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Glaucomys sabrinus.

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Glaucomys sabrinus (Shaw, 1801)

Northern Flying Squirrel

Sciurus hudsonius Gmelin, 1788:153. Type locality mouth of Severn River, Ontario. A homonym of *Sciurus hudsonius* Gmelin, *antea*, p. 147, which is assignable to *Tamiasciurus hudsonicus* (Erxleben, 1777).

Sciurus sabrinus Shaw, 1801:157. A renaming of *Sciurus hudsonius* Gmelin.

?*Pteromys canadensis* E. Geoffroy Saint-Hilaire, 1803:170. Type locality from North America, probably Quebec.

Sciurus labradorius Ord, 1815:292. Nomen nudum.

Pteromys alpinus Richardson, 1828:519. Type locality Jasper House, Alberta.

Pteromys oregonensis Bachman, 1839:101. Type locality from pine woods of the Columbia, near the sea. Probably near St. Helens, Columbia Co., Oregon (Rhoads, 1897).

Sciuropterus yukonensis Osgood, 1900:25. Type locality Camp Davidson, Yukon River, near Alaska-Canada boundary, Yukon.

Glaucomys bullatus A. H. Howell, 1915:113. Type locality Sawtooth (=Alturas) Lake, E base of Sawtooth Mountains, Idaho.

CONTEXT AND CONTENT. Order Rodentia, Suborder Sciuromorpha, Superfamily Sciuroidea, Family Sciuridae, Subfamily Petauristinae (Simpson, 1945). The genus *Glaucomys* consists of two Recent species, *G. volans* (Linnaeus, 1758) and *G. sabrinus* (Shaw, 1801). Twenty-five subspecies were recognized by Hall (1981) as follows:

G. s. alpinus (Richardson), 1828:519, see above.

G. s. bangsi (Rhoads), 1897:321. Type locality Raymond, Idaho Co., Idaho (*bullatus* Howell, a synonym).

G. s. californicus (Rhoads), 1897:323. Type locality near Squirrel Inn, 5,200 ft, San Bernardino Mountains, San Bernardino Co., California.

G. s. canescens Howell, 1915:111. Type locality Portage la Prairie, Manitoba.

G. s. coloratus Handley, 1953:191. Type locality Bald Knob, 5,000 ft, 3.5 mi S summit of Mt. Mitchell, Yancey Co., North Carolina.

G. s. columbiensis Howell, 1915:111. Type locality Okanagan, British Columbia.

G. s. flaviventris Howell, 1915:112. Type locality head of Bear Creek, 6,400 ft, Trinity Co., California.

G. s. fuliginosus (Rhoads), 1897:321. Type locality Cascade Mountains, near Martin Station, about 8,000 ft, Kittitas Co., Washington.

G. s. fuscus Miller, 1936:143. Type locality Cranberry Glades, 3,300 ft, Pocahontas Co., West Virginia.

G. s. goodwini Anderson, 1943:55. Type locality Berry Mountain Camp, junction Berry Mountain Brook and Grand Cascapedia River, about 1,500 ft, Matane Co., Quebec.

G. s. gouldi Anderson, 1943:56. Type locality Frizzleton, Inverness Co., Cape Breton Island, Nova Scotia.

G. s. griseifrons Howell, 1934:64. Type locality Lake Bay, Prince of Wales Island, Alaska.

G. s. klamathensis (Merriam), 1897:225. Type locality Fort Klamath, 4,200 ft, Klamath Co., Oregon.

G. s. lascivus (Bangs), 1899:69. Type locality Tallac, El Dorado Co., California.

G. s. latipes Howell, 1915:112. Type locality Glacier, British Columbia.

G. s. lucifugus Hall, 1934:1. Type locality 12 mi E Kamas, Summit Co., Utah.

G. s. macrotis (Mearns), 1898:353. Type locality Hunter Mountain, 3,300 ft, Catskill Mountains, Greene Co., New York.

G. s. makkovikensis (Sornborger), 1900:48. Type locality Makkovik, Labrador.

G. s. murinauralis Musser, 1961:120. Type locality Timid Springs, 10,300 ft, 1 mi N Big Flat Guard Station, Tushar Mountains, Beaver Co., Utah.

G. s. oregonensis (Bachman), 1839:101, see above. (*olympicus* Elliot, a synonym).

G. s. reductus Cowan, 1937:79. Type locality Lonesome Lake, Atnarko River, approximately 52°10'N, 125°45'W, British Columbia.

G. s. sabrinus (Shaw), 1801:157, see above (*canadensis* E. Geoffroy Saint-Hilaire, may be a synonym according to Howell, 1918:31).

G. s. stephensi (Merriam), 1900:151. Type locality Sherwood, 2,500 ft, Mendocino Co., California.

G. s. yukonensis (Osgood), 1900:25, see above.

G. s. zaphaeus (Osgood), 1905:133. Type locality Helm Bay, Cleveland Peninsula, southeastern Alaska.

DIAGNOSIS. *Glaucomys sabrinus* (Figs. 1 and 2) is the larger of the two species of *Glaucomys* with total length more than 260 mm (Hall, 1981). This species is distinguished from *G. volans* by hairs on the venter being grayish-white at the tips and lead gray (plumbeous) at the base, rather than white at the base. Greatest length of skull is 36 mm or more (less than 36 mm in *G. volans*; Jackson, 1961). The tail is uniform grayish buff and dark apically, whereas in *G. volans* it is paler below without a dark tip (Jackson, 1961). The hindfoot is 34 mm or more (32 mm or less in *G. volans*; Howell, 1918).

The baculum (Fig. 3) is relatively short, broad, and in dorsal view is sinusoidal. Its base is concave from an end view. The right side is concave and the left side is convex for about two-thirds of the length; following a constriction the left side becomes concave, then the concavity is twisted to the upper surface so that the tip is spoon-like. There is a prominent tooth-like projection at the constriction. The length is 6.3 to 7.3 mm; greatest shaft width is 1.7 to 2.1 mm (Burt, 1960). In dorsal view, the os clitoridis is steeply triangular with its left side strongly curved and right side indented smoothly from the base to about the middle; a thickened ridge on

FIGURE 1. An adult female northern flying squirrel, *Glaucomys sabrinus macrotis*, from Baraga County, Michigan. Photograph by Nancy Wells-Gosling.

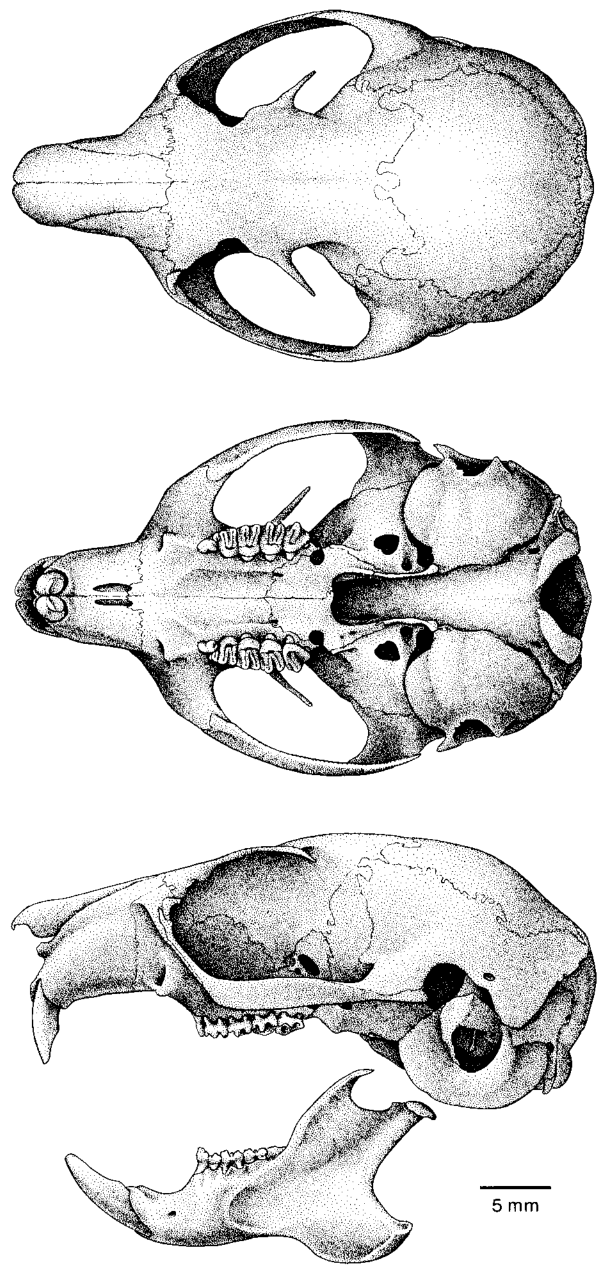

FIGURE 2. Dorsal, ventral, and lateral view of cranium and lateral view of mandible of *Glaucomys sabrinus sabrinus* from Beltrami Co., Minnesota (UMMZ 83617). Prepared by Margaret Van Bolt.

the ventral left edge follows the margin of the bone. Its length is 1.5 mm (Layne, 1954).

GENERAL CHARACTERS. The northern flying squirrel (Fig. 1) is similar in appearance to the southern flying squirrel, but larger and more robust with thicker pelage and richer coloration. Color of pelage varies widely according to subspecies and season (Howell, 1918). Hall (1981:450) described it as, "upper parts varying from cinnamon to pecan brown according to subspecies; tail above from cinnamon to fuscous or even blackish, usually darkest near tip; tail below varying from pinkish cinnamon to nearly black; underparts white or creamy white often washed with some shade of buffy or yellowish; sides of head and sometimes face gray, often with wash of buff, cinnamon, or fuscous."

On either side of the body, a furred patagium extends from the forelegs to the hindlegs from ankle to wrist, and is supported by a slender, cartilaginous, styliform process that articulates with the bones of the wrist. The tail is long, about 80% of the length of head and body, and densely furred with distichous hairs presenting a dorso-ventrally flattened appearance; its tip is rounded. Mystacial vibrissae are long; one or two superciliaries usually are present. Contrary to Pocock (1922), ulnar and interramal vibrissae are present. There are four tubercles at the base of toes on the hindfeet, with no metatarsal pads. Forefeet have three tubercles at the bases of toes, one at base of rudimentary pollex, and one on the outer edge of the palm (Pocock, 1922). Four pair of mammae are present: one pectoral, two abdominal, one inguinal (Howell, 1918; Thorington and Heaney, 1981).

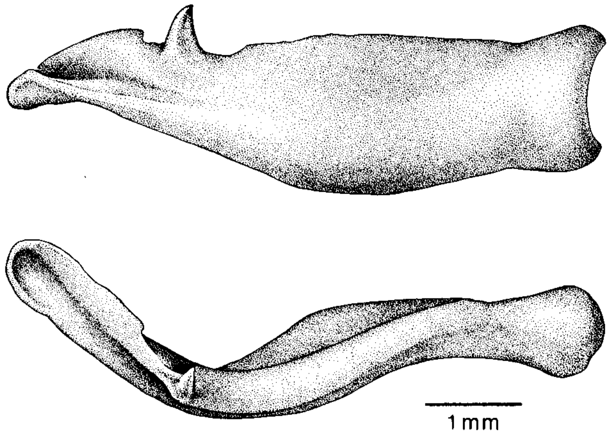

FIGURE 3. Lateral and dorsal view of baculum of *Glaucomys sabrinus* from Cheboygan Co., Michigan (UMMZ 82633). Prepared by Margaret Van Bolt.

Two palatal lobes of hairy integument extend inward from the cheeks and can be brought together behind the incisors. Two smaller lingual lobes jut inwards on each side of the tongue (Pocock, 1922). The eye is large and dark, with a black orbital ring. The ear is large, rounded, broadly pointed, and sparsely haired, with a membranous auricula and small tragus, antitragus, and conchal lobe. The posteriorly inflated conchal cavity is relatively larger than in other squirrels, which probably results in increased sonic perception, useful during the nocturnal activity of *Glaucomys*. The manus is relatively longer and weaker than in tree squirrels; the claws are exceptionally deep at the base and are strongly compressed and arched. Digits 3 and 4 are subequal, as are digits 2 and 5 (Bryant, 1945).

The dental formula is i 1/1, c 0/0, p 2/1, m 3/3, total 22. Incisors are slender and procumbent, only slightly recurved; the enameled surface is finely crenulated (Bryant, 1945). Cusps on the outer side of the upper toothrow are without subsidiary cusplets. The P3 are small and terete with a simple crown. The P4 are subquadrate, nearly as large as the M1, with the parastyle ridge rising to form a cusp. Transverse ridges of the upper molars are continuous. Maxillary toothrows are approximately parallel (Howell, 1918, 1938).

The skull (Fig. 2) is lightly constructed and somewhat flattened. The braincase is unusually deep and inflated. Nasals are abruptly depressed anteriorly. The dorsal profile of the skull from nasals to postfrontal region is nearly straight, but abruptly depressed to occiput. Frontals are long and narrow; interorbital and postorbital regions are constricted, with a deep interorbital notch. Infraorbital foramina are oval, vertical, and situated above the P3; zygomatic plates tilt upward at an angle of approximately 65° to basiocranial axis; the zygomata are appressed, slightly convergent anteriorly, and have nearly parallel sides. Temporal ridges are weak and widely separated (not uniting to form a sagittal or nuchal crest). Postorbital processes are broad at the base, tapering abruptly to a point. They project to about the middle of the temporal fossa and are depressed at the tip (Hall, 1981; Howell, 1938). The mastoidal portion of the temporal bones is highly inflated. Auditory bullae are large, subcircular in outline, and smoothly rounded. Pterygoids are slender and rather low; the hamular processes usually touch the audital bullae. The diastemal portion of the mandible is deep and the alveolar border is slightly above the level of the anterior end of the mandible. Coronoid processes are relatively short. A posterior projection of the angular process is absent (Fig. 2; Bryant, 1945; Howell, 1918).

In comparing *Glaucomys sabrinus* and *G. volans* to other North American sciurids, Bryant (1945) noted the following postcranial skeletal characters as being especially distinctive in *Glaucomys*. The lumbar region is short, with the transverse processes of lumbar vertebrae directed craniad but small and inclined nearly ventrad. The sternum is short. The manubrium is Y-shaped and wider than long, with the clavicular notches and first costal pits respectively on the cranial and caudal surfaces of the two cranial branches being near the tips. Scapulae have a straight axillary border; the axillary ridges are low, and the infraspinous fossa is shallow. The vertebral border is inclined strongly ventrad. The base of the coronoid process is massive and long, with the metacromion rounded and rudimentary and the acromion reduced to a short knob. The clavicle is relatively short and slender; the coracoclavicular fossa is reduced and the sternal end is nearly as large as the acromial end. The humerus is long and slender, with low, short deltoid and lateral epicondylar ridges. The condyles are relatively short and deep. The radius and ulna have the distal halves fused. The radius is long and slender, its distal end the weakest part of shaft. The ulna is long and slender, its olecranon short and tricipital ridge strong; the tuberosity is minute and the shaft reduced distally to a filament of bone. The pubic-ischial symphysis is short. The slender, long femur has its distal end reduced. The distal part of the fibula is fused to the caudolateral surface of the tibia with the length of the fused area unusually great (about 37% of tibia). The tibial tuberosity is weak and popliteal fossa nearly flat. The metatarsus is long, narrow, and weak.

Sexual dimorphism in color or size is not evident, but geographical variation in size is prominent. Average external measurements (mm) and extremes (in parentheses) for 16 adult *G. s. macrotis* from New York and New England (Howell, 1918) are: total length, 275.6 (263.0 to 290.0); length of tail, 126.4 (115.0 to 135.0); length of hindfoot, 36 (34 to 38); ear length, 18.8 (16.0 to 20.0). Skull measurements for 11 adults from the same region are: greatest length, 37.3 (36.0 to 38.7); zygomatic breadth, 22.6 (21.9 to 23.5); mastoidal breadth, 17.6 (17.2 to 18.0); least interorbital breadth, 6.9 (6.2 to 7.3); least postorbital breadth, 9.2 (8.6 to 9.9); length of nasals, 10.7 (10.0 to 11.5); length of maxillary toothrow, 7 (6.4 to 7.7).

Average external measurements and extremes for 10 adult *G. s. latipes* from British Columbia, Idaho, and Montana (Howell, 1918) are: total length, 342 (315 to 368); length of tail, 153 (145 to 161); length of hindfoot, 41.4 (38.0 to 44.0). Skull measurements for 7 adults are: greatest length, 42.9 (41.6 to 44.2); zygomatic breadth, 24.5 (24.0 to 25.4); mastoidal breadth, 19.5 (19.0 to 20.0); least interorbital breadth, 8.3 (8.0 to 8.8); least postorbital breadth, 8.8 (8.0 to 9.1); length of nasals, 13.3 (12.5 to 14.0); length of maxillary toothrow, 8.3 (7.9 to 9.0).

DISTRIBUTION. Northern flying squirrels occur in forested regions over most of northern North America (Fig. 4). The flora of inhabited areas typically is dominated by conifers, but often is mixed coniferous-deciduous forest and occasionally strictly broadleaf deciduous forest (Baker, 1983; Weigl, 1977; Wells-Gosling, 1982). The range probably is continuous across North America through central Canada, but disjunct populations occur in the southern Appalachian Mountains (North Carolina, Tennessee, and West Virginia), the Black Hills (South Dakota and Wyoming), the southern Rocky Mountains (Utah and Idaho), and Sierra Nevada (California). Several islands off the coast of British Columbia, Nova Scotia, and Prince Edward Island also support populations of these squirrels. The northern limit of distribution generally is the edge of continuous forest, but northern limits (and limiting factors) are not well established (Harper, 1961; Manville and Young, 1965; Youngman, 1975).

FOSSIL RECORD. Two late Miocene to early Pliocene flying squirrel species were described from the Cuyama Valley of California and designated as *Sciuropterus* by James (1963), but assigned to *Cryptopterus* by Mein (1970). James (1963) suggested these specimens might be ancestral to *Glaucomys*, but Mein (1970) was skeptical. Robertson (1976) described a new species of *Cryptopterus* from the latest Pliocene of Florida, but it too lacked basic features indicating it was ancestral to *Glaucomys*.

Fossils of *G. sabrinus* are known from localities of late Pleistocene and Recent age (Fig. 4). These localities include Baker Bluff Cave, Bootlegger Sink, Clark's Cave, Eagle Cave, Natural Chimneys, New Paris No. 4, Peccary Cave, Potter Creek Cave, Robinson Cave, and Samwel Cave (Kurtén and Anderson, 1980). Kurtén and Anderson (1980) provided faunal descriptions for these localities.

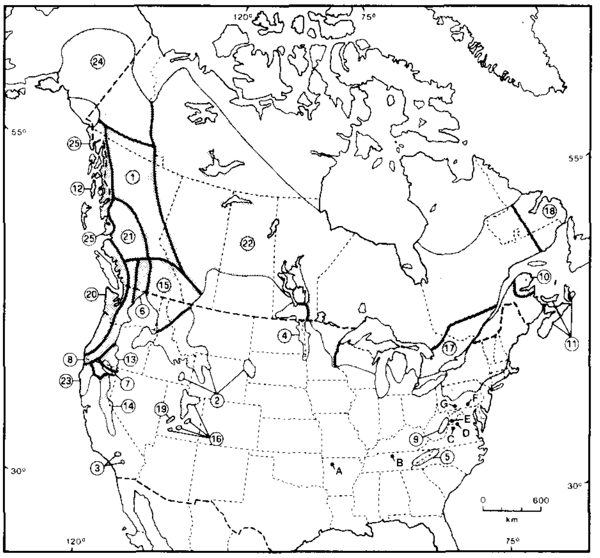

FIGURE 4. Distribution of *Glaucomys sabrinus*. Subspecies are as follows: 1, *G. s. alpinus*; 2, *G. s. bangsi*; 3, *G. s. californicus*; 4, *G. s. canescens*; 5, *G. s. coloratus*; 6, *G. s. columbiensis*; 7, *G. s. flaviventris*; 8, *G. s. fuliginosus*; 9, *G. s. fuscus*; 10, *G. s. goodwini*; 11, *G. s. gouldi*; 12, *G. s. griseifrons*; 13, *G. s. klamathensis*; 14, *G. s. lascivus*; 15, *G. s. latipes*; 16, *G. s. lucifugus*; 17, *G. s. macrotis*; 18, *G. s. makkovikensis*; 19, *G. s. murinauralis*; 20, *G. s. oregonensis*; 21, *G. s. reductus*; 22, *G. s. sabrinus*; 23, *G. s. stephensi*; 24, *G. s. yukonensis*; 25, *G. s. zaphaeus*. Fossil localities outside of the current range of the species are indicated by letters: A, Peccary Cave, Arkansas; B, Robinson Cave, Tennessee; C, Clark's Cave, Virginia; D, Natural Chimneys, Virginia; E, Eagle Cave, West Virginia; F, Bootlegger Sink, Pennsylvania; G, New Paris No. 4, Pennsylvania. Prepared by Margaret Van Bolt.

FORM AND FUNCTION. The skeletal structure of the limbs in *Glaucomys* (and other petauristines) is grossly similar to that of other sciurids except for the presence of the styliform process ("accessory carpal" of Gupta, 1966) that articulates with the fifth metacarpal, the unciform, and pisiform bones of the wrist. This process supports the anterior margin of the patagium during a glide (Gupta, 1966). *G. sabrinus* lacks a significant uropatagium, as is true for all small flying squirrels, but the broad tail adds 20 to 30% to the gliding surface, giving *G. sabrinus* a "wing-loading" coefficient of 50 newtons/m^2, which is two to three times the wing-loading typical for bats. High wing-loading results in these squirrels functioning aerodynamically similar to certain types of Rogallo-wing hang gliders, with the musculature of the patagium and forelimbs allowing control over aspect ratio, billow, glide ratio, and speed of glide (Thorington and Heaney, 1981). Development and attachment of the gliding muscles in *Glaucomys* suggests this genus may be evolutionarily more primitive than flying squirrels in the genera *Pteromys*, *Petinomys*, and *Petaurista* (Johnson-Murray, 1977).

The oviduct of female *G. sabrinus* lacks a periovarial sac, and has a large loop on the ampulla and numerous smaller convolutions along the length of the tube (Beck, 1972). *G. sabrinus* has a low encephalization index compared with *Cynocephalus* and *Iomys*. However, all three exhibit similar subdivision of the brain, possibly a result of general parallelism in ecological conditions and behavior (Pirlot and Kamiya, 1982).

The baculum of *G. sabrinus* more closely resembles that of *Hylopetes* of Asia than it does *G. volans* (Burt, 1960). Burt (1960) speculated that the ancestral *G. sabrinus* stock may have become separated from the parental stock and migrated to North America at a later date than *G. volans*. An immunological study by Hight et al. (1974) tended to support this view.

ONTOGENY AND REPRODUCTION. Copulatory behavior is similar to that seen in *G. volans*, consisting of series of intromissions lasting about 15 s and occurring at intervals of 15 to 30 s. During coition females emit a "churring" sound, and following each series of intromissions the male produces a long nasal "whine" and licks his genitalia. When mounted, the male grasps the female with his front legs just anterior to her flanks, and quickly strokes her venter during rapid series of intromissions. After ejaculation the hindlegs of the male often straighten and extend posteriorly (Muul, 1969).

The gestation period was reported as 37 to 42 days (Muul, 1969; Soper, 1973). Litters usually contain two to four young, but sometimes as few as one (Rust, 1946) and rarely as many as six (Soper, 1970).

Although Doutt et al. (1977), Hamilton and Whitaker (1979), and Seton (1929) suggested that *Glaucomys sabrinus* may produce two or even three litters per year, probably only one litter is produced per female per year (Cowan, 1936; Jackson, 1961). Mating occurs in late March through May (Jackson, 1961; Muul, 1969; Soper, 1970, 1973). Young usually are born in late May through June, but in the Upper Peninsula of Michigan, Dice and Sherman (1922) found a female with five small embryos on 6 July, evidence of a late summer litter. In Humboldt Co., California, 5-week-old squirrels were found on 15 December at an elevation of 900 m (Raphael, 1984).

Newborn squirrels weigh 5 to 6 g and measure 70 mm in total length (Booth, 1946; Jackson, 1961; Muul, 1969). They have transparent skin that lacks pigment and hair, but the patagium is clearly evident. Eyes and ears are closed and toes fused together. At 6 days of age vibrissae appear and the toes separate. Fine hair covers the head, neck, and shoulders by day 8. Brownish-black pigment colors the dorsum and fine hair appears on most of the body by day 11. At 2 weeks of age, the top of the head and shoulders has thick brown hair and white fur grows on the muzzle. Almost all the back and sides are cloaked with hair by 18 days and the young crawl awkwardly. Lower incisors erupt on day 26. On day 32, eyes open and fine white hairs cover the venter. The tail definitely is flattened in appearance (Booth, 1946). Young can walk and begin to emerge from the nest at 40 days of age (Muul, 1969). They eat solid food shortly thereafter. Weaning occurs at about 2 months of age (Booth, 1946; Jackson, 1961), but the young may remain with the female for some time. A female carries young grasped in her teeth to retrieve them or move them to a new nest.

Normal longevity probably is less than 4 years (Jackson, 1961).

ECOLOGY. Throughout their extensive continental range, northern flying squirrels inhabit a wide variety of woodland habitats. In the southern Appalachian Mountains this species is distributed at altitudes of 1,000 to 1,830 m in forests of spruce (*Picea*)-fir (*Abies*) and mixed hemlocks (*Tsuga*) and adjacent mature hardwoods (Handley, 1953; Weigl, 1977, 1978; Weigl and Osgood, 1974). The first record of *G. sabrinus* from Pennsylvania was from a tract of large beech (*Fagus*), yellow birch (*Betula alleghaniensis*), and sugar maple (*Acer saccharum*) (Doutt, 1930). In southeastern New York, optimal habitat for *G. sabrinus* contained beech, sugar maple, red oak (*Quercus rubra*), various birches and other deciduous trees, and some hemlock and white pine (*Pinus strobus*) (Connor, 1960). Squirrels also were taken from pure beech-maple forests and stands of red spruce (*Picea rubens*), balsam fir (*Abies balsamea*), and hemlock. A flying squirrel was found on the summit of Mt. Marcy, Essex Co., New York at 1,630 m, 135 m above timber line (Gordon, 1961). In the Great Lakes region, northern flying squirrels were found in beech-maple stands, hemlock forests, and also in white cedar (*Thuja occidentalis*) swamps, spruce-fir forests, and jack pine (*Pinus banksiana*) barrens (Jackson, 1961; Manville, 1949). In Alaska, they inhabit the extensive taiga forests of white spruce (*Picea glauca*) and paper birch (*Betula papyrifera*) interspersed with groves of quaking aspen (*Populus tremuloides*; Dice, 1921; Mowrey and Zasada, in press). In Alberta, squirrels were found in mixed woods with tall conifers, or semi-open woods, from the lowest valleys up to an altitude of 1,980 to 2,130 m (Soper, 1970). In southwestern Utah, squirrels were trapped in Engelmann spruce (*Picea engelmannii*) habitats at elevations ranging from 2,400 to 3,140 m and in stream-bottom stands of white fir (*Abies concolor*) with cottonwood (*Populus*) at an elevation of 2,970 m (Musser, 1961). In Lassen Co., California, flying squirrels were found in stands of ponderosa pine (*Pinus ponderosa*), lodgepole pine (*Pinus contorta*), and mixed red fir (*Abies magnifica*) and white fir (McKeever, 1960).

In captivity, *G. volans* and *G. sabrinus* tolerated each other and often shared nestboxes (Muul, 1968; Weigl, 1978). However, *G. volans* was dominant and more aggressive and sometimes displaced *G. sabrinus* from a box although the reverse situation never occurred (Weigl, 1977). Under experimental conditions, *G. sabrinus* selected either deciduous or coniferous habitat, whereas *G. volans* strongly selected deciduous habitat (Weigl, 1978). *G. volans* may have a greater ability to locate and control tree cavities, and to displace *G. sabrinus* from hardwood forest, especially if conifers are absent. Also, *G. volans* breeds earlier than *G. sabrinus* and, in areas of sympatry, may usurp the tree cavities as nesting sites. However, the two species occasionally occur in the same woodlot (Connor, 1960; Osgood, 1935; Wells-Gosling, 1982), although perhaps only temporarily (Weigl, 1978). Southern flying squirrels have a *Strongyloides* sp. parasite that may be debilitating or lethal to northern flying squirrels in some parts of their range (Weigl, 1977).

Northern flying squirrels inhabit two types of nests, those inside tree cavities or abandoned woodpecker holes, and those outside protective enclosures (Cowan, 1936; Howell, 1918; Rust, 1946; Weigl and Osgood, 1974). Cowan (1936) divided outside nests into two general types: larger ones of 31-cm diameter entirely encased in twigs, bark, and roots with one or two entrances, usually housing a female and her brood; and smaller outside nests of about 18-cm diameter built on platforms of sticks or on top of an abandoned bird nest, housing single animals. He considered outside nests generally unsuitable for winter use and thought that cavities were the main winter quarters, although squirrels occasionally have been found to use outside nests during winter. Most nests Cowan (1936) investigated also were used as feeding platforms.

In northern Idaho, squirrels constructed outside nests of dried grass lined with lichens and fastened to the tree at heights of 3.7 to 4.6 m (Rust, 1946). In Oregon, some nests were inside the masses of moss that draped tree branches (Bailey, 1936). Flying squirrels were radiotracked to nests inside witches' brooms on trees infected with rust disease in Alaska. Brooms were 0.5 to 1.0 m in diameter. After a sharp drop in temperature in late October, the squirrels aggregated within the brooms and shifted away from use of tree cavities (Mowrey and Zasada, in press). Flying squirrels have been found to inhabit abandoned red squirrel nests (Jackson, 1961).

When ambient temperatures were 4 to 15°C, temperatures inside nests ranged from 27 to 36°C and varied only 1 to 3°C while the animal was inside. After the animal entered the nest, it took 15 to 20 min to establish the stable nest temperature (Weigl and Osgood, 1974).

Nests are lined with finely shredded bark, moss, lichens, feathers, grass, pine needles, leaves, fur, or other available material (Bailey, 1929; Bailey, 1936; Jackson, 1961; Rust, 1946). Height of nests above the ground ranges from 1 to 18 m (Bailey, 1929; Cowan, 1936; Jackson, 1961; Manville, 1942; Weigl and Osgood, 1974). Cooper (1860) reported a nest containing three young squirrels under a log on the ground.

The home range encompasses 0.8 to 1.2 ha (Seton, 1929). Population density ranges from 1 squirrel/3 ha to 10 animals/ha under favorable habitat (Jackson, 1961; Mowrey and Zasada, in press). Squirrels in Pennsylvania and North Carolina had a home range radius of 100 to 200 m (Weigl and Osgood, 1974). On the Alaskan taiga, squirrels foraged around a 2-km circuit in about 6 h in the summer and each animal required 31 ha of optimal habitat, although ranges of individual animals overlapped (Mowrey and Zasada, in press). Retention of travel corridors and scattered, tall spruce trees were recommended forest management procedures to provide flying squirrel habitat on the Alaskan taiga (Mowrey and Zasada, in press).

Avian predators of northern flying squirrels include barn owls (*Tylo alba*; Cowan, 1942), barred owls (*Strix varia*; Seton, 1929), great horned owls (*Bubo virginianus*; Connor, 1960; Cowan, 1942; Jackson, 1961), goshawks (*Accipiter gentilis*; Jackson, 1961), and red-tailed hawks (*Buteo jamaicensis*; Luttich et al., 1970). A pair of spotted owls (*Strix occidentalis*) can consume about 500 squirrels annually (Heinrichs, 1983).

Mammalian predators include martens (*Martes americana*; Murie, 1961; Smith, 1978; Zielinski et al., 1983), domestic house cats (*Felis catus*; Connor, 1960; Toner, 1956), wolves (*Canis lupus*; Voigt et al., 1976), lynxes (*Lynx lynx*; Nellis et al., 1972), weasels (*Mustela*), and foxes (*Vulpes* and *Urocyon*; Seton, 1929). A flying squirrel was found in the stomach of a trout in British Columbia (Seton, 1929). Occasionally squirrels die after entangling the gliding skin in barbed wire (Crowe, 1943; Findley, 1945).

Food habits of this species are not well documented. Records of food items include acorns, hazelnuts, beechnuts, and other nuts; conifer and hardwood seeds (Connor, 1960; Jackson, 1961; Smith and Aldous, 1947); buds, staminate cones, and catkins (Connor, 1960; Jackson, 1961; Weigl, 1978); wild fruits, and insects (Bailey, 1936; Foster and Tate, 1966; Jackson, 1961; Soper, 1970). They also consume tree sap and were observed to chew away the bark between sapsucker (*Sphyrapicus* sp.) holes to increase the flow (Foster and Tate, 1966; Schmidt, 1931). In the past, many were drowned in sap buckets (Merriam, 1886). They reputedly consume roosting birds captured at night and eat eggs (Ingles, 1937; Ingles, 1954; Jackson, 1961), but more investigation is needed on this aspect of their diet (Bailey, 1936). Vertebrate flesh was found in stomach contents of squirrels taken in New York (Connor, 1960). Successful trapping baits include "Funsten" mink bait, dried prunes, rolled oats, and oatmeal, bread, nuts, grain, "a bunch of cotton," sausage, bacon, and other types of meat, biscuits, apples, peanut butter, and a dead mouse (Bailey, 1936; Cahn, 1937; Connor, 1960; Goodwin, 1929; Handley, 1953; Jackson, 1961; Merriam, 1886; Schmidt, 1931; Sumner, 1927; Weigl and Osgood, 1974; Whitlow and Hall, 1933).

Northern flying squirrels cannot be maintained on a diet of white spruce seeds; thus, these seeds probably are not a prime dietary item in the wild (Brink and Dean, 1966). Fungi and lichens may be the predominant or only foods eaten at certain times of the year (Connor, 1960; Cowan, 1936; Maser et al., 1978; McKeever, 1960; Mowrey et al., 1981; Tevis, 1953; Wrigley, 1969). In Alaska, *G. sabrinus* foraged at fungal caches of red squirrels (Mowrey and Zasada, in press). Food storing behavior is documented poorly; perhaps northern flying squirrels do not cache food at all (Ingles, 1965). Water may be obtained from green vegetation or moisture on food (Jackson, 1961).

Numerous parasites have been recorded from northern flying squirrels. In northeastern Oregon, an examination of 29 flying squirrel nests revealed 35 taxa of ectoparasites, whereas 29 taxa of ectoparasites were found on the 31 squirrels examined (Whitaker et al., 1983). Flea (Siphonaptera) species confined to flying squirrels include *Opisodasys pseudarctomys* (Benton and Cerwonka, 1960; Haas and Wilson, 1973; Holland and Benton, 1968), *O. vesperalis* (Spencer, 1956), *Epitedia faceta* (Larson, 1983), and *Tarsopsylla octodecimdentata coloradensis* (Holland, 1949), whereas *Orchopeas howardii* (Benton and Cerwonka, 1960; Benton et al., 1969), *Monopsyllus vison* (Benton et al., 1971; Holland, 1949), and *Orchopeas caedens* (Larson, 1983; Robert and Bergeron, 1977) are generalized squirrel fleas. *Orchopeas nepos* and *Megarthroglossus divisus exsecatus* (Holland, 1949) are mainly parasites of red squirrels, but sometimes are found on flying squirrels. *Monopsyllus ciliatus* (Spencer, 1956), *M. eumolpi* (Stark, 1959), *M. wagneri* (Stark, 1959), *Opisocrostis bruneri* (Benton et al., 1971), *Orchopeas leucopus* (Timm, 1975), and *Epitedia stanfordi* (Stark, 1959) have been found on flying squirrels but probably are of accidental occurrence.

Lice (Anoplura) include *Hoplopleura trispinosa*, *Microphthirus uncinatus*, and *Neohaematopinus sciuropteri* (Ferris, 1951; Spencer, 1956). Mites and ticks include *Acaropsellina summersi*, *Camincheyletus glaucomys*, *Eucheyletia oregonensis* (Smiley and Whitaker, 1981), *Haemogamasus ambulans*, *H. reidi* (Keegan, 1951; Redington, 1971), *Hirstionyssus occidentalis* (=*punctatus*) (Allred and Beck, 1966), *Hyperlaelaps microti* (Scholten et al., 1962), *Ixodes marxi* (Bequaert, 1945; Martell et al., 1969), *I. pacificus* (Spencer, 1956), and *Neotrombicula microti* (Jackson, 1961). Endoparasites include Nematoda, *Citellinema bifurcatum* (Doran, 1955), *Syphacia thompsoni* (Doran, 1955; Rausch and Tiner, 1948; Tiner and Rausch, 1949); Cestoda, *Andrya sciuri* (Rausch, 1947; Rausch and Tiner, 1948), *Catenotaenia pusilla* (Rausch and Tiner, 1948), *Moneococestus thomasi* (Rausch and Maser, 1977), and *Hymenandrya* sp. (Rausch and Rausch, 1982); and Protozoa, *Eimeria dorneyi* (Soon and Dorney, 1969), and *E.* cf. *sciurorum* (Dorney, 1962).

BEHAVIOR. Squirrels exhibited a biphasic nocturnal activity pattern in late summer. The animals first left the nest shortly after sundown and returned after 2 h (average 118 min). A few hours before sunrise they were again active for a shorter period of time (average 76 min). Each squirrel had its own characteristic activity schedule. Heavy cloud cover tended to advance onset of activity. Inclement weather delayed the time of departure from the nest, but did not preclude activity although the squirrels seemed reluctant to glide during rain, high wind, or fog (Weigl and Osgood, 1974). Occasionally, *G. sabrinus* are active during the day (McIntyre, 1950; Soper, 1923; Tanner, 1927).

Northern flying squirrels are active throughout the winter (Jackson, 1961; Merriam, 1886) in temperatures as low as −24°C (Connor, 1960) and probably lower. Tracks and signs often are seen in the snow, and the squirrels travel under the shelter of conifer branches and fallen logs (Connor, 1960, 1966), or along snowshoe hare runways (Keith and Meslow, 1966). They dig tunnels to reach food buried under the snow (Connor, 1960, 1966). During winter they often enter traps, apparently in search of food, and sometimes become nuisances for professional trappers (Hamilton and Whitaker, 1979; Merriam, 1886; Soper, 1942). There are no indications that northern flying squirrels enter torpor similar to that observed in *G. volans* (Muul, 1968).

Considerable time is spent foraging on the ground, the animal progressing in a series of short jumps. When carrying a large piece of food it may hop on the hindlegs (Coventry, 1932; Jackson, 1961). Maximum running speed is about 13 km/h (Jackson, 1961).

Although the squirrels travel on the ground, they usually glide from tree to tree. In Alaska, squirrels favored the tallest spruce trees as launching sites. They took off at a height approximately 3 m below the tree top and usually landed less than 1 m from the ground on another tree. Mean gliding distance was 19.7 m (range 1.8 to 48.2 m; Mowrey and Zasada, in press). A squirrel was observed to glide more than 90 m down a mountainside (Klugh, 1924). Another leapt from a 15-m tree, described a semi-circle and landed 21 m away from the starting point (Coventry, 1932).

Squirrels aggregate for warmth in winter (Banfield, 1974; Manville, 1948; Seton, 1929; Weigl and Osgood, 1974), but this behavior is not as thoroughly documented as for the southern flying squirrel. In the Blue Mountains of Oregon, the sexes were segregated 97% of the time (Maser et al., 1981). Sexes also were apparently segregated in Virginia (Osgood, 1935). Females raise their families without assistance from males. Defense of nesting areas against males and other females as observed in some populations of the southern flying squirrel has not been confirmed in *G. sabrinus* (Madden, 1974).

In a group of 13 squirrels that frequented a feeding station, adults dominated the younger squirrels and sometimes chased them away, but subadults shared food amicably. Occasionally, two squirrels fought over a piece of food; the altercations lasted only a few seconds and were accompanied by clucking noises (Coventry, 1932).

Northern flying squirrels are not highly vocal. Their call is a low, soft chirp (Jackson, 1961). They emit a clucking or chuckling sound when disturbed (Banfield, 1974; Coventry, 1932).

GENETICS. Rausch and Rausch (1982) described karyotypes from *G. sabrinus* that contained 28 bi-armed metacentric-subtelocentric and 18 acrocentric autosomes, whereas *G. volans* displayed 30 and 16, respectively. Sex chromosomes of the two species were similar in morphology and banding pattern, with a medium-sized submetacentric X, and a small submetacentric Y. Total length of individual chromosomes differed between the two species; the female complement was 65 μm in *G. volans* and 86 μm in *G. sabrinus*. The two species of *Glaucomys* were karyotypically distinct from each other and also differed from *Pteromys volans*, which has a diploid number of 38 (Rausch and Rausch, 1982).

Although the hemoglobin of *Glaucomys volans* is isoelectric with human hemoglobin A, that of *G. sabrinus* is slower. Several *G. sabrinus* showed a second major hemoglobin fraction, isoelectric with human hemoglobin A, indicating a possible polymorphism of the hemoglobin molecule (Johnson, 1968). Antigenic divergence and differences in the two-dimensional starch gel patterns of serum proteins were evident between the two species of *Glaucomys* (Hight et al., 1974).

REMARKS. The generic name is derived from the Greek *glaukos* (gray) and *mys* (mouse). The specific epithet, *sabrinus*, is derived from the Latin name for the river Severn in England, but refers to the type locality of the species, the Severn River region of northwestern Ontario (Shaw, 1801).

The subspecies *Glaucomys sabrinus coloratus* is listed as a threatened population in North Carolina (Weigl, 1977).

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