

MISCELLANEOUS PUBLICATIONS NO. 38
MUSEUM OF ZOOLOGY
UNIVERSITY OF MICHIGAN

REVISION OF *SCIURUS VARIE-*
GATOIDES, A SPECIES OF
CENTRAL AMERICAN
SQUIRREL

BY
WILLIAM P. HARRIS, Jr.

ANN ARBOR
UNIVERSITY OF MICHIGAN
September 4, 1937

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FREDERICK M. GAIGE
Director of the Museum of Zoology

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REVISION OF *SCIURUS VARIEGATOIDES*, A SPECIES OF CENTRAL AMERICAN SQUIRREL

INTRODUCTION

Fifteen geographical races of the species *Sciurus variegatoides* are recognized in the present revision (Map 1). Previously these forms have been assigned to a number of species. After a study of three hundred and eight specimens of the large tree squirrels of this group taken at many localities in Central America, from Guatemala to Panamá, there seems to be no alternative but to assign all of these forms to a single species, for, (1) each subspecies, except for minor individual variations, is locally quite constant; and (2) whenever the ranges of two or more of these subspecies meet, intergradation is either clearly illustrated or, with reasonable certainty, may be assumed to exist.

Nelson (1899: 71-82) in his revision of the squirrels of Mexico and Central America recognized the following eight species of this group: *thomasi*, *dorsalis*, *adolphei*, *boothiae*, *belti*, *variegatoides*, *managuensis*, and *goldmani*. I regard these forms, together with *rigidus* and *melania*, which Nelson regarded as synonyms of *dorsalis*, as subspecies of *variegatoides*. The forms *bangsi*, *underwoodi*, *atrirufus*, *austini*, and *helveolus*, which were named subsequent to Nelson's revision, also are considered races of the species *variegatoides*. The present classification previously has been suggested in part by Goldman (1920: 136) who considered *adolphei*, *dorsalis*, *melania*, and *helveolus* as subspecies of *variegatoides*, and by Dickey (1928: 8) who reduced *goldmani* to subspecific rank. *Sciurus boothiae annalium* Thomas is considered a synonym of *adolphei* in the present treatment.

The wide and singularly striking diversity of color and color pattern in this group of squirrels and the few specimens available to earlier workers have made the classification of the group difficult. The excellent series of specimens of squirrels collected in Costa Rica by Austin Smith and the fine series from El Salvador in the Dickey collection have been most helpful in working out the relationships of the group.

Thanks are due to the authorities of the United States National Museum, the American Museum of Natural History, the Museum of Comparative Zoology, Field Museum, the California Institute of Technology, the Academy of Natural Sciences of Philadelphia, and the Carnegie Museum for the generous loan of specimens.

Capitalized names of colors refer to Robert Ridgway's *Color Standards and Color Nomenclature* (Washington, 1912).

SCIURUS VARIEGATOIDES OGILBY

DISTRIBUTION.—Central Guatemala and southern Mexico to the Canal Zone in Panamá.

EXTERNAL CHARACTERS.—Size large, tail long, about 50 per cent of the total length; general coloration extremely variable, postauricular patches white to reddish; pelage shiny, coarse and bristly. Mammae, eight.

CRANIAL CHARACTERS.—Premolars, 2/1, except in *helveolus* where the number is 1/1; skull short, broad, dorsal outline flattened or slightly swollen at the frontal region, nasals about equal in length to the interorbital breadth, rostrum short and broad.

RELATION TO OTHER SPECIES.—There is no evidence of intergradation between *Sciurus variegatoides* and either *S. griseoflavus* or *S. yucatanensis*. The northern limit of the range of *variegatoides* in northwestern Guatemala is adjacent to and perhaps overlaps the range of *griseoflavus*. *S. griseoflavus* differs from *variegatoides* in having softer and longer pelage; postauricular patches, when present, are small, indistinct, and of a grayish color; back, grizzled yellowish brown. In northeastern Guatemala *variegatoides* meets and perhaps overlaps the range of *yucatanensis*, which differs from *variegatoides* in having a much smaller skull, softer and longer pelage, grizzled black and gray coloration above, grizzled buffy and black below, and black postauricular patches.

SCIURUS VARIEGATOIDES VARIEGATOIDES OGILBY

1839 *Sciurus variegatoides* Ogilby, *Proc. Zool. Soc. London*: 117.

1842 *Macrozous pyladei* Lesson, *Rev. Zool., Paris*, 5: 130, April, 1842 (*nomen nudum*); *Nouv. Tabl. Regne Anim., Mamm.*: 112.

1843 *Sciurus griseocaudatus* Gray, "Voyage of 'Sulphur,'" *Mammalia*, 2: 34, Pl. 13, Fig. 2; Pl. 18, Figs. 7-12.

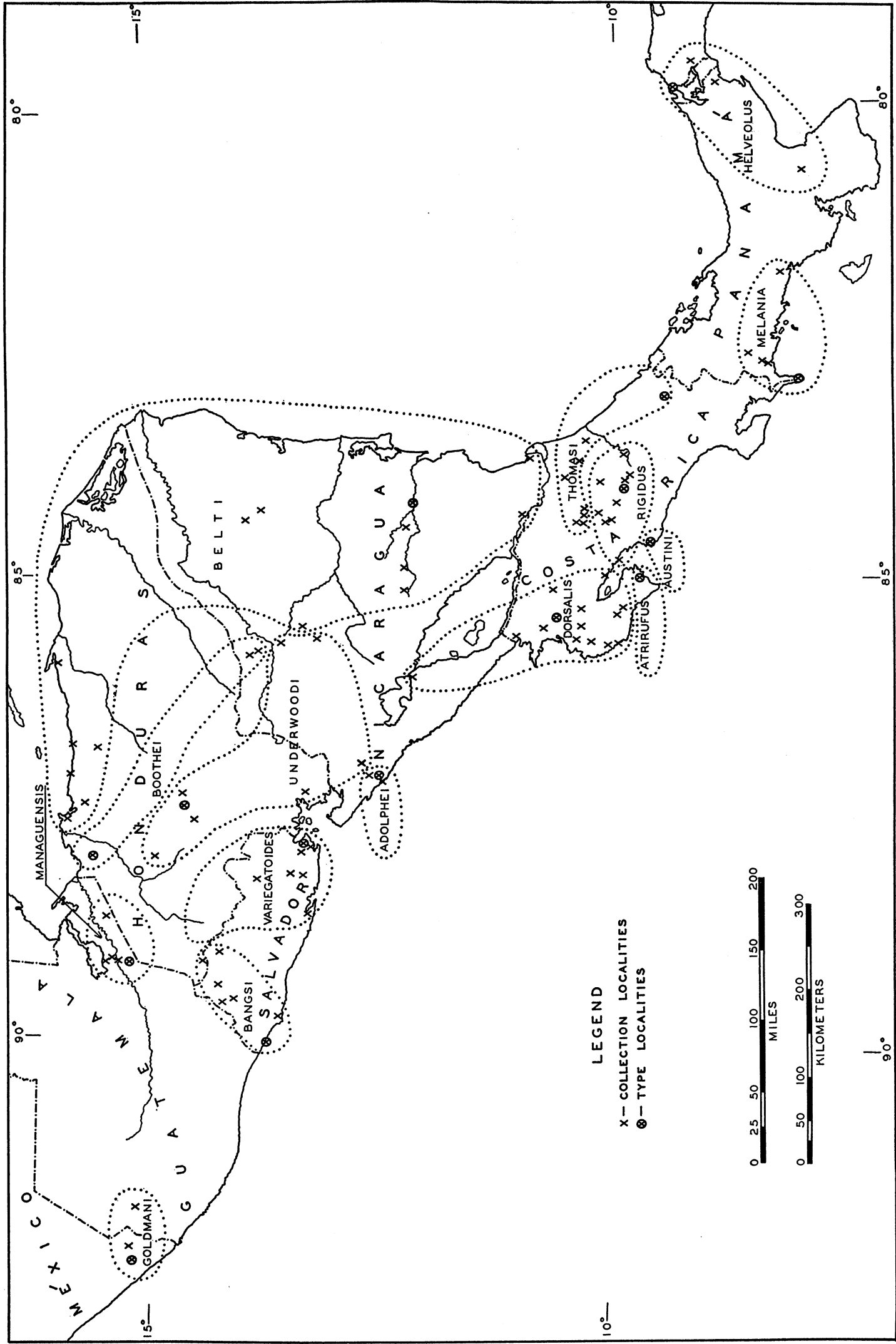
1857 *Sciurus pyladei* Baird, *Mamm. N. Amer.*: 282.

TYPE LOCALITY.—El Salvador, Central America. Assumed to be in the vicinity of San Carlos, Department of La Unión, El Salvador (Nelson, 1899: 81; and Allen, 1910: 103). Type in the British Museum.

DISTRIBUTION.—From the Pacific Coast of southeastern El Salvador throughout the Departments of La Unión, San Miguel, and Usulután.

DIAGNOSIS.—Pelage coarse, stiff, shiny, and rather sparse. Color of the upperparts when viewed at a distance appearing dull yellowish or orange-gray washed with black. Underparts and postauricular patches yellowish orange. Tail above, black washed with white; below, with median buffy area (Pl. II, Fig. 3).

CHARACTERS.—Upperparts, including back, head, sides, outside of legs, and feet, grizzled Ochraceous-Buff and black. Hairs of the back and sides sooty black at base, followed by a median buffy band, and tipped with black. Ears with narrow black border. Postauricular patches and back of ears



MAP 1.—Distribution of the subspecies of *Sciuurus variegatoides*.

Ochraceous-Buff. Cheeks and chin paler than back. Toes like back, but with fewer black hairs. Underparts, including inside of legs, varying from Light Ochraceous-Buff to Ochraceous-Orange with occasional traces of white spotting on throat and axillae. Tail above, black washed with white; below, with median line like back, bordered with black and edged with white. Hairs of tail above, black tipped with white; below, with three black bands separated by two buffy bands and tipped with white.

VARIATION.—Seventeen specimens from southeastern El Salvador show little individual variation. The specimen upon which Nelson based his description of this form (No. 7020 U.S.N.M., from La Unión, Salvador), was compared with the type by Oldfield Thomas who reported the specimens to be identical. No specimens are available from western Honduras along the border of El Salvador, but *variegatoides* probably occupies this region and intergrades with *managuensis* and *belti* in southeastern Guatemala.

SPECIMENS EXAMINED.—Eighteen.

El Salvador: Department of La Unión, La Unión, 1 (U.S.N.M.); Pine Peaks, Volcán Conchagua (altitude, 3500 feet), 2 (Dickey); Lake Olomega (altitude, 200 feet), 2 (Dickey). Department of Usulután, Puerto Del Triunfo (sea level), 1 (Dickey). Department of San Miguel, Río San Miguel (altitude, 225 feet), 3 (Dickey); Volcán San Miguel (altitude, 2600 feet), 2 (Dickey); Monte Cacaguatique (altitude, 3500 feet), 2 (Dickey); Lake Olomega (altitude, 200 feet), 5 (Dickey).

SCIURUS VARIEGATOIDES UNDERWOODI GOLDMAN

1932 *Sciurus boothiae underwoodi* Goldman, *Journ. Wash. Acad. Sci.*, 22, No. 10: 275 (May 19).

TYPE LOCALITY.—Monte Redondo, about thirty miles northwest of Tegucigalpa, Honduras (altitude, 5100 feet). Type: adult male (skin and skull), No. 250219, United States National Museum (Biol. Surv. collection), collected by C. F. Underwood, December 8, 1931. Original number 644.

DISTRIBUTION.—Highlands of central Honduras and northern Nicaragua.

DIAGNOSIS.—Upperparts paler and grayer than *variegatoides* and similar to *goldmani*. A buff lateral line usually present on the sides separating the color of the back from the color of the underparts. Postauricular patches usually buffy, but sometimes white. Underparts white except when occasional broadening of lateral line somewhat reduces the amount of white on the belly.

CHARACTERS.—Upperparts, including back, head, sides, and outside of legs, grizzled Ochraceous-Buff to yellowish gray and black. The feet black or like the outside of legs. Hairs of back and sides sooty black at base followed by a median buffy band and tipped with black. Ears edged with black; tufts scanty and indistinctly tawny. Postauricular patches and back

of ears Ochraceous-Buff or white. Cheeks and chin paler than back. A lateral line of Ochraceous-Buff usually present. Underparts and inside of legs usually white, but sometimes chiefly Ochraceous-Buff with white spotting on the axillae, throat, and lower abdomen. Tail above black washed with white. Tail below has median line like back, bordered with black and edged with white. Hairs of tail above, black tipped with white; below, with three black bands separated by two buffy bands and tipped with white.

VARIATION.—There is considerable variation within this race. The form most nearly approaches *boothiae* in appearance, but the upperparts are paler, more grayish, and the underparts are generally white although often with a considerable amount of buff. The ear patches are generally buffy, but sometimes white. The variation in this form suggests intergradation with *bangsi* and *variegatoides* on the west and with *boothiae* on the east. The gray of the upperparts, while not as pale as in *bangsi*, suggests intergradation with that form as does also the presence in some specimens of white ear patches and white belly without the lateral buffy line. The underside of the tail, however, has the buffy banding of the hairs in the median area, which is absent in *bangsi*. The buffy color present on the belly of some specimens approaches in tone the buff found in *variegatoides*. The darker specimens from Monte Redondo in the north suggest intergradation with *boothiae*. The specimens from Matagalpa and San Raphael del Norte, which Allen (1910: 102) described as *variegatoides*, are here included with *underwoodi* although it is recognized that they show intergradation with *variegatoides*. I have assigned to *underwoodi* ten specimens in the American Museum of Natural History in the following manner: Three from Matagalpa (A.M.N.H. Nos. 28411, 28412, 28444) and one from San Raphael del Norte (A.M.N.H. No. 28438), which Allen first in 1908 assigned to *Sciurus griseoflavus*; these four and three additional ones from San Raphael del Norte (A.M.N.H. Nos. 29240, 29245, 29246) assigned by Allen in 1910 to *Sciurus variegatoides*; and three more specimens, previously unrecorded, from Matagalpa and Volcán El Viejo (A.M.N.H. Nos. 41388 (not typical), 41389, 41231), taken by Richardson from 1910 to 1917. The range of *underwoodi*, previously limited to the type locality, is now extended from Monte Redondo in the north to Matagalpa in the south, east to El Viejo, and west to San Raphael del Norte.

When more material is available the relationships of *underwoodi* to other forms can be more clearly understood, and the limits of its range better defined.

SPECIMENS EXAMINED.—Forty-four.

Honduras: Department of Comayagua, Lake Yojoa, 2 (A.M.N.H.); Monte Redondo, 6 (M.Z.U.M.), 5 (A.M.N.H.), 1 (M.C.Z.); La Flor Archaga, 4 (M.C.Z.); Comayabuela, 1 (M.C.Z.). Department of Tegucigalpa, Hatillo, 9 (M.C.Z.). Department of Choluteca, Cantarranas, 2 (A.N.S.P.).

Nicaragua: Department of Matagalpa, Matagalpa, 9 (A.M.N.H.). Department of Matagalpa, San Raphael del Norte, 4 (A.M.N.H.). Department of Chinandega, Volcán El Viejo, 1 (A.M.N.H.).

SCIURUS VARIEGATOIDES GOLDMANI NELSON

1898 *Sciurus goldmani* Nelson, *Proc. Biol. Soc. Wash.*, 12: 149-150 (June 3).

1928 *Sciurus variegatoides goldmani* Dickey, *Proc. Biol. Soc. Wash.*, 41: 8 (Feb. 1).

TYPE LOCALITY.—Huehuetán, Chiapas, Mexico. Type, No. 77903, United States National Museum (Biol. Surv. collection).

DISTRIBUTION.—Southeastern Chiapas, Mexico, and adjacent parts of Guatemala.

DIAGNOSIS.—Upperparts yellowish gray washed with black, similar to *variegatoides*; postauricular patches and underparts white; no lateral line.

CHARACTERS.—Upperparts, including back, head, sides, and outside of legs, grizzled Ochraceous-Buff and black. Hairs of back sooty black at base with median buffy band and tipped with black. Back of ears and inconspicuous tuft, tawny. Postauricular patches white. Cheeks and chin grizzled gray. Feet similar to back, but paler and with more gray. Lateral line absent. Underparts and inside of legs white. Tail above, black washed with white; below, with very broad cinnamon or grayish median line bordered with black and edged with white. Hairs of tail above, black tipped with white; below, with three black bands separated by two buffy or grayish bands and tipped with white.

VARIATION.—*S. v. goldmani* is the most northern form of the shiny, coarse-haired squirrels of the *variegatoides* group. All the specimens of this race examined are similar and show no particular individual variation.

SPECIMENS EXAMINED.—Five.

Mexico: Department of Chiapas, Huehuetán, 1 (A.M.N.H.).

Guatemala: Department of Escuintla, Concepción del Mar, 2 (Field Mus.), 1 (M.C.Z.), no locality, 1 (U.S.N.M.).

SCIURUS VARIEGATOIDES BANGSI DICKEY

1928 *Sciurus variegatoides bangsi* Dickey, *Proc. Biol. Soc. Wash.*, 41: 7 (Feb. 1).

TYPE LOCALITY.—Barra de Santiago, Department of Ahuachapán, El Salvador. Type, adult male (skin and skull), No. 12746, collection of Donald R. Dickey; collected April 3, 1927, at sea-level by G. D. Stirton.

DISTRIBUTION.—Western El Salvador from the Department of Chalatenango south and west to the seacoast in the Department of Ahuachapán, possibly ranging into southern Guatemala.

DIAGNOSIS.—Upperparts light gray washed with black. This form is by far the palest of the squirrels included in the *variegatoides* group and lacks any trace of buffy wash. Underparts and postauricular patches white (Pl. II, Fig. 2).

CHARACTERS.—Upperparts, including back and head, grizzled pale olive-gray and black with buffy wash. Sides and outside of legs like back, but paler. Hairs of back sooty black at base with median band of very light buff and tipped with black. Back of ears like back with black border and buffy tuft reduced to minimum. Postauricular patches pure white. Cheeks and chin light pepper and salt gray. Feet light gray. Toes white. Underparts and inside of legs white. Tail above and below black washed with white. Hairs of tail above, black, tipped with white; below, with two black bands separated by a white band and tipped with white.

VARIATION.—This form is represented by sixteen specimens, in the D. R. Dickey collection, from western El Salvador. Nearest externally to *goldmani*, but lighter and grayer than the grayest of that form, with fewer black hairs through the pelage of the back, and no trace of the rusty wash which gives tone to the whole dorsal pelage of *goldmani*. Face much lighter (light pepper and salt gray) than in the dark-faced *goldmani*. Two specimens from San José del Sacare in the Department of Chalatenango, El Salvador, and two specimens (A.M.N.H.) from Ocototec in Honduras, are intergrades between *bangsi* and *variegatoides*. One specimen (No. 12440) from Los Esesmiles has the light gray color of the back typical of *bangsi*, but with the brown ear patches and buffy tinge of the underparts. One specimen (No. 12712) from San José del Sacare, and the two from Ocototec (Nos. 124826-7), more closely resemble *variegatoides* in the color of the back underparts and ear patches, but are somewhat paler particularly on the underparts.

SPECIMENS EXAMINED.—Eighteen, from the collection of D. R. Dickey. El Salvador: Department of Sonsonate, Hacienda Chilata (altitude sea-level), 2. Department of Chalatenango, Los Esesmiles (altitude 8000 feet), 1; San José del Sacare (altitude 3600 feet), 6. Department of Santa Ana, El Tablán (altitude 1450 feet), 1. Department of Ahuchapán, Barra de Santiago (sea-level), 6. Honduras: Department of Ocototec, Plan del Rancho, 2.

SCIURUS VARIEGATOIDES BOOTHIAE GRAY

- 1842 *Sciurus richardsoni* Gray, *Ann. and Mag. Nat. Hist.*, 10: 264 (not *Sciurus richardsoni* Bachman, 1838).
 1843 *Sciurus boothiae* Gray, *List Spec. Mamm. Brit. Mus.*: 139.
 1845 *Sciurus fuscovariegatus* Schinz, *Synopsis Mamm.*, 2: 15-16.
 1867 *Macroxus boothiae* Gray, *Ann. and Mag. Nat. Hist.*, Ser. 3, 20: 424.

TYPE LOCALITY.—“Honduras” assumed to be in the vicinity of San Pedro Sula, Nelson (1899: 77). Type in the British Museum.

DISTRIBUTION.—Mountains on the border of central parts of Honduras and Nicaragua, and San Pedro Sula, Honduras.

DIAGNOSIS.—Upperparts contrasting strongly with *variegatoides* in being a duller more yellowish brown more heavily washed with black. Postauricular patches tawny and underparts white with occasional trace of tawny lateral line.

CHARACTERS.—Upperparts, including back, head, sides, and outside of legs, grizzled Ochraceous-Tawny and black. Hairs of back and sides sooty black at base followed by median tawny band and tipped with black. Back of ears tawny edged with black. Postauricular patches Ochraceous-Tawny. Cheeks and chin like back, but paler. Feet black or like back. Occasional trace of tawny lateral line. Underparts and inside of legs white. Tail above, black washed with white; below, with median line like back, bordered with black and edged with white. Hairs of tail above, black tipped with white; below, with three black bands separated by two buffy bands and tipped with white.

VARIATION.—*S. v. boothiae* is distinguished from *belti* in having the underparts white or creamy instead of reddish, upperparts slightly more brownish, and ear patches paler and less brilliantly reddish. Specimens from San Juan, Jalapa, and Jicara in Nicaragua, and San Pedro Sula in Honduras, are typical except that the narrow line of dull reddish brown along the flanks, which Nelson describes as typical, is absent from all but one. More specimens are needed to establish the range of this form. In assigning specimens to *boothiae* and *belti* I have followed in general the practice of Allen and Nelson. The two forms are closely related and so variable that individual specimens are difficult of assignment. The nine specimens from Río Coco, included under *boothiae* by Allen in 1910, I have assigned to *belti* because the color of the underparts more closely approaches that form.

SPECIMENS EXAMINED.—Nine.

Nicaragua: Department of Segovia, Jalapa, 4 (A.M.N.H.); Jicara, 1 (A.M.N.H.); San Juan, 1 (A.M.N.H.).

Honduras: Department of San Pedro Sula, 2 (U.S.N.M.); Laguna, 1 (A.N.S.P.).

SCIURUS VARIEGATOIDES BELTI NELSON

1899 *Sciurus boothiae belti* Nelson, *Proc. Wash. Acad. Sci.*, 1: 78 (May 9).

1910 *Sciurus boothiae* Allen, *Bull. Amer. Mus. Nat. Hist.*, 28: 101 (in part).

TYPE LOCALITY.—Escondido River, fifty miles from Bluefields, Nicaragua. Type, adult female (skin and skull), No. 36477, United States National Museum (Biol. Surv. collection). Collected by Charles W. Richmond, November 22, 1892.

DISTRIBUTION.—Eastern slopes of mountains of Honduras and Nicaragua to the Atlantic Coast, including approximately the entire eastern halves of these countries.

DIAGNOSIS.—Upperparts yellowish brown washed with black; postauricu-

lar patches tawny; underparts normally uniform rusty rufous, but variable in tone and frequently with white spotting on throat, chest, axillae, and lower abdomen.

CHARACTERS.—Upperparts, including back, head, sides, and outside of legs, grizzled Ochraceous-Tawny and black. Hairs of back and sides sooty black at base followed by median tawny band and tipped with black. Back of ears tawny edged with black. Postauricular patches Ochraceous-Tawny. Cheeks and chin like back, but paler. Feet like back or black. Lateral line absent. Underparts and inside of legs Ochraceous-Tawny to Ochraceous-Orange. These parts are mainly uniform in color, especially in specimens from the vicinity of the type locality, but sometimes with a considerable amount of white spotting on the throat, axillae, and lower abdomen. Tail above, black washed with white; below, with median line like back bordered with black and edged with white. Hairs of tail above, black tipped with white; below, with three black bands separated by two buffy bands and tipped with white.

VARIATION.—This subspecies occupies the coastal regions of Honduras and Nicaragua and intergrades with *boothiae* in the mountains to the west. Throughout this region it shows great variability in the color of the underparts. When more material is available it may be found that there are several recognizable local races. Specimens from the vicinity of Bluefields and the Escondido River are typical. The color of the upperparts is only slightly variable, some of these specimens being somewhat paler and others having a little heavier wash of black. The color of the underparts varies in the tone of the rufous and in the amount of white spotting. Although the type has been described as having uniform rusty rufous on the underparts a topotype has a slight trace of white spotting in the regions of the axillae and lower abdomen. This would lend support to the supposition that the uniform rusty rufous represents an extreme development that is not necessarily characteristic of the group in which the specimens herein listed are included.

The only specimen available from south of the type locality is a melanistic specimen from Greytown, Nicaragua (U.S.N.M. No. 16412). This specimen shows some rufous banding of the hairs on the head, back, and underparts.

A description of thirty-four specimens from the coastal regions of Honduras will illustrate the variations in this group.

One specimen (M.C.Z. No. 23885) from Lancetilla has the feet the same rusty rufous as the belly, the median area of which is white. The back shows less black than the topotypes.

Two specimens from La Ceiba are paler on the back and have larger and more brilliant ear patches than the topotypes. The feet and legs are washed with black and tinged with Orange-Rufous. The underparts of one specimen are of a uniform but deeper shade of rufous, and the other specimen has the

median area of the underparts clear white from the throat to the lower abdomen. These specimens are approaching *managuensis*.

In three specimens from Yaruca the upperparts are like those of the topotypes. The underparts are a dark grizzled brownish rufous with varying amounts of white spotting. This grizzled effect is caused by banding of the hairs which are lead-colored at the base, succeeded by a band of Orange-Rufous, followed by a black band, and tipped with Orange-Rufous.

A specimen (U.S.N.M. No. 23825, a captive) originally taken at Carmelina is slightly paler on the upperparts. The color of the subterminal bands of the hairs is bleached to yellowish white showing only a tinge of rufous just below the black tip of the hair. The median area of the underside of the tail is similarly paler. The underparts are slightly paler than in the topotypes.

One specimen collected by C. H. Townsend at Truxillo in 1887 has the underparts uniform cream white. Except for the more reddish color of the grizzled upperparts and more brilliant color of the ear patches, in which respects it resembles the topotypes of *belti*, this specimen might at first glance be assigned to *boothiae*.

Three specimens taken by C. H. Townsend in 1887 on the Río Segovia show a heavier wash of black with a paler banding of the hairs of the upperparts than do the topotypes. All three show some white spotting on the underparts, the general color of which is rusty rufous in two and grizzled reddish brown in one, caused by orange banding of the hairs in this region.

One specimen (A.M.N.H. No. 41230) taken by Richardson in 1917, at Los Sabalos on the Río San Juan near the border of Nicaragua and Costa Rica, is like the topotypes of *belti* but has slightly paler upperparts and indistinct ear patches.

Nine specimens taken by Richardson in 1908, on the Río Coco at an altitude of 1000 feet, show intergradation with *boothiae*. Allen (1910: 101) assigned these to *boothiae*, but remarked that they graded toward *belti*. He stated that "they differ from the first series (*boothiae* from San Juan, Jicaro, and Jalapa) in having the suffusion of the dorsal pelage more yellowish, and the white of the ventral surface mainly restricted to the breast and lower abdomen, which regions are mainly white, these two areas being usually connected by a narrow median line of white. In one adult and one young example the ventral surface, exclusive of the usual white area, is grizzled dark rufous gray." As I have restricted *boothiae* to those specimens with uniform white underparts from the localities listed under the description of this form it would seem more consistent to assign the specimens from Río Coco to *belti*. In them the color of the back, ear patches, and the rufous tone of the underparts is quite within the range of variation of *belti*.

Another group of thirteen specimens taken by Richardson in 1907-1909

at Matagalpa, Uluce, Peña Blanca, Savala, and Chontales are included in this form. Allen assigned them to this group (1908: 659, and 1910: 101). They are very similar to specimens from Río Coco, but differ from these in having more rusty rufous and less white on the underparts. Otherwise, they are similar to the specimens of this region, all of which grade toward *boothiae*. Although the specimens from Matagalpa bear the same locality name as other specimens assigned to *underwoodi* they presumably came from farther east. They show some approach to the latter form but intergrade with *boothiae* rather than *underwoodi*, which here intergrades with *variegatoides*.

SPECIMENS EXAMINED.—Forty.

Nicaragua: Department of Zelaya, Arroyo Escondido, fifty miles from Bluefields, 3 (U.S.N.M., Biol. Surv. collection). Department of Chontales, Greytown, 1 (U.S.N.M.); Los Sabalos on the Río San Juan, 1 (A.M.N.H.); Peña Blanca, 2 (A.M.N.H.); Chontales, 2 (A.M.N.H.); Río Sigua, 2 (M.Z.U.M.). Department of Segovia, Río Segovia, 3 (U.S.N.M.); Río Coco, 9 (A.M.N.H.). Department of Matagalpa, Matagalpa, 3 (U.S.N.M.); Uluce, 4 (A.M.N.H.); Savala, 1 (A.M.N.H.); Eden, 1 (C.M.).

Honduras: Department of Yoro, Yaruca (south slope of coast range behind La Ceiba, altitude, 1000 feet), 3 (M.C.Z.). Department of Atlantida, Lancetilla, 1 (M.C.Z.); La Ceiba, 2 (M.C.Z.); Carmelina, 1 (U.S.N.M.). Department of Colón, Truxillo, 1 (U.S.N.M.).

SCIURUS VARIEGATOIDES ADOLPHEI (LESSON)

1842 *Macroxus adolphei* Lesson, *Rev. Zool.*, 5: 130 (*nomen nudum*). *Nouv. Table. Règne Animal, Mamm.*: 112-113.

1899 *Sciurus adolphei* Nelson, *Proc. Wash. Acad. Sci.*, 1: 73-74 (May 9).

†1905 *Sciurus boothiae annatum* Thomas, *Ann. and Mag. Nat. Hist.*, 7th Ser., 16: 309-310 (September).

1920 *Sciurus variegatoides adolphei* Goldman, *Mammals of Panama, Smith. Misc. Coll.*, 69, No. 5: 136.

TYPE LOCALITY.—Realejo, Nicaragua. Type in the Muséum National d'Histoire Naturelle, Paris.

DISTRIBUTION.—Known only from Corinto and Realejo on the east coast of Nicaragua and from Volcán Chinandega.

DIAGNOSIS.—Upperparts yellowish gray washed with black, similar to *variegatoides*, but grayer and more strongly overlaid with black. Postauricular patches white. Underparts grizzled grayish with white spotting.

CHARACTERS.—Upperparts, including back, head, sides, and outside of legs, grizzled Ochraceous-Buff and black. Hairs of back and sides sooty black at base followed by a median buffy band and tipped with black. Back of ears like back, but paler and without black edges. Postauricular patches white. Cheeks and chin grizzled dark gray. Feet like back or black. Lateral line absent. Underparts and inside of legs a grizzled grayish buff

similar in color to the upperparts but paler and with white spotting on the throat, chest, axillae, and lower abdomen. Tail above black washed with white, below with median line like back, bordered with black and edged with white. Hairs of tail above, black tipped with white; below, with three black bands separated by two buffy bands and tipped with white.

VARIATION.—This form has a rather small range on the west coast of Nicaragua in the vicinity of the type locality. Allen (1910: 103) described two specimens from Chinandega as being typical, except in minor particulars, of the form described by Lesson. He also pointed out that these were not at all like the one specimen from Nicaragua, without definite locality, described by Nelson (1899: 73) as *adolphei*. An additional specimen taken by Richardson in 1917 at Corinto is practically a topotype. It is similar to those previously recorded by Allen. *S. v. adolphei* resembles *bangsi* in the color of the back, but has a heavier wash of black than average specimens of the latter form. The two specimens from Chinandega and one from Corinto are the only ones available of this form, but they are sufficiently distinctive to indicate the recognition of this race of limited range. Additional specimens are needed from north and south of Realejo more clearly to define its range and relationships with other races. Thomas' description of *annalium* seems to refer to this form. He describes the two specimens collected by Dyson in "Honduras" as being similar to *boothiae* on the back, but with dull grizzled grayish underparts and white postauricular patches. The description of *annalium* by Thomas is based on characters all of which are quite variable. The character of grizzled gray underparts is confined to the one race, *adolphei*, as far as the specimens examined by me indicate. The locality given by Thomas for *annalium* is indefinite, and there is no way of telling where the specimens were taken.

SPECIMENS EXAMINED.—Three.

Nicaragua: Department of Chinandega, Volcán Chinandega, 2 (A.M.N.H.); Corinto, 1 (A.M.N.H.).

SCIURUS VARIEGATOIDES MANAGUENSIS NELSON

1898 *Sciurus boothiae managuensis* Nelson, *Proc. Biol. Soc. Wash.*, 12: 150 (June 3).

TYPE LOCALITY.—Río Managua, Guatemala. Type, No. 62476, United States National Museum.

DISTRIBUTION.—Department of Isabal, and probably Zacapa, in eastern Guatemala.

DIAGNOSIS.—Back grizzled yellowish brown, underparts and postauricular patches Ochraceous-Orange. This subspecies is very similar to *variegatoides*, but is a darker more vividly colored form.

CHARACTERS.—Upperparts, including back, head, sides and outside of legs, grizzled Ochraceous-Orange to Ochraceous-Buff and black. Hairs of

back sooty black at base with median buffy band and tipped with black. Back of ears like back, bordered with black, and with an inconspicuous tawny tuft. Postauricular patches, underparts, and inside of legs Ochraceous-Orange to Ochraceous-Buff. Cheeks and chin like back, but paler. Feet like back, but with toes sometimes clear Ochraceous-Orange or Ochraceous-Buff. Tail above, black washed with white; below, with broad median area like back bordered with black and edged with white. Hairs of tail above, black tipped with white; below, with three black bands separated by two buffy bands and tipped with white.

VARIATION.—This subspecies, which is similar in coloration to *variegatoides*, as has been noted above, has a more vivid coloration, which is characteristic of the humid tropical rain forests of the east coast of Central America. Three specimens from the Río Managua are topotypes. A fourth specimen taken at Quiragua was a captive for some time in the National Zoological Park in Washington. Two of the Río Managua specimens have a grayish banding of the hairs of the back. The captive specimen from Quiragua has a pinkish tinge to the banding of the hairs and color of the underparts. A fifth specimen from the Department of Izabal, Guatemala, has the yellowish color of the underparts similar to that of *variegatoides*, but richer than specimens of this form from El Salvador. The color of the upperparts of this specimen is similar to that of *belti*.

SPECIMENS EXAMINED.—Five.

Guatemala: Department of Izabal, Río Managua, 3 (U.S.N.M.), Quiragua, 1 (U.S.N.M.). Department of Izabal, Bobos, 1 (Field Mus.).

SCIURUS VARIEGATOIDES AUSTINI HARRIS

1933 *Sciurus variegatoides austini* Harris, *Occ. Papers Mus. Zool. Univ. Mich.*, No. 266: 1-4 (June 28).

TYPE LOCALITY.—Las Agujas, Province of Puntarenas, Costa Rica. Type, adult male (skin and skull), No. 65118, Museum of Zoology, University of Michigan; collected by Austin Smith, September 22, 1931.

DISTRIBUTION.—Known only from the vicinity of Las Agujas, a small settlement on a sandy peninsula with coconut palms and mangrove trees, thirty miles south of the city of Puntarenas.

DIAGNOSIS.—Color of upperparts a mixture of black, white, and Orange-Cinnamon. Head grizzled gray with a patch of rufous on the forehead. Underparts rufous. Postauricular patches white (Plate II, Fig. 1).

CHARACTERS.—Back, from nape to base of tail, with broad band of grizzled Orange-Cinnamon, black and white, widest behind the ears and over the lumbar region, narrow over the shoulders, and tapering towards the tail. Hairs of back black at base with a subterminal band of Orange-Cinnamon, and with a sprinkling of black hairs tipped with white. Head dark grizzled

gray with patch of Vinaceous-Cinnamon. Back of ears grizzled gray bordered with black. Postauricular patches white. Cheek and chin gray to yellowish gray. Sides, outside of legs, feet, underparts, and inside of legs Cinnamon-Rufous. Hairs of sides black at base tipped with Cinnamon-Rufous. Black hairs with white tips form a whitish stripe across the flanks to the base of the tail in all specimens, extending along the sides as a lateral line in a few specimens. More or less white spotting on throat, axillae, and lower abdomen. Tail above, black washed with white; below, with median area like underparts, bordered with black and edged with white. Hairs of tail above, black tipped with white; below, Cinnamon-Rufous at base with broad subterminal band of Cinnamon-Rufous and tipped with white.

VARIATION.—In the type and nine paratypes the only variation is in the color of the feet, some of which are darker than others, and in the tinge of color of the heads and backs. This race, although closely related to *dorsalis* and *rigidus*, is readily distinguished from either of these forms. The rufous legs and the color of the back, which appears from a distance to be a mixture of shiny black and silver, gives this form a striking appearance. Specimens from Chomes are intermediate between *austini* and *dorsalis*, and those from Puntarenas are intermediate between *austini* and *rigidus*.

SPECIMENS EXAMINED.—Sixteen.

Costa Rica: Province of Puntarenas, Chomes, 5 (M.Z.U.M.); Las Agujas, 10 (M.Z.U.M.); Costa Rica, 1 (Carnegie Mus.).

SCIURUS VARIEGATOIDES ATRIRUFUS HARRIS

1930 *Sciurus adolphei atrirufus* Harris, *Occ. Papers Mus. Zool. Univ. Mich.*, No. 219: 1-4 (Oct. 15).

TYPE LOCALITY.—Tambor, Nicoya Peninsula, Costa Rica. Type, adult male (skin and skull), No. 59842, Museum of Zoology, University of Michigan. Collected November 28, 1928, by Austin Smith.

DISTRIBUTION.—Known only from the vicinity of Tambor, a small settlement at sea level on the Bay of Ballena at the southeast extremity of the Nicoya Peninsula.

DIAGNOSIS.—Similar in color pattern to *dorsalis*, but median area of back uniform black and underparts, sides, and ear patches rufous (Pl. I, Fig. 1).

CHARACTERS.—Back with broad band of black, extending forward in stripes above the eyes, wide behind the ears and over the lumbar region, narrow over the shoulders, and tapering toward the tail. Hairs of back black with a few hairs between the shoulders, rump, and sides with Cinnamon-Rufous subterminal bands. Top of head, sides, postauricular patches, legs, and underparts Cinnamon-Rufous. Cheeks and chin like top of head, but paler and more yellowish. Ears Cinnamon-Rufous bordered with black. Hairs of sides and underparts black at base, tipped with Cinnamon-Rufous.

Some specimens have a few white hairs on axillae and throat. Tail above, black washed with white; below, with median band of Cinnamon-Rufous. Hairs of tail above, black tipped with white; below, Cinnamon-Rufous at base, followed by a black band, and tipped with white.

VARIATION.—This form was described by Gray (1867: 423) under *Macroxus dorsalis* as variety No. 6, but was not named. According to Austin Smith the examples of this form (*Macroxus dorsalis* variety No. 6) were taken by Enrique Arce at Lepanto on the east coast of the Nicoya Peninsula, fifteen miles from Tambor.

This is a well-marked form which is locally quite constant. The color of five specimens taken at Tambor varies only slightly in the color tone of the underparts. Three of these specimens have the color of the underparts as follows: one, Chestnut, one, Hazel, and one, Kaiser-Brown. Intergradation with *dorsalis* farther north in the Nicoya Peninsula has been discussed under *dorsalis*.

SPECIMENS EXAMINED.—Five.* All from the type locality.

SCIURUS VARIEGATOIDES DORSALIS GRAY

1848 *Sciurus dorsalis* Gray, *Proc. Zool. Soc. London*: 138.

1867 *Macroxus dorsalis* Gray, *Ann. and Mag. Nat. Hist.*, 3rd Ser., 20: 423.

1899 *Sciurus adolphi dorsalis* Nelson, *Proc. Wash. Acad. Sci.*, 1: 74.

1920 *Sciurus variegatoides dorsalis* Goldman, "Mammals of Panama," *Smith. Misc. Coll.*, No. 5: 136.

TYPE LOCALITY.—Assumed to be Liberia, Costa Rica (Nelson, 1899: 74). Erroneously given as Caracas, Venezuela. Type in the British Museum.

DISTRIBUTION.—Southwestern Nicaragua and northwestern Costa Rica from Lake Managua to Puntarenas, and from the Pacific Coast eastward to the summit of the Tileran Mountains. In Costa Rica this form is found throughout the Province of Guanacaste (except in the extreme southern end of the Nicoya Peninsula) and also in the northern coastal region of the Province of Puntarenas south to Chomes.

DIAGNOSIS.—Typical *dorsalis* is distinguished by a median area of black from nape to base of tail, postauricular patches white, sides, head, and legs grizzled gray, white or tawny underparts (Pl. I, Figs. 3-4).

CHARACTERS.—Back, from nape to base of tail, with broad band of black, widest behind the ears and over the lumbar region, narrow over the shoulders and tapering toward the tail. Hairs of back black; sometimes with few scattered hairs having buffy band. Hairs of fresh pelage are black, but fade to chocolate with exposure. Top and sides of head, sides, and outside of legs and feet, gray slightly grizzled with brown. Forehead sometimes with patch of white or Tawny. Hairs of sides black at base, tipped with white or buffy. Back of ears and postauricular patches white. Underparts and inside of legs white or Tawny. Tail above black washed with white; below,

with median line like color of the underparts bordered with black and edged with white. Hairs of tail white, reddish or black at base tipped with white, or sometimes with two black and two white bands alternating and beginning with black at the base.

VARIATION.—This form shows a wide range of variability. Specimens from the localities of Liberia, La Cruz, El Pelón, Miravalles, and Posa del Tempisque in Costa Rica, and one specimen from Tipitapa in Nicaragua, may be regarded as typical. The color of the underparts is usually white, but sometimes Tawny. The top of the head is always lighter than the back and varies from white to dark grizzled gray. The hairs of the back of most specimens are clear black, which fades to chocolate after the molt. In other specimens there is a sprinkling of black hairs tipped with white or a sprinkling of hairs which have a subterminal buffy band and are tipped with black. These variations do not seem to be peculiar to any one locality, but occur together in the different localities and in widely separated regions. For instance, at Liberia, all three types of variation are found (white, cream, or Tawny underparts and backs with clear black hairs or with sprinkling of black hairs tipped with white); at Miravalles specimens have both creamy or Tawny underparts and either clear black hairs or banded hairs on the backs. Specimens from the widely separated regions of Tipitapa and Posa del Tempisque are very similar; the heads, sides, and legs being clear white. One specimen from Posa del Tempisque has the underparts cream white, another has clear white underparts. The former has a sprinkling of banded hairs on the back, and the latter has a sprinkling of white tipped hairs. One specimen from Bebedero (U.S.N.M. Nos. 5760/3748, taken by Alfaro in 1885), two from Chomes, and five from Miravalles show the same sort of variation which seems to indicate intergradation with *rigidus*. These specimens, in general, have the dorsal stripe a uniform blackish color, although the hairs have a median buffy band, which in some specimens imparts a slightly grizzled effect. They also have a brownish cast to the lower half of the sides due to the normal gray tips to the hairs being replaced with buff. The specimen taken by Alfaro at Liberia has the reddish color of the underparts extending to the feet, which is still more characteristic of *rigidus*.

Dr. Otto Koller (1934: 169–194) collected fourteen squirrels at Bebedero in 1934. He noted an extreme amount of variation among these specimens in the color of the back, sides, and underparts, similar to specimens at hand from both this locality and from Ballena.

The region of Tempate and Ballena is one of intergradation between *dorsalis* and *atrirufus*. One specimen from Tempate and two from Ballena closely resemble typical *dorsalis* in color and pattern. They have the dark dorsal stripe and light-colored head, sides, and underparts. Two have the hairs of the back black tipped with white, and one has the hairs tipped

with black and banded with buff. The remaining specimens from these two localities have the sides, underparts, and legs varying from Yellow Ocher to Ochraceous-Orange. The heads are grizzled gray with the forehead tinged with buff. All these specimens have the dark pattern on the back with the hairs either white tipped or buffy banded.

Eighteen specimens from 27 de Abril, Las Huecas, San Juanillo, Cerros de San Juan, and Oja Ancha also show intergradation between *dorsalis* and *atrivirufus*. The underparts of these specimens are much more richly colored than are those taken farther north, varying from Ochraceous-Buff to Cinnamon-Rufous. The heads of all are grizzled gray with a buffy patch on the foreheads like the color of underparts and have dark streaks over the eyes like the color of the backs. The color of the dorsal stripe is extremely variable; the hairs being either entirely black, black with white tips, black banded with buffy, or black banded with buffy and tipped with white. A light lateral line is present in some and absent in others. Some specimens from Oja Ancha are very similar to *austini*, but this is not true of the series as a whole.

SPECIMENS EXAMINED.—Fifty-five.

Nicaragua: no definite locality, 1 (U.S.N.M.). Department of Managua, Tipitapa, 1 (A.M.N.H.).

Costa Rica: Province of Guanacasta, Liberia, 3 (U.S.N.M.), 2 (M.Z.U.M.); Miravalles, 3 (Field Mus.), 5 (Carnegie Mus.). Remaining specimens all from the Museum of Zoology, University of Michigan collection, El Pelón, 2; La Cruz, 1; Bebedero, 1; Chomes, 2; 27 de Abril, 3, Los Huecos, 1, San Juanillo, 7; Cerros de San Juan, 3; Oja Ancha, 3; Poso del Tempisque, 1; Tempate, 5; Ballena, 11.

SCIURUS VARIEGATOIDES RIGIDUS PETERS

1863 *Sciurus rigidus* Peters, *Monatsber. K. Pr. Akad. Wiss., Berlin*: 652-653.

1867 *Sciurus intermedius* Gray, *Ann. and Mag. Nat. Hist.*, 3rd Ser., 20: 421.

1867 *Macroxus nicoyana* Gray, *ibid.*: 423.

1930 *Sciurus adolpheï rigidus* Harris, *Occ. Papers Mus. Zool. Univ. Mich.*, No. 219: 1-4.

TYPE LOCALITY.—San José, Costa Rica, type collected by Dr. Hoffman and Dr. Von Frantzius.

DISTRIBUTION.—Mountains and valleys of central Costa Rica from Puntarenas east to Juan Viñas, and from Liberia in the north to Cartago in the south, and possibly throughout the Cordillera de Talamanca into Panamá.

DIAGNOSIS.—Upperparts grizzled grayish brown. Head usually paler and grayer than back. Postauricular patches white. Underparts and legs bright rufous.

CHARACTERS.—Upperparts, including back, sides, and flanks, grizzled Ochraceous-Orange and black. Head paler and grayer than back. Hairs

of back sooty black at base followed by median buffy band and tipped with black. Back of ears like back bordered with black. Postauricular patches white. Cheeks and chin yellowish gray. Forelegs, underparts, and feet Orange-Rufous. The color of the forelegs extends well up on the shoulders as in *dorsalis*. Hairs of sides black at base and tipped with Orange-Rufous. More or less white spotting on throat, axillae, and lower abdomen. Tail above, black washed with white; below, with median area like underparts bordered with black and edged with white. Hairs of tail above, black tipped with white; below, Orange-Rufous at base with subterminal band of Orange-Rufous tipped with white.

VARIATION.—This form was considered by Nelson to be a color phase of *dorsalis*. After examining additional material besides that available to Nelson, I (Harris, 1930: 1-4) found the two forms to have distinct geographic ranges and considered them as subspecies. *S. rigidus* is found in central Costa Rica and possibly ranges into Panamá. It intergrades with *dorsalis*, and *thomasi* where the ranges of these forms are adjacent or overlap. The ranges of *rigidus* and *thomasi* overlap on the north and east along the Carribean watershed. A specimen (Field Mus. No. 4746) from Alajuela is an example of intergradation between *thomasi* and *rigidus*. This specimen has the black back and richly colored underparts typical of *thomasi*, but the top of the head and white ear patches are like *rigidus*. On the east intergradation with *thomasi* is illustrated by two specimens (U.S.N.M.) from Juan Viñas which resemble *thomasi* in having the banding of the hairs of the back more reddish and the back more heavily overlaid with black than typical *rigidus*, but the color of the ear patches and underparts like the latter. Most specimens show more or less white spotting on the underparts, and three specimens from different localities (Tres Rios, San José, and San Mateo) indicate that the black of the back fades to brown with age and wear. The banding and tips of the hairs show some variation, which may be the result of age and wear. The former varying from Tawny to yellowish gray, and the latter from black to chocolate. These differences of hair color occur together in specimens taken at the same localities at the same seasons. Some individual variation is also shown in the amount of rufous on the shoulders, which is present in some and absent in others. Intergradation with *dorsalis* is discussed under that form. In the absence of specimens from the Cordillera de Talamanca south of Cartago and from the coastal regions of Costa Rica and Panamá south of Las Agujas it is impossible to extend the range of this form farther south at this time. There are, however, nine specimens (U.S.N.M.), without definite locality, labeled West Coast of Central America (collected by Captain Dow), Costa Rica, and Panamá, which are distinctly of the *rigidus* type. These specimens, together with a specimen from Remedios, Panamá, suggest the possibility of an extension of the range of this

form much farther south. Further discussion of this question is given under *melania*.

SPECIMENS EXAMINED.—Thirty-six.

West coast of Central America: 3 (U.S.N.M.).

Costa Rica: no definite locality, 5 (U.S.N.M.); Province of San José, San José, 2 (U.S.N.M.). Province of Cartago, Cartago, 2 (M.Z.U.M.); Juan Viñas, 2 (Biol. Surv. collection); La Carpintera, 1 (Field Mus.); Agua Caliente, 1 (M.Z.U.M.); San Ramón de Tres Ríos, 2 (Field Mus.). Province of Alajuela, Alajuela, 2 (U.S.N.M.), 1 (Field Mus.); San Mateo, 1 (U.S.N.M.); Zarceró, 6 (M.Z.U.M.); Esparta, 3 (M.Z.U.M.). Province of Puntarenas, Puntarenas, 5 (M.Z.U.M.).

SCIURUS VARIEGATOIDES THOMASI NELSON

1899 *Sciurus thomasi* Nelson, *Proc. Wash. Acad. Sci.*, 1: 71 (May 9).

TYPE LOCALITY.—Talamanca, Costa Rica. Type, Nos. 12044/2367, United States National Museum. Collected by William Gabb.

DISTRIBUTION.—Humid tropical forests of eastern Costa Rica, probably from the border of Nicaragua to Panamá, westward in the south to Talamanca, and in the north to Santa Clara.

DIAGNOSIS.—Similar to *belti*, but much blacker above and with much darker and richer ear patches and underparts (Pl. II, Fig. 4).

CHARACTERS.—Upperparts, including back, head, sides, outside of legs, and feet, grizzled Ochraceous-Orange and black. Sides with lighter wash of black. Hairs of sides and back sooty black at base followed by median band of Ochraceous-Orange and tipped with black. Back of ears tawny bordered with black. Cheeks and chin like back, but paler. Underparts, inside of legs, and postauricular patches Orange-Rufous. Tail above, black washed with white; below, with median area like underparts, bordered with black and edged with white. Hairs of tail above, black tipped with white; below, with three black bands beginning at the base, separated by two reddish bands and tipped with white.

VARIATION.—This is a dark and richly-colored form extending over a wide range in the Caribbean rain forest. The fourteen specimens in the collection representing this race, although from rather scattered and distant localities, are remarkably uniform in color. The only variation seems to be in the slight trace of white spotting on the abdomen, found in three specimens, and in the coloration of the feet, which are grizzled like the back in some specimens and pure black in others. Intergradation with *rigidus*, as described under that name, and its similarity to *belti* would suggest the possibility of intergradation with that form along the Atlantic coast region south of Bluefields.

SPECIMENS EXAMINED.—Eighteen.

Costa Rica: Province of Limón, Talamanca, 1 (U.S.N.M.); Pacuare, 1

(M.Z.U.M.); Jiminez, 2 (M.Z.U.M.). Province of Alajuela, Santa Clara, 2 (U.S.N.M.); La Vieja, 1 (M.Z.U.M.); San Carlos, 3 (M.Z.U.M.); Villa Quesada, 1 (M.Z.U.M.); Guapiles, 5 (Carnegie Mus.). Province of Cartago, no definite locality, 2 (U.S.N.M.).

SCIURUS VARIEGATOIDES MELANIA (GRAY)

1867 *Macroxus melania* Gray, *Ann. and Mag. Nat. Hist.*, 3rd Ser., 20: 425.

1920 *Sciurus variegatoides melania* Goldman, "Mammals of Panama," *Smith. Misc. Coll.*, 69, No. 5: 136.

TYPE LOCALITY.—Point Burica, Costa Rica. Given by Gray as West Coast of America, Point Burica (Kellet and Wood). Type in the British Museum.

DISTRIBUTION.—Pacific slopes of the mountains, coastal plains, and islands of western Panamá and adjacent parts of Costa Rica.

DIAGNOSIS.—Usually occurring in a melanistic phase, but with a gray phase similar to *rigidus*, although somewhat paler on the head and flanks.

CHARACTERS.—The pelage of *melania* is nearly black all over. When the pelage is fresh the color is practically black, but when viewed close at hand and in the proper light is seen as dark Seal-Brown which fades, with exposure and wear, to Chestnut-Brown, except on the feet which remain black.

VARIATION.—This black form seems to be quite constant in coloration throughout a definite range and, therefore, should be considered a geographic race of *variegatoides* which it resembles in size, skull characters, and characters of pelage. It possibly has a gray phase as will be brought out later in this discussion. Nelson (1899) assumed it to be a melanistic phase of *dorsalis* although he apparently had no specimens for comparison. Later, Bangs (1902: 22), on the basis of twenty-one specimens from Bugaba, Boqueti, Panamá, recognized it as a valid species. Goldman (1920: 136), with whom the author is in agreement, considered *melania* a subspecies of *variegatoides*. In 1856, ten years before Gray's original description of *Sciurus melania*, Selater (1856: 139) referred to a "black species, difficult to distinguish" and said, by the collector, Bridges, to be common in the vicinity of David and Boco Chicas. Thomas (1903: 40) records specimens of this form from the islands of Sevilla, Insoleta, Cebaco, and Brava.

Two specimens from Panamá, one (A.M.N.H.) from Remedios, and one (U.S.N.M. from a captive) from Panamá, may represent either a gray phase of *melania*, an extension of the range of *rigidus*, or the presence of another and yet unrecognized geographic race. The specimen from Remedios is of the grizzled backed "*rigidus* type" as recognized by Allen (1904: 66). This specimen has the color of the underparts typical of *rigidus* and the black tips of the hairs of the back faded to brown, which is characteristic of this form. It has a rather poorly-defined grayish stripe on the flanks and sides like the intergrades between *ridigus* and *austini* from the vicinity of Punt-

arenas. The twenty-seven specimens of *melania* examined from Panamá are nearly uniform in color. All show more or less fading of the black color which turns to brown with time and exposure. The old brown hairs are replaced with black hairs when the animal molts.

SPECIMENS EXAMINED.—Twenty-eight.

Panamá: Province of Chirique, Boquerón, 16 (A.M.N.H.), 10 (Field Mus.); Divala, 1 (Field Mus.); Remedios, 1 (A.M.N.H.).

SCIURUS VARIEGATOIDES HELVEOLUS GOLDMAN

1912 *Sciurus variegatoides helveolus* Goldman, *Smith. Misc. Coll.*, 56, No. 36: 3 (Feb. 19).

TYPE LOCALITY.—Corozal, Canal Zone, Panamá. Type, adult male, No. 171540, United States National Museum (Biol. Surv. collection), collected by E. A. Goldman, June 15, 1911. Original number 21166.

DISTRIBUTION.—Pacific coastal region of Panamá from the Canal Zone westward to the vicinity of Santiago.

DIAGNOSIS.—Similar in general appearance to *dorsalis* except that the color of the sides and underparts is cream instead of gray. Anterior premolar absent.

CHARACTERS.—Back, from top of head to base of tail, with broad band of black or grizzled pale buff and black or brown, widest behind the ears and over the lumbar region, narrow over the shoulders and tapering towards the tail. Hairs of back black or sooty black at base with median band of pale buff tipped with black or brown. Back of ears white bordered with black. Postauricular patches white. Cheeks and chin like back, but paler and with less black. Sides, outside of legs, and feet cream color. Hairs of sides black at base and tipped with white. Tail above, black washed with cream; below, with median area like underparts bordered with black and edged with white. Hairs of tail above, black tipped with white; below, cream color at base with subterminal band of cream and tipped with cream.

VARIATION.—This form resembles *dorsalis* in color pattern, but differs in pelage color from typical *dorsalis* both on the back and underparts. Judging from the specimens in hand, it seems that the hairs of the fresh pelage of the back come in, after the molt, with black tips which rapidly fade to brown or buff. The only individual variation shown is in the slightly more buffy color of the underparts and median area of the underside of the tail of some specimens. This may be the result of age and stain. One specimen (A.M.N.H.) from Santiago de Colorado, Panamá, the molt being partly completed, is entirely black with a patch of the old faded brown pelage on the rump. The skull of the specimen is missing, but it would seem best to assign it to this form rather than to *melania* as it bears the same data and locality as two other normal specimens of *helveolus*. The skulls of all the specimens examined lack the small anterior premolar present in other members of the *variegatoides* group.

SPECIMENS EXAMINED.—Ten.

Panamá: Province of Veraguas, 3 (A.M.N.H.); Canal Zone, Corozal, 2 (U.S.N.M.); near Panamá City, 5 (M.C.Z.).

DISCUSSION

Sciurus variegatoides is noteworthy among mammals for the 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 a grizzled all-over coloration.

The range of the species is from Mexico to the eastern part of Panamá, a distance of something over one thousand miles. The width of the range is much less, for in some places Central America is rather narrow, varying from about three hundred to less than fifty miles across. Within this geographic district no less than fifteen subspecies of these squirrels must be recognized.

MEASUREMENTS

Nelson (1899: 15-16), in his review of the Central American and Mexican squirrels, believed that some of the forms of the *variegatoides* group were differentiated by differences in body size and in skull measurements. My tabulation of measurements of the considerable number of specimens now available does not support this supposition.

There is a considerable amount of variation in size among the specimens taken at any one locality. Some of this variation in size is undoubtedly due to age, but I have not been able to detect any size difference between the sexes. There is also apparently considerable individual variation in size between the adult specimens taken at any one locality.

On the contrary, there do not seem to be any certain differences between the average body measurements of the various subspecies. In Table I measurements of three races, *dorsalis*, *variegatoides*, and *bangsi* are presented. These subspecies are the only ones of which sufficient numbers are available to give a basis for statistical analysis. Even these series are not fully comparable because the body measurements of *dorsalis* were not all taken by the same collector. All the other races have measurements within the general limits of those of the three subspecies which are tabulated.

None of the differences in total length between the three subspecies are of statistical significance. The mean total length of *variegatoides* exceeds that of *dorsalis* by 15.0 ± 6.53 mm., a difference which is 2.3 times its standard error, and of doubtful significance. This is the greatest difference between any two of the races.

In condylo-premaxillary skull length *bangsi* exceeds *variegatoides* by $1.74 \pm .55$ mm. and exceeds *dorsalis* by $1.50 \pm .46$ mm. These differences

TABLE I
 MEASUREMENTS OF THREE SUBSPECIES OF *SCIURUS VARIEGATOIDES*
 Means and standard errors, in millimeters

	<i>variegatoides</i>	<i>bangsi</i>	<i>dorsalis</i>
Total length	542.92 ± 3.24	539.50 ± 5.34	527.909 ± 5.66
Tail length	272.08 ± 2.70	268.50 ± 6.68	271.818 ± 4.68
Hind foot	64.29 ± 0.72	65.00 ± 0.76	65.818 ± 0.51
Condyllo-premaxillary length	54.171 ± 0.408	55.914 ± 0.367	54.418 ± 0.283
Zygomatic breadth	35.143 ± 0.228	35.393 ± 0.212	34.309 ± 0.175
Premaxilla to palatine notch	30.950 ± 0.217	31.621 ± 0.219	31.173 ± 0.258
Interorbital breadth	20.028 ± 0.227	20.500 ± 0.159	20.809 ± 0.228

are each 3.2 times their standard errors and therefore are statistically significant.

In zygomatic breadth of skull *dorsalis* averages small. The skull of *variegatoides* is wider than *dorsalis* by $.83 \pm .29$ mm. and the skull of *bangsi* is wider by $1.08 \pm .27$ mm. These differences are, respectively, 2.9 and 3.9 times their standard errors and are significant.

It appears that there is no difference of importance between the body measurements of these three races, but there is a significant difference in the dimensions of the skull between our series of *dorsalis* and the other two races. The number of specimens available in each of the series is few, however, and it is not at all certain that the specimens are of comparable age. It is not assured, therefore, whether these differences in skull measurements would hold if larger series were available. Among all the geographic races recognized here, there is no single specimen belonging to any one group that cannot be closely matched by single individuals in some other race in both body and skull measurements.

SKULL VARIATION

The skulls of the *variegatoides* group of squirrels are rather variable. When series of skulls from single localities are studied, it can be seen that there is a wide difference in the width of the nasals, the slope of the rostrum, the flatness of the frontal region, and the inflation of the premaxillaries directly anterior to the frontals.

In a series of six skulls of *bangsi* from Barra de Santiago, El Salvador, No. 12761 (Dickey collection) has a markedly different appearance from No. 12763 (Pl. III). These are both adult male specimens and, judging from the amount of wear on the teeth, are of comparable age. The larger specimen, No. 12763, has a much wider rostrum than No. 12761; also the frontal region is slightly flatter, and the parietal ridges are less widely separated. The differences between these two skulls are clearly only individual. In contrast to these skulls is another one, No. 12762, which is also from an adult

male, but the teeth do not show much wear. This skull is the smallest of the series, and the variation here is undoubtedly in part due to age. The largest male skull of this series is larger than any of the females.

In another series of six skulls of *bangsi* from San José del Sacare there is a similar amount of variation and the extremes are shown by two adult female specimens, Nos. 12725 and 12726. One specimen, No. 12725, is slightly older and has a broader rostrum and more depressed frontal region than the other. This large female, in contrast to the preceding series, is larger than any of the males in the series.

In a series of seven specimens of *bangsi* from Lake Olomega, El Salvador, the smallest specimen, No. 10361, is a female with narrower rostrum than other specimens of comparable age of both sexes. The largest specimen, which has the widest rostrum and most depressed frontal region, is the oldest male. There seems, therefore, to be no consistent difference between the sexes in skull characters.

The considerable amount of individual and age variation in the skulls of the species *variegatoides* masks any geographic variation which possibly may occur, and no diagnostic skull character distinguishing the several subspecies has been discovered.

COLOR PATTERN

In *Sciurus variegatoides*, exclusive of the tail and feet, there are five principal color areas on the body: the dorsal stripe, postauricular patches, forehead, underside of body (including the inside of the legs), and the sides of the body and outside of the legs. In Table II the color of these areas in the several races is tabulated. It will be noted that the black phase of *melania* is the only form which is nearly uniformly colored all over the body. All the other races and also the gray phase of *melania* are marked with more or less conspicuous color patterns.

All the subspecies have large postauricular patches, which are always of a color contrasting with the color of the back. Usually the color of the postauricular patch closely matches the color of the underparts. In *underwoodi*, which has either white or pale buffy underparts, the ear patches may be either of these colors and may or may not match the color of the underparts. In *austini* and *rigidus*, the ear patches are white, although the underparts are reddish, as is also the case with both the reddish and white color phases of the underparts of *austini*. In the strongly colored races, *thomasi*, *atrirufus*, and *belti*, the ear patches are rich red brown.

A strongly-marked dorsal stripe is present in *atrirufus*, *dorsalis*, *austini*, and *helveolus*. In these forms the dorsal stripe is black or blackish, and reaches from the base of the tail forward over the back. In its best development the dorsal stripe extends between the ears, but in some specimens of *dorsalis* it terminates just behind the postauricular patches. Narrow black

TABLE II
COLOR AREAS OF THE SUBSPECIES OF *SCIURUS VARIAGATOIDES*

SUBSPECIES	BACK	FOREHEAD	SIDES OF BODY AND OUTSIDE OF LEGS	UNDERPARTS AND INSIDE OF LEGS	WHITE SPOTTING ON UNDERPARTS	POST-AURICULAR PATCH
<i>goldmani</i>	Grizzled black and Ochraceous-buff	Like back	Like back	White	White
<i>variagatoides</i>	Grizzled black and Ochraceous-buff	Like back	Like back	Ochraceous-buff to Ochraceous-orange	Occasional	Buff
<i>bangsi</i>	Grizzled black and Pale Olive-gray	Like back	Like back	White	White
<i>managuensis</i>	Grizzled black and Ochraceous-orange	Like back	Like back	Ochraceous-orange	None	Reddish
<i>underwoodi</i>	to Ochraceous-buff Grizzled black and Ochraceous-buff to Yellowish gray	Like back	Like back	White or Ochraceous-buff	Occasional	Reddish or White
<i>adolphi</i>	Grizzled Ochraceous-buff heavily washed with black	Like back	Like back	Grizzled gray	Present	White
<i>boothiae</i>	Grizzled black and Ochraceous-tawny	Like back	Like back	White	Reddish
<i>belti</i>	Grizzled black and Ochraceous-tawny	Like back	Like back	Ochraceous-tawny	Present	Reddish
<i>dorsalis</i>	Black	Grizzled gray	Grizzled	White or Orange-rufous	Occasional trace	White
<i>atrivivus</i>	Black	Cinnamon-rufous	Cinnamon-rufous	Cinnamon-rufous	Occasional trace	Reddish
<i>austini</i>	Grizzled black and Orange-cinnamon	Grizzled gray with patch of Vinea-ceous cinnamon	Cinnamon-rufous	Cinnamon-rufous	Present	White
<i>rigidus</i>	Grizzled black and Ochraceous-orange	Like back	Like back	Orange-rufous	Present	White
<i>thomasi</i>	Grizzled Ochraceous-orange heavily washed with black	Like back	Like back	Brilliant Orange-rufous	Occasional trace	Reddish
<i>melania</i> (black phase)	Black	Black	Black	Black	Absent	Absent
<i>hebeolus</i>	Black	Like back	Cream	Cream	Absent	Absent

or blackish lines, more or less continuous with the dorsal stripe, extend from between the ears forward above each eye, usually terminating just in front of the eye. The two dark lines outline the back and sides of the color area of the forehead (Pl. I, Fig. 3). Two narrow lateral extensions of the dorsal stripe mark the posterior edges of the postauricular color patches, and form a partial dark collar around the upper part of the neck.

In those subspecies which have dorsal stripes the underside of the body and inside of the legs are a uniform color, which varies in the different subspecies from a dark tone of red to cream and to nearly white. The side of the body and outside of the legs in *atrirufus*, *helveolus*, and in some specimens of *dorsalis* are the same color as the underparts of the body. In the specimens of *dorsalis* which have white underparts, however, the sides are grayish, intermediate between the color of the underparts and that of the dorsal stripe.

The forehead is colored the same as the sides of the body in *atrirufus* and in *dorsalis*, but in *helveolus* the forehead patch is intermediate between the colors of the dorsal stripe and of the sides.

Quite another type of pattern is characteristic of those subspecies of *variegatoides* which do not have a dorsal stripe (Pl. II, Figs. 2-4). In these races there are only two main color areas on the body besides the ear patches. The color of the upperparts extends down over the sides of the body and meets that of the underparts at a rather sharp line. In all these forms, except in intergrades with races having dorsal stripes, the entire upperparts, including the forehead and the outside of the legs and feet, are grizzled, and the underparts are of a solid color, which is broken only by the occasional presence of small white spots or more rarely by small areas of gray along the side.

Some intergrades of *dorsalis* with *atrirufus*, *austini*, and *rigidus* have a narrow whitish line bordering each side of the dorsal stripe (Pl. I, Fig. 2).

The color of the forehead usually matches that of the sides of the body. For example specimens of *dorsalis* with gray or white sides have the forehead colored correspondingly, and intergrades between typical *dorsalis* and *atrirufus* have reddish foreheads matching the color of the sides of these specimens. Exceptions to this rule are found in all specimens of *helveolus* and in some specimens of *austini* where the color of the forehead is the same as that of the back. There seems also to be a correlation between the color of the sides of the body and the sides of the head, which are usually of the same color; but in *rigidus*, *atrirufus*, *dorsalis*, and in intergrades between these races the sides of the head remain light although the sides of the body may be dark reddish.

The underparts are extremely variable among the subspecies of *variegatoides*. The underside in each specimen is usually of a uniform color, red-

dish, gray, cream, or white, with the exception that whenever the underparts are reddish there are always a few specimens which have some white spotting in the region of the axillae, throat, and lower abdomen. The extent of this white spotting varies from a few white hairs to rather large areas, or even to the extent of covering the entire underparts. The only form in which the agouti type of coloration seems to be normal on the ventral surface is *adolphei*.

A tendency to white underparts occurs in many of the red-bellied squirrels of the Americas, either as white spotting or complete replacement of red by white. In *underwoodi* and *dorsalis* the red of the underparts seems to be entirely replaced by white in some specimens from regions where other specimens show little or no trace of ventral white spotting. I am in agreement with Allen (1915: 230) that the occurrence of white underparts is of little diagnostic value when considered alone. It may also be noted here that in the fox squirrel, *Sciurus niger rufiventer*, there occur occasional specimens in which the reddish color of the hairs of the underparts is replaced with black, and in these specimens the subterminal bands of the hairs of the back are also black instead of reddish. In some parts of Central America, as in other parts of the world, these variations in ventral color and in color pattern tend to become locally constant and then may contrast sharply with characters of the populations of adjacent areas.

The color of the feet is generally the same as that of the sides of the body and legs, the only independent variation being a slight variability in the number of black-tipped hairs present.

COLOR BANDS ON THE HAIRS

The guard hairs of the back and sides of the body in most subspecies of *variegatoides* are of the agouti type, and each hair is made up of several bands of color, giving a grizzled appearance to the upperparts. In Figure 1 is shown a diagrammatic cross section through the middle of the body of a

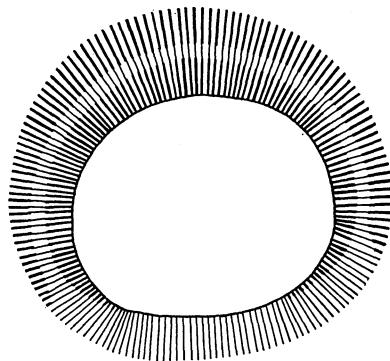


FIG. 1. Hypothetical cross section through the middle of the body of *Sciurus variegatoides rigidus*, showing the color bands on the hairs. This subspecies has no dorsal stripe.

specimen of a subspecies such as *rigidus*. The guard hairs on the sides and dorsal part of the body are shown to be marked by three bands: a basal blackish band, a median band of buff or whitish which is similar in color to the hairs of the underparts, and a long black tip.

On the underparts of the body the hairs usually are not banded. In some specimens of *underwoodi* and of *belti*, however, small areas along the outer edge of the underparts are gray or buff, due to the presence of banded hairs, and in *adolphei* the hairs of most of the undersurface are banded, giving a dark grayishness to the undersurface of the body.

In those subspecies which have a dorsal stripe the banding on the hairs is like that represented in Figure 2. The guard hairs of the dorsal stripe itself are mostly completely black or the bands are faint. A few of the guard hairs, however, especially on the anterior part of the back, may have buff subterminal bands.

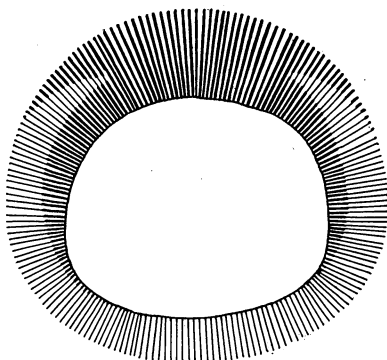


FIG. 2. Hypothetical cross section through the middle of the body of *Sciurus variegatoides dorsalis*, showing the color bands on the hairs. This subspecies has a conspicuous black dorsal stripe.

On the sides of the body in *atrirufus*, *dorsalis*, and *helveolus* the guard hairs have in general only two color bands: a basal black band, which diminishes in its width from the dorsal stripe downward to the lower edge of the side where it disappears, and a wide terminal portion which has the same color as the hair of the underparts of the body, and carries the ventral color upward to where it meets the dorsal stripe. Over a narrow area at the edge of the dorsal stripe the hairs have three bands, a black tip being added.

In many specimens of *dorsalis* the basal color of the double-banded hairs of the side shows through, and the side, therefore, is apparently of a different color from either the underparts or the dorsal stripe. An underfur of woolly gray and white hairs adds to this effect. In *atrirufus* and in some specimens of *dorsalis*, on the contrary, the color of the tips of the hairs on the side is sufficiently intense to obscure that of the bases of the hairs, and

the sides in these specimens are apparently colored like the underparts of the body.

The peculiar lateral stripe found in some intergrades between *dorsalis*, and *atrirufus* (Pl. I, Fig. 2), *austini*, or *rigidus* is produced by the addition of white or whitish tips to some of the hair along the outer edge of the dorsal stripe. This is illustrated diagrammatically in Figure 3. Some of the hairs of the lateral line are black for most of their length, with a short white tip; others, lower down on the sides of the body, have a narrow buff intermediate

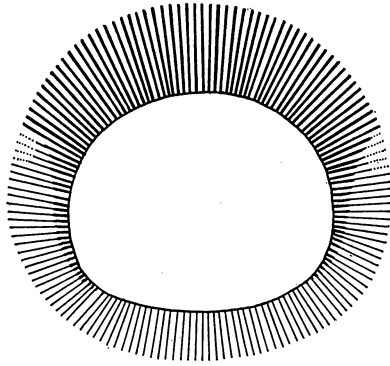


FIG. 3. Hypothetical cross section through the middle of the body of an intergrade between *Sciurus variegatoides dorsalis* and *S. v. atrirufus*, showing the color bands on the hairs. This specimen has a whitish edging along the dorsal stripe.

band between the black base and the whitish tip. A specimen which has no white lateral line often has a few white-tipped hairs in the dorsal stripe itself.

The tail in all subspecies of this group is, on the dorsal side, a mixture of black and white. The hairs are long, black, and tipped with white. The tail has a median ventral area similar in color to that of the underside of the body, because of a band of that color on the hair. In those subspecies with reddish underparts the tail hairs often have as many as five bands of color: the hair is dark at the base followed by two buffy bands separated by two black bands and tipped with white. The buffy band nearest the tip is often greatly reduced or absent.

MOLT

Seasonal changes in pelage color seem not to be important in this species. However, specimens from any one locality in series large enough fully to determine either the time or nature of seasonal changes in the pelage have not been collected. Neither are there available specimens taken at every month of the year. Judging from the material at hand 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. In some of the forms there is an increase in the proportion of black hairs of the feet after the molt. Its beginning stage occurs most often in specimens taken in April and May, and most of the skins in fresh pelage were taken in September and October. Individuals in molt are also found in November, December, February, and July, and there seems little uniformity in the season when it occurs in different individuals. Molt is evident in some individuals from nearly every month of the year, but is least evident in early fall. It is possible that each individual molts only once per year, but the evidence is not conclusive that this is so.

PERSISTENCE OF RACIAL CHARACTERS

The characters of at least some of these races of squirrels are indicated to have remained the same for many generations. Three specimens of *rigidus* taken at Alajuela in 1886 by A. Alfaro are almost identical in color and color pattern with two specimens from Cartago secured by Austin Smith in 1933. In the period of forty-seven years between these two collections there has been no detectable change in this district in the characters of the race, although the environment of the area has been considerably modified in this time by agricultural developments.

ENVIRONMENTAL RELATIONSHIPS

The climates of Central America are as complex as the topography of the region and change with remarkable abruptness with slope exposure and altitude. On the Atlantic slope the climate is generally that of the tropical rain forest, and the rainfall is distributed more or less throughout the year. The central highlands and Pacific coast region have a period of winter drought, but the latter region is considerably drier and warmer than the highland throughout the year (Sapper, 1932: 59).

Without having visited Central America it is difficult to draw any but general conclusions about correlations between the coat colors of these squirrels and climate, habitat, or other environmental conditions.

In general the darkest and most intensely colored forms, with reddish underparts and ear patches, live in the regions of heaviest rainfall. These dark forms are *thomasi*, *belti*, and *managuensis*, and their ranges extend from the tropical lowlands of the Caribbean Coast to the eastern slopes of the central highlands (Map 1). This region has heavy precipitation and dense forests.

S. v. atrirufus is also a dark form, but it is found on the Pacific side. The mountains of the central part of the Nicoya Peninsula, however, have considerably more rainfall than the rest of the Pacific Coast of Costa Rica and Nicaragua (Sapper, 1932: 31, Fig. 2).

On the Pacific slope of Central America are found the pale forms *gold-*

mani, *bangsi*, *dorsalis*, and *helveolus*, all of which have white ear patches and white underparts. In this area the amount of rainfall is considerably less than on the Caribbean slope, and the forest is much less dense.

Those specimens of *dorsalis* from Oja Ancha on the Nicoya Peninsula having reddish underparts were taken, according to Austin Smith, in regions with dark red clay soil. Furthermore, the palest specimens of the *dorsalis* series, which have whitish underparts, were taken on isolated limestone hills near Ballena (Pl. I, Fig. 4). These facts, although meager, suggest a possible correlation between the color of the pelage and of the soil at the places where the squirrels live.

A correlation between the character of the pelage of certain squirrels and of the climate was noted by Nelson (1899: 21). Tropical species tend to have much thinner and coarser pelage than species of the Transition and Boreal Zones. This trend in the character of the pelage is not apparent in the subspecies of the *variegatoides* group, even when specimens from sea level are compared with those from altitudes as high as 5000 feet near Cartago. All the squirrels of the *variegatoides* group have stiff, coarse, and rather short pelage, no matter at what altitude they live.

VARIATION IN SOME OTHER SPECIES OF SQUIRRELS

Several similar cases of extreme variation in color and color pattern among the geographical races of a single species of squirrel are found in other parts of the world.

Seven subspecies of *Callosciurus sladini* described by Thomas and Wroughton (1916: 230-235) occur between the Chindwin and Irrawaddy rivers in Upper Burma. These races are relatively stable in character at their type localities, which are about thirty miles apart. Except in one case, they intergrade wherever the ranges overlap. These races are found only on the east bank of the Chindwin River from Hkamti south two hundred and fifty miles to Yin. The Chindwin River seems to form a barrier to the western dispersal of the species, and the extent of the range eastward is unknown except in a few forms which reach the Irrawaddy River. From north to south the body color becomes paler in four successive races, then becomes abruptly darker in the next two, and more rufous in the succeeding form. The abrupt change from the pale form (*baringtoni*) to the darker forms (*millardi* and *sladini*) takes place south of the Uyu River, which is the only eastern tributary of the Chindwin and which seems to form a barrier to intergradation between the races of *sladini*. According to Morris (1936: 671) the darker forms in the north are associated with dense jungle country and the paler forms with lighter deciduous forests, but he does not find the same sort of correlation in the rich coloration of the three most southerly forms. It is interesting to note that in *rubex*, the most southerly

of the *sladini* races, the reddish color of the underparts is occasionally replaced by white, as occurs sometimes in *dorsalis* in Costa Rica.

From the east to the west coasts of Equatorial Africa forty-seven races of squirrels have been referred by Ingoldby (1927: 471-487) to *Heliosciurus gambianus*. From east to west along latitude ten degrees north occur a number of small pale races, and correspondingly small pale races occur also along latitude ten degrees south. In the intervening regions there are found a number of much larger dark races, which intergrade in various directions. A peculiar feature of this species is that similar races occur both north and south of the equator, which, though separated by the ranges of darker and larger forms, are almost indistinguishable. The darker forms are said to be associated with areas of heavier forests and of more rainfall than exists in the localities occupied by the paler forms.

Another interesting instance of racial variation has been described by Banks (1931: 1335-1348) in the species *Sciurus prevostii* from Sarawak. The eight races of this species found in Borneo are locally constant, but intergrade where their ranges come together, and the ranges of all but four overlap. Along the banks of two rivers running westward there is no intergradation between the races on opposite banks. Other rivers do not seem to form barriers to dispersal. Banks finds nothing, climate least of all, to explain the differences of racial color, but admits that adequate meteorological data are lacking. In the area of intergradation of two races (*caroli* and *griseicauda*) he found certain specimens having characters common to both parent races, but having some characters peculiar to themselves. These, he states, may possibly be nonintermediate hybrids. The similarity between some races of the *prevostii* species found respectively in Borneo and in Sumatra may be considered as evidence for discontinuous distribution.

Serebrennikov (1931: 493-495) describes three forms of *Sciurus vulgaris* from Siberia with tails and ear-tufts respectively black, brown, and red. Although these forms sometimes occur together, they tend to be more abundant separately in the forests of cedar, fir and larch, and pine, respectively. He further states: "The darker the forest (i.e., the more cedar and fir prevailing), the damper is the microclimate, the greater the elevation of land, the darker are the squirrels; and vice versa, in dry, light pine forests on flat areas, light squirrels are found."

The *variegatoides* group illustrates the same sort of variation and intergradation that the three above-mentioned species have shown. All show intergradation where the ranges of two races lie adjacent or are not separated by physical barriers. The *gambianus* and the *prevostii* groups differ from the *sladini* and *variegatoides* groups, however, in having some discontinuous distribution. It is likely that similar amounts of variation in color and color pattern will be found in other species of squirrels when careful studies are made.

The relationship between the colors and color patterns of the geographic races of all these various groups of squirrels, and the environment is uncertain. A general tendency for the occurrence of dark-colored races in regions of heavy rainfall and dense vegetation, and conversely of pale-colored races in regions of scanty rainfall and more open forests is evident. Almost nothing is known about the soil colors and other features of the environments in relation to the habits of any of these squirrels. No correlation between the color patterns of these squirrels and of their habitat seems to have been suggested. Whether or not the colors and color patterns of the various races of these squirrels are in part adaptive is, therefore, uncertain. Critical ecological studies of any of these forms would be very desirable.

SUMMARY

Sciurus variegatoides ranges from southeastern Mexico to the Panama Canal Zone, a distance of over one thousand miles. A great amount of variation occurs in this range, and fifteen geographic races are recognized. Intergradation between the races is of a blending type for general color tone, while it seems to be of an alternative type for the color of the postauricular patches and for the occurrence of the dorsal stripe. Pale-colored races such as *goldmani*, *bangsi*, and *dorsalis* occur in general in regions with arid climate, and dark-colored races, such as *thomasi* and *belti*, are found in regions of heavy rainfall.

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PLATE I

Skins of several subspecies of *Sciurus variegatoides*; about one-fourth natural size.

- FIG. 1. *S. v. atrirufus*; Tambor, Costa Rica.
- FIG. 2. Intergrade between *atrirufus* and *dorsalis*; San Juanillo, Costa Rica.
- FIG. 3. Typical *dorsalis*; El Pelón, Costa Rica.
- FIG. 4. Very pale *dorsalis*; Ballena, Costa Rica.

PLATE II

Skins of several subspecies of *Sciurus variegatoides* (*continued*).

- FIG. 1. *S. v. austini*; Las Agujas, Costa Rica.
- FIG. 2. *S. v. bangsi*; San José del Sacare, Salvador.
- FIG. 3. *S. v. variegatoides*; Lake Olomega, Salvador.
- FIG. 4. *S. v. thomasi*; mountains above Peralta, Costa Rica.



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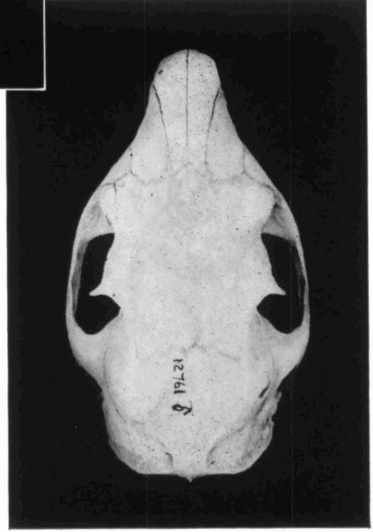
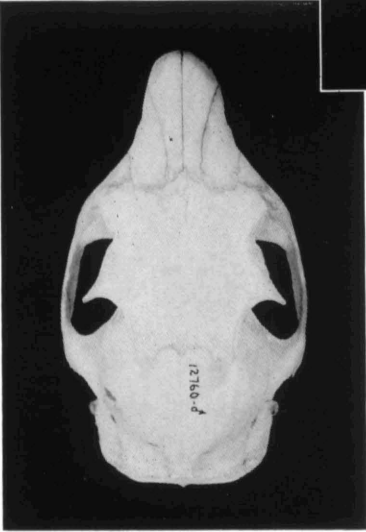
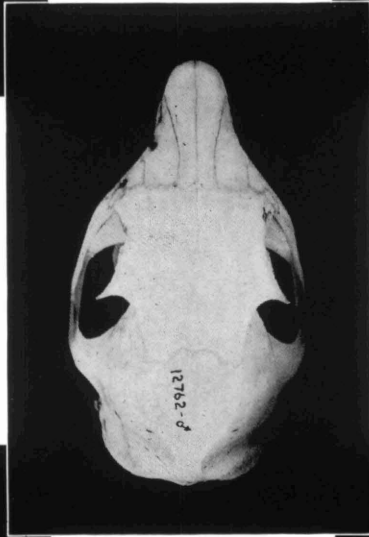
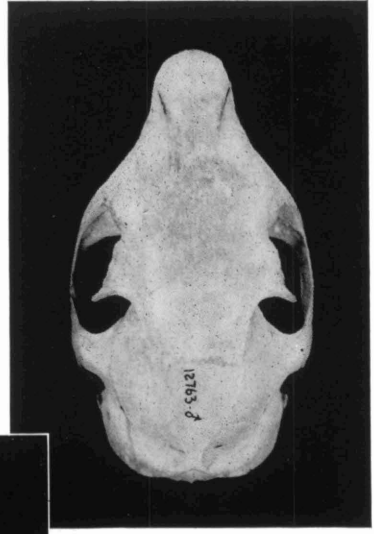
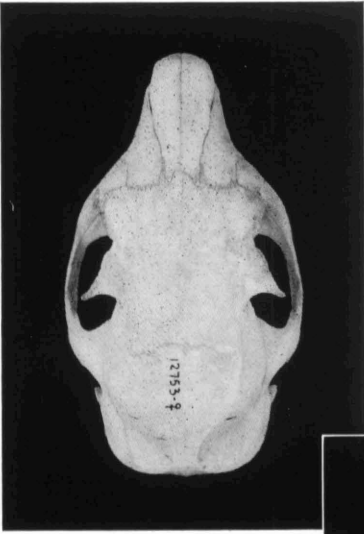
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PLATE III

Variation in adult skulls of *Sciurus variegatoides bangsi*; somewhat less than natural size. From Barra de Santiago, Salvador.



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