

THE DIFFICULTIES OF IDENTIFYING FLYING SQUIRRELS (SCIURIDAE: PTEROMYINI) IN THE FOSSIL RECORD

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ABSTRACT—Two problems are examined in this paper: (1) the identification of flying squirrels in the fossil record by means of their teeth; and (2) the identification of features of the limbs that indicate that the animals were gliders. Dental features vary widely among flying squirrels and among other squirrels, and a thorough survey demonstrates that most features that have been used to distinguish fossil flying squirrels are also found in some tree squirrels. A review of the descriptions of fossil flying squirrels reveals few convincing arguments that these animals actually belong to the Pteromyini and none to support the hypothesis that they were gliding animals. Recent flying squirrels exhibit a number of distinguishing morphological features in their carpal and tarsal bones and at the proximal and distal ends of their long bones. Some of these morphological structures are obligatory features required for gliding locomotion in squirrels and hence are diagnostic of flying squirrels.

INTRODUCTION

There is a long-standing disagreement on the relationship of flying squirrels to other squirrels. Some paleontologists have argued that flying squirrels evolved from paramyids independent of other squirrels (Major, 1893; Mein, 1970; de Bruijn and Unay, 1989). Most others have classified flying squirrels within the Sciuridae (Simpson, 1945; Hoffmann et al., 1993; McKenna and Bell, 1997), and recent molecular studies support the view that they evolved from one particular group of tree squirrels, long after the Sciuridae evolved from paramyids (Mercer and Roth, 2003; Stepan et al., 2004).

In this paper, we address two problems related to this disagreement. The first is the problem of identifying fossils that belong to the lineage of the Recent Pteromyini, the ancestors of modern flying squirrels or their close relatives. The second problem is determining whether the fossil animals display morphological features that clearly suggest that they were gliders. In the paleontological literature, the main focus has been on the first problem, and it has been almost completely based on dental morphology, for the obvious reason that teeth are all we have for most taxa. We propose to examine the criteria that have been used to distinguish flying squirrels in the fossil record, and to determine if they are supported by the dental morphology of Recent squirrels, both flying squirrels and all others. Second, we submit a list of postcranial characters that should be retrievable and recognizable in the fossil record and that would demonstrate that the fossils were derived from squirrels that could actually glide.

Fossils have long been identified as belonging to flying squirrels. Major (1893) described *Sciuropterus albanensis* (= *Albanensia albanensis*), comparing it with *Pteromys phaeomelas* (= *Aeromys tephromelas*), and suggested that several other fossil squirrels were in fact flying squirrels. He reviewed a number of Eocene rodents that showed “analogies” to the dental morphology of Recent flying squirrels, but he included rodents of several different families and even some primates. The feature on which he focused was that “all have in common an elegant sculpturing of the enamel, which gives often a crenate appearance to the cusps or crests” (Major, 1893:193). It is clear in his writing that Major believed this morphological similarity strongly implied phylogenetic affinity, and that he considered

flying squirrels to have originated from Eocene forms different from those that gave rise to the other squirrels. An Eocene origin of flying squirrels, independent from the origin of other squirrels, has more recently been argued by de Bruijn and Unay (1989), based on Oligocene fossils purported to be flying squirrels. It has also been suggested that flying squirrels evolved twice from different groups of tree squirrels (Black, 1972; Hight et al., 1974), but this is not supported by morphology (Thorington, 1984; Thorington et al., 2002) or molecular studies (Mercer and Roth, 2003).

There are now 21 genera of fossil flying squirrels recorded in the literature (McKenna and Bell, 1997). Of these, eight genera include extant species. This is a surprisingly high diversity of fossil flying squirrels. There are fewer genera of fossil tree squirrels (13 genera), although extant tree squirrels (approximately 25 genera) are more diverse than extant flying squirrels (15 genera) (Hoffmann et al., 1993; Thorington et al., 1996).

McKenna (1962) detailed the dental morphology of all genera of extant flying squirrels, documenting the differences among them, but it was not his purpose to present features that distinguish flying squirrels from other squirrels. He placed the genera of Recent flying squirrels into five groups, as follows.

1. The *Glaucomys* group (*Glaucomys*, *Eoglaucomys*, *Pteromys*, *Olisthomys*, and *Petaurillus*), with the exception of *Olisthomys* (*Petinomys setosus*), has a simple low-crowned, upper cheek tooth pattern, free of heavy crenulation.
2. The *Iomys* group (*Iomys*) has an enlarged and discrete hypcone.
3. The *Petinomys* group (*Aeromys*, *Petinomys*, “*Petinomys*” *vordermanni*, and *Hylopetes*) has varying degrees of crenulation along the occlusal surface.
4. The *Trogopterus* group (*Trogopterus*, *Pteromyscus*, and *Belomys*) has highly cuspidate teeth, with ectolophes having angular styles.
5. The *Petaurista* group (*Petaurista*, *Aeretes*, and *Eupetaurus*) has high-crowned teeth, with cross lophs connecting principle crests. These patterns vary in complexity between genera and species, but tend to wear flat with age.

McKenna (1962) demonstrated the diversity of dental patterns among flying squirrels (Fig. 1), but the teeth of other squirrels

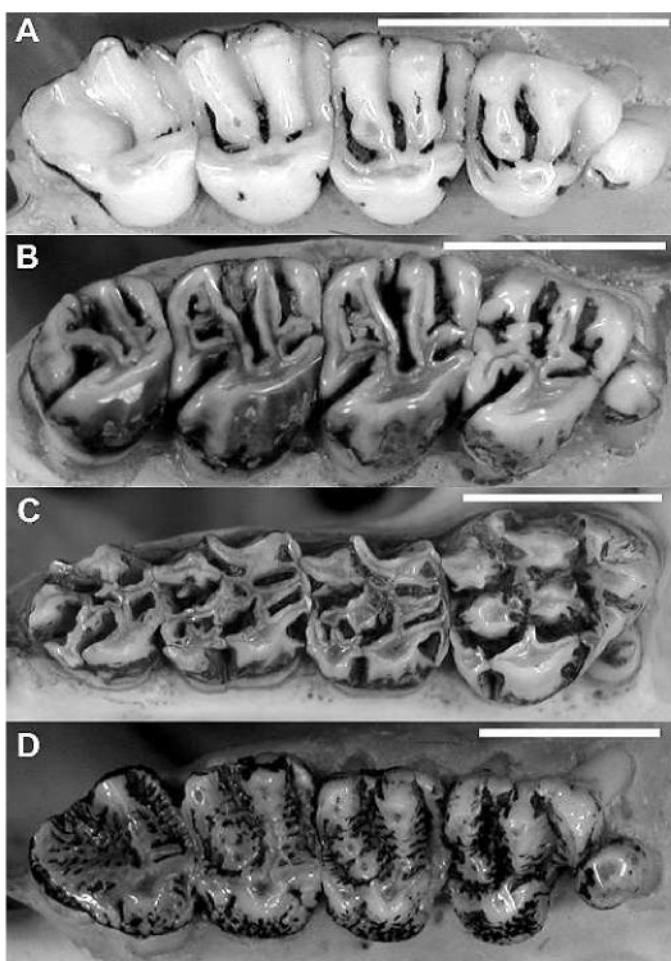


FIGURE 1. Upper tooth rows of four species of flying squirrels showing the diversity of tooth patterns. **A**, *Eoglaucomys fimbriatus* (P4–M3 equals 11.1 mm); **B**, *Petaurista petaurista* (P4–M3 equals 15.55 mm); **C**, *Trogopterus xanthipes* (P4–M3 equals 16.1 mm); **D**, *Aeromys tephromelas* (P4–M3 equals 17.3 mm). Scale bars equal 5 mm.

are equally diverse, making it difficult to distinguish between flying and other groups of squirrels.

Mein (1970) re-analyzed McKenna's characters and came to different conclusions about the supra-generic groupings of flying squirrels. He listed the features of each of his groups, but like McKenna, it was not his purpose to distinguish between flying squirrels and other squirrels. Mein's groups were:

- I. The *Glaucomys* group consisting of *Glaucomys*, *Eoglaucomys*, and *Iomys*. This combined McKenna's *Glaucomys* and *Iomys* groups, while excluding *Pteromys*. Mein did not examine *Petaurillus*, but he surely would have included it in this group because it exhibits the group's diagnostic characters. These characters are the combination of smooth enamel and absence of lophules, with other common features being absence of the metaloph on M3, no mesostyle, presence of an anterior sinuside (anterior valley), and absence of an anteroconid. He placed two genera of fossils in this group, *Cryptopterus* and *Petauria*, and also suggested that the group includes the fossil flying squirrels of North America.
- II. The *Petaurista* group, including McKenna's *Trogopterus* group and *Pteromys*, consists of the genera *Pteromys*, *Trogopterus*, *Pteromyscus*, *Belomys*, *Aeretes*, *Petaurista*, and *Eupetaurus*. It is characterized by the combination of

smooth enamel and presence of lophules. Other common characters are presence of a metaloph on M3 and presence of a mesostylid in the form of a crest attached to the metaconid. In this group Mein included the fossil genera *Miopetaurista*, *Forsythia*, and *Pliopetaurista*.

- III. The *Petinomys* group, which is almost the same as McKenna's, includes *Petinomys*, *Hylopetes*, and *Aeromys*. It is characterized by pitted enamel and no or few lophules. Other common characters are the absence of a metaloph on M3 and of a hypolophid. In this third group Mein included the fossils *Blackia* and *Pliopetes*.

By presenting a different interpretation of groups within the crown clade of flying squirrels, Mein raises a further problem in recognizing fossil flying squirrels. If there is no single set of characters that distinguish the teeth of flying squirrels, one needs to determine the several sets of characters that distinguish the different groups of flying squirrels, and how each set distinguishes them from other squirrels. If the phylogenetic relationships within the crown clade are unclear, this becomes a more difficult problem. This problem is further documented by Thorington et al. (2002). In this phylogenetic study based on morphological characters, dental characters alone mixed flying squirrels and tree squirrels. Flying squirrels formed a monophyletic group only when postcranial characters were added to the analysis.

In a seminal paper, James (1963) noted ten features by which the teeth of flying squirrels could be distinguished in the fossil record from the teeth of other squirrels. These features have been accepted and used extensively since then. Presumably, their acceptance is the reason why most subsequent authors have not felt obligated to justify their identification of fossils as flying squirrels. However, Engesser (1979), Pratt and Morgan (1989), and Emry and Korth (1996) raised doubts about the identification of flying squirrels from teeth in the fossil record. We share these doubts as illustrated by the similarity in dental morphology exhibited by the squirrels in Figures 2 and 3. In this paper we review James' (1963) dental characters, identifying which flying squirrels exhibit which characters, but also listing tree and ground squirrels that exhibit these same characters. We then propose a series of postcranial characters that do distinguish flying squirrels from other clades of tree and ground squirrels.

MATERIALS AND METHODS

We examined skulls and postcranial skeletons of squirrels in the United States National Museum (USNM) collection, both grossly and under the microscope. The list of specimens examined is given in Appendix 1.

RESULTS

Dental Characters

James (1963) noted ten features by which the teeth of flying squirrels could be identified in the fossil record and distinguished from the teeth of other squirrels. In his words, "The dentitions of the Petauristinae can be distinguished from those of the Sciurinae by the possession of some or all of the following characters . . ." (James, 1963:88). We list these below, noting in which genera of flying squirrels each occurs and whether it also occurs in any genus of tree or ground squirrels. This tabulation clearly demonstrates that no single one of his dental characters discriminate flying squirrels from other squirrels, and that no flying squirrel exhibits all of these characters. His descriptions are given in quotation marks.

1. "Occlusal surface of teeth usually heavily crenulated, at least in early stages of wear" (James, 1963:88).

Flying squirrels: Pitting and crenulations are characteristic of *Hylopetes*, *Petinomys* (Fig. 3A), and *Aeromys*, as noted by

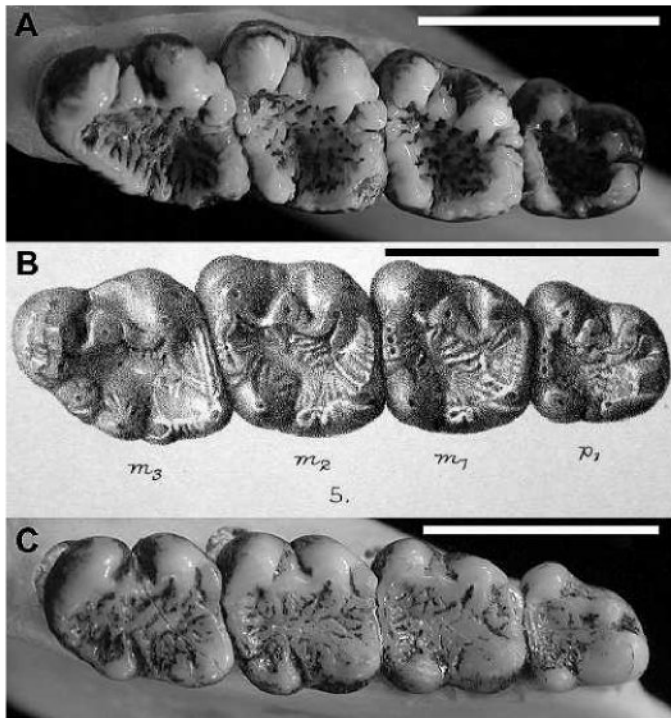


FIGURE 2. Lower tooth rows of **A**, flying squirrel, *Aeromys tephromelas* (p4–m3 equals 12.6 mm); **B**, Major's (1893) fossil squirrel, *Sciuropterus albanensis*; (m3 equals 4, m2 equals 3.5, m1 equals 3, p4 equals 2.5 mm); and **C**, tree squirrel, *Ratufa affinis* (p4–m3 equals 12.8 mm), all illustrating similar “elegant sculpturing of the enamel” (Major, 1893: 193). Scale bars equal 5 mm.

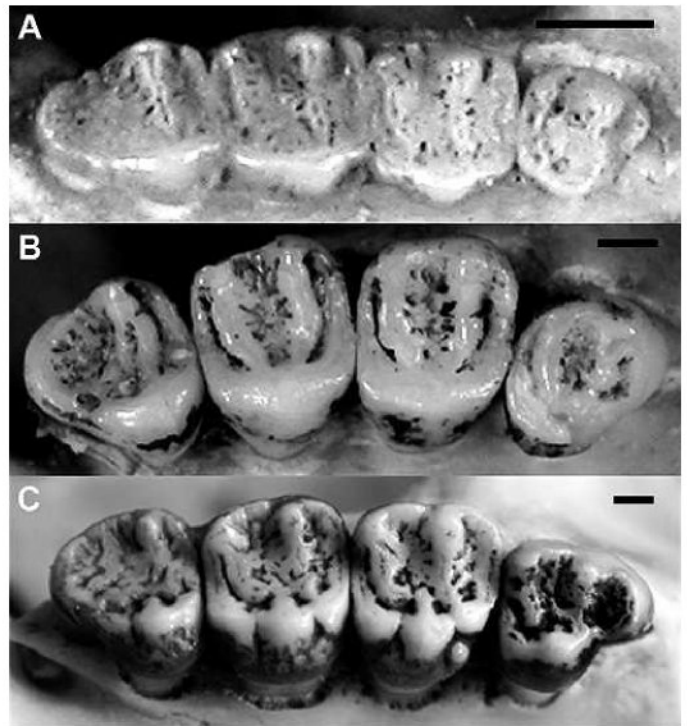


FIGURE 3. Pitting and crenulation on upper tooth rows of three squirrels. **A**, Asian flying squirrel, *Petinomys vordermanni* (P4–M3 equals 5.2 mm); **B**, African tree squirrel, *Protoxerus stangeri* (P4–M3 equals 10.7 mm); and **C**, Asian giant tree squirrel, *Ratufa bicolor* (P4–M3 equals 15.05 mm). Note lophules on *Protoxerus* and *Ratufa*. Scale bars equal 1 mm.

McKenna (1962) and subsequently by Mein (1970). We have tried to make a distinction between pitted enamel and crenulated (folded) enamel, but a gradation between the two blurs the distinction, particularly in *Aeromys*.

Other squirrels: Pitting is prominent on unworn teeth of the African squirrels *Protoxerus* (Fig. 3B) and *Heliosciurus*. Occasional pitting is seen in the African *Paraxerus* and in the Asian genera, on the lower molars of *Callosciurus*, *Lariscus*, and *Prosciurillus*. Crenulations are most prominent in the Asian giant tree squirrels, *Ratufa* (Fig. 3C), and some are evident on the lower molars of the same three Asian genera, *Callosciurus*, *Lariscus*, and *Prosciurillus*.

2. “Protocone and hypocone distinct, connected by narrow loph with deep pit on lingual surface of crown directly below loph” (James, 1963:88).

Flying squirrels: James was probably referring to the protocone-hypocone complex of *Pteromyscus* (Fig. 4A), *Belomys*, and *Trogopterus*. However, there is a distinct hypocone in *Iomys* and a small hypocone in *Aeromys*. In both a narrow loph connects the two cones on at least some teeth and there is a small to deep depression on the lingual side of the loph.

Other squirrels: Distinct protocone and hypocone without a connecting loph are seen in the Asian ant-eating *Rhinosciurus*. Small hypocones with a narrowing loph connecting them with the protocones are evident in the African *Protoxerus*, *Heliosciurus*, and *Paraxerus*, in the Asian *Callosciurus* (Fig. 4B), *Dremomys*, and *Prosciurillus*, and in the Asian giant squirrel *Ratufa macroura*.

3. “P4 triangular resulting from large, well-developed parastyle and reduced anterior cingulum” (James, 1963:88).

Flying squirrels: A somewhat triangular P4 occurs in *Glaucomys*, *Petaurillus*, *Petinomys*, *Aeromys*, *Belomys*, and

Pteromyscus, but in some cases trapezoidal would be a better description. The teeth seem best characterized by the reduction of the lingual end of the anterior cingulum, which is more developed in the other genera of flying squirrels.

Other squirrels: A similar triangular P4 is common in other squirrels, *Sciurus* and *Microsciurus*, the African genera *Heliosciurus* and *Epixerus*, the African ground squirrels *Atlantoxerus* and *Xerus*, the Indian striped squirrel *Funambulus*, the giant squirrels, *Ratufa*, and the Asian pygmy squirrel, *Nannosciurus*.

4. “Lophs complicated by presence of protolophules and metalophules in some genera” (James, 1963:88).

Flying squirrels: The more complex teeth are found in *Petaurista*, *Aeretes*, *Trogopterus*, *Belomys*, *Pteromyscus*, *Eupetaurus*, *Pteromys*.

Other squirrels: Lophules are prominent features on the teeth of *Protoxerus* (Fig. 3B), *Ratufa* (Fig. 3C), *Paraxerus*, and *Xerus erythropus*.

5. “Accessory lophs arising from protocone, extending into central valley and infrequently into anterior valley” (James, 1963:88).

Flying squirrels: Medial mesolophs are seen in *Hylopetes* and *Petinomys*.

Other squirrels: A prominent mesoloph occurs in all species of *Ratufa*.

6. “Attrition similar to that in Paramyinae, cutting action developed between parametaconid and lingual surface of protocone, and between entoconid and lingual face of hypocone” (James, 1963:88).

Remarks: The “parametaconid” is now regarded as the metaconid. We did not examine this character. It seems to have been completely neglected in the literature of fossil

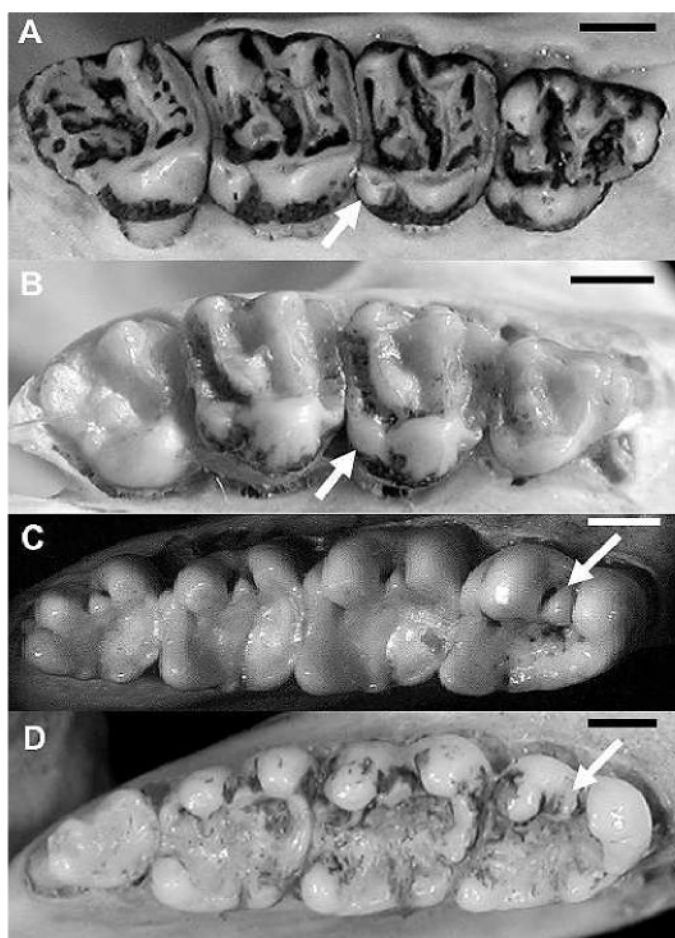


FIGURE 4. **A, B**, hypocones (arrow) on upper teeth of two squirrels. **A**, Asian flying squirrel *Pteromyscus pulverulentus* (P4–M3 equals 8.4 mm); **B**, Asian tree squirrel *Callosciurus prevostii* (P4–M2 equals 7.1 mm). **C, D**, mesoconids (arrow) on lower teeth of two squirrels. **C**, American flying squirrel *Glaucomys sabrinus* (p4–m3 equals 8.65 mm); **D**, American tree squirrel *Tamiasciurus hudsonicus* (p4–m3 equals 8.75 mm). Scale bars equal 1 mm.

flying squirrels. Also, the retention of an ancestral character is not a good basis for defining or recognizing a derived group.

7. “Mesostyles may be present on P4 to M2” (James, 1963:88).
Flying squirrels: Seen in most *Hylopetes*, *Petinomys*, *Aeromys*, *Petaurista*, *Trogopterus*, *Belomys*, and *Pteromyscus*.

Other squirrels: Present in all specimens examined of *Sciurus*, *Tamiasciurus*, *Ratufa*, most species of *Paraxerus*, and some specimens of *Protoxerus* and *Paraxerus poensis*.

8. “Mesoconid distinct” (James, 1963:88).
Flying squirrels: Mesoconids are found in all flying squirrels (Fig. 4C).

Other squirrels: A distinct mesoconid is visible in *Sciurus*, *Tamiasciurus* (Fig. 4D), *Sciurotamias*, *Protoxerus*, *Heliosciurus*, and *Ratufa*. It is also commonly present in the paramyids.

9. “Parametaconid high, entoconid distinct, and metastylid present in some specimens” (James, 1963:88).

Flying squirrels: The metaconid is the highest conid in all genera, most distinctively in p4. The entoconid is consistently the smallest conid, but is distinct in all genera. In *Iomys*, *Aeromys*, *Eoglaucmys*, *Pteromys*, *Petinomys genibarbis*, *Petinomys fuscocapillus*, *Petinomys lugens*, *Trogop-*

terus, *Belomys*, and *Pteromyscus*, the entoconid is more bulbous in occlusal view. In the remaining genera, the entoconid is as wide or only slightly wider than the posterolophid.

Other squirrels: The combination of these three features is found in *Sciurus*, *Tamiasciurus*, *Ratufa*, and *Paraxerus*.

10. “Groove present on lingual surface of lower cheek teeth opposite connection of protolophid and protoconid” (James, 1963:88).

This is the lingual diagonal flexid illustrated by McKenna (1962:fig. 5). It is prominent in some species with high-crowned teeth, forming between the mesostylid and the entoconid. In other species it is present as a groove, as described by James, or only as a notch, or not at all, and the transition from “groove present” to “groove absent” is somewhat arbitrary.

Flying squirrels: *Petaurista*, *Aeretes*, *Trogopterus*, *Belomys*, *Pteromyscus*, *Pteromys*, *Eupetaurus*, *Aeromys*, *Eoglaucmys*, *Glaucomys*, *Hylopetes phayrei* (but not *H. nigripes*), *Petinomys* (*P. genibarbis*, *P. lugens*, and *P. vordermanni*, but not *P. setosus*), and *Iomys*.

Other squirrels: *Ratufa*, *Protoxerus*, *Paraxerus vexillarius* (m1 and m2 only), *Sciurus* (p4 and m2), *Tamiasciurus douglassii* (but not *T. hudsonicus*), *Sundasciurus hippurus* (m2), *Marmota*, *Cynomys*, and some *Spermophilus* (*S. beecheyi* and *S. franklinii*, but not *S. columbianus*, *S. tridecemlineatus*, and *S. lateralis*).

This documents that no single one of these dental characters enables us to distinguish flying squirrels from other squirrels in the Recent fauna, and it is doubtful that any would work better for identifying flying squirrels in the fossil record. Because a combination of features might enable us to do so, we examined the combinations used by Mein (1970) to discriminate among his three groups of flying squirrels. Mein examined the structure of the enamel surface in both fossil and modern flying squirrels, and

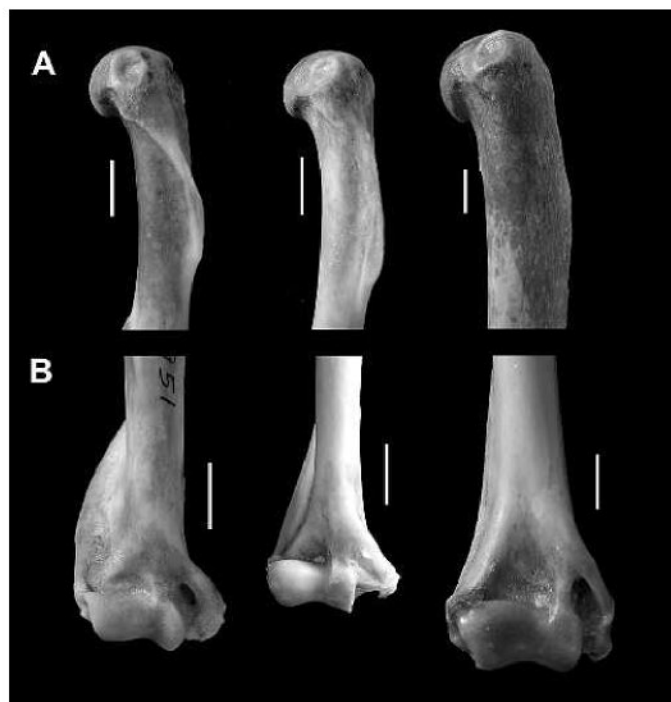


FIGURE 5. **A**, Proximal and **B**, distal ends of humeri in three squirrels: from left to right, American ground squirrel *Spermophilus beecheyi*; Asian tree squirrel *Callosciurus prevostii*; and Asian flying squirrel *Petaurista petaurista* (scale bars equal 5 mm). See text for distinguishing characteristics.

believing this characteristic to be of greatest systematic value, he used it to classify the modern flying squirrels into three groups. We have listed these groups below and noted which of the non-flying squirrels show the characteristics common within each group.

1. Enamel smooth, absence of lophules—*Glaucomys*, *Eoglaucomyss*, *Iomys*.

Other common characters: absence of the metaloph on M3; no mesostyle; presence of an anterior sinuside (anterior valley); absence of anteroconid" (Mein, 1970:51).

Other squirrels: Smooth enamel and the absence of lophules occurs in specimens of *Atlantoxerus*, *Epixerus*, *Funisciurus*, *Rubrisciurus*, *Sciurotamias*, *Spermophilus*, *Sundasciurus*, and *Tamiasciurus*. These characteristics also occur in some species of *Callosciurus* (*C. prevostii*), *Dremomys* (*D. everetti*), *Paraxerus* (*P. poensis*, *P. boehmi*, and *P. cepapi*), *Sciurus* (*S. niger*, *S. carolinensis*, *S. stramineus*, *S. aberti*, and *S. griseus*), *Tamioops* (*T. swinhoei*), and *Xerus* (*X. rutilus* and *X. inauris*). Specimens examined of *Exilisciurus*, *Funambululus*, *Glyphotes*, *Lariscus*, *Microsciurus*, and *Tamioops mclellandi* contained all of the characteristics for group one.

2. Smooth enamel, presence of lophules—*Pteromys*, *Trogopterus*, *Pteromysscus*, *Belomys*, *Aeretes*, *Petaurista*, *Eupetaurus*.

Other common characters: presence of a metaloph on M3; presence of a mesostylid in the form of a crest attached to the metaconid" (Mein, 1970:51).

Other squirrels: Both the *Rhinosciurus* and *Xerus erythropus* specimens examined showed smooth enamel, lophules, and a metaloph on M3. Neither species, however, had the mesostylid.

3. Pitted enamel, no or few lophules—*Petinomys*, *Hylopetes*, *Aeromys*.

Other common characters: no metaloph on M3; no hypolophid" (Mein, 1970:52).

Other squirrels: The combination of all four of these features can be found in *Callosciurus notatus*, *Callosciurus flavimanus*, *Dremomys pernyi*, *Heliosciurus*, *Menetes*, *Nannosciurus*, *Prosciurillus*, *Ratufa macroura*, *Sciurus granatensis*, and *Sciurus vulgaris*. Other specimens showing some of these characteristics include *Paraxerus vexillarius*, *Protoxerus*, *Ratufa affinis*, and *Ratufa bicolor*.

Clearly, the combinations of characters cited for the *Glaucomyss* group (group one) and the *Hylopetes* group (group three) do not adequately discriminate flying squirrels from other squirrels. Mein's *Petaurista* group (group two) is the most distinctive and easily discriminated from other squirrels by their teeth. However, the difficulties are compounded if the *Hylopetes* group is combined in the *Glaucomyss* group and if *Aeromys* is included in the *Petaurista* group, as argued by Thorington et al. (2002) and supported by Mercer and Roth (2003). With these latter groupings of genera it becomes difficult, perhaps impossible, to cite combinations of dental characters that distinguish the two groups from one another and either of them from other squirrels.

Postcranial Characters

The complete long bones of flying squirrels are easily distinguished from those of tree squirrels and ground squirrels, because they are much longer and more gracile. If complete long bones are not available, one can still recognize the long bones of Recent flying squirrels by features of their proximal and distal ends. In addition, there are trenchant features of carpal and tarsal bones that characterize flying squirrels, tree squirrels, or ground squirrels. These anatomical features are described below, with the presumption that many of them will also distinguish the bones of flying squirrels in the fossil record. Unfortunately, postcranial bones of fossil squirrels are seldom found and rarely

described. If these bones can be identified, as we contend, this direct hard evidence will enable us to determine when gliding evolved and test the conclusions based on molecular data.

Humerus—The proximal end of the humerus is distinctive in flying squirrels (Fig. 5). In some ground squirrels (*Marmota*, *Cynomys*, *Spermophilus beecheyi*) and tree squirrels (*Callosciurus prevostii*, *C. erythraeus*), the deltoid ridge is broad proximally and narrows distally. In others it is narrower (*Sciurus*), but it still has obvious lateral and medial edges. In flying squirrels it is less prominent, shorter, and narrower still, more like a knife edge. The deltoid ridge is more laterally directed in ground squirrels than in tree squirrels, and it is even less laterally directed in flying squirrels, principally because the ridge is less prominent. We were not able to distinguish flying squirrels from other squirrels on the basis of the sphericity of the humeral head, the size or shape of the greater or lesser tubercles, or the insertion of the infraspinatus muscle on the greater tubercle. Tree squirrels and ground squirrels can be distinguished by the insertion of the infraspinatus, but flying squirrels look like tree squirrels in this respect.

The distal end of the humerus differs among squirrels in several ways (Fig. 5). Tree squirrels and especially ground squirrels have a large lateral epicondylar ridge, extending to the lateral edge of the epicondyle, for the origin of the brachioradialis and the extensor carpi radialis longus and brevis muscles. In most flying squirrels (except *Eoglaucomyss*), this ridge is greatly reduced and does not extend to the lateral edge of the epicondyle. The medial epicondylar process of all flying squirrels is also relatively smaller than that of tree or ground squirrels, unlike the robust epicondyle of ground squirrels or the more elongate epicondyle of tree squirrels. The distal end of the trochlea is sharply angled in tree squirrels, less sharply angled in ground squirrels, and in flying squirrels it is even more gradually angled. For this character, we find the distinction between tree squirrels and ground squirrels to be ambiguous in some cases (e.g., *Callosciurus notatus* compared with *Spermophilus columbianus*), but there is no ambiguity between the sharply angled trochlea of tree squirrels and the gradually angled trochlea of flying squirrels.

Between the radial fossa and the medial epicondyle, the shaft of the humerus takes a ridge-like form in tree squirrels, but it is flat to slightly ridged in ground squirrels. In flying squirrels, this ridge is very narrow and prominent. Although we sometimes have difficulty distinguishing tree and ground squirrels by this character, we found no overlap in appearance between flying squirrels and other squirrels. On the extensor surface of the humerus, the medial edge of the trochlea is distinctly angled in *Sciurus*, *Ratufa*, and *Callosciurus prevostii*. It is much more in line with the long axis of the bone in other squirrels, including flying squirrels. This character is probably useful only in distinguishing some tree squirrels from flying squirrels. Because there is little difference between flying squirrels and *Tamiasciurus* and *Callosciurus notatus*, it is not safe to use this feature to distinguish flying squirrels from tree squirrels.

Radius—It is difficult to distinguish different kinds of squirrels from the proximal end of the radius. The circumference of the proximal articular surface differs slightly in shape, however, and ground squirrels have a slight concavity to the circumference on the dorsal surface of the radius. This gives the circumference a slight kidney-shape, which we have not seen in flying squirrels (more circular) and which is rare in tree squirrels (only seen in *Tamiasciurus*).

At the distal end of the radius, the flexor surface of ground squirrels is quite flat. It is round in flying squirrels and many tree squirrels (*Sciurus*, *Tamiasciurus*, *Callosciurus*, *Ratufa*), but it is flatter in the African tree squirrels (*Protoxerus*, *Heliosciurus*, *Funisciurus*), except for the small species of *Paraxerus* (*P. cepapi* and *P. poensis*).

On the lateral side of the radius, opposite the ulna, a small

distal process supports the first compartment, for the tendon of the abductor pollicis muscle. In flying squirrels, this process is more prominent, more pointed, and more separated from the styliiform process of the radius than it is in other squirrels.

Ulna—The olecranon process exhibits some subtle differences between flying squirrels and other squirrels. In flying squirrels, the olecranon is shorter than in tree squirrels and ground squirrels (Fig. 6). Also, the medial edge of the end of the olecranon process extends farther medially in ground squirrels, less medially in tree squirrels, and least in flying squirrels. The radial notch on the ulna has a different orientation relative to the humeral notch in tree, flying, and ground squirrels. The planes of the radial and humeral articular surfaces differ least in the tree squirrels, more in the flying squirrels, and most in the ground squirrels, which have a sharp angle of separation between the two articular surfaces.

The distal end of the ulna is less robust in flying squirrels, and it lacks the distinct groove on the dorsal lateral surface for the tendon of the extensor carpi ulnaris muscle. In North American tree squirrels (*Sciurus*) this groove is very prominent. It is less prominent in other tree squirrels and in ground squirrels, but more prominent than in flying squirrels. On the flexor surface of the distal end of the ulna, there is a distinct ridge for the origin of the pronator quadratus muscle in tree and ground squirrels. It is most prominent in ground squirrels, weaker in tree squirrels, and absent in flying squirrels, many of which lack the pronator quadratus.

Carpal Bones—The pisiform bone of flying squirrels is distinct from that of tree and ground squirrels. In flying squirrels, the pisiform has a strong articulation with the scapholunate bone, as well as with the triquetrum and the distal end of the ulna (Thorington, 1984). This scapholunate process of the pisiform is lacking in all tree and ground squirrels. In *Petaurista*, *Trogopterus*, and several other genera of Southeast Asian flying squirrels, there is also a distinct triquetral process that extends dorsally between the triquetrum and the scapholunate. This is not present



FIGURE 6. Proximal ends of ulnae in three squirrels: from top to bottom, American prairie dog *Cynomys ludovicianus*; Asian flying squirrel *Aeromys tephromelas*; and American tree squirrel *Sciurus carolinensis* (scale bars equal 5 mm). Note differences in shapes and relative lengths of the olecranon processes and orientation of radial notches (arrow).

in the *Glaucomys* group of flying squirrels. Thus, the shape of the pisiform bone is diagnostic of flying squirrels and can be diagnostic of particular groups of flying squirrels (Thorington and Darow, 2000:fig 3; Thorington et al., 2002:fig 9). The scapholunate bone of flying squirrels is also diagnostic because other squirrels lack the distinctive articular facet for the scapholunate process of the pisiform.

Femur—Among Recent squirrels, one can distinguish tree squirrels, marmotine ground squirrels, xerine ground squirrels, and flying squirrels from the relative sizes and positions of the lesser and third trochanters of the femur (Fig. 7). In most tree squirrels, the lesser trochanter is large and medial, extending medially as far as or farther than the middle of the femoral head. It is similarly positioned, although slightly shorter, in many flying squirrels (*Glaucomys*, *Eoglaucomys*, *Iomys*), but in spermophiline ground squirrels it extends posteromedially and usually is even shorter. The femoral neck is elongate in the xerine ground squirrels, particularly *Xerus*, causing the lesser trochanter to appear relatively much shorter. In one African tree squirrel, *Pro-*

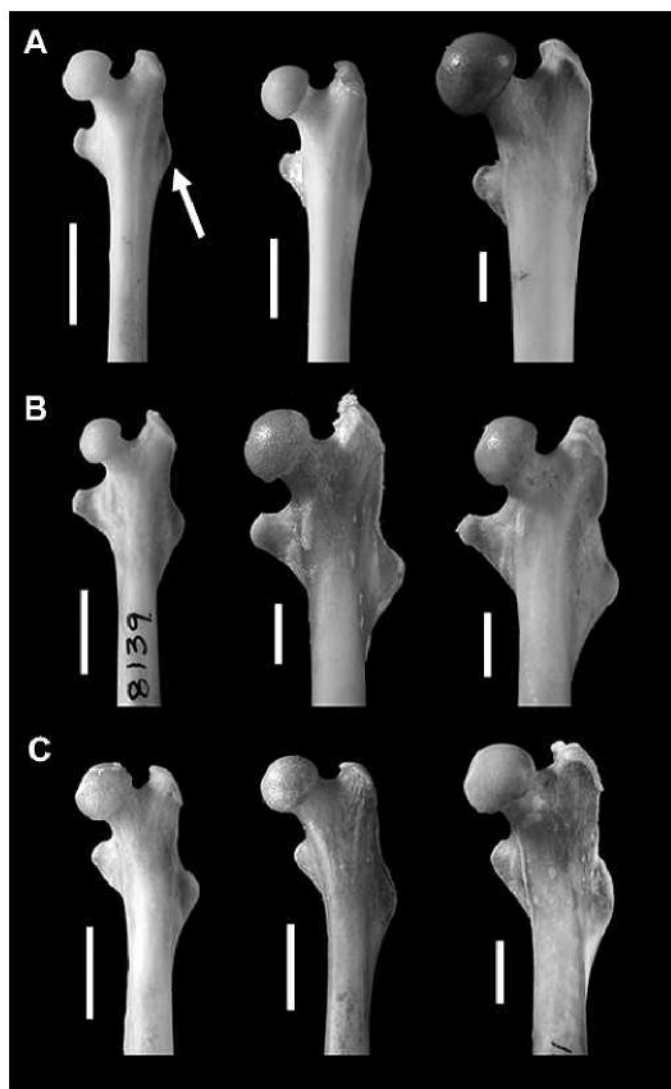


FIGURE 7. Anterior views of the proximal ends of femora of nine squirrels. **A**, (left to right) flying squirrels *Glaucomys volans*, *Iomys horsfieldii*, and *Petaurista petaurista*; **B**, tree squirrels *Microsciurus alfari*, *Sciurus carolinensis*, and *Callosciurus prevostii*; and **C**, ground squirrels *Ammospermophilus leucurus*, *Spermophilus tridecemlineatus*, and *Spermophilus beecheyi* (scale bars equal 5 mm). Note differences in size of lesser trochanters and third trochanters (arrow).

toxerus stangeri, the lesser trochanter is short. In other African tree squirrels it is long (*Funisciurus*), to very long (*Heliosciurus*). The lesser trochanter is short in the large flying squirrels (*Petaurista*, *Eupetaurus*, *Aeromys*, *Trogopterus*) unlike tree squirrels and smaller flying squirrels. A prominent third trochanter lies opposite or slightly distal to the lesser trochanter in tree squirrels, and is similarly positioned in marmotine ground squirrels. In some giant tree squirrels, *Ratufa bicolor* and *Ratufa macroura*, the third trochanter extends as a prominent ridge, distally and slightly posteriorly on the proximal 3/4 of the femur. In xerine ground squirrels, the third trochanter is prominent and distal to the position of the lesser trochanter. In all flying squirrels, however, the third trochanter and the trochanteric ridge are much reduced and lie opposite or slightly proximal to the lesser trochanter.

The distal end of the femur has few characters that functionally differentiate among squirrels. In large flying squirrels (*Petaurista*, *Aeromys*), however, the patellar groove is broader and shallower than in tree, ground, or small flying squirrels.

Tibia—At the proximal end of the tibia, the popliteal fossa is more pronounced in ground squirrels than in tree or flying squirrels (Fig. 8). In ground squirrels, it is limited medially and laterally by low bony ridges, particularly prominent on the medial side. In tree squirrels the fossa has distinct edges or low ridges, separating it from the lateral surfaces of the bone. In the large

flying squirrels (*Petaurista*, *Eoglaucomys*), the edges of the fossa are indistinct, with only rounded edges separating the fossa from the medial and lateral surfaces of the bone. In the small flying squirrels (*Glaucmys*, *Iomys*) the fossa is more distinct, similar to the condition in tree squirrels. The cnemial crest on the cranial surface of the tibia is pronounced in ground squirrels, less pronounced in tree squirrels, and not very distinct in flying squirrels (Fig. 8).

At the distal end of the tibia, the tibio-fibular articulation is long in small flying squirrels (e.g., *Glaucmys*) and short in large flying squirrels. It is relatively short in all tree and ground squirrels. The distal articular surface mirrors the trochlea of the astragalus. In ground squirrels the medial portion of the articular surface is relatively larger than in tree squirrels and flying squirrels. The posterior process at the distal end of the tibia is long in tree squirrels, shorter in ground squirrels, and variable among flying squirrels, relatively long in *Petaurista* but short in *Glaucmys*. In the *Glaucmys* group, there is a small tubercle on the anterior surface at the distal end of the tibia. This is highly diagnostic, because it is the origin of the tibio-carpalis muscle, which extends from the wrist to the ankle along the edge of the patagium and is found only in flying squirrels (Thorington et al., 1996:fig. 2; Thorington et al., 2002:fig. 11). The tubercle occurs in *Glaucmys*, *Eoglaucomys*, *Iomys*, *Hylotropes*, *Petinomys*, and *Petaurillus*, but not in the other genera of Recent flying squirrels, in which the muscle takes origin from the metatarsals.

Astragalus—The medial edge of the trochlea for articulation with the tibia is much smaller than the lateral edge in tree squirrels and flying squirrels. The two edges are much more similar in size in ground squirrels. In flying squirrels, the trochlear surface is more 'V'-shaped than in other squirrels, to match a sharper ridge on the distal articular surface of the tibia. In tree squirrels and ground squirrels the middle of the trochlear surface, between the medial and lateral edges, is a more rounded groove.

The neck of the astragalus of tree squirrels (*Sciurus*, *Tamiasciurus*, *Ratufa*, *Callosciurus*, *Sundasciurus*) has a small pit just distal to the medial side of the trochlear surface. This pit is also found in chipmunks (*Tamias*). It is absent in ground squirrels and flying squirrels. It is also absent in African tree squirrels (*Protoxerus*, *Heliosciurus*, *Funisciurus*, and *Paraxerus*), but there is a slight groove on the neck at the base of the medial side of the trochlear surface in these genera. Because of the 'V'-shaped groove of the trochlear surface of flying squirrels, the edge of the neck adjoining the trochlea is also 'V'-shaped.

On the plantar surface of the astragalus there are two facets for articulation with the calcaneus: the proximal astragalo-calcaneal articulation and the sustentacular articulation. There is commonly a sulcus between the two facets (Fig. 9), within which lies the astragalo-calcaneal interosseous ligament and synovial tissue of the joints. In some squirrels, the facets are confluent and the sulcus is reduced to a pit for the origin of the astragalar end of the ligament. The sulcus is completely missing in all genera of flying squirrels, but also it is greatly reduced in the North American tree squirrels (*Sciurus*, *Tamiasciurus*), some African tree squirrels (*Funisciurus*, *Paraxerus*), and some basal members of the Marmotini (*Tamias*, *Sciurotamias*; the sulcus is very narrow in *Spermophilus beecheyi* and *S. variegatus*). The sulcus is prominent in the Asian tree squirrels (*Ratufa*, *Callosciurus*, *Sundasciurus*), and therefore its presence or absence cleanly distinguishes between Asian tree and flying squirrels.

Calcaneus—In ground squirrels, the calcaneus is cruciform, with the sustentacular process aligned opposite the peroneal process (Fig. 10). In tree and flying squirrels, the sustentacular process is more distal than the peroneal process, so that the two are aligned diagonally relative to the main axis of the calcaneus. The sustentacular process is triangular in *Sciurus* and it is elongate in *Ratufa*. It is round, conforming closely to the circular shape of the articular process, in ground squirrels (*Spermophilus*, *Cyno-*

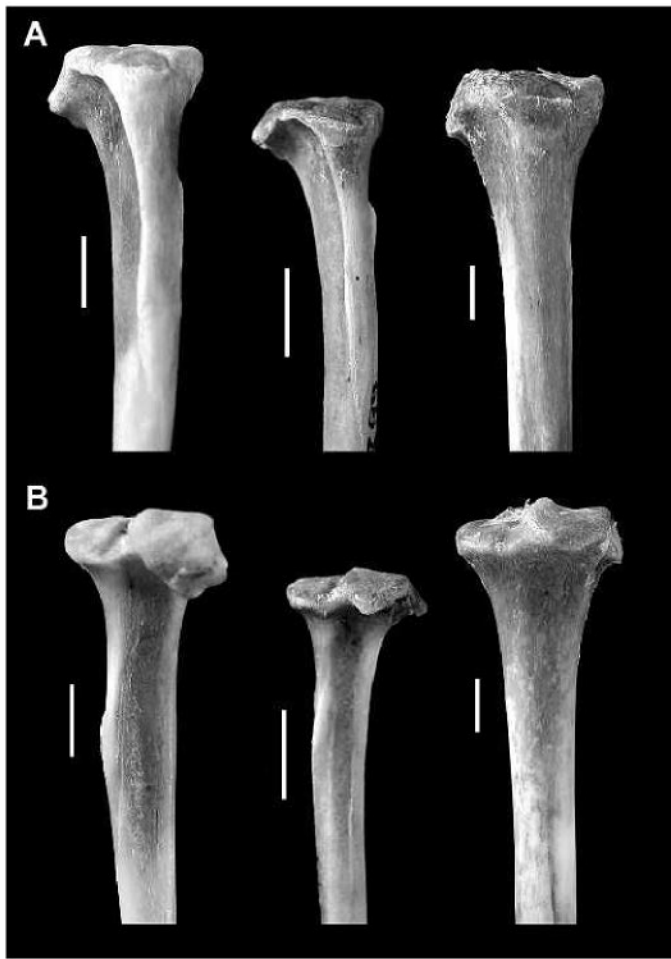


FIGURE 8. Proximal ends of tibiae of three squirrels, **A**, anterior view, **B**, posterior view. Left to right, American ground squirrel *Spermophilus beecheyi*, Asian tree squirrel *Callosciurus notatus*, and Asian flying squirrel *Petaurista petaurista* (scale bars equal 5 mm). Note differences in cnemial crests and popliteal fossae.

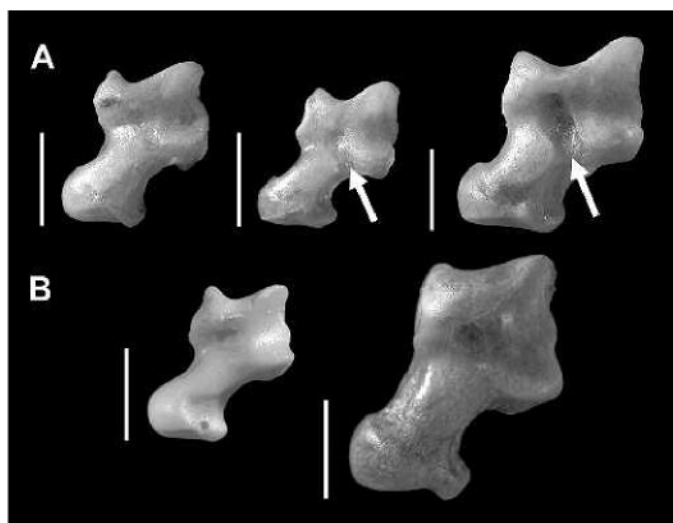


FIGURE 9. Plantar surfaces of astragali of five squirrels. **A**, (left to right) tree squirrels *Sciurus carolinensis*, *Callosciurus prevostii*, and *Ratufa bicolor*; **B**, flying squirrels *Eoglaucomys fimbriatus* and *Petaurista petaurista* (scale bars equal 5 mm). Note presence or absence of sulcus (arrows).

mys, and *Xerus*) and in some of the Asiatic tree squirrels (*Callosciurus*), but not in flying squirrels. There is a distinct sulcus between the two articular surfaces for the astragalus in most squirrels (including flying squirrels, *Ratufa*, *Callosciurus*, *Protoxerus*, *Heliosciurus*, and *Funisciurus*), but it is practically absent in *Sciurus* and *Tamias*, and it is small in *Spermophilus beecheyi* and *Paraxerus cepapi*. Plantar and medial to the cuboid articulation there is a prominent process in ground squirrels, which is much smaller in flying and tree squirrels. There is always a ridge between the peroneal process and the heel in flying squirrels. It is rarely present in tree squirrels (*Tamiasciurus*) and ground squirrels.

DISCUSSION

Our understanding of Sciuridae phylogeny and classification has changed extensively in the last two years. Two molecular studies, each using three genes, six in total, strongly support the same phylogeny, with a few minor differences between them (Mercer and Roth, 2003; Steppan et al., 2004). Both strongly support the monophyly of flying squirrels and place them as the sister group of one lineage of tree squirrels, the Sciurini. The morphology of modern squirrels is generally concordant with this molecular phylogeny. Mercer and Roth (2003) included all but one genus of modern flying squirrels and found two main groups, a *Glaucomys* group of six genera and a *Petaurista* group of eight genera. These are the same two groups suggested by Thorington and Darrow (2000) on the basis of ankle and wrist morphology and found to be among the most parsimonious groupings in a subsequent study of 80 morphological characters (Thorington et al., 2002). However, in the Mercer and Roth cladogram, two genera in the *Petaurista* group seem strangely placed, particularly with reference to tooth morphology. These are *Aeretes*, which has teeth very similar to *Petaurista* but is placed as a sister group of *Trogopterus*, and *Aeromys* placed as a sister group of *Eupetaurus*, in spite of their very different teeth. Because Steppan et al. (2004) included only *Glaucomys* and *Petaurista*, their analysis is uninformative about the positions of *Aeretes* and *Aeromys*.

Mercer and Roth (2003) carefully tested the appropriateness of a molecular clock and estimated dates for nodes in their phy-

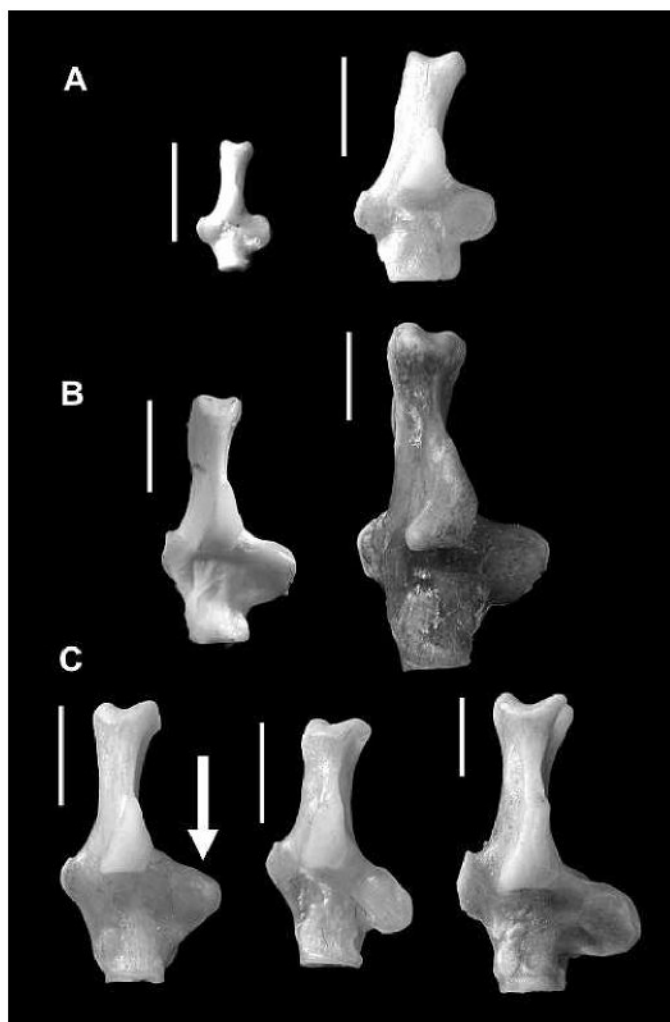


FIGURE 10. Dorsal views of calcanei of seven squirrels. **A**, (left to right) ground squirrels *Tamias striatus* and *Spermophilus beecheyi*; **B**, flying squirrels *Eoglaucomys fimbriatus* and *Petaurista petaurista*; and **C**, tree squirrels *Sciurus carolinensis*, *Callosciurus prevostii* and *Ratufa bicolor* (scale bars equal 5 mm). Note cruciform shape in ground squirrels, triangular sustentacular process (arrow) in *Sciurus*, and elongate sustentacular process in *Ratufa*.

logeny, providing an hypothesis of flying squirrel phylogeny readily compared with the fossil record. If they had used *Palaeosciurus* instead of *Douglasciurus* to root the sciurid tree (Heissig, 2003), their divergence dates would have been slightly younger. They suggest that flying squirrels and the Sciurini (*Sciurus*, etc.) diverged in the early Miocene. This is discordant with the description of flying squirrels from the Oligocene, in particular of *Oligopetes* described by Heissig (1979) from Germany, and the explicit statement by de Bruijn and Unay (1989:144) that their observations provide “strong support for the hypothesis of Major (1893) and Mein (1970) that the Petauristinae and Sciurinae do not share a common ancestor.” The justification for considering *Oligopetes* to be a flying squirrel is provided by de Bruijn and Unay (1989:140): “The complete absence of a protoconule and the near absence of a metaconule in M1–2, the U-pattern formed by the protoloph and the metaloph of the M1–2, and the shape of the occlusal surface of the cheek teeth in *Oligopetes* all indicate that we are dealing with true flying squirrels.” None of these characters truly distinguish flying squirrels from other squirrels, most of which lack protoconules and meta-

conules and a number of which exhibit the 'U'-pattern. Furthermore, Cuenca Bescos and Canudo (1992) illustrated *Oligopetes* with both protoconule and metaconule, and they note the presence of these in *Oligopetes*, *Forsythia*, *Miopetaurista*, and *Pliopetaurista*. However, we agree that the combination of characters causes the teeth to look remarkably like those of *Hylopetes* and *Petinomys*. There is approximately a 25 million year gap between *Oligopetes* and *Hylopetes*, and therefore de Bruijn and Unay (1989) did not synonymize the two.

In contrast, Mercer and Roth (2003) present a case for *Hylopetes* and *Petinomys* evolving within the *Glaucomys* group in the mid- to late Miocene, approximately at the time that *Hylopetes* (formerly *Pliopetes*, synonymized by Bouwens and de Bruijn, 1986) appeared in the fossil record. Furthermore, in the cladogram, the most basal members of the *Glaucomys* group are *Eoglaucomys* and *Glaucomys*, both of which show a more 'V'-shaped arrangement of protoconule and metaconule, suggesting that ancestral members of this group in the early Miocene would have shared this characteristic with the tree squirrels of the same period.

These differing interpretations of the molecular and paleontological data may be irresolvable with present evidence. Stepan et al. (2004) included only *Glaucomys* and *Petaurista* in their analysis and Thorington et al. (2002) were not able to resolve the position of *Hylopetes* and *Petinomys* with morphological data, so neither study helps to support the cladistic placement of these two genera by Mercer and Roth (2003). The absence of non-dental material of *Oligopetes* and the long gap in the fossil record makes the interpretation of de Bruijn and Unay (1989) less than compelling.

Mercer and Roth (2003) depict the divergence of flying squirrels from the Sciurini in the early Miocene. Early Miocene fossils purported to be flying squirrels include the genera *Petauristodon*, *Miopetaurista*, *Aliveria*, and *Blackia* (McKenna and Bell, 1992). The genus *Sciurion* was informally described by Skwara (1986) as a "flying squirrel," because it has enamel crenulations in the basin of unworn cheek teeth. However, Skwara declined to assign it formally to the flying squirrels, because these features are found in some paramyids and some species of *Prosciurus*. She allocated it only to the Sciuridae, where it was listed also by McKenna and Bell (1997). The identification of *Petauristodon* as a flying squirrel has been questioned by Pratt and Morgan (1989), with whom we agree, as elaborated below in our discussion of the astragalus. *Blackia* seems to be considered a flying squirrel because of its extensively rugose and pitted enamel (Mein, 1970). These features have evolved independently in at least two lineages of flying squirrels and three of tree squirrels, but no tree squirrel exhibits the extreme condition of the enamel of *Blackia*. The simplicity and pattern of *Blackia*'s cusps and lophes seem unlike those of any modern flying squirrels, and Mein (1970) considered it unlikely to be directly ancestral to any. Stronger justification for allocating *Blackia* to the flying squirrels is desirable.

Aliveria is a reasonable candidate for an early flying squirrel, as noted by de Bruijn et al. (1980), and the occurrence of flying squirrels at this time is concordant with the molecular data (Mercer and Roth, 2003). *Shuanggouia* of the middle Miocene is similar to *Aliveria* and was allocated to flying squirrels because of this (Qiu and Liu, 1986). *Aliveria* and *Shuanggouia* exhibit the convergent protoconule and metaloph of other sciurids with some features suggesting they are closely related to *Albanensia* of the middle and late Miocene (McKenna and Bell, 1997) and *Miopetaurista*. However, the justification for calling these flying squirrels seems principally to be the crenulated enamel of the talonid basin on some of them. We do not find this convincing because it is not characteristic of the basal members of either the *Glaucomys* group (*Eoglaucomys*, *Glaucomys*) or the *Petaurista* group (*Petaurista*). In this respect, interpretation of the fossil

record is discordant with expectations based on the molecular analysis. In clarifying the distinction between *Albanensia* and *Miopetaurista*, Daxner-Höch and Mein (1975) did not state why they consider these flying squirrels. *Albanensia* has rugose enamel and a strong hypocone and lacks a free mesostyle and mesostylid; *Miopetaurista* has smooth enamel, lacks a hypocone, and has a free-standing mesostylid. None of these features are diagnostic of flying squirrels; in fact, *Petaurista philippinensis* exhibits a different combination of strong hypocone, smooth enamel, and free mesostyle on the M1–2. Although the large P4 and the occurrence of lophules on *Albanensia* are suggestive as precursors of the complex high-crowned *Petaurista* teeth, these features might be expected to evolve in common among folivorous squirrels.

Forsythia is described (Mein, 1970) as a flying squirrel of the middle (?) Miocene, with converging protoconule and metaloph and a combination of distinctive 'flying squirrel' features. Mein (1970) compared it with *Pteromys* and *Glaucomys*, but he did not state explicitly why he considered it to be a flying squirrel. He may have considered some crenulations on the lower molars to be diagnostic.

Two other genera of flying squirrels have been described from the middle Miocene of Asia: *Meinia* and *Parapetaurista*. There are imprints of the body and a partial skeleton of *Meinia*, but only the teeth were described in English by Qiu (1981). Dimensions of some of the postcranial elements are also provided in the Chinese description, and the illustration suggests that there are distal tibia, tarsal bones, and carpal bones. Qiu (1981) considered *Meinia* to be a flying squirrel, closest to *Blackia* in form and pattern of molars and rugosity of the enamel. The figures do not persuade us that it is very similar to *Blackia*, but if it is, it is subject to the same questions that we pose for identifying *Blackia* as a flying squirrel. *Meinia*, however, has postcranial elements that may answer these questions. *Parapetaurista* is compared by Qiu and Liu (1986) with *Miopetaurista*, although it seems more comparable to *Albanensia*, because both have rugose enamel, hypocones, and lack free-standing mesostyles and mesostylids.

Two genera, *Pliopetaurista* and *Pliosciuropterus* are reported to occur first in the late Miocene (McKenna and Bell, 1992). Qiu (1991) cited similarities between *Pliopetaurista rugosa* and *Petaurista* in the general patterns of P4 and M3 and details of DP4. Comparing his illustrations with specimens of *Petaurista philippinensis*, *P. alborufus*, and *P. xanthipes*, we are intrigued by his suggestion that *Pliopetaurista rugosa* is in the lineage leading to *Petaurista*. In contrast, the holotype of *Pliopetaurista meini* illustrated by Black and Kowalski (1974; plate xv, fig. 1) appears to resemble *Callosciurus* (e.g., *C. prevostii*) more closely than any flying squirrel, especially in the metaloph of M1–2 with its prominent metaconule narrowly connected to the metacone and not to the protocone. In his description of *Pliosciuropterus*, Sulimski (1964) listed and illustrated the similarities and differences between it, *Pteromys*, and *Petaurista*. He presents a reasonable, though not convincing argument that *Pliosciuropterus* is a "flying squirrel" (his quotation marks).

Flying squirrels of the Pliocene and Pleistocene are attributed to recent genera and to four of the fossil genera discussed above, *Miopetaurista*, *Blackia*, *Pliopetaurista*, and *Pliosciuropterus*. A fifth genus, known only as a fossil, is the middle Pleistocene *Petauria*. The teeth illustrated by Dehm (1962) for the type of *Petauria* closely resemble the well-worn teeth of some species of *Petaurista* (c.f. *P. philippinensis*), and possibly this genus should be considered a synonym of *Petaurista*. If fossils are correctly attributed to Recent genera of flying squirrels, there is almost certainty that they were gliding animals. Publications detailing such attributions of Pliocene and Pleistocene fossils are strongly persuasive to us (e.g., Guilday, 1962; Guilday et al., 1964, 1977; Chaimanee, 1998). In these publications, reference to postcranial

elements is rare (Guilday, 1962) even when it is likely that they were collected (Guilday et al., 1964, 1977).

One problem with the attributions of fossils to Recent genera is the difficulty of distinguishing between *Hylopetes* and *Petinomys* by teeth alone. Bouwens and de Bruijn (1986) concluded that it was not possible. This question needs to be revisited, because it is unclear what species and specimens they examined. They noted that they accepted the names on the specimen labels but they did not cite the specimen numbers or their geographic origin. The identifications included "*Hylopetes saggita*," but the type specimen of this species is reported to be a *Petinomys* (Hill, 1960, 1962; Corbet and Hill, 1992). Also, they listed "*Petinomys bartelsi*," which is now considered to be a *Hylopetes* (Corbet and Hill, 1992; Hoffmann et al., 1993). In addition, there are two groups of *Hylopetes* that can be distinguished by the prominence or absence of a mesostyle on P4 and M1 (Thorington et al., 1996), and Chaimanee (1998) seems to have successfully distinguished between two species of *Hylopetes* and two species of *Petinomys* from the Pleistocene of Thailand. Therefore it seems likely that a careful review of all the species of *Hylopetes* and *Petinomys* would permit more precise identifications of Pliocene and Pleistocene fossils of these squirrels.

It is probable that Recent flying squirrels are monophyletic (Thorington, 1984; Thorington et al., 2002; Mercer and Roth, 2003), but fossil lineages demonstrated to be gliding squirrels need not be closely related to the Recent ones. Gliders have evolved among at least seven different lineages of mammals, so there is no reason to assume among squirrel fossils that the demonstration of flying squirrel morphology is also a demonstration that the fossil belongs to the Pteromyini. The opposite is also possible, that the Pteromyini and the Sciurini diverged before gliding evolved in the former. Until there is clear evidence supporting either of these possibilities, however, we prefer the hypothesis that gliding morphology evolved once in the Sciuridae at the base of the radiation of the Pteromyini.

In distinguishing among ground squirrels, tree squirrels, and flying squirrels in the fossil record, it is desirable to choose features that are functionally important for these different ways of life. Diet varies greatly among Recent squirrels, and with a few specialized exceptions it varies independent of terrestrial, arboreal, and gliding habits. Many small ground squirrels, tree squirrels, and flying squirrels feed extensively on seeds, insects, and other rich sources of nutrition. In contrast, large squirrels feed more extensively on leaves and other vegetation. There is no reason to expect a tighter correlation among fossil squirrels. This does not preclude dental features from being good indicators of lineages over geologically short periods of time, but it should raise concerns about interpretations of lineages traced by dental features over tens of millions of years. This is the crux of our concern with identifying flying squirrels in the fossil record solely from teeth. Our concern is furthered by our survey of the dental features that have been used to distinguish fossil flying squirrels. Many of these features appear to be widespread among Recent squirrels that are not flying squirrels. We submit that such identifications of fossils as flying squirrels should be carefully argued with full consideration and exclusion of alternative hypotheses.

We have not examined the dental features of paramyid rodents and compared them with the features of flying squirrels, because we are not convinced of their relevance. Morphological evidence suggests, although not conclusively, that flying squirrels are derived from ancestral tree squirrels, not directly from paramyids. Flying squirrels have male reproductive tracts that are remarkably similar to those of other squirrels. These tracts include the bulbar gland and penile duct, which are unique to tree squirrels (Mossman et al., 1932). Unfortunately the primitive state of the male reproductive tract in paramyids is unknown. Flying squirrels share the sciurimorph jaw musculature (Bryant, 1945), but sciuromorphy has evolved repeatedly in rodents. Mo-

lecular data strongly support the origin of flying squirrels from tree squirrels (Mercer and Roth, 2003; Steppan et al., 2004), but of course, paramyids were not included in their analyses. Finally, any anatomical features of paramyids retained in sciurids are symplesiomorphies and not useful for phylogenetic assessments, in spite of their interest for other evolutionary studies.

A number of postcranial features do appear to correlate well with terrestrial, arboreal, or gliding habits of Recent squirrels. We consider the function of these features, in the hope that there are reasons to consider them functional correlates, independent of lineage. If so, then these features can better be argued to be indicative of these habits, even among fossil squirrels.

The robust deltoid ridge of the humerus in ground squirrels and tree squirrels serves for the insertion of the pectoralis and deltoid muscles. The strong distal insertion of these muscles on the humerus increases the power of forelimb flexion but reduces flexibility at the shoulder joint. The less robust deltoid ridge in flying squirrels probably allows increased flexibility at the shoulder joint for gliding. A similar but less extreme difference can be seen in a comparison of the non-gliding marsupial *Gymnobelideus* and the closely related gliding marsupial, *Petaurus*, of Australia. Therefore we submit that this difference will distinguish flying squirrels in the fossil record as well, although we cannot assess how early in their history it will be evident.

In flying squirrels, the reduction of the lateral epicondylar ridge must represent a reduction in the leverage of the extensor muscles for flexion of the elbow joint, with a concomitant increase in the ease with which the elbow joint can be extended. This might be expected of a gliding mammal, so we find the strong lateral epicondylar ridge of *Eoglaucomys* to be a surprise, in contrast with the reduced ridge on all other flying squirrels we have studied.

The third trochanter of the femur may be analogous. The reduction of the trochanter and the trochanteric ridge in flying squirrels reflects a reduction in the muscle mass and power of the superficial gluteal muscle. However, it is not obvious that this would have much effect on flexibility at the hip joint and thus a more plausible explanation for this universal characteristic of Recent flying squirrels should be sought. There is a similar reduction in the size of the insertion of this muscle in the gliding marsupial *Petaurus*.

Pronation and supination at the wrist joint is reduced or absent in flying squirrels. The pronator quadratus muscle is absent in many species, and the pisiform bone articulates with both the scapholunate and the triquetral bones, probably to increase stability at the wrist joint for control during gliding (Thorington, 1984; Thorington et al., 1998; Thorington and Darrow, 2000). Distinguishing morphological features that are associated with these changes are the reduction of the distal end of the ulna, the absence of the ridge on the ulna for the origin of the pronator quadratus, the shape of the pisiform bone, and the articular facet on the scapholunate for the pisiform. Among fossil sciurids, these features should distinguish flying squirrels from all others.

In the hind limb, there are a number of features that distinguish ground squirrels from tree squirrels and flying squirrels. Some of these can plausibly be linked to the digging activities and burrowing habits of ground squirrels, so the presence of these characters can be used to argue that a fossil was not a flying or tree squirrel. These include the orientation of the lesser trochanter, which is directed posteriorly and medially in ground squirrels. This trochanter is the point of insertion of the psoas major and iliacus muscles, which effect the recovery phase or protraction of the femur. In tree and flying squirrels the tip of the lesser trochanter lies medial to the axis of rotation of the femur, taken as a line between the head and the medial condyle of the femur, but lateral to this axis in ground squirrels. Accordingly, these muscles should provide for greater lateral rotation of the femur in tree and flying squirrels and greater medial rotation in

ground squirrels. It is plausible that this contributes to the toes-out posture of tree-climbing squirrels but a more toes-in posture for burrowing ground squirrels.

The existence of a small tubercle on the anterior surface of the distal end of the tibia would be an unambiguous demonstration that a fossil was a flying squirrel. This highly diagnostic feature is the origin of the tibio-carpalis muscle, which extends along the lateral edge of the flight membrane and is found only in flying squirrels, although the tubercle is not found in all flying squirrels.

In flying squirrels the calcaneal surface of the astragalus exhibits derived features. The two calcaneal articular surfaces are enlarged and occlude the sulcus, contrary to the condition seen in many other squirrels. The ancestral condition, a prominent sulcus, is known in fossil squirrels (*Douglassciurus*) and in Asian tree squirrels (Emry and Thorington, 1982). The derived morphology permits greater mobility of the ankle joint and is associated with extreme plantar inversion of the foot in gliding. The foot is held so that the sole is parallel to the flight membrane and to the slip stream of the air passing over it. This must decrease turbulence and drag during gliding and increase the lift/drag ratio and the ratio of glide distance to vertical drop. Presumably, this is a requisite condition for efficient gliding, because the inverted foot is seen during glides in four of the six Recent mammal groups that glide (flying squirrels, colugos, sugar gliders, and greater gliders; adequate photographs of the feather tail glider and the scaly tailed flying squirrels are not available). An occluded sulcus on the plantar surface of the astragalus is also seen in North American tree squirrels, permitting the reversal of the foot during headfirst descent of trees. If the North American tree squirrels are ancestral to or a sister group of the flying squirrels, as is probable, then the occluded sulcus is a synapomorphy of these two groups. Although not diagnostic of flying squirrels alone, it is probably characteristic of all Recent and fossil flying squirrels. If this assessment is correct, then Pratt and Morgan (1989) were right to doubt that *Petauristodon* of the early Miocene, Florida, was a flying squirrel, because it has a prominent astragalal sulcus. The irony would be that specimens of *Petauristodon* were the basis for James' (1963) assessment of the 10 dental features that distinguish flying squirrels from other squirrels.

In conclusion, we submit that identifications of flying squirrels in the fossil record, based on teeth alone, should be carefully reviewed and verified, with particular concern for other squirrels with similar dental characteristics. The 'gold standard' for such identifications should be associated postcranial remains exhibiting diagnostic features found only in Recent flying squirrels.

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APPENDIX 1

Listed below are the USNM specimens that were examined for this paper. **Abbreviations:** p, postcrania; s, skull.

Family Sciuridae

Subfamily Ratuffinae: Indo-Malayan giant squirrels

- Ratufa affinis*: 300928 (s)
Ratufa bicolor: 277614 (s), 573966 (p)
Ratufa indica: 322077 (p), 355785 (s)
Ratufa macroura: 256734 (s)

Subfamily Sciurinae: Tree squirrels and flying squirrels

Tribe Sciurini: Holarctic and Neotropical tree squirrels

- Douglassciurus jeffersoni*: 243981 (p)
Microsciurus mimulus: 309030 (s), 309033 (s)
Microsciurus alfari: 338138 (p), 338139 (p)
Sciurus carolinensis: 348323 (s), 398573 (s), 505573 (p), 527930 (s)
Sciurus deppei: 244939 (p), 244942 (p)
Sciurus niger: 38860/4044 (s), 583337 (p)
Sciurus vulgaris: 152686 (s)
Tamiasciurus douglasii: 549262 (s), 549263 (s)

- Tamiasciurus hudsonicus*: 39012/14913 (s), 564078 (p)
- Tribe Pteromyini: Flying squirrels
Aeromys tephromelas: 481192 (s), 196743 (p)
Eoglaucmys fimbriatus: 173362 (s), 173363 (p), 326363 (p), 353243 (p)
Eupetaurus cinereus: uncataloged specimen (p)
Glaucmys sabrinus: 129708 (s), 141952/A49822 (p), 530557 (p), 551843 (p)
Glaucmys volans: 293439 (s), 329701 (s), 397077 (p), 505618 (p), 506226 (s)
Hylopetes nigripes: 477995 (s)
Hylopetes phayrei: 260623 (s)
Iomys horsfieldii: 292654 (p)
Petaurista petaurista: 197320 (p), 326359 (s)
Petinomys genibarbis: 488672 (s)
Petinomys lugens: 252319 (s)
Petinomys setosus: 488676 (s)
Petinomys vordermanni: 481148 (s)
Pteromys volans: 237587 (s)
Trogopterus xanthipes: 258250 (p)
- Subfamily Callosciurinae: Oriental squirrels
Callosciurus erythraeus: 255367 (p)
Callosciurus notatus: 155680 (p), 574899 (p)
Callosciurus prevostii: 300947 (s), 300949 (s), 574902 (p)
Dremomys everetti: 292615 (s)
Funambulus pennanti: 328003 (s)
Lariscus insignis: 498572 (s)
Nannosciurus borneanus: 198077 (p)
Rhinosciurus laticaudatus: 488519 (s)
Sundasciurus hippurus: 488405 (s)
Sundasciurus lowii: 396658 (p)
- Subfamily Xerinae: Ground squirrels and African tree squirrels
- Tribe Xerini: African ground squirrels
Xerus inauris: 368419 (p)
Xerus rutilus: 484010 (p)
- Tribe Protoxerini: African tree squirrels
Epixerus ebii wilsoni: 543105 (p)
Funisciurus anerythrus: 402914 (s), 539401 (p)
Funisciurus pyrropus: 539425 (p)
Heliosciurus rufobrachium: 439137 (s), 439165 (s), 539426 (p), 543110 (p)
Paraxerus cepapi: 295201 (p)
Paraxerus palliatus: 182804 (s)
Paraxerus poensis: 539393 (p), 539394 (p)
Paraxerus vexillarius: 540771 (s)
Protoxerus stangeri: 481824 (p), 539438 (s), 539439 (p), 539440 (s), 539443 (s)
- Tribe Marmotini: Holarctic ground squirrels
Ammospermophilus leucurus: 578030 (p)
Cynomys ludovicianus: 35012 (p), 65030 (s)
Marmota flaviventris: 94251 (s)
Marmota monax: 157613 (s), 191374 (p)
Spermophilus beecheyi: 44259 (s), 484951 (p), 484954 (p), 484955 (p)
Spermophilus columbianus: 81930 (s), 275817 (s), 398302 (p), 398303 (p)
Spermophilus franklinii: 497840 (s)
Spermophilus lateralis: 176460 (s)
Spermophilus mexicanus: 79569 (s)
Spermophilus tridecemlineatus: 48457 (s), 398258 (p)
Spermophilus variegatus: 248462 (p), 349320 (p)
Tamias dorsalis: 501006 (p), 501007 (p)
Tamias minimus: 397141 (p), 527615 (p)
Tamias striatus: 349628 (p), 364947 (p)