

ARBOREALITY IN TREE SQUIRRELS (SCIURIDAE)

RICHARD W. THORINGTON, JR., AMY M. L. MILLER, AND
CHARLES G. ANDERSON

*Department of Vertebrate Zoology, Smithsonian Institution,
Washington, D.C. 20560 (RWT)*

*Department of Ecology, Evolution, and Marine Biology, University of California,
Santa Barbara, CA 93106 (AMLM)*

*Department of Zoology, University of Tennessee,
Knoxville, TN 37916 (CGA)*

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, *Dougllassia* (formerly *Protosciurus*), from the late Eocene is considered to have been an arboreal squirrel (Emry and Thorington, 1982). Thus, arboreality may be primitive for squirrels, although the European *Palaeosciurus* 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 Tamiina, 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 Tamiini) 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, *Dougllassia jeffersoni* (formerly *Protosciurus* c.f. *jeffersoni*), from the late Eocene, 35 Ma, was a tree squirrel (Emry and Thorington, 1982; Emry and Korth, 1996). The earliest chipmunks date from the early Miocene, ca. 25 Ma

(Black, 1963; Bruijn, 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 masseteric 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

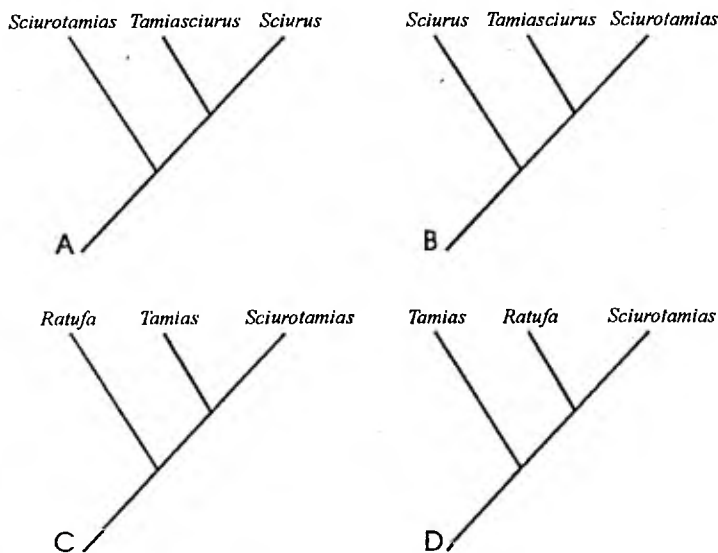


Fig. 1.—Sister-group hypotheses examined: A. Commonly accepted hypothesis that *Sciurus* and *Tamiasciurus* are more closely related to each other than either is to *Sciurotamias*, B. Moore's (1959) hypothesis that *Tamiasciurus* and *Sciurotamias* are more closely related to each other, C. Milne-Edwards' (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 transbullar septa. Therefore, the primitive modal number for squirrels is equivocal and could be two or three transbullar 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).

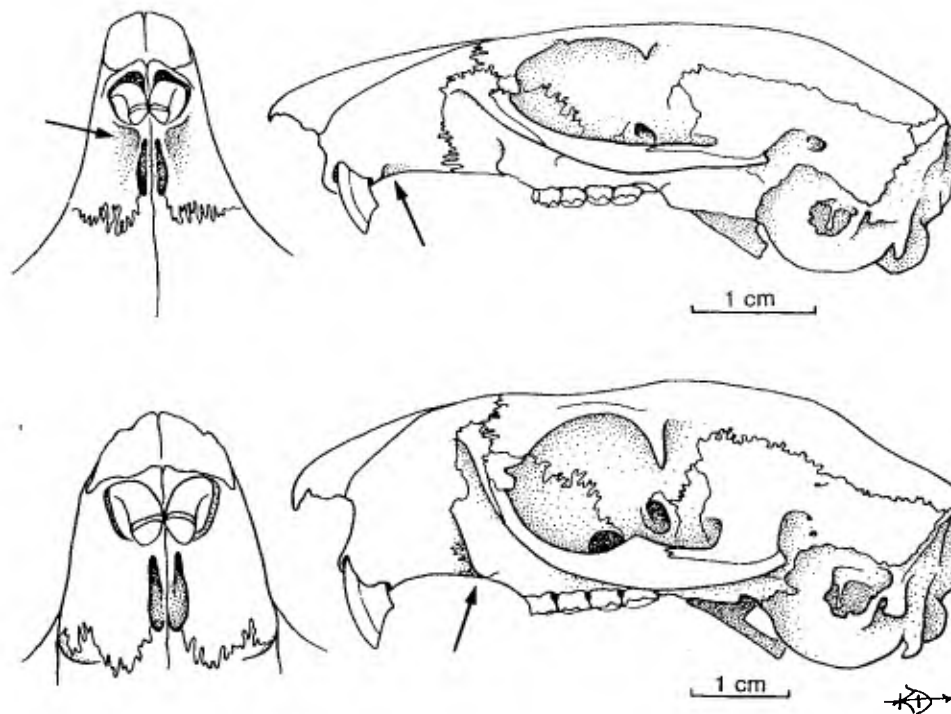


Fig. 2.—Ventral views of rostrum and lateral views of skulls of *Sciurotamias davidianus*, USNM 155219, (above) and *Ratufa bicolor*, USNM 481228, (below). Arrows indicate fossae behind the incisors of *Sciurotamias* and the position of the infraorbital foramen of *Ratufa*. Note also the large sphenopalatine foramen in the orbit and the presence of the temporal foramen in *Ratufa*.

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 supra-orbital 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 rachelae* 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: *Ratufa*.
 (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 *Ratufa* 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 *Spermophilinus bredai* 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*, *Ratufa*.
 (1a) Lateral pterygoid ridge weak and not diverging: *Sciurotamias*.
 (1b) Lateral pterygoid ridge prominent, diverging from medial ridge postero-laterally: *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 on the lateral side of the foramen ovale. In *Ratufa*, 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 condoni*, as shown by Black (1963), is most similar to that of *Ratufa*, 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: *Ratufa*.

In *Protosciurus condoni*, 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*, *Ratufa*.
 (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 *Ratufa* (Fig. 2) appears to have a flat profile because of its large size.

Character 13. Squamosal suture (Fig. 2)

- (0) High: *Tamiasciurus*, *Sciurotamias*, *Tamias*, *Ratufa*.
 (1) Low, extending less than half way from the root of the zygoma to the notch of the postorbital process: *Sciurus*.

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

Character 14. Cheek pouches

- (0) Absent: *Sciurus*, *Tamiasciurus*, *Ratufa*.
 (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 rachelae* of the early Miocene; they are weakly present in *Protospermophilus angusticeps* of the late middle Miocene; and they are deep in *Protospermophilus malheurensis* also of the late Middle Miocene (Black, 1963). They are also present in *Spermophilinus bredai* 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*, *Ratufa*.
 (1) Short: *Sciurotamias*, *Tamias*.

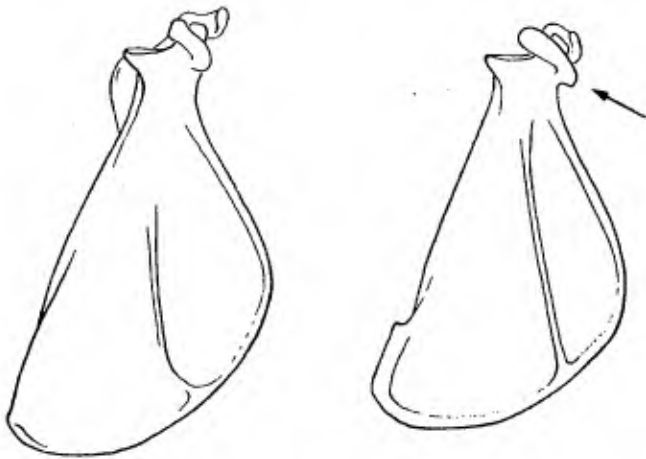


Fig. 3.—Medial views of scapulae of *Sciurotamias davidianus*, USNM 258508, (left) and *Tamiasciurus hudsonicus*, USNM 505581, (right). Note length of coracoid process (arrow) and prominence of fossa for teres major muscle.

The coracoid of *Douglassia* was broken, but it was clearly similar to *Sciurus* and larger than in ground squirrels.

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*, *Sciurotamias*

(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 capitata, 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*.

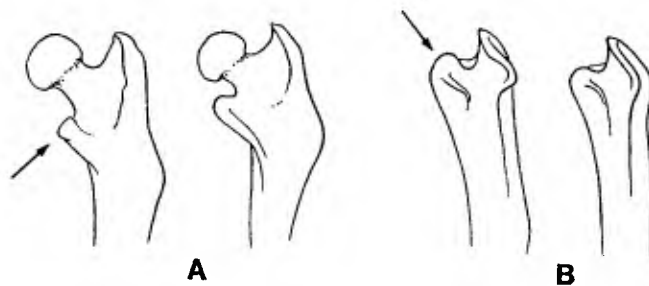


Fig. 4.— (A) Posterior views of proximal ends of femora, and (B) medial views of distal ends of tibiae of *Sciurotamias davidianus*, USNM 258508, (left) and *Tamiasciurus hudsonicus*, USNM 564083, (right). Arrows indicate lesser trochanter of femur and the anterior process of the medial malleolus of 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: *Sciurus*, *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: *Sciurus*, *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): *Sciurus* (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. *Sciurus*, *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: *Sciurus*, *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;

Protoxerini: *Heliosciurus* illustrated but misidentified by Kingdon, 1974; 372; Funambulini: *Funisciurus* illustrated but misidentified by Kingdon, 1974; 373; *Funambulus* (in part), Siddiqi, 1938; Ratufini: *Ratufa*, Prasad, 1954; Sciurini: *Sciurus*, Mossman, et al., 1932; Marmotini: *Tamias*, *Spermophilus*, 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 *Sciurus* 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, but 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.

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: Delto-pectoral 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.

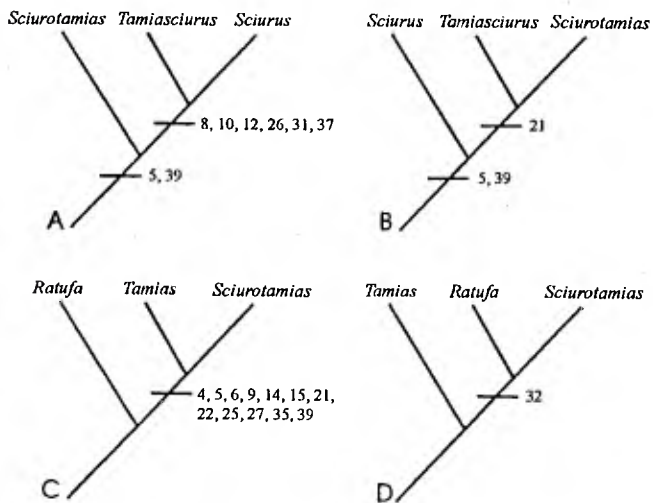


Fig. 5.— Sister-group hypotheses examined. A.-D. as in Fig. 1, but with shared derived characters plotted on them. Numbers correspond to character list in text. Uniquely derived characters not plotted.

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 *Sciurotamiina*. 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 place-

ment 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

We thank V. Louise Roth, Robert S. Hoffmann, and two anonymous reviewers for their helpful recommendations. Special thanks are due to Karolyn Darrow, who assisted with the extensive final revision of the manuscript and prepared all the figures.

LITERATURE CITED

- BLACK, C. G. 1963. A review of the North American Tertiary *Sciuridae*. *Bulletin of the Museum of Comparative Zoology, Harvard University*, 130:100-248.
- BRUIJN, H. DE AND P. MEIN 1968. On the mammalian fauna of the Hipparion beds in the Calatayud-Teruel basin (Prov. Zaragoza, Spain). Part V. The *Sciuridae*. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, series B*, 71:74-90.
- BRUIJN, H. DE., A. J. VAN DER MEULEN, AND G. KATSIKATSOS. 1980. The Mammals from the Lower Miocene of Aliveri (Island of Evia, Greece). *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, series B*, 83:241-261.
- BRYANT, M. D. 1945. Phylogeny of Nearctic *Sciuridae*. *The American Midland Naturalist*, 33:257-390.
- CALLAHAN, J. R. 1976. Systematics and biogeography of the *Eutamias obscurus* complex (Rodentia: *Sciuridae*). Ph.D. dissertation., University of Arizona, Tucson, 184 pp. (as cited in Callahan and Davis, 1982).
- CALLAHAN, J. R., AND R. DAVIS. 1982. Reproductive tract and evolutionary relationships of

- the Chinese rock squirrel, *Sciurotamias davidianus*. *Journal of Mammalogy*, 63:42-47.
- CORBET, G. B. AND J. E. HILL. 1992. *Mammals of the Indomalayan Region*. Oxford University Press, New York, 488 pp.
- ELLERMAN, J. R. 1940. The families and genera of living rodents. Volume I. Rodents other than Muridae. Trustees of the British Museum (Natural History), London, 689 pp.
- EMRY, R. J., AND W. W. KORTH. 1996. The Chadronian Squirrel "*Sciurus*" *jeffersoni* Douglass, 1901: A new generic name, new material, and its bearing on the early evolution of Sciuridae (Rodentia). *Journal of Vertebrate Paleontology*, 16:775-780.
- EMRY, R. J., AND R. W. THORINGTON, JR. 1982. Descriptive and comparative osteology of the oldest fossil squirrel, *Protosciurus* (Rodentia: Sciuridae). *Smithsonian Contributions to Paleobiology*, 47:1-35.
- GROMOV, I. M., D. I. BIBIKOV, N. I. KALABUKOV, AND M. N. MEIER. 1965. Nazemnye belich'i (Marmotinae). *Fauna SSSR*, 3:1-467. (In Russian).
- HAFNER, M. S., L. J. BARKLEY, AND J. M. CHUPASKO. 1994. Evolutionary genetics of New World tree squirrels (tribe Sciurini). *Journal of Mammalogy*, 75:102-109.
- HILL, W. C. 1936. The penis and its bone in Ceylonese Squirrels; with special reference to its taxonomic importance. *Ceylon Journal of Science (B)*, 20:99-113.
- . 1940. On the penis of *Ratufa macroura melanochra*. *Ceylon Journal of Science (B)*, 22:131-134.
- HIGHT, M. E., M. GOODMAN, AND W. PRYCHODKO. 1974. Immunological studies of the Sciuridae. *Systematic Zoology*, 23:12-25.
- HOFFMANN, R. S., C. G. ANDERSON, R. W. THORINGTON, JR., AND L. R. HEANEY. 1993. Family Sciuridae. Pp. 419-465, in *Mammal Species of the World: a taxonomic and geographic reference*, (D.E. Wilson and D.M. Reeder, eds.), Smithsonian Institution Press, Washington, D.C., 1206 pp.
- KINGDON, J. 1974. *East African Mammals: an atlas of evolution in Africa*. Vol. II. Part B (Hares and Rodents). Academic Press, London.
- LAVOCAT, R. 1973. Les rongeurs du Miocene d'Afrique orientale. *Memoires et Travaux de l'Institut Montpellier*, 1:1-284.
- MILLER, G. S., Jr. 1901. The subgenus *Rhinosciurus* of Trouessart. *Proceedings of the Biological Society of Washington*, 14:22.
- MILNE-EDWARDS, A. 1867. Description de quelques especes nouvelles d'ecureuils de l'ancien continent. *Revue et Magasin de Zoologie*, 2:193-232.
- . 1871. Etudes pour servir a l'histoire de la faune mammalogique de la Chine. Pp. 67-229, in *Recherches pour servir a l'histoire naturelle des mammifères: comprenant des considerations sur la classification de ces animaux*, (H. Milne-Edwards and A. Milne-Edwards, 1868-1874). Paris: G. Masson, 394pp.
- MOORE, J. C. 1959. Relationships among the living squirrels of the Sciurinae. *Bulletin of the American Museum of Natural History*, 118:153-206.
- MOSSMAN, H. W., J. W. LAWHAN, AND J. A. BRADLEY. 1932. The male reproductive tract of the Sciuridae. *American Journal of Anatomy*, 51:89-155.
- PRASAD, M. R. N. 1954. The male genital tract of two genera of Indian squirrels. *Journal of Mammalogy*, 35:471-485.
- QIU, Z. 1991. The Neogene mammalian faunas of Ertente and Harr Obo in Inner Mongolia (Nei Mongol), China.-8. Sciuridae (Rodentia). *Senckenbergiana lethaea* 71:223-255.
- SIDDIQI, M. A. H. 1938. The genito-urinary system of the Indian ground squirrel (*Funambulus palmarum*). *Proceedings of the National Academy of Science of India*, 1:1-10.
- VIANEY-LIAUD, M. 1974. *Palaeosciurus goti* nov. sp., ecureuil terrestre de l'Oligocene moyen du Quercy. *Donnees nouvelles sur l'apparition des Sciurides en Europe*. *Annales Paleontologique (Vertebrata)*, Paris, 60:103-122.
- WAHLERT, J. H. 1985. Cranial foramina of rodents. Pp. 311-332, in *Evolutionary relationships among rodents: A multidisciplinary analysis* (W. P. Luckett and J-L. Hartenberger, eds.). Plenum Press, New York, 721 pp.
- . 1991. The Harrymyinae, a new Heteromyid subfamily (Rodentia, Geomorpha), based on cranial and dental morphology of *Harrymys* Munthe, 1988. *American Museum of Natural History Novitates*, 3013:1-23.

SPECIMENS EXAMINED (all USNM):

- Ratufa affinis*—post-crania: 151757, 198121.
Ratufa affinis pyrsonota—skulls: 251673, 257716, 257720.
Ratufa affinis sandakanensis—skulls: 292564, 292565.

VIRGINIA MUSEUM OF NATURAL HISTORY

- Ratufa bicolor*—post-crania: 464512.
Ratufa bicolor fretensis—post-crania: 49703.
Ratufa bicolor palliata—penis: 546334.
Ratufa bicolor smithi—skulls: 320803-320807.
Ratufa indica—skulls: 38010, 355785; penis/baculum: 548661. post-crania: 308415.
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—post-crania: 297850, 505573, 505575, 548048.
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 striatus ohionensis—skulls: 308622, 308623, 308626, 308636, 308640.
Tamias townsendi ochrogenys—skulls: 96110, 96112, 97146, 97337, 97339.
Tamias townsendi townsendi—skulls: 24423, 24424, 57124, 69373, 69375.
Tamiasciurus douglasii albolimbatus—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 albiaticola—skulls: 55796, 50853, 268992, 294450.
Tamiasciurus hudsonicus baileyi—skulls: 66447, 168950, 168951.
Tamiasciurus hudsonicus columbiensis—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.