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Journal of Mammalogy, Vol. 77, No. 1 (Feb., 1996), 69-83.

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VALIDITY OF THREE GENERA OF FLYING SQUIRRELS: *EOGLAUCOMYS*, *GLAUCOMYS*, AND *HYLOPETES*

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Ellerman (1947) reduced the genus *Eoglaucmys* to a subgenus of *Hylopetes*. Burt (1960) suggested that *Glaucmys sabrinus* was more closely related to *Hylopetes* than to *Glaucmys volans*. We tested these two hypotheses by examining morphological evidence of bacula, foot pads, musculature, crania (especially teeth), and postcrania (especially wrists and ankles). Our data contradict these hypotheses and support recognition of three distinct clades.

Key words: *Eoglaucmys*, *Glaucmys*, *Hylopetes*, flying squirrels, systematics

We investigate two hypotheses about flying squirrels: that Himalayan flying squirrels, subgenus *Eoglaucmys*, are closely related to and should be included in the genus *Hylopetes* from Southeast Asia; and that the North American genus of flying squirrels, *Glaucmys*, is a composite, and the northern *Glaucmys sabrinus* is more closely related to *Hylopetes* than it is to the southern *Glaucmys volans*.

Ellerman (1947) included *Eoglaucmys* in the genus *Hylopetes* with the comment that the differences between them did not seem to be of more than subgeneric importance. This evaluation was followed by Ellerman and Morrison-Scott (1966), McLaughlin (1967), Honacki et al. (1982), McLaughlin (1984), Corbet and Hill (1992), and Hoffmann et al. (1993). It is counter to the evaluation of Thomas (1908), Howell (1915), and McKenna (1962), who considered *Eoglaucmys* closely related to *Glaucmys*, on the basis of similar dental morphology. Thomas (1908) even maintained these flying squirrels in a single genus; but Howell (1915) described *Eoglaucmys* as a distinct genus, and Pocock (1923) documented that the bacula are dramatically different. Most workers (includ-

ing Ellerman, 1940) maintained *Eoglaucmys* as a distinct genus until 1947.

Burt (1960) was the author of the second hypothesis. He showed that the baculum of *G. sabrinus* is very different from the baculum of *G. volans*. On the basis of similarities between bacula of *G. sabrinus* and two species of *Hylopetes*, as figured by Pocock (1923), Burt (1960) argued that *G. sabrinus* was more closely related to *Hylopetes* than to *G. volans*. Based on this evidence, Muul (1968) developed the idea that *G. volans* and *G. sabrinus* invaded North America sequentially. Burt's (1960) observation that the two species of *Glaucmys* have very different bacula has been verified (Wells-Gosling and Heaney, 1984). Also, Hight et al. (1974) reported a significant immunological difference between the two species. However, the two have been retained in the same genus by all subsequent authors. Here we examine the morphology of bacula, foot pads, musculature, crania, and postcrania to test these hypotheses.

MATERIALS AND METHODS

We have studied the morphology of all specimens listed in Appendix I, paying particular attention to cranial morphology, external features visible on skins, bacula as available, wrist and

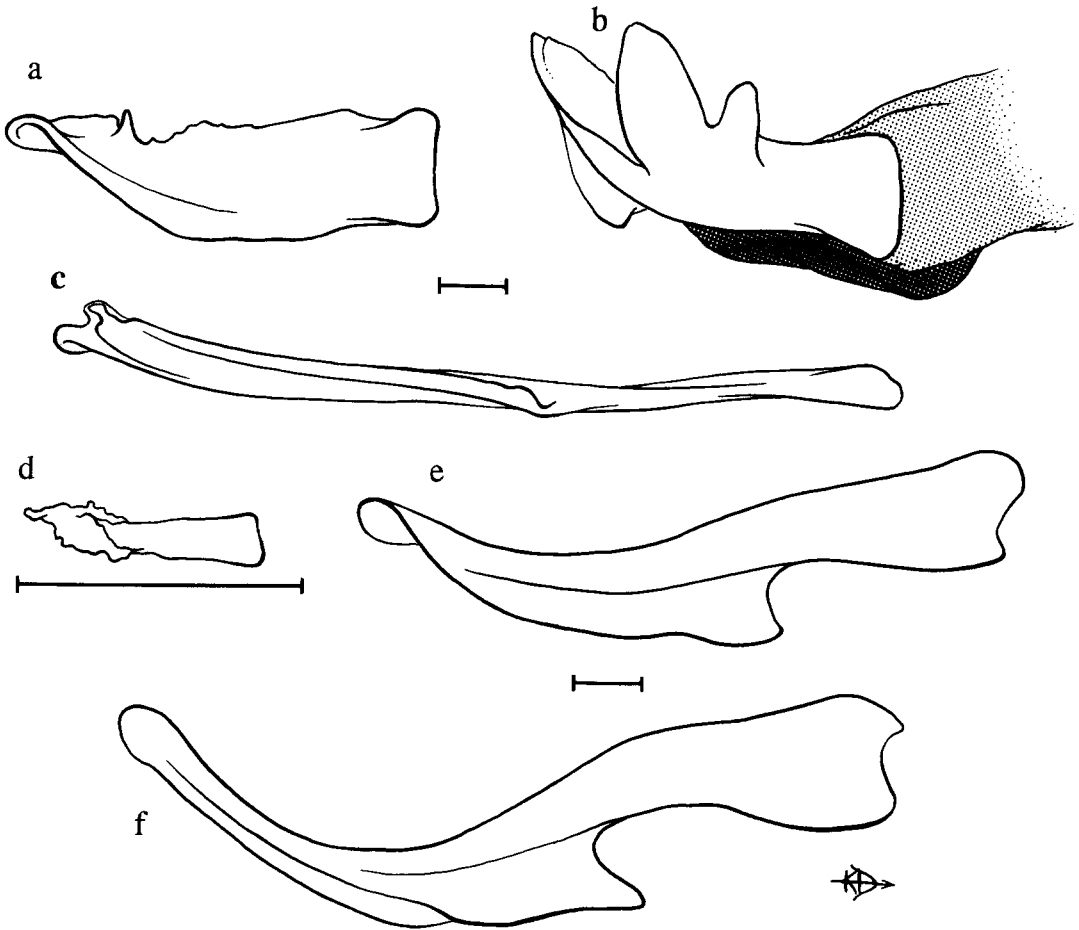


FIG. 1.—Bacula of flying squirrels, left side with distal end at left: a) *Glaucomys sabrinus*; b) *Eoglaucomys fimbriatus*; c) *Glaucomys volans*; d) *Hylopetes spadiceus*; e) *Hylopetes phayrei*; f) *Hylopetes alboniger*. In b, the dark stipple is cartilage, and the pale stipple is muscle. Scale bars are 1 mm. Note that d is shown at a different scale from the other five.

ankle morphology, and selected muscles. Wrists and ankles were removed from dried skins or fluid-preserved specimens, bones were separated one at a time, and all articular surfaces were studied using a microscope. Specimens are from the United States National Museum, (USNM).

In Appendix 1, we also present a brief statement of our taxonomic interpretations. This is particularly important for *Hylopetes* because our usage of names differs from others who have recently studied the genus.

COMPARISONS

Baculum.—Bacula of the three genera have been figured and discussed by Pocock

(1923), Didier (1953), White (1953), Burt (1960), Dolan and Carter (1977), Chakraborty (1981), and Wells-Gosling and Heaney (1984). Our discussion is based on these papers and our independent observations of bacula (Fig. 1). The baculum of *G. volans* is a long, straight, slender rod with a narrow crest on the left side. The crest is variable and seldom as extensive as illustrated by Pocock (1923), but we found it to be present in four of the five specimens we examined. The illustrations of Burt (1960) and Dolan and Carter (1977), drawn from the right side, do not show this crest. We

did not observe a secondary serrated portion at the proximal end of the baculum as figured by Didier (1953). The baculum of *G. sabrinus* differs from *G. volans*; it is laterally compressed, has a spine on its dorsal edge, lacks a crest, and is more spatulate at the distal end. The baculum of *Eoglaucomy*s is a short, stout rod with an irregularly-shaped distal end. In *E. fimbriatus*, the distal end is s-shaped in cross section with a flat mitten-like projection at one end of the "s." The baculum of *E. baberi*, figured by Chakraborty (1981), appears completely different from the baculum of *E. fimbriatus*, figured by Pocock (1923). In fact, these two are not different, but are simply different views of the same morphology, as verified by our specimens. Bacula of *Hylopetes alboniger* and *H. phayrei* are curved rods with a distal crest, which spirals from the left side at the distal tip of the rod to the ventral surface at mid-shaft. Lengths of these bacula, as reported by Pocock (1923) are 13 and 11 mm. In contrast, the baculum of *H. spadiceus* from Viet Nam is a short straight rod, only 1 mm in length.

The primitive morphology of the baculum of flying squirrels is difficult to determine. However, the peculiar shape of the baculum of *Eoglaucomy*s, with its mitten-like projection, probably is derived. Contrary to the assessment of Burt (1960), the baculum of *G. sabrinus* is dissimilar to bacula of *Hylopetes* figured by Pocock (1923); it lacks a crest, it is laterally compressed, and it has a dorsal spine. It also is different from the baculum of *H. spadiceus*. The baculum of *G. volans* is more similar to *H. alboniger* and *H. phayrei* because it has a crest. This is the only trait shared among genera, and because of the different orientations of the crests we are uncertain of the homologies. However, no matter what is primitive, Burt (1960) correctly pointed out that bacula of *G. sabrinus* and *G. volans* are different from one another. Possibly both are derived, as may be the two bacular morphologies in *Hylopetes*. However, the baculum of *Petinomys fuscicapillus* is similar

to bacula of *H. alboniger* and *H. phayrei* (Pocock, 1923), a similarity that could be used to argue that the morphology of *H. alboniger* is primitive for *Hylopetes*.

Foot pads.—Foot pads of flying squirrels were illustrated by Pocock (1922). Our observations of *Eoglaucomy*s and *Glaucomy*s are the same as those illustrated by him in figures 55 and 56. There is no significant variation in pads of the forefoot within or between these two genera and *Hylopetes*. On the hind foot, there are no major differences between the four plantar pads at the base of the digits, but there are significant differences in the metatarsal pads. In *Eoglaucomy*s, there is a small lateral metatarsal pad and a large medial metatarsal pad. In *Hylopetes*, the lateral metatarsal pad is absent, and the medial pad is prominent. In *Glaucomy*s, both metatarsal pads are absent. Because both metatarsal pads are present in diverse tree squirrels and some flying squirrels, we consider the presence of pads primitive and their absence derived, which agrees with Heaney (1985).

Musculature associated with gliding.—Johnson-Murray (1977) compared musculature of *Glaucomy*s, *Pteromy*s, *Petinomys*, and *Petaurista*. Muscles of *Glaucomy*s were studied previously by Bryant (1945) and Gupta (1966). We have additional observations.

No features in gliding musculature clearly allow separation of clades among flying squirrels. Johnson-Murray (1977) illustrated one characteristic that seems to have this potential, the position of humerodorsalis III relative to humerodorsalis I. However, because this feature varies within taxa, as she noted, it is not useful in distinguishing clades. Several muscles show degrees of specialization from primitive to derived, but whether these represent clades or grades of evolution is unclear. One of these muscles is the tibiocarpalis, found only in flying squirrels. Gupta (1966) reported that it originated from the distolateral end of the tibia in *Glaucomy*s. We found that it originated from a distinctive anterior tubercle at the

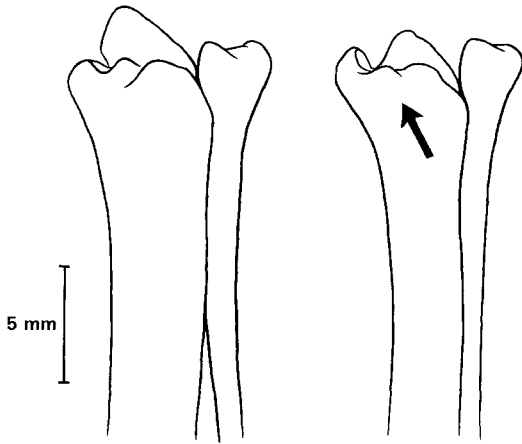


FIG. 2.—Distal end of right tibiae (anterior view) of *Sciurus carolinensis* (left) and *Eoglaucomys fimbriatus* (right). Arrow points to tubercle on *Eoglaucomys* for origin of the tibiocarpalis muscle, found only in flying squirrels.

distal end of the tibia (Fig. 2). The tubercle is present in *Glaucomys*, *Eoglaucomys*, *Hyllopetes*, and *Iomys*; and we have observed the origin of tibiocarpalis from the tubercle in *Glaucomys*, *Eoglaucomys*, and *Hyllopetes*. The tubercle is absent in *Petaurista*, *Eupetaurus*, *Aeromys*, and *Trogopterus*, among flying squirrels, and absent in all other squirrels we have examined. Johnson-Murray (1977) reported that tibiocarpalis originated from the dorsum of metatarsal I in *Pteromys* and from the dorsum of metatarsal II in *Petaurista*. These data can be interpreted in several ways. The origin on the anterior tubercle, on metatarsal I, or on metatarsal II, could each be considered independently derived. Alternatively, the more proximal origin on the anterior tubercle could be considered primitive among flying squirrels and the more distal origins derived. In the latter instance, origins on the foot could be shared-derived or independently derived features. We hypothesize that the gliding membrane migrated gradually during evolution, down the leg to the foot, and that the origin of the tibiocarpalis on the metatarsals is more derived than origin on the tubercle. If the metatarsal insertions differ consistently between taxa, as

suggested by Johnson-Murray (1977), we would treat them as independently derived.

A third feature of the musculature is the insertion of semitendinosus III (Figure 3 in Johnson-Murray, 1977). All squirrels, except flying squirrels, have a bicapital semitendinosus inserting on the tibial crest. In flying squirrels, a third head (semitendinosus III) takes origin from the caudal vertebrae. Its insertion can be divided into two states. In some flying squirrels it fuses with semitendinosus I and II, and insertion on the tibial crest is similar to the condition in tree squirrels. In other flying squirrels, semitendinosus III does not combine with the other heads but inserts independently on the calcaneus, a derived condition never found in tree squirrels. The paper of Johnson-Murray (1977) is somewhat confusing on the distribution of these states because the text does not agree with the labeling of her figure 3. In *Glaucomys*, the fused muscles insert on the tibial crest, as reported. In *H. spadiceus*, semitendinosus III becomes tendinous above the middle of the tibia and inserts on the calcaneus. This condition is similar to the description of Johnson-Murray (1977) of the condition in *Pteromys* and to her illustration of the condition in *Petinomys*. We found an intermediate condition in *Eoglaucomys*. While most of the fibers of semitendinosus III combine with the fibers of semitendinosus I and II to insert on the tibial crest, some fibers of semitendinosus III insert on a long tendon that extends the length of the lower leg to insert on the medial side of the calcaneus.

A fourth feature is the extent of insertion of the humerodorsalis III on the skin of the forearm. Insertion of humerodorsalis III just on the wrist is known only in *Pteromys* (Johnson-Murray, 1977). In *Glaucomys*, the insertion extends the length of the forearm, as illustrated by Gupta (1966). We confirmed this by dissection in *G. volans* and by examining skins of *H. spadiceus*, *H. platyurus*, *Petinomys setosus*, and *P. genibarbis*. When skins of these taxa are held up to the light, the distribution of the opaque

TABLE 1.—Dental characteristics. If *Sciurus* is used as an outgroup (Hight et al., 1974), polarities are changed in two cases; smooth enamel and the absence of the isthmus on the metaloph.

Character	<i>Glaucomys</i>	<i>Eoglaucomys</i>	<i>Hylopetes</i>
Enamel:	Smooth ^a	Irregular	Pitted and grooved ^a
Maxillary teeth:			
Upper PM3	Unicuspid	Bicuspid ^a	Unicuspid
Anterior cingulum	Anteroloph indistinct	Anteroloph distinct ^a	Anteroloph indistinct
Metaloph	Isthmus absent ^a	Isthmus indistinct	Isthmus present
Lateral mesoloph	Absent	Rare	Present ^a in four of five species
Medial mesoloph	Rare	Absent	Present ^a in four of five species
Mandibular teeth:			
Anterior cingulum	pm4 style distinct ^a	pm4 style absent	pm4 style absent
Ectolophids on some teeth	Present	Absent ^a	Present
Fossettes	Small grooves	Prominent ^a	Present, but small

^a Probably derived features, using the fossil *Protosciurus* (Emry and Thorington, 1982) as a primitive outgroup.

muscle fibers can be seen through the more transparent skin.

Teeth.—The dental morphology of flying squirrels was examined previously by McKenna (1962). Here we make detailed comparisons of the three genera, *Glaucomys*, *Eoglaucomys*, and *Hylopetes*, and summarize our conclusions about polarities (Table 1) using the fossil squirrel, *Protosciurus*, as an outgroup.

Enamel varies from smooth to pitted and grooved (Fig. 3). In *Glaucomys*, it is smooth. In *Eoglaucomys*, the enamel is generally smooth, although some grooves are present but inconspicuous in the basin of M3. On the lower teeth, irregularities in the enamel of the basins of m1, m2, and m3, are increasingly prominent posteriorly. While these tend to wear into pits and grooves, they are not patterned as in *Hylopetes*. In *Hylopetes*, pits and grooves are conspicuous on all teeth. The teeth of *H. spadiceus*, *H. platyurus*, and *H. nigripes* are etched with shallow, pin-prick pits, and in *H. alboniger* and *H. phayrei*, the enamel is more deeply grooved. Grooves and pits

tend to be arranged in dense parallel rows, giving a distinctly patterned appearance.

Maxillary teeth.—Among the maxillary teeth, the third premolar varies from being a single cusp to being bicuspid. This is obvious in unworn teeth, but the distinction becomes obscured with wear. In *Glaucomys*, PM3 is unicuspid. In *Eoglaucomys*, PM3 is grooved on the lingual side and, in four of seven specimens examined, is bicuspid. PM3 is unicuspid in *Hylopetes*.

PM4, M1, and M2 have a single buccal loph, formed either from a protocone alone or from a fused protocone and hypocone. They have an anterior cingulum, a protoloph connecting the protocone with the paracone, and a metaloph connecting the protocone with the metacone. Variation occurs in the extent to which protoloph and metaloph connect directly to protocone or are separated from it by a narrow groove. A mesostyle may be present between paracone and metacone, and it may have a mesoloph associated with it. A medial mesoloph may also occur, connected with protocone and lying between protoloph and

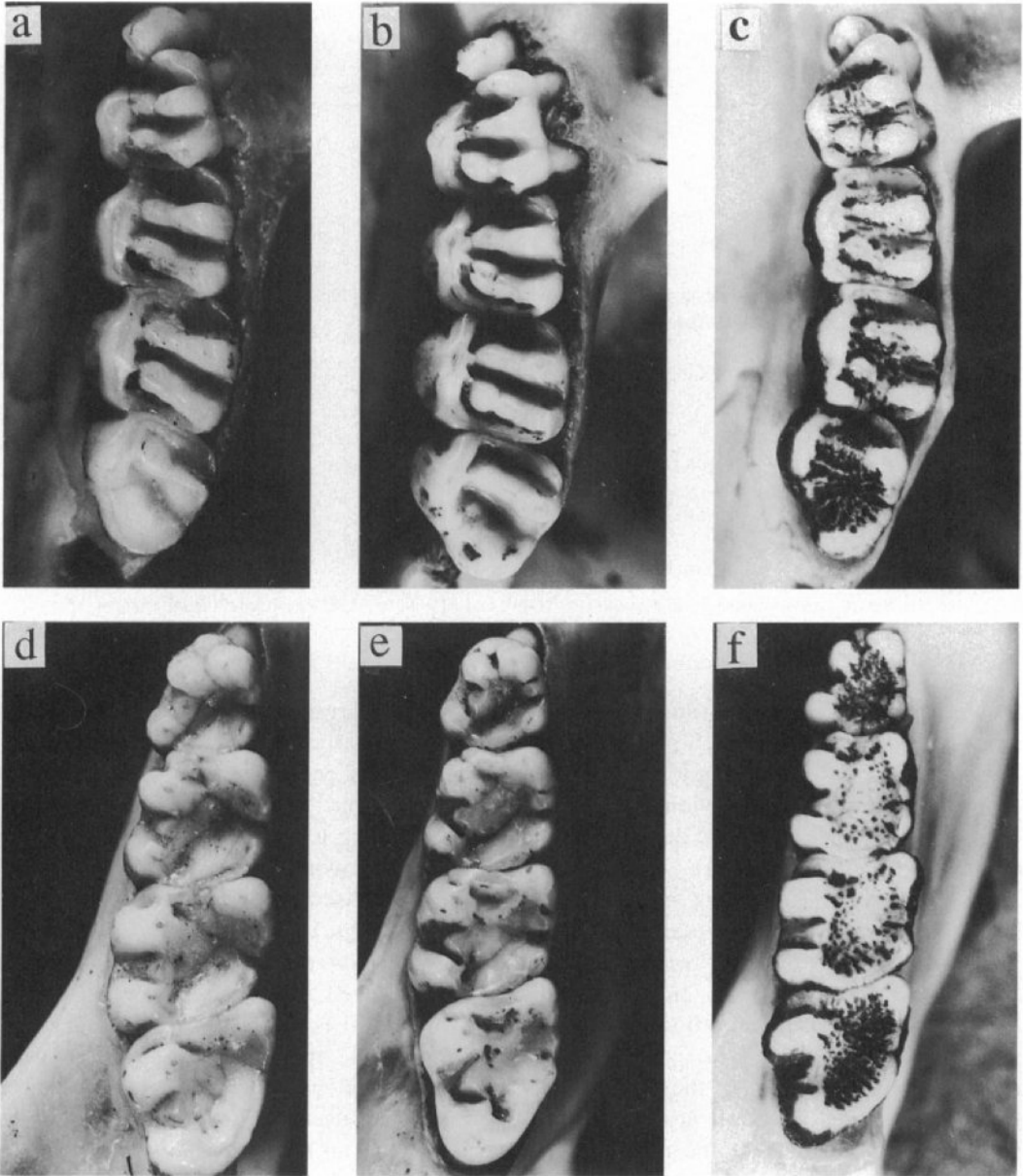


FIG. 3.—Left maxillary (a–c) and mandibular (d–f) toothrows: a,d) *Glaucomys sabrinus*; b,e) *Eoglaucmys fimbriatus*; c,f) *Hylopetes spadiceus*.

metaloph, but not connected to the mesostyle.

On the anterior cingulum, the parastyle varies from prominent to absent, usually in an anterior to posterior gradient. In *Glaucomys*, there is a distinct parastyle on both

PM4 and M1, but it is not connected by an anteroloph to the protocone. On M2, the parastyle is less distinct and, on M3, is indistinct. In *Eoglaucmys*, PM4 and M1 have both a distinct parastyle and a distinct anteroloph connecting it to the protocone.

On M2 and M3, the parastyle and the anteroloph are progressively less distinct. The distinctness of the anteroloph is due in part to the depth of the basin lying between it and the protoloph. PM4 and M1 in *Hylopetes* appear as in *Glaucomys*, except that the parastyle is indistinct on M1 of *H. platyurus* and indistinct on M2 of all five species. In *H. nigripes*, the basin between the anteroloph and the protoloph is almost as deep as in *Eoglaucmys*, but the anteroloph does not connect to the protocone.

A protoloph is present on PM4, M1, M2, and M3 of all three genera. It exhibits little variation except for the presence or absence of a small protoconule. In *Glaucomys*, there is a small protoconule present on the protoloph of PM4 in some *G. sabrinus*. In *Eoglaucmys*, small protoconules are only rarely present. In *Hylopetes*, protoconules are absent, but there is usually a narrow isthmus on the protoloph close to the protocone.

A metaloph is present on PM4, M1, and M2 of all three genera, but varies in its connection to the protocone and in the presence or absence of metaconules. In *Glaucomys*, the metaloph is present as a continuous loph between metacone and protocone, but is sometimes notched near the protocone. There is not a distinct isthmus connecting the metaloph with the protocone. In both species of *Glaucomys*, there also is a metaconule present on PM4. In *Eoglaucmys*, the metaloph is deeply notched near the protocone. Metaconules are present on PM4 and M1. In *Hylopetes*, the metaloph is notched close to protocone on PM4, M1, and M2 of *H. alboniger* and *H. phayrei*, only on PM4 of *H. nigripes*, but not at all in *H. spadiceus* and *H. platyurus*. The metaloph usually is connected by a narrow isthmus to the protocone (in *H. nigripes*, the isthmus is seen only on PM4). There is a metaconule present on PM4 of *H. alboniger*, *H. nigripes*, *H. spadiceus*, on PM4, M1, and M2 of *H. phayrei*. Metaconules are absent in *H. platyurus*.

A mesostyle sometimes is present and

may or may not be accompanied by a mesoloph. In *Glaucomys*, there is a mesostyle present on PM4, M1, and M2 of *G. volans*, and, in *G. sabrinus*, a mesostyle is present on PM4, but sometimes absent on M1 and M2; in both species the mesoloph is absent. In *Eoglaucmys*, a mesostyle rarely is present on PM4 (one of seven), and M1 (two of seven), and only weak to moderate on M3 (seven of seven). A weak mesoloph is only rarely present (one of seven). In *Hylopetes*, both mesostyles and mesolophs are present on PM4, M1, M2, and M3 of *H. alboniger* and *H. phayrei*; on PM4 and M1 of *H. spadiceus*; on PM4 (one of six), M1 (six of six) and M2 (one of six) of *H. platyurus*. A mesostyle without an accompanying mesoloph is occasionally present (two of five) on PM4 of *H. nigripes*.

A medial mesoloph sometimes is present extending from the protocone toward the mesostyle. Its presence is correlated with the presence of a mesostyle. In *Glaucomys*, presence of a medial mesoloph is rare (*G. volans*, one of four; *G. sabrinus*, zero of five) and in *Eoglaucmys* it is absent (zero of seven). In *Hylopetes*, the medial mesoloph is absent on *H. nigripes*; present on PM4, M1, M2, and M3 of *H. alboniger*, *H. phayrei*, and *H. spadiceus*; and present on M1, M2, and present but weak on M3 (three of five) in *H. platyurus*.

Mandibular teeth.—On the mandibular teeth, there is variation in the anterior cingulum of pm4, in the presence of fossettes at the anterior edge of the molars, and in the presence or absence of stylids on the buccal and lingual sides of the teeth. On the anterior cingulum of pm4 a free standing cusp may be present. In *Glaucomys*, there is a prominent cingulum with a free standing cusp in *G. sabrinus* and in some *G. volans* (two of four). In *Eoglaucmys*, the cingulum is distinct, but lacks a free-standing cusp. In *Hylopetes*, the cingulum is distinct and without a free-standing cusp in *H. nigripes*, *H. phayrei*, *H. platyurus*, and *H. spadiceus*. The cingulum is indistinct in *H. alboniger*.

Fossettes or grooves may occur anterior and medial to protoconid. In *Glaucomys*, grooves are present. These are deeper in *G. sabrinus* than in *G. volans*. In *Eoglaucmys*, there are prominent fossettes anterior and medial to protoconid on m1, m2, and m3. In *Hylopetes*, where fossettes are present, they appear more like deep crenulations than like the fossettes of *Eoglaucmys*. Small, but distinct, fossettes occur on m1, m2, and m3 of *H. alboniger* and *H. phayrei*, sometimes on m1 of *H. spadiceus*, on m3 of *H. platyurus*, and on m1 and m2 of *H. nigripes*.

Ectostylids generally are present on the buccal side of the teeth, but are not always accompanied by an ectolophid. In *Glaucomys*, there is an ectostylid present on pm4, but it lacks an ectolophid. In m1 and m2, an ectostylid is present and an ectolophid extends from stylid to labial margin. Both ectostylid and ectolophid are weak on m3. In *Eoglaucmys*, an ectostylid is present on pm4, m1, m2, and m3. An ectolophid is absent, so there appears to be a shelf between the base of the ectostylid and the labial margin of the tooth. In *Hylopetes*, ectostylids and ectolophids are prominent on all teeth in *H. alboniger* and *H. phayrei*. In *H. platyurus*, an ectostylid with ectolophid occurs on m1, m2, and m3, but on pm4, the ectolophid is absent. In *H. spadiceus*, ectostylid and ectolophid occur on m2 and m3; a weak ectostylid occurs without ectolophid on pm4 and m1. In *H. nigripes*, ectostylid occurs with a weak ectolophid on all teeth.

Mesostylids vary from absent to distinct and when present are most prominent on the anterior mandibular teeth. In *Glaucomys*, a mesostylid is absent in *G. volans* and present only weakly on pm4 and m1 of *G. sabrinus*. In *Eoglaucmys*, the mesostylid is distinct on pm4, m1, and m2, but only sometimes distinct on m3 (three of seven). In *Hylopetes*, the mesostylid is distinct on pm4, m1, and m2 of *H. alboniger* and *H. spadiceus*, weak on pm4, m1, and m2 of *H.*

nigripes, and distinct only on pm4 and m1 of *H. phayrei* and *H. platyurus*.

In summary, the teeth of *Glaucomys* are distinguished by smooth enamel, distinct cusp on anterior cingulum of pm4, and fossettes present only as grooves. *Eoglaucmys* is distinctive because of its irregular enamel, bicuspid PM3, distinct anteroloph, the absence of ectolophids, and presence of prominent fossettes. *Hylopetes* is distinguished by its pitted and grooved enamel, the distinct isthmus on the metaloph, and presence of small fossettes.

Wrist morphology.—In squirrels, the proximal joint of the wrist lies between the two bones of the forearm and three carpal bones. Radius articulates with scapholunate, and ulna articulates with a socket formed by triquetrum and pisiform. In non-gliding squirrels, there is a ligamentous connection between radius and ulna that permits movement at their distal end. In pronation and supination, radius rotates relative to the distal end of ulna, changing the relative position and orientations of these two bones. The corresponding movement between scapholunate and the combined triquetrum and pisiform is allowed by the joint between scapholunate and triquetrum. In flying squirrels, the distal ends of radius and ulna are tightly bound in a syndesmosis and there is no movement possible between these two bones. Pronation and supination are accomplished by rocking the ulna at the elbow joint. This eliminates the need for movement between scapholunate and triquetrum in these species, and permits evolution of the distinctive morphology of the flying-squirrel wrist.

All flying squirrels share a number of derived features in the wrist (Thorington, 1984), among which is the articulation of pisiform with scapholunate. In the primitive condition, which exists in most mammals, pisiform articulates with triquetrum and not with the lunate or scapholunate. In all flying squirrels examined, a process of the pisiform (Fig. 4) articulates with the ulnar side of scapholunate (Fig. 5), forming a triangle

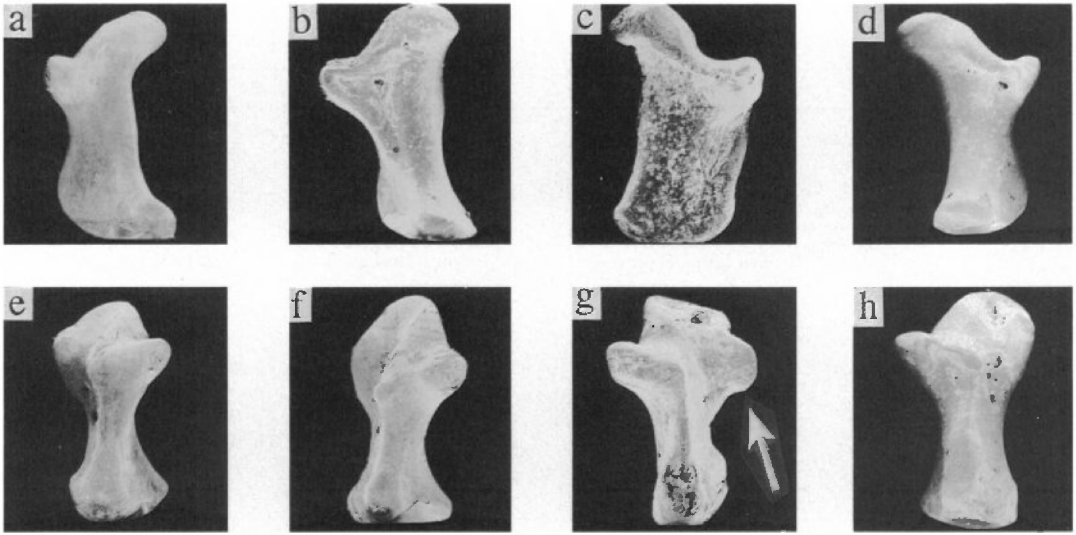


FIG. 4.—Proximal (a–d) and ulnar (e–h) views of pisiform bones, with dorsal surface up (dorsal-palmar height given in parentheses): a,e) *Glaucomys sabrinus*, left side (3.5 mm); b,f) *Glaucomys volans*, left side (2.5 mm); c,g) *Hylopetes spadiceus*, right side (2.8 mm); d,h) *Eoglaucomys fimbriatus*, right side (5.4 mm). Arrow in g points to distinctive flange on *Hylopetes*.

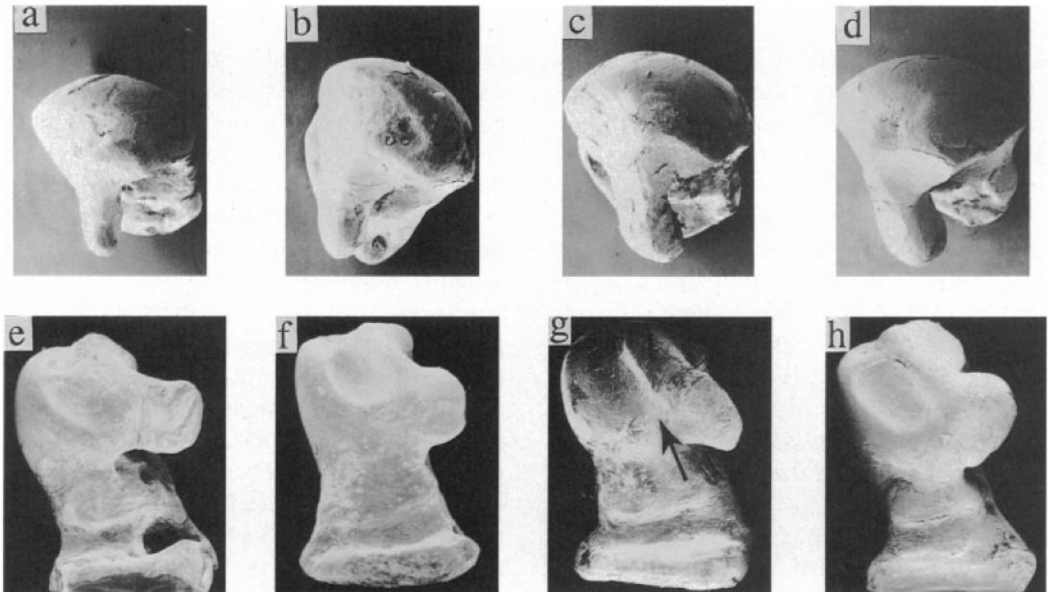


FIG. 5.—Scapholunate bones; ulnar views, proximal side up (a–d) and palmar views, proximal side on the left (e–h) with ulnar-radial width given in parentheses: a,e) *Glaucomys sabrinus* (3.1 mm); b,f) *Glaucomys volans* (2.6 mm); c,g) *Hylopetes spadiceus* (2.7 mm); d,h) *Eoglaucomys fimbriatus* (5.6 mm). Arrow in g points to distinctive groove on *Hylopetes*.

TABLE 2.—*Summary of differences in carpal bones. The shared states of Glaucomys and Eoglaucomys are all considered to be primitive.*

Bone	<i>Glaucomys</i>	<i>Eoglaucomys</i>	<i>Hylopetes</i>
Pisiform	Twisted	Twisted	Relatively untwisted
Flange for triquetral articulation	Absent	Absent	Present
Scapholunate	Triquetral facet extends onto hamate process	Does not extend onto process	Extensive facet on process
Centrale-hamate articulation	Almost	Present	Extensive
Scapholunate-capitate articulation	Present	Present	Absent
Centrale-metacarpal II articulation	Present	Present	Absent, except in <i>H. nigripes</i>

of articulations between the three bones and eliminating movement between them. This process and the articulation are not the same in all flying squirrels, however (Table 2). If pisiform is examined from the proximal side, its dorsal end has the shape of an inverted boot (Fig. 4). The toe is the process that articulates with scapholunate and the instep forms part of the articulation for ulna. In all three genera, the body of pisiform is twisted, so that the palmar crest lies at a different angle from the axis of the boot. In *Hylopetes*, the twisting is slight, but in *Glaucomys* and *Eoglaucomys*, the twisting of pisiform causes the crest to lie almost 90° from the axis of the boot. On its distal surface, pisiform articulates with triquetrum. In *Hylopetes* alone, there is an additional flange on the radial side of the bone for this articulation (Fig. 4g). Thus, in shape and position of articular surfaces, *Glaucomys* and *Eoglaucomys* are similar and both differ from the derived morphology of *Hylopetes*.

There is a difference in the articulation of scapholunate with pisiform between these two groups. In *Glaucomys* and *Eoglaucomys*, the facet on scapholunate is similar to the bowl of a spoon, near and extending onto the hamate process of scapholunate (Fig. 5). In *Hylopetes*, the facet

is a distinct and more extensive groove on the proximal surface of the hamate process, suggesting that this is a stronger articulation between the two bones.

Pisiform bone articulates with triquetrum. The primitive morphology for flying squirrels is probably that found in most other mammals; a simple small articulation, commonly trapezoidal in shape, lying adjacent to the articular surface for ulna. In flying squirrels, this articulation appears to be reinforced by a more extensive facet, commonly a ventral strip, between the two bones. This reinforcement is associated with the attachment of styliiform cartilage to both bones. In gliding position, the wrist is strongly dorsi-flexed and inverted, and the styliiform cartilage forms the curved tip of the flight membrane. The stability of the base of the cartilage is a significant feature of the wrist of flying squirrels because of its aerodynamic importance. In *Glaucomys*, *Eoglaucomys*, and *H. nigripes*, the ventral extension of the facet lies along a ridge on triquetrum, which fits in a groove on the distal side of pisiform. In *H. spadiceus*, the ventral extension of triquetrum does not articulate with a groove, but rather it wraps around a small distal process of pisiform. In *H. phayrei*, there is strong ligamentous bonding of the ridge and groove, but there

is no bone-to-bone articulation. Thus, except for the presence of the distinctive flange on pisiform in *Hylopetes*, the variability of pisiform-triquetral articulation is not useful in distinguishing between the three genera.

Articulation between triquetrum and scapholunate lies near the dorsal surface of both bones in most mammals and in some flying squirrels. This is probably the primitive condition for flying squirrels. In some species, the articulation migrates ventrally onto the hamate process of scapholunate. This migration is least in *Eoglaucomys*, more in *Glaucomys*, and most extensive in *Hylopetes*. In *Hylopetes*, a groove at the ventral end of the facet on triquetrum articulates with the ulnar edge of the hamate process of scapholunate (Fig. 5). In *H. nigripes* and *H. phayrei*, articulation extends about one-half way down the process, and in *H. spadiceus*, it extends even further.

The midcarpal joint lies between two carpals of the proximal row (scapholunate and triquetrum) and four carpals of the distal row (hamate, capitate, lesser multangular, and greater multangular). Centrale lies between the two rows, in the middle of the joint. Ventrally, centrale is tightly bound by ligaments to scapholunate, but it exhibits no tendency to fuse with scapholunate in any squirrels we have studied. Articulations of centrale vary significantly among squirrels. Among tree squirrels, centrale seems never to articulate with hamate. In some flying squirrels, such as the two species of *Glaucomys*, centrale and hamate almost articulate. In *Eoglaucomys*, the two carpals definitely articulate, but just barely. In these two genera, there is a distinct articulation between capitate and scapholunate. In *Hylopetes*, however, articulation between centrale and hamate completely blocks the articulation of capitate with scapholunate.

Articulation between centrale and metacarpal II also is variable. In almost all squirrels, metacarpal II extends proximally between capitate and lesser multangular, where it articulates with centrale. This ar-

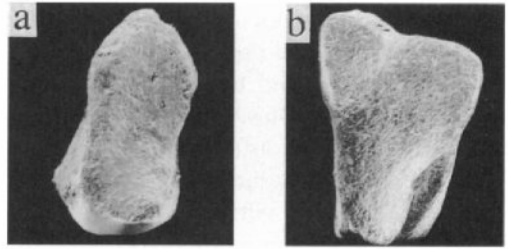


FIG. 6.—Radio-distal views of centrale, dorsal side up (dorsal-palmar height given in parentheses): a) *Hylopetes spadiceus* (1.0 mm); b) *Eoglaucomys fimbriatus* (2.1 mm). Note distinctive facet on upper left corner of b for articulation with metacarpal II. This is absent in *Hylopetes*.

ticulation is found in *Glaucomys*, *Eoglaucomys*, and in *H. nigripes* (Fig. 6). In some flying squirrels, centrale and metacarpal II do not touch, although they come close to one another when the wrist is dorsi-flexed. This condition is seen in *H. alboniger*, *H. phayrei*, *H. spadiceus*, and *H. platyurus*.

In the midcarpal joint, centrale articulates with both lesser and greater multangular bones. In *Glaucomys* and *Eoglaucomys*, the articulating facet between lesser multangular and centrale is only slightly twisted. In *Hylopetes*, the facet is much more strongly twisted; the plantar portion on the centrale faces distally and the dorsal portion faces radially. Articulation of centrale with greater multangular varies; it is almost absent in *G. volans*, a prominent elliptical facet on *G. sabrinus* and *Hylopetes*, and a more extensive facet on *Eoglaucomys*. Our observations are summarized in Table 2.

Foot morphology.—Morphology of the foot in flying squirrels is conservative and in most features similar to the morphology of *Sciurus*. However, as noted by Bryant (1945), flying squirrels do not show as deep a pit on the dorsal surface at the base of the neck of the astragalus. This condition is seen in *Protosciurus* and in North American ground squirrels and is, therefore, probably primitive while the deep pit seen in *Sciurus* probably is derived.

The cuboid articulates medially with cu-

neiform III and navicular. In *Sciurus*, the dorsal articulation of cuneiform III with cuboid is separate from the more plantar articulation of navicular. In all three genera of flying squirrels, articulations of cuneiform III and navicular are contiguous. A plantar articulation between cuneiform III and cuboid is present in all three genera of flying squirrels, but is variable among species of *Sciurus*. In casts of *ProtoSciurus*, these articulations are unclear so the polarity of these characters is presently unknown.

Proximal processes of metatarsals I and V appear to be derived in flying squirrels. The proximal process of metatarsal V, for insertion of the peroneus brevis muscle, is elongate relative to those seen in tree squirrels. The proximal process of metatarsal I, for the insertion of the peroneus longus muscle is directed more proximally and less laterally in flying squirrels than in tree squirrels. Both these features are present in *Glaucomys*, *Eoglaucomys*, and *Hylopetes*.

DISCUSSION

The evidence presented in this paper support the independence of the three genera *Glaucomys*, *Eoglaucomys*, and *Hylopetes*. *Glaucomys* is distinguished by five derived characters: absence of both medial and lateral metatarsal pads, smooth enamel, a distinct style on pm4, and lack of an isthmus on metaloph. *Eoglaucomys* is distinguished by five derived characters; insertion of semitendinosus III on both tibia and calcaneus, a bicuspid PM3, a distinct anteroloph, absence of ectolophids, and presence of prominent fossettes. *Hylopetes* is distinguished by eight derived characters; absence of lateral metatarsal pad, insertion of semitendinosus III on calcaneus alone, pitted and grooved enamel, a relatively untwisted pisiform, presence of a flange on pisiform for articulation with triquetrum, an extensive triquetral facet on the hamate process of scapholunate, an extensive articulation between centrale and hamate, and ab-

sence of a scapholunate-capitate articulation.

No shared-derived characters support Ellerman's (1947) hypothesis that *Eoglaucomys* is closely related to *Hylopetes*. In two characters, insertion of semitendinosus III muscle and presence of a centrale-hamate articulation, *Eoglaucomys* is intermediate between the primitive state exhibited by *Glaucomys* and the derived state of *Hylopetes*. This provides weak support for Ellerman's hypothesis. The hypothesis is contradicted by two other characters; medial mesoloph and triquetral facet on scapholunate, in which *Glaucomys* is intermediate between the primitive state of *Eoglaucomys* and the derived state of *Hylopetes*.

The derived features of *Glaucomys*, shared by both species, contradict the hypothesis of Burt (1960) that *G. sabrinus* is more closely related to *Hylopetes* than to *G. volans*. Furthermore, *G. sabrinus* does not share any derived features with *Hylopetes*.

Neither of the hypotheses of Ellerman (1947) and Burt (1960) appear tenable. The evidence supports the argument that all three genera have had long independent histories and that *Glaucomys*, *Eoglaucomys*, and *Hylopetes* should be retained as distinct genera of flying squirrels.

ACKNOWLEDGMENTS

An earlier version of this manuscript was reviewed by L. R. Heaney, R. S. Hoffmann, and V. L. Roth, whose substantive and critical comments have helped us improve it. Figs. 1 and 2 were drawn by K. Darrow. Photographs for Fig. 3 were taken by D. Schmidt.

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Submitted 5 December 1994. Accepted 13 April 1995.

Associate Editor was Patricia W. Freeman.

APPENDIX I

Taxonomic interpretations.—*Hylopetes* is a genus of ca. 10 species (Corbet and Hill, 1992). They are characterized by the pitted and grooved enamel of their teeth, a simple dental pattern with hypocone absent, and the two septa in their tympanic bullae. Having two septa in the bullae is probably a primitive feature of flying squirrels, as in other squirrels (Thorington et al., in

press). The simple dental pattern also may be primitive. The pitted and grooved enamel is probably a derived feature (Table 1), but it is found in Oligocene fossils reputed to be flying squirrels (de Bruijn and Unay, 1989). Thus, none of these features argues persuasively that members of this genus are closely related to each other. Features of the carpal bones (Table 2) do appear to be derived characters defining the genus.

Among the species of *Hylopetes*, we have studied five. There are at least two species on the mainland of Asia that exhibit the following characteristics; they lack an inflation of the mastoid bone and they have prominent mesostyles on their upper premolar 4 and molars 1 and 2. These two are *Hylopetes alboniger* and *Hylopetes phayrei*. The former has relatively small bullae and the latter has large bullae. According to Pocock (1923), they have similar bacula (Fig. 1). Although all their shared characteristics could be primitive, their many detailed morphological similarities suggest that these two species are closely related. On the Malay Peninsula, there are two species (Muul and Liat, 1971) that share the following characteristics: the mastoid bone is greatly inflated and mesostyles on their premolar 4 and molars 1 and 2 are small to absent. We call the larger species *Hylopetes spadiceus* and the smaller species *Hylopetes platyurus*. There has been much confusion about the application of names to these species. Hill (1962) recognized two species, *Hylopetes spadiceus* with relatively larger bullae and *Hylopetes lepidus* (including *H. platyurus*) with relatively smaller bullae. We think that the name *H. lepidus* (with a type locality in Java) should be restricted to the animals from Borneo and Java, which have only slightly inflated mastoids. Our usage differs from that of Muul and Liat (1971) and Askins (1977), who use the name *H. lepidus* for the larger species and *H. platyurus* for the smaller species. In the Philippines, there is another species of this genus, *Hylopetes nigripes*, a large species with mastoid only slightly inflated and with mesostyles absent on the molars. Corbet and Hill (1992) suggest that *Hylopetes nigripes* is a subspecies of *Hylopetes alboniger*, but the absence of mesostyles makes this seem unlikely. The species, *bartelsi*, *sipora*, and *winstoni*, which we have not studied, probably are assignable to *Hylopetes* (Corbet and Hill, 1992).

Eoglaucomys, either as a genus or a subgenus,

contains one or two species, *baberi* and *fimbriatus* (Chakraborty, 1981). It has a simple dental morphology, with the hypocone absent and almost no pits and grooves on its teeth. It lacks any inflation of the mastoid and usually lacks mesostyles on its upper molars. The bacula have been figured by Pocock (1923) and by Chakraborty (1981). The former shows the side views, with the cartilage removed. The latter illustrates a ventral view with the cartilage in place (Fig. 1). The relatively smaller premolar of *Eoglaucomys fimbriatus*, described and illustrated by Chakraborty (1981), appears to be a deciduous PM4, compared to the permanent PM4 of his *Eoglaucomys baberi*. Thus, we believe that the evidence for separating *Eoglaucomys baberi* as a distinct species should be reexamined. We identify our specimens as *Eoglaucomys fimbriatus*.

Specimens examined (USNM).—Aeromys. Tibia: 196743. *Eoglaucomys fimbriatus*. Skulls: 35490; 173361; 173362; 201086; 353243; 353245; 353246. Bacula: 326364; 353231; 353232; 353234; 353236. Foot pads: 173361–173368; 326363–326365; 353230–353233. Tibia: 173365. *Glaucomys volans volans*. Skulls: 72572; 72934. Bacula: 397075; 457978. Tibia: 397082; 397083; 397105; 505618; 505623; 536967. Musculature: 457978. *Glaucomys volans oaxacensis*. Bacula: 329702; 329703. *Glaucomys v. querceti*. Skulls: 61798; 309248. Foot pads: 72572; 72574; 72933; 78695; 111305; 194002; 194003. Baculum: 397035. *Glaucomys v. guerreroensis*. Foot pads: 329701; 329702; 329703. *Glaucomys v. saturatus*. Tibia: 325962. Foot pads: 178361–178364; 178367; 178368. *Glaucomys sabrinus sabrinus*. Skulls: 25354; 193999. Foot pads: 233271; 243062; 243063. *Glaucomys s. macrotis*. Tibia: 524544; 551841. *Glaucomys s. yukonensis*. Skulls: 210286; 234675; 242498; 242501. Foot pads: 241745; 241746; 246077. *Glaucomys s. zaphaeus*. Foot pads: 15509; 136135; 136136; 136138; 136139. *Hylopetes alboniger lenonardi*. Skulls: 37875; 253608. Foot pads: 253611. *Hylopetes nigripes*. Skulls: 477992; 477995; 477997; 477998; 478009. Foot pads: 478002–478010. *Hylopetes phayrei*. Skulls and foot pads: 261083; 294889; 294893. *Hylopetes platyurus*. Skulls and foot pads: 488618; 488626; 488629; 488635; 488636. *Hylopetes spadiceus*. Skulls and foot pads: 488656; 488639; 488664; 489453; 489456. Baculum: 321151. Muscula-

ture: 321151. *Iomys horsfieldii*. Tibia: 292654. *Petaurista batuana*. Tibia: 49660. *Petaurista elegans banksi*. Tibia: 292647. *Petaurista grandis*. Tibia: 307073. *Petaurista lylei*. Tibia: 257844. *Petaurista* sp. Tibia: 254807. *Trogopterus xanthipes*. Tibia: 258520, 268872.

Specimens illustrated.—*Eoglaucmys fimbriatus*. Teeth: 35490. Carpals: 353243. Baculum: 353232. Tibia: 173365. *Glaucmys sabri-*

nus. Carpals: 235940. Baculum: 108665(?). *Glaucmys sabrinus yukonensis*. Teeth: 242501. *Glaucmys volans*. Pisiform: 525962. Scapholunate: 536967. Baculum: 273523. *Hylopetes spadiceus*. Teeth: 489453. Carpals: 488638. Baculum: 321151. *Hylopetes phayrei*. Baculum: redrawn from Pocock (1923). *Hylopetes alboniger*. Baculum: redrawn from Pocock (1923). *Sciurus carolinensis*. Tibia: 505573.