Sciurus variegatoides Ogilby, 1839
Variegated Squirrel

Sciurus variegatoides Ogilby, 1839:117. Type locality “west coast of South America [assumed to be in the vicinity of San Carlos, Department de La Unión, El Salvador—Harris, 1937:8].”

Macrochaeta ptilata Lesson, 1842:112. Type locality “San-Carlos (Centre Amérique).” El Salvador.

Macrochaeta adelphi Lesson, 1842:112. Type locality “Realejo (Nicaragua) Centre Amérique.”

Sciurus richardsonii Gray, 1842:264. Type locality “Honduras.”

Not Sciurus richardsonii Bachman (=Tamiasciurus).


Sciurus griseoaudatus Gray, 1843:34. Type locality “West Coast of America.”

Sciurus fuscovariegatius Schinz, 1845:15. Type locality “Honduras.”


Sciurus rigidus Peters, 1863:652. Type locality “San José in Costa Rica.”

Sciurus intermedius Gray, 1867:421. Type locality “Guatemala.”

Macrochaeta nicoyana Gray, 1867:423. Type locality “Costa Rica, Nicoya.”


Sciurus goldmani Nelson, 1898:149. Type locality “Huehuatan, Chiapas, Mexico.”

Sciurus thomasi Nelson, 1899:71. Type locality “Talamanca, Costa Rica.”

CONTEXT AND CONTENT. Order Rodentia, Suborder Sciuromorpha, Family Sciuridae, Subfamily Sciurinae, Genus Sciurus, Subgenus Sciurus (Wilson and Reeder, 1993). Based upon structure of the hyoid bones, S. variegatoides also has been placed into the subgenus Neosciurus (Hoffmeister and Hoffmeister, 1991). The genus Sciurus contains 28 species (Wilson and Reeder, 1993). Fifteen subspecies of S. variegatoides are recognized (Hall, 1981):

S. v. adelphi (Lesson, 1842:112), see above (annulatum Thomas is a synonym).

S. v. atripilus Harris, 1930:2. Type locality “Tambor on the Nicoya Peninsula, Costa Rica.”


S. v. belti Nelson, 1899:78. Type locality “Escondido River, 50 miles from Bluefields, Nicaragua.”

S. v. boothi Gray, 1843:139, see above (richardsonii Gray and fuscovariegatius Schinz are synonyms).

S. v. dorsalis Gray, 1849:138, see above.

S. v. goldmani Nelson, 1898:149, see above.

S. v. helecrisus Goldman, 1912:39. Type locality “Corozal, Canal Zone, Panama.”

S. v. loewyi McPherson, 1972:191. Type locality “1 rd mi S Paso Real, Rio Escuadra, Province of Puntarenas, Costa Rica; . . . at an altitude of 150 meters in the Tropical Forest portion of the Valle del General.”

S. v. managuensis Nelson, 1898:150. Type locality “Managua River, Guatemala.”

S. v. melanica (Gray, 1867:425), see above.

S. v. rigidus Peters, 1863:652, see above (austini Harris, intermedius Gray, and nicoyana Gray are synonyms).

S. v. thomasi Nelson, 1899:71, see above.

S. v. underwoodi Goldman, 1932:275. Type locality “Monte Redondo, about 30 miles northwest of Tegucigalpa, Honduras (altitude 5,100 feet).”

S. v. variegatoides Ogilby, 1839:117, see above (griseoaudatus Gray and pylades Lesson are synonyms).

DIAGNOSIS. The range of S. variegatoides is at least partially sympatric with the ranges of S. aureogaster, S. deppei, S. granatensis, and S. richmondi. S. variegatoides has a greater total length (510–560 mm) and length of tail (240–305 mm), compared with <447 mm and <195 mm, respectively, for S. deppei, S. granatensis, and S. richmondi (Hall, 1981). In Panama, S. variegatoides also is distinguished from other Sciurus inhabiting the region by its long black and white tail, the individual hairs of which are broadly tipped with white (Goldman, 1920). Where the range of S. variegatoides meets the range of S. aureogaster (the ranges overlap only in Chiapas and Guatemala), S. variegatoides is distinguished by its feet being whitish and slightly speckled with black (not frosted buffy black or blackish as in S. aureogaster), and the underparts are white or rarely pigmented (instead of orange or chestnut and often black-flecked—Hall, 1981).

In Costa Rica, S. variegatoides (Fig. 1) is larger and has longer pelage than S. granatensis, and the tail of S. variegatoides is grizzled. Some populations of S. variegatoides have a prominent brown patch on the back, with pale-colored sides; other populations

have a grizzled appearance with a rusty color on the limbs. There usually is a prominent white postauricular patch. *S. variegatoidea* also differs from *S. granatensis* in occurring in relatively drier, more open, and more disturbed habitat. These species often are sympatric in Costa Rica (Heaney, 1983) at the interface of dry forest and rainforest (D. H. Janzen, in litt.). In Panama, *S. variegatoidea* and *S. granatensis* can be distinguished in the field by color and size. *S. variegatoidea* has a black dorsal stripe, pale-gray sides, and lacks reddish pelage, whereas *S. granatensis* consistently has a dark red-brown dorsum and a reddish tail. Near Paraiso, Panama, *S. variegatoidea* is significantly larger than *S. granatensis* in length of head and body (264 versus 254 mm), length of tail (252 versus 205 mm), and length of hind foot (59 versus 55 mm—Glanz, 1984).

*Sciurus variegatoidea*, *S. colliei*, and *S. yucatanensis* are strikingly similar in color and pattern of pelage, although they differ in size. *S. yucatanensis* essentially is a smaller version of the western and southwestern populations of *S. variegatoidea*. Differences in pelage features between the two are of the same magnitude as those between adjacent, slightly differentiated, and intergrading subspecies of *S. variegatoidea*, but *S. yucatanensis* is smaller in cranial and external dimensions than nearby populations of *S. variegatoidea* (Mussser, 1968), and *S. variegatoidea* lacks black postauricular patches (Hall, 1981). *S. variegatoidea* and *S. yucatanensis* may hybridize (Mussser, 1968).

In color and pattern, *S. variegatoidea* from Chiapas and Guatemala closely resemble the southernmost population of *S. colliei* (S. c. nuchalis). Like *S. c. nuchalis*, *S. variegatoidea* has variable buff and black upperparts, which cover the sides and thighs that are grayish in *S. colliei*. The white or buff-tinted postauricular patches of *S. variegatoidea* are larger and more distinct than in *S. colliei*, the upperparts are paler (not as black), the feet are white and are usually peppered instead of fronted black or black, the underparts are white, and the tail is variegated buff. There is no melanistic phase in *S. variegatoidea*. The Chiapas-Guatemala population of *S. variegatoidea* also resembles *S. colliei* in external dimensions, but *S. variegatoidea* is appreciably smaller in cranial measurements, and sphenopalatine vacuities occur more frequently (Mussser, 1968).

**GENERAL CHARACTERS.** The variegated squirrel is a large long-tailed species (Goodwin, 1934) with shiny, coarse, and bristly pelage. The upperparts are highly variable in color, from blackish to grizzled yellowish-gray. Dorsally, the tail is black with a heavy wash of white, sometimes appearing faintly annulated. Ventrally, the tail has a median area of tawny to dark rufous, bordered with black and edged with white. The underparts are white to rich cinnamon-buff. When the underparts are not entirely white, then white inguinal, axillary, and gular patches usually are present. There is no rump patch. The dorsal patch on the shoulder usually is absent or faint (Hall, 1981).

The variegated squirrel has great variation in color and in color pattern among its subspecies. The colors vary from nearly white or cream through yellow and reddish brown to pure black. The patterns vary from the presence of dorsal and lateral stripes and forehead patches to an overall grizzled coloration. The darkest and most intensely colored subspecies (*S. v. bettii*, *S. v. managuensis*, and *S. v. thomasi*), with reddish underparts and ear patches, live in the regions of heaviest rainfall. Their ranges extend from the tropical lowlands of the Caribbean coast to the eastern slopes of the central highlands, a region with heavy precipitation and dense forests. *S. v. atriprasus* also is a dark subspecies, but is found on the Pacific side in the mountains of the central part of the Nicoya Peninsula, where it has considerably more rainfall than the rest of the Pacific coast or Costa Rica and Nicaragua. On the Pacific slope of Central America are found the pale subspecies *S. v. bangsi*, *S. v. dorsalis*, *S. v. goldmani*, and *S. v. helvolus*, all of which have white ear patches and white underparts. In this area, the amount of rainfall is considerably less than in the Caribbean slope, and the forest is less dense. Pelage color of *S. v. dorsalis* also may vary in relation to soil color (Harris, 1937). There is considerable individual variation in size among adults of *S. variegatoidea* with one locality in the U.S. (Fig. 3). The single locality show a wide difference in width of nasals, slope of the rostrum, flatness of the frontal region, and inflation of the premaxillaries directly anterior to the frontals (Harris, 1937).

There is no sexual dimorphism in size. Averages of external and cranial measurements (in mm) of *S. v. bangsi*, *S. v. dorsalis*, and *S. v. variegatoidea*, respectively, are: total length, 540, 528, 543; length of tail, 269, 272, 272; length of hind foot, 65, 66, 64; condylo-maxillaries length, 55.9, 54.4, 54.2; zygomatic breadth, 35.4, 34.3, 35.1; distance from premaxilla to palatine notch, 31.6, 31.2, 31.0; interorbital breadth, 20.5, 20.8, 20.0 (Harris, 1937).

**DISTRICTION.** The variegated squirrel occurs from southern Chiapas, Mexico, to central Panama (Fig. 3; Hall, 1981), and occupies arid and humid tropical forests from sea level to 2,500 m elev. (Elliot, 1904; Giacalone et al., 1987; Harris, 1930; Nelson, 1899; Wilson, 1983). The genus *Sciurus* evolved by the early Miocene (Black, 1972). No fossils of *S. variegatoidea* are known.

**FORM AND FUNCTION.** The dental formula of the variegated squirrel is i 1/1, c 0/0, p 2/1, m 3/3, total 22 (Hall, 1981). The hyoid apparatus consists of a single basihyal and paired
thryohyal, ceratohyal, and stylohyals; the basihyal is thick, triangular in section, and fuses with the short thyrohyal at an early age (Hoffmeister and Hoffmeister, 1991).

The only important seasonal change in pelage color is a gradual fading of the black of the black-backed forms to dull chocolate, and an abrupt change at molt to brighter and more intense colors. The proportion of black hairs on the feet increases after the molt in some subspecies. Molting begins most often in April and May, and most are in fresh pelage in September and October. Individuals in molt also occur in November, December, February, and July; molt is evident in some individuals from nearly every month of the year, but is least evident in early autumn. It is possible that individuals molt only once per year (Harris, 1937).

The baculum (os penis) of S. variegatoides (Fig. 4) is most like bacula of S. aureogaster, S. colliae, and S. yucatanensis. The basal portion of the shaft is circular or nearly so in cross section. The shaft tapers distally, with an apparent twist, to its smallest diameter, which is called the neck. At this point the shaft usually curves dorsally and expands into a broad circular disc that is concave on the right side and convex on the left. Ventral to this expanded disc is a spur. In S. variegatoides, the baculum has a large base, tapers to a narrow neck, and has a relatively small expanded tip, with the edges curled over in most individuals. There is no supplementary spur, but a tuberosity is present just posterior to the main spur. The posterior edge of the disc is rounded and a right angle is formed with the shaft. There may be a dorsal keel on the shaft. Averages and ranges of measurements (in mm) of four bacula from Costa Rica and one from Panama are: length, 12.1 (11.5–12.4); length of expanded tip, 2.6 (2.4–2.7); height of tip, 3.0 (2.7–3.6); height of base, 3.0 (2.7–3.3); width of base, 2.4 (2.1–2.9)—Burt, 1960).

The basiheum (os clitoris) of S. variegatoides has no evidence of a crest on the left side of the shaft or disc, and the ventral projection is blunt. Length of the basiheum is 3.9 mm, and width of the disc is 2.0 mm (Layne, 1954). Females have eight mammae (Goodwin, 1946); one pair pectoral, two pair abdominal, and one pair inguinal.

**ONTOMETRY AND REPRODUCTION.** In Panama, the breeding season for S. variegatoides may be in April or May (Enders, 1935). The average number of young in a litter probably varies from four to six (Goodwin, 1946). The dark color of adult S. v. melania also is present in young (Bangs, 1902).

**ECOLOGY.** The variegated squirrel occurs in tropical-evergreen forests, in rainforests, in drier and partly deciduous tropical forests surrounding lagoons, and in forests of nut palms (Palmaceae) intermixed with figs (Ficus) and other tropical broadleaf trees on the coastal plain. Farther inland, S. variegatoides occurs in tropical rainforest that has been thinned. This is typical habitat for the species in Chiaapas and Guatemala. The variegated squirrel does not occur in pine (Pineus) and oak (Quercus) forests above the rainforest or cañetal zone in Chiaspa or Guatemala, although it lives in pine-oak habitats farther south in Honduras and Nicaragua (Musser, 1968). In Guatemala, S. variegatoides inhabits the arid tropical forest region along the western coast at elevations ranging from sea level to ca. 1,050 m (Goodwin, 1934). In Costa Rica, the variegated squirrel lives in coastal lowlands, deciduous forest, and riparian vegetation below ca. 400 m elev., farmland and urban sprawl at 900–1,200 m elev., and evergreen forests and associated pastures and fields at 1,500–1,900 m elev. (Wilson, 1983). S. variegatoides is abundant at lower elevations in the Canal Zone and western Panama, where it occurs in fruit groves, scrub, and semi-open country (Handley, 1966).

In Panama, S. variegatoides lives in nests that are compactly constructed of leaves and located in the tops of tall, slender trees. The nests usually are placed on a limb at its juncture with the main stem against which the nest rests for additional support. There may be as many as one nest to every 2.4 ha (Enders, 1935).

**Scirius variegatoides** consumes hard-shelled seeds in fruits, such as *Scheelea rotstra*, *S. zonensis* (Bradford and Smith, 1977; Fleming, 1970); D. H. Janzen (in litt.), and *Crescentia alata* (Janz, 1982b), and softer, thinner-shelled seeds in fruits, such as *Guazuma ulmifolia* (Janz, 1982c, in litt.), *Quercus oleoides* (Bouck, 1961), and *Sterculia aptata* (Janz, 1972, in litt.). Fungi also are consumed (Gomez, 1983). In Costa Rica, the variegated squirrel eats various kinds of fruits and nuts (Goodwin, 1946).

Near Paraiso, Panama, foods eaten by S. variegatoides included seeds of species of Anacardiaceae (*Mangifera indica*, *Spondias mombin*), Burseraceae (*Bursera simaruba*), Bombacaceae (*Ochroma pyramidale*), Cochlospermaceae (*Cochlospermum vitifolium*), Leguminosae (*Enterolobium cyclocarpum*), Moraceae (*Cecropia*, *Ficus insipida*), Palmaceae (*Astracorys standleyanus*, *Scheelea zonensis*), Rubiaceae (*Genipa americana*), Sapindaceae (*Cupania, Paulinia*), Sterculiaceae (*Guazuma ulmifolia*), Tiliaceae (*Apeiba tiboubr*, *Luehea species*), Ulmaceae (*Tremia micrantha*), and unidentified vines. Palms were relatively unimportant in the diet. The three fruits whose seeds the variegated squirrel ate most frequently (48% of its diet) included guanaco (Guazuma ulmifolia), and two larger drupes, the introduced mango (*Mangifera indica*) and the hogplum (*Spondias mombin*). S. variegatoides consumed seeds of all immature and most mature fruits it took, but discarded the thick-shelled seeds of mature mungos and hogplums. The variegated squirrel seems to prefer not to penetrate the hard shells protecting certain seeds (Glanz, 1984; D. H. Janzen, in litt.).

**Scirius variegatoides**, the larger species, tends to occur in drier and more variable habitat than the smaller S. granatensis (Heaney, 1984). In some areas of Panama, S. variegatoides seems to occur in older and denser woodland than S. granatensis, although S. variegatoides also occurs in the open growth of abandoned plantations (Aldrich and Bole, 1937). In other parts of Panama, S. variegatoides occurs in the second growth of comparatively small trees, whereas S. granatensis tends to occur in more mature forests (Enders, 1935). Near Paraiso, Panama, S. variegatoides and S. granatensis overlap in some habitats, but S. variegatoides shows a broader variety of habitats than S. granatensis; S. variegatoides occupied dry deciduous forest more often than other habitat types. Compared with S. granatensis, the diet of S. variegatoides includes more soft fruits and flowers and less hard-shelled nuts. The percentage of feeding sessions devoted to categories of foods for S. variegatoides and S. granatensis, respectively, are: palm and legume nuts, 3.9, 72.6; large, hard fruits, 7.8, 7.9; soft drupes and berries, 61.1, 10.4; cashew, 1, 3; capuchate or arillate fruits, 7.8, 2.6; flowers, 13.0, 0; bark, fungi, and insects, 6.5, 2.6 (Glanz, 1984). Near Rodman, Panama, S. variegatoides occurs sympatrically with S. granatensis, but only one S. variegatoides was observed; it was
running along a Scheelea palm frond carrying a nut in its mouth. Two months later, a S. granatensis was seen running along the same palm (Enoch, 1970).

In Volcán Poás National Park, Costa Rica, S. variegatoides is sympatric with three other species of squirrels. Of 302 sightings of squirrels, Synthecosciurus brochus accounted for 170 (56.3%) of the sightings, S. granatensis 84 (27.8%), S. variegatoides 15 (5.0%), and Microsciuroides olfersi 1 (0.3%). S. variegatoides occurred at ca. 2,500 m elev. in mature, undisturbed forest that was dominated by Quercus, Clusia odorata, Diodonpyxis pittieri, Podocarpus, and Brunellia costaricensis. This forest had many trees of large girth, which often were composed of two to four trees intertwined into composite trunks. Branches carried heavy loads of bromeliads, orchids, mosses, and liverworts. Sightings frequencies of S. variegatoides was 0.02 individuals/km, compared, with 0.46 for S. brochus and 0.42 for S. granatensis. S. variegatoides occurred in disturbed forests, but was not observed during census walks. S. variegatoides also was observed with S. brochus in pasture edges at 2,450 m elev. in habitats characterized by isolated trees that were remnants of the old forest, including Quercus, Podocarpus, Drimys granadensis, Magnolia poasana, and Miconia corticata (Giaccalone et al., 1987).

The Chiapas-Guatemala populations of S. variegatoides occur in tropical broadleaf forests while S. aureogaster occupies either the pine and conifer forests of the Sierra Madre de Chiapas and Guatemalan highlands or the lowland-scrub and tropical-deciduous forests west of Pico Vernal. Although the two species overlap elevantionately, they are not known to occur at the same locality (Musser, 1968).


The only ectoparasites reported from S. variegatoides are the chigger Microtrombicula nicaraguensis (Webb and Loomis, 1970) and the louse Enderleinellus honshinum (Kim, 1966). No endoparasites are known.

In Mexico, the variegated squirrel is considered to be a "fragile" species in some parts of its range (Gelabals and Navarro L., 1991). Three subspecies of S. variegatoides (S. v. melania, S. v. variegatoides, and S. v. underwoodi) have been identified in zoos (Dolan and Moran, 1969).

BEHAVIOR. The variegated squirrel is diurnal and arboreal (Goodwin, 1946; Handley, 1966), but it occasionally descends to the ground. In Costa Rica, S. variegatoides is very arboreal; in ca. 100 ft of observation, it was observed on the ground only once, and then only for a few seconds while it crossed a small open area (Boucher, 1981). In Panama, the average height that S. variegatoides is active aboveground is 3.5 m (Glanz, 1984).

In Panama, the variegated squirrel is wary (Aldrich and Bole, 1937). Hunting pressure on S. variegatoides could favor quieter foraging behavior, and hence less grooming on palm nuts by this species (Glanz, 1984). In mid-June, S. variegatoides was observed in mango trees in an old clearing. The variegated squirrels made rapid motions while cutting and feeding on the ripe fruit. This species is not especially shy, but one that had been watching a human observer ran down a tree trunk and started rapidly off along the ground, carrying a large mango in its mouth (Goldman, 1920). A young male S. variegatoides was a playful and friendly pet. He had been taken from a nest while very young and reared by humans. He was not active after dusk (Enders, 1935).

In Costa Rica, the variegated squirrel was seen feeding on acorns in oak (Q. xoleoides) trees, picking them from the branches or cutting them loose with the teeth. S. variegatoides ate them singly, holding them in the front paws and cutting off pieces of shell with the incisors, and then biting off pieces of kernel. Although variegated squirrels often dropped many pieces, including nearly whole acorns on occasion, they never were seen carrying whole acorns more than a few meters. Variegated squirrels thus appear to be important as predispersal seed-predators on large-seeded fruits; there was no sign of them ever caching food in trees or on the ground (Boucher, 1981).

In Costa Rica, S. variegatoides retrieves fallen ripe fruits of Crescentia alata by picking up a fruit in its mouth and carrying it up 1–3 m in a tree. It may spend as much as 15 min gnawing a hole in the side of the fruit, and then it cuts into the pulp, dropping pulp fragments and removing the seeds. The seeds are chewed and swallowed. After feeding this way for 30 min, the fruit is discarded and the variegated squirrel moves on to another activity. There is no evidence to suggest that S. variegatoides caches or otherwise distributes seeds of C. alata (Janz, 1982). Nothing is known concerning the genetics of S. variegatoides.

REMARKS. Sciurus variegatoides, S. collliae, and S. yucatanensis may be fragmented segments of one species whose geographic range once extended along the Pacific lowlands and uplands from Sonora to southern Guatemala, across eastern Guatemala into the Yucatan Peninsula, and throughout Central America to Panama. Geographic distributions of segments now represented by S. variegatoides and S. yucatanensis remain relatively intact and the two may still connect (geographically and genetically) through eastern Guatemala and northwestern Honduras. The Pacific segment in Mexico, however, was fragmented and the northwestern populations now represented by S. collliae are at present separated from the southeastern populations (S. variegatoides) by a different and closely related species, S. aureogaster. Pelage features and known ecology of S. variegatoides, S. collliae, and S. yucatanensis are in harmony with this hypothesis. So too is the geographic distribution of external and cranial dimensions of the three forms. Although the three differ in these features, the extremes are encompassed in S. collliae, which grades clinaly from a small squirrel about the size of S. yucatanensis to one larger than S. variegatoides. The original, continuously distributed species may have been as variable in external and cranial dimensions (Musser, 1968).

A squirrel, S. variegatoides, from El Salvador that was brought back in 1838 to the Zoological Society of London by Captain Sir Edward Belcher of the Royal Navy was named by Ogilby (1839). This squirrel may have been one of the first mammalian specimens preserved from Central America, although Leseon (1842) described Macreusus adolphi (=S. v. adolphii) from Nicaragua only a short time later (Baker, 1991).

Sciurus is from the Latin meaning squirrel (Jaeger, 1955). The specific epithet variegatoides probably refers to the variable coloration of this species. S. variegatoides also has been referred to as black-backed (Gray, 1849), varied (Allen, 1877), mottled (Nelson, 1898), Costa Rica, Nicaragua, banded-backed, Honduras, Escondido River, Rio Managua, Goldman's (Nelson, 1899), Thomas', banded-back, Gray's black (Elliot, 1904), Underwood's (Goldman, 1932), Austin's variegated, Nicoya Peninsula, Gray's variegated, Peters' variegated, Thomas' variegated, Costa Rican black (Goodwin, 1946), Costa Rican variegated, Nicaraguan variegated, and Panamanian variegated squirrel (Dolan and Moran, 1969).

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