

Glaucomys volans. By Patricia G. Dolan and Dillard C. Carter

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Glaucomys Thomas, 1908

Glaucomys Thomas, 1908:5. Type species *Mus volans* Linnaeus.

CONTEXT AND CONTENT. Order Rodentia, Suborder Sciuromorpha, Superfamily Sciuroidea, Family Sciuridae, Subfamily Petauristinae (Simpson, 1945). The genus *Glaucomys* includes two Recent species, *volans* (Linnaeus, 1758) and *sabrinus* (Shaw, 1801). All fossil and subfossil specimens are assigned to one of these two species.

Glaucomys volans (Linnaeus, 1758)

Southern Flying Squirrel

[*Mus*] *volans* Linnaeus, 1758:63. Type locality fixed by Elliot (1901:109) as Virginia.

Sciurus petaurista Erxleben, 1777:435. A renaming of *Mus volans* Linnaeus.

Sciurus volucella Pallas, 1778:351. A renaming of *Mus volans* Linnaeus.

Pteromys virginianus Tiedemann, 1808:451. A renaming of *Mus volans* Linnaeus.

Sciuropterus americanus, Desmarest, 1827:140. A renaming of *Sciurus volucella* Pallas.

Pteromys cucullatus Fischer, 1829:365. Type locality questionably Virginia; based on "*Sciurus, Virginianus, volans*" Seba (1734).

Sciuropterus silus Bangs, 1896:163. Type locality top of Katis Mountain, near White Sulphur Springs, West Virginia.

CONTENT. Howell (1918) recognized five subspecies; Hall and Kelson (1959), eight; and Goodwin (1961) added two new subspecies to bring the total to 10 as included here.

G. v. chontali Goodwin, 1961:3. Type locality Santo Domingo, Chontecomatlán, Yautepec, Oaxaca, altitude about 7000 feet.

G. v. goldmani (Nelson, 1904:148). Type locality 20 mi. SE Teopisca, Chiapas.

G. v. herreranus Goldman, 1936:463. Type locality Mountains of Veracruz.

G. v. madrensis Goldman, 1936:463. Type locality Sierra Madre, Chihuahua.

G. v. oaxacensis Goodwin, 1961:11. Type locality San Pedro Jilotepec, Tehuantepec, Oaxaca, altitude about 5000 feet.

G. v. querceti (Bangs, 1896:166). Type locality Citronelle, Florida.

G. v. saturatis Howell, 1915:110. Type locality Dothan, Alabama.

G. v. texensis Howell, 1915:110. Type locality 7 mi. NE Sour Lake, Texas.

G. v. underwoodi Goodwin, 1936:1. Type locality Zambrano, Tegucigalpa, Honduras, "a village on the main road to Lake Yojoa and the north coast, about halfway between Tegucigalpa and Comayagua; altitude 4500 feet."

G. v. volans (Linnaeus, 1758:63). Type locality fixed by Elliot (1901:109) as Virginia (*silus* Bangs, *cucullatus* Fischer, and *nebrascensis* Swenk, 1915:151, are synonyms).

DIAGNOSIS. Hairs on venter are white to base. Baculum is unlike those of other sciurids; long and slender, twisted shaft with basal end slightly expanded; shaft widest at about midpoint, where a groove starts and continues to distal end; terminates in a double condylelike structure with groove of shaft continuing to near anterior edge of one of the "condyles" (see figure 1). Os clitoridis essentially rod-shaped, proximal end with hook-like projection directed ventrolaterally (figure 1). There are 20 acrocentric chromosomes.

GENERAL CHARACTERS. Forelimbs and hind limbs are connected from wrist to ankle by a loose fold of fully haired skin; tail is densely haired, broad, dorsoventrally flattened, almost parallel sided, and has the tip rounded (see figure 2); vibrissae on dorsal surface of ungual phalanges of hind foot extend beyond tips of claws. Skull (figure 3) is lightly constructed; nasals are short and abruptly depressed at tip; dorsal profile of skull is almost straight from nasals to postfrontal region and is abruptly depressed to occiput; frontals are long and narrow, their postorbital processes are broad at base, narrow distally, and curved slightly downward; occiput is broad; petrosal is enlarged, exposed posteriorly, and uplifting squamosal dorsolaterally; tympanic bullae are inflated. Incisors are slender, only slightly recurved; third premolar is relatively well developed, its crown forms part of occlusal surface of dental series; molars are without subsidiary cusplets on labial side; lower molars have subsidiary cusplets between primary cusps on both labial and lingual sides. Dental formula is $i\ 1/1, c\ 0/0, p\ 2/1, m\ 3/3$, total 22.

Selected measurements in millimeters of adults are: total length, 198 to 255; length of tail, 81 to 120; length of hind foot, 21 to 33; ear, 13 to 23; greatest length of skull, 32 to 37.2; cranial depth, 16.5 to 17.8; zygomatic breadth, 18.5 to 22.2; interorbital constriction, 6.2 to 9.2; postorbital breadth, 8.2 to 10.0; mastoidal breadth, 16.0 to 19.4; length of nasals, 8.0 to 11.6; maxillary toothrow, 5.9 to 7.1; breadth of palate across molars, 7.9 to 8.8. Published records of body weights (46.5 to 85 grams) are variable; sexual dimorphism and clinal variation are not really evident. The pelage is of moderate length (about 12 mm), dense, fine, and silky in texture. According to season and subspecies, color of upperparts is drab, pinkish, cinnamon, sayal brown, pale snuff brown, hair brown, bright ochraceous tawny, or yellowish wood brown; bases of hairs are deep neutral gray; sides of face are smokie gray, often shaded with fuscous or buff, cheeks and nose sometimes white; borders of patagium are fuscous, clove brown, or blackish brown above; forefeet are buffy white, hair brown, or grayish buff; hind feet are hair

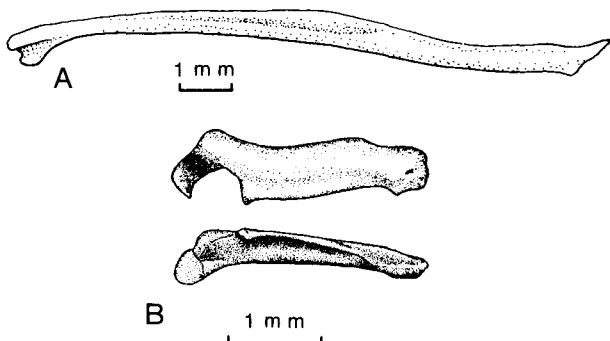


FIGURE 1. Os penis (A) and os clitoridis (B) of *Glaucomys volans*. Drawings after Burt (1960) and Layne (1954), respectively.



FIGURE 2. Southern flying squirrel from Ithaca, New York (photograph by D. M. Payne).

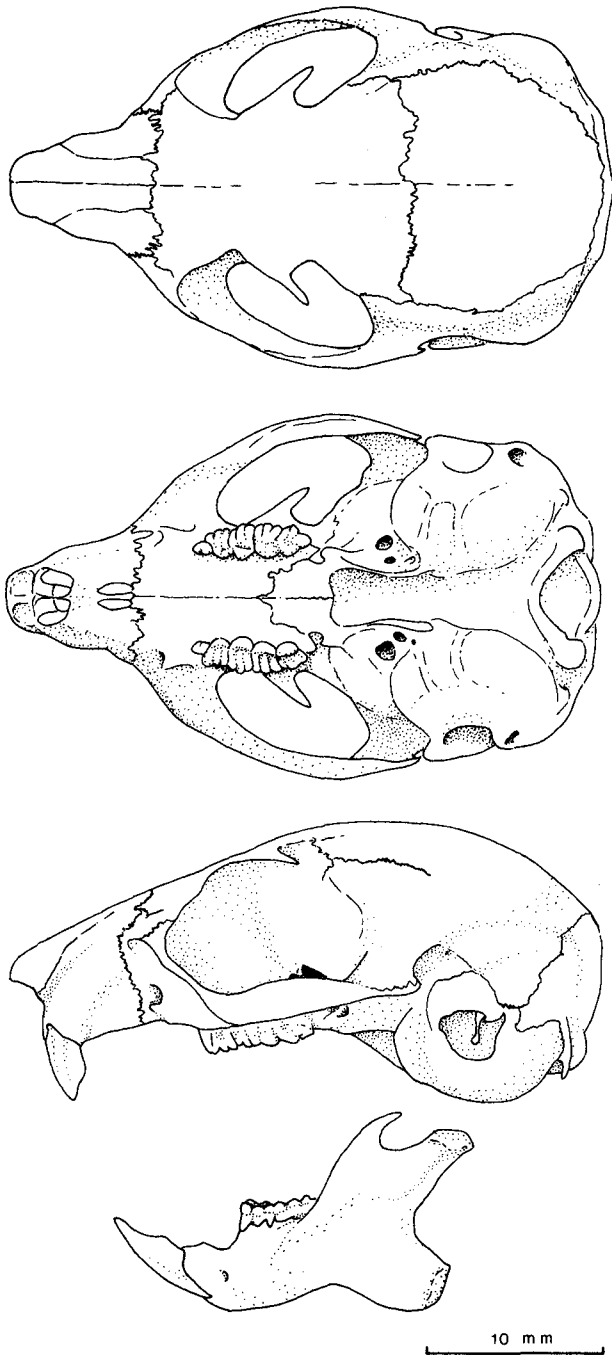


FIGURE 3. Dorsal, ventral, and lateral views of skull, and lateral view of lower jaw of *Glaucomys volans saturatus* (TTU 9667, female, from 8 mi. NW Warren, Bradley Co., Arkansas).

brown, fuscous, or mouse gray; the toes in *G. v. volans* are white in winter; tail is hair brown, snuff brown, verona brown, fuscous, or drab above and pinkish cinnamon, vinaceous cinnamon, or pinkish buff beneath; underparts are creamy white and often edged with pinkish cinnamon, vinaceous cinnamon, or pinkish buff.

DISTRIBUTION. The southern flying squirrel is found in temperate to subtemperate pine-hardwood forests from southernmost Quebec southward through the eastern half of the United States to Honduras (see Youngman and Gill, 1968; Hall and Kelson, 1959; Layne, 1974; Goodwin, 1961; figure 4). In North America north of México, four subspecies are recognized, *volans* in the north and *texensis*, *saturatus*, and *querceti*, from west to east, in the south. The geographic range of these four races, as a group, is more or less continuous, none being clearly separated from the others. In México and Central America, six subspecies are recognized, each occurring in an isolated, sub-

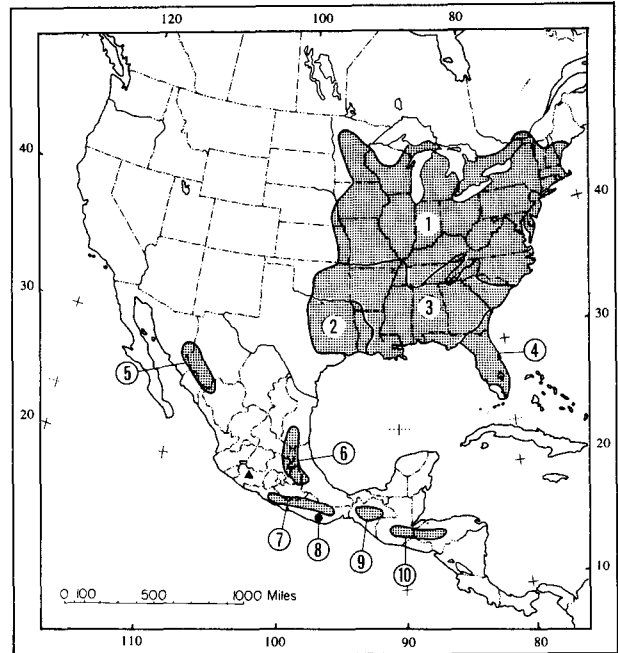


FIGURE 4. Distribution of *Glaucomys volans*. Subspecies are: 1, *G. v. volans*; 2, *G. v. texensis*; 3, *G. v. saturatus*; 4, *G. v. querceti*; 5, *G. v. madrensis*; 6, *G. v. herreranus*; 7, *G. v. oaxacensis*; 8, *G. v. chontali*; 9, *G. v. goldmani*; and 10, *G. v. underwoodi*. A sight record (Hooper, 1952), 9 km. (by highway) S. Pátzcuaro, Michoacán, is indicated by a closed triangle. Stippled areas represent geographic range based on marginal records, except for *madrensis*, which is known only by the holotype taken from the Sierra Madre de Chihuahua.

temperate, montane habitat. *G. v. madrensis* is known by specimens reported to have come from the Sierra Madre Occidental in Chihuahua. Perhaps this subspecies occurs in suitable habitat in mountains from Sonora south to the Río Grande de Santiago drainage in Nayarit and northern Jalisco. *G. v. herreranus* may have a similar distribution in the Sierra Madre Oriental, from southern Nuevo León and western Tamaulipas south to southwestern Puebla and west-central Veracruz where the elevation drops off toward the Río Santo Domingo. A sight record (Hooper, 1952), from 9 km (by highway) S Pátzcuaro, Michoacán, may represent this subspecies inasmuch as temperate and subtemperate forest extend westward along the transvolcanic cordillera to Michoacán. Locality records indicate that *oaxacensis* occurs in suitable habitat throughout the Sierra Madre del Sur, which is separated from the transvolcanic cordillera by the Balsas Basin, tropical deciduous forest, and thorn scrub.

A subspecies, *G. v. chontali*, known only from the type locality near Cerro Neveria, Oaxaca, may be restricted to a small mountain range that extends east from the drainage of the Río Verde to that of the Río Tehuantepec and is delimited to the north by the Río Atoyac and Río Tequisistlan. *G. v. goldmani* should inhabit pine-oak forests throughout the Chiapan highlands and probably the Cuchumatanes of Guatemala. *G. v. underwoodi* is known from Tecpan, Guatemala, east to the Department of Tegucigalpa, Honduras, a distribution that corresponds to an isolated pine-oak forest habitat.

FOSSIL RECORD. *Glaucomys volans* is known as a fossil only from Pleistocene deposits in North America. The earliest record, assigned to the Illinoian, is from Cumberland Cave, Maryland (Guilday, 1971). Other deposits in Augusta County, Virginia (Guilday, 1962), and Bedford County, Pennsylvania (Guilday *et al.*, 1964), date from post Wisconsin times, approximately 11,300 years BP. Cranial material from Overton County, Tennessee (Guilday *et al.*, 1969), has not been accurately dated and may be pre-Wisconsin or post-Wisconsin, or assignable to that age.

The species is thought to have originated in Asia (Burt, 1960) and to have migrated in the middle Miocene across northern Canada, then southward through the eastern United States (Muul, 1968). Most of the North American continent at this time supported an Arcto-Tertiary forest of diverse deciduous and coniferous trees. The Southwest, however, was occupied by a

Madro-Tertiary vegetation of xeric woodland, chaparral, grassland, and thorn forest—an unsuitable habitat for an animal like *G. volans*.

With the advent of the Pliocene, general drying conditions took place in the Southwest, and the Arcto-Tertiary vegetation of the Northwest was replaced by boreal forests so that the range of a deciduous forest species, like *volans*, was reduced to the eastern half of North America (Weigl, 1969). The Pleistocene produced further range modifications for the species as glacial advances altered sea levels and climate, and consequently the vegetation found south of the glacial margin. Muul (1968) suggested that *G. volans* was excluded from the northern United States during glaciation, at which time it probably spread into Middle America. Weigl (1969) also supported this view of a recent invasion of Middle America, arguing that there is little differentiation between the American flying squirrels and the Mexican races, and that the vegetation present in the Southwest throughout late Cenozoic times has afforded little opportunity for a southward migration of a mesic woodland species.

The supposed migratory route traversed by *volans* is through southern Texas along a woodland corridor produced by glacially associated climatic changes. However, fossil evidence to support this hypothesis is unavailable from any of the excavations along the assumed route, nor have fossil remains been found in Pleistocene deposits in Florida (Bader, 1957; Sherman, 1957), even though palynological data indicate suitable habitat (Watts, 1971). Elucidation of the distribution of the species during this period clearly must await the discovery of new fossil material.

FORM. Mucous glands are absent in the oral lips and angle of *G. volans*, but sudoriferous (sweat) glands are present, although atrophic, and sebaceous glands are moderately developed (Quay, 1965). The functional role of the sudoriferous and sebaceous glands is unknown, but they may serve in "marking" stored nuts (Muul, 1968; Avenoso, 1969). Anal musk glands are absent (Schwartz and Schwartz, 1959).

In the upper epididymis, spermatozoa form cylindrical masses in which the heads form the peripheral surface; the tails are directed toward the center of this cylinder and adhere to each other. The form of these cylindrical bodies and the degree of cohesion of spermatozoa are altered as they pass through the epididymis and probably reflect changes in the cohesive properties of the maturing spermatozoa (Martan and Hruban, 1970). Hruban *et al.* (1971) described the fine structure of the spermatozoa and their spatial arrangement in the upper epididymis. Histological and histochemical comparisons of spermatozoa from sexually active and inactive *G. volans*, and a study of epididymal influence on spermatozoan behavior were undertaken by Perkins (1974).

The os penis of *G. volans* is little more than a long (12.1 to 12.8 mm), slender, twisted bone with a slightly expanded distal end (Burt, 1960). Layne (1954) described the os clitoridis as essentially a rod-shaped structure, the proximal end of which forms a hook-like projection directed ventrolaterally. Adult length was 2.7 mm, and relative size when compared with bacula was 0.22.

Adaptations in myology and osteology, associated with a glissant habit, were recorded in detail by Peterka (1936) and contrasted with fossorial and arboreal strategies in other sciurids. More recently, Gupta (1966) has reported on the attachment and relationship of the musculature associated with the accessory cartilage and the gliding membrane.

FUNCTION. Endogenous activity rhythms have been studied, with the conclusion that light serves as the primary entraining factor. Due to a circadian rhythm of sensitivity to light, predictable phase shifts in activity patterns occur when animals, held under constant dark conditions, are subjected to light-shocks (DeCoursey, 1960a, 1960b).

Photoperiod has been implicated in the timing of the reproductive cycle. According to Muul (1969), the annual minimum photoperiod may trigger reproductive activity, and the annual maximum photoperiod may produce the postreproductive regression of the gonads—exposure to long photoperiods inhibited testicular descent. Gonadal development was independent of temperature cues.

Photoperiod apparently also serves as the cue for intensive nut storing. Decreasing day length appears to be the important factor involved in triggering the onset of the behavior, whereas a reduction in storing activity appears to be dependent on increasing day length (Muul, 1965, 1968).

At 37°C and pH 7.40, the partial pressure of oxygen required for half saturation of blood in the southern flying squirrel was 39 mm of mercury (Hall, 1965). Relatively higher oxygen affinities of hemoglobin measured in five other species of sciurids apparently is related to their lower metabolic requirements or habitation of oxygen-poor environments. In a comparative study of the hemoglobins of *G. volans* and *G. sabrinus*, Weigl (1969)

found four distinctive hemoglobin types, two in each species, with little evidence of intraspecific variation. The taxonomic significance of this finding has yet to be ascertained.

Two subspecies of the southern flying squirrel, *volans* and *querceti*, differed in their basal metabolic rates (870 as opposed to 1040 mm³ of oxygen per hour per gram of body weight) and mean body temperatures (37.8 as opposed to 37.4°C). Additional data on evaporative water loss, behavioral responses to high temperatures, and conductance (heat loss) are taken as further evidence for the existence of physiological adaptations that allow the more southern subspecies, *querceti*, to cope with the high daytime temperatures to which its arboreal nests in Florida are subjected (Dolan, unpublished data). Neumann (1967) recorded shifts in the upper and lower critical limits of the thermoneutral zone and changes in basal rates of metabolism that were correlated with season. Rate of heat loss (110 mm³O₂/hr/g°C) appears fairly uniform throughout the geographic range of the species in the United States, suggesting insulative qualities of the pelage are similar (Dolan, unpublished data; Morrison and Ryser, 1951; Muul, 1968). Neumann (1967) found no seasonal variation in pelage conductance.

Muul (1968) reported occasional torpidity in southern flying squirrels and recorded rectal body temperatures of 22 and 29.4°C for two individuals (normal resting body temperature, approximately 39°C). He further postulated that the condition is produced by prolonged cold stress and reduced food supplies, but was unable to induce torpidity under laboratory conditions. True hibernation is unknown in this species.

ONTOGENY AND REPRODUCTION. Two peaks in parturition (April and May, August and September), throughout the range in the United States, are indicated by published records (Connor, 1960; Hibbard, 1935; Lowery, 1974; Uhlig, 1956). However, it is not known conclusively whether a single female participates in both the spring and autumn breeding periods. Sollberger (1943) observed that captive females mated only once during a year. Furthermore, there is some question as to whether females from late summer litters breed during their first spring (Jordan, 1948).

The gestation period is 40 days, and young are born blind, deaf, hairless (with the exception of mystacial vibrissae), and pink in color. Average litter size is three to four (range two to seven), and mean body weight at birth is 3 to 5 g. The patagium is clearly evident in newborns. Notes on postpartum development are provided by Hatt (1931), Muul (1970), Rand and Host (1942), Sollberger (1943), and Svihla (1930). Young are weaned at approximately six to eight weeks, but remain with the female if a second litter is not produced (Muul and Alley, 1963).

Reproductive data are not available for the isolated populations in México and Middle America.

ECOLOGY. Estimates of population density have ranged from two to five squirrels per hectare (Burt, 1940; Jackson, 1961; Jordan, 1948) to as many as 12 (Sollberger, 1943). Little information is available on home range size, but areas of 1.6 to 2 hectares (Schwartz and Schwartz, 1959) and 0.41 for females and 0.53 for males (Madden, 1974) have been calculated. Sex ratios of males to females have been reported at 1:2 (Jordan, 1956) and 3:2 (Burt, 1940). However, Burt did not think his findings represented the true ratio.

The only published record of homing in flying squirrels (McCabe, 1947) concerns a toe-clipped female that returned six days following release 1.6 km from point of capture. If the animal traveled through the trees, the return route measured 2.8 km.

Flying squirrels are among the most carnivorous of North American sciurids and are reputed to consume not only insects and other invertebrates but also birds, eggs, nestlings, and carrion when available (Connor, 1960; Schwartz and Schwartz, 1959; Seton, 1929; Stoddard, 1920; Svihla, 1930). Plant matter consists of a wide variety of items: nuts, seeds, berries, fruits, blossoms, buds, fungi, lichens, and bark (Jordan, 1948; Muul and Alley, 1963; Sollberger, 1940). Nuts may be stored in the nest, in cracks, cavities, or unfinished woodpecker holes, in the forks of branches, or even in the ground. Nut storing behavior peaks in November, and nut selection and processing have been described in detail by Muul (1968) and Avenoso (1969).

It is doubtful that the nocturnal habits of flying squirrels confer any special immunity from predation. Owls and domestic cats definitely take their toll of individuals (Connor, 1960; Hall and Blewett, 1964; Mumford and Handley, 1956; Sollberger, 1943). The rat snake, *Elaphe obsoleta*, also has been reported feeding on *G. volans* (Pearson, 1954). Potential predators probably include bobcats, raccoons, weasels, and hawks.

Apparently, one complete molt occurs annually; it begins in September or early October and is completed by late November (Jackson, 1961). The lateral pelage is replaced first, then the dorsal fur, and finally the hair on the head and shoulders (Howell, 1918).

Captive animals begin to show signs of age at three years; five years probably represents the average life span (Sollberger, 1943), and potential longevity may approximate 10 years (Schwartz and Schwartz, 1959).

It is evident from the literature that flying squirrels utter several distinct calls, but inasmuch as a systematic study of the vocal repertoire of these animals has never been undertaken, the information in this area remains in the form of scattered observations. The young do produce detectable high-pitched squeaks, and possibly other notes that may be ultrasonic. Muul and Alley (1963) suggested that the production of high frequency sounds emitted during gliding may serve as a form of echolocation. Adults make sounds resembling the chirping of birds, a "chuck, chuck" note, a high-pitched "tseet," and a soft sneeze-like call (Sollberger, 1940; Perkins, 1873; Schwartz and Schwartz, 1959; MacClintock, 1970).

Flying squirrels generally travel by gliding in a descending curve from one tree to another. These glides are normally 6 to 9 m in length, although more extensive glides (30 m or more) have been reported. The record is approximately 90 m, made when a squirrel glided down a slope (Klugh, 1924). The remarkable agility in gliding is evinced by an ability to make 90 and 180° turns in avoiding obstacles.

The genus *Glaucomys* includes the only strictly nocturnal tree squirrels in North America. Nevertheless, a few accounts in the literature show that *G. volans* may occasionally be abroad before dark (Kelker, 1931; Kennicott, 1857; Jackson, 1961; personal observation, 1971).

A prolonged study of activity patterns in captive flying squirrels (Muul, 1968) housed in an outside enclosure revealed that animals are more or less active throughout the night during warm months (July to October). However, as ambient temperature decreased in the winter (November to February), trimodal and sometimes bimodal patterns of activity became discernible with "peaks following sunset, sometimes around midnight, and before dawn. . . . The occasional bursts of activity apparently represent feeding times" (Muul, 1968:44). This is in contrast to Sollberger's (1940) conclusion that flying squirrels are inactive during cold weather.

Tree cavities are preferred nest sites, and woodpecker holes comprise an important percentage of the cavities (Muul, 1968; Sollberger, 1940). Entrance ways usually measure 40 to 50 mm in diameter, large enough to admit flying squirrels, but small enough to exclude the larger tree squirrels with which they may compete for nest sites. Interiors are lined most often with finely divided inner bark, although moss, lichens, feathers, and leaves may be used on occasion. In Florida, Spanish moss (*Tillandsia*) is the most common nesting material (Ivey, 1959; Moore, 1947). Nests average 4.5 to 6 m above the ground, but may be situated anywhere from 1.5 to 12 m or more in height.

Flying squirrels may usurp old nests of birds, gray squirrels, and fox squirrels, modifying them for their own use (Jackson, 1961; MacClintock, 1970; Sollberger, 1943). Although Sollberger (1943) remained skeptical of the ability of *G. volans* actually to construct such a nest, the numerous observations of the species in outside dens seems to suggest his suspicions were unwarranted. Many of these records are of females with young (Landwer, 1935; Layne, 1958; Snyder, 1921). Svihla (1930) observed a captive female that abandoned a nest box and built a nest of Spanish moss, oak leaves, and twigs in a corner of the cage. Characteristically, complete outside nests have an outer shell of small sticks and leaves, and an inner lining of finely shredded material, usually bark. Palmetto fibers occasionally may be substituted for bark in southern portions of the range. Moore (1947) described other nests in hanging streamers of Spanish moss in Florida, some of which lacked interior linings.

Muul (1968) recognized two general categories of nests: primary nests, those used more or less continuously, and secondary nests or retreats. There are usually several of the latter, and they serve variously as sheltered stations for feeding and defecating, as well as refuges should the primary nest be disturbed or destroyed. Defecatoria not only function to keep the primary nest clean but may well be important in diverting the attention of predatory animals away from the main nest site. Considering the number of nest sites required per individual or family group, their availability may be an important factor in limiting population size (Muul, 1968). Laboratory encounters between *G. sabrinus* and *G. volans* showed *volans* to be slightly more successful in controlling nest sites, a resource probably competed for in the wild (Weigl, 1969). Weigl suggested, however, that the northern limit of the range of the southern flying squirrel is determined not by competition with *sabrinus*, but rather by the availability of certain mast species, particularly the oaks and hickories, which provide an important part of the diet of *volans* during winter.

Muul (1968) further documented the use of subterranean sites, probably as retreats along escape routes rather than actual

TABLE 1. Parasites infecting the southern flying squirrel, *Glaucomys volans*.

Ectoparasites	Source
Mites	
<i>Psorergates glaucomys</i>	Ah <i>et al.</i> , 1973
<i>Euhaemogamasus ambulans</i>	Lowery, 1974
<i>Trombicula microti</i>	Lowery, 1974
<i>Haemolaelaps megaventralis</i>	Lowery, 1974
Lice	
<i>Haploplura trispinosa</i>	Lowery, 1974
<i>Neohaematopinus sciuropteri</i>	Lowery, 1974
<i>Enderleinellus replicatus</i>	Lowery, 1974
Fleas	
<i>Opisodasys pseudarctomys</i>	Connor, 1960
<i>Eptedia faceta</i>	Connor, 1960
<i>Orchopeas howardii</i>	Lowery, 1974
<i>Peromyscopsylla catatina</i>	Connor, 1960
<i>Conorhinopsylla stanfordi</i>	Lowery, 1974
<i>Leptopsylla segnis</i>	Lowery, 1974
Endoparasites	
Protozoa	
<i>Eimeria parasciurorum</i>	Bond and Bovee, 1957
<i>Eimeria glaucomydis</i>	Roudabush, 1937
<i>Trypanosoma denysi</i>	Lowery, 1974
Acanthocephala	
<i>Moniliformis clarki</i>	Lowery, 1974
Cestoda	
<i>Raillietina bakeri</i>	Kinsella, personal communication
Nematoda	
<i>Capillaria americana</i>	Lowery, 1974
<i>Citellinema bifurcatum</i>	Lowery, 1974
<i>Enterobius sciuri</i>	Lowery, 1974
<i>Syphacia thompsoni</i>	Lowery, 1974
<i>Strongyloides robustus</i>	Kinsella, personal communication

nests, although he did not specify. Moore (1947) thought he might have found a below-ground nest for *G. volans*, but the data do not warrant such a conclusion. As far as is known, no authentic record of subterranean nesting in the species exists.

In both the eastern United States and Middle America, the southern flying squirrel occupies a general habitat best characterized simply as deciduous forest. In the more northerly reaches of its range, the species also inhabits mixed woodlands of hardwoods and conifers, particularly where hardwoods predominate. Muul (1968) gave a detailed account of the diverse plant associations harboring *G. volans* in the northern United States.

These squirrels in the eastern United States are found primarily at low elevations, but in Middle America they occur usually between 1200 and 3000 m on the forested, high mountain slopes where cloud forest habitat prevails (Goodwin, 1961; Hooper, 1952). The only published record of the species from lowland tropical forests was provided by Koopman and Martin (1959), on the basis of subfossil skeletal material from Tamaulipas.

Diseases and parasites. Osteomalacia, which is clinically characterized by lameness of the affected animal, has been induced in captive flying squirrels (Sheldon *et al.*, 1971). Partial alopecia (loss of hair) has been observed in another group of captive animals (Sheldon, 1971). Both maladies apparently stem from nutritional deficiencies.

The single specimen of *G. volans* known to have rabies is thought to have contracted the virus as a result of contact with an infected bat (Venters, 1962). This represents the first confirmed report of rabies in a Florida rodent.

Parasitological data for the species are summarized above in Table 1.

BEHAVIOR. Flying squirrels form winter aggregations, presumably for the purpose of thermoregulation (Muul, 1968; Sollberger, 1943); it is not known if these represent basically family groupings or if extrafamilial individuals are included.

Territoriality was believed limited to female defense of brood nest trees (Muul, 1968; Sollberger, 1943)—males do not assist in the care of young. However, Madden (1974) recently described

territorial behavior generalized to include the entire home range in a population of breeding females in New York. Males did not maintain territories.

Females will go to great lengths to retrieve young removed from the nest (Stack, 1925). Muul (1970) studied this behavior in detail and found that it was strongest during a 40-day postpartum period. In this interval, females retrieved extrafamilial litters as readily as their own, but preferred younger individuals. Muul also noted that the females seemed to be attracted primarily by sounds emitted by the young, and that these vocalizations may, in part, be ultrasonic. An hormonal basis for the retrieval response is proposed in view of the fact that after about 40 days postpartum, aggression replaced retrieval behavior in encounters with all extrafamilial individuals, regardless of age. This behavioral change occurred independently of the stage of development of the young in the female's care. Sollberger (1940, 1943) noted that lactating females are much less likely to bite, and one of us (Dolan) has observed this also for females with young.

Kelker (1931) and Sollberger (1943) described courting and mating in flying squirrels.

GENETICS. Nadler and Sutton (1967) examined a single female *G. volans* and reported a diploid number of 48 chromosomes and a fundamental number of 74 chromosomal arms. The karyotype contained 12 metacentric, 16 submetacentric, and 20 acrocentric autosomes; the X chromosomes were not identified. Karyotypically, *G. volans* is distinguishable from *sabrinus* by the number of acrocentric chromosomes (20 as opposed to 18), the sex chromosomes in *sabrinus* are a submetacentric and a minute chromosome. The chromosomal similarity of the two species argues for a closer relationship (Nadler and Sutton, 1967) than is suggested by their markedly different bacula and os clitorides.

Moore (1965) was unable to demonstrate sexual dimorphism of nuclei in interphase somatic cells taken from *G. volans*.

REMARKS. The generic name is derived from the Greek *glaukos* (gray) and *mys* (mouse). The specific name *volans* is the Latin word for "flying."

The etymology of subspecific names is as follows: *goldmani* and *underwoodi* honor E. A. Goldman and C. F. Underwood, respectively, collectors of type specimens; *herrerae* refers to Professor L. Herrera, who presented E. A. Goldman with the only other specimens known from México in 1926; *chontali* is in reference to the Chontal Indians, which are native to the area of the type locality; *madrensis* and *oaxacensis* denote the type localities, Sierra Madre de Chihuahua and San Pedro Jilotepec, Oaxaca, México, respectively. Although not specified, *saturatus* probably refers to the darker pelage characteristic of that race, and *texensis* to the general geographic distribution of that subspecies. The derivation of *querceti* is uncertain but may refer to a dweller of oak trees.

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