SYMPOSIUM ON THE GRAY SQUIRREL

INTRODUCTION

This symposium is an innovation in the regional meetings of professional game and fish personnel. When I was asked to serve as chairman of the Technical Game Sessions of the 13th Annual Conference of the Southeastern Association of Game and Fish Commissioners this seemed to be an excellent opportunity to collect most of the people who have done some research on the gray squirrel to exchange information and ideas and to summarize some of this work for the benefit of game managers and other biologists. Many of these people were not from the southeast and surprisingly not one of the panel members is presenting a general resume of one aspect of squirrel biology with which he is most familiar.

The gray squirrel is also important in Great Britain but because it causes extensive damage to forests. Much work has been done over there by Monica Shorten (Mrs. Vizoso) and a symposium on the gray squirrel would not be complete without her presence. A grant from the National Science Foundation through the American Institute of Biological Sciences made it possible to bring Mrs. Vizoso here. It is hoped that this symposium will set a precedent for other symposia at future wildlife conferences.

VAGN FLYGER.

THE RELATIONSHIPS OF THE GRAY SQUIRREL, SCIURUS CAROLINENSIS, TO ITS NEAREST RELATIVES

By DR. J. C. MOORE

INTRODUCTION

It seems at least slightly more probable at this point in our knowledge of the living Sciuridae, that the northeastern American gray squirrel's oldest known ancestors came from the Old World rather than evolved in the New. If this is certainly the case, then we know that some of the gray squirrel's ancestors spread to the New World a good many million years ago, because there are several fossil squirrels from North America known from the lower Miocene which seem to represent tree squirrels (Bryant 1945, p. 339). If they did come from the Old World, we know that the ancestral tree squirrels must have come across an isthmus or land bridge where the Bering Strait now separates Alaska from Siberia, for Simpson (1947) has shown that many kinds of mammals had crossed the Bering Land Bridge, in both directions, during periods of the middle Cenozoic, and because it now seems quite well established (Simpson, 1947, pp. 657-671) that no other land route was available to emigrants from the Old World.

There is much evidence that during the Pleistocene there were successive periods when the sea invaded and receded, alternately covering and baring the land connecting Siberia and Alaska (Hopkins, 1959, p. 1524). But there is also some evidence that no forests grew on the land bridge during these times (Hopkins, 1959, p. 1527). If that is true, no tree squirrel population could have spread onto and across it, and it seems possible therefore that the most recent crossing of the Bering land bridge by tree squirrels may very likely have been as long ago as Pliocene. After consideration of the slight difference in skull series in the American Museum and baculum characters (Howell, 1938) between the Eurasian red squirrel, *Sciurus vulgaris,* and the North American gray squirrel, *Sciurus carolinensis,* the present writer is of the opinion that the gray squirrel is the closest North American relative of the Asiatic red.

That seems to be nearly all that can be said about the early ancestors of the northeastern American gray squirrel. Tree squirrels have generally left very few fossils, and thus far, at any rate, very little is known about their evolution. However, reasonable speculation is possible about the separation of the gray

squirrel species from its nearest southern relative. A growing body of data is being advanced which indicates that during the Pleistocene, the southward extension of the continental glaciers into southern Illinois, Indiana, and Ohio (Flint, 1957, p. 321) inflicted a cold, nearly boreal climate upon the Southeastern Coastal Plain (Blair, 1958; Dorf, 1959, fig. 5). This change of climate appears to have wiped out certain species of vertebrates each of which must have been previously occupying the whole sweep of the Southeastern Coastal Plain, until their only remnants survived at the tip of peninsular Florida and far south into Mexico (Blair, 1958). When the glaciers retreated, permitting the return of what Dorf (1959) calls subtropical climatic conditions, and vegetation, the refugee species must have spread northward from Florida and Mexico and reoccupied the Southeastern Coastal Plain. Two parts of a species kept separate for so long a time as a glacial period may evolve characteristics different enough to estrange the two populations and prevent them from interbreeding when they expand onto the old range and reestablish contact. Then there are two species where there had been one.

Whether this mechanism could work on the gray squirrel depends upon the extent to which this species is adapted to cool temperate climate. Because of the extension of its present range north to the Canadian border toward the northern limits of cool temperate climate (Dorf, 1959, fig. 7), one could consider the gray squirrel too well adapted to cool climate to have been separated into two parts around the gulf at all, let alone pruned back all the way to Yucatan and the tip of peninsular Florida, by Pleistocene glacial climate.

ZOOLOGICAL VALIDITY OF SUBGENERA

Before exploring further for the gray squirrel's nearest relative to the south, we need to reconsider some matters of its presently accepted classification which need revision and which may be obscuring our goal. The problem of what the relationship of the gray squirrel is to its nearest relative has actually not been well studied since 1899 when E. W. Nelson recognized all of the four really good species of the genus *Sciurus* in the United States as distinct subgenera. Nelson (1899) also sorted the Mexican and Central American squirrels into several subgenera, and although this was an excellent work in its time, it may be seen to be very badly out of date with present concepts of how a species is distinguished, by study of the mapped distributions of his alleged species presented by Hall and Kelson (1959, vol. 1).

Nearly 40 years after Nelson's work, and just incidental to revision of the North American ground squirrels, Howell (1938) proposed a general classification of North American squirrels at the level of genera and subgenera. In this classification Howell refused to admit as valid all of the tropical subgenera that Nelson (1899) had recognized (except *Guerlinguetus*), but included them as species in the subgenera *Neosciurus* and *Parasciurus*. Consequently, in Howell's classification the gray squirrel, instead of constituting a subgenus alone, became the type species of a large subgenus including 16 species of Mexican and Central American squirrels. The North American fox squirrel, *Sciurus niger*, instead of constituting a subgenus by itself as Nelson (1899) classified it, became type species of a subgenus including (according to Howell, 1938) five species of the west and the tropics. The only skull character of possibly subgeneric significance upon which separation of these two "subgenera" rests, is the consistent presence in the gray squirrel's alleged subgenus of the vestigial pair of third upper premolar teeth, and the consistent absence of these in the fox squirrel's subgenus. In the absence of a better classification of these tree squirrels, Miller and Kellogg (1955) have followed Howell (1938) in their "List of North American Recent Mammals." Hall and Kelson (1959) also felt obliged to follow Howell's (1938) classification in their "Mammals of North America."

In a recent study of the relationships of the squirrels (Sciurinae) as indicated by the characteristics of their skulls, the writer acquired a familiarity with the degree of distinction acceptable for distinguishing subgenera in dealing with the 37 genera of this nearly worldwide subfamily. In the course of that study the writer could discover no justification, and in spite of the above men-

tioned implications of possible separation since as long ago as the Pliocene, still cannot find any, for distinguishing the northeastern American gray squirrel, *Sciurus carolinensis,* as a subgenus distinct from the Eurasian red squirrel, *Sciurus vulgaris.* Nor, in fact, have any such characters been proposed. Their skulls and their bacula are alike, and no combination of external and internal features suggests in the present author's opinion (and see Table I) a distinction greater than that of species. It is here proposed that the subgenus *Neosciurus* based on the gray squirrel be dropped. It and the two synonyms of it (*Echinosciurus* Trouessart, 1880; *Baiosciurus* Nelson, 1899) become synonyms of the typical subgenus *Sciurus.*

TABLE I

ESTIMATED DEGREE OF TAXONOMIC AFFINITY BETWEEN THE GRAY SQUIRREL AND ITS NEAREST RELATED SPECIES. NUMERALS 1 TO 4 RESPECTIVELY INDICATE MOST TO LEAST AFFINITY

	niger	*vulgaris*	*negligens*	*alleni*	*aureogaster*
Skull (teeth)	2	1	1	2	1
Body Pelage	3	2	2	1	4
Ear Pelage	2	3	1	1	1
Tail Pelage	3	2	1	1	3
Body Size	2	1	2	1	2
Habitat	2	2	2	1	2
Habits	1	2	3	1	1

The only character of possible subgeneric significance that appears to distinguish the fox squirrel, *Sciurus niger,* and its subgenus, *Parasciurus,* from the eastern gray squirrel and the typical subgenus, *Sciurus,* is the consistent absence of the third upper premolar teeth. The presence or absence of the vestigial third upper premolar teeth is a character which the writer (1959) has found to be diagnostic for polytypic subgenera, genera, subtribes, and tribes of squirrels. In none of these taxa, however, was it found to be the only character of consequence distinguishing so high a taxonomic category. Neither the skulls nor the published illustrations of the bacula of the fox squirrel and other species assigned to the subgenus *Parasciurus* by Howell (1938) show any other distinguishing character of consequence. It is here proposed that the subgenus *Parasciurus* Trouessart, 1880, be dropped. It and the subgenus *Araeosciurus* Nelson, 1899, become synonyms also of the typical subgenus *Sciurus.* With these ill-defined and possibly even unnatural, subgeneric categories so removed, several more species may be recognized as distinct from the gray squirrel at the species level. These nearest relatives include the Palaearctic tree squirrel, *Sciurus vulgaris,* the fox squirrel, *Sciurus niger,* and many apparently too finely split species of Mexico and Central America.

NEAREST MEXICAN RELATIVES OF S. CAROLINENSIS

Which species have already been considered to show the closest relationship to the gray squirrel? The rather diminutive gray squirrels, *Sciurus deppei* and *Sciurus negligens* of the Tropical Zone of eastern Mexico in Tamaulipas and San Luis Potosí are placed nearest to *S. carolinensis* by Miller and Kellogg (1955, p. 239) implying that those authors considered *deppei* and *negligens* to be the closest relatives of *carolinensis.* Hall and Kelson (1959, p. 372) have expressed an emphatically different opinion by placing 10 other species between *negligens* (as a subspecies of *deppei*) and *carolinensis,* and by placing the fire-bellied squirrel *S. aureogaster* next to *S. carolinensis.*

The ranges of *aureogaster* and *deppei negligens* as mapped by Hall and Kelson (1959, pp. 373 and 382) are sympatric, and so located that the range of either one is consonant with the concept of its origin having been by separation from what is now *carolinensis* during a glacial period. Dalquest (1953, p. 89) points out that the small squirrel *negligens,* lives in greater abundance in the Upper Tropical Zone of the eastern slopes of the mountains in San Luis Potosí in eastern Mexico, and is scarcer in the Lower Tropical Zone of the coastal plain to the east. Dalquest (1953, p. 89) describes in *negligens* peculiari-

ties of habit for a tree squirrel, that, together with its small size, suggest specialization both for the tropical forest habitat and for coexisting in this habitat with a larger species of ordinary size. "Shy and retiring, they are relatively inactive as compared with other Tree Squirrels. The animals live in the deep shade, and only rarely are they seen on twigs and small branches. They are commonly [observed] on the ground and seem to spend most of their lives on the lower parts of the trees, less than thirty feet from the ground. One to three ball-like leaf nests, each about a foot in diameter, were found in some trees. Nests were observed six to twenty feet from the ground in dense mango trees. . . ."

Sciurus oculatus alleni of northeastern Mexico has so many of the pelage and other external characters almost identical in every way to those of *Sciurus carolinensis* as to be distinguishable from it at the species level, only by lacking the third upper premolars. In particular the tail hairs of *Sciurus oculatus alleni,* like those of *Sciurus carolinensis* when fully grown out, possess four or five blackish bands consisting of a longer subterminal one and three or four shorter proximal ones. (The tail hairs of *Sciurus niger* and some forms in the southwestern United States apparently closely related to it, generally possess no more than three black bands, and proximal ones tend to approximate the subterminal one in length.) The geographic location of the range of *Sciurus oculatus* is consonant with the concept of separation from *Sciurus carolinensis* during one or more glacial periods of the Pleistocene by the invasion of boreal climate into the Southeastern Coastal Plain.

In the present paper *Sciurus alleni* is regarded as a subspecies of *oculatus* rather than as a species distinct from *oculatus* for the following reasons. In San Luis Potosí Dalquest (1953, p. 86) reports *oculatus shawi* to be occupying oak forests of the mountains west of the Sierra Madre. Dalquest remarks that *alleni* and *oculatus shawi* are "strikingly similar" and sustains *alleni* as a species apart from *oculatus* only on the basis of "slightly smaller size, under parts white rather than buffy, and postauricular spots absent." Baker (1956, p. 214) notes that "In *alleni* from Coahuila there are . . . postauricular spots conspicuous on some specimens but less so on others." (Baker examined 13 specimens of *alleni* and Dalquest but six.) The present writer observes conspicuous light postauricular spots of pelage in some *alleni* material in the United States National Museum. In view of the meager morphological difference between *alleni* and *oculatus shawi,* their correspondence of habitat, and their geographic proximity, it seems probable that their present geographic separation has not been of great duration and that differentiation has not reached a point at which the two populations would fail to interbreed freely if rejoined.

Dalquest (1953, p. 87) reports that *Sciurus* [*oculatus*] *alleni* lives in the oak forests capping the main crest of the Sierra Madre of the Mexican State of San Luis Potosí. The eastern slopes and lowlands of this state from the oak forested crest of this mountain range downward, Dalquest says, are tropical, and *alleni* does not occur there. The tropical forest areas are inhabited instead by the fire-bellied squirrel, *Sciurus aureogaster* (Dalquest, 1953, p. 84) as well as *Sciurus (deppei?) negligens.* Significantly Dalquest points out that farther north [in the Mexican State of Tamaulipas] where the lowlands east of the Sierra Madre are desert instead of tropical forest habitats, *alleni* does descend into the lowlands along streams and rivers. This certainly suggests that some species, probably *aureogaster* but possibly even *negligens,* is dominant to *alleni* in the tropical habitats and replaces it there.

Dalquest (1953, p. 84) does note that *aureogaster* is "less common at the upper edge of the Upper Tropical Zone than at lower elevations." Thus, even though *negligens* and *aureogaster* do occur together in the Tropical Zone, and seem adjusted by differences in size and habits to coexistence without fatal competition, each is reported as more abundant where the other is less.

Of the three species whose ranges do suggest the possibility of origin by separation from what is now *Sciurus carolinensis,* then, *Sciurus aureogaster* differs most greatly from *carolinensis* in pelage characters, and these are indeed very different. (Nelson, 1899, recognized the two as type species of two subgenera primarily on this degree of difference.) *Sciurus negligens* (as Dalquest,

1953, p. 88, regarded it, declaring that it should remain a species until intergradation with *deppei* is definitely established) or *Sciurus deppei negligens* (as Hooper, 1953, p. 4, considered it, evidently not doubting that intergradation does occur [1]) has considerably less difference in pelage characters from *carolinensis*. It is noted, and it may be significant, that the subspecies (?) of *deppei* and *oculatus* which are geographically closest to the range of the species *carolinensis*, display pelage character evidence of being closest to it taxonomically as well. Both *aureogaster* and *negligens* have become adapted to the tropical forest community, which is in some ways more distinct from the temperate climate habitat of *carolinensis* than is the Upper Sonoran Zone habitat to which *oculatus alleni* is adapted. Thus *oculatus alleni* is essentially like *carolinensis* in pelage characters and in habits and differs from it primarily in the one morphological feature, absence of the third pair of upper premolars. In view of the lack of other notable differences, the tooth character is taken to indicate no more than a good specific difference between *oculatus alleni* and *carolinensis*. The differences, thus, between *carolinensis* and each of the other three species are fewest, and, I think perhaps taxonomically least, in the case of *oculatus alleni*. The similarities in pelage characters, habit, and habitat between *carolinensis* and the geographically nearest form of each of the other three species seem also greatest in the case of *oculatus alleni*. See Table I.

HYPOTHETICAL HISTORY

A recapitulation of the hypothetical history of the separation of the two species will indicate better the reasons for emphasizing habitat in the above comparison of three species in regard to which is most closely related to the species *carolinensis*. When a Pleistocene glacial period intruded what Erling Dorf (1959, map 5) calls "cool temperate" climate on the Southeastern Coastal Plain, it drove what he calls "sub-tropical" climate (Dorf designates the present climate of the Southeastern Coastal Plain north to the Virginia line "subtropical" in his map 7) to the southern tip of Florida and south to what is now the Mexican state of Tabasco (Dorf, 1959, map 5). It drove the "subtropical" vegetation (which presumably would have constituted the habitat of the gray squirrel stock in the Southeastern Coastal Plain during the interglacial periods) south to these places. (It is primarily the fossil vegetation from which Dorf drew his inferential maps of the climate.) Moving south along with forest types to which it was adapted, the gray squirrel stock could very well have been separated by the Gulf of Mexico into eastern and western populations.

In the most extreme view, it might be conceived that each glacial period so separated the gray squirrel population into two parts and kept them separated long enough to allow them to differentiate beyond the point at which the two populations would interbreed if reunited by the northward migration with their habitat upon the retreat of the glacier. Thus several species might hypothetically have been so produced from the one gray squirrel stock by this one mechanism during the Pleistocene (for example *alleni, negligens, aureogaster* and still another species which has subsequently been competed out of existence in northeastern Mexico).

In the most conservative view, separation into two populations need not have been produced around the head of the Gulf of Mexico, but the single population must have been cold-adapted enough to maintain its range around the northern rim of the Gulf. At the same time its southern extremity must have reached deep into southern Mexico. Upon the retreat of the glacier and movement of the plant communities northward, it is evident that the vegetation also moved up the east slope of the Sierra Madre Oriental and that the tropical vegetation moved north and replaced it in the lowlands. Desert and grassland then replaced forest in response to diminution of rainfall in lowlands of Tamaulipas and Texas, thus cutting off the "subtropical" forest with its population of squirrels on the mountain. Tropical flora must then have infiltrated the "subtropical"

1 The present writer cast some further doubt that they do intergrade, in reporting at the annual meeting of the American Society of Mammalogists of June, 1959, that in the collections of the American Museum of Natural History the nine parous female specimens of *negligens* on which functional pairs of mammae could be confidently counted, all had four pair; whereas the 14 of *deppei deppei* and 3 of *deppei matagalpae* all had three pair.

forest and in many instances out-competed the "subtropical." Martin and Harrell (1957, p. 473) find 29 per cent of the trees of their cloud forest, Upper Tropical Zone, to be species that have conspecific relatives or closely related species disjunctly located in the eastern United States. While the flying squirrel and vole apparently would have had no tropical species moving up with the tropical vegetation to compete for their niches, the relict gray squirrel population had a tropical-adapted competitor in the species we recognize now as *S. aureogaster*. If the gray squirrel population occupied the pine-oak forest of the summit as well as the moist, mostly tropical, upper slope, then *aureogaster* has evidently outcompeted and replaced it in the tropical portion, and that gray squirrel population is now identifiable as *alleni*. But if the gray squirrel population being cut off in Mexico had entered only the tropical environments and adapted by further reduction in size and restriction of habits and feeding, to ways that avoided fatal competition with *aureogaster,* then it may survive there still and be identifiable as *negligens*.

DISCUSSION

The evidence regarding the closeness of these forms to *carolinensis* is assembled in Table I, together with similar data for other species. The first four kinds of data represent original observations of museum specimens, but since the field experience of the present author has not included northeastern Mexico, the last three are entirely from literature cited in text. The unit values shown in Table I are not transferable from one line of the table to another, and it would be far from valid, of course, to add these arbitrary figures and compare the totals. Table I does strongly hint, however, that if ecological niches may be considered in this relationship (which they surely should), that *alleni* is the closest relative of *carolinensis*.

From a study of the arboreal flora and vertebrate fauna of a cloud forest area within the moist Tropical Zone area of the eastern slope of the Sierra Madre Oriental in Tamaulipas north of where Dalquest worked, Martin and Harrell (1957, p. 479) conclude 1. that some of the evident relationships between this cloud forest area and the forest flora and fauna of the southern Appalachians and Southeastern Coastal Plain are a result of pre-Pliocene connection by continuous forest ("sweet gum, hard maple, beech, evergreen magnolia, etc." and lungless salamanders) but that 2. some presumably do result from "a cool savanna or open woodland corridor" having extended across the arid Texan barrier during the Pleistocene (two snakes, *Storeria occipitomaculata* and *Rhadinaea laureata;* and barred owl, *Strix varia;* a flying squirrel, *Glaucomys volans;* and a vole, *Pitymys pinetorum*).

From the fact that Dalquest (1953, p. 11) considers *Glaucomys volans* and *Pitymys quasiater* "confined, or nearly" confined, to the Upper Tropical Zone (and Martin, 1955, p. 355, corroborates this in *Glaucomys*), and the occupation of this Upper Tropical Zone by many forest trees of northern affinities, one might expect the nearest Mexican relative of *Sciurus carolinensis* to occur there also. However, if a potentially competing species was already present both in the Upper Tropical Zone (as seems to have been the case), and another in the oak and pine forest capping the sierra (but there is no evidence that this was so), it seems more likely to the present writer that the intruded population of gray squirrel stock would be better adapted to compete more successfully against the species in the oak and pine habitat. Nevertheless, the evidence of Martin and Harrell (1957) suggests otherwise, and inasmuch as the taxonomic evidence of Table I is equivocal, it is uncertain whether *negligens* or *alleni* is the closest relative of *carolinensis*.

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writer is especially grateful to Dr. George H. Lowery, Director of the Museum of Natural Science, Louisiana State University.

SUMMARY

The subgenera *Neosciurus* and *Parasciurus* are regarded as insubstantial, and the eastern gray squirrel is classified in the subgenus *Sciurus* with *Sciurus vulgaris, Sciurus niger,* and many Mexican and Central American species differentiated from it only at the species level. Its nearest relative is shown to be most probably *Sciurus oculatus alleni* and the separation of *Sciurus carolinensis carolinensis* from *oculatus alleni* seems rather satisfactorily explained either by the theory of a boreal climate bisecting the warm adapted biota of the Southeastern Coastal Plain during Pleistocene glacial intrusions, or by the hypothesis that the plants and animals of the Southeastern Coastal Plain including the gray squirrel population, were forced far south into Mexico, and that upon withdrawal of the glacier, fragments of this biota ascended the mountains and became isolated with their squirrel populations by intrusion of desert conditions at lower elevations. Both *Sciurus oculatus alleni* and *Sciurus (deppei?) negligens* could have originated from *Sciurus carolinensis* by one of these mechanisms, but it is uncertain which of the two would have originated the most recently.

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QUESTIONS

Flyger: We don't always find upper premolars present in our gray squirrel.

Moore: This does not surprise me because there is frequently some variation in taxonomic characters.

Shorten: What subspecies of gray do we have in Britain? We have some black squirrels introduced in one or two parts of Britain.

Moore: This is certainly a point in favor of the northern subspecies.

Uhlig: Dr. Mosby, what are the weights of the southern subspecies that you have handled?

Mosby: 450-500 grams.

Moore: I would hesitate to accept weights as a taxonomic character. Scheffer has found considerable decrease in weights of fur seals in recent years.

Sharp: Is there a relative of Tamiasciurus in Asia?

Moore: A Chinese rock squirrel and African ground squirrels appear to be the closest relatives.

Clark: Squirrels may have evolved rapidly because a nasal mite found in gray squirrels at Patuxent is similar to a mite found in an African squirrel (Funisciurus).

Moore: I would say, nevertheless, that these two squirrels are about as far apart as any tree squirrels can be.

Johnson: You say that *Sciurus* has many more species here and only one species in Eurasia. Do you therefore say the squirrels went over there or came over here?

Moore: I have a theory that they came over here but it would take me too long to go into this at present. I hope to publish on this soon.

CURRENT KNOWLEDGE OF TREE SQUIRREL REPRODUCTIVE CYCLES AND DEVELOPMENT[1]

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Knowledge of the reproductive behavior and physiology of a particular species is a prerequisite to its successful management. In those wild species which can adapt to life in artificial surroundings (mink, fox) considerable information has accumulated regarding length of estrus, type of estrous cycle, reproductive development, nutritional balance required for successful breeding, etc., all of which aid in the successful propagation and management. In tree squirrels, however, artificial propagation has been generally unsuccessful. Consequently, much of the information on reproductive cycles in tree squirrels has been acquired by empirical means.

A review of the literature reveals almost complete agreement that tree squirrels have two main breeding seasons per year. Each mating period is rather restricted in time although it vvaries somewhat with latitude and perhaps with age, nutrition, climatic conditions and possibly even with population density.

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