebrate populations and emphasized the need for studies that measure empirically the extent and effect of gene flow among populations of vertebrates. According to Jackson and Pounds (1979), these studies should be designed to assess the effects on gene flow of extrinsic barriers to dispersal (such as rivers) using populations that are in similar selective regimes. Thus, with selection held constant, the role of gene flow in dedifferentiating populations could be ascertained. Jackson and Pounds reasoned that if gene flow is the major factor in maintaining similarities among populations, there should be more differences between populations separated by a barrier (even though they are in similar selective regimes) than there are differences between populations separated by distance alone. The methodology of this study follows most suggestions of Jackson and Pounds (1979), and the experimental design (described in a later section) is similar to that used by Pounds and Jackson (1981) in their study of sceloporine lizards.

Several studies have demonstrated that rivers act as barriers to gene flow among vertebrate populations (Biggers and Dawson, 1971; Capparella, 1987; Davis, 1940; Dice, 1939, 1949; Grinnell, 1927; Haffer, 1974; Hershkovitz, 1963, 1982;
McLaughlin, 1958; Pounds and Jackson, 1981; Vaurie, 1968). Studies by Haffer (1974), Vaurie (1968), and Capparella (1987) were designed to investigate evolutionary relationships among populations of South American birds. Each of these studies concluded that large rivers, such as the Amazon, Orinoco, and Napo, are barriers to dispersal and, hence, gene flow in many species of Amazonian birds; Capparella (1987) presents striking evidence of allozymic differentiation among cross-river samples in several species of sedentary understory birds. Hershkovitz (1963, 1982) also emphasized the role of the Amazon as a barrier to dispersal among populations of the primate genera *Calliobus* and *Saguinus*.

Several studies have demonstrated the impact of riverine barriers on gene flow in rodents. Dice (1939) reported that the Columbia River of Washington, Idaho, and Oregon constituted a barrier to gene flow in the deer mouse, *Peromyscus maniculatus*. Later, Dice (1949) determined that the Snake River in Washington and Oregon is also a barrier to gene flow among populations of this species. Several studies of the morphology of pocket gophers of the family Geomyidae (Grinnell, 1927; Davis, 1940; McLaughlin, 1958) have also concluded that rivers act as barriers to dispersal and gene flow in these fossorial rodents.

Relatively few studies have utilized biochemically detectable traits to assess the effects of river systems on gene flow among mammalian populations. Smith and Patton (1980)
analyzed electrophoretic and morphometric data from pocket gopher (*Thomomys*) populations separated by the Colorado River. They reasoned that the electrophoretic data were more accurate reflections of the zoogeographic history of the populations than were the morphometric data. From the genic data, Smith and Patton (1980) concluded that populations on opposite banks of the river are more similar to each other than are adjacent populations on the same side of the river. They attributed the lack of detectable gene flow between populations on the same side of the river to physiographic barriers. In contrast, Biggers and Dawson (1971) concluded that the absence of a certain allozymic allele in old-field mouse (*Peromyscus polionotus*) populations north of a river in South Carolina indicated that the river system (and associated riverine habitats) presented formidable barriers to dispersal and, hence, gene flow in that species. Thus, these two studies (Biggers and Dawson, 1971; Smith and Patton, 1980) yielded contradictory results regarding riverine effects on gene flow in mammals.

This review illustrates the fact that although rivers are often assumed to prevent effective dispersal and gene flow in many vertebrate groups, few studies have documented the effects of river systems on these evolutionary processes in mammals. In particular, no studies have been conducted to assess the effects of the Mississippi River, the longest and widest river in North America, on mammalian zoogeography. The lower Mississippi River
presents a unique opportunity for the study of the impact of river systems on zoogeography because of its impressive width and, hence, potential as a barrier to gene flow. Much is known of the historical physiography of the Mississippi delta because of the Mississippi's importance in commerce and petrochemical exploration, which has led to detailed historical accounts and geological mapping of channel changes, flooding, and deltaic formation. As such, the Mississippi River delta is probably the most-studied delta region in the world in terms of its geology and physiography. In contrast, very little is known of the historical zoogeography of mammals in this region.

The present study focuses heavily on the river's role in shaping the evolutionary history of two species of tree squirrels (genus Sciurus) in the lower Mississippi valley. The role of the Mississippi River in restricting gene flow among populations has been underemphasized in past studies of fox squirrels, S. niger, and gray squirrels, S. carolinensis (Lowery, 1974; Lowery and Davis, 1942; Weigl et al., in press; Weigl et al., in prep.). This investigation not only provides new information on electrophoretic and morphologic variation among fox and gray squirrel populations, but, more importantly, this new information will be interpreted in light of the river's role as a barrier to gene flow in mammals.
Previous Studies of Geographic Variation
in Fox and Gray Squirrels

Fox squirrels (*Sciurus niger*) and gray squirrels (*S. carolinensis*) occur sympatrically throughout most of eastern North America; their ranges are approximately coincident with the distribution of eastern temperate forests. These animals are conspicuous mammals because of their diurnal habits, and they have been hunted for food and sport for over two hundred years. Yet, despite their high visibility and widespread distribution, very few studies have investigated geographic variation in these species.

The only comprehensive investigation of geographic variation in fox squirrels is an ongoing study by Peter Weigl and his colleagues at Wake Forest University. Weigl et al. (in press) describe spectacular differences between fox squirrels that inhabit the southeastern Gulf Coastal Plain and animals that are north and west of this region: northern and western fox squirrels are moderately large (600–900 g) and reddish; southeastern animals are larger (900–1200 g) and exhibit three color morphs: gray, agouti, and black. The southeastern squirrels often have black masks and always have distinctive white markings on the nose, ears, and feet.

No comprehensive study has been conducted to assess geographic variation in gray squirrels throughout the range of
this species. Indeed, very few studies have examined geographic variation in *S. carolinensis*, even on a regional basis (Barnett, 1977; Havera and Nixon, 1978).

In a review of the distributional ranges and habitats of fox and gray squirrels, Bakken (1952) noted the striking overlap in geographic range between *S. niger* and *S. carolinensis*. According to Bakken (1952), coexistence (= syntopy) occurs where there is overlap in habitat utilization and along margins of adjacent, exclusive habitats. Bakken (1952) reported that syntopy in fox and gray squirrels is most evident in the northern and western portions of their ranges, and coexistence occurs in limited areas throughout portions of their joint range. Bakken's (1952) data were insufficient for him to determine the degree of coexistence between these species in Louisiana and southwestern Mississippi, although he considered them to be syntopic in eastern Texas. According to Lowery (1974), the habitat requirements of these two species in Louisiana are remarkably similar, and both species are common or abundant throughout the state.

Fox and gray squirrels are well-suited to a comparative study of geographic variation; their natural history and habitat preferences are extensively documented because of their popularity as game species in eastern North America (Baker, 1944; Bakken, 1952, and references therein; Brown anad Yeager, 1945; Lowery, 1974; Redmond, 1949; Weigl et al., in press). Moreover, these species have very similar (if not identical) diets (Allen, 1943, 1952; Baumgartner, 1939; Davison, 1964; Goodrum, 1961;
Packard, 1956; Smith, 1970; Uhlig, 1955); they occur sympatrically throughout most of eastern North America (Hall, 1981) and syntopically in many habitats in the lower Mississippi River valley (Bakken, 1952; pers. obs.). Because of these similarities, patterns of variation in each of these species can be used as a "control" for assessing geographic variation in the other species, and both species together serve as "replicates" for inferring potential mechanisms that may be responsible for geographic patterns of morphologic and electrophoretic variation in tree squirrels in the lower Mississippi River valley.

Objectives of This Study

In this study, I analyze morphologic and electrophoretic characters to assess geographic variation in two syntopic species of tree squirrels, the fox squirrel (Sciurus niger) and the gray squirrel (S. carolinensis), in the lower Mississippi River valley. This region was chosen because of the striking patterns of morphological variation present among populations of tree squirrels in this area (Lowery, 1974, Lowery and Davis, 1942), which is even more spectacular because this region represents a very small portion of these species' distributional ranges. This study is the first report of electrophoretically detectable variation among populations of fox squirrels, and it is the second such report for gray squirrels, the first being a study by

According to Hall (1981) and Lowery (1974), there are two subspecies of *S. carolinensis* (*carolinensis* and *fuliginosus*), and five subspecies of *S. niger* (*limitis, rufiventer, ludovicianus, subauratus, and bachmani*) in the lower Mississippi River valley. Distinguishing pelage and/or size characteristics have been described for each of these named forms. In this report, single epithets (e.g., *carolinensis, bachmani*) will be used to refer to the subspecies of tree squirrels. The distributional ranges of the subspecies of *S. niger* and *S. carolinensis* in the lower Mississippi River valley are shown in Figures 1 and 2.

The principal goal of this study is to identify the evolutionary forces that have influenced the historical origin and present state of geographic variation in fox squirrels and gray squirrels in the lower Mississippi River valley. Toward this end, I will: 1) use allozymic and morphometric analyses to assess patterns of geographic variation among conspecific populations of tree squirrels; 2) determine whether or not morphological and biochemical characters are congruent in the patterns of variation they reveal within and between species; and 3) interpret patterns of differentiation in light of potential causal mechanisms, including past and present vegetational distributions and past and present channels of the lower Mississippi River.
MATERIALS AND METHODS

Sampling Design and Allocation of Specimens to A Priori Groups

The sampling protocol of this study was designed to allow investigation of potential geographical and ecological correlates of variation in *S. carolinensis* and *S. niger* in the lower Mississippi River valley. Sampling localities were chosen so that the geographic location of samples for each species approximated two east-west transects through Louisiana and Mississippi, one northern and one southern. Samples from Arkansas, Texas, and Tennessee were also included for comparative purposes. This experimental design resulted in sampling from different habitat types and insured that most subspecific taxa were represented by at least three samples. The sampling design also allowed comparison of genetic distances estimated between pairs of cross-river samples (that are in similar selective regimes) with genetic distances estimated between pairs of samples that are not separated by the Mississippi River (and may or may not be in similar selective regimes) but are separated by geographic distances equal to or greater than the width of the river. If the river is an effective barrier to gene flow, and if gene flow rather than natural selection is the primary force that maintains genetic homogeneity within species, the genic
dissimilarities between cross-river samples should be greater than those between geographically equidistant samples on the same side of the river. Conversely, if selection is the main force in sustaining genetic homogeneity within a species, similar selective regimes should maintain similarities among populations, whether or not they are separated by the river.

For electrophoretic analyses, each sample was assigned to two a priori groups: "riverbank" (e.g., east-bank) and subspecies (e.g., *carolinensis*, *ludovicianus*); samples for morphologic analyses were assigned only to subspecies. The term "riverbank" refers to the location of each sample in relation to the present Mississippi River channel; samples of each species were assigned to "east-bank" and "west-bank" groups. Individuals of each species were tentatively assigned to subspecies based on pelage characteristics and specific collecting locality according to currently recognized distributional ranges (Figs. 1 and 2). Assignment of specimens to a priori groups was made to facilitate description of geographic patterns of variation in relation to current taxonomy and does not necessarily imply evolutionary relationships per se among populations.

**Morphometric analyses**

One hundred forty-nine specimens of *Sciurus niger* and 142 specimens of *Sciurus carolinensis* were included in this study.
All were determined to be adults based on the presence of permanent, fully erupted fourth, upper premolars. For each species, specimens from geographically adjacent collecting localities were pooled to increase sample sizes and to increase the discriminating power of univariate and multivariate analyses. This pooling resulted in 19 samples of fox squirrels and 18 samples of gray squirrels from Arkansas, Louisiana, Mississippi, Tennessee, and Texas. General collecting localities, sample codes, subspecific assignment of each sample, and sample sizes are listed in Tables 1 and 2. I will refer to these samples by sample codes in subsequent discussions. The geographic location of samples is depicted in Figures 3 and 4, and specific collecting localities and sample sizes are listed in Appendix I, which includes a list of museum collections in which specimens are deposited.

The following cranial and mandibular measurements were made to the nearest 0.1 mm with digital calipers for each specimen:

- total skull length (MAX_LEN),
- width between the zygomatic arches (ZYG_WDTH),
- width of the posterior braincase (BRN_WDTH),
- width of the braincase posterior to the supra-orbital processes (LST_POST),
- height of skull at the pterygoid processes (MAX_HT),
- width of the infra-orbital processes (INFR_BR),
- diastemal length (DIAST),
- toothrow length (TOOTH),
- width of M3 (MLR_WDTH),
- width of P4 (PML_WDTH),
- distance between the posterior palatine foramina (PAL_WDTH),
- width of the foramen magnum (FOR_WDTH),
width of the articular process (ART_WDTH), mandibular height (MAND_HT), and mandibular length (MAND_LEN). Figure 5 illustrates measurements used in this study, with the exception of ART_WDTH.

Statistical analyses were performed using the following commercially available computer packages: Statistical Analysis System (SAS; SAS Institute, Inc., 1985a, 1985b), Biomedical Data Programs (BMDP; Dixon, 1981), and Numerical Taxonomic System of Analysis (NT-SYS; Rohlf et al., 1974). Specimens with missing data (due to damaged or missing bones) for more than three variables were excluded from all analyses. The procedure BMDP-AM was used to tabulate the number of missing values for each character and to determine whether or not patterns existed in the missing data. Because there was no discernible pattern of missing values, I estimated replacement values for missing data with the multiple regression option of BMDP-AM. For each sample, data from specimens with valid measurements for all variables were used to compute a regression equation, from which a value for the variable with missing data was estimated. In this way, relationships among characters were determined for each sample, then estimation of each missing value for a certain variable was accomplished by regressing that variable on all other variables for a particular specimen. Using this routine, measurements were estimated for 48 specimens of S. niger and 45 specimens of S. carolinensis. Subsequent analyses were performed on the original
data sets (which included individuals with missing measurements) as well as the "complete" data sets (for which values were estimated to replace missing data). The results of these analyses did not differ in detail, and results will be reported only for analyses of the "complete" data sets.

In order to assess the degree of non-geographic variation in the characters examined, I used four routines of multivariate analysis of variance (MANOVA procedure of SAS) to test the hypothesis that there are no significant differences due to gender within each species. Fox squirrels were represented by 58 females, 75 males, and 16 specimens of undetermined gender; gray squirrels were represented by 70 females, 68 males, and 4 specimens of unknown gender. There were no significant differences between sexes in any of these tests (see also Kramm et al., 1975; Havera and Nixon, 1978; and Lindsay, 1981, 1986); therefore, all individuals from each sample were pooled in subsequent analyses to increase sample sizes and to increase the discriminating power of univariate and multivariate analyses.

I used the UNIVARIATE procedure of SAS to compute descriptive statistics (mean, standard error, and coefficient of variation) for each character by sample. For each species, the MANOVA procedure of SAS was used to test the hypothesis that sample centroids are significantly heterogeneous in multivariate space. Next, patterns of phenetic relationships among samples of each species were investigated using cluster analysis. For each
species, the NT-SYS package was used to compute product-moment correlation coefficients for each pair of character means in order to determine which characters exhibit similar patterns of variation. Next, NT-SYS was used to variance-standardize character means for each sample and to compute a taxonomic distance measure for each pairwise comparison of samples. These distance measures were used to construct a sample-by-sample matrix, from which a phenogram based on the taxonomic distance between each pair of samples was obtained by using the unweighted pair-group method with arithmetic averaging (UPGMA) analysis described by Sneath and Sokal (1973). Cophenetic correlation coefficients were computed for each phenogram in order to evaluate the degree to which the phenogram represents the distance matrix from which it was derived. In order to elucidate further patterns of phenetic similarity among samples within species, the PRINCOMP procedure of SAS was used to perform a principal components analysis (PCA) on variance-standardized character means for each sample. PCA identifies linear combinations of variables that best summarize character variation among samples and reduces a large number of variables to a smaller number of dimensions while retaining maximum spread among sampling units.
Electrophoretic analyses

Ninety-one specimens of *Sciurus niger* representing 14 populations and 107 specimens of *S. carolinensis* representing 10 populations were analyzed using standard protein electrophoresis procedures. General collecting localities, sample codes, subspecific assignment of each sample, and sample sizes are listed in Tables 3 and 4. Subsequent discussions will refer to these sampling localities by sample codes. The geographic location of each sample is depicted in Figs. 6 and 7; specific collecting localities and sample sizes are listed in Appendix II. Techniques for tissue preparation and staining followed those described in Harris and Hopkinson (1976) and Selander et al. (1971). Samples of heart, liver, kidney, and skeletal muscle were used to make aqueous extracts of proteins. Kidney and liver samples were available for all specimens; heart and skeletal muscle were used when available.

Twenty-eight enzyme systems that are encoded by 35 presumptive gene loci were assayed; numerous side-by-side comparisons of electromorphs were made to insure correct assessment of relative mobilities. Electromorphs were assumed to represent alleles and were assigned unique letters, with "A" designating the most common allele; the most anodal locus was designated as "locus 1" for enzymes in which the product of more
than one gene locus (isozyme) was interpretable. Buffer systems, and the enzymes for which they were used, were as follows: Poulik (Poul) for superoxide dismutase (SOD), fumarase (FUM), glycerol-3-phosphate dehydrogenase (G3PD), lactate dehydrogenase (LDH-1,-2), mannose phosphate isomerase (MPI), octanol dehydrogenase (ODH), peptidase A (which uses valyl-leucine as substrate; PEPA), peptidase B (leucyl-glycyl-glycine as substrate; PEPB), peptidase C (leucyl-alanine as substrate; PEPC), peptidase D (phenylalanyl-proline as substrate; PEPD), peptidase S (val-leu, leu-ala, or leu-gly-gly as substrate; PEPS), phosphoglucone isomerase (PGI), and sorbitol dehydrogenase (SDH); tris-citrate, pH 8.0 (TC8) for adenylate kinase (AK), creatine kinase (CK-1,-2), glucose-6-phosphate dehydrogenase (G6PD), glutamate dehydrogenase (GLUD), glutamate oxaloacetate transaminase (GOT-1,-2), isocitrate dehydrogenase (IDH-1,-2); and tris-citrate pH 7.0 (TC7) for acid phosphatase (ACP), adenosine deaminase (ADA), aconitase (ACN-1,-2), guanine deaminase (GDA), malate dehydrogenase (MDH-1,-2), malic enzyme (ME), nucleoside phosphorylase (NP), 6-phosphogluconate dehydrogenase (6PGD), and phosphoglucomutase (PGM-1,-2). Gels made with TC8 and TC7 buffers were subjected to 80 milliamperes of current for 4.5 h; Poulik gels were subjected to 150 volts for 5 h.

The BIOSYS-1 program of Swofford and Selander (1981) was used to summarize and to analyze statistically the
electrophoretic results. Using this program, I determined allelic and genotypic frequencies and the percentage of polymorphic loci for each sample. Allelic and genotypic frequency data were then used in a series of analyses to estimate genetic variation within and among conspecific populations. Slatkin's (1981, 1985a) method was used to estimate gene flow among conspecific populations. This analysis uses allelic frequency data to estimate levels of gene flow among natural populations (the procedure estimates $N_m$, the average number of migrants that have been exchanged among demes). Slatkin's (1981) simulations showed that the conditional average frequency of an allele, $p(i)$, is basically independent of the assumed selection intensity and mutation rate but depends heavily on the overall level of gene flow. In his 1981 publication, he provided a method to assess qualitatively levels of gene flow among populations as low, moderate, or high. In 1985, Slatkin introduced a technique to quantify his qualitative assessments; he showed that the logarithm of $N_m$ is approximately linearly related to the logarithm of the average frequency of alleles found in only one sample, $p(1)$. With computer simulations he further demonstrated that this relationship is relatively insensitive to changes in parameters of the model other than $N_m$ and the number of individuals sampled per population.

For each sample, mean heterozygosity was calculated as the average proportion of heterozygous individuals at the loci
examined (direct-count method), and the expected heterozygosity (averaged over all loci) assuming Hardy-Weinberg equilibrium was calculated for each sample using Nei's (1978) formula that corrects for small sample sizes. Genotypic proportions observed at each polymorphic locus were tested for conformation to the proportions expected under Hardy-Weinberg equilibrium.

Chi-square tests using Levene's (1949) correction for small sample sizes were used to test for goodness-of-fit between observed and expected numbers of heterozygous individuals at each locus.

Nei's (1977) and Wright's (1978) $F_{IS}$ and $F_{IT}$ statistics, which take into account all samples for locus-level calculations, were also used to estimate departure from Hardy-Weinberg equilibrium. For these statistics, the subscript "I" represents individual variation, "S" represents variation within a sample, and "T" represents total variation present. Therefore, $F_{IS}$ estimates genetic differentiation of individuals relative to the sample they comprise, and $F_{IT}$ measures genetic differentiation of individuals relative to all samples pooled (Nei, 1977). Mean $F_{IS}$ (calculated over all loci) for a set of samples indicates the average deviation from values based on Hardy-Weinberg expectation for all loci within each sample; mean $F_{IT}$ indicates the overall deviation from Hardy-Weinberg expectation for all loci within all samples pooled. Positive values of $F_{IS}$ and $F_{IT}$ represent a deficiency of heterozygotes, negative values indicate an excess
of heterozygous individuals.

F-statistics ($F_{ST}$) of Nei (1977) and Wright (1978) were also used to estimate levels of genetic differentiation among populations. $F_{ST}$ can be regarded as the actual amount of differentiation among samples at a given locus in relation to the maximum amount of differentiation possible. Thus, an $F_{ST}$ value of zero indicates a lack of differentiation among samples, which is the null hypothesis. A value of 1.0 for $F_{ST}$ indicates maximum differentiation (fixation for alternate alleles in different samples), although in cases where only two populations are considered, an $F_{ST}$ value of 1.0 is not possible if the locus under consideration is represented by more than two alleles (Wright, 1978). For this study, I used two different formulae for calculating $F_{ST}$: 1) Nei's (1977) method, which measures the amount of differentiation among subpopulations relative to the limiting amount under complete fixation (Nei called this "$G_{ST}$"; and 2) Wright's (1978) formula, which measures the amount of differentiation in absolute terms, and incorporates a correction for error due to small sample size (the notation for this term is "$F_{DT}$"; the subscript "D" represents variation within a deme). Wright's (1978) formula that does not correct for sample size yields values identical to Nei's (1977) method (Swofford and Selander, 1981; this study). To test for significant departures of $F_{ST}$ values from zero at individual loci, I used the Chi-square test of Workman and Niswander (1970) to test an M by N
contingency table against the model of panmixia. For this test, 
M is the number of populations and N is the number of alleles and 
there are \((M-1)(N-1)\) degrees of freedom. Mean \(F_{ST}^{\text{mean}}\) 
calculated over all loci for a set of samples indicates the 
overall amount of differentiation among samples relative to the 
total amount of variation present. Wright (1978) did not discuss 
methods for testing the significance of \(F_{ST}^{\text{mean}}\) values, but he stated 
that values greater than 0.25 suggest very great differentiation, 
and that differentiation is moderately great among populations 
for which values of \(F_{ST}^{\text{mean}}\) range from 0.15 to 0.25.

\(F_{ST}^{\text{mean}}\) is an empirical estimate of relative amounts of genetic 
differentiation. To assess patterns of divergence among 
populations, I examined variation at selected individual loci 
using single-locus techniques; I then employed cluster analyses 
in which differentiation among conspecific populations was 
considered at all loci combined. In the single-locus analyses, 
each variable locus was first analyzed cladistically using the 
method described by Patton and Avise (1983) and Honeycutt and 
Williams (1982). For this analysis, relationships of ingroup 
(conspecific) populations were assessed using individuals of the 
other species as an outgroup. Using this technique, any ingroup 
electromorph also present in the outgroup was considered 
pleisiomorphic (primitive); therefore, it was discounted in the 
analysis. All alleles at a given locus that were not present in 
the outgroup were treated as autapomorphic (uniquely derived) or
synapomorphic (shared derived) characters. For those loci at which no electromorphs were shared with the outgroup, all allelic variants were presumed derived. This analysis permitted the identification of primitive and derived alleles for interpretation of patterns of variation revealed by subsequent analyses. Allelic distributions at selected loci were superimposed onto maps using pie diagrams to represent allelic frequencies for each sample. With this approach, the distribution of apomorphic and plesiomorphic alleles was portrayed in a geographic context for each species.

Differentiation among populations of each species at all loci combined was estimated using the genetic distance measures of Nei (1978) and Rogers (1972). Rogers' (1972) distance \( D_R \) was used to examine genetic distances among populations in a priori groups (subspecies and riverbank), then all samples within each species were clustered using UPGMA (Sneath and Sokal, 1973) and the distance-Wagner procedure of Farris (1972; mid-point rooting; multiple addition criterion of Swofford, 1981, maxtree=30, branch length optimization suppressed). Rogers' (1972) distance measure was used in these procedures because the properties of this statistic conform to those of a metric (Sneath and Sokal, 1973; Swofford and Selander, 1981; also see Rogers, 1986). In order to identify stable nodes in the distance-Wagner phenogram, I performed a jackknifing routine as described by Lanyon (1985). In jackknifing, a series of Wagner trees are
constructed, each of which includes $n-1$ samples, where $n$ is the total number of samples in the data set. Thus, for each species, I omitted each sample in turn and generated $n-1$ trees, resulting in 13 additional trees for *S. niger* and 9 additional trees for *S. carolinensis*.

**RESULTS AND DISCUSSION**

*Sciurus niger*

Morphometric analyses.—Table 5 lists means and standard deviations of cranial and mandibular characters for each sample, and Table 6 lists correlations among characters. For each character (except LST_POST), analysis of variance revealed highly significant differences ($P < 0.0001$) among samples. Four routines of MANOVA were used to test the hypothesis that there are no significant morphometric differences among samples. Each of the four tests had results that were significant at $P < 0.0001$: Hotelling-Lawley's Trace ($F = 3.84$); Pillai's Trace ($F = 2.06$); Wilk's Criterion ($F = 2.67$); and Roy's Maximum Root Criterion ($F = 38.37$). Because each of these $F$-values was highly significant, additional analyses were used to elucidate patterns of variation among samples. Toward this end, cluster analysis and principal components analysis were performed to evaluate
variation among samples using all characters simultaneously.

The results of a UPGMA analysis of taxonomic distances among character means for the 19 samples of fox squirrels are shown in Figure 8. Two very distinct clusters are apparent at the 6.97 distance level: the lower cluster is composed of samples from the Atchafalaya River basin of south-central Louisiana (the Atchafalaya River is the vestige of one of the original distributaries of the Mississippi River), the Mississippi River floodplain, and central Texas (NL_3, NL_7, NL_9, NL_5 and NX_1); the upper cluster is subdivided into two groups at the 4.70 level. One of these includes samples from Arkansas, Texas, Mississippi, Tennessee, and Louisiana (NA_1, NX_2, NM_1, NT_1, NL_1, NX_3, NL_8, and NT_2); the other consists of samples from Louisiana, Mississippi, and Texas (NL_2, NM_2, NL_4, NL10, NX_4, and NL_6).

Principal components were extracted to summarize character variation among localities. Values for the loadings, which indicate correlations of characters with the first and second principal components are listed in Table 7. Principal component one (PC I) had positive correlations for all characters, and each character contributed approximately equally to this component; therefore, PC I probably represents size. For PC II, LST_POST had the highest positive loading, which indicates that this character has the greatest influence on this component. However,
because analysis of variance indicated that differences among samples for this character are not statistically significant, the meaning of variation for PC II is not easily interpretable.

Bivariate plots of the 19 samples are presented in Figure 9. In this figure, PC I accounts for 78.9% of the total variance, and PC II accounts for 5.9% of the variance. Samples NL_3, NL_5, NL_7, and NX_1 had high, negative scores for PC I; thus, individuals from the Mississippi River floodplain and central Texas are the smallest animals included in this study. Samples from east-central Texas (NX_4), central and western Louisiana (NL_6, NL_2, NL_4), central Mississippi (NM_2), and extreme southeastern Louisiana (NL10) included some of the largest individuals in this study, as indicated by the high, positive scores of these samples for PC I. For PC II, sample NL_6 had a high, positive score, and samples NT_2 and NX_4 had high, negative scores. This may indicate that animals from southwestern Louisiana have relatively broad anterior braincases (large LST_POST) and that the anterior braincases of animals from east-central Texas and southwestern Tennessee are relatively narrow.

The multivariate analyses of 15 cranial and mandibular characters indicate that there is substantial morphological differentiation among samples of *S. niger* from the lower Mississippi River valley and Texas. Furthermore, the differentiation is structured so that there are striking patterns of geographic variation in these squirrels: cluster and principal
components analyses (Figs. 8 and 9) identify four geographically defined groups of samples, which correspond to previously described subspecies. Individuals that inhabit the Mississippi River floodplain and the Atchafalaya River basin of south-central Louisiana (samples NL_5, NL_9, NL_7, and NL_3) clustered with animals from central Texas (NX_1) in both analyses (Figs. 8 and 9), indicating phenetic similarity among fox squirrels in these geographic regions. Samples from Arkansas, western Louisiana, and eastern Texas (NA_1, NL_1, NL_2, NL_4, NL_6, NX_2, NX_3, and NX_4) were placed with samples from Tennessee, Mississippi, and the extreme eastern portion of south Louisiana (NT_1, NT_2, NM_1, NM_2, NL_8, and NL10) in Figures 8 and 9. Because phenotypically similar forms (animals from central Texas and the Mississippi River floodplain) are separated by animals that are very different (individuals from eastern Texas and western Louisiana), samples that are geographically proximal did not always cluster together (e.g., NL_3 from northeastern Louisiana did not cluster with either NM_2 (central Mississippi) or NL_2 (north-central Louisiana), and NL_9 was not placed with either NL_8 or NL10, although all are from southeastern Louisiana). Conversely, samples that are distant geographically occasionally clustered together, indicating their phenotypic similarity; for example, NL10 from southeastern Louisiana clustered with NX_4 from east-central Texas, NA_1 (northern Arkansas) with NX_2 (southeastern Texas), and NL_5 (east-central Louisiana) with NX_1
(central Texas). However, geographically proximal samples did cluster together within subgroups (e.g., NL_1 from northwestern Louisiana clustered with NX_3 from northeastern Texas and samples from south-central Louisiana, NL_7 and NL_9 clustered together).

This pattern of geographic variation in fox squirrels was described by Lowery and Davis (1942), although they did not quantify their comparisons. They recognized four clearly defined subspecies in the lower Mississippi River valley and Texas: a smaller, western form that is restricted to central Texas (limitis), a larger form characteristic of eastern Texas and western Louisiana (ludovicianus), another smaller form that is restricted to the floodplain of the Mississippi River and the Atchafalaya River basin (subauratus), and another, larger form that occurs throughout Mississippi, most of Alabama and the extreme eastern portion of southern Louisiana (bachmani). Thus, in a west-to-east transect across the lower Mississippi River valley, fox squirrels vary geographically so that a subspecies that is characterized by smaller individuals alternates with a subspecies in which individuals are on average much larger.

Although I did not quantify pelage-color variation in fox squirrels, my incidental examination of study skins while measuring skulls for this investigation confirms Lowery's (1974) description of pelage variation among specimens of S. niger from the lower Mississippi River valley. The subspecies can be identified by striking differences in pelage coloration: limitis
and *ludovicianus* each have pale yellow-orange venters and yellowish-gray dorsal coloration; the venter of *subauratus* is darker and more orangish-yellow, and its dorsum is much darker gray; and *bachmani* is similar in color to *subauratus*, but all individuals of *bachmani* are marked with white on the nose, ears, feet, and tail. My morphological analyses also indicate that animals from eastern Arkansas and western Tennessee (*rufiventer*) are in the same size class as *bachmani* and *ludovicianus*. The specimens of *rufiventer* I examined were similar to *ludovicianus* in pelage coloration.

Weigl et al.'s (in press; in prep.) extensive investigation of geographic variation, ecology, feeding behavior, habitat preferences, and natural history of *S. niger* is the most comprehensive study of southeastern fox squirrels to date, and my results can be interpreted in light of their findings. Weigl et al. (in press; in prep.) report spectacular differences in color and size between eastern and western subspecies of fox squirrels. They describe eastern subspecies as being generally much larger and observed that all subspecies of *S. niger* that occur east of the Mississippi River and Appalachian Mountains (*bachmani*, *niger*, *shermani*, *cinereus*, and *avicennia*) are characterized by white markings on the nose, ears, and feet. Weigl et al. (in press) report that the primary habitat of fox squirrels in North Carolina and much of the southeast is open, mature, pine-oak forest (especially longleaf pine and turkey oak), along with some
adjacent hardwood, bottomland, and swamp woodland. They further state that the eastern subspecies' large size appears to be related to the presence of longleaf pine, which does not occur in most of the northern and western portions of this species distributional range. Large body size is a definite advantage in handling bulky longleaf pine cones, which are a crucial food source for many southeastern populations during late summer and early fall (Weigl et al., in press). These cones are excellent sources of energy (each one may contain over 60,000 calories); however, they are extremely large (up to 29 cm and 490 g) and thus are difficult to manipulate. Comparative feeding studies by Weigl et al. (in press) demonstrated the importance of body size in feeding on these cones: (larger) North Carolina fox squirrels (weighing approximately 1000 g) were far superior to (smaller) western fox squirrels (800 g) and North Carolina gray squirrels (500 g) in their ability to carry, handle, and gnaw longleaf pine cones. In the present study, the largest animals inhabit the longleaf pine forests of extreme southeastern Louisiana (NL10), central and western Louisiana (NL_2, NL_4, NL_6), and central-eastern Texas (NX_4). The smallest animals in my study occupy what appear to be trophically poor habitats: the Mississippi River floodplain and Atchafalaya River Basin of south central Louisiana (NL_3, NL_5, NL_7, NL_9) and the western limits of the eastern deciduous forest (NX_1).

In summary, my analyses confirmed Lowery and Davis' (1942)
observations that individuals assigned to *limitis* and *subauratus* are approximately equal in size and are smaller than specimens assigned to *ludovicianus* and *bachmani*, which are also approximately equal in size. Moreover, my findings support the currently recognized geographic distributions of these forms: they are linearly distributed in an alternating pattern from west to east so that a subspecies characterized by smaller individuals alternates with one characterized by larger individuals. This pattern is evident from central Texas to at least central Mississippi. In light of these findings, and until additional studies are available, I recommend retention of the current subspecific epithets (Hall, 1981) to recognize geographic variation among these populations of *S. niger*.

**Electrophoretic analyses.**—Seventeen of 35 loci were monomorphic for the same allele across all 14 samples: ACN-1, ACN-2, AK-1, AK-2, GDA, G3PD, GLUD, GOT-1, GOT-2, LDH-1, LDH-2, MDH-2, PEPA, PEPC, PEPS, SDH, and SOD. Nine loci were polymorphic for alleles that were present in two or more samples: ACP, ADA, FUM, IDH-1, ME, MPI, NP, PEPB, and PGM-1. Allelic designations and allele frequencies for the eighteen polymorphic loci are shown in Table 8. The mean number of alleles per locus was either 1.1 or 1.2 for each sample. Table 8 also indicates the following statistics for each sample: percent polymorphism
(P), which was calculated using loci for which the frequency of the most common allele was <95%; direct-count estimates of mean heterozygosity (H); and expected mean number of heterozygotes (H_{exp}), which was calculated using Nei's (1978) unbiased estimate and assuming Hardy-Weinberg equilibrium. Percentage of polymorphic loci (P) ranged from 5.7% (NA, NX, and NS) to 22.9% (NT). The average H calculated over all populations of fox squirrels in this study was 4.5% and ranged from 2.1% (NP) to 9.5% (NT). There were no apparent geographically related patterns in levels of genic variation as measured by levels of heterozygosity or polymorphism, and these values for fox squirrels are comparable to values for mammals reported by Nei and Graur (1984), Nevo (1978), and Powell (1975).

For five samples (NF, NK, NM, NT, and NV), Chi-square tests revealed significant deviation from Hardy-Weinberg expectations at certain loci ("-" denotes heterozygote deficiency, "+" indicates heterozygote excess at a given locus): NF (CK -, ME -); NK (PEPB +); NM (PGM-1 -); NT (MDH-1 -); NV (G6PD -, IDH-2 -). There was no obvious pattern in these deviations, geographic or otherwise, and the general absence of departure from Hardy-Weinberg expectations in S. niger is consistent with the findings of many allozymic studies of sexually outbreeding organisms (Smith et al., 1982).

Slatkin's (1985a) technique for estimating levels of gene flow among populations uses alleles that are unique to a single
sample (called "private" alleles by Neel, 1973). Twelve loci were polymorphic for private alleles in fox squirrels; the loci and samples in which these alleles occurred were as follows: NE (6PGD), NF (CK, IDH-1), NH (PGM-2), NK (ME, PGM-1), NT (MDH-1, PE PD, PGI), NV (G6PD, IDH-2), and NX (ODH). Among all samples, 12 private alleles were present, the average frequency of each allele \( \bar{p}(1) \) was 0.297 and the estimated amount of gene flow among populations, corrected for sample size \( (N_m) \) was 0.34. This estimate is comparable to that reported for Peromyscus polionotus by Slatkin (1985a). Recalculation of these values using only samples with ten or more individuals (NJ, NH, NE, and NA) resulted in estimates of \( \bar{p}(1) = 0.045 \) and \( N_m = 8.05 \) (after correcting for sample size). This estimate is similar to the value for Drosophila willistoni calculated by Slatkin (1985a), and according to Slatkin (1981, 1985a, 1985b) it represents high levels of gene flow.

F-statistics and the results of the heterogeneity Chi-square analyses for each of the polymorphic loci are presented in Table 9. The mean value of \( F_{IS} \) was -0.067, indicating an overall heterozygote excess within these samples. The mean value of \( F_{IT} \) was 0.336, which suggests that there was a deficiency of heterozygotes within samples pooled over all loci. The uncorrected \( F_{ST} \) for the 14 samples of fox squirrels is 0.378. The corrected \( F_{ST} (F_{DT}) \) value is 0.305. Thus, despite high estimated levels of gene flow among samples \( (N_m = 8.05) \), 30-40%
of the electrophoretically detectable variation is among-sample variation, rather than within-sample variation. Recalculation of these values for Louisiana and Mississippi samples only (i.e., without NT, NX, and NK) resulted in an uncorrected $F_{ST}$ of 16.4% and a value of 9.6% after correction for small sample size. All of these values are comparable to $F_{ST}$ estimates for other mammals, which range from 0 to 0.8 (Barrowclough, 1983) and are "moderately great" according to Wright (1978).

Comparison of values for $F_{IS}$, $F_{IT}$, and $F_{ST}$ for each polymorphic locus (Table 9) with allelic frequency distributions (Table 8) aids in the interpretation of the F-statistics. For example, ACP and FUM have low values for $F_{ST}$, and low, negative values for both $F_{IT}$ and $F_{IS}$. These loci are polymorphic in only two samples, and the alleles other than the common one occur in relatively low frequencies. In contrast, ADA has a high $F_{ST}$, a high, negative $F_{IS}$, and a high, positive $F_{IT}$. This locus is polymorphic in all samples except NS, and two or more alleles are in high frequency in most samples. MPI also has a high $F_{ST}$, a high, negative $F_{IS}$, and a positive $F_{IT}$. However, the $F_{IT}$ for MPI is lower than the $F_{IT}$ value for ADA because MPI is polymorphic in only 6 of 14 populations, although (like ADA) both alleles are in relatively high frequency in samples that are polymorphic at MPI.

Side-by-side comparisons of electromorphs revealed that Sciurus carolinensis and S. niger are fixed for alternate alleles at four loci: GDA, PGI, PEPD, and PEPA. The locus-by-locus
cladistic analysis of *S. niger* (Table 10; *S. carolinensis* was the outgroup) indicated that alleles ADA^A^, IDH-1^A^, MPI^A^, NP^A^, NP^B^, and PGM-1^A^ are shared with gray squirrels. These were, therefore, considered primitive alleles in fox squirrels, and they were discounted in locus-by-locus analyses of relationships within *S. niger*.

The geographic distribution of alleles at all loci that were polymorphic in six or more samples is depicted in Figures 10-14. $F_{ST}$ values for each of these loci had highly significant Chi-square values (Table 9). Figures 10-14 depict the following geographic distributions of synapomorphic alleles: at the MPI locus (Fig. 10), the $B$ allele is present in all samples east of the Mississippi River, and it is absent from all west-bank samples; the PGM-1^B^ (Fig. 11) and ADA^C^ (Fig. 12) alleles occur primarily in samples west of the river. Both alleles at NP (Fig. 13; Table 10) are shared with *S. carolinensis*, therefore inferences made from allelic distributions at this locus are tenuous. The geographic distribution of the IDH-1^B^ allele (Fig. 14) is not readily interpretable.

Table 11 summarizes values of Nei's (1972) and Rogers' (1972) genetic distance estimates for pairwise comparisons of the 14 samples of fox squirrels analyzed in this study. For these samples, Rogers' distance estimates ($D_R$) ranged from 0.014 (NE-NB) to 0.139 (NX-NK), and the average distance among populations was 0.047. These values are comparable to genetic
distance estimates among mammalian populations reported by Avise and Aquadro (1982), Ayala (1975), and Selander and Johnson (1973).

Inspection of these values in relation to the geographic distance between samples and whether or not the samples are separated by the Mississippi River reveals a pattern that may be attributable to the presence of the river (see Fig. 6 and Table 11). For example, the genetic distance estimated between samples NP and NW (separated by the river) is 0.042. This value is more than twice that estimated between samples NP and NM (0.018), which are both west of the river but are separated by a geographic distance that is more than twice the distance between NP and NW. In other words, geographically proximal samples separated by the Mississippi River are genetically more distinct than are geographically distant samples on the same side of the river. This pattern is evident in other comparisons; for example, the distance values between NP and other west-bank samples are as follows: NV, 0.042; NA, 0.019; NJ, 0.027. In contrast, genetic distances estimated between NP and geographically closer or equidistant east-bank samples are generally larger than these values: NE, 0.032; NF, 0.053; NS, 0.031. Similar results obtain for distances estimated between NM and other west-bank samples (NJ, 0.016; NB, 0.021; NA, 0.015; NP, 0.018; NV, 0.029) versus distances estimated between NM and east-bank samples that are geographically closer or equidistant.
(NH, 0.029; NE, 0.032; NF, 0.037; NW, 0.037). Examination of average \( D_R \) among subspecific populations (Table 12) and average \( D_R \) values among riverbank populations (Table 13) reveals similar patterns of differentiation among populations. For example, Table 12 shows that the average distance between \textit{ludovicianus} populations (0.029) is the same as the average of values obtained from pairwise comparisons of \textit{subauratus} populations (0.029); each of these values is slightly higher than averaged distances among populations of \textit{subauratus} and \textit{ludovicianus} (0.027). In contrast, the average distance between populations of \textit{bachmani} (0.024) is much lower than average distances among \textit{bachmani-ludovicianus} (0.036) or \textit{bachmani-subauratus} (0.039) populations. Similarly, Table 13 illustrates that the average distance among populations separated by the Mississippi River (0.061) is larger than the average of values from pairwise comparisons among populations east of the Mississippi River (0.049). These values (especially the average value for pairwise comparisons among west-bank populations, 0.057) may be inflated somewhat by the inclusion of samples NX, NK, and NT, which are geographically distant from Louisiana and Mississippi populations (Fig. 6). However, similar relative distance values were obtained when these samples were omitted (Table 13). That is, genetic distances estimated between opposite-bank samples are on average higher than are genetic distances estimated between pairs of samples from either the east or west bank of the river.
The phenogram resulting from UPGMA cluster analysis of Rogers' (1972) distance estimates (Fig. 15) reflects an east-west pattern of differentiation among samples from Louisiana and Mississippi. Noteworthy features of this dendrogram include the following: samples NK (Arkansas) and NT (Tennessee) cluster together and are distinct from all other samples; samples NF, NH, NW, and NS, all of which are east of the river, cluster together; and samples NA, NM, NJ, NP, and NV, all of which are west of the river, form another grouping. An exception to the east-west dichotomy of samples in this dendrogram is the placement of NE, which clusters with NB and other "west-bank" samples.

The distance-Wagner tree (Fig. 16) identifies the same major groups; the most notable discrepancy between the UPGMA phenogram (Fig. 15) and the distance-Wagner tree (Fig. 16) is the placement of sample NX. The distance-Wagner procedure clustered NX with west-bank samples from Louisiana, whereas according to the UPGMA phenogram, NX is almost as genetically distinct from Louisiana and Mississippi samples as are NT and NK.

The jackknifing procedure identified the following "stable" nodes: NA–NP was supported in 11 of the 11 trees that included both samples, NB–NE (10 of 11), NB–NE grouped with NM in 7 of the 10 possible trees; the grouping of NA–NP, NB–NE, and NM was supported in 5 of 8 trees; NV–NX with NJ in 10 of 10; NW–NS (8 of 11); the grouping of NW–NS, with NF and NH in 6 of 9; and the rooting of the tree at the NK–NT branch was present in all 11
trees that included both of these samples.

In summary, electrophoretically-detectable patterns of geographic variation in fox squirrels, as revealed by multilocus and single-locus analyses (Figs. 10-16), are not congruent with the morphological patterns described earlier (Figs. 8 and 9). Despite estimates of high levels of gene flow among populations in this species (Nm = 8.05), examination of allelic distributions and genetic distances among samples suggests a north-south grouping of samples in which "northern" samples from Arkansas and Tennessee cluster together, and all "southern" samples from Texas, Louisiana, and Mississippi cluster together. There is a further subdivision within the "southern" cluster: samples are separated into "east-bank" and "west-bank" clusters, with the exception of NE, which is an east-bank sample that is placed with the "west-bank" cluster. The placement of NE with "west-bank" samples will be addressed in a subsequent section.

Sciurus carolinensis

Morphometric analyses.—Table 14 lists means and standard deviations of cranial and mandibular characters for each sample; Table 6 lists correlations among characters. Analysis of variance revealed highly significant differences (P < 0.0001) among samples for each character except MAX_HT, PAL_WIDTH.
ART_WIDTH, and MAND_HT. Four routines of MANOVA were used to test
the hypothesis that there are no significant morphometric
differences among samples. As in the S. niger analysis, each of
the four tests had results that were significant at $P < 0.0001$:
Hotelling-Lawley's Trace ($F = 3.07$); Pillai's Trace ($F = 2.09$);
Wilk's Criterion ($F = 2.55$); and Roy's Maximum Root Criterion ($F$
$= 20.32$). Because each of these $F$-values was highly significant,
additional analyses were used to elucidate patterns of variation
among samples; cluster analysis and principal components analysis
were performed to evaluate all characters simultaneously.

The results of a UPGMA analysis of taxonomic distances among
caracter means for the 18 samples are shown in Figure 17. Two
very distinct clusters are apparent at the 6.40 distance level:
the upper cluster is composed of samples from Arkansas,
Tennessee, and north-central Louisiana (CA_1, CT_2, CT_3, and
CL_2); and the lower cluster is further subdivided into two
clusters at the 5.80 level. One of these consists of samples
from southeastern Louisiana (CL_9 and CL_12), and the other
includes all other samples in this study. Sample CL_5 from
southwestern Louisiana is almost as distinct from the latter
grouping as are CL_9 and CL_12. CL_4, CT_1, and CX_1 also form a
relatively distinct cluster.

Results of the principal component analysis are presented in
Figure 18 and Table 15. Principal component one (PC I) accounts
for 49.7% of the total variance, and PC II accounts for 13.6% of
the variance. Characters MAX_LEN, ZYG_WIDTH, BR_WIDTH, and DIAST had the highest loadings for PC I (Table 15). As with *S. niger*, PC I probably portrays size because all characters exhibit relatively high, positive correlations with this axis. For PC II, LST_POST, INFR_BR, and PAL_WIDTH had high positive loadings. In Figure 18, samples CL_9 and CL12 (the southernmost populations) have high negative values for PC I and are comprised of the smallest individuals in this analysis. Samples from northern Louisiana, Tennessee, and Arkansas (CL_2, CT_3, CT_2, and CA_1) are comprised of the largest animals in this study, as indicated by high, positive scores for PC I. For PC II, CA_1 (Arkansas) and CL12 (southeastern Louisiana) have high, negative values for PC II; animals in these samples have relatively narrow anterior braincases (LST_POST), rostra (INFR_BR), and hard palates (PAL_WIDTH). In contrast, individuals in CL_3 from northeastern Louisiana have broader skulls in these respects, as reflected by the high, positive value that this sample scored for PC II.

Multivariate analyses of 15 cranial and mandibular characters indicate that there is morphological differentiation among samples of *S. carolinensis* from the lower Mississippi River valley. Furthermore, cluster and principal components analyses (Figs. 17 and 18) identified a pattern of clinal variation in size: there is a decrease in average size of individuals from north to south, and individuals from the Atchafalaya basin and
coastal swamps of Louisiana are, on average, the smallest individuals in this study. Animals from northern localities, Tennessee and Arkansas (CT_2, CT_3, and CA_1), were the largest individuals, and animals from localities in southeastern Louisiana (CL_9 and CL12) were the smallest individuals in this study. Animals from western Louisiana, eastern Texas, and Mississippi (CL_4, CX_1, and CM_1) are intermediate in size. There were no detectable differences in size among samples separated by the Mississippi River.

This pattern of morphological differentiation in gray squirrels is similar to patterns of variation described for this species by Lowery (1974), although he based taxonomic assignment of specimens on subtle differences in pelage coloration, rather than on skeletal characters. Lowery (1974) evidently was unable to detect the variation in size that I report here, perhaps because he did not use multivariate techniques, and he did not examine specimens from as far north as Tennessee and Arkansas. During my incidental inspection of study skins while measuring skulls, I was unable to detect the geographically structured patterns of pelage coloration that Lowery (1974) described. According to Lowery, individuals of "fuliginosus are darker than the darkest examples of carolinensis," but I was unable to see consistent differences in pelage coloration among specimens I examined. Nonetheless, my findings indicate that there is a north-south clinal pattern of morphological variation in S.
carolinensis that is approximately coincident with the geographic distributions Lowery (1974) and Hall (1981) described for carolinensis and fuliginosus; gray squirrels increase in size from south to north in a pattern of roughly concentric arcs that are centered in the Mississippi River delta region. As with S. niger, until additional studies are available, I recommend retention of the present subspecific epithets in recognition of the geographic variation among these population of S. carolinensis.

Electrophoretic analyses.—Twelve of 35 loci were monomorphic for the same allele across all 10 samples: ACN-2, AK-i, CK, GDA, G3PD, G6PD, IDH-2, LDH-2, MPI, PEPA, PEPC, and PEPS. Allelic designations and allele frequencies for the 23 polymorphic loci are shown in Table 16. Nine loci were polymorphic for alleles that occurred in two or more samples: ACN-1, ACP, ADA, 6PGD, PGM-1, MDH-2, GOT-1, PEPD, and PG1. Mean number of alleles per locus ranged from 1.1 (value for 6 samples) to 1.5 (CTS).

Table 16 also indicates the following statistics for each sample: percent polymorphism (P), which was calculated using loci for which the frequency of the most common allele was <95%; direct-count estimates of mean heterozygosity (H); and the expected mean number of heterozygotes (He, exp), which was calculated using Nei's (1978) unbiased estimate and assuming
Hardy-Weinberg equilibrium. Percent polymorphism ranged from 0% (CJ) to 22.9% (CE), and the average P for gray squirrels was 11.4%. Average $\bar{H}$ calculated over all samples in this study is 2.8%; values ranged from 0.5% (CJ) to 4.3% (CE). There were no apparent geographically related patterns in levels of genic variation as measured by heterozygosity and polymorphism, and as for fox squirrels, the values for $\bar{H}$ and P in gray squirrels (Table 16) are comparable to values generally reported for mammals (Nei and Graur, 1984; Nevo, 1978; Powell, 1975).

Chi-square tests revealed significant deviations from Hardy-Weinberg equilibrium for two samples, CH and CTS. These samples had heterozygote deficiencies at the following loci: CH (PGI, GLUD, GOT-2, 6PGD); and CTS (ME, MDH-1, PEPB). As with S. niger, the general agreement between observed and expected numbers of heterozygotes in S. carolinensis is consistent with the findings of many allozymic studies of sexually outbreeding organisms (Smith, et al., 1982).

Slatkin's (1985a) technique for estimating levels of gene flow among populations uses alleles that are unique to a single sample (called "private" alleles by Neel, 1973). Seventeen of the polymorphic loci were characterized by alleles unique to a single sample. The samples and loci were as follows: CA (ODH, ADA), CB (SDH), CE (FUM, MDH-2), CH (ADA, GLUD, GOT-2, ME, NP, PGM-1), CV (SOD), CTS (AK-2, IDH-1, LDH-1, MDH-1, PEPB, PGM-2, ME). Using all samples, 20 private alleles were present, the
average frequency of each allele \( p(l) \) was 0.0645 and the estimated amount of gene flow among populations (\( N_m \)), corrected for sample size, was 4.21. This estimate is higher than that reported for other mammals by Slatkin (1985a). Recalculation of these values using only samples with ten or more individuals (CH, CJ, CW, CE, and CS) resulted in estimates of \( p(l) = 0.036 \) and \( N_m = 10.41 \) (after correcting for small sample sizes). As with \( S. niger \) (\( N_m = 8.05 \)), this estimate for \( S. carolinensis \) is similar to Slatkin's value for \( Drosophila willistoni \), and it represents high levels of gene flow according to Slatkin (1981, 1985a, 1985b).

F-statistics and the results of the heterogeneity Chi-square analysis for each of the polymorphic loci are presented in Table 17. The mean value of \( F_{IS} \) is 0.072, which indicates overall heterozygote deficiency within each sample, and the mean value for \( F_{IT} \) (0.167) indicates an overall heterozygote deficiency among all samples combined. The \( F_{ST} \) for the ten samples of gray squirrels is 0.102 (uncorrected) and 0.056 (corrected), indicating that 5-10% of the genetic variance in gray squirrels is distributed among populations. Recalculation of \( F_{ST} \) values for samples from Louisiana and Mississippi (i.e., omitting CTS) yielded estimates of 10.4% (uncorrected) and 5.5% (corrected), which are essentially the same as estimates calculated for all ten samples. These \( F_{ST} \) values are lower than those estimated among Louisiana and Mississippi samples of \( S. niger \) (16.4%
uncorrected, 9.6% corrected), indicating that fox squirrel populations in the lower Mississippi River valley are more highly differentiated genetically than are gray squirrel populations in this region. I will comment on this difference in $F_{ST}$ values in a subsequent section.

The following alleles were shared with *S. niger*, and therefore were identified as symplesiomorphs in *S. carolinensis* in the locus-by-locus cladistic analysis (Table 10): ACN-1$^C$, ACP$^B$, ADA$^A$, 6PGD$^A$, and PGM-1$^B$. These alleles were discounted in analyses of relationships among populations of gray squirrels. The geographic distribution of alleles at loci that were polymorphic in four or more samples is depicted in Figures 19-23. Of these loci, $F_{ST}$ values for ACN-1 and ADA had highly significant Chi-square values (Table 17). Geographic distributions of synapomorphic alleles were as follows: the ACN-1$^B$ allele (Fig. 19) is present in all samples east of the Mississippi River and is absent from all west-bank samples; the 6PGD$^B$, 6PGD$^C$ (Fig. 20), and PGM-1$^C$ (Fig. 21) alleles are present only in samples east of the river. There is no apparent geographic pattern in the distribution of the ADA$^B$ allele (Fig. 22). The B allele at ACP (Fig. 23) is sympleisiomorphic (Table 10).

Table 18 summarizes values of Nei's (1978) and Rogers' (1972) genetic distance estimates for pairwise comparisons of the 10 samples of gray squirrels analyzed in this study. Values of
$D_R$ for these samples ranged from 0.011 (CJ-CA) to 0.039 (CA-CTS; CB-CTS), and the average distance estimate among populations was 0.025. As for fox squirrels, these values are comparable to genetic distance estimates among mammal populations reported by Avise and Aquadro (1982), Ayala (1975), and Selander and Johnson (1973). Distance estimates among samples of gray squirrels show a pattern similar to that seen in fox squirrels, although the trend is somewhat weaker in gray squirrels. That is, geographically proximal samples that are separated by the Mississippi River often are genetically more distinct than are geographically more distant samples that are located on the same side of the river. For example, estimated distance values between CA and other west-bank samples are as follows: CB, 0.020; CJ, 0.011; CV, 0.021, whereas the distances estimated for CA-CW and CA-CE are much larger (0.032 and 0.030, respectively), even though CW and CE are geographically closer to CA than are most of the west-bank samples. This relationship does not always obtain (e.g., distances estimated between CS-CB (0.018) and CS-CJ (0.015) are less than estimated distances between CS-CE (0.028) and CS-CH (0.025)).

Average distances estimated among subspecific (Table 19) and opposite-bank (Table 20) samples also show patterns of east-west differentiation. The average distance among samples west of the river (0.015) is much less than the average distances among populations on opposite sides of the Mississippi River (0.026).
The value for distances among east-bank populations apparently is not inflated by inclusion of sample CTS, which is genetically (and geographically) the most distant gray squirrel sample in this study (Table 18); recalculation of these values omitting CTS results in very minor changes (Table 20), perhaps because samples CW and CH are fairly distinct genetically from the other Louisiana and Mississippi samples (Table 18).

The phenogram resulting from UPGMA cluster analysis of Rogers' (1972) distance estimates (Fig. 24) illustrates a pattern of relationships similar to that seen for S. niger (Fig. 15); however, the east-west dichotomy in clusters of gray squirrel samples is not as distinct as was seen in samples of fox squirrels. I will comment on the relative amounts of east-west differentiation in these species in a subsequent section.

Noteworthy features of the UPGMA dendrogram for S. carolinensis (Fig. 24) include the following: CTS is distinct from all other samples; samples CA, CJ, CB, and CV (all of which are west of the river) form a group; and samples CW and CH cluster together. The distance-Wagner tree for gray squirrels (Fig. 25) identified similar groups of samples and placed all west-bank samples (CA, CB, CJ, CV) into a discrete group. The most notable difference between the UPGMA phenogram (Fig. 24) and the distance-Wagner tree (Fig. 25) is that CW and CH are placed with CTS, and the tree is rooted midway between this cluster and all other samples. The jackknifing procedure identified the
following "stable" nodes: the CA-CJ, CB, and CV group was
supported in 5 of the 5 trees that included all of these samples;
and the placement of CH-CTS with CW occurred in 7 of 7 trees.

In summary, electrophoretically detectable geographic
variation in gray squirrels, as revealed by multilocus and
single-locus analyses (Figs. 19-25), are not congruent with
patterns of morphological differentiation described earlier (Figs.
17 and 18). In spite of estimates of high levels of gene flow
among populations of *S. carolinensis* (*N_m* = 10.41), all samples of
gray squirrels from west of the Mississippi River form a cluster
distinct from other samples in this study. This pattern is
congruent with the results obtained from similar analyses of data
from fox squirrels, although the east-west trends were much more
pronounced in *S. niger* than in *S. carolinensis*.

The only other published study of electrophoretically
detectable geographic variation among populations of tree
squirrels, that of Havera and Nixon (1978), reported no
differentiation among the samples they examined. Havera and
Nixon (1978) made comparisons among samples of *S. carolinensis*
from Pennsylvania, North Carolina, northern Illinois, and
southern Illinois. From their report, it is unclear whether or
not side-by-side comparisons of electromorphs were made among all
samples. Additionally, Havera and Nixon (1978) did not report
estimates of *H* and *P* from their analyses because all individuals
were (apparently) homozygous for the same allele at each of the
"approximately 24" and "about 25" genetic loci they assayed. Because of these differences, comparisons between this study and Havera and Nixon's (1978) are not possible.

Changes in the Vegetation of Eastern North America During the Last 40,000 Years: Potential Effects on Evolution in Tree Squirrels of the Genus Sciurus

According to Black (1963, 1972), tree squirrels of the genus Sciurus have been present in North America and Eurasia since the early Miocene, and Moore (1959a, 1959b, 1961) proposed that Palearctic Sciurus vulgaris invaded North America (via a Bering land bridge), and its descendants diverged to produce species endemic to the New World. However, evolutionary relationships among New World species of Sciurus are poorly understood: examination of fossil material (Black, 1963, 1972), morphological studies (Moore, 1959b), and biochemical studies (Hight et al., 1974, Ellis and Maxson, 1980; Moncrief, unpubl. data) have done little to clarify affinities among species. Thus, phylogenetic relationships between S. niger and S. carolinensis remain unclear at this time, although there is considerable evidence (Black, 1963, 1972; Hafner, 1984) that progenitors of these species have been in North America since the late Oligocene-early Miocene boundary, approximately 25 million years before present.

Having established the presence of Sciurus in North America
before the Pleistocene, it is now appropriate to consider
disruptions and allowed divergence of ancestral populations in
order to suggest potential causal mechanisms for patterns of
differentiation in fox and gray squirrels. The present
distribution of fox squirrels and gray squirrels is delimited by
the distribution of eastern temperate deciduous forests; thus,
knowledge of the past distribution of these forests is crucial to
proposing past distributional ranges of tree squirrel populations
that are the presumed ancestors of squirrels that presently
inhabit the lower Mississippi River valley. Temperate deciduous
forests currently occur in eastern North America approximately to
the United States-Canada border and east to the Atlantic
coastline; the western boundary of temperate deciduous forests
extends north from central Texas, through central Oklahoma and
eastern Kansas, to the United States-Canada border. Delcourt and
Delcourt (1981, 1984) provide lucid summaries of palynological
evidence for spatial and temporal distribution of paleovegetation
during the late Quaternary in eastern North America. The oldest
time plane they were able to examine is 40,000 years before
present (Y.B.P.) because this date represents the effective limit
for age documentation using the radiocarbon-dating techniques
they employed. Delcourt and Delcourt's (1981, 1984) findings
that are pertinent to this study include the following:

1. During the last major period of glaciation, which lasted
from 80,000 to as recently as 10,000 years ago, climatic conditions in much of eastern North America would have been intolerable for temperate deciduous forests.

2. There were marked contrasts in phytogeographic patterns between glacial and interglacial periods, and there were also vegetational responses to shorter-term climatic oscillations; more than 60% of the last 40,000 years has been characterized by environmental conditions transitional between glacial and nonglacial regimes. There is broad similarity in vegetation types mapped by Delcourt and Delcourt for 40,000 Y.B.P., 25,000 Y.B.P., and 14,000 Y.B.P.

3. Cool-temperate hardwood species were, without question, displaced during glacial maxima; previously proposed refugial areas in southern Florida and Mexico have been refuted by Braun (1950). Delcourt and Delcourt (1981, 1984) suggest that ravines and slope habitats adjacent to major river valleys across the southeast provided refugia for these mesic, deciduous forest taxa.

4. The vegetation in most of the Deep South has remained relatively stable during the last 40,000 years: a widespread forest mosaic of oaks, hickories, and southern pine has persisted in sandy upland sites.

5. During peak, or full, glacial times (the last of which occurred ca. 18,000 Y.B.P.), the Laurentide Ice Sheet extended southward nearly to the confluence of the Ohio and
Mississippi rivers, and white spruce and tamarack extended southward in the alluvial valley of the Mississippi River to Louisiana (Fig. 26). At this time, a steep climatic gradient ran from northern Mississippi across central Alabama and Georgia, separating boreal from warm-temperate vegetation. South of this climatic boundary, a forest of oaks, hickories, and southern pines covered much of the Gulf and Atlantic coastal plains.

6. At approximately 16,500 Y.B.P., climatic amelioration resulted in initial disintegration and northward retreat of the Laurentide Ice Sheet, and a surge of meltwater was carried down the Mississippi River. Spruce persisted in the alluvial valley of the Mississippi River until about 12,500 Y.B.P., when it was replaced by cypress-gum, which was present in the lower Mississippi River valley until it was extensively disrupted by white settlers approximately 200 years ago. Coastal swamps and marshes formed in southern Louisiana with the late-Holocene development of major deltaic systems by the Mississippi River, which began approximately 5,000 to 7,000 Y.B.P. (Kolb and Van Lopik, 1958).

From this summary, it is evident that vegetational changes in the lower Mississippi valley beginning at least 18,000 Y.B.P. may have presented potentially major impediments to east-west
dispersal in tree squirrels. White spruce and tamarack were present in a broad north-south band adjacent to the Mississippi River and separated otherwise continuous oak-hickory southern pine forest for up to 5,000 years. This band of boreal forest may have provided a major, long-term barrier to west-east dispersal of squirrels whose descendants inhabit warm-temperate forests.

**Recent Geologic and Physiographic History of the Lower Mississippi River Valley**

Numerous geologic and physiographic analyses of the lower Mississippi valley have yielded a detailed record of course changes made by major distributaries of the river and resulting deltaic formations (Adams and Baumann, 1980; Doering, 1956; Frazier, 1967; Gunter, 1952; Kolb, 1963; Kolb and Van Lopik, 1958; Saucier, 1963, 1974). Kolb and Van Lopik (1958) have published an extensive summary of current knowledge of the geologic and physiographic history of the Mississippi River and its deltaic regions. Historical features pertinent to this study include the following:

1. Five to seven thousand years ago, lobate deltas were formed at the mouth of the ancestral Mississippi River, displacing gulf waters then at the latitude of Baton Rouge, Louisiana (approximately 180 km north of the present gulf);
this arm of the sea was referred to as the "Pontchartrain Embayment" by Fisk (1944).

2. Beginning 5,000 years ago, a sequence of major deltaic complexes were formed at the mouth of the primary distributaries of the Mississippi River. In order of their formation, these deltas are named Sale-Cypremort, Cocodrie, Teche, St. Bernard, Lafourche, Plaquemines, and Balize (Fig. 27).

3. The present delta (Balize) is different in size, shape, and distributary characteristics from all previous deltaic complexes. It is only one-tenth the size of several of the premodern deltas and is described as "bird's foot" in shape, which contrasts with the triangular outline of earlier deltas. The major distributary channels of the ancient deltas, in addition to being more numerous, were narrower and deeper than those of the Balize complex.

According to Kolb and Van Lopik's (1958) summary, land at or below the approximate latitude of Baton Rouge has been deposited by various distributaries of the Mississippi River within the last 5,000 to 7,000 years, and the lower Atchafalaya basin has been partitioned by varying numbers of major river channels. During the last 5,000 or so years, the entire lower delta region has literally been in a state of flux, creating a dynamic system in which river channels may have alternately impeded dispersal
and gene flow in tree squirrels, then effected reunion of previously separated populations via oxbows and cross-cuts of river channels.

**Patterns of Variation in Fox and Gray Squirrels:**

**Potential Effects of the Mississippi River on Differentiation in Tree Squirrels**

Examination of patterns of morphological differentiation in *S. carolinensis* and *S. niger* reveals that, in both species, individuals from the Atchafalaya River basin and the floodplain of the lower Mississippi River (*S. carolinensis fuliginosus* and *S. niger subauratus*) are smaller than animals from surrounding areas. The traditional interpretation of this geographic variation is that small size in these populations is an adaptive response to environmental factors in this region (Antonovics, 1971; Burnett, 1983; James, 1970; Johnston and Selander, 1971). Thus, according to the traditional viewpoint, these populations are genetically differentiated from populations in adjacent regions due to natural selection for small size. Scenarios might be proposed in which animals from the floodplain are smaller because they are, of necessity, more arboreal due to floods and standing water; or it might be suggested that animals from these regions are smaller because these areas are relatively warmer and more humid (James, 1970). However, electrophoretic analyses
suggest that neither species exhibits genetic differentiation among samples from the Mississippi River floodplain and those in (adjacent) western Louisiana; thus, these data do not support the traditional interpretation that genetic differentiation is congruent with morphological differences. It is, of course, possible that *fuliginosus* and *subauratus* differ from conspecifics at gene loci that were not analyzed in this study.

An alternative interpretation for the smaller size of tree squirrels in the Mississippi River floodplain and Atchafalaya River basin is that this reduction in body size may represent an environmentally induced, nongenetic response to a trophically poor habitat. The vegetation in this region is cypress and hardwoods, and frequent flooding in the spring presumably reduces access to nuts and seeds buried by squirrels and limits utilization of vegetation that might otherwise be available to squirrels feeding on the ground. This flooding occurs (and may limit food resources) during a potentially critical time period: many litters are being weaned during the mid-spring floods, so that nutritional resources are scarce during an important stage of individual growth and development.

In their review of geographic variation in fox squirrels, Weigl et al. (in press) also attributed the smaller size of *subauratus* individuals to poor food resources, and they noted that animals assigned to *S. n. avicennia* (which also inhabit in a poor trophic region, the cypress wetlands of southern Florida)
are smaller than animals found in the pine-oak forests of
northern Florida (S. n. shermani). In another study, Bakken
(1952) compared subspecies distributions and habitats of fox
squirrels and gray squirrels throughout their ranges; he noted
that the distributional range of the subspecies of gray squirrel
from southern Florida (S. carolinensis extimus) is coincident
with that of S. n. avicennia. Bakken (1952) suggested that
subspecies of fox and gray squirrels in southern Florida "may
have been influenced similarly by ecological conditions." Fox
squirrels from central Texas, S. n. limitis, inhabit the western
limit of the eastern deciduous forests. Like subauratus and
fuliginosus, these animals are smaller than conspecifics from
adjacent regions; this effect in limitis may also be an
environmentally induced, nongenetic response to trophic
conditions that are apparently poor for tree squirrels.

Patton and Brylski (in litt.) similarly attributed body size
differences in pocket gophers (Thomomys bottae) to differences in
nutritional quality of available food. In one of the few studies
of its kind, Patton and Brylski (in litt.) examined morphological
variation among genetically undifferentiated natural populations
of pocket gophers that inhabit areas with vastly different food
resources: their natural habitat of desert scrub and the
artificial environment of irrigated alfalfa fields. Animals from
desert scrub populations are significantly smaller than those
found in alfalfa; "common-garden" feeding experiments of gophers
born in the laboratory indicate that these differences are
directly related to nutritional conditions after weaning and that
growth rate is very labile in pocket gophers.

Thus, in the present study, small size in *fuliginosus*,
*subauratus*, and *limitis* may result from nutritional conditions
and may be environmentally induced and nongenetic. This view is
in contrast to (but not inconsistent with) Weigl et al.'s (in
press) interpretation of factors responsible for the size
differences between eastern and western fox squirrels. Weigl et
al. (in press) present considerable evidence that the large size
of eastern fox squirrels is an adaptive response that facilitates
utilization of longleaf pine cones as the primary food resource
during certain times of the year. They have conducted extensive
ecological and behavioral investigations on North Carolina
populations of fox squirrels, and their comparative feeding
studies demonstrated that (larger) eastern fox squirrels are far
superior to (smaller) western fox squirrels and gray squirrels in
their ability to handle and carry these large, bulky cones.
Weigl et al. (in press) attribute the eastern squirrels' superior
ability to manipulate longleaf pine cones to its much larger body
size, and they conclude that natural selection has produced
larger squirrels in the southeastern United States because
longleaf pine cones provide the only available food for these
squirrels during late summer and early fall. They point out that
large fox squirrels also occur in those regions west of the
Mississippi River (e.g., west-central Louisiana) in which longleaf cones are potentially the primary food resource in late summer and early fall. Therefore, large size in *ludovicianus* and *bachmani* may be the result of natural selection for efficient utilization of limited food resources, and may represent an adaptive response to the environment. Other recent morphological studies of geographic variation in mammals (Lindsay, 1986; Schmitz and Lavigne, 1987) have attributed size differences to efficiency in exploitation of food sources. Lindsay (1986) presented evidence that red squirrels have undergone selection for size that corresponds to geographic changes in conifer cone morphology. Similarly, Schmitz and Lavigne (1987) attributed size variation in canids to selection for utilization of certain prey species. McNab (1971) also pointed out this relationship between size of food items and geographic variation in tree squirrels and carnivores. Thus, large size in *ludovicianus* and *bachmani* may be an adaptive (i.e., genetically based) response to environmental factors; however, there are no electrophoretically detectable genetic differences that correspond to morphological differentiation and distinguish *ludovicianus* (west-central Louisiana, longleaf pines) from *subauratus* (Mississippi River floodplain, bottomland hardwoods).

This discussion of potential causes of size variation in tree squirrels is somewhat speculative. However, both adaptive and nonadaptive interpretations of small size in *S. niger*...
subauratus and S. carolinensis fuliginosus emphasize environmental effects induced by the Mississippi River. Further insight into the factors responsible for morphologic differentiation among populations of fox and gray squirrels from the lower Mississippi River valley may be obtained through cross-transplantation experiments of the sort performed by James (1983) and "common-garden" experiments such as those conducted by Patton and Brylski (in litt.). Such experiments may allow more definitive statements to be made regarding factors that affect size in S. niger and S. carolinensis; however, logistical problems involved in live-trapping and cross-transplanting squirrels or maintaining wild-caught tree squirrels in captivity for long periods of time make these studies impractical at this time.

In addition to the broad similarity in patterns of morphological differentiation within fox and gray squirrels in the lower Mississippi River valley, both species exhibit east-west divergence in allozymic characters that is approximately coincident with the Mississippi River. For each species, alleles that are present on one side of the river do not occur in any of the opposite-bank populations, suggesting that the Mississippi River has been (and may still be) a barrier to gene flow in both species. This pattern exists at different loci in fox and gray squirrels, discounting the view that alleles at these structural gene loci are acted upon by natural selection.
That is, if natural selection produced differences among eastern and western populations, it is logical to assume that the same loci would exhibit east-west patterns in both fox and gray squirrels. This is not the case; the patterns are present at different loci in these two species, and my data are consistent with the view that allozymic differences among populations result from random mutation and chance fixation of alleles that are neutral with respect to natural selection. My data also suggest that the river has impeded (and may still impede) gene flow in both species. For example, the B allele at MPI is characteristic of east-bank _S. niger_ (Fig. 10), and ACN-1^B_ (Fig. 19) is characteristic of east-bank samples of _S. carolinensis_. Additionally, the PGM-1^B_ allele (Fig. 11) is present in only one east-bank sample of _S. niger_, as is the C allele at ADA (Fig. 12). And finally, the C allele at 6PGD (Fig. 20) is present in 4 of 6 east-bank populations of _S. carolinensis_, whereas this locus is completely monomorphic for the A allele in samples west of the river. It might be argued that sample sizes used in this study are inadequate to rule out sampling error; for example, because of small sample sizes, there might have been omission of west-bank individuals that possess east-bank "marker" alleles at MPI and ACN-1. However, it should be noted that for these loci, the east-bank "marker" allele is present in samples that include only three or seven individuals (NW and CEP, respectively). Sample sizes of most west-bank samples are at least as large as
this, weakening the argument that inadequate sample sizes resulted in sampling error.

The dichotomy between eastern and western populations is also clearly evident in pelage coloration differences among fox squirrel populations. All southern subspecies of *S. niger* that occur exclusively east of the Mississippi River (*bachmani*, *niger*, *shermani*, *cinereus*, and *avicennia*) have distinctive white markings on the nose, ears, and feet. This is undoubtedly genetically based variation, and these white markings constitute a synapomorphic trait that unites these populations of *S. niger*. As with morphometric variation, the traditional interpretation is that these markings have an adaptive function. Weigl et al. (in press) suggested that they are disruptive coloration and are, therefore, a predator-defense mechanism. In this vein, Richard Kiltie of the University of Florida (in litt.) has conducted experiments with captive red-tailed hawks (*Buteo jamaicensis*), which are the largest hawks known to prey on fox squirrels. He presented the hawks with variably-colored squirrel models against various tree-bark backgrounds to determine the birds' ability to detect squirrels with more or less black on the dorsum. Kiltie's (in litt.) preliminary results indicate that variable patches of black hairs may have an adaptive advantage; he did not comment on the effect of varying amounts of white on the extremities, however. An alternative, "nonadaptive" explanation is that the
white markings serve no discernible function and are effectively neutral to selection. The fact that western fox squirrels lack these white markings, and yet may be equally susceptible to predation by hawks, supports this contention. Hafner and Hafner (1987) offered a similar "nonadaptive" interpretation to account for the presence of white "belts" and "headspots" in some populations of Central American pocket gophers. Further investigations using techniques similar to those employed by Kiltie (in litt.) are necessary before more conclusive statements can be made regarding the functional significance of white markings in bachmani and other eastern subspecies of S. niger.

Not all fox squirrels east of the current Mississippi River channel have white markings: individuals from East Baton Rouge Parish (NL_9) are "typical" subauratus that phenotypically (size and coloration) resemble west-bank populations from the Mississippi River floodplain and Atchafalaya River basin. Intergradation between bachmani and subauratus in Louisiana occurs in a narrow zone just east of East Baton Rouge Parish; individuals in this area average slightly larger, and some exhibit white on the nose and feet. Congruent with morphological patterns of differentiation, animals from East Baton Rouge Parish (sample NE) are electrophoretically most similar to west-bank samples. Yet the East Baton Rouge population shares the MPI\textsuperscript{B} allele with other east-bank populations. It may be of further interest to note that the "marker" allele MPI\textsuperscript{B} is present in
lower frequency in the East Baton Rouge sample (5%) than in other east-bank samples (17%-33%). This result obtains in spite of the fact that NE is represented by more individuals (N = 10) than all but one other east-bank sample of S. niger (NH; N = 13). Thus, the low frequency of MPI\(^B\) in the East Baton Rouge sample appears not to result from sampling error, rather this allele may have only recently been introduced into populations in East Baton Rouge Parish. Gray squirrels exhibit a similar pattern of allozymic differentiation; some east-bank samples of S. carolinensis (CE, CEP, and CS) are electrophoretically more similar to west-bank samples than to other east-bank samples (e.g., CW and CH). Yet, as with MPI\(^B\) in S. niger, all east-bank samples of S. carolinensis share the ACN-1\(^B\) allele.

I interpret these data as evidence of secondary contact following in situ allopatric differentiation that resulted from separation of populations by a physical barrier to gene flow, namely the Mississippi River and associated riverine habitats (Endler, 1977). In a reexamination of data presented by Baker (1981) and Grenbaum (1981), Hafner (1982) suggested a similar interpretation for the distribution of electrophoretically detectable alleles at a Honduran contact zone between cytotypes of Uroderma bilobatum. Hafner (1982) proposed a scenario of secondary contact after allopatric divergence between Honduran populations of U. bilobatum on either side of the Golfo de Fenesco, which bisects the Pacific versant corridor of lower
tropical forest habitat to which these bats are restricted. In interpreting results obtained in the present study, I suggest that populations of tree squirrels in the vicinity of Baton Rouge, and those south and east of Baton Rouge (south of the Tunica Hills region of Louisiana), at one time may have been located west of the Mississippi River channel. At that time, alleles that are now characteristic of east-bank or west-bank populations (e.g., MPI^B, ACN-1^B, and the alleles for white markings in fox squirrels) appeared and were disseminated via gene flow throughout populations on one side of the river or the other. Subsequent shifts in the major distributary channel of the river (perhaps within the last 5,000-7,000 years; Fig. 27) may have effected passive transfer of populations in southeastern Louisiana from one bank of the river to the other. Under this scenario, the land presently defined as East. Baton Rouge Parish was recently transferred to the eastern bank of the Mississippi River channel. Subsequent dispersal of individuals allowed gene flow with populations to the east, which were previously cross-river populations. In turn, certain alleles (e.g., MPI^B and ACN-1^B) characteristic of east-bank populations were introduced into populations that had been passively transferred to the east bank.

East-west patterns of divergence in electrophoretic and morphologic characters are more striking in fox squirrels than in gray squirrels. Electrophoretically detectable differentiation
among fox squirrel populations in the lower Mississippi River valley is much more pronounced than that found among gray squirrel populations: corrected $F_{ST}$ ($\bar{F}_{DT}$) values are 30.5% for S. niger (Table 9) versus 5.6% for S. carolinensis (Table 17). Additionally, Rogers' (1972) genetic distance values among populations of fox squirrels ranged from 0.014 to 0.139 and averaged 0.047 (Table 11), whereas these values ranged from 0.011 to 0.039 and averaged 0.025 (Table 18) in gray squirrels. Cluster analyses of these genetic distance values revealed a much more pronounced east-west dichotomy in S. niger (Figs. 15 and 16) than in S. carolinensis (Figs. 24 and 25). Examination of morphologic characters reveals spectacular east-west pelage color differences in fox squirrels; in contrast, Lowery (1974) reported that variation in pelage color among gray squirrel populations (which I was unable to detect) is present in a north-south orientation.

These observations on the relative amounts of east-west divergence in tree squirrels in the lower Mississippi River valley may be interpretable in light of habitat preferences of extant populations. Bakken (1952) and Weigl et al. (in press) note that gray squirrels tend to be restricted more to closed-canopy oak-hickory forests, swamps, and bottomlands; fox squirrels prefer more open pine stands, pine slashings, and old burns with standing pine. Thus, gray squirrels seem to prefer wetter, denser forests. It is, therefore, possible that
river-induced vegetational changes in the lower Mississippi River valley may have acted as a weaker barrier to dispersal in gray squirrels than in fox squirrels. That is, fox squirrels may be more divergent morphologically and allozymically than gray squirrels because ancestral fox squirrel populations were isolated in eastern and western refugia for a longer period of time.

Conclusions

In summary, my analyses indicate that there is geographic variation in morphology and allozymes among populations of *S. carolinensis* and *S. niger* in the lower Mississippi River valley. Patterns of differentiation in morphologic and allozymic characters are similar between species; however, morphometric variation is not congruent with allozymic variation within either species. Morphological analyses indicate that within each species, individuals in the Mississippi River floodplain and the Atchafalaya River basin are smaller than animals from adjacent regions. The smaller size of floodplain individuals may be a nongenetic response to environmental factors, although additional studies are necessary to support or refute this interpretation. Electrophoretic analyses do not reveal patterns consistent with size differences. Rather, within each species, there is genetic
differentiation among eastern and western populations, as defined by their geographic location relative to the present Mississippi River channel. This trend in allozymic differentiation is more pronounced in fox squirrels than in gray squirrels.

This study provides considerable evidence that the lower Mississippi River has influenced phenotypic differentiation in fox and gray squirrels and that the river has impeded (and may still impede) gene flow in these species. The role of the river as a barrier to dispersal and gene flow may have resulted from direct effects, because the Mississippi River may be a substantial physical barrier to a large, scansorial rodent such as a tree squirrel. It is also highly likely that the river has affected dispersal and gene flow in tree squirrels indirectly due to environmental and vegetational shifts that occurred in the alluvial valley of the Mississippi River during the late Quaternary. The results of this study suggest that the Mississippi River may have profoundly affected the distribution and historical biogeography of mammal species in this region. Additional studies are needed to assess the potential influence of the lower Mississippi River on evolution in other species of terrestrial organisms.


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Table 1.—Listing of samples of *Sciurus niger* used in morphometric analyses.
Specific collecting localities are given in Appendix I.

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Table 2.—Listing of samples of *Sciurus carolinensis* used in morphometric analyses. Specific collecting localities are given in Appendix I.

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Table 3.—Listing of samples of *Sciurus niger* used in electrophoretic analyses. Specific collecting localities are given in Appendix II.

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<td>Holmes</td>
<td>13</td>
<td><em>bachmani</em></td>
</tr>
<tr>
<td>10.</td>
<td>NS</td>
<td>St. Tammany</td>
<td>5</td>
<td><em>bachmani</em></td>
</tr>
<tr>
<td>11.</td>
<td>NW</td>
<td>West Feliciana</td>
<td>3</td>
<td><em>bachmani</em></td>
</tr>
<tr>
<td>12.</td>
<td>NX</td>
<td>Atascosa</td>
<td>1</td>
<td><em>limitis</em></td>
</tr>
<tr>
<td>13.</td>
<td>NK</td>
<td>Greene</td>
<td>5</td>
<td><em>rufiventer</em></td>
</tr>
<tr>
<td>14.</td>
<td>NT</td>
<td>Haywood, McNairy, Trousdale</td>
<td>3</td>
<td><em>rufiventer</em></td>
</tr>
</tbody>
</table>
Table 4.—Listing of samples of *Sciurus carolinensis* used in electrophoretic analyses. Specific collecting localities are given in Appendix II.

<table>
<thead>
<tr>
<th>sample</th>
<th>code</th>
<th>county</th>
<th>sample size</th>
<th>subspecies</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>CB</td>
<td>Bossier</td>
<td>3</td>
<td><em>carolinensis</em></td>
</tr>
<tr>
<td>2.</td>
<td>CJ</td>
<td>Jackson, Bienville, Winn</td>
<td>12</td>
<td><em>carolinensis</em></td>
</tr>
<tr>
<td>3.</td>
<td>CH</td>
<td>Holmes</td>
<td>18</td>
<td><em>carolinensis</em></td>
</tr>
<tr>
<td>4.</td>
<td>CV</td>
<td>Vernon, Rapides</td>
<td>7</td>
<td><em>carolinensis</em></td>
</tr>
<tr>
<td>5.</td>
<td>CTS</td>
<td>Shelby, Tipton</td>
<td>16</td>
<td><em>carolinensis</em></td>
</tr>
<tr>
<td>6.</td>
<td>CA</td>
<td>Acadia, Lafayette</td>
<td>5</td>
<td><em>fuliginosus</em></td>
</tr>
<tr>
<td>7.</td>
<td>CE</td>
<td>East Baton Rouge</td>
<td>16</td>
<td><em>fuliginosus</em></td>
</tr>
<tr>
<td>8.</td>
<td>CEP</td>
<td>East Baton Rouge</td>
<td>7</td>
<td><em>fuliginosus</em></td>
</tr>
<tr>
<td>9.</td>
<td>CW</td>
<td>West Feliciana</td>
<td>11</td>
<td><em>fuliginosus</em></td>
</tr>
<tr>
<td>10.</td>
<td>CS</td>
<td>St. Tammany</td>
<td>12</td>
<td><em>fuliginosus</em></td>
</tr>
</tbody>
</table>
Table 5.—Means and standard deviations of 15 cranial and mandibular characters for 19 samples of *Sciturus niger*. Abbreviations for samples are given in Table 1; abbreviations for characters are given in text.
Table 6.—Character correlations among IS cranial and mandibular characters for 19 samples of *Sclurus niger* (above diagonal) and 18 samples of *Sclurus carollinensis* (below diagonal). Abbreviations for characters are given in text.

<table>
<thead>
<tr>
<th>character</th>
<th>MAX_LEN</th>
<th>ZYG_WIDTH</th>
<th>BRN_WIDTH</th>
<th>LST_POST</th>
<th>MAX_HT</th>
<th>INFR_BR</th>
<th>DIASY</th>
<th>TOOTH</th>
</tr>
</thead>
<tbody>
<tr>
<td>MAX_LEN</td>
<td>--------</td>
<td>0.938</td>
<td>0.969</td>
<td>0.599</td>
<td>0.834</td>
<td>0.764</td>
<td>0.961</td>
<td>0.836</td>
</tr>
<tr>
<td>ZYG_BR</td>
<td>0.637</td>
<td>--------</td>
<td>0.933</td>
<td>0.619</td>
<td>0.927</td>
<td>0.868</td>
<td>0.911</td>
<td>0.839</td>
</tr>
<tr>
<td>BRN_WIDTH</td>
<td>0.767</td>
<td>0.692</td>
<td>--------</td>
<td>0.538</td>
<td>0.840</td>
<td>0.782</td>
<td>0.814</td>
<td>0.825</td>
</tr>
<tr>
<td>LST_POST</td>
<td>0.115</td>
<td>0.215</td>
<td>0.491</td>
<td>--------</td>
<td>0.665</td>
<td>0.690</td>
<td>0.595</td>
<td>0.596</td>
</tr>
<tr>
<td>MAX_HT</td>
<td>0.486</td>
<td>0.446</td>
<td>0.684</td>
<td>0.559</td>
<td>--------</td>
<td>0.815</td>
<td>0.783</td>
<td>0.814</td>
</tr>
<tr>
<td>INFR_BR</td>
<td>0.659</td>
<td>0.645</td>
<td>0.656</td>
<td>0.486</td>
<td>0.657</td>
<td>--------</td>
<td>0.723</td>
<td>0.839</td>
</tr>
<tr>
<td>DIASY</td>
<td>0.874</td>
<td>0.817</td>
<td>0.898</td>
<td>0.341</td>
<td>0.600</td>
<td>0.652</td>
<td>--------</td>
<td>0.723</td>
</tr>
<tr>
<td>TOOTH</td>
<td>0.716</td>
<td>0.467</td>
<td>0.567</td>
<td>-0.046</td>
<td>0.431</td>
<td>0.222</td>
<td>0.576</td>
<td>0.352</td>
</tr>
<tr>
<td>MLR_WIDTH</td>
<td>0.610</td>
<td>0.548</td>
<td>0.680</td>
<td>0.204</td>
<td>0.303</td>
<td>0.464</td>
<td>0.637</td>
<td>0.341</td>
</tr>
<tr>
<td>PML_WIDTH</td>
<td>0.701</td>
<td>0.538</td>
<td>0.730</td>
<td>0.210</td>
<td>0.498</td>
<td>0.512</td>
<td>0.711</td>
<td>0.341</td>
</tr>
<tr>
<td>PALWIDTH</td>
<td>0.204</td>
<td>0.503</td>
<td>0.434</td>
<td>0.254</td>
<td>0.350</td>
<td>0.545</td>
<td>0.367</td>
<td>0.033</td>
</tr>
<tr>
<td>FOR_WIDTH</td>
<td>0.369</td>
<td>0.377</td>
<td>0.457</td>
<td>-0.127</td>
<td>0.060</td>
<td>0.043</td>
<td>0.443</td>
<td>0.383</td>
</tr>
<tr>
<td>ART_WIDTH</td>
<td>0.266</td>
<td>0.321</td>
<td>0.095</td>
<td>0.000</td>
<td>0.390</td>
<td>0.326</td>
<td>0.072</td>
<td>0.050</td>
</tr>
<tr>
<td>MAND_HT</td>
<td>0.765</td>
<td>0.792</td>
<td>0.670</td>
<td>-0.116</td>
<td>0.316</td>
<td>0.579</td>
<td>0.648</td>
<td>0.550</td>
</tr>
<tr>
<td>MAND_LEN</td>
<td>0.614</td>
<td>0.430</td>
<td>0.606</td>
<td>-0.023</td>
<td>0.299</td>
<td>0.286</td>
<td>0.612</td>
<td>0.313</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>character</th>
<th>MLR_WIDTH</th>
<th>PML_WIDTH</th>
<th>PAL_WIDTH</th>
<th>FOR_WIDTH</th>
<th>ART_WIDTH</th>
<th>MAND_HT</th>
<th>MAND_LEN</th>
</tr>
</thead>
<tbody>
<tr>
<td>MAX_LEN</td>
<td>0.643</td>
<td>0.761</td>
<td>0.855</td>
<td>0.755</td>
<td>0.785</td>
<td>0.931</td>
<td>0.929</td>
</tr>
<tr>
<td>ZYG_BR</td>
<td>0.785</td>
<td>0.692</td>
<td>0.855</td>
<td>0.762</td>
<td>0.866</td>
<td>0.967</td>
<td>0.938</td>
</tr>
<tr>
<td>BRN_WIDTH</td>
<td>0.858</td>
<td>0.762</td>
<td>0.854</td>
<td>0.702</td>
<td>0.717</td>
<td>0.918</td>
<td>0.915</td>
</tr>
<tr>
<td>LST_POST</td>
<td>0.312</td>
<td>0.440</td>
<td>0.561</td>
<td>0.527</td>
<td>0.698</td>
<td>0.641</td>
<td>0.563</td>
</tr>
<tr>
<td>MAX_HT</td>
<td>0.687</td>
<td>0.539</td>
<td>0.815</td>
<td>0.680</td>
<td>0.860</td>
<td>0.892</td>
<td>0.904</td>
</tr>
<tr>
<td>INFR_BR</td>
<td>0.674</td>
<td>0.734</td>
<td>0.815</td>
<td>0.594</td>
<td>0.791</td>
<td>0.850</td>
<td>0.774</td>
</tr>
<tr>
<td>DIASY</td>
<td>0.819</td>
<td>0.773</td>
<td>0.706</td>
<td>0.714</td>
<td>0.738</td>
<td>0.871</td>
<td>0.906</td>
</tr>
<tr>
<td>TOOTH</td>
<td>0.750</td>
<td>0.764</td>
<td>0.882</td>
<td>0.695</td>
<td>0.754</td>
<td>0.865</td>
<td>0.849</td>
</tr>
<tr>
<td>MLR_WIDTH</td>
<td>--------</td>
<td>0.658</td>
<td>0.643</td>
<td>0.698</td>
<td>0.685</td>
<td>0.770</td>
<td>0.832</td>
</tr>
<tr>
<td>PML_WIDTH</td>
<td>0.215</td>
<td>--------</td>
<td>0.717</td>
<td>0.497</td>
<td>0.552</td>
<td>0.723</td>
<td>0.678</td>
</tr>
<tr>
<td>PAL_WIDTH</td>
<td>0.008</td>
<td>0.094</td>
<td>--------</td>
<td>0.595</td>
<td>0.735</td>
<td>0.831</td>
<td>0.824</td>
</tr>
<tr>
<td>FOR_WIDTH</td>
<td>0.323</td>
<td>0.511</td>
<td>0.150</td>
<td>--------</td>
<td>0.760</td>
<td>0.818</td>
<td>0.750</td>
</tr>
<tr>
<td>ART_WIDTH</td>
<td>0.382</td>
<td>0.207</td>
<td>0.349</td>
<td>-0.065</td>
<td>--------</td>
<td>0.621</td>
<td>0.805</td>
</tr>
<tr>
<td>MAND_HT</td>
<td>0.535</td>
<td>0.566</td>
<td>0.232</td>
<td>0.281</td>
<td>0.281</td>
<td>--------</td>
<td>0.932</td>
</tr>
<tr>
<td>MAND_LEN</td>
<td>0.553</td>
<td>0.478</td>
<td>0.121</td>
<td>0.652</td>
<td>0.168</td>
<td>0.422</td>
<td>--------</td>
</tr>
</tbody>
</table>
Table 7.—Character loadings for 15 cranial and mandibular characters for 19 samples of *Sciurus niger*. Abbreviations for characters are given in text.

<table>
<thead>
<tr>
<th>character</th>
<th>PCI</th>
<th>PCII</th>
</tr>
</thead>
<tbody>
<tr>
<td>MAX_LEN</td>
<td>0.280</td>
<td>-0.149</td>
</tr>
<tr>
<td>ZYG_WDTH</td>
<td>0.284</td>
<td>0.065</td>
</tr>
<tr>
<td>BRN_WDTH</td>
<td>0.276</td>
<td>-0.225</td>
</tr>
<tr>
<td>LST_POST</td>
<td>0.197</td>
<td>0.678</td>
</tr>
<tr>
<td>MAX_HT</td>
<td>0.264</td>
<td>0.212</td>
</tr>
<tr>
<td>INFR_BR</td>
<td>0.256</td>
<td>0.181</td>
</tr>
<tr>
<td>DIAST</td>
<td>0.268</td>
<td>-0.170</td>
</tr>
<tr>
<td>TOOTH</td>
<td>0.263</td>
<td>-0.006</td>
</tr>
<tr>
<td>MLR_WDTH</td>
<td>0.242</td>
<td>-0.420</td>
</tr>
<tr>
<td>PML_WDTH</td>
<td>0.225</td>
<td>-0.280</td>
</tr>
<tr>
<td>PAL_WDTH</td>
<td>0.259</td>
<td>-0.019</td>
</tr>
<tr>
<td>FOR_WDTH</td>
<td>0.230</td>
<td>0.044</td>
</tr>
<tr>
<td>ART_WDTH</td>
<td>0.252</td>
<td>0.301</td>
</tr>
<tr>
<td>MAND_HT</td>
<td>0.281</td>
<td>0.021</td>
</tr>
<tr>
<td>MAND_LEN</td>
<td>0.276</td>
<td>-0.092</td>
</tr>
</tbody>
</table>
Table 8.— Alphabetic designation of electromorphs, mean heterozygosity (H\textsuperscript{\textdagger}), and percent polymorphism (P\textsuperscript{\textdagger}) at 13 polymorphic loci assayed across 14 samples of Sclerus nigra. Allelic frequencies for polymorphic loci are indicated in parentheses. Abbreviations for samples are given in Table 3; abbreviations for loci are given in text.

<table>
<thead>
<tr>
<th>Sample</th>
<th>MA</th>
<th>SB</th>
<th>HE</th>
<th>WF</th>
<th>NH</th>
<th>NJ</th>
<th>NK</th>
<th>NH</th>
<th>WP</th>
<th>NT</th>
<th>NV</th>
<th>NK</th>
<th>WH</th>
<th>NS</th>
</tr>
</thead>
<tbody>
<tr>
<td>W</td>
<td>0.026</td>
<td>0.036</td>
<td>0.041</td>
<td>0.048</td>
<td>0.051</td>
<td>0.034</td>
<td>0.073</td>
<td>0.024</td>
<td>0.021</td>
<td>0.095</td>
<td>0.057</td>
<td>0.057</td>
<td>0.034</td>
<td></td>
</tr>
<tr>
<td>H</td>
<td>0.033</td>
<td>0.033</td>
<td>0.035</td>
<td>0.065</td>
<td>0.047</td>
<td>0.049</td>
<td>0.057</td>
<td>0.040</td>
<td>0.030</td>
<td>0.123</td>
<td>0.062</td>
<td>0.057</td>
<td>0.057</td>
<td></td>
</tr>
</tbody>
</table>
| N  | 5.7 | 11.4 | 17.1 | 17.1 | 11.4 | 11.4 | 8.6 | 2.2 | 2.9 | 17.1 | 5.7 | 11.4 | 5.7 | 100
Table 9.—F-statistics averaged over polymorphic loci for 14 samples of *Scicurus niger* and contingency chi-square analysis of $F_{ST}$. $I$ = individual, $S$ = sample, $T$ = total, $D$ = data; $F_{DT}$ = estimate of $F_{ST}$ calculated using Wright’s (1978) correction for small sample sizes.

<table>
<thead>
<tr>
<th>locus</th>
<th>$F_{IS}$</th>
<th>$F_{IT}$</th>
<th>$F_{ST}$</th>
<th>$F_{DT}$</th>
<th>alleles</th>
<th>$X^2$</th>
<th>DF</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>ACP</td>
<td>-0.065</td>
<td>-0.008</td>
<td>0.053</td>
<td>0.000</td>
<td>3</td>
<td>8.38</td>
<td>13</td>
<td>0.818</td>
</tr>
<tr>
<td>ADA</td>
<td>-0.171</td>
<td>0.199</td>
<td>0.316</td>
<td>0.221</td>
<td>2</td>
<td>97.86</td>
<td>26</td>
<td>0.000</td>
</tr>
<tr>
<td>CK</td>
<td>1.000</td>
<td>1.000</td>
<td>0.157</td>
<td>0.086</td>
<td>2</td>
<td>25.31</td>
<td>13</td>
<td>0.021</td>
</tr>
<tr>
<td>FUM</td>
<td>-0.042</td>
<td>-0.006</td>
<td>0.035</td>
<td>0.000</td>
<td>2</td>
<td>4.94</td>
<td>13</td>
<td>0.976</td>
</tr>
<tr>
<td>G6PD</td>
<td>1.000</td>
<td>1.000</td>
<td>0.134</td>
<td>0.072</td>
<td>2</td>
<td>22.84</td>
<td>13</td>
<td>0.044</td>
</tr>
<tr>
<td>IDH-1</td>
<td>-0.308</td>
<td>-0.012</td>
<td>0.226</td>
<td>0.149</td>
<td>3</td>
<td>64.13</td>
<td>26</td>
<td>0.000</td>
</tr>
<tr>
<td>IDH-2</td>
<td>1.000</td>
<td>1.000</td>
<td>0.134</td>
<td>0.072</td>
<td>2</td>
<td>23.41</td>
<td>13</td>
<td>0.037</td>
</tr>
<tr>
<td>MDH-1</td>
<td>1.000</td>
<td>1.000</td>
<td>0.317</td>
<td>0.203</td>
<td>2</td>
<td>55.32</td>
<td>13</td>
<td>0.000</td>
</tr>
<tr>
<td>ME</td>
<td>0.357</td>
<td>0.783</td>
<td>0.663</td>
<td>0.621</td>
<td>3</td>
<td>221.33</td>
<td>26</td>
<td>0.000</td>
</tr>
<tr>
<td>MPI</td>
<td>-0.184</td>
<td>0.064</td>
<td>0.209</td>
<td>0.126</td>
<td>2</td>
<td>39.05</td>
<td>13</td>
<td>0.000</td>
</tr>
<tr>
<td>NF</td>
<td>-0.154</td>
<td>0.108</td>
<td>0.226</td>
<td>0.158</td>
<td>2</td>
<td>28.25</td>
<td>13</td>
<td>0.008</td>
</tr>
<tr>
<td>ODH</td>
<td>-1.000</td>
<td>-0.037</td>
<td>0.481</td>
<td>0.222</td>
<td>2</td>
<td>77.50</td>
<td>13</td>
<td>0.000</td>
</tr>
<tr>
<td>PEPB</td>
<td>-0.765</td>
<td>-0.063</td>
<td>0.397</td>
<td>0.318</td>
<td>2</td>
<td>69.28</td>
<td>13</td>
<td>0.000</td>
</tr>
<tr>
<td>PEPD</td>
<td>1.000</td>
<td>1.000</td>
<td>0.849</td>
<td>0.823</td>
<td>2</td>
<td>146.92</td>
<td>13</td>
<td>0.000</td>
</tr>
<tr>
<td>6PGD</td>
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<td>-0.004</td>
<td>0.047</td>
<td>0.000</td>
<td>2</td>
<td>8.14</td>
<td>13</td>
<td>0.834</td>
</tr>
<tr>
<td>PG1</td>
<td>-0.500</td>
<td>-0.024</td>
<td>0.317</td>
<td>0.203</td>
<td>2</td>
<td>55.98</td>
<td>13</td>
<td>0.000</td>
</tr>
<tr>
<td>PGM-1</td>
<td>0.182</td>
<td>0.519</td>
<td>0.426</td>
<td>0.379</td>
<td>3</td>
<td>60.40</td>
<td>26</td>
<td>0.000</td>
</tr>
<tr>
<td>PGM-2</td>
<td>-0.040</td>
<td>-0.003</td>
<td>0.036</td>
<td>0.000</td>
<td>2</td>
<td>5.80</td>
<td>13</td>
<td>0.953</td>
</tr>
<tr>
<td>mean</td>
<td>-0.067</td>
<td>0.336</td>
<td>0.378</td>
<td>0.305</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>totals</td>
<td></td>
<td></td>
<td>0.305</td>
<td></td>
<td>1015.07</td>
<td>286</td>
<td>0.000</td>
<td></td>
</tr>
</tbody>
</table>
Table 10.—Alphabetic designations of alleles for polymorphic loci at which the same allele(s) was present in both species.

<table>
<thead>
<tr>
<th>locus</th>
<th>niger</th>
<th>carolinensis</th>
</tr>
</thead>
<tbody>
<tr>
<td>ACN-1</td>
<td>A</td>
<td>C</td>
</tr>
<tr>
<td>ACP</td>
<td>A</td>
<td>B</td>
</tr>
<tr>
<td>ADA</td>
<td>A</td>
<td>A</td>
</tr>
<tr>
<td>IDH-1</td>
<td>A</td>
<td>A</td>
</tr>
<tr>
<td>MPI</td>
<td>A</td>
<td>A</td>
</tr>
<tr>
<td>NP</td>
<td>A</td>
<td>A</td>
</tr>
<tr>
<td>NP</td>
<td>B</td>
<td>B</td>
</tr>
<tr>
<td>6PGD</td>
<td>A</td>
<td>A</td>
</tr>
<tr>
<td>PGM-1</td>
<td>A</td>
<td>B</td>
</tr>
</tbody>
</table>
Table 11.—Rogers' (1972; below diagonal) and Nei's (1972; above diagonal) genetic distances for 14 samples of *Sclerus nigra* assayed at 35 loci.

<table>
<thead>
<tr>
<th>sample</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>9</th>
<th>10</th>
<th>11</th>
<th>12</th>
<th>13</th>
<th>14</th>
</tr>
</thead>
<tbody>
<tr>
<td>NA</td>
<td>---</td>
<td>0.008</td>
<td>0.013</td>
<td>0.010</td>
<td>0.004</td>
<td>0.095</td>
<td>0.002</td>
<td>0.005</td>
<td>0.046</td>
<td>0.007</td>
<td>0.036</td>
<td>0.013</td>
<td>0.003</td>
<td></td>
</tr>
<tr>
<td>NB</td>
<td>0.030</td>
<td>---</td>
<td>0.002</td>
<td>0.008</td>
<td>0.012</td>
<td>0.006</td>
<td>0.097</td>
<td>0.004</td>
<td>0.006</td>
<td>0.038</td>
<td>0.011</td>
<td>0.066</td>
<td>0.008</td>
<td>0.007</td>
</tr>
<tr>
<td>NE</td>
<td>0.039</td>
<td>0.014</td>
<td>---</td>
<td>0.013</td>
<td>0.017</td>
<td>0.012</td>
<td>0.108</td>
<td>0.008</td>
<td>0.009</td>
<td>0.047</td>
<td>0.018</td>
<td>0.074</td>
<td>0.007</td>
<td>0.012</td>
</tr>
<tr>
<td>NF</td>
<td>0.045</td>
<td>0.033</td>
<td>0.045</td>
<td>---</td>
<td>0.005</td>
<td>0.009</td>
<td>0.088</td>
<td>0.009</td>
<td>0.017</td>
<td>0.031</td>
<td>0.010</td>
<td>0.060</td>
<td>0.007</td>
<td>0.005</td>
</tr>
<tr>
<td>NH</td>
<td>0.034</td>
<td>0.039</td>
<td>0.048</td>
<td>0.030</td>
<td>---</td>
<td>0.009</td>
<td>0.094</td>
<td>0.009</td>
<td>0.020</td>
<td>0.037</td>
<td>0.007</td>
<td>0.043</td>
<td>0.005</td>
<td>0.003</td>
</tr>
<tr>
<td>WJ</td>
<td>0.018</td>
<td>0.029</td>
<td>0.039</td>
<td>0.038</td>
<td>0.033</td>
<td>---</td>
<td>0.091</td>
<td>0.003</td>
<td>0.007</td>
<td>0.019</td>
<td>0.003</td>
<td>0.041</td>
<td>0.009</td>
<td>0.008</td>
</tr>
<tr>
<td>NK</td>
<td>0.104</td>
<td>0.120</td>
<td>0.133</td>
<td>0.117</td>
<td>0.119</td>
<td>0.106</td>
<td>---</td>
<td>0.088</td>
<td>0.101</td>
<td>0.047</td>
<td>0.086</td>
<td>0.116</td>
<td>0.107</td>
<td>0.105</td>
</tr>
<tr>
<td>WM</td>
<td>0.015</td>
<td>0.021</td>
<td>0.032</td>
<td>0.037</td>
<td>0.029</td>
<td>0.016</td>
<td>0.105</td>
<td>---</td>
<td>0.004</td>
<td>0.039</td>
<td>0.005</td>
<td>0.044</td>
<td>0.010</td>
<td>0.008</td>
</tr>
<tr>
<td>NF</td>
<td>0.019</td>
<td>0.025</td>
<td>0.032</td>
<td>0.053</td>
<td>0.045</td>
<td>0.027</td>
<td>0.117</td>
<td>0.018</td>
<td>---</td>
<td>0.051</td>
<td>0.014</td>
<td>0.054</td>
<td>0.016</td>
<td>0.015</td>
</tr>
<tr>
<td>NT</td>
<td>0.097</td>
<td>0.089</td>
<td>0.100</td>
<td>0.076</td>
<td>0.087</td>
<td>0.089</td>
<td>0.087</td>
<td>0.091</td>
<td>0.108</td>
<td>---</td>
<td>0.038</td>
<td>0.089</td>
<td>0.043</td>
<td>0.040</td>
</tr>
<tr>
<td>NV</td>
<td>0.032</td>
<td>0.044</td>
<td>0.056</td>
<td>0.067</td>
<td>0.035</td>
<td>0.020</td>
<td>0.108</td>
<td>0.029</td>
<td>0.042</td>
<td>0.092</td>
<td>---</td>
<td>0.035</td>
<td>0.011</td>
<td>0.010</td>
</tr>
<tr>
<td>NJ</td>
<td>0.063</td>
<td>0.088</td>
<td>0.099</td>
<td>0.094</td>
<td>0.073</td>
<td>0.046</td>
<td>0.139</td>
<td>0.070</td>
<td>0.075</td>
<td>0.138</td>
<td>0.067</td>
<td>---</td>
<td>0.056</td>
<td>0.056</td>
</tr>
<tr>
<td>NW</td>
<td>0.039</td>
<td>0.030</td>
<td>0.029</td>
<td>0.029</td>
<td>0.025</td>
<td>0.035</td>
<td>0.127</td>
<td>0.037</td>
<td>0.042</td>
<td>0.089</td>
<td>0.044</td>
<td>0.086</td>
<td>---</td>
<td>0.004</td>
</tr>
<tr>
<td>NS</td>
<td>0.026</td>
<td>0.029</td>
<td>0.035</td>
<td>0.025</td>
<td>0.018</td>
<td>0.029</td>
<td>0.119</td>
<td>0.031</td>
<td>0.041</td>
<td>0.080</td>
<td>0.038</td>
<td>0.080</td>
<td>0.015</td>
<td>---</td>
</tr>
</tbody>
</table>
Table 12.—Rogers' (1972) genetic distance between subspecies of Sciurus niger. Included in this study. Range for distance values is indicated in parentheses.

<table>
<thead>
<tr>
<th>subspecies</th>
<th>samples</th>
<th>ludovicianus</th>
<th>subauratus</th>
<th>bachmani</th>
<th>limitis</th>
<th>rufiventer</th>
</tr>
</thead>
<tbody>
<tr>
<td>ludovicianus</td>
<td>4</td>
<td>0.029</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.018–0.044)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>subauratus</td>
<td>3</td>
<td>0.029</td>
<td>0.027</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.014–0.056)</td>
<td>(0.018–0.032)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>bachmani</td>
<td>4</td>
<td>0.036</td>
<td>0.039</td>
<td>0.024</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.026–0.047)</td>
<td>(0.029–0.053)</td>
<td>(0.15–0.030)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>limitis</td>
<td>1</td>
<td>0.070</td>
<td>0.081</td>
<td>0.083</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.062–0.088)</td>
<td>(0.070–0.099)</td>
<td>(0.073–0.094)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>rufiventer</td>
<td>2</td>
<td>0.101</td>
<td>0.109</td>
<td>0.102</td>
<td>0.138</td>
<td>0.087</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.089–0.120)</td>
<td>(0.091–0.133)</td>
<td>(0.076–0.127)</td>
<td>(0.138–0.139)</td>
<td>(0.087–0.087)</td>
</tr>
</tbody>
</table>
Table 13.—Rogers' (1972) genetic distance between west-bank and east-bank samples of Sciurus niger (values for 14 samples below diagonal, values for 11 samples—NT, NK, NX excluded—above diagonal). Range for distance values is indicated in parentheses.

<table>
<thead>
<tr>
<th>riverside samples</th>
<th>west</th>
<th>east</th>
<th>west</th>
<th>east</th>
</tr>
</thead>
<tbody>
<tr>
<td>west</td>
<td>8/6</td>
<td>0.057</td>
<td>-----</td>
<td>0.026</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.015-0.139)</td>
<td></td>
<td>(0.015-0.044)</td>
</tr>
<tr>
<td>east</td>
<td>6/5</td>
<td>0.061</td>
<td>0.049</td>
<td>-----</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.014-0.138)</td>
<td>(0.015-0.100)</td>
<td></td>
</tr>
<tr>
<td>Sample</td>
<td>MAX_LEN</td>
<td>ZYG_WIDTH</td>
<td>BRN_WIDTH</td>
<td>LST_POST</td>
</tr>
<tr>
<td>--------</td>
<td>---------</td>
<td>-----------</td>
<td>-----------</td>
<td>----------</td>
</tr>
<tr>
<td>CA_1</td>
<td>61.1 ± 0.83</td>
<td>33.3 ± 0.98</td>
<td>24.4 ± 0.59</td>
<td>17.5 ± 0.75</td>
</tr>
<tr>
<td>CL_1</td>
<td>57.9 ± 0.89</td>
<td>31.9 ± 0.88</td>
<td>23.4 ± 0.29</td>
<td>18.5 ± 1.05</td>
</tr>
<tr>
<td>CL_2</td>
<td>59.8 ± 0.86</td>
<td>33.8 ± 0.91</td>
<td>23.7 ± 1.06</td>
<td>17.5 ± 0.23</td>
</tr>
<tr>
<td>CL_3</td>
<td>57.1 ± 1.47</td>
<td>32.7 ± 0.06</td>
<td>23.8 ± 0.20</td>
<td>18.2 ± 0.23</td>
</tr>
<tr>
<td>CL_4</td>
<td>59.0 ± 1.26</td>
<td>33.5 ± 1.06</td>
<td>23.6 ± 0.47</td>
<td>17.8 ± 0.63</td>
</tr>
<tr>
<td>GL_1</td>
<td>58.8 ± 1.08</td>
<td>33.0 ± 0.66</td>
<td>23.2 ± 0.38</td>
<td>18.4 ± 0.53</td>
</tr>
<tr>
<td>GL_2</td>
<td>57.9 ± 1.74</td>
<td>32.1 ± 1.13</td>
<td>23.2 ± 0.66</td>
<td>17.8 ± 0.66</td>
</tr>
<tr>
<td>GL_3</td>
<td>58.3 ± 1.28</td>
<td>32.4 ± 0.84</td>
<td>22.9 ± 0.59</td>
<td>17.4 ± 0.79</td>
</tr>
<tr>
<td>CL_5</td>
<td>58.5 ± 0.69</td>
<td>32.3 ± 0.78</td>
<td>23.3 ± 0.43</td>
<td>17.8 ± 0.64</td>
</tr>
<tr>
<td>CL_6</td>
<td>56.5 ± 0.93</td>
<td>31.3 ± 0.78</td>
<td>22.5 ± 0.31</td>
<td>17.4 ± 0.56</td>
</tr>
<tr>
<td>CL_7</td>
<td>58.1 ± 1.27</td>
<td>32.8 ± 1.07</td>
<td>22.9 ± 0.51</td>
<td>17.6 ± 0.32</td>
</tr>
<tr>
<td>CL_8</td>
<td>58.1 ± 1.88</td>
<td>31.8 ± 0.61</td>
<td>23.0 ± 0.85</td>
<td>17.7 ± 0.20</td>
</tr>
<tr>
<td>CL_9</td>
<td>57.6 ± 0.58</td>
<td>32.3 ± 0.73</td>
<td>22.1 ± 1.41</td>
<td>16.7 ± 1.12</td>
</tr>
<tr>
<td>CT_1</td>
<td>58.0 ± 0.75</td>
<td>33.5 ± 1.23</td>
<td>23.4 ± 0.55</td>
<td>18.5 ± 0.46</td>
</tr>
<tr>
<td>CT_2</td>
<td>58.0 ± 1.47</td>
<td>32.8 ± 1.28</td>
<td>23.6 ± 0.70</td>
<td>17.7 ± 0.90</td>
</tr>
<tr>
<td>CT_3</td>
<td>61.0 ± 0.77</td>
<td>33.7 ± 0.66</td>
<td>23.9 ± 0.29</td>
<td>18.0 ± 0.44</td>
</tr>
<tr>
<td>CX_1</td>
<td>59.9 ± 1.33</td>
<td>32.6 ± 1.07</td>
<td>23.5 ± 0.61</td>
<td>17.8 ± 0.74</td>
</tr>
</tbody>
</table>

**Table 2:** Abbreviations for characters are given in text.
Table 15.—Character loadings for 15 cranial and mandibular characters for 19 samples of *Sciurus carolinensis*. Abbreviations for characters are given in text.

<table>
<thead>
<tr>
<th>character</th>
<th>PCI</th>
<th>PCII</th>
</tr>
</thead>
<tbody>
<tr>
<td>MAX LEN</td>
<td>0.330</td>
<td>-0.188</td>
</tr>
<tr>
<td>ZYG WDTH</td>
<td>0.320</td>
<td>0.052</td>
</tr>
<tr>
<td>BRN WDTH</td>
<td>0.335</td>
<td>0.092</td>
</tr>
<tr>
<td>LST POST</td>
<td>0.115</td>
<td>0.493</td>
</tr>
<tr>
<td>MAX HT</td>
<td>0.235</td>
<td>0.283</td>
</tr>
<tr>
<td>INFR BR</td>
<td>0.264</td>
<td>0.366</td>
</tr>
<tr>
<td>DIAST</td>
<td>0.343</td>
<td>0.012</td>
</tr>
<tr>
<td>TOOTH</td>
<td>0.231</td>
<td>-0.245</td>
</tr>
<tr>
<td>MLR WDTH</td>
<td>0.267</td>
<td>-0.098</td>
</tr>
<tr>
<td>PML WDTH</td>
<td>0.297</td>
<td>-0.119</td>
</tr>
<tr>
<td>PAL WDTH</td>
<td>0.148</td>
<td>0.362</td>
</tr>
<tr>
<td>FOR WDTH</td>
<td>0.182</td>
<td>-0.399</td>
</tr>
<tr>
<td>ART WDTH</td>
<td>0.143</td>
<td>0.184</td>
</tr>
<tr>
<td>MAND HT</td>
<td>0.271</td>
<td>-0.123</td>
</tr>
<tr>
<td>MAND LEN</td>
<td>0.238</td>
<td>-0.270</td>
</tr>
</tbody>
</table>
Table 16.—Alphabetic designation for electromorphs, mean heterozygosity (H), number of expected heterozygotes (H<sub>exp</sub>; Nai, 1978), and percent polymorphism (P) at 23 polymorphic loci assayed across 10 samples of *Sciurus carolinensis*.

Allelic frequencies for polymorphic loci are indicated in parentheses. Abbreviations for samples are given in Table 4; abbreviations for loci are given in text.

<table>
<thead>
<tr>
<th>locus</th>
<th>sample</th>
<th>CA</th>
<th>CB</th>
<th>CE</th>
<th>CH</th>
<th>CJ</th>
<th>CR</th>
<th>CV</th>
<th>CW</th>
<th>CTS</th>
<th>CEP</th>
</tr>
</thead>
<tbody>
<tr>
<td>ACH-1 A</td>
<td>CH</td>
<td>(.83)</td>
<td>(.94)</td>
<td>(.75)</td>
<td>(.17)</td>
<td>(.06)</td>
<td>(.25)</td>
<td>(.86)</td>
<td>(.68)</td>
<td>(.86)</td>
<td>(.71)</td>
</tr>
<tr>
<td>ACP A</td>
<td>A</td>
<td>(.92)</td>
<td>(.92)</td>
<td>(.92)</td>
<td>(.08)</td>
<td>(.06)</td>
<td>(.04)</td>
<td>(.86)</td>
<td>(.96)</td>
<td>(.96)</td>
<td>(.93)</td>
</tr>
<tr>
<td>ADA A</td>
<td>(.70)</td>
<td>(.94)</td>
<td>(.97)</td>
<td>(.96)</td>
<td>(.08)</td>
<td>(.06)</td>
<td>(.04)</td>
<td>(.86)</td>
<td>(.96)</td>
<td>(.96)</td>
<td>(.93)</td>
</tr>
<tr>
<td>A2X A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>(.96)</td>
<td>(.93)</td>
</tr>
<tr>
<td>FUM A</td>
<td>A</td>
<td>(.97)</td>
<td>(.03)</td>
<td>(.94)</td>
<td>(.94)</td>
<td>(.94)</td>
<td>(.94)</td>
<td>(.94)</td>
<td>(.94)</td>
<td>(.94)</td>
<td>(.94)</td>
</tr>
<tr>
<td>GLUD A</td>
<td>A</td>
<td>(.94)</td>
<td>(.94)</td>
<td>(.94)</td>
<td>(.94)</td>
<td>(.94)</td>
<td>(.94)</td>
<td>(.94)</td>
<td>(.94)</td>
<td>(.94)</td>
<td>(.94)</td>
</tr>
<tr>
<td>GOT-1 A</td>
<td>A</td>
<td>(.91)</td>
<td>(.97)</td>
<td>(.97)</td>
<td>(.09)</td>
<td>(.03)</td>
<td>(.03)</td>
<td>(.03)</td>
<td>(.03)</td>
<td>(.03)</td>
<td>(.03)</td>
</tr>
<tr>
<td>GOT-2 A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>(.96)</td>
<td>(.96)</td>
</tr>
<tr>
<td>IDR-1 A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
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<td>A</td>
<td>(.97)</td>
<td>(.97)</td>
</tr>
<tr>
<td>LDH-1 A</td>
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<td>A</td>
<td>A</td>
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<td>(.96)</td>
<td>(.96)</td>
</tr>
<tr>
<td>MDH-1 A</td>
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<td>(.96)</td>
</tr>
<tr>
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<td>A</td>
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<td>A</td>
<td>(.96)</td>
<td>(.96)</td>
</tr>
<tr>
<td>NE A</td>
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<td>A</td>
<td>A</td>
<td>A</td>
<td>(.87)</td>
<td>(.87)</td>
</tr>
<tr>
<td>NP A</td>
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<td>A</td>
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<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>(.87)</td>
<td>(.87)</td>
</tr>
<tr>
<td>ODN A</td>
<td>(.90)</td>
<td>(.90)</td>
<td>(.90)</td>
<td>(.90)</td>
<td>(.90)</td>
<td>(.90)</td>
<td>(.90)</td>
<td>(.90)</td>
<td>(.90)</td>
<td>(.90)</td>
<td>(.90)</td>
</tr>
<tr>
<td>PEP-B A</td>
<td>A</td>
<td>A</td>
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<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
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<td>A</td>
<td>(.94)</td>
<td>(.94)</td>
</tr>
<tr>
<td>PEP-D A</td>
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<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
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<td>A</td>
<td>A</td>
<td>A</td>
<td>(.94)</td>
<td>(.94)</td>
</tr>
<tr>
<td>SFCD A</td>
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<td>(.84)</td>
<td>(.84)</td>
<td>(.84)</td>
<td>(.84)</td>
<td>(.84)</td>
<td>(.84)</td>
<td>(.84)</td>
<td>(.84)</td>
<td>(.84)</td>
</tr>
<tr>
<td>PCLI A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>(.95)</td>
<td>(.95)</td>
</tr>
<tr>
<td>PCH-1 A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>(.96)</td>
<td>(.96)</td>
</tr>
<tr>
<td>PCH-2 A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>(.96)</td>
<td>(.96)</td>
</tr>
<tr>
<td>SDH A</td>
<td>A</td>
<td>(.83)</td>
<td>(.83)</td>
<td>(.83)</td>
<td>(.83)</td>
<td>(.83)</td>
<td>(.83)</td>
<td>(.83)</td>
<td>(.83)</td>
<td>(.83)</td>
<td>(.83)</td>
</tr>
<tr>
<td>SOO A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>(.93)</td>
<td>(.93)</td>
</tr>
</tbody>
</table>

Mean H = 0.028 ± 0.005; mean H<sub>exp</sub> = 0.027 ± 0.004; mean P = 0.096 ± 0.007.
Table 17.—F-statistics averaged over polymorphic loci for 10 samples of *Sciurus carolinensis* and contingency chi-square analysis of $F_{ST}$.  
$I = $ individual;  
$S = $ sample;  
$T = $ total;  
$D = $ deme;  
$F_{DT} = $ estimate of $F_{ST}$ calculated using Wright's (1978) correction for small sample sizes.

<table>
<thead>
<tr>
<th>locus</th>
<th>$F_{IS}$</th>
<th>$F_{IT}$</th>
<th>$F_{ST}$</th>
<th>$F_{DT}$</th>
<th>alleles</th>
<th>$X^2$</th>
<th>DF</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>ACHN-1</td>
<td>-0.038</td>
<td>0.086</td>
<td>0.120</td>
<td>0.069</td>
<td>3</td>
<td>40.40</td>
<td>18</td>
<td>0.002</td>
</tr>
<tr>
<td>ACP</td>
<td>-0.112</td>
<td>-0.035</td>
<td>0.069</td>
<td>0.013</td>
<td>2</td>
<td>12.68</td>
<td>27</td>
<td>0.178</td>
</tr>
<tr>
<td>ADA</td>
<td>-0.062</td>
<td>0.042</td>
<td>0.098</td>
<td>0.042</td>
<td>4</td>
<td>35.73</td>
<td>27</td>
<td>0.000</td>
</tr>
<tr>
<td>AK2</td>
<td>-0.043</td>
<td>-0.004</td>
<td>0.038</td>
<td>0.000</td>
<td>2</td>
<td>7.62</td>
<td>9</td>
<td>0.573</td>
</tr>
<tr>
<td>FUM</td>
<td>-0.032</td>
<td>-0.003</td>
<td>0.028</td>
<td>0.000</td>
<td>2</td>
<td>5.59</td>
<td>9</td>
<td>0.780</td>
</tr>
<tr>
<td>GLUD</td>
<td>1.000</td>
<td>1.000</td>
<td>0.050</td>
<td>0.024</td>
<td>2</td>
<td>9.09</td>
<td>9</td>
<td>0.429</td>
</tr>
<tr>
<td>GOT-1</td>
<td>-0.085</td>
<td>-0.012</td>
<td>0.067</td>
<td>0.039</td>
<td>2</td>
<td>12.77</td>
<td>9</td>
<td>0.173</td>
</tr>
<tr>
<td>GOT-2</td>
<td>1.000</td>
<td>1.000</td>
<td>0.050</td>
<td>0.024</td>
<td>2</td>
<td>9.87</td>
<td>9</td>
<td>0.361</td>
</tr>
<tr>
<td>IDH-1</td>
<td>-0.037</td>
<td>-0.004</td>
<td>0.032</td>
<td>0.000</td>
<td>2</td>
<td>6.53</td>
<td>9</td>
<td>0.685</td>
</tr>
<tr>
<td>LDH-1</td>
<td>-0.032</td>
<td>-0.003</td>
<td>0.028</td>
<td>0.000</td>
<td>2</td>
<td>5.71</td>
<td>9</td>
<td>0.768</td>
</tr>
<tr>
<td>MDH-1</td>
<td>1.000</td>
<td>1.000</td>
<td>0.057</td>
<td>0.027</td>
<td>2</td>
<td>11.48</td>
<td>9</td>
<td>0.244</td>
</tr>
<tr>
<td>MDH-2</td>
<td>-0.112</td>
<td>-0.020</td>
<td>0.083</td>
<td>0.045</td>
<td>3</td>
<td>31.91</td>
<td>18</td>
<td>0.022</td>
</tr>
<tr>
<td>ME</td>
<td>0.805</td>
<td>0.825</td>
<td>0.103</td>
<td>0.074</td>
<td>3</td>
<td>29.61</td>
<td>18</td>
<td>0.041</td>
</tr>
<tr>
<td>NP</td>
<td>-0.029</td>
<td>-0.003</td>
<td>0.025</td>
<td>0.000</td>
<td>2</td>
<td>4.97</td>
<td>9</td>
<td>0.837</td>
</tr>
<tr>
<td>ODH</td>
<td>-0.111</td>
<td>-0.010</td>
<td>0.091</td>
<td>0.000</td>
<td>2</td>
<td>20.30</td>
<td>9</td>
<td>0.016</td>
</tr>
<tr>
<td>PEPB</td>
<td>1.000</td>
<td>1.000</td>
<td>0.057</td>
<td>0.027</td>
<td>2</td>
<td>11.48</td>
<td>9</td>
<td>0.244</td>
</tr>
<tr>
<td>PEPD</td>
<td>0.212</td>
<td>0.302</td>
<td>0.115</td>
<td>0.085</td>
<td>2</td>
<td>22.64</td>
<td>9</td>
<td>0.007</td>
</tr>
<tr>
<td>6PGD</td>
<td>0.083</td>
<td>0.147</td>
<td>0.069</td>
<td>0.039</td>
<td>4</td>
<td>22.13</td>
<td>27</td>
<td>0.731</td>
</tr>
<tr>
<td>PG1</td>
<td>0.526</td>
<td>0.545</td>
<td>0.041</td>
<td>0.007</td>
<td>2</td>
<td>8.18</td>
<td>9</td>
<td>0.316</td>
</tr>
<tr>
<td>PGM1</td>
<td>0.115</td>
<td>0.230</td>
<td>0.130</td>
<td>0.094</td>
<td>5</td>
<td>40.52</td>
<td>36</td>
<td>0.277</td>
</tr>
<tr>
<td>PGM2</td>
<td>-0.032</td>
<td>-0.003</td>
<td>0.028</td>
<td>0.000</td>
<td>2</td>
<td>5.65</td>
<td>9</td>
<td>0.774</td>
</tr>
<tr>
<td>SDH</td>
<td>-0.200</td>
<td>-0.017</td>
<td>0.153</td>
<td>0.011</td>
<td>2</td>
<td>34.50</td>
<td>9</td>
<td>0.000</td>
</tr>
<tr>
<td>SOD</td>
<td>-0.077</td>
<td>-0.007</td>
<td>0.065</td>
<td>0.000</td>
<td>2</td>
<td>14.35</td>
<td>9</td>
<td>0.110</td>
</tr>
</tbody>
</table>

**mean**  
0.072  0.167  0.102  0.056

**totals**  
423.71  297  0.000
Table 18.—Rogers' (1972; below diagonal) and Nel's (1972; above diagonal) genetic distances for 10 samples of *Sclerus carollinensis* assayed at 15 loci.

<table>
<thead>
<tr>
<th>Sample</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>9</th>
<th>10</th>
</tr>
</thead>
<tbody>
<tr>
<td>CA</td>
<td>----</td>
<td>0.004</td>
<td>0.004</td>
<td>0.007</td>
<td>0.002</td>
<td>0.007</td>
<td>0.003</td>
<td>0.007</td>
<td>0.007</td>
<td>0.005</td>
</tr>
<tr>
<td>CB</td>
<td>0.020</td>
<td>----</td>
<td>0.004</td>
<td>0.005</td>
<td>0.002</td>
<td>0.004</td>
<td>0.002</td>
<td>0.005</td>
<td>0.007</td>
<td>0.003</td>
</tr>
<tr>
<td>CE</td>
<td>0.030</td>
<td>0.030</td>
<td>----</td>
<td>0.004</td>
<td>0.002</td>
<td>0.005</td>
<td>0.002</td>
<td>0.005</td>
<td>0.005</td>
<td>0.003</td>
</tr>
<tr>
<td>CH</td>
<td>0.036</td>
<td>0.030</td>
<td>0.032</td>
<td>----</td>
<td>0.004</td>
<td>0.003</td>
<td>0.004</td>
<td>0.002</td>
<td>0.003</td>
<td>0.002</td>
</tr>
<tr>
<td>CJ</td>
<td>0.011</td>
<td>0.012</td>
<td>0.020</td>
<td>0.026</td>
<td>----</td>
<td>0.005</td>
<td>0.001</td>
<td>0.005</td>
<td>0.005</td>
<td>0.002</td>
</tr>
<tr>
<td>CS</td>
<td>0.025</td>
<td>0.018</td>
<td>0.028</td>
<td>0.025</td>
<td>0.015</td>
<td>----</td>
<td>0.004</td>
<td>0.003</td>
<td>0.007</td>
<td>0.001</td>
</tr>
<tr>
<td>CV</td>
<td>0.021</td>
<td>0.016</td>
<td>0.022</td>
<td>0.031</td>
<td>0.012</td>
<td>0.021</td>
<td>----</td>
<td>0.004</td>
<td>0.005</td>
<td>0.002</td>
</tr>
<tr>
<td>CW</td>
<td>0.032</td>
<td>0.027</td>
<td>0.031</td>
<td>0.020</td>
<td>0.023</td>
<td>0.021</td>
<td>0.025</td>
<td>----</td>
<td>0.003</td>
<td>0.002</td>
</tr>
<tr>
<td>CTS</td>
<td>0.038</td>
<td>0.039</td>
<td>0.035</td>
<td>0.030</td>
<td>0.032</td>
<td>0.039</td>
<td>0.033</td>
<td>0.028</td>
<td>----</td>
<td>0.004</td>
</tr>
<tr>
<td>CEP</td>
<td>0.024</td>
<td>0.016</td>
<td>0.023</td>
<td>0.020</td>
<td>0.013</td>
<td>0.012</td>
<td>0.014</td>
<td>0.017</td>
<td>0.030</td>
<td>----</td>
</tr>
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</table>
Table 19.—Rogers' (1972) genetic distance between subspecies of *Sciurus carolinensis* included in this study. Range for distance values is indicated in parentheses.

<table>
<thead>
<tr>
<th>subspecies</th>
<th>samples</th>
<th>fuliginosus</th>
<th>carolinensis</th>
</tr>
</thead>
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<tr>
<td>fuliginosus</td>
<td>5</td>
<td>0.024</td>
<td>(0.012-0.032)</td>
</tr>
<tr>
<td>carolinensis</td>
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<td>0.024</td>
<td>0.026</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>(0.011-0.039) (0.012-0.039)</td>
</tr>
</tbody>
</table>
Table 20.—Rogers' (1972) genetic distance between west-bank and east-bank samples of *Sciurus carolinensis* (values for 10 samples below diagonal, values for 9 samples—CTS excluded—above diagonal). Range for distance values is indicated in parentheses.

<table>
<thead>
<tr>
<th>riverside</th>
<th>samples</th>
<th>west</th>
<th>east</th>
<th>west</th>
<th>east</th>
</tr>
</thead>
<tbody>
<tr>
<td>west</td>
<td>4/4</td>
<td>0.015</td>
<td>----</td>
<td>0.015</td>
<td>0.024</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.011-0.021)</td>
<td>(0.011-0.021)</td>
<td>(0.013-0.036)</td>
<td></td>
</tr>
<tr>
<td>east</td>
<td>6/5</td>
<td>0.026</td>
<td>0.026</td>
<td>----</td>
<td>0.023</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.013-0.039)</td>
<td>(0.012-0.039)</td>
<td>(0.012-0.032)</td>
<td></td>
</tr>
</tbody>
</table>
Fig. 1.—Distribution of *Sciurus niger* subspecies in the lower Mississippi River valley; after Hall (1981), Lowery (1974), and Lowery and Davis (1942).
Fig. 2.—Distribution of *Sciurus carolinensis* subspecies in the lower Mississippi River valley; after Hall (1981) and Lowery (1974).
Fig. 3.—Location of samples of *Sciurus niger* used in morphometric analyses.
Fig. 4.—Location of samples of *Sciurus carolinensis* used in morphometric analyses.
Fig. 5.—Cranial and mandibular characters measured for morphometric analyses. Characters are labeled as follows: A) MAX_LEN, B) ZYG_WDTH, C) BRN_WDTH, D) LST_POST, E) MAX_HT, F) INFR_BR, G) DIAST, H) TOOTH, I) MLR_WDTH, J) PML_WDTH, K) PAL_WDTH, L) FOR_WDTH, M) MAND_HT, N) MAND_LEN. ART_WDTH is not illustrated. Abbreviations for characters are given in text.
Fig. 6.—Location of samples of *Sciurus niger* used in electrophoretic analyses.
Fig. 7.—Location of samples of *Sciurus carolinensis* used in electrophoretic analyses.
Fig. 8.—Phenogram based on UPGMA cluster analysis of taxonomic distance among 19 samples of Sciurus niger. Cophenetic correlation is 0.742.

(ludovicianus, subauratus, bachmanii, limitis, rufiventer).
Fig. 9.—Plot of first and second principal components for 19 samples of *Sciurus niger*. 
Fig. 10.—Distribution of allelic frequencies at MPI locus in *Sciurus niger*. 
Fig. 11.—Distribution of allelic frequencies at PGM-1 locus in Sciurus niger.
Fig. 12.—Distribution of allelic frequencies at ADA locus in Sciurus niger.
Fig. 13.—Distribution of allelic frequencies at NP locus in *Sciurus niger*.
Fig. 14.—Distribution of allelic frequencies at IDH-1 locus in *Sciurus niger*.
Fig. 15.—Phenogram based on UPGMA cluster analysis of Rogers' (1972) genetic distance estimated among 14 samples of Sciurus niger. Goodness-of-fit statistics are as follows: Farris (1972) "F" = 0.756, Prager and Wilson (1976) "F" = 14.318, percent standard deviation (Fitch and Margoliash, 1967) = 19.395, and cophenetic correlation = 0.947. (E = east-bank, W = west-bank; Id = ludovicianus, su = subsuratus, ba = bachmani, lm = limitis, ru = rufiventer).
Fig. 16.—Distance-Wagner tree for 14 samples of *Sciurus niger* based on Rogers' (1972) genetic distance estimates, rooted at the midpoint and generated using the multiple addition criterion of Swofford (1981, maxtree = 30, branch-length optimisation suppressed). Goodness-of-fit statistics are as follows: Farris (1972) "F" = 0.776, Prager and Wilson (1976) "F" = 14.697, percent standard deviation (Fitch and Margoliash, 1967) = 29.655, and cophenetic correlation = 0.962. (E = east-bank, W = west-bank; ld = *ludovicianus*, su = *subauratus*, ba = *bachmani*, lm = *limitis*, ru = *rufiventer*).
Fig. 17.—Phenogram based on UPGMA cluster analysis of taxonomic distance among 18 samples of 
Sciurus carolinensis. Cophenetic correlation is 0.718.

(fu = fuliginosus, ca = carolinensis).
Fig. 18.—Plot of first and second principal components for 18 samples of *Sciurus carolinensis*. 
Fig. 19.—Distribution of allelic frequencies at ACN-1 locus in *Sciurus carolinensis*.
Fig. 20.—Distribution of allelic frequencies at 6PGD locus in *Sciurus carolinensis*.
Fig. 21.—Distribution of allelic frequencies at PGM-1 locus in *Scirurus carolinensis*.
Fig. 22.—Distribution of allelic frequencies at ADA locus in Sciurus carolinensis.
Fig. 23.—Distribution of allelic frequencies at ACP locus in *Sciurus carolinensis*.
Fig. 24.—Phenogram based on UPGMA cluster analysis of Rogers’ (1972) genetic distances estimated among 10 samples of Sciurus carolinensis.

Goodness-of-fit statistics are as follows: Farris (1972) "F" = 0.164, Prager and Wilson (1976) "F" = 14.922, percent standard deviation (Fitch and Margoliash, 1967) = 20.280, and cophenetic correlation = 0.835. (E = east-bank, W = west-bank; fu = fuliginosus, ca = carolinensis).
Fig. 25.—Distance-Wagner tree for 10 samples of *Sciurus carolinensis* based on Rogers' (1972) genetic distance estimates, rooted at the midpoint and generated using the multiple addition criterion of Swofford (1981, maxtree = 30, branch-length-optimization suppressed. Goodness-of-fit statistics are as follows: Farris (1972) "F" = 0.131, Prager and Wilson (1976) "F" = 11.923, percent standard deviation (Fitch and Margoliash, 1967) = 18.545, and cophenetic correlation = 0.930. (E = east-bank, W = west-bank; fu = *fuliginosus*, ca = *carolinensis*).
Fig. 26.—Paleovegetation map of eastern North America for 18,000 years before present (modified from Delcourt and Delcourt, 1981, 1984). Forest types (B-H) are labeled as follows: B) cool-temperate mixed northern conifer-hardwood forest, C) warm-temperate oak-hickory-southern pine forest, D) sand dune scrub, E) jack pine-spruce-fir forest, F) mixed mesophytic hardwood forest, G) spruce-jack pine forest, H) cypress-gum forest; A indicates glacial ice.
Fig. 27.—Premodern (1-6) and modern (7) deltaic complexes of the Mississippi River (modified from Kolb and Van Lopik, 1958).
APPENDIX I

SPECIMENS EXAMINED

Morphometric Analyses

Acronyms for museum collections are as follows:

LSUMZ = Louisiana State University Museum of Zoology
MSU = McNeese State University
MSUMZ = Memphis State University Museum of Zoology
TCWC = Texas Cooperative Wildlife Collection, Texas A&M University
USL = University of Southwestern Louisiana

Sciurus niger

ARKANSAS. Greene Co.: 3 1/2 mi. W Paragould on Hwy 25, 3 (MSUMZ); 8 mi. W Paragould, 2 (MSUMZ).

LOUISIANA. Acadia Par.: 1 1/2 mi. N Rayne, 1 (USL); 5 mi. S Eunice, 1 (LSUMZ). Allen Par.: 3 mi. N, 1 mi. E Reeves, 1 (MSU); West Bay Game Management Area, 1 (MSU); Whiskey Chitto Creek, 10 mi. W Oberlin, 3 (LSUMZ), 12 mi. W Mamou, Kastaw Creek, 1 (USL). Ascension Par.: 3 mi. SE Burnside, 1 (LSUMZ); 4 mi. SE St. Gabriel, 1 (LSUMZ); 1 mi. E Geismar, 1 (LSUMZ); 4 mi. W
Gonzales, 1 (LSUMZ); Sorrento, 1 (LSUMZ). Avoynelles Par.: 5 mi. S Cottonport, 1 (USL); 4 mi. N Bunkie, 1 (LSUMZ); 15 mi. N Marksville, 1 (LSUMZ); 3 mi. W Marksville-Echo Highway, 1 (LSUMZ); 20 mi. NE Marksville, 1 (LSUMZ); 5 mi. SW Effie, 1 (LSUMZ); 1 mi. SE Cottonport City Hall, 1 (USL); Ring Levee outside Hamburg, 1 (USL); Lake Callahan, 1 mi. S Cottonport City Hall, 1 (USL); 1 mi. SE Cottonport City Hall, 1 (USL); Lake Callahan, 1 (USL); 2 1/2 mi. ENE Mansura, 1 (USL). Beauregard Par.: Old River, 7 mi. SW Merryville, 1 (MSU); Persimmon (sic) Gap Marsh, 10 mi. S Hwy. 27 Derrider, 1 (MSU); 7 7/10 mi. N, 1 9/10 mi. S Merryville (in Vernon Par.), 1 (MSU). Bienville Par.: 1 mi. S, 3 mi. W Saline, 1 (LSUMZ). Bossier Par.: 1 mi. NE Red Point, 1 (LSUMZ); 4 mi. N Princeton, 1 (LSUMZ); Bossier Air Force Base, 2 mi. N main gate, 2 (LSUMZ); 2 mi. E Midway, 1 (LSUMZ); Barksdale Air Force Base, 2 (LSUMZ). Cado Par.: 5 mi. NW Keithville, 1 (LSUMZ). Calcasieu Par.: Interstate 10, ca. 4 mi. W Sulfur, 2 (MSU); 2 mi. S, 5 1/2 mi. E Dequincy, 1 (MSU); 10 mi. W West Lake, 1 (MSU). East Baton Rouge Par.: Baton Rouge, 2 (LSUMZ); University, 3 (LSUMZ); University, 1 (LSUMZ); 1 1/2 mi. E University, 1 (LSUMZ); Lindsay, 1 (LSUMZ); 3 mi. S University, 1 (LSUMZ); 7 mi. SW Zachary, 1 (LSUMZ); 6 mi. S University, 1 (LSUMZ); LSU campus, 1 (LSUMZ). East Feliciana Par.: ca. 4 mi. NW Clinton, Beechgrove Plantation, 4 (LSUMZ), 4 mi. N, 4 mi. W Clinton, 1 (LSUMZ); 1 mi. NE Clinton, 1 (LSUMZ); Clinton, 1 (LSUMZ). Evangeline Par.: 9 mi. N Ville Platte, 1 (USL); 1 1/2
mi. N Chataigner, 1 (USL). **Iberia Par.**: 5 mi. W New Iberia, 2
mi. S LA 14, 3 (USL); 1 mi. S Lafayette {in Lafayette Par.}, 1
(USL); Week's Island Road, 1 (USL); New Iberia Navy Base, 1
(USL); Lake Dauterive, 1 (USL). **Iberville Par.**: 3 1/4 mi. NW
Bayou Sorrel, 1 (LSUMZ); 8 mi. S Bayou Pigeon, 1 (LSUMZ);
Carville, 1 (LSUMZ); 1/2 mi. S Jct. Bayou Manchac and Old Perkins
Road, 1 (LSUMZ). **Jackson Par.**: Jackson-Bienville Wildlife
Management Area, 1 (LSUMZ). **Jefferson Davis Par.**: no specific
locality, 1 (MSU). **Lafayette Par.**: 1/2 mi. N Carencro Post
Office, 1 (USL); Lafayette, 10 (USL); 2 1/2 mi. E Lafayette
Courthouse-Beaver Park, 1 (USL); 1 mi. NE Lafayette Airport, 1
(USL); 5 mi. SE Lafayette, 1 (USL). **La Salle Par.**: Catahoula
Lake, Jena, 1 (LSUMZ). **Livingston Par.**: 9 mi SE LSU lakes, 1
(LSUMZ). **Madison Par.**: 5 mi. E Lamar {in Franklin Par.}, 4
(LSUMZ). **Pointe Coupee Par.**: 1 mi. E Melville, {in St. Landry
Par.}, 1 (USL); Ventress, 4 (LSUMZ). **Rapides Par.**: Bayou Boeuf
Rd., 5 mi. off Lecompte-Forest Hill Rd., 1 (USL); 15 mi. S
Alexandria, 1 (LSUMZ); 1 mi. N Pineville City Hall, 1 (USL). **St.
Helena Par.**: 5 mi. S Greensburg, 2 (LSUMZ). **St. Landry Par.**:
Melville, 1 (USL); 2 mi. S Opelousas, 3 (USL); 2 mi. E
Arnandville, 1 (USL); 6 mi. S Parish Courthouse, Opelousas, 3
(USL). **St. Martin Par.**: Lake Martin, 2 (USL); Cade, 2 (USL); 2
mi. SE St. Martinsville {sic}, 1 (USL); S Evangeline State Park,
St. Martinville, 1 (USL); Catahoula Woods, 1 (USL); 1 mi. E St.
Martinville, 1 (USL). **St. Tammany Par.**: 6 mi. E Folsom, 1
(LSUMZ); 3 mi. NE Lacombe, 1 (LSUMZ); 2 1/2 mi. NE Bush, 1 (LSUMZ); 5 mi. N Slidell, 1 (LSUMZ); 2 mi. S Lacombe, 1 (LSUMZ); 4 1/2 mi. E Abita Springs on Hwy 36, 1 (LSUMZ). Tensas Par.: 1 mi. S St. Joseph, 1 (LSUMZ); 12 mi. W St. Joseph, 2 (LSUMZ); 20 mi. NW St. Joseph, 2 (LSUMZ). Vernon Par.: 1 mi. E Fort Polk, 1 (MSU); 5 mi. E Simpson, 1 (LSUMZ); 3 mi. E Simpson, 1 (LSUMZ); 3 mi. S, 2 mi. E Fort Polk (T.1S, R.8W, sec.11), 1 (LSUMZ); 9 mi. E Fort Polk (T.1N, R.7W, sec.24), 1 (LSUMZ); Fort Polk Wildlife Management Area, 1 (LSUMZ). Washington Par.: 5 mi. N, 1 mi. W Bogalusa, 1 (LSUMZ); 3 km. N Bogalusa on Hwy 21, 1 (LSUMZ); 12 mi. E Franklinton, 1 (LSUMZ); Sheridan, Lee Memorial Forest, 1 (LSUMZ); 5 mi. E, 2 mi. S Mount Herman, 1 (LSUMZ); 2 3/4 mi. W Angie, 1 (LSUMZ); 2 mi. N, 3 mi. E Angie, 1 (LSUMZ). West Feliciana Par.: 1 1/2 mi. N, 1 mi. W Jackson, 2 (LSUMZ). Winn Par.: 1 mi. S, 2 mi. E Readhimer, 2 (LSUMZ); 1 mi. W Readhimer, 2 (LSUMZ).

MISSISSIPPI. Holmes Co.: 8 mi. S, 1 mi. W Durant, 1 (LSUMZ); 5 mi. S, 1 mi. W Durant, 3 (LSUMZ). Marshall Co.: 7 mi. S Waterford, 2 (MSUMZ); 1 1/2 mi. SE Law’s Hill, 1 (MSUMZ). Panola Co.: 2 mi. SW Sardis, 3 (MSUMZ). Tate Co.: Chigger Ridge Farm, Blue Grass Community, 1 (MSUMZ).

TENNESSEE. Fayette Co.: 2 mi. SW Grand Junction, 3 (MSUMZ); 5 mi. E Moscow, 1 (MSUMZ). Shelby Co.: Jct. New Allen and
Raleigh-Frayser Rds., 2 (MSUMZ); Memphis, Union and Peabody, 1 (MSUMZ); 2 mi. W McKellar Lake, 1 (MSUMZ); Memphis, proposed coal gasification plant site, 2 (MSUMZ).

**TEXAS.**

(TCWC). **Trinity Co.**: 15 mi. SW Trinity, 1 (TCWC); 12 mi. E Trinity, 3 (TCWC); Trinity, 1 (TCWC); Riverside, 1 (TCWC). **Wood Co.**: 3 mi. SE Quitman, 2 (TCWC).

*Sciurus carolinensis*

**ARKANSAS. Stone Co.**: cave at Mud Springs, 1 (MSUMZ); 3 mi. N Fifty-six, 1 (MSUMZ); 2 mi. N Fifty-six, 3 (MSUMZ).

**LOUISIANA. Acadia Par.**: 4 1/2 mi. SE Crowley, 1 (USL); 1/2 mi. S Egan near Bayou Jonah, 1 (USL). **Allen Par.**: no specific locality, 1 (MSU). **Avoyelles Par.**: 2 1/2 mi. N Morrow, 2 (USL); 5 mi. S Dupont, 1 (USL); 5 mi. S Cottonport, 1 (USL); 3 mi. N Morrow, 1 (USL). **Bienville Par.**: Bienville, 1 (LSUMZ); 15 mi. NW Gibsland, 1 (LSUMZ); 3 mi. N, 5 mi. W Saline, 1 (LSUMZ). **Beauregard Par.**: no specific locality, 1 (MSU). **Caddo Par.**: 3 mi. S, 1 mi. W Blanchard, 1 (LSUMZ); 3 mi. S, 1 1/2 mi. W Blanchard, 1 (LSUMZ); Rodessa, 1 (LSUMZ). **Calcasieu Par.**: no specific locality, 1 (MSU); Lake Charles, 6 (MSU); ca. 4 mi. W Sulfur, 2 (MSU); Maplewood, Thomas Ashford House, 1 (MSU); ca. 10 mi. W Sulfur, 2 (MSU); 6 mi. S Pecan Grove, Lone Star Plantation Road, 2 (MSU); 1 mi. S, 1 mi. E Gillis, 2 (MSU); 2 mi. W Lake Charles, 1 (MSU). **East Baton Rouge Par.**: Indian Mound, 6 (LSUMZ); 12 mi. S University, 1 (LSUMZ); 1 mi. W Airport, 1
(LSUMZ); 3 mi. S University, 1 (LSUMZ); 20 mi. N Baton Rouge, 2
(LSUMZ); 7 mi. E Baton Rouge, 2 (LSUMZ); 2 mi. N, 3 mi. E
Zachary, 1 (LSUMZ). **Iberia Par.**: Grand Lake, 1 (LSUMZ); Avery
Island, 1 (LSUMZ). **Iberville Par.**: 4 mi. SW Rosedale, 1 (LSUMZ);
3 mi. S Rameh, 1 (LSUMZ); Indian Village, 1 (LSUMZ); Bayou Sorrel
below Plaquemine, 1 (LSUMZ). **Jackson Par.**: Jackson-Bienville
Wildlife Management Area, 4 (LSUMZ). **Jefferson Par.**: Metairie, 1
(USL); 1 mi. W New Orleans, 1 (USL); 2 mi. E of Lake
Pontchartrain Causeway along levee, 1 (USL). **Jefferson Davis
Par.**: Lake Arthur, 1 (MSU); 3 mi. N Elton, 2 (MSU); no specific
locality, 1 (MSU). **Lafayette Par.**: 1 mi. NE Lafayette Airport, 2
(USL); Lafayette, 2 mi. SW Courthouse, 1 (USL). **Lafourche Par.**:
4 mi. SE Raceland, 1 (USL). **Madison Par.**: 20 mi. S, 4 mi. W
Tallulah, 1 (LSUMZ); 20 mi. S, 5 mi. W Tallulah, 1 (LSUMZ).
**Natchitoches Par.**: Provencal, 1 (LSUMZ); Lotus, 1 (LSUMZ).
**Orleans Par.**: 3 mi. SW Algiers, 1 (LSUMZ); 4 mi. E New Orleans, 1
(LSUMZ). **Plaquemines Par.**: Fanny, 4 (LSUMZ). **Rapides Par.**: 18
mi. S Alexandria, 1 (USL); 8 mi. W LeCompte near border of
Alexandria State Forest, 2 (USL); 9 mi. SW Alexandria, 1 (LSUMZ);
7 mi. W Woodworth, 1 (LSUMZ); 2 mi. W LeCompte, 1 (LSUMZ). **St.
Bernard Par.**: Toca Village, 4 (LSUMZ). **St. Landry Par.**: 1 1/2
mi. N of Morrow, 1 (USL); Thistlewaite Game Management Area, 11
(USL), 2 (LSUMZ); 5 mi. W Melville, 1 (USL); 3 mi. N Port Barre
Courthouse, 2 (USL); 10 mi. SE Krotz Springs, 1 (LSUMZ); 1/4 mi.
S Palmetto, 1 (LSUMZ). **St. Mary Par.**: Cypremont Point, 1 (USL);
4 mi. W Morgan City, 1 (USL); 2 1/2 mi. E Jeanerette, 3 (LSUMZ). 
St. Tammany Par.: 4 mi. E Bush, 1 (LSUMZ); 2 1/2 mi. N Covington, 1 (LSUMZ); Covington, 1 (LSUMZ); 1 mi. S Sun, 1 (LSUMZ); 1 mi. NW Pearl River, 1 (LSUMZ); 6 mi. S Bainsville, 1 (LSUMZ); 2 1/10 mi. S, 8/10 mi. E Pearl River, 1 (LSUMZ); 1 1/2 mi. SW Pearl River, 1 (LSUMZ); Slidell, 4 (LSUMZ). 
Tensas Par.: 4 mi. S, 2 mi. E Newellton, 1 (LSUMZ). 
Union Par.: 4 mi. N Marion on Cecil Creek, 2 (LSUMZ). 
Vernon Par.: 1 mi. N, 11 mi. E DeRidder (in Beauregard Par.), 1 (MSU); Fort Polk Wildlife Management Area, 5 (LSUMZ); 9 mi. S Flatwoods, 1 (LSUMZ); 4 mi. NE Hicks, 1 (LSUMZ); 5 mi. W Hineston, 1 (LSUMZ); 10 mi. W Merryville, 1 (MSU). 
West Feliciana Par.: 1 1/2 mi. N, 1 mi. W Jackson, 8 (LSUMZ).

MISSISSIPPI. Holmes Co.: 5 mi. S, 1 mi. W Durant, 5 (LSUMZ); 7 mi. S, 1 mi. W Durant, 3 (LSUMZ).

TENNESSEE. Hardeman Co.: Grand Junction, 1 (MSUMZ); Chickasaw State Park, 1 (MSUMZ); Teague, 5 (MSUMZ). 
Houston Co.: 2 mi. N McKinnon, 10 (MSUMZ). 
Shelby Co.: Memphis, 2 (MSUMZ); no specific locality, 2 (MSUMZ); Jct. New Allen and Raleigh-Frayser Rds., 1 (MSUMZ); 1 mi. E Germantown, 1 (MSUMZ); 3 mi. E Jct. Austin-Peay Hwy. and Loosahatchie River, 1 (MSUMZ); Audubon Park, Memphis, 1 (MSUMZ); Millington Naval Air Station, 1 (MSUMZ); Memphis, 1/4 mi. W Jct. Union and Cleveland, 1 (MSUMZ); Hall Rd. between Macon Rd. and Walnut Grove Rd., 1 (LSUMZ).
TEXAS. **Hardin Co.**: 9 mi. N Silsbee, 1 (TCWC); Goat Island, Pine Island Bayou, 1 (TCWC). **Polk Co.**: 1 8/10 mi. NNW Segno, 1 (TCWC), 5 8/10 mi. N Dallardsville (on FM 1276), 1 (TCWC); 5 2/10 mi. W Dallardsville, 1 (TCWC); 4 6/10 mi. NNW Dallardsville, 2 (TCWC). **Trinity Co.**: 16 mi. SW Trinity, 1 (TCWC); 11 mi. SW Trinity, 1 (TCWC); 8 mi. S Apple Springs, 1 (TCWC). **Tyler Co.**: 2 mi. SW Dam B Reservoir, 1 (TCWC); 1 1/2 mi. S, 1 8/10 mi. W Town Bluff, 1 (TCWC); 10 8/10 mi. S Woodville, 2 (TCWC); 12 mi. S Woodville, 1 (TCWC).
APPENDIX II

SPECIMENS EXAMINED

Electrophoretic Analyses

**Sciurus niger**

**ARKANSAS.** Greene Co.: 3 1/2 mi. W Paragould (5).

**LOUISIANA.** Acadia Par.: 5 mi. S Eunice (12). Ascension
Par.: 3 mi. W Prairieville (3). Bienville Par.: 3 mi. N, 5 mi. W
Saline (2); 1 mi. S, 3 mi. W Saline (1). Bossier Par.: Fillmore
(1); Barksdale Air Force Base, (4). East Baton Rouge Par.: Baton
Rouge, LSU campus (6). East Feliciana Par.: ca. 4 mi. NW
Clinton Beechgrove Plantation (4); Idlewild Experiment
Station (1); 1 mi. N St. Francisville (1). Grant Par.: 17 km N
Manchac and Old Perkins Rd. (1); Bayou Paul Rd. (1). Jackson
Par.: Jackson-Bienville Wildlife Management Area (3). Madison
Par.: 5 mi. E Lamar (in Franklin Par) (7). Pointe Coupée Par.:
Ventress (4). St. Tammany Par.: Covington (5). Vernon Par.: 3
mi. S, 2 mi. E Fort Polk (T1S, R8W, sec. 11) (1); 9 mi. E Fort
Polk (T1N, R7W, sec. 24) (1); Fort Polk Wildlife Management Area
(3). West Feliciana Par.: 1 1/2 mi. W Jackson (4). Winn Par.: 1
Sciurus carolinensis

LOUISIANA. Acadia Par.: 5 mi. S Eunice (4). Bienville Par.: 3 mi. N, 5 mi. W Saline (1); 4 mi. N, 2 1/4 mi. W Saline (1). Bossier Par.: Barksdale Air Force Base (3). East Baton Rouge Par.: Baton Rouge, LSU campus (10); Baton Rouge, 735 Highland Park Dr. (1); Baton Rouge, Junction Menlo and Highland Rds. (1); Baton Rouge, 1/4 mi. E Jct. Highland and Lee Rds. (on Highland) (1); Baton Rouge, 1/8 mi. N Jct. Highland and Staring Rds. (on Staring) (1); Baton Rouge, 4244 Swire Rd. (1); Baton Rouge, Kenilworth Subdivision (1); Pride (7). Jackson Par.: Jackson-Bienville Wildlife Management Area (8). Lafayette Par.: 1 1/2 km E Johnson St., 5 km S Ridge Rd. (1). Rapides Par.:
Deville off Flagon Creek bottom (1). **St Tammany Par.**: 2 mi. S Folsom (3); Slidell (4); 2 mi. N Waldheim (5). **Vernon Par.**: Fort Polk Wildlife Management Area (6). **West Feliciana Par.**: 1 1/2 mi. N, 1 mi. W Jackson (12). **Winn Par.**: 1 mi. W Readhimer (1); 1 mi. S, 2 mi. E Readhimer (1).

**MISSISSIPPI.** Holmes Co.: 5 mi. S, 1 mi. W Durant (11); 7 mi. S, 1 mi. W Durant (5); 8 mi. S, 1 mi. W Durant (2).

**TENNESSEE.** Shelby Co.: Jct. Macon and Collierville-Arlington Rds., Fisherville (1); Jct. Macon and Pisgah Rds., (1); Shelby Forest State Park (1); Memphis (12). **Tipton Co.**: Munford (1).
CURRICULUM VITAE
Nancy D. Moncrief
May, 1987

EDUCATION

Louisiana State University, 1981-present; Ph.D. in Zoology, expected August 1987.
Major subject area: evolutionary biology
Minor subject area: vertebrate physiology

Texas Tech University, May 1982; course: "Field Methods (in Karyology),"
taught by Dr. Robert J. Baker, Texas Tech Center at Junction, Junction, TX.

Major subject area: evolutionary biology

University of Oklahoma, June-July 1978; course: "Natural History of Vertebrates,"
taught by Dr. Howard W. McCarley, University of Oklahoma Biological Field Station,
Lake Texoma.

Memphis State University, 1974-1978; B.S. in Biology (cum laude), May 1978.
Major subject area: vertebrate zoology

RESEARCH AND ACADEMIC POSITIONS

Curatorial Assistant, Division of Mammals, Museum of Zoology, Louisiana State
University. Performed routine curatorial duties in addition to identifying and
cataloging specimens. Fall 1982; Spring and Fall 1984; Fall 1985; Spring, Summer,
and Fall 1986.

Research Assistant, National Science Foundation (NSF) grant to Mark S. Hafner.
Performed karyology and protein electrophoresis investigations. Summer 1982;
Summer 1984; Spring 1985.

Teaching Assistant, Department of Zoology and Physiology, Louisiana State University.
Taught laboratories in introductory zoology, mammalogy, and mammalian physiology.
Fall 1981; Spring 1982; Spring and Fall 1983.

Research Assistant, Savannah River Ecology Laboratory, Aiken, SC. Performed protein
electrophoresis investigations. Summer 1983.

Curatorial Assistant, Division of Mammals, Museum of the High Plains, Fort Hays State
University. Performed routine curatorial duties in addition to identifying and
cataloging specimens. Fall 1979 - Summer 1981.

Research Assistant, NSF grant to Jerry R. Choate and Hugh H. Genoways. Performed
karyology and extensive field investigations. Summer 1979.

Teaching Assistant, Department of Biological Sciences, Fort Hays State University.
(taught laboratories in introductory zoology, anatomy and physiology, and
mammalogy) Spring and Fall 1979.

152
GRANTS AND AWARDS

1986. Travel Award from The Graduate School, Louisiana State University. Financed travel to professional meetings.


1 April 1985-1 April 1986. $1410

1983. National Science Foundation Dissertation Improvement Grant BSR-8312805 (awarded in my behalf to Dr. H. S. Hafer). "The Effects of the Lower Mississippi River on Gene Flow among Mammalian Populations."

1 November 1983-10 October 1985. $6,000


1 April 1983-1 April 1984. $480

1982. Travel Award from The Graduate School, Louisiana State University. Financed travel to professional meetings.

FIELD EXPERIENCE


Iowa, Kansas, and Missouri: Collection and preparation of mammals in Kansas, northern and eastern Missouri and southern Iowa. Summer 1979; Summer 1980.

Tennessee: Live-trapping, collection and preparation of mammals throughout the state. Summer and Fall 1977; Spring and Summer 1978.


SOCIETY AFFILIATIONS

American Society of Mammalogists (served on Membership committee 1981-1985; appointed to Education and Graduate Students Committee 1985)
Southwestern Association of Naturalists
The Wildlife Society
Society for the Study of Evolution
Society of Systematic Zoology
American Association for the Advancement of Science

PAPERS PRESENTED AT SCIENTIFIC MEETINGS


THESIS AND PUBLICATIONS


DOCTORAL EXAMINATION AND DISSERTATION REPORT

Candidate: Nancy D. Moncrief

Major Field: Zoology

Title of Dissertation: Geographic Variation in Morphology and Allozymes within Tree Squirrels, Sciurus niger and S. carolinensis, of the Lower Mississippi River Valley

Approved:

[Signature]
Major Professor and Chairman

[Signature]
Dean of the Graduate School

EXAMINING COMMITTEE:

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W. Harman

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Albert H. Meier

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Jim T. Chamber

Date of Examination:

June 9, 1987