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Sciurus aberti.

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Sciurus aberti Woodhouse, 1853

Abert's Squirrel

Sciurus dorsalis Woodhouse, 1853*a*:110. Type locality San Francisco Mountains, Coconino County, Arizona (preoccupied by *Sciurus dorsalis* Gray, 1848).
Sciurus aberti Woodhouse, 1853*b*:220, a renaming of *S. dorsalis* Woodhouse.
Sciurus castanotus Baird, 1855:332. Type locality "the Mimbres," New Mexico.
Sciurus castanonotus Baird, 1858, an emendation of *castanotus*, stated to have been a typographical error for *castanonotus*.
Sciurus alberti Gray, 1867:417, a *lapsus* for *aberti*.

CONTEXT AND CONTENT. Order Rodentia, Suborder Sciuromorpha, Family Sciuridae, Genus *Sciurus*, Subgenus *Otosciurus*. Hall and Kelson (1959) recognized two species within *Otosciurus*, *Sciurus aberti* and *S. kaibabensis*. Cockrum (1960), however, regarded the Kaibab squirrel only as a subspecies of Abert's squirrel. The classification of Hall and Kelson will be followed in this account. Eight subspecies of *S. aberti* were recognized:

S. a. aberti Woodhouse, 1853:110, see above (*castanonotus* Baird a synonym).
S. a. barberi Allen, 1904:207. Type locality Colonia García, Chihuahua.
S. a. chuscensis Goldman, 1931:133. Type locality Chusca Mts., 9000 ft., New Mexico.
S. a. durangi Thomas, 1893:50. Type locality Ciudad Ranch, 100 mi. W Durango, Durango.
S. a. ferreus True, 1894:241. Type locality Loveland, Larimer Co., Colorado.
S. a. mimus Merriam, 1904:130. Type locality Hall Peak, S end Cimarron Mountains, Mora Co., New Mexico.
S. a. navajo Durrant and Kelson, 1947:79. Type locality 1 mi. E Kigalia Ranger Station, 30 mi. W Blanding, Natural Bridges National Monument Road, 8000 ft., San Juan Co., Utah.
S. a. phaeurus Allen, 1904:205. Type locality La Ciénega, 7500 ft., Durango.

DIAGNOSIS. Abert's squirrel and its close relative, the Kaibab squirrel, have long and broad ears that bear pronounced tufts or tassels in the winter pelage. The tail is short and unusually broad. The upper parts, including the tail, are mainly gray and the underparts are white (in the Kaibab squirrel the tail is white above and below and the underparts are dark gray to black). The lateral line is usually black and distinct. The skull is short and broad and the frontal area is flattened. The braincase is depressed and inflated laterally. The rostrum is narrow and laterally compressed. The nasals are long (equalling the interorbital breadth). There are two upper pairs and one lower pair of premolars.

GENERAL CHARACTERS. The long ears bear the tassels or tufts that give the species one of its vernacular names. The tassels may exceed 25 mm in length and reach their maximum length during the winter months. In summer the tufts are much reduced in size and may be completely absent. Keith (1965) studied the length of the ear tufts of Abert's squirrel in Arizona. Mean length was 0 to 5 mm from July through September; it increased rapidly to 25 mm in October, and then increased gradually to a high of 40 mm in February and March. The tufts then decreased in size to 20 mm by June.

Abert's squirrel is a relatively large squirrel and there appears to be no major difference in size between males and females. The ranges of external measurements (all in millimeters) for the species as given by Hall and Kelson (1959) are: total length, 463 to 584; length of tail, 195 to 255; length of hind foot, 65 to 80. Armstrong (1972) presented selected cranial measurements of the holotype (a young adult female) and two additional females of *S. a. ferreus* from Colorado: greatest length of skull, 57.8, 60.2, 60.4; condylobasal length, 52.0, 56.2, 55.9; zygomatic breadth, 34.3, 35.9, 35.9; interorbital breadth, 18.7, 19.4, 21.1; postorbital breadth, 18.3, 18.0, 18.4; length of nasals, 19.4, 18.0, 18.4; mastoid breadth, 24.4, 25.6, 25.5; length of maxillary toothrow, 11.0, 11.0, 11.1. Additional measurements were provided by Allen (1895), McKee (1941), Warren (1942), Armstrong (1972), and Keith (1965).

Ramey and Nash (1976*a*) studied morphological variation among three allopatric subspecies in Colorado and Arizona, *S. a. ferreus*, *S. a. mimus*, *S. a. aberti*. Analyses were made for total length, length of tail, length of hind foot, length of ear from the notch, and body weight. No differences between the sexes were significant. Significant differences among the three subspecies were found for total length, length of hind foot, and body weight. Although McKee's (1941) data had indicated a consistent cline of decreasing size from central Arizona to northcentral Colorado, the data analyzed by Ramey and Nash did not show any consistent differences in size among the three subspecies.

DISTRIBUTION. This species is found in Ponderosa or yellow pine (*Pinus ponderosa*) communities of the Southwest, usually between 1800 and 3000 m, in portions of Wyoming, Colorado, New Mexico, Arizona, and Utah in the United States and in the Sierra Madre Occidental from Northern Sonora and Chihuahua to southern Durango in México. All subspecies live in close association with Ponderosa pine, which provides both shelter and food. Although the species usually is confined to Ponderosa forests, Findley *et al.* (1975) indicated that these squirrels are common in mixed conifer forests in many New Mexican canyons.

Many populations are relatively isolated as a result of the discontinuous distribution of stands of Ponderosa pine. Abert's squirrel is rather scarce throughout much of its range, but is abundant at times in some localities.

Much of the known geographic range of the species occurs in relatively remote and inaccessible areas, an observation confirmed by the fact that one subspecies, *S. a. navajo*, was not discovered in Utah until 1947. Additional extensions of the distribution of the species have been made known in recent

FIGURE 1. Photograph of *Sciurus aberti ferreus* taken in Larimer County, Colorado.

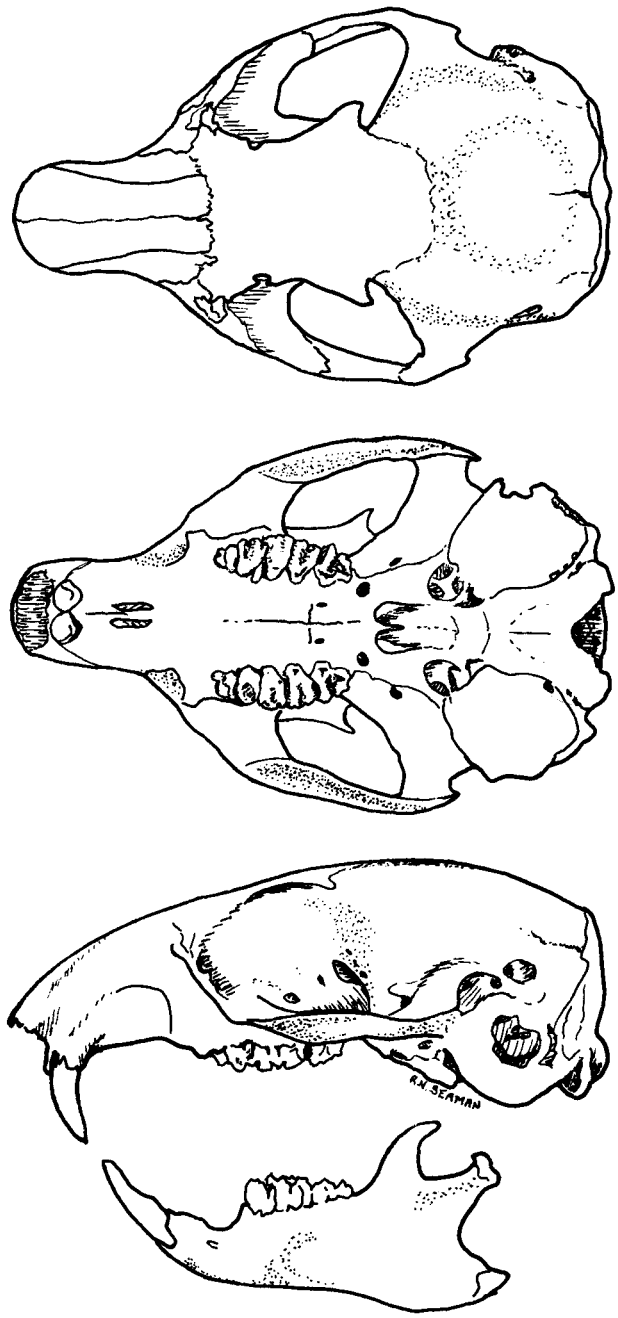

FIGURE 2. Skull and jaw of *Sciurus aberti*: from top to bottom, dorsal view, ventral view, lateral view, and lateral view of lower jaw.

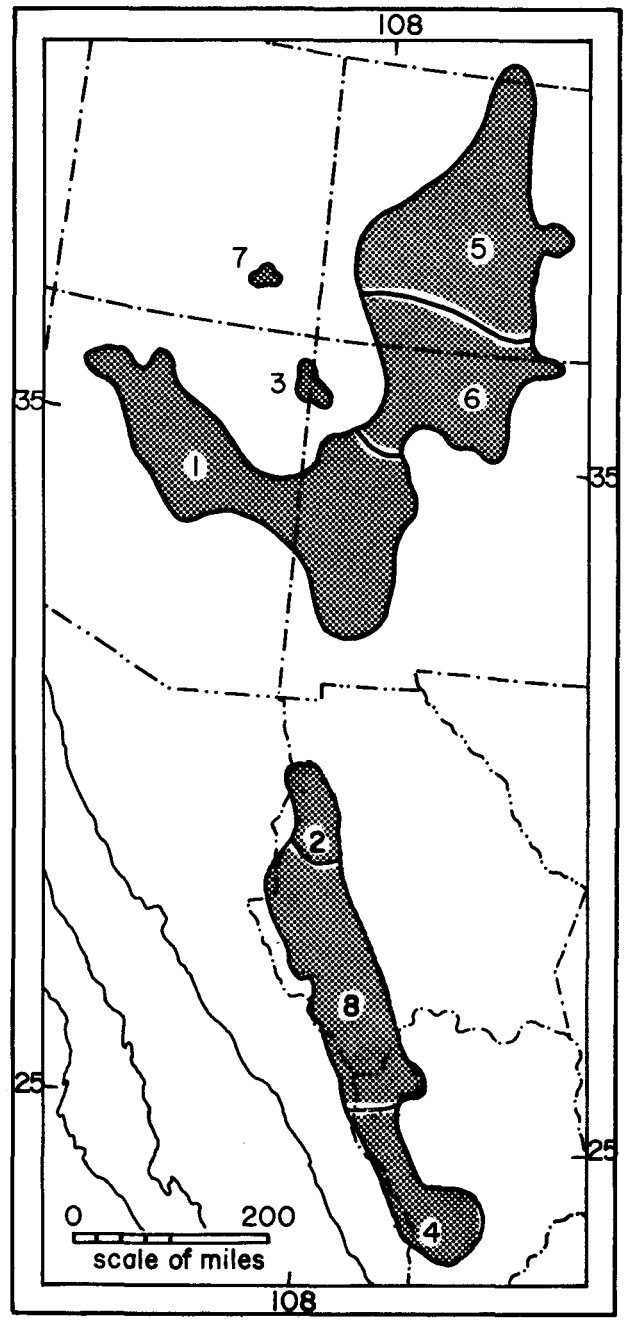

FIGURE 3. Range of *Sciurus aberti* and its subspecies (modified from Hall and Kelson, 1959, and Anderson, 1972). Subspecies are: 1, *S. a. aberti*; 2, *S. a. barberi*; 3, *S. a. chuscensis*; 4, *S. a. durangi*; 5, *S. a. ferreus*; 6, *S. a. mimus*; 7, *S. a. navajo*; 8, *S. a. phaeurus*.

years. It is thought that these extensions reflect the increased observations of additional researchers rather than actual extension of the range of the species.

Brown (1965) reported an extension of the known geographic range of Abert's squirrel into Wyoming at a locality 1.2 km north of the Colorado-Wyoming state line. He doubted that the geographic range of the species extended more than 8 to 16 km inside Wyoming because of the lack of suitable Ponderosa pine habitat.

Ramey and Nash (1971) studied the distribution of Abert's squirrel in Colorado and reported that the range extended eastward to include the Black Forest regions of El Paso and Elbert counties and that it also extended westward into Montezuma county.

FOSSIL RECORD. The fossil record helps little in understanding the evolutionary development of the species. Matthew (1924) reported one well-preserved lower jaw from the Upper Snake Creek beds near Agate, Nebraska, dating from the Middle Pliocene. Although the specimen is not distinguishable from the jaw of modern *S. aberti*, Matthew also commented that it might represent some other large western black squirrel. He also noted (p. 84) that the jaw was "a little too large, too deep-jawed and heavy-toothed for the common eastern gray squirrel."

Bryant (1945) in his study of the phylogenetic relationship of the Nearctic Sciuridae reported two right maxillaries (*Sciurus* sp.) from the Hemingfordian, middle Miocene, in Oregon, but the specimens were far too fragmentary for the determination of any precise relationship.

FORM. There are few anatomical studies on Abert's squirrel. It presents an outstanding example of coat color polymorphism. The polymorphism appears limited to the north-central part of Colorado and is confined to the subspecies *Sciurus aberti ferreus* (Ramey and Nash, 1971). Early biologists,

including Warren (1910) typically identified three color phases: gray, brown, and black. However, more recent studies indicate that coat color exhibits a continuous variation as far as the intensity of brown is concerned (Ramey, 1972). Study of coat color polymorphism by Ramey utilized the presence or absence of the so-called agouti phase, which may be recognized from the characteristic banded pattern. The agouti category included specimens previously described as gray and the nonagouti category contained the melanistic squirrels, including the brown and black phases. The frequency of melanistic animals was 67.5% in north-central Colorado and approached 100% in the Black Forest region east of Colorado Springs. Ramey and Nash (1976*b*) found that the polymorphism seemed to be a balanced one as frequencies of the color phases have been fairly stable since the turn of the century. Frequencies of morphs revealed no obvious associations with elevation, temperature, humidity, or data on evaporation or freezing.

Direct breeding tests for the inheritance of coat color have not been performed. Cases are known in which a single female had a mixed litter of both gray and melanistic forms. Rockwell (1916) reported that squirrels of any two or three of the coat colors may be born of the same parents.

Occurrence of coat color polymorphism in states other than Colorado has been reported, but it has not been studied in any depth. Ligon (1927) reported that approximately 85% of the San Mateo Mountains population was in the black phase.

Findley *et al.* (1975) noted that on certain mountain ranges in New Mexico many individuals are black-bellied and that most of the squirrels in the Sandia and Manzano mountains are black-bellied, but they did not give specific data on frequencies.

Keith (1965) described molt in the species in Arizona. The spring molt commences under the forelegs and is nearly complete ventrally before molting begins on the back and finally on the tail. Most individuals have finished molting by July. More white hairs are found on the back in the summer fur than in the winter coat, and, in addition, the white on the venter is more sharply defined.

Molting during autumn is not as sharply defined and additional hairs develop to form the longer and thicker hairs characteristic of the winter coat. Growth of the new ear tassels or tufts also commences about this time in October. Keith indicated that the general coloring of the summer fur was much paler, an observation confirmed by Ramey (1973) for Abert's squirrel in Colorado.

FUNCTION. Virtually no physiological information is available concerning this species. Johnson (1974) reported a single band of hemoglobin in a single specimen of *Sciurus aberti ferreus*. Seaman (1975), however, noted that populations in Colorado are polymorphic for hemoglobin, some individuals having a "single" hemoglobin and others a "double" hemoglobin.

ONTOGENY AND REPRODUCTION. Hall and Kelson (1959) reported that three or four young usually are born in April or May and that there often is more than one litter each year, especially in the southern parts of the range. However, it is difficult to find specific information concerning breeding in the species. Keith (1965) observed that in 1954 squirrels bred only once in central Arizona. The duration of gestation was estimated to be 40 days and the mean litter size was 3.4. The young weighed 12 g at birth and were 60 mm long.

Farentinos (1972*a*) determined that gestation required about 46 days in northern Colorado. Mean litter size was 3.2 for five litters with a range from two to four.

The young are born naked and with their eyes and ears covered by membranes. Vibrissae are present on the face and the toes bear well-developed claws. Keith (1965) provided the following summary of development of six young squirrels taken from nests when about two weeks old and held in captivity:

"At two weeks of age these squirrels had thin short hair on their tails, sides, and backs, but their chests and abdomens were bare. When handled they grasped firmly with their claws and often squealed loudly. Their eyes were closed and their ears had only small openings. At six weeks of age the squirrel's pelage resembled the adult's winter coat—the legs and tail were long and appeared out of proportion to the rest of the body. The hairs of the tail lay flat, giving the tail a terete appearance. The ears hung over the sides of the face and were held upright only when the squirrels were attentive. Their eyes opened at about this age, and the young spent less time sleeping and became more active.

"At seven weeks of age the tail had broadened and was carried over the back. The ears were always held erect. Young squirrels scratched and sat on their haunches like adults. They ceased to take only milk in their diet and ate mushrooms and the inner bark of pine twigs. The exact age of independency in the wild is not known. In captivity the young first ventured from the nests at about seven weeks, but it was not until they were about nine weeks of age that they climbed to the ground. The young were weaned at about ten weeks of age. They could probably have survived without the care of the mother at that time, but they did not reach mature size until they were 15 to 16 weeks old. Their weight averaged about 170 g at five weeks, 195 g at six weeks, 242 g at seven weeks, and 355 g at nine weeks of age."

Juvenile males do not possess definitive scrota. In adult males the testes are abdominal during early to late autumn. The testes begin to descend by February and are fully descended by mid-March. Keith (1965) reported that testes volume increased during February from an average of about 465 mm^3 to about 2,600 mm^3. The testes remain large until August and then begin to regress again.

ECOLOGY AND BEHAVIOR. Observations of the breeding behavior of Abert's squirrel have been made by several authors including Rice (1957), Keith (1965), and Farentinos (1972*b*). Mating chases similar to those described for other tree squirrels also have been described for *Sciurus aberti*. Mating chases or bouts typically involve several males and a female in estrus. Chases usually begin early in the morning and last until dusk with a mean duration of 11 hours (Farentinos, 1972*b*). Aggressive encounters between dominant males and females are common at this time. Portions of the account by Farentinos may be used as an illustrative example. "During a mating bout an oestrous female typically moved through the forest, often in response to the advancing dominant male or a subordinate, or passively left an area while feeding, which she engaged in frequently throughout a bout. Whenever the female moved to another tree or some other part of the forest the males ran behind, thus the name 'mating chase.' The dominant male, if aware that the female had left, usually headed the entourage with the subordinate males following. The term 'mating chase' is somewhat inappropriate in describing this mass movement of squirrels, in that the pursuit of the female by the males appeared to be a following response rather than an active chase. The female often ran on the ground from one tree to another with the male troop running behind. When the female reached a tree she often jumped to the base of the trunk and paused (sometimes for over a minute) before ascending. The pursuing males usually stopped a meter or so short of the female and remained motionless until she began to climb the tree, at which time they followed in response."

Little behavior associated specifically with courtship has been observed. Although the dominant male usually succeeded in copulating first, subordinate males also frequently copulated (Farentinos, 1972*b*). In his observations of 73 copulations involved in six mating chases Farentinos observed that 25 copulations were made by dominant males, 17 by subordinate males which were dominant in other mating chases and 31 by completely subordinate males.

Copulation usually consists of three distinct phases following mounting of the female by the male. The first phase consists of a series of rapid pelvic thrusts followed by a phase of slower and deeper thrusts and finally a phase of inactivity during which the penis remains inserted. The mean duration of copulation was estimated to be 72.2 seconds (Farentinos, 1972*b*). Dominance was found to be correlated with which male was first to copulate and also with the number of times a male copulated.

Nests typically are built in the branches of ponderosa pine (V. Bailey, 1931; Cahalane, 1947; Farentinos, 1972*c*; Goldman, 1928; Keith, 1965; Warren, 1910). Keith observed that nests also were found in cavities of Gambel oaks and in branches of cottonwoods. Nests also were built within "witches brooms" or pathogenic growths of small pine twigs caused by dwarf mistletoe infection (Farentinos, 1972*c*). Keith noted in Arizona that trees with nests varied from .3 to 1.0 m diameter at breast height (d.b.h.) and that the nests were built 4.9 to 27 m above ground in trees that were 6 to 34 m in height. Nests were constructed of pine twigs that were 13 mm or less in diameter and varied in length from .2 to .6 m. The inside diameter of nests ranged from 102 to 254 mm and the outside diameter from .3 to 1.0 m. There usually was only one opening per nest although some nests were found with two or three openings. Frequently more than one nest is utilized.

Patton and Green (1970) and Patton (1975) extended the studies of Keith on tree characteristics of nest sites in Arizona. They concluded that the most important components of nest cover were tree density, diameter, and a grouped distribution of trees. Out of 302 nest sites, 80% of the nest trees were 280 to 560 mm d.b.h. with a mean value of 442 mm. Nests usually were located on a limb or against the tree trunk 9 to 15 m above ground. Good squirrel cover was found to contain uneven-aged ponderosa pine stands with trees spaced in small even-aged groups within the stand.

Abert's squirrels utilize ponderosa pine extensively as a source of food during the entire year. The inner bark, seeds,

terminal buds, and staminate flowers are eaten. These squirrels also feed on fleshy fungi, carrion, and bones and antlers (Keith, 1965). They apparently do not store food in large caches but have been reported to bury single pine cones in shallow pits (F. M. Bailey, 1932). Squirrels may show a preference for certain trees when feeding on the inner bark (Goldman, 1928; Pearson, 1950). Patton (1974) made a detailed study of the composition of the inner bark of ponderosa pine twigs. In Arizona in September, twigs were not highly nutritive, consisting of only 4.6% protein, 7.0% fat, and 41.7% fiber. During the winter the inner bark of the twigs comprises the staple diet. Squirrels actually consume less than 10% of the weight of twigs that are cut. Patton (1974) estimated that the average weights in grams for a sample of 50 twigs were: inner bark (the source of food)—13.0 g, outer bark (litter)—62.5 g, peeled twigs (litter)—65.0 g.

During a 10-year study from 1956–1965 in central Arizona, Larson and Schubert (1970) found that Abert's squirrel reduced the Ponderosa pine cone production by one-fifth. The proportion of the cone crop cut by squirrels varied from 0.3% in 1961 to 74.8% in 1959.

Abert's squirrels are strictly diurnal, becoming active shortly before sunrise and returning to their nests before sunset. Keith (1965) observed them to travel frequently from tree to tree and they were seen to jump distances between trees of up to 2.4 m. He determined the average home range in Arizona to be 7.3 ha (range, 4.05 to 9.71 ha) during the summer and autumn. Home ranges were considerably reduced in winter under snow cover to about 2.02 ha. Ramey (1973) determined the mean home range to be 8.13 ha in spring and summer in the Black Forest of Colorado. Subadult males, if they formed home ranges, tended to have larger home ranges than adult males (2.87 ha more in spring and 5.22 ha more in summer). Home ranges of adult females averaged 2.18 ha more than adult males during the summer.

Population numbers appear to fluctuate widely over time and space. Trowbridge and Lawson (1942) found about 30/km^2 in Arizona in 1941. Keith (1965) reported densities of only 2.5 to 5/km^2 in 1954 over the same regions. Ramey (1973) estimated densities of 30/km^2 in the Black Forest of Colorado in the summer of 1970 and 12/km^2 in the spring of 1971. Farentinos (1972*a*) determined the density to be 82/km^2 in Boulder County during the autumn of 1970 and 114/km^2 by the autumn of 1971. Cahalane (1947) suggested that population cycles might be related to cyclic variations in the biomass of the pine seed crops.

Farentinos (1974) studied intraspecific communication among Abert's squirrels and noted that they use a variety of auditory, olfactory, tactile, and visual cues. Visual and vocal signals were observed to be delivered over a wide range of intensity. A wide range of stimuli could evoke certain displays. The alarm display, for example, could be initiated by predators, conspecifics, and even inanimate objects.

The ecological relationship of the red squirrel, *Tamiasciurus hudsonicus*, and Abert's squirrel was studied by Ferner (1974) in Boulder County, Colorado. Red squirrels usually are not common in pure stands of Ponderosa pine within the range of Abert's squirrel, although they are found in Ponderosa pine outside the range of Abert's squirrel. Ferner considered that the habitat separation of the two species may be due in part to possible competitive exclusion.

GENETICS. Nadler and Sutton (1967) reported a diploid number of 40 chromosomes from a single male specimen. The karyotype contained 14 metacentric and 24 submetacentric chromosomes and was indistinguishable from that of *S. carolinensis* and *S. niger*. A large unpaired metacentric and an unpaired acrocentric were thought to represent the X and Y chromosomes, respectively. Based on their karyotypic analysis Nadler and Sutton felt that the subgenus *Otosciurus* may not be distinguishable from the subgenus *Sciurus*.

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