ABSTRACT.—The purpose of this paper is to examine the hypothesis that arboreality evolved more than once among extant tree squirrels. The North American fossil, Douglassia (formerly Protosciurus), from the late Eocene is considered to have been an arboreal squirrel (Emry and Thornton, 1982). Thus, arboreality may be primitive for squirrels, although the European Palaeoscinrus from the early Oligocene was probably terrestrial (Vianey-Liaud, 1974). It is unclear how these are related to the Recent tree squirrels, the Sciurini of the Americas and Northern Eurasia, the Ratufini and Callosciurini of Southern Asia, and the Protoxerini and Funambulini, mostly of Africa. Three hypotheses of relationships among Recent squirrels imply a terrestrial origin for some group of tree squirrels: Moore (1959) hypothesized that Sciurotamias and Tamiasciurus are closely related and that the North American red squirrel is derived from a terrestrial ancestor, Callahan and Davis (1982) hypothesized that Sciurotamias and Ratufa are closely related and suggested a terrestrial origin for the Asian giant tree squirrels, and Moore (1959) also suggested that the African tree squirrels, Protoxerini and Funambulini, may have evolved from xerine ground squirrels. A review of morphological evidence suggests that Sciurotamias is more closely related to chipmunks, the Tamini, than to either Tamiasciurus or Ratufa. This contradicts the first two hypotheses cited above and the suggestion that arboreality evolved independently in these two tree squirrels. We cite reasons for doubting the third hypothesis, that African tree squirrels have a terrestrial origin, but do not critically examine it in this paper.

INTRODUCTION

The squirrel family, Sciuridae, includes two radiations of ground squirrels (Marmotini, Xerini) and a larger number of radiations of tree squirrels in South America, North America, Eurasia, and Africa. Formerly, it was presumed that arboreal squirrels evolved from terrestrial squirrels. For example, Black (1963) considered the chipmunks (tribe Tamini) the basal group from which all other squirrels evolved. Similarly, Moore (1959) thought that the African tree squirrels were derived from the African ground squirrels. However, the earliest fossil squirrel, Douglassia jeffersoni (formerly Protosciurus c.f. jeffersoni), from the late Eocene, 35 Ma, was a tree squirrel (Emry and Thornton, 1982; Emry and Korth, 1996). The earliest chipmunks date from the early Miocene, ca. 25 Ma (Black, 1963; Brujin, et al., 1980). Thus, it is possible that arboreality is primitive for squirrels and that extant terrestrial squirrels have evolved from tree squirrels once among the Marmotini of North America and Eurasia, independently in the Xerini of Africa and Southern Asia, and also independently in most tribes of tree squirrels. We here examine several hypotheses that arboreality has evolved more than once in the family Sciuridae.

Moore (1959) proposed that Sciurotamias, the Chinese rock squirrel, and Tamiasciurus, the North American red squirrel, are closely related, and that the red squirrel evolved from a terrestrial rock squirrel ancestor, similar to S. davidianus. Callahan and Davis (1982) presented an alternative hypothesis about Sciurotamias, arguing that
it is closely related to Ratufa. They explicitly suggested that Ratufa evolved from a terrestrial ancestor. Thus, the unresolved phylogeny of Sciurotamias, the Chinese rock squirrel, is central to the question of whether arboreality evolved more than once among tree squirrels.

Moore (1959) also suggested that the African tree squirrels evolved from the xerine ground squirrels. This hypothesis has not received careful consideration from subsequent investigators. Moore listed four characters shared by the Xerini and the Protoxerini. One of these is the separation of the buccinator and masticatory foramina. This condition is primitive for rodents (Wahlert, 1991) and therefore does not serve as a good phylogenetic indicator. A second is the prominence of the masticatory tubercle, but this is found in only one genus in the Protoxerini. Therefore, it is likely that it evolved independently in the Protoxerini and the Xerini. This leaves two characters, long orbits and short interorbital width, purportedly supporting Moore's hypothesis. In details the orbits of the Xerines and the Protoxerines are very different, however, especially in the shapes of the lacrimal, jugal, and maxillary bones. On the basis of cranial evidence, Lavocat (1973) considered the earliest fossil squirrels in Africa to be tree squirrels derived from southwest Asia. This also weakens Moore's speculation; but we will not critically examine it in this paper.

In this contribution, we examine and test four hypothesized sister groups: Tamiasciurus-Sciurus, Tamiasciurus-Sciurotamias, Tamias-Sciurotamias, and Ratufa-Sciurotamias (Fig. 1), challenging the two proposed ground squirrel-tree squirrel hypotheses, each with an alternative hypothesis.

THE STATUS OF THE TAMIASCIURINI

Moore (1959) created a tribe, the Tamiasciurini, for Tamiasciurus and Sciurotamias because both have three transbullar septa, a rare condition among squirrels. Both Moore (1959) and Black (1963) noted that Tamiasciurus is polymorphic for two and three transbullar septa. Corbet and Hill (1992) list two transbullar septa for Sciurotamias forresti and three for Sciurotamias davidianus. Thus, both genera are polymorphic for number of transbullar septa. Callahan and Davis (1982) showed that Sciurotamias lacks the specialized reproductive tract of Tamiasciurus. These observations detract from the likelihood that Moore's hypothesis is a good one, but do not test it. The hypothesis would be falsified by finding many derived features shared by Sciurus and Tamiasciurus, but not by Sciurotamias. It is not falsified by showing that proposed synapomorphies of Tamiasciurus and Sciurotamias are invalid. Bryant (1945) described many osteological and myological similarities between Sciurus and Tamiasciurus, concluding that Tamiasciurus should not be considered a distinct genus from Sciurus. He was very careful to distinguish between primitive and derived characters, but he did not study Sciurotamias. Similarly, the immunological study by Hight et al. (1974) and the protein electrophoresis study by Hafner et al. (1994) suggested that Sciurus and Tamiasciurus are closely related, but neither study

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Fig. 1.—Sister-group hypotheses examined: A. Commonly accepted hypothesis that Sciurus and Tamiasciurus are more closely related to each other than either is to Sciurotamias, B. Moore's (1959) hypothesis that Tamiasciurus and Sciurotamias are more closely related to each other, C. Milne-Edwards' (1871) hypothesis that Sciurotamias is closely related to chipmunks, and D. Callahan and Davis (1982) hypothesis that Sciurotamias is more closely related to Ratufa.
included Sciurotamias, so they do not contradict Moore’s hypothesis. In spite of the logical weaknesses of these “tests” of Moore’s hypothesis, his concept of the Tamiasciurini (Tamiasciurus + Sciurotamias) has been almost completely abandoned (Hoffmann et al., 1993).

THE STATUS OF THE RATUFINI

Moore (1959) placed the genus Ratufa by itself in the tribe Ratufini. Callahan and Davis (1982) described the reproductive tract of Sciurotamias, compared it with that of Ratufa and suggested that the two genera are closely related and should both be included in the tribe Ratufini. We disagree. In many ways these two genera are remarkably different squirrels. To us, figure 4 of Prasad (1954:479) showing the baculum of Ratufa and the glans penis with many ridges and a ventral sulcus, looks very different from figure 3 of Callahan and Davis (1982:45) showing the glans penis of Sciurotamias with four simple annuli. Thus, we question the basis for their placement of Sciurotamias in the Ratufini. They list the cheek pouch and the hoof-like pollex as supporting evidence. However, Sciurotamias has a cheek pouch and Ratufa lacks one. Furthermore, we have observed that Ratufa’s “hoof-like pollex” is supported by a modified first phalanx and a broad, flattened terminal phalanx, but the pollex of Sciurotamias is not. Again, these criticisms do not test their hypothesis, which has generally been accepted (e.g., Corbet and Hill, 1992; Hoffmann, et al., 1993). To test it, we compare it with the earlier hypothesis that Sciurotamias is most closely related to the chipmunks (Milne-Edwards, 1867; Miller, 1901; Ellerman, 1940; Gromov, et al., 1965; Callahan, 1976).

CHARACTER LIST AND POLARITY ASSESSMENTS

We test the hypotheses of the following sister-groups: Tamiasciurus-Sciurus, Tamiasciurus-Sciurotamias, Tamias-Sciurotamias, and Ratufa-Sciurotamias, by re-examining the characters included in studies by Bryant (1945), Moore (1959), and others. We have added other characters from our studies of wrists and ankles. Our polarity assessments are based on the morphologies of Protosciurus crania, as described by Black (1963), and postcrania of Douglassia, as described by Emry and Thorington (1982), of Paleosciurus as described by Vianey-Liaud (1974), and of primitive rodents, as assessed by Wahlert (1985, 1991). We consider the closely related Douglassia and Protosciurus to be the most primitive sciurids and the best outgroup for all the other sciurids (Emry and Thorington, 1982). Our assessment of the primitive state is listed as (0). different derived states are listed as (1a) and (1b), and sequentially derived states are listed as (1) and (2). We indicate uncertainty of polarities with a question mark (?) and do not use these characters in our assessment.

Character 1. Transbullar septa

(0) Two septa: Sciurus (most), Tamiasciurus (few), Sciurotamias forresti, Tamias.

(0) Three septa: Sciurus anomalus, Tamiasciurus (most), Sciurotamias davidianus.

(1) No septa: Ratufa.

Black (1963) described Protosciurus condoni and noted that the type specimen has two and one-half transbular septa. Therefore, the primitive modal number for squirrels is equivocal and could be two or three transbular septa. Lack of septa is derived.

Character 2. External auditory meatus

(0) Flange on anterior superior edge; portion of bulla anterior and superior to the meatus not swollen: Sciurus, Tamiasciurus, Tamias, Ratufa.

(1) Lacks flange; portion of bulla anterior and superior to it swollen: Sciurotamias.

The primitive condition in rodents is an unswollen bulla (Wahlert, 1991). Black’s (1963) illustration of Protosciurus condoni shows a flange and unswollen bulla. Therefore, the condition in Sciurotamias is considered derived.

Character 3. Postglenoid region of the squamosal (Fig. 2)

(?) Pierced by both postglenoid and subsquamosal foramina: Sciurus (most), Tamiasciurus (most), Ratufa (most).

(?) Second foramen posterior to glenoid higher on skull, as if it were a supraglenoid foramen: Sciurotamias, Tamias.

The pattern of foramina behind the glenoid is quite variable individually. They are sometimes absent, sometimes fused, and sometimes multiple, particularly in Sciurus. The primitive condition in squirrels is not clear and it may also have been variable. This is in agreement with Wahlert’s (1974) assessment for primitive rodents.

Character 4. Temporal foramen at squamosal-parietal suture (Fig 2)

(0) Present: Sciurus, Tamiasciurus, Ratufa affinis (most).

(1) Absent: Sciurotamias, Tamias, Ratufa other species (most).
The presence of a foramen at the squamosal-parietal suture is primitive for rodents (Wahlert, 1974), and probably primitive for squirrels (Wahlert, 1991). It is neither mentioned nor figured by Black (1963) in Protosciurus.

**Character 5. Supraorbital notch (Fig. 2)**

(0) Absent or inconspicuous: *Ratufa* (usually).

(1) Open and usually trenchant: *Sciurus, Tamiasciurus, Sciurotamias, Tamias*.

Black (1963) comments on the absence of the supraorbital notch in *Protosciurus condoni*, but it appears to be present in his plate 3, figure 1a. Vianey-Liaud (1974) shows prominent supraorbital notches in *Palaeosciurus goti*. We have considered its presence to be derived in squirrels, but it is possible that this polarity should be reversed.

**Character 6. Sphenopalatine foramen (Fig. 2)**

(0) Large, approximately size of sphenoidal fissure: *Sciurus* (most), *Tamiasciurus, Ratufa*.

(1) Sphenopalatine foramen small: *Sciurus granatensis, Sciurotamias, Tamias*.

Black (1963) illustrates the sphenopalatine foramen in *Protosciurus condoni*, showing it to be large. We take this to be primitive for squirrels.

**Character 7. Sharp anterior edge of zygomatic arch (Fig. 2)**

(0) Does not extend onto the premaxillary bone: *Sciurus griseus* (the anterior masseter extends onto the premaxillary bone but the sharp ridge does not), *Tamiasciurus, Sciurotamias, Tamias* (most).

(1) Extends onto the premaxillary bone: *Sciurus* (most, but barely in *S. anomalus* and *S. granatensis*), *Tamias* (some), *Ratufa*.

The evolution of sciuromorphy involves the migration of the masseter onto the zygomatic plate and side of the rostrum. The more the masseter musculature extends onto the premaxillary bone, the more derived we consider it.

**Character 8. Angle of zygomatic plate (Fig. 2)**

(0) More horizontal: *Sciurotamias, Tamias*.

(1) More vertical: *Sciurus, Tamiasciurus, Ratufa*.

Black (1963) describes the evolution of the zygomatic plate from a more horizontal angle to a more vertical angle in his treatments of Miocene *Protosciurus rachetiae* and *Sciurus*. The derived condition is associated with the enlargement of the area for origin of the anterior portion of the deep lateral masseter muscle.
Character 9. Length of infraorbital canal (Fig. 2)

(0) Moderately long: Sciurus, Tamiasciurus.
(1a) Long, extending to maxillary-premaxillary suture: Rattus.
(1b) Short, barely extending onto the side of the rostrum: Sciurotamias.
(2b) Short, not extending onto the side of the rostrum: Tamias.

In Protosciurus, the infraorbital canal is moderately long, according to Black (1963). The long canal of Rattus is clearly derived. The short canal of Sciurotamias and Tamias is probably also derived. It is further derived in Tamias, because the ventral head of the maxillonasalis muscle passes through the infraorbital foramen to insert on the orbital margin (Bryant, 1945). A large infraorbital foramen and very short canal, like those seen in Tamias, are reported in Spermophilus brerai of the middle Miocene (Bruin and Mein, 1968). This is not seen in Sciurotamias. Our polarity assessment is in disagreement with Wahlert (1985).

Character 10. Ectopterygoid region

(0?) Lateral pterygoid ridge prominent, parallel to, or diverging slightly from medial pterygoid ridge posteriorly: Tamias, Rattus.
(1a) Lateral pterygoid ridge weak and not diverging: Sciurotamias.
(1b) Lateral pterygoid ridge prominent, diverging from medial ridge posterolaterally: Sciurus, Tamiasciurus.

In Tamias, the pterygoid plate is narrow. The lateral pterygoid ridge terminates posteriorly between the medial side and the middle of the foramen ovale and parallels the medial pterygoid (ectopterygoid) ridge. In Sciurus and Tamiasciurus, the pterygoid plate is broad. The lateral ridge diverges posteriorly from the medial ridge and terminates posteriorly from the foramen ovale. In Rattus, the lateral ridge terminates in the middle of the foramen ovale and the wings of the medial pterygoid extend ventrally, not toward the bullae like those of chipmunks and the other tree squirrels. The pterygoid region of Protosciurus conondi, as shown by Black (1963), is most similar to that of Rattus, although the wing of the medial pterygoid is unknown, so the other two morphologies are considered to be derived.

Character 11. Posterior edge of palate

(0) Behind M3: Sciurus, Tamiasciurus, Sciurotamias, Tamias.
(1) At the level of M3: Rattus.

In Protosciurus conondi, the posterior edge of the palate is figured as being slightly behind M3 (Black, 1963: plate 3, figure 1c) and we therefore consider this primitive.

Character 12. Dorsal profile of skull

(0) Flat: Sciurotamias, Tamias, Rattus.
(1) Rounded: Sciurus, Tamiasciurus.

The primitive condition for squirrels is the flat profile, as seen in the fossil record (Black, 1963). This feature is allometric, being related to relative brain volume. Therefore, small squirrels have more rounded cranial profiles and large squirrels flatter profiles. For their size, tree squirrels have more rounded profiles than do chipmunks, and Rattus (Fig. 2) appears to have a flat profile because of its large size.

Character 13. Squamosal suture (Fig. 2)

(0) High: Tamiasciurus, Sciurotamias, Tamias, Rattus.
(1) Low, extending less than halfway from the root of the zygoma to the notch of the postorbital process: Sciurus.

The squamosal almost reaches the postorbital notch in Protosciurus conondi according to Black (1963), therefore we consider this to be primitive.

Character 14. Cheek pouches

(0) Absent: Sciurus, Tamiasciurus, Rattus.
(1) Present: Sciurotamias, Tamias.

There are fossae anterolateral to the incisive foramina in squirrels with cheek pouches (Fig. 2), for the origin of the dorsal pouch muscle. Therefore, it is possible to document the evolution of cheek pouches in North American fossils. The fossae are absent in Protosciurus rachaelae of the early Miocene; they are weakly present in Protospermophilus angusticeps of the late middle Miocene; and they are deep in Protospermophilus maiheuensis also of the late Middle Miocene (Black, 1963). They are also present in Spermophilus brerai of the middle Miocene (Bruin and Mein, 1968). Accordingly, we treat cheek pouches as being derived, and assume they date from the Early Miocene, when Tamias appears in the fossil record, or slightly earlier. The fossae are also present in Spermophilopsis and Xerus princeps. This needs further study.

Character 15. Coracoid process of scapula (Fig. 3)

(0) Long: Sciurus, Tamiasciurus, Rattus.
(1) Short: Sciurotamias, Tamias.
Character 16. Axillary ridge relative to the surface of scapula
(0?) Perpendicular and high: Sciurus, Tamiasciurus.
(1a?) Perpendicular and low: Ratufa.
(1b?) Perpendicularity intermediate and high: Sciurotamias.
(2?) Least perpendicular but high Tamias.
Sciurid scapulae are very rare in the fossil record and we know of none that show the axillary ridge.

Character 17. Flange near caudal angle of scapula for teres major muscle (Fig. 3)
(0?) Prominent: Sciurus, Tamiasciurus, Ratufa.
(1?) Small: Sciurotamias.
(2?) Almost absent: Tamias.

Character 18. Subscapular spine (Fig. 3)
(0?) Single: Sciurus, Tamiasciurus, Sciurotamias, Tamias.
(1?) Sometimes double: Ratufa.
The broken scapula of Douglassia jeffersoni shows a single subscapular spine.

Character 19. Metacromion process of scapula
(0?) Less broad and at angle to plane of scapula: Sciurus, Tamiasciurus, Sciurotamias.
(1a?) Narrow and abruptly parallel to plane of scapula: Ratufa.

(1b?) Broad and most parallel to plane of scapula: Tamias.
The metacromion process is unknown for fossil sciurids.

Character 20. Acromion process of scapula
(0?) Broad: Sciurus, Tamiasciurus, Ratufa.
(1?) Narrow: Sciurotamias, Tamias.

Character 21. Deltoid and pectoral ridges of humerus
(0) Deltoid ridge weak proximally: Sciurus, Ratufa.
(1) Deltoid ridge prominent proximally, diverging from pectoral ridge: Tamiasciurus, Sciurotamias, Tamias.
In Douglassia the deltoid and pectoral ridges are damaged, but appear similar to those of Sciurus.

Character 22. Orientation of delto-pectoral crest of humerus
(0) Directed medially with prominent bicipital groove: Sciurus, Tamiasciurus, Ratufa.
(1) Directed laterally with less distinct bicipital groove: Sciurotamias, Tamias.
This region was broken on Douglassia but appeared to be similar to Sciurus.

Character 23. Entepicondylar foramen of humerus
(0) Usually present: Sciurus, Tamiasciurus, Ratufa.
(1) Usually absent: Tamias striatus.
The entepicondylar foramen is commonly present in rodents, including most Recent squirrels, Douglassia, and Paleosciurus.

Character 24. Medial epicondyle of humerus
(0) Elongate medially: Sciurus, Tamiasciurus, Sciurotamias, Ratufa.
(1) Not elongate: Tamias.
The medial epicondyle was elongate in Douglassia and in Paleosciurus.

Character 25. Extent of the radial notch on ulna
(0) Approximately one-third the width of the semilunar notch: Sciurus, Tamiasciurus, Ratufa.
(1) Approximately one-half of the width of the semilunar notch: Sciurotamias.
(2) More than one-half of width of the semilunar notch: Tamias.
This feature in Douglassia is very similar to that in Sciurus.
Character 26. Prominent ridge for pronator quadratus muscle on ulna
(0) Present: Tamias, Sciurotamias.
(1) Absent: Sciurus, Tamiasciurus, Ratufa.
The ridge is prominent in Douglassia.

Character 27. Groove on pisiform bone
(0) Pisiform ungrooved: Sciurus, Tamiasciurus, Ratufa.
(1) Radial side of pisiform grooved near palmar end: Sciurotamias, Tamias.
The pisiform of Douglassia is ungrooved, so this is presumed to be the primitive condition. The derived condition is not unique to Sciurotamias and Tamias, it is also found in Callosciurus to which they are not closely related (based on other evidence).

Character 28. Shape of triquetrum
(0) Triquetrum elongate and gracile: Sciurus, Tamiasciurus, Tamias, Ratufa.
(1) Triquetrum short and robust: Sciurotamias.
The shape of the triquetrum in Sciurotamias appears to be unique among squirrels and we think that it is derived.

Character 29. Ventral articulation of metacarpal III and metacarpal IV
(0) Present: Sciurus carolinensis, S. griseus, S. granatensis, Sciurotamias davidianus, Tamias, Ratufa.
(1) Absent: Sciurus niger, Tamiasciurus hudsonicus.
Loss of this articulation is rare and is presumed to be derived. The presence of the derived condition in Tamiasciurus and only part of Sciurus can be interpreted in two ways. First, it may be independently derived in the two genera. Second, it may indicate that some species of Sciurus are more closely related to Tamiasciurus than they are to other species of Sciurus.

Character 30. Centrale-greater Multangular articulation
(0) Absent: Sciurus, Tamiasciurus, Sciurotamias.
(1) Present: Tamias, Ratufa.
Primitively in squirrels the centrale articulates distally with capitate, metacarpal II, and lesser multangular. In several lineages it extends radially, toward the pollex, and also articulates with greater multangular.

Character 31. Articulation of metacarpal III and hamate.
(0) Corner of hamate beveled: Sciurotamias, Tamias, Ratufa.
(1) Corner of hamate square: Sciurus, Tamiasciurus.
The hamate is slightly beveled in Douglassia. The loss of this feature appears to be correlated with the narrowing of the hand and particularly metacarpal III.

Character 32. Lateral iliac ridge
(0) Broad, distinct ridge: Sciurus, Tamiasciurus.
(1a) Broad, indistinct ridge: Tamias.
(1b) Narrow, distinct ridge: Sciurotamias, Ratufa.
The iliac ridge of Douglassia is more pronounced than in most Recent squirrels, but is approximated by some Sciurus.

Character 33. Dorso-ventral depth of pelvic basin
(0?) Deep: Sciurus, Tamiasciurus, Ratufa.
(1?) Shallow: Sciurotamias, Tamias.
It is not possible to determine this in Douglassia.

Character 34. Pubic symphysis
(0?) Normal: Sciurus, Tamiasciurus, Sciurotamias, Ratufa.
(1?) Short: Tamias.
The pubic symphysis of chipmunks is shorter than the ascending ramus of the pubis, and the anterior end does not extend cranially to the posterior edge of the acetabulum. This seems to be unique to Tamias and is probably derived.

Character 35. Lesser trochanter of femur
(Fig. 4)
(0) Directed medially: Sciurus, Tamiasciurus, Ratufa.
(1) Directed postero-medially: Sciurotamias, Tamias.

Fig. 4.—(A) Posterior views of proximal ends of femora, and (B) medial views of distal ends of tibiae of Sciurotamias davidianus, USNM 258508, (left) and Tamiasciurus hudsonicus, USNM 564083, (right). Arrows indicate lesser trochanter of femur and the anterior process of the medial malleolus of the tibia.
The lesser trochanter of *Douglassia* is directed medially. This appears to be the case in *Palaeosciurus goti* as well (Vianey-Liaud, 1974).

**Character 36. Popliteal fossa of tibia**

(0) Deep with medial and lateral ridges: *Tamiasciurus*, *Sciurotamias*, *Tamias*.

(1) Shallow and unridged, sometimes with medial ridge: *Sciuris*, *Ratufa*.

In *Douglassia*, the popliteal fossa is prominent.

**Character 37. Relative lengths of the anterior and posterior processes of the medial malleolus of tibia (Fig. 4)**

(0) Anterior process slightly shorter than the posterior process: *Tamias*, *Sciurotamias*.

(1) Anterior process distinctly shorter than the posterior process: *Sciuris*, *Tamiasciurus*, *Ratufa*.

The anterior and posterior processes are approximately the same length in *Douglassia* and *Palaeosciurus goti*.

**Character 38. Tarsal foot pads**

(0?) Two: *Sciurotamias forresti*, *Ratufa*, *Sciurus niger* (rare), *S. vulgaris* (rare).

(1?) One (hallucal): *Sciuris* (most), *Tamiasciurus hudsonicus* (rare).

(2?) None: *Tamiasciurus douglassi*, *T. hudsonicus* (most), *Sciurotamias davidianus*, *Tamias*.

We hypothesize that the presence of two tarsal pads is primitive and that loss of one or both is derived. However, in view of the great variation in this character, we are not very confident of this polarity.

**Character 39. Two calcaneal facets on astragalus**

(0) Separated by a shallow groove: *Ratufa*.

(1) Confluent. *Sciuris*, *Tamiasciurus*, *Sciurotamias*, *Tamias*.

In *Douglassia* the two facets are separated by a groove.

**Character 40. Reproductive tract**

(0) Large bulbo-urethral glands and presence of penile duct: *Sciuris*, *Sciurotamias*, *Tamias*, *Ratufa*.

(1) Absence of separate bulbo-urethral glands and absence of penile duct. *Tamiasciurus*.

Large, distinctive bulbo-urethral glands occur in the flying squirrels and five tribes of the Sciurinae, as listed below, suggesting that they are primitive for the family Sciuridae.

Pteromyinae (= Petauristinae): *Glaucomys*, *Mossman*, et al., 1932;


Large bulbo-urethral glands and a penile duct are absent in both *Tamiasciurus* (*Mossman*, et al., 1932) and *Funambulus palmarum* (Prasad, 1954).

**Character 41. Shape of baculum**

(0?) Baculum nearly symmetric and simple — almost rod shaped, with distal end bent dorsally: *Tamias*, *Sciurotamias*, and *Ratufa*.

(1a?) Baculum asymmetric and flattened at tip. *Sciurus*.

(1b?) Baculum absent or minuscule. *Tamiasciurus*.

There is no clear evidence on which to base a polarity assessment for the baculum of squirrels. A simple, symmetric baculum would be a good model from which to derive the complex symmetrical bacula of ground squirrels and the complex asymmetric bacula of some other squirrels. Another alternative is that the bacular morphology of *Sciuris* is close to primitive, because it is found in such a diverse group of squirrels as *Sciurillus*, *Rheithrosciurus*, and *Petaurista*.

A feature not included in our list above is the external morphology of the glans penis, cited by Callahan and Davis (1982) as their justification for placing *Sciurotamias* in the *Ratufini*. We think that the penile morphologies of *Ratufa* and *Sciurotamias* are both derived but not homologous with one another. The morphology of the glans penis of *Ratufa* is illustrated by Hill (1936, 1940) and Prasad (1954) but interpretation of these drawings is not straightforward. The difference between the illustrations of Hill (1936, 1940) and Prasad (1954) appears to be in their definitions of dorsal and ventral. In comparing the three papers, Prasad (1954) should be viewed upside down. It also seems that the baculum illustrated in Hill (1936) is upside down relative to his illustrations of the penis. In either orientation it is difficult to visualize how the baculum could fit inside the illustrated penis.

All three publications clearly illustrate 12-23 ridges or folds, with a ventral sulcus on the glans penis of *Ratufa*. According to Callahan and Davis (1982), the ornamentation of the penis of *Sciurotamias* consists of four annuli, three going completely around the penis. No ventral sulcus is shown or described. To us this seems very different
from the morphology of Ratufa, and we do not consider the two to be homologous.

CHARACTERS SUPPORTING SISTER-GROUP HYPOTHESES

We examined two competing hypotheses (Figs. 5A and 5B) for the phylogenetic placement of Tamiasciurus, Moore's hypothesis that Tamiasciurus and Sciurotamias form a sister group, and the alternative hypothesis that Tamiasciurus forms a sister group with Sciurus. The more strongly supported hypothesis is that it forms a sister group with Sciurus. Two characters, 5 and 39, are shared by both pairs and hence are shown at the base of the tree. The remaining six characters include three in the cranium, two in the forelimb, and one in the hindlimb.

Derived characters shared by Tamiasciurus and Sciurus:
Character 5: Supraorbital notch present.
Character 8: Vertical angle of zygomatic plate.
Character 10: Posteriorly diverging lateral pterygoid ridges.
Character 12: Rounded skull profile.
Character 26: Reduced ridge on ulna for pronator quadratus muscle.
Character 31: Absence of beveled corner of hamate.
Character 37: Anterior process distinctly shorter than the posterior process of medial malleolus of tibia.
Character 39: Confluent astragalus facets.

Sciurotamias        Tamiasciurus    Sciurus
---                   ---             ---
4, 5, 6, 9, 14, 15, 21, 22, 23, 27, 33, 39

Fig. 5.—Sister-group hypotheses examined. A-D. as in Fig. 1, but with shared derived characters plotted on them. Numbers correspond to character list in text. Uniquely derived characters not plotted.

Derived characters shared by Tamiasciurus and Sciurotamias:
Character 5: Supraorbital notch present.
Character 21: Deltoid and pectoral ridges diverge proximally.
Character 39: Confluent astragalus facets.

The hypothesis proposed by Callahan and Davis (1982), that Sciurotamias forms a sister group with Ratufa (Fig. 5D), is supported by only one character. The original hypothesis of Milne-Edwards (1871), that the Chinese rock squirrel is more closely related to chipmunks (Fig. 5C), is supported by twelve derived characters not shared with Ratufa. Nine of these characters are not shared with either Ratufa or Tamiasciurus -- four of the cranium, four of the forelimb, and one of the femur.

Derived characters shared by Sciurotamias and Tamias:
Character 4: Temporal foramen absent.
Character 5: Supraorbital notch present.
Character 6: Small sphenopalatine foramen.
Character 9: Short infraorbital canal.
Character 14: Cheek pouch present.
Character 15: Short coracoid process of scapula.
Character 21: Deltoid and pectoral ridges of humerus diverge proximally.
Character 22: Deltopectoral crest directed laterally.
Character 25: Radial notch on ulna large.
Character 27: Pisiform grooved.
Character 35: Lesser trochanter of femur directed postero-medially.
Character 39: Confluent astragalus facets.

Derived character shared by Sciurotamias and Ratufa:
Character 32: Narrow, distinct lateral iliac ridge.

The characters we consider to be strongest are those associated with the zygomatic plate, the infraorbital canal, and the cheek pouch. These appear to have evolved early in the evolutionary history of squirrels (Black, 1963) and, based on our personal observations, show little interspecific and intergeneric variation. A smaller number of derived characters supports the tree squirrel hypothesis than the chipmunk-rock squirrel hypothesis. This probably results from tree squirrels retaining more features of the primitive squirrel morphology.
Tamias lacks several derived features of other members of the Marmotini, as described by Bryant (1945): a second subscapular spine, the triangular cross-section of the ilium, and the flaring of the ilium, for example. In these characters Sciurotamias is like Tamias, appearing to be primitive within the tribe.

DISCUSSION

The taxonomic position of Sciurotamias, its behavior, and its use of habitat, are central to the question of whether arboreality evolved more than once among tree squirrels. Moore (1959) placed it with Tamiasciurus on the basis of the presence of three transbullar septa. Callahan and Davis (1982) placed it with Ratufa on the basis of their perception of the similarity of bacular and penile morphologies. We contend that the similarities in transbullar septa and bacula are primitive and that the features of the penis are not homologous. Our observations lead us to conclude that Sciurotamias belongs within the tribe Marmotini. While we contend that the characters shared by Sciurotamias and Tamias are derived features of the Marmotini, we do not consider them to be derived features linking Sciurotamias with Tamias within the Marmotini. Thus, we provisionally place Sciurotamias within its own subtribe, the Sciurotamini. Although one species of Sciurotamias, S. davidianus, is called a "rock squirrel" and is considered to be terrestrial, the other species, S. forresti is described as an arboreal tree squirrel. Unfortunately, little is known about its anatomy or ecology. Similarly, some species of Tamias are quite arboreal, and others forage readily in trees. We suspect that this says more about the versatility of small squirrels and their retention of climbing abilities than it does about any independent evolution of arboreality. However, if cheek pouches evolved as an adaptation for terrestrial foraging, then arboreal squirrels with cheek pouches are potentially very interesting. Accordingly, the biology of Sciurotamias forresti of southern China deserves study.

We agree with Black (1963) that the Tamiasciurini is not a valid tribe. We concur with his return of Tamiasciurus to the Sciurini, but not with his placement of Sciurotamias in the Callosciurini. Qiu (1991) also places the Sciurotamias lineage in the Callosciurini, although he argues convincingly that Sinotamias, a fossil from the upper Miocene of Inner Mongolia, is ancestral to Sciurotamias and is closely related to Spermophilus, of the Marmotini. We think his evidence better supports our conclusion. Our placement of Sciurotamias close to Tamias agrees with the earlier assessments of Milne-Edwards (1871), Miller (1901), Ellerman (1940), Gromov et al. (1965), and the initial conclusions of Callahan (1976).

Emry and Thorington (1982) presented evidence that Douglassia jeffersoni (of the late Eocene) was an arboreal squirrel. Black (1963) argued that Protosciurus rachelae of the early Miocene was a good morphological ancestor of the primitive Sciurus of the middle Miocene. Therefore, it is reasonable to contend that the tribe Sciurini has arboreal roots that extend back into the Eocene. The other tribes of tree squirrels probably share ancestry with the Sciurini in the Oligocene. Thus, it is probable that their common ancestor was arboreal, and that arboreality evolved only once in the extant Sciuridae.

ACKNOWLEDGMENTS

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LITERATURE CITED


CALLAHAN, J. R., AND R. DAVIS. 1982. Reproductive tract and evolutionary relationships of...


**SPECIMENS EXAMINED (all USNM):**

*Ratufa affinis*—post-crania: 151757, 198121.

*Ratufa affinis* pyrsonota—skulls: 251673, 257716, 257720.

*Ratufa affinis* sandakanensis—skulls: 292564, 292565.
Ratufa bicolor—post-crania: 464512.
Ratufa bicolor fretensis—post-crania: 49703.
Ratufa bicolor palliata—post-crania: 546334.
Ratufa bicolor smithi—skulls: 320803-320807.
Sciurotamias davidianus davidianus—skulls: 155110, 155219, 155125-155127, 548431; post-crania: 258505, 258510, 285511, 258516.
Sciurotamias davidianus consobrinus—skulls: 258511-258513, 544436; post-crania: 258506, 258509.
Sciurotamias forresti—skulls: 255138 (occipital region broken).
Sciurus aberti aberti—skulls: 158892, 159332, 167027.
Sciurus anomalus—skulls: 37412, 152748, 152749.
Sciurus carolinensis carolinensis—skulls: 234368-234370; post-crania: 256047, 397180.
Sciurus carolinensis pennsylvanicus—skulls: 234368-234370; post-crania: 256047, 397180.
Sciurus granatensis—skulls: 318405, 318408, 318409; post-crania: 387805, 540703.
Sciurus griseus griseus—skulls: 43041, 242332, 274351.
Sciurus niger—skulls: 167740, 177744, 177801; skin: 248132 (only one tarsal pad); post-crania: 347957, 397159.
Sciurus vulgaris—skulls: 105106, 105107, 121351; skin: 121351 (juv., has two tarsal pads).
Tamias dorsalis dorsalis—skulls: 23695, 23696, 24882, 32090, 32093.
Tamias dorsalis merriami—skulls: 22723, 22808, 41773, 41776, 41783.
Tamias striatus fisheri—skulls: 62602, 86680, 86686, 86834, 260250; penises/bacula: 2 uncatalogued specimens from Mountain Lake, VA; post-crania: 364947, 396281, 505612, 505613.
Tamias striatus griseus—skulls: 17313, 226948, 227426, 229004, 232129; post-crania: 349628.
Tamias striatus lysteri—skulls: 30225, 30230, 30239, 43415, 96939; post-crania: 500999, 564115.
Tamias townsendi ochrogenys—skulls: 96110, 96112, 97146, 97337, 97339.
Tamias townsendi townsendi—skulls: 24423, 24424, 57124, 69373, 69375.
Tamiasciurus douglasii albopilatus—skulls: 548848, 548849.
Tamiasciurus douglasii douglasii—skulls: 166892, 166893, 231804, 231805.
Tamiasciurus douglasii mearnsi—skulls: 25169, 25171.
Tamiasciurus douglasii mollipilosus—skulls: 23992, 24028.
Tamiasciurus hudsonicus albieticola—skulls: 55796, 50853, 268992, 294450.
Tamiasciurus hudsonicus baileyi—skulls: 66447, 168950, 168951.
Tamiasciurus hudsonicus columbiaensis—skulls: 202835, 202836.
Tamiasciurus hudsonicus dakotensis—skulls: 213689, 213690.
Tamiasciurus hudsonicus dixiensis—skulls: 158041, 158042.
Tamiasciurus hudsonicus fremonti—skulls: 48209, 48210; post-crania: 564078.
Tamiasciurus hudsonicus loquax—post-crania: 397070, 397151, 397152, 505579, 505587, 506645, 551803, 564084.
Tamiasciurus hudsonicus hudsonicus—post-crania: 564083.
Within the Sciuridae there are three broad categories of locomotor types: tree squirrels, which tend to live in forests and nest in trees or fallen logs; ground squirrels, which inhabit more open habitats and nest in burrows; and the inaccurately named "flying" squirrels, which unlike the other two forms typically are nocturnal and capable of gliding between trees using a patagium stretching from wrist to ankle as an airfoil. Variation exists within and to some extent blurs differences between these categories: Flying squirrels are otherwise arboreal. Among arboreal squirrels, foraging may be Squirrels belong to the family Sciuridae, which is made up of small- to medium-sized rodents. Other members of the family include chipmunks, marmots and prairie dogs. Squirrels range in length from 5 inches up to 3 feet. They are native to Canada, North America, South America, Asia, Africa and Europe, and have been introduced into Australia. Since they are tree squirrels, they spend a majority of their time in trees where they eat, sleep and rest. They often live in areas with other tree squirrel species like the fox squirrel. One way to tell the eastern gray squirrel apart from other species of tree squirrel is by the gray fur on the top of its body and its white underside. They weigh up to 1.5 pounds, measure between 18 and 20 inches in length, and have a broad and bushy tail. Tree squirrels are distributed throughout Eurasia and America, and grouped in the tribe Sciurini (Black, 1963; Wilson & Reeder, 2005). Sciurini comprehends the genera Sciurus, Syn-theosiurus, Microsciurus, Tamiasciurus and Rheinthrosciurus. Among these, the genus Sci-urus, with seven subgenera and 28 species (Wilson & Reader, 2005), is the most diverse and widespread, with representatives in Eur-asia (S. vulgaris), the Japan Islands (S. lis), the Middle East (S. anomalus) and the Americas. Nuclear DNA phylogeny of the squirrels (Mammalia: Rodentia) and the Evolution of arboreality from c-myc and rag1. Molecular Phylogenetics and Evo-lution, 30, 703-719. Villalobos, F. (2013).