

THE NEOTROPICAL VARIEGATED SQUIRREL, *SCIURUS VARIEGATOIDES* (RODENTIA: SCIURIDAE) IN NICARAGUA, WITH THE DESCRIPTION OF A NEW SUBSPECIES

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ABSTRACT

The Neotropical variegated squirrel, *Sciurus variegatoides*, is represented in Nicaragua by five known subspecies—*adolphei*, *belti*, *boothiae*, *dorsalis*, and *underwoodi*. Analyses of morphometrics, color, and color patterns of 394 specimens from throughout the country and all available literature support the retention of these subspecies, but also reveal the presence of a sixth population of these squirrels, which is worthy of description and recognition as a new subspecies. This new subspecies is confined to Isla de Ometepe in Lago de Nicaragua. Variegated squirrels on Ometepe are on average the smallest variegated squirrels in the country in most cranial measures; however, in postorbital breadth, the island population averages larger than the samples from the surrounding mainland. This island population is the smallest and most distinctive of any population of variegated squirrels from throughout the species' geographic range. The baculum is distinct in size, shape, and angle of the disc. Ometepe variegated squirrels have a distinctive albeit a highly variable color pattern. Although there are some color differences between the populations found on the north island (Volcán Concepción) and the south island (Volcán Maderas), all specimens from Ometepe are regarded as belonging to a single subspecies because there are no discernable differences in cranial measures. Throughout Nicaragua's Pacific lowland dry tropical forest region, there is no evidence of integration between *S. variegatoides dorsalis* with *S. v. adolphei*, the subspecies occurring to the north; between *S. v. dorsalis* and *S. v. underwoodi*, the subspecies occurring to the east and northeast; or between *S. v. adolphei* and *S. v. underwoodi* in the northwest. The Central Depression region of Nicaragua appears to be a significant geographic barrier to gene flow between taxa. In the Central Highlands, there are regions of intergradation between *S. v. belti* and *S. v. underwoodi* and between *S. v. belti* and *S. v. boothiae*. The taxa of *S. variegatoides* found in the country are described and mapped by critically evaluating the historical collecting sites, all published literature, and data presented herein.

Key words: biodiversity, biogeography, Central America, color pattern variation, geographic variation, Mammalia, morphology, Neotropics, subspecies novum, taxonomy

INTRODUCTION

The Neotropical variegated squirrel *Sciurus variegatoides* Ogilby, 1839 (Rodentia: Sciuridae) is the largest and most widely distributed of the squirrels found in Central America. Variegated squirrels occur from southwestern Chiapas through central Panama and range in elevation from sea level to 2,600 m; however, they are most abundant at elevations below 1,500 m. *Sciurus variegatoides* occupies a wide array of habitats, including lowland dry and wet forests, as

well as premontane and montane forests, but it favors second-growth, disturbed, and heterogeneous habitats where it tends to nest in the largest trees available.

This is often the most conspicuous squirrel in much of the Central American forests. Because of its size and at times abundance, variegated squirrels play important ecological roles in Neotropical ecosystems as they feeds on seeds, fruits, fungi, insects, and smaller

vertebrates. It can be the principal handler of seeds, especially as seed predators of palms, but can also increase seed dispersal and germination by caching. This species can be quite abundant locally, especially in agricultural situations. It can do considerable damage feeding on developing bananas (*Musa*, Musaceae), coconuts (*Cocos nucifera*, Arecaceae), coffee beans (*Coffea* sp., Rubiaceae), cacao pods (*Theobroma cacao*, Malvaceae), papaya (*Carica papaya*, Caricaceae), and other crops.

Sciurus variegatoides is one of the most variable species of all mammals with respect to color; hence the English common name, variegated squirrel, is especially appropriate. Fifteen subspecies, based primarily on color, currently are recognized (Harris 1937; McPherson 1971; Hall 1981), acknowledging the considerable geographic variation within the species, yet little systematic or ecological information is available for most populations (Best 1995). The species ranges in pelage color from nearly black to steely gray, or grizzled gray, to reds, and to having a broad, black dorsum with white, red, bright orange, or light orange sides and ventrum (Harris 1937; Reid 2009; Thorington et al. 2012).

As currently defined, this broadly distributed and highly variable squirrel has continued to be recognized as a single species, although there is considerable size and color variation among subspecies. Interestingly, there appears to be little, and in some cases no, introgression in color morphs between several of the subspecies; although between some, there is a narrow zone of introgression. There has been no revisionary work since Harris's classic review of the species (Harris 1937). A considerable number of specimens have become available since Harris's work and a re-assessment

of distributions and status of several of the taxa are now possible. In the absence of genetic information for these subspecies, and given localities of intergradation between them as documented below, *S. variegatoides* is treated as a single, widespread, variable species herein.

In a recent review of the squirrels of Nicaragua, Medina-Fitoria et al. (2018) reported range extensions for southern flying squirrels (*Glaucomys volans*) and pygmy squirrels (*Microsciurus alfari*) and reviewed the then known distributions of these and *S. granatensis*, *S. richmondi*, and *S. variegatoides*. They provide descriptions and a useful key to the species of sciurids in the country, their conservation status, and color images of each. In their report on the variegated squirrels found on Isla de Ometepe, they provided two images of free-ranging animals demonstrating some of the color variation found in the island population and stated that these squirrels were of uncertain taxonomic status.

Between February 1964 and the spring of 1968, several field parties from University of Kansas led by J. Knox Jones, Jr. and James Dale Smith, collected mammals and their ectoparasites throughout Nicaragua. Herein, these collections are reported along with other specimens housed in museums to re-examine the systematic status of several populations of *S. variegatoides* focusing on the taxa found in Nicaragua. One goal is to build a better understanding of the geographic variation in this species and to re-evaluate the diversity that is currently recognized. The field parties from Kansas were the first to collect mammal specimens at several localities on Isla de Ometepe, the large volcanic island in Lago de Nicaragua. The tree squirrels on Ometepe represent a previously unrecognized taxon, which is described below as part of this species complex.

METHODS AND MATERIALS

A total of 394 specimens of *Sciurus variegatoides* from throughout Nicaragua comprise the basis of this report, with additional specimens examined from throughout the species' range and a review of the published literature to assess distributions, morphology, and color variation. All measurements in the accounts that follow are in millimeters and weights are given in grams (g) or kilograms (kg). Cranial measurements were taken by Genoways with digital calipers accurate

to the nearest 0.1 mm as defined by Hall (1981) and include the following: greatest length of skull (GLS), condylobasal length (CBL), zygomatic breadth (ZB), interorbital breadth (IOB), postorbital breadth (POB), mastoid breadth (MB), length of nasals (LN), length of palatal bridge (PB), and length of maxillary toothrow (LTR). External measurements and reproductive data are those recorded on specimen labels by the collector.

Statistical analyses were performed using Minitab (Minitab, Inc., State College, Pennsylvania, USA). There is no secondary sexual dimorphism in size in these squirrels and given the small sample sizes, assessment of sexual dimorphism was not feasible; thus measurements of males and females were pooled in analyses of variation among groups. A number of principal component analyses were undertaken using either individual localities or small geographic areas as units beginning with 27 operational groupings. Individuals deemed intergrades as judged by external color characteristics were not included in morphometric analyses. Based on these results, six groups that represent taxonomic and geographic units were formed for the final principal components analysis. Discriminant function analysis was used to assess morphological differences and to maximize group discrimination (Strauss 2010). See Table 1 (in ANALYSES) for taxon-specific descriptive statistics (mean, standard deviation, and range). Differences among groups were analyzed for the six operational groupings and for pairwise comparisons.

Harris's (1937) color terminology was followed in describing the coloration of these squirrels to provide the user with a standard, uniform set of descriptors for the various colors and because Harris did an outstanding job of elucidating the patterns present.

Specimens reported in the systematics accounts below are housed in the following museums: American Museum of Natural History, New York (AMNH); British Museum (Natural History) London, UK [BM(NH)]; Muséum national d'Histoire naturelle, Paris, France (MNHN); Museum of Texas Tech University, Lubbock (TTU); University of Kansas Museum of Natural History, Lawrence (KU); and National Museum of Natural History, Washington, DC (NMNH). Timm's research on Central American mammals was undertaken with the approval of the University of Kansas Institutional Animal Care and Use Committee.

HISTORICAL REVIEW

The Irish naturalist William Ogilby first made the species *Sciurus variegatoides* known to science in 1839 based on a specimen sent to him by Captain Belcher from the coast of El Salvador (Ogilby 1839). Only three years later, Lesson (1842) reported the first specimen of this species from Nicaragua when he described *Macroxus Adolphei* from El Realejo near Chinandega on the Pacific coast of the country. This taxon, which is now known under the name *Sciurus variegatoides adolphei*, is believed to be confined to the tropical dry forest of extreme northwestern Nicaragua (Genoways and Timm 2005). The other subspecies of Neotropical variegated squirrel originally described from Nicaragua is *Sciurus boothiae belti* Nelson, 1899. Charles W. Richmond (1893:480–481), who collected the holotype on 22 November 1892, described the type locality as follows: “The International Planting Company's plantation, or ‘I. P.,’ as it is familiarly called, is 50 miles from Bluefields [along Escondido River]. A creek joins the river at this plantation, and affords an excellent means of reaching the heavy forest in the rear.” This description places the type locality well within the lowland tropical wet forest that originally covered much of eastern Nicaragua.

John Edward Gray, long-serving botanist and zoologist at the British Museum, described several taxa of Mexican and Central American *Sciurus*, two of which are considered valid subspecies of *S. variegatoides* with geographic ranges extending into Nicaragua. The earliest was *Sciurus richardsoni* Gray, 1842 from Honduras; however, this name is preoccupied by *Sciurus richardsoni* Bachman, 1839, so in 1843 Gray renamed this taxon as *Sciurus boothiae*. He later described *Sciurus dorsalis* Gray, 1849, based on two specimens supposedly from Caracas, Venezuela, but he (Gray 1867) later corrected the type locality to Costa Rica, where (Nelson 1899:74) wrote “specimens from Liberia, Costa Rica, are typical.” On this basis, Liberia, Costa Rica, is considered to be the restricted type locality of the strikingly and distinctly colored dry forest squirrel *Sciurus variegatoides dorsalis*.

The first systematic revision of *S. variegatoides* was undertaken by Edward W. Nelson in 1899. Within the squirrels now considered to represent *S. variegatoides*, Nelson recognized six species—*S. adolphei*, *S. boothiae*, *S. goldmani*, *S. managuensis*, *S. thomasi*, and *S. variegatoides*. Nelson (1899:79) treated *dorsalis*

as a subspecies of *S. adolphei* because specimens of *adolphei* appeared to “differ from *S. a. dorsalis* mainly in its darker color.” Nelson (1899) described *Sciurus thomasi* as a distinct species because he concluded that specimens from La Carpintera, Costa Rica, represented both *thomasi* and *dorsalis*. On the other hand, Nelson (1899) described the taxon *belti* as a subspecies of *S. boothiae* because “*S. boothiae* grades into *S. b. beltii* to the south.” Also, Nelson (1899) placed two taxa, currently considered valid subspecies—*rigidus* and *melania*—as junior synonyms of *S. adolphei dorsalis*.

Subsequent to Nelson’s revision of the group, Allen (1908) reported 12 specimens of these squirrels from five localities in western and northern Nicaragua. Two years later, Allen (1910) presented information on an additional 25 specimens from seven localities in Nicaragua and summarized the taxonomy of squirrels in these two collections. These specimens were all collected by William B. Richardson, who in many cases used local names for his work sites, which have challenged subsequent researchers to precisely locate (see below). Allen (1910) divided the specimens from Nicaragua into two species—*S. boothiae* and *S. variegatoides*—the former including the nominate subspecies and *beltii* and the latter including the nominate subspecies and *adolphei*.

Between 1912 and 1933, five additional taxa, now associated with *S. variegatoides*, were described and named. Only one of these taxa—*underwoodii* Goldman, 1932—has ultimately been associated with squirrels in Nicaragua, with the type locality in Honduras. Two of the new taxa were from Costa Rica—*atrirufus* Harris, 1930 and *austini* Harris, 1933—one from Panama—

helveolus Goldman, 1912—and the other from El Salvador—*bangsi* Dickey, 1928. Goldman (1912), Dickey (1928), and Harris (1933) used *variegatoides* as the specific epithet for the new taxa and Dickey (1928) placed earlier species names, such as *goldmani*, in the species *S. variegatoides*.

Harris (1937) revised this group of squirrels bringing them all into the species *S. variegatoides*, with 15 recognized subspecies. This is the same basic arrangement, with a few modifications, still used for the Neotropical variegated squirrel today (Hall 1981). Harris mapped the geographic ranges of five subspecies of *S. variegatoides* as including parts of Nicaragua—*adolphei*, *beltii*, *boothiae*, *dorsalis*, and *underwoodii*. He considered *S. v. beltii* to occupy much of eastern half of the country in the Caribbean Lowlands, an area of tropical wet forests. Two subspecies occurred on the Pacific Coast, with *S. v. dorsalis* west of Lago de Nicaragua along the southwest coast and *S. v. adolphei* along the northwest coast in the Department of Chinandega. These taxa occur in a much drier area than *beltii* including much of the arid tropical scrub forests. The last two subspecies—*boothiae* and *underwoodii*—occur in the montane areas of central and northern Nicaragua.

Subsequent to Harris’s revision (1937), only two taxonomic changes have been made regarding these squirrels. Hall and Kelson (1952) arranged *S. v. austini* as a junior synonym of *S. v. rigidus* in central Costa Rica. The distinctive populations from two valleys in southwestern Costa Rica separated by the Cordillera de Talamanca from more northern and eastern populations were described as *S. v. loweryi* McPherson, 1971, bringing the number of recognized subspecies back to 15.

HISTORICAL COLLECTING SITES

One of the early professional collectors of bird and mammal specimens in Nicaragua was William B. Richardson. In 1891, Richardson settled in Matagalpa, Nicaragua, to grow coffee, and over the years he collected a number of specimens for museums in England and the United States. The collections of mammals that he made in Nicaragua for the American Museum of Natural History from 1904 to 1908 contained a significant number of Neotropical variegated squirrels. Many of the Nicaraguan collecting localities visited

by Richardson were small villages not found on most maps, then or now, or were given as nonspecific geographic features. “He never gave distance and direction from a locality and seldom included the Departamento. His handwriting was not always clear and he sometimes used cryptic abbreviations” (Howell 1993, 2010:3). Because the material collected by Richardson included a number of important scientific specimens, his localities have long been a challenge to researchers (Allen 1908, 1910; Buchanan and Howell 1965; Jones and

Genoways 1970, 1971; Jones and Yates 1983; Jones and Engstrom 1986; Howell 1993, 2010; McCarthy et al. 1999; Rossi et al. 2010).

Because Richardson's squirrel specimens are important to the study of *Sciurus variegatoides* in Nicaragua, the latest thinking on the placement of his relevant collecting locations are provided below.

Departamento de Boaco:

Chontales [probably near Tierra Azul, 30 km NNE Boaco, 12°41'N, 85°30'W; Jones and Genoways 1971; Jones and Engstrom 1986]

Departamento de Chinandega:

Volcán de Chinandega [Rossi et al. 2010 believed this to be the same as San Cristóbal volcanic complex, which is composed of five volcanoes including San Cristóbal (main cone), El Chonco, Moyotepe, Volcán Casita (site visited by a University of Kansas field party), and La Pelona (12°42'N, 87°01'W)]

Volcán Viejo [Volcán El Viejo is an alternative more local name for San Cristóbal]

Departamento de Jinotega:

Peña Blanca [in southern part of the Department of Jinotega at 13°15'N, 85°41'W; Buchanan and Howell 1965:549; Jones and Engstrom 1986]

San Rafael del Norte [13°13'N, 86°07'W on modern maps]

Río Coco [has been one of the most difficult of Richardson's localities to pinpoint, but Howell (1993, 2010) presented a persuasive case for the site to have been located in the vicinity of the village of Santa Cruz on modern maps, with its coordinates being 13°27'N and 85°55'W. The village is on the south side of the Río Coco and thus within Departamento de Jinotega. The birds and mammals collected by Richardson at "Santa Cruz" and "Río Coco" are from a remarkably varied group of habitats in Nicaragua, including Caribbean slope, humid lowland forest, highland pine forest, humid montane (cloud) forest, and Pacific slope thorn scrub and deciduous

forest edge. When Richardson collected some distance away from the village, with no other named place nearby, he appeared to have used only "Río Coco" as his locality (Howell 1993, 2010). The squirrels appear to have a relationship with the Caribbean slope so probably were from near the river.]

Departamento de Madriz:

San Juan [San Juan de Telpaneca, 13°32'N, 86°17'W, on modern maps]

Departamento de Matagalpa:

Lavala [a misinterpretation of Richardson's spelling of Savala, located at 45 km ENE of Matagalpa; Buchanan and Howell 1965:549; Jones and Genoways 1970]

Matagalpa [12°56'N, 85°55'W on modern maps, but may cover more than one location according to Harris (1937)]

Río Grande [probably on the Río Grande de Matagalpa near the mouth of the Río Upá, 200 m, 13°15'N, 85°41'W; Jones and Genoways 1971; Jones and Engstrom 1986]

Río Tuma [probably near El Tuma on the Río Tuma, 13°08'N, 85°44'W; Rossi et al. 2010]

Sebaco [Sébaco, on modern maps at 12°51'N, 86°06'W in northwestern Departamento de Matagalpa]

Uluce [12°53'N, 85°37'W; Jones and Engstrom 1986]

Vijagua [= Bijagua, a small village near Guasaca, 13°07'N, 85°41'W, about 35 km NE Matagalpa; Buchanan and Howell 1965; Jones and Genoways 1971; Jones and Engstrom 1986]

Departamento de Nueva Segovia:

Jalapa [13°55'N, 86°07'W on modern maps]

Jicaro [13°43'N, 86°08'W on modern maps]

Departamento de Río San Juan:

Los Sabalos [= Boca de Sabalos, at confluence of Río Sabalos and Río San Juan, 11°03'N, 84°28'W]

In addition to Richardson's localities, three other historic collecting sites in Nicaragua deserve comment. Dr. L. F. H. Birt of Greytown in the southeastern-most part of the country, who was associated with the Nicaragua Canal Company, collected a large number of mammals, reptiles, fishes, and birds in the late 1880s and donated them to the Smithsonian. His collections include a single *S. variegatoides* from Greytown. This specimen came to the National Museum of Natural History prior to 1888 from the Nicaragua Canal Company (True 1889). Greytown has changed names over the years from San Juan del Norte to San Juan de Nicaragua, but is now officially Greytown. Greytown appears on modern maps at 10°55'N, 83°41'W in the Departamento de Río San Juan.

A second site is Escondido River, "50 miles above Bluefields," where a series of Neotropical varie-

gated squirrels was collected by Charles W. Richmond, Curator of Ornithology of the National Museum of Natural History, between August and November of 1892 (Richmond 1893). This site, which is the type locality for *S. v. belti*, was determined by Jones and Genoways (1971) to be the I. P. Plantation, 3 km S, 13 km E Rama currently located in the South Caribbean Coast Autonomous Region of the country.

Harris (1937) reported a specimen of *S. v. belti* from Edén, Departamento de Matagalpa. This specimen, which is deposited in the Carnegie Museum of Natural History, was not examined for this study and this locality is not shown on modern maps of Nicaragua. However, Ulmer (1995) gives a good description of this site and the history of specimens from there. Specimens from Edén were obtained in 1922 by an expedition from the Academy of Natural Sciences of Philadelphia lead by Wharton Huber and J. Fletcher Street. They described Edén as a gold mining town located at 14°00'N, 84°26'W (213 m), which places the site in the North Caribbean Coast Autonomous Region and not in Matagalpa.

PHYSIOGRAPHIC SETTING

Nicaragua is generally divided into three physiographic regions—Pacific, Central Highlands, and Caribbean Lowlands (Taylor 1963). Neotropical variegated squirrels occur in all three regions, and the climate and environment of the individual regions have influenced the variation in these squirrels. The Pacific region features a chain of 40 volcanoes extending from Volcán Cosigüina on the Golfo de Fonseca in the northwest to Volcán Maderas on Isla de Ometepe in the south (Arguello et al. 2018). Those volcanoes northwest of Lago de Managua are collectively known as the Cordillera de los Marrabios and the chain of volcanoes continues in Costa Rica as the Cordilleras de Guanacaste and Tilarán. This line of volcanoes lies just west of a large crustal rift formed by the subduction of the Cocos plate under the Caribbean plate (van Wyk de Vries 1993). This subduction zone forms the Central Depression of Nicaragua, which contains six freshwater lakes, with the largest being Lago de Managua and Lago de Nicaragua (Taylor 1963). Rainfall in this region is highly seasonal, with a marked rainy season from May to August, with the wettest period in July.

The Pacific region extends about 75 km inland from the coast and is characterized by relative flat, low-lying land except for the volcanic peaks. This region has high temperatures, moderate rainfall, and strong seasonal droughts. These low lands are characterized by dry tropical forest and grasslands (Sabogal 1992) or semi-evergreen rainforest (Taylor 1963), with common plants such as bull horn acacia (*Vachellia collinsii* = *Acacia collinsii*), Spanish elm (*Cordia alliodora*), white manjack (*Cordia dentata*), quickstick (*Gliricidia sepium*), and hog plum (*Spondias purpurea*) (Sabogal 1992). Since prehistoric times, the Pacific region has been heavily impacted by human activity, including significant harvests of large, valuable hardwood trees; agriculture—large ranches for raising cattle and mules, and crops primarily cotton, sugar cane, and rice in the lowlands and coffee at higher elevations; and building of communities and cities. The forests on the slopes of the volcanoes are taller because of the cooler temperatures and additional moisture as well as less timber harvest, but there are also treeless areas as a result of volcanic activity and landslides. Some of the larger

trees in these areas are kapok (*Ceiba pentandra*), hog plum, and chelate (*Ficus insipida*). Two subspecies of squirrels occur in this region—*S. v. adolphei* to the north and *S. v. dorsalis* to the south.

Lying in the Pacific region is Isla de Ometepe, which is situated in Lago de Nicaragua and comprised of two stratovolcanoes. Volcán Concepción (1,600 m), the larger of the two, is the northern island and connected to Volcán Maderas (1,400 m) by a narrow, low elevation isthmus (Istmo de Istián). Concepción is an active volcano that has erupted recently. Maderas, southernmost and smaller of the two, has not been active in historical times last erupting perhaps 3,000 years ago. Isla de Ometepe is home to a previously undescribed population of *S. variegatoides* described below.

The Central Highlands is a triangular-shaped area extending south from Honduras, that consists of three ancient major mountain ranges and several minor ones. These rugged mountains historically were covered in forest, but significant clearing has taken place. Dividing these mountains are deep valleys with rivers that generally flow to the east. The western slopes of these mountains are drier than the eastern slopes, with a flora that Taylor (1963) called Seasonal Evergreen Rainforest, but little of this mature forest remains. Regenerating forests have such trees as papelillo (*Miconia argentea*), pink shower tree (*Cassia grandis*), and aguacatillo (*Nectandra salicifolia*). The moister eastern slopes were covered in forests that Taylor (1963) classified as Lower Montane Rainforest, which grades toward the Caribbean Lowland forests. Some of the important trees in this zone are Mexican elm (*Ulmus mexicana*), oak (*Quercus lancifolia*), snowbell (*Styrax argenteus*), and mastic (*Mastichodendron capiri*). The subspecies

S. v. underwoodi occurs in the lower elevations of the western slopes of the Central Highlands and *S. v. belti* seems to be found in the moister areas of the eastern slopes of the highlands probably following the valleys of the major river systems. Harris (1937) found that *belti* from this area show influences of *S. v. boothiae* and results presented below support this conclusion. Found in this region is highest point in Nicaragua, Pico Mogotón at 2,103 m, which is located on the Honduran border in the Departamento de Nueva Segovia (Arguello et al. 2018). The subspecies *S. v. boothiae* appears to be associated with these highest elevations in the Departamento de Nueva Segovia.

The Caribbean Lowlands occupy the eastern half of Nicaragua and are composed of low, level plains that at some points are 100 km wide (Arguello et al. 2018). South of Lago de Nicaragua Caribbean Lowland Tropical Moist Forest extends as far west–southwest as the Cordilleras de Guanacaste and Tilarán. This hot, humid region was covered in Lowland Evergreen Rainforest (Taylor 1963). Large areas of these forests are mature stands of trees, although species such as mahogany (*Swietenia*, Meliaceae) have been selectively logged and new areas have been opened recently in anticipation of the construction of a new canal. These forests are characterized by high biodiversity of plant species. Some of the major tree species in this area include cabbage bark (*Andira inermis*), crabwood (*Carapa nicaraguensis*), tamarindo montero (*Dialium guianense*), tonka bean tree (*Dipteryx panamensis*), Guácimo Colorado (*Luehea seemannii*), and roble coral (*Terminalia amazonia*) (Taylor 1963). Occurring throughout these lowland areas are squirrels representing *S. v. belti*. This subspecies also penetrates the Central Highlands, probably following the large eastward flowing rivers.

ANALYSES

Morphometric variation.—To gain a broader understanding of the relationship among the populations of *Sciurus variegatoides* in Nicaragua, nine cranial measurements from specimens available for study were recorded. Three analyses on these measurements—derived standard univariate statistics, principal components analysis, and a discriminate function analysis were performed. Squirrels were grouped into

taxonomic groups taking care to not include intergrades between them and a group from Isla de Ometepe where the squirrels have not been described previously. This created six groups for final analyses.

Table 1 presents univariate statistics for the six groups. The squirrels from Isla de Ometepe averaged smaller than the other five groups in seven of the

Table 1. Standard statistics for six subspecies of *Sciurus variegatoides* from Nicaragua. The samples are as follows: new subspecies, Isla de Ometepe; *S. v. adolphei*, departments of Chinandega and León; *S. v. belti*, North and South Caribbean Coast Autonomous Region; *S. v. boothiae*, Departamento de Nueva Segovia; *S. v. dorsalis*, departments of Carazo, Granada, Managua, Masaya, and Rivas; *S. v. underwoodi*, departments of Estelí, Jinotega, Madriz, and Matagalpa.

Statistics	GLS	CBL	ZB	IOB	POB	MB	LN	PB	LTR	
				Isla de Ometepe						
Mean ± SE (N = 42)	55.3 ± 0.15	50.2 ± 0.16	32.3 ± 0.11	18.5 ± 0.10	18.8 ± 0.08	23.1 ± 0.08	17.1 ± 0.11	18.4 ± 0.10	10.6 ± 0.04	
Range	52.6–57.1	48.4–52.2	30.0–33.7	17.2–20.1	17.8–19.8	22.3–24.7	15.3–19.1	16.7–19.7	9.8–11.2	
				<i>Sciurus variegatoides adolphei</i>						
Mean ± SE (N = 33)	61.4 ± 0.22	56.5 ± 0.23	34.9 ± 0.14	20.5 ± 0.12	18.6 ± 0.13	25.2 ± 0.10	18.8 ± 0.17	20.5 ± 0.14	11.8 ± 0.07	
Range	58.4–63.2	53.2–58.6	32.8–36.4	19.0–22.4	17.0–19.9	24.1–26.6	16.7–20.4	19.2–22.2	11.1–12.5	
				<i>Sciurus variegatoides belti</i>						
Mean ± SE (N = 39)	57.1 ± 0.19	52.6 ± 0.20	33.4 ± 0.14	19.5 ± 0.11	18.5 ± 0.15	23.5 ± 0.21	16.9 ± 0.16	19.3 ± 0.11	11.6 ± 0.05	
Range	54.9–59.6	49.7–54.5	31.8–34.9	18.2–21.6	17.4–19.3	22.8–25.1	14.8–18.8	17.4–20.8	11.0–12.2	
				<i>Sciurus variegatoides boothiae</i>						
Mean ± SE (N = 19)	57.7 ± 0.36	52.9 ± 0.32	33.5 ± 0.23	19.7 ± 0.24	18.7 ± 0.19	24.1 ± 0.15	17.4 ± 0.20	19.5 ± 0.18	11.4 ± 0.11	
Range	55.2–60.5	50.2–56.2	32.1–35.5	17.7–21.1	17.0–20.6	22.9–25.2	15.9–19.1	18.5–21.4	10.6–12.3	
				<i>Sciurus variegatoides dorsalis</i>						
Mean ± SE (N = 52)	59.9 ± 0.16	54.6 ± 0.17	34.7 ± 0.14	20.5 ± 0.11	19.3 ± 0.12	24.7 ± 0.14	18.7 ± 0.12	20.4 ± 0.07	11.7 ± 0.06	
Range	57.5–62.8	52.7–57.4	31.6–35.8	18.8–22.9	17.4–21.9	20.2–26.7	17.1–20.3	19.4–21.4	10.7–12.9	
				<i>Sciurus variegatoides underwoodi</i>						
Mean ± SE (N = 28)	58.4 ± 0.21	53.7 ± 0.21	34.0 ± 0.16	19.7 ± 0.15	18.9 ± 0.13	24.1 ± 0.13	17.5 ± 0.14	19.6 ± 0.10	11.3 ± 0.08	
Range	56.1–60.3	51.0–55.9	32.3–35.7	17.7–21.5	17.3–20.4	22.9–25.4	14.8–18.5	18.4–20.6	10.6–12.1	

measurements, with the exceptions being postorbital breadth and length of nasals. In postorbital breadth, squirrels from Isla de Ometepe average larger than the samples of *adolphei*, *belti*, and *boothiae* and matched the average of the sample of *underwoodi*. Only specimens identified as *dorsalis* at 19.3 mm average larger than the island group at 18.8 mm. The sample of *belti* had on average the shortest nasal bones followed by the island population. It is worth noting that the range of measurements for greatest length of skull and condylobasal length for the sample from Isla de Ometepe does not overlap the range of these measurements from the other two groups of squirrels from western Nicaragua—*adolphei* and *dorsalis*.

The sample of *adolphei* from northwestern Nicaragua is on average the largest squirrels from Nicaragua in seven of the nine cranial measurements, the exceptions being postorbital breadth and interorbital breadth in which both *adolphei* and *dorsalis* average 20.5 mm. The samples of *dorsalis* from southwestern Nicaragua closely tracked the variation in *adolphei*, averaging the second largest in seven measurements, with the exceptions being postorbital breadth in which they averaged the largest and interorbital breadth where *dorsalis* averaged the same as *adolphei*. Examining the other three groups—*belti*, *boothiae*, and *underwoodi*—their mean values fall in the middle between the previous groups and so broadly overlap each other that there are no discernable morphometric differences.

A number of principal component analyses were undertaken either using individual localities or small geographic areas as units beginning with 27 operational groupings. Based on these results, six groups that represent taxonomic and geographic units for the final principal components analysis were formed. The results of this analysis are shown in Figure 1 and Table 2. Table 2 presents the component loadings for all characters. Loadings in PC 1 are all negative and fall between -0.294 and -0.398 except for postorbital constriction at -0.116 . These results indicate that overall size is the dominant factor in this component and it accounts for just over 64% of the variation among these samples. The second component is dominated by a negative value of 0.903 for postorbital breadth. This component deals with shape of the cranium with all length measurements being negative and all breadth measurements being positive and accounts for just less

than 12% of the variation among these samples. Each of the remaining components account for 7.9% or less of the variation. The units in Figure 1 do overlap, but form three groups across the first principal component. On the far left are representatives of *S. v. adolphei* and *S. v. dorsalis* with the highest negative values, indicating that they are the largest individuals for the species in Nicaragua as seen in the univariate analysis. These taxa are the two confined to the drier Pacific lowlands of western Nicaragua. These two taxa show some separation in the second component with *S. v. dorsalis* toward the top of the plot indicating heavier influence by breadth measurements and *S. v. adolphei* nearer the bottom of the plot indicating more influence from length measurements. Along PC 1, *S. v. adolphei* and *S. v. dorsalis* do not overlap the variation in the population from Isla de Ometepe. This is important because the Ometepe population is separated from the mainland Departamento de Rivas populations of *S. v. dorsalis* only by about a 6-kilometer water gap. In the middle of PC 1 are representatives of three taxa—*belti*, *boothiae*, and *underwoodi*—which are the taxa that occur in the Central Highlands and Caribbean Lowlands. These three taxa broadly overlap each other and fill the gap between the representatives of the other two groups. There is no separation morphometrically of these three taxa from each other. These three taxa also overlap with the larger taxa—*adolphei* and *dorsalis*—and larger individuals from Isla de Ometepe but the overlap is not extensive. No additional separation of the groups in PC 2 are discernable.

Discriminate function analyses were performed on the same groups used in the principal components analysis, resulting in a classification matrix presented in Table 3. The sample from Isla de Ometepe had the highest classification success with only one of the 42 squirrels being misclassified. At the opposite end of the scale was the sample of *S. v. boothiae* in which only five members of the sample of 19 squirrels were correctly identified, with misidentifications falling into all groups except *S. v. adolphei*. These results indicate that the taxon *S. v. boothiae* is not defined morphometrically. The remaining four samples have correct classification percentages falling between 64% and 80%, indicating that there is a certain level of morphometric definition to these groups. Half of the misidentified *adolphei* (4) were identified as *dorsalis* and half of the misidentified *dorsalis* (7) were identified as *adolphei* clearly indi-

Table 2. Principal component loadings for nine cranial measurements in 213 specimens of *Sciurus variegatoides* from Nicaragua.

Measurement	PC I	PC II
Greatest length of skull	-0.398	-0.118
Condylobasal length	-0.395	-0.129
Zygomatic breadth	-0.373	0.092
Interorbital breadth	-0.339	0.267
Postorbital breadth	-0.111	0.903
Mastoid breadth	-0.349	0.047
Length of nasals	-0.293	-0.187
Length of palatal bridge	-0.354	-0.135
Length of maxillary toothrow	-0.294	-0.139
Percent of variance explained	64.1%	11.9%

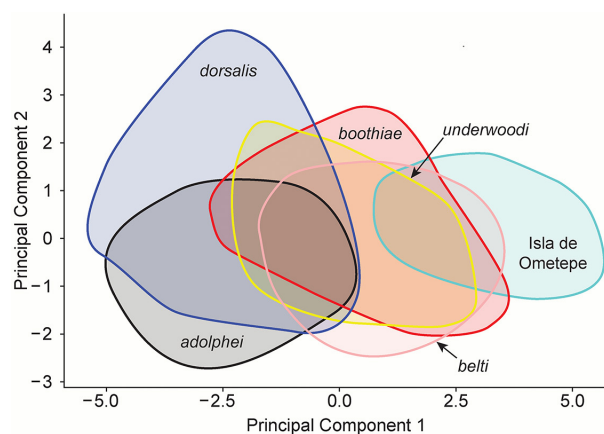


Figure 1. Specimen scores described as ellipses from principal component loadings circumscribing factor scores on CV 1 and CV 2 of nine cranial variables of the six subspecies of *Sciurus variegatoides* we recognize in Nicaragua. Principal component 1 accounts for 64.1% and principal component 2 accounts for 11.9% of the variance explained by specimen scores of 213 specimens for nine cranial measurements (GLS, CBL, ZB, IOB, POB, MB, LN, PB, and LTR) to show the relationships of these taxa. Axes are scaled relative to their eigenvalues (proportion of the variation explained). The colors used on the ellipses are as follows: black, *S. v. adolphei*; pink, *S. v. belti*; red, *S. v. boothiae*; blue, *S. v. dorsalis*; turquoise, *S. v. ometepensis*, the new subspecies described; and yellow, *S. v. underwoodi*.

cating that these two large-sized taxa of squirrels can be defined morphometrically but are actually closely related. The three medium-sized groups of squirrels occupying the Central Highlands and Caribbean Lowlands show in the discriminate analysis that they are close morphometrically, with *belti* being the most distinct of the group with nearly 80% correct identifications. Four of the misidentified *belti* classify as *boothiae*, which becomes understandable where there are several intergrades along the eastern edge of the Central Highlands (see subspecies accounts). Along the western edge of the Central Highlands, *boothiae* and *underwoodi* account for five misidentifications of each other.

Among the six groups studied morphometrically, it is the population from the Isla de Ometepe that represents a sixth taxonomic unit in Nicaragua. Its individuals are on average the smallest of the Neotropical variegated squirrels in the country, and indeed the smallest of any population of variegated squirrels from throughout the species' geographic range. This difference is particularly striking in comparison to the geographically adjacent populations of *S. v. dorsalis*.

Color variation.—Color in mammals is a combination of two forms of melanin. Eumelanin creates black, gray, and dark brown tones. Sulfur-containing

Table 3. Classification matrix resulting from a discriminate function analysis of nine cranial measurements from six subspecies of *Sciurus variegatoides* occurring in Nicaragua.

Input Group	Classification Group					
	<i>adolphei</i>	<i>belti</i>	<i>boothiae</i>	<i>dorsalis</i>	Isla de Ometepe	<i>underwoodi</i>
<i>adolphei</i>	25	0	0	7	0	1
<i>belti</i>	0	31	4	1	0	2
<i>boothiae</i>	2	4	5	2	1	5
<i>dorsalis</i>	4	1	3	39	0	2
Isla de Ometepe	0	1	2	0	41	0
<i>underwoodi</i>	2	2	5	3	0	18
Total N	33	39	19	52	42	28
N correct	25	31	5	39	41	18
Percentage	75.8%	79.5%	26.3%	75.0%	97.6%	64.3%

pheomelanin creates yellow, orange, and red tones. Hershkovitz (1968) attributed white coloration to bleaching or lack of deposition of melanin in the developing hair. Agouti colored hair is a pattern characterized by alternating blackish and reddish–tan bands. Production and deposition of one melanin can be switched off, and that of the other switched on, depending on hair type.

As Harris (1937) accurately described, the dorsal hairs are generally three banded (see exceptions below) and hairs on the ventrum generally are not banded. The terminal and middle band coloration of the dorsum hairs determines the overall coloration of the individual. Hairs along the sides are generally two banded, but this is highly variable between subspecies. The tail in all subspecies of *S. variegatoides* appears as a mix of long black and white hairs interspersed; however, all hairs are black basally and some have white tips.

Both males and females of most subspecies of *S. variegatoides* have conspicuous, distinctive, and similar tan, orange, or white ear patches. These are generally referred to as “postauricular patches,” and as Harris (1937) notes, these are generally in sharp contrast to the dorsal coloration and interestingly often match the venter coloration. On all specimens of variegated squirrels examined from throughout the species’ range,

these distinctive hairs are on the posterior/medial surface of the pinna itself and generally proceed posteriorly appearing to be a full 10 mm or more post fleshy pinna, albeit in some, it is the length of the hairs on the ear that give the impression of a larger patch. Thus, they might best be termed “auricular patches.” These hairs are generally silkier in texture than the more course surrounding guard hairs and are generally shorter in length. There is considerable variation in the size and color of the patch but in most taxa these are in sharp contrast to the body coloration. Thus, the auricular patch is a variable character both geographically as well as within populations, and, as a diagnostic character to identify geographic forms, is best used in combination with other characters. These distinctive auricular patches almost certainly have a social function (Ancillotto and Mori 2017).

The color and color pattern of the subspecific populations are discussed in the following individual systematic accounts. This information will emphasize the unique character of these colors and color patterns. The above analyses match closely those of Harris (1937) who was truly a keen observer and provided clear, succinct descriptions. The unique and highly variable population of squirrels on Isla de Ometepe is herein considered to be an undescribed subspecies and is described below.

SYSTEMATIC ACCOUNTS

Sciurus variegatoides ometepensis,
new subspecies

Figs. 2–6

Holotype.—KU 115306, adult male skin and skull, obtained on 25 March 1968 and prepared by Jerry R. Choate (field number CJR 941). Skin and skull in excellent condition (Figs. 2–4). All teeth fully erupted and moderately worn, cranium with advanced fusion of basicranial synchondroses (Fig. 4). Skin with fleshy penis and baculum attached and extended (Fig. 3).

Measurements of the holotype.—KU 115306: total length, 500; length of tail, 223; length of hind foot, 62; length of ear, 30; greatest length of skull, 56.0; condylobasal length, 51.1; zygomatic breadth, 32.5; interorbital breadth, 19.3; postorbital breadth, 19.8; mastoid breadth, 23.4; length of nasals, 16.6; length of palatal bridge, 19.0; and length of maxillary toothrow, 10.3.

Type locality.—Nicaragua: Departamento de Rivas; Isla de Ometepe, 2 km N Mérida.

Geographic range.—This new subspecies is confined to Isla de Ometepe in Lago de Nicaragua, encompassing Volcán Concepción (1,610 m) to the northwest and Volcán Maderas (1,394 m) to the southeast and connected by a low, narrow isthmus (Istmo de Istián) into a single island (Fig. 5). The island has an area of some 276 square kilometers.

Paratypes (6).—Nicaragua: Departamento de Rivas; Isla de Ometepe, 2 km N Mérida (KU 115312, 115319); Mérida (KU 115337); Santa Ana (KU 115301); 3 km NE Moyogalpa (KU 110399); and 6 km E Moyogalpa (KU 110396).

Etymology.—The specific epithet is an adjective in the genitive case and formed by adding “ensis” to the stem of the island’s name and is applied in reference to the subspecies distribution on Isla de Ometepe in Lago de Nicaragua. The island’s name is derived from the Nahuatl words *ome* (two) and *tepetl* (mountain), meaning “two mountains.” This gives the subspecies the common name of the Neotropical variegated squirrel from the place of two mountains.

Nomenclatural statement.—A life science identifier (LSID) number was obtained for the new subspecies (*Sciurus variegatoides ometepensis*): urn:lsid:zoobank.org:pub:F4DA74D8-5D54-46D8-95D0-FC3C73D60E34.

Diagnosis.—A large tree squirrel (order Rodentia, suborder Sciuromorpha, family Sciuridae, subfamily Sciurinae, tribe Sciurini, genus *Sciurus*, subgenus *Sciurus*) mass 400–500 g in mature adults; total length 500+ mm, variably colored with long tail (47–51% of total length). *Sciurus variegatoides* is the largest tree squirrel occurring in Central America. Cranial size smallest among populations of *S. variegatoides* in Nicaragua and throughout the geographic range of the species, with a proportionally broad postorbital region (Table 1). Incisors, 1/1; premolars, 2/1, anterior one minute; molars, 3/3. Jugal twisted posteriorly revealing medial surface when viewed from above. Mammary formula: 1 pectoral + 2 post-axillary + 1 inguinal. Dorsum variously colored ranging from brown–agouti to a lighter brown–tan, and in some individuals nearly blond appearing (Fig. 3). All dorsal hairs are black at base and either black or tan terminally, including on the blond-colored animals. Ventral fur bright orange–chestnut in all specimens examined except for very dark animals some of which have a black venter. Large, pronounced, and generally bright white auricular patches covering the basal 2/3s of pinnae extend as far posteriorly as 15+ mm. The tail is a mix of white tipped and black or pale brown hairs throughout giving an appearance typical of other Nicaraguan subspecies or considerably paler.

Description.—A small member of the *Sciurus variegatoides* complex confined to Isla de Ometepe in Lago de Nicaragua, with variable pelage color and color patterns, but centering around a pattern of a mixture of dark and tan producing a dark agouti-type or pale agouti-type appearance. Individuals range in color from blond to nearly black (see Fig. 3). Dorsally, all hairs have two or three bands, a black basal band and either tan, brown, or black (rarely) terminal band. Hairs of the ventrum are unicolor bright chestnut–orange. Hind feet are chestnut, orange, or dark agouti.

General anatomy of skull and dentition in *S. v. ometepensis* (Fig. 4) conforms in all major features with that in other species in the subgenus (e.g., see Harris 1937). Measurements of skull for nine cranial dimensions of 42 specimens of *S. v. ometepensis* are provided Table 1.

The baculum has a large, expanded base, circular in cross section; the shaft tapers to a narrow neck and terminates in a distal expanded, circular scoop-shaped disc at a 45° angle to the shaft (Fig. 6). The anterior and ventral margins of the disc are rounded with the edges slightly curled. The disc is concave on the right side and convex on the left. A bluntly pointed somewhat posteriorly curved dorsal spur is present dorsally. Measurements of the baculum of a paratype (KU 115312) are: length, 12.8 mm; height of base, 3.4 mm; width of base, 2.7 mm; and length of expanded tip, 2.2 mm. Total length and width of base of *S. v. ometepensis* were larger than the ranges for five individuals from other populations (length, 11.5–12.4, mean = 12.1 mm; height of base, 2.7–3.3, mean = 3.0 mm), whereas the length of expanded tip is smaller than the range (2.4–2.7, mean = 2.6 mm) provided by Burt (1960). On the other hand, width of base is within the range Burt provided (2.1–2.9, mean = 12 mm).

Comparisons.—Compared to all Nicaraguan Neotropical variegated squirrels most individuals of *ometepensis* are small, usually the smallest. In size, there is some overlap with the subspecies east and northeast of Lago de Nicaragua—*belti*, *boothiae*, and *underwoodi*. The only specific comparison that is really needed is to the geographically adjacent population of *S. v. dorsalis* occurring on the mainland of Departamento de Rivas about 6 km to the west of the island (*S. v. adolphei* farther to the northwest is even larger than *dorsalis* and *S. v. beltii* to the east is also larger than *ometepensis*). The range of the measurements for greatest length of skull and condylobasal length for *ometepensis* do not overlap the ranges for the larger *dorsalis* or *adolphei*. The mass of mature *S. v. ometepensis* is in the range of 450–500 g for mature adults, whereas it is in the range of 500–600+ g for mature *S. v. dorsalis*.

In gross morphology, the baculum of *S. variegatoides ometepensis* differs from other northern members of *S. variegatoides* complex as provided by Burt (1960) in that the disc is at a 45° angle rather than a

90° angle, less curling of the margin of the disc, more sharply pointed spur, and lack of a tuberosity and notch posterior to the spur present in other *S. variegatoides* among other details. The baculum differs from that of the more southern taxon, *S. v. thomasi* (KU 26958), in the disc margin being less curled, and in having a more sharply pointed spur. It has a narrower attachment of the disc and is less rugose posterior to the disc. The disc on both is at a 45° angle to the shaft.

Sciurus v. ometepensis differs from *S. v. dorsalis* in that it lacks a broad dark dorsal stripe, which is present in all specimens of *dorsalis*, extending from the nape of the neck to the base of the tail. *Sciurus v. dorsalis* is paler in color (with exception of the dark dorsal stripe), often white laterally and ventrally.

Remarks.—*Sciurus variegatoides ometepensis* is the most variable in color and color patterns of the subspecies in the species complex. In addition to the overall description of color presented above, a single specimen (KU 115308, see Fig. 3) from 2 km N Mérida is black in overall appearance. The hairs on the dorsum are of two types—some primarily black throughout their length, and others are two banded with a long black basal band (8–10 mm) and a short tip of agouti to orange. These two color patterns of hair are not evenly distributed over the dorsum. Black hairs predominate on the head and shoulders and two-banded hairs predominate over the lower back and hips. The overall appearance is black, but on closer inspection, the brownish orange is clearly visible. The two-banded hairs continue along the dorsal tail, and the overall tail appearance is black. The ventrum has unicolored hairs as is typical of variegated squirrels and is black throughout. The auricular patches are confined to the back of the pinnae and the two-banded hairs are concentrated along the edges of the pinnae. Hind feet are black. The overall appearance of the tail is dark with a 40 mm tip of dirty white or tan color (see Fig. 3). The 50 mm prior to the blonde tip the agouti brown band becomes longer and imparts a brownish color to the tail. This individual or any of the other black appearing individuals described below are not considered as fully melanistic because all individuals evaluated have banded dorsal hairs with black predominating but with a tan or agouti band either centrally or terminally. Additional images of *S. v. ometepensis* are provided by Medina-Fitoria et al. (2018), who contributed significantly to knowledge

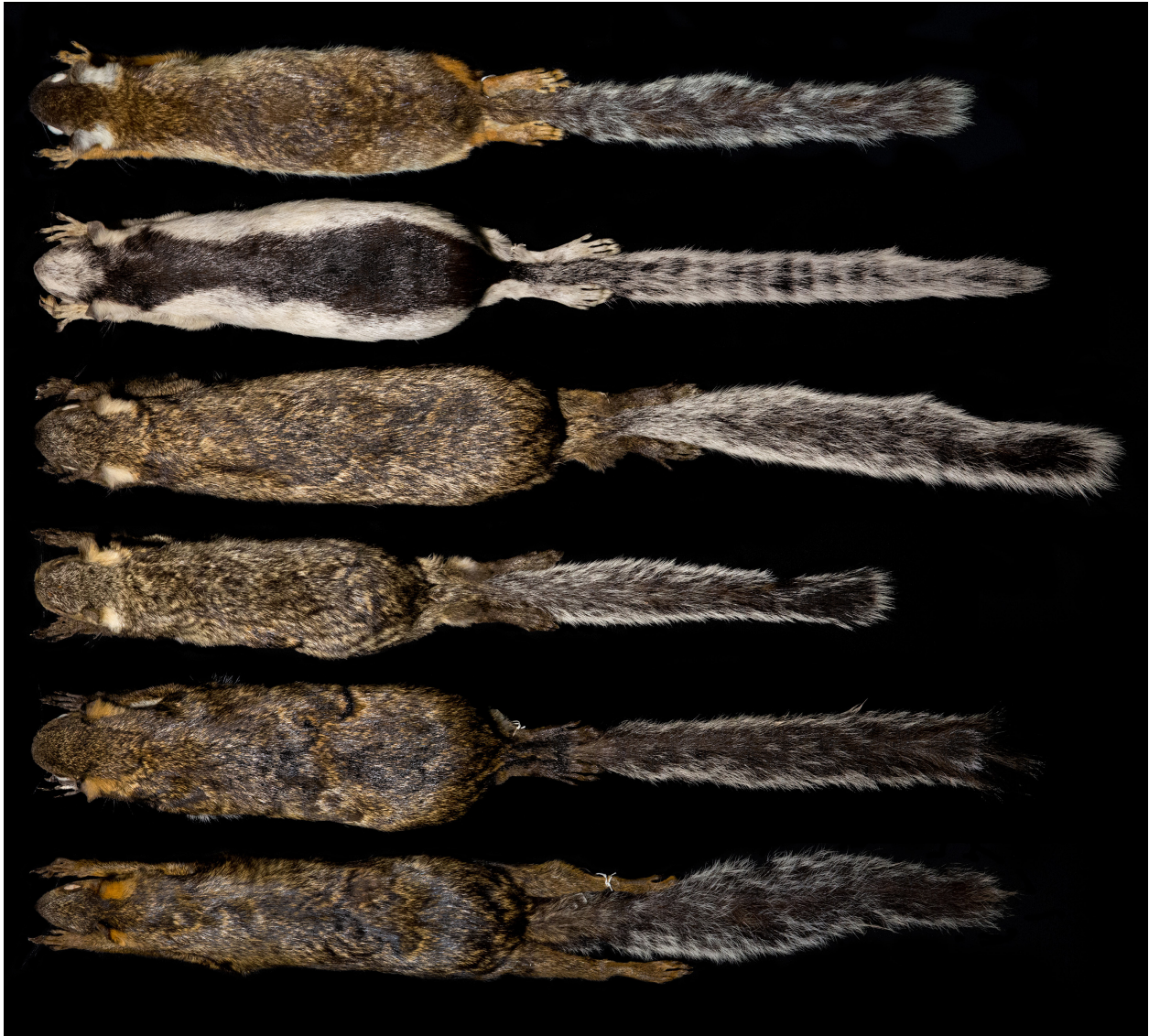


Figure 2. Variation in color and color patterns in the dorsum (left; this page) and ventrum (right; opposite page) of six subspecies of *Sciurus variegatoides* from Nicaragua. From top to bottom: *S. v. ometepensis*, KU 115306 (holotype), Departamento de Rivas, 2 km N Mérida, Isla de Ometepe; *S. v. dorsalis*, KU 110386, Departamento de Carazo, 3 km N, 4 km W Diriamba; *S. v. adolphei*, KU 106349, Departamento de Chinandega, Hacienda Bellavista, Volcán Casita; *S. v. underwoodi*, KU 97912, Departamento de Madriz, Darailí, 5 km N, 14 km E Condega; *S. v. boothiae*, KU 110361, Departamento de Nueva Segovia, 1.5 km N, 1 km E Jalapa; and *S. v. belti*, KU 99464, Departamento de Jinotega, Hacienda La Trampa, 5.5 km N, 16 km E Jinotega. Scale: total length of holotype = 500 mm.

of the color variation found in this subspecies. They report that these squirrels occur from the lowlands up to 1,000 m.

This new subspecies is confined to Isla de Ometepe in Lago de Nicaragua separated from the mainland

of the Departamento de Rivas to the west by just over 6 km. The island consists of two volcanic cones, the associated low, flat volcanic aprons, and a narrow isthmus connecting the two islands into one. The aprons around the Ometepe volcanoes have been heavily impacted by human occupation and agricultural activities,



Figure 2. (cont.)

which has expanded extensively since the University of Kansas field research in the late 1960s. The large collection of squirrels from the southern island from 2 km N Mérida and the one individual from Mérida were taken from large trees that remained in the area fringing the dirt roads and footpaths that paralleled the coast. Among these trees were such species as West Indian cedar (*Cedrela odorata*), mango (*Mangifera indica*), sandbox tree (*Hura crepitans*), gumbo limbo (*Bursera simaraba*), and chelate (*Ficus trigonata*), along with an assortment of acacias and other shorter thorn-covered trees and bushes. The squirrels from 2 km N, 3 km E

Mérida were obtained from trees on the slopes of Volcán Maderas. Some areas of the slopes were heavily vegetated, whereas other areas were more open as the result of past landslides. Among the important trees in this area were kapok (*Ceiba petrandia*), molenillo (*Lueha candida*), balsa (*Ochroma pyramidale*), stinking toe tree (*Cassia grandis*), and spiny cedar (*Pachira quinata*). On the northern end of the island the situation was similar with squirrels from 3 km NE Moyogalpa coming from forest fragments on the apron of the volcano and those from 6 km E Moyogalpa coming from the western slope of Volcán Concepción and those from

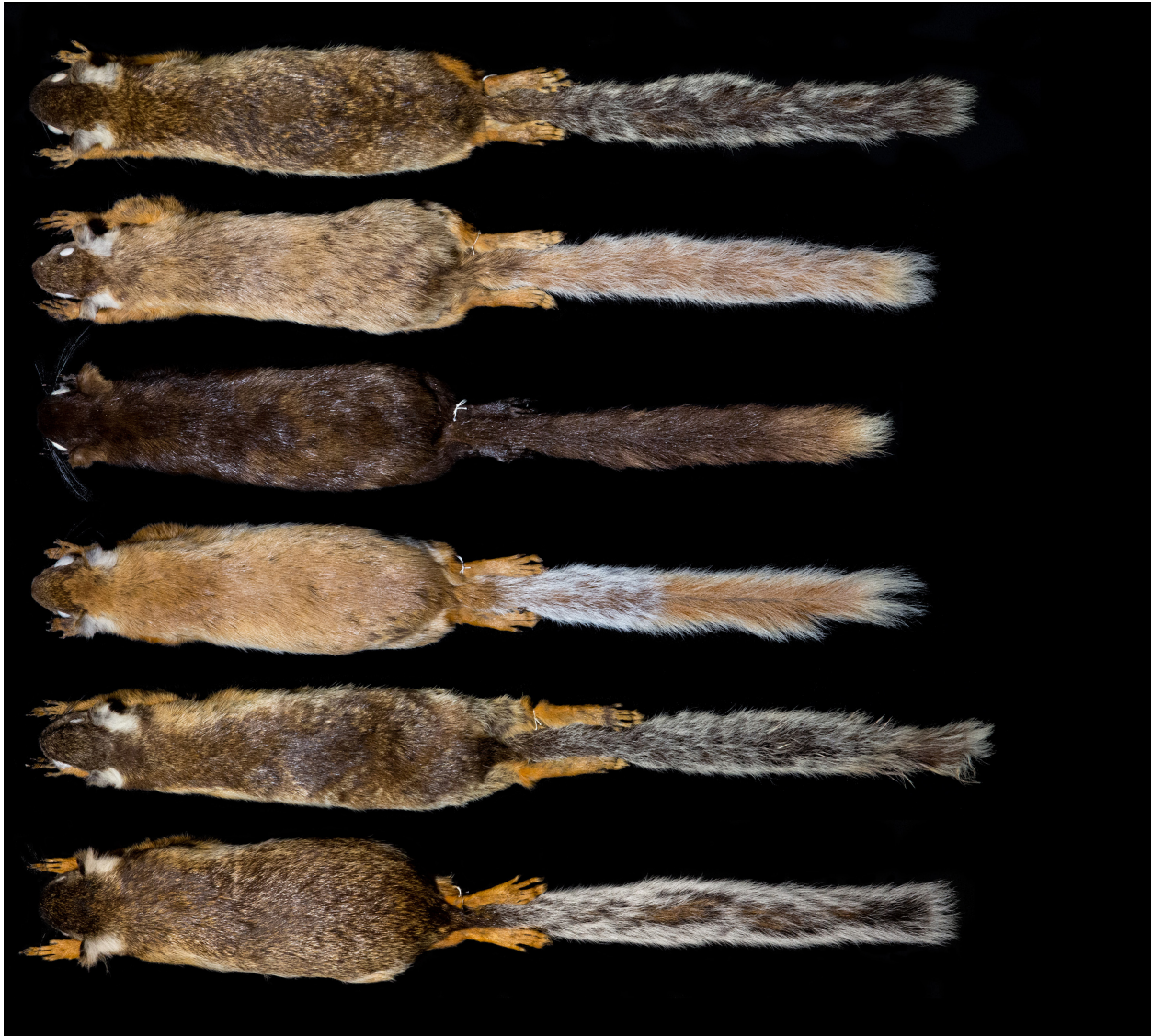


Figure 3. Variation in color and color patterns in the dorsum (left; this page) and ventrum (right; opposite page) of six individuals of *Sciurus variegatoides ometepensis* from Isla de Ometepe, Departamento de Rivas, Nicaragua. From top to bottom: South Island—KU 115306 (holotype), 2 km N Mérida; KU 115325, 2 km N Mérida; KU 115308, 2 km N Mérida; KU 115319 (paratype), 2 km N Mérida; Isthmus—KU 115301 (paratype), Santa Ana; and North Island—KU 110399 (paratype), 3 km NE Moyogalpa. Scale: total length of holotype = 500 mm.

1.5 km W Altagracia were from the northern slope. There was evidence of recent volcanic activity on this cone. The specimens from Santa Ana came from the area of the isthmus where soil conditions were moister and where stands of trees were in the wetter areas and agricultural fields occupied the intervening areas.

A specimen from northeast of Mérida (KU 115334) taken on 7 April 1968 is a juvenile with only M1 erupted and M2 starting to erupt. A dental variation was noted in KU 110396, which is missing the left upper P3. Based on the University of Kansas series of squirrels collected in Nicaragua, Emerson (1971)

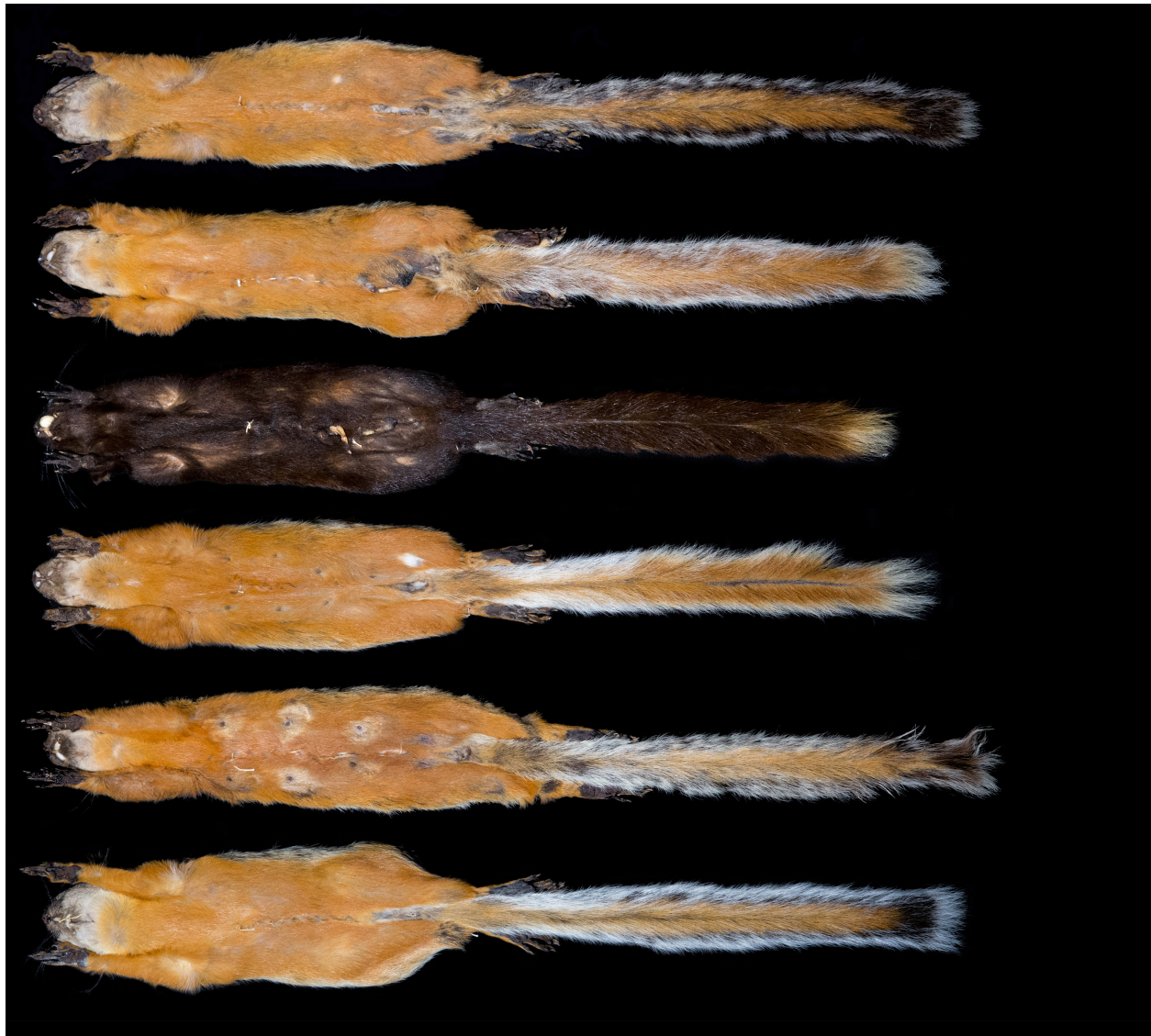


Figure 3. (cont.)

reported the squirrel sucking louse *Enderleinellus hondurensis* Werneck (Phthiraptera: Hoplopleuridae) from three subspecies in the *S. variegatoides* complex—*S. v. belti*, *S. v. underwoodi*, and a specimen of *S. v. ometepensis* from Mérida on Isla de Ometepe (KU 115326). The holotype of *E. hondurensis* is from a specimen of *S. v. underwoodi* from Honduras.

In addition to *Sciurus variegatoides*, species of mammals collected or observed on Isla de Ometepe include *Philander* sp., *Balantiopteryx plicata*, *Rhynchonycteris naso*, *Saccopteryx bilineata*, *Noctilio*

albiventris, *Noctilio leporinus*, *Artibeus intermedius*, *Artibeus jamaicensis*, *Dermanura tolteca*, *Carollia perspicillata*, *Carollia subrufa*, *Chiroderma villosum*, *Desmodus rotundus*, *Glossophaga leachii*, *Glossophaga soricina*, *Phyllostomus discolor*, *Platyrrhinus helleri*, *Sturnira hondurensis*, *Sturnira parvidens*, *Uroderma convexum*, *Alouatta palliata*, *Cebus capucinus*, *Sylvilagus floridanus*, *Oligoryzomys fulvescens*, *Oryzomys couesi*, *Peromyscus nicaraguae*, *Peromyscus stirtoni*, *Sigmodon hirsutus*, *Liomys salvini*, *Odocoileus virginianus*, and the introduced black rat, *Rattus rattus*.



Figure 4. Dorsal, ventral, and lateral view of the cranium and lateral view of the right dentary of an adult male *Sciurus variegatoides ometepensis* from 2 km N Mérida, Isla de Ometepe, Departamento de Rivas, Nicaragua (holotype, KU 115306); greatest length of skull = 56.0 mm.

Specimens examined (50).—Departamento de Rivas: Isla de Ometepe [*North Island*], Volcán Concepción, 1.5 km W Altagracia [= Alta Gracia] (2, 1 ♂, 1 ♀, KU 115294–295); Volcán Concepción, 3 km NE Moyogalpa (4, 3 ♂♂, 1 ♀, KU 110397–400); Volcán Concepción, 6 km E Moyogalpa (2 ♂♂, KU 97914, 110396). Isla de Ometepe [*Istmo de Istián*], Santa Ana (7, 5 ♂♂, 2 ♀♀, KU 115296–302). Isla de Ometepe [*South Island*], 2 km N Mérida (31, 26 ♂♂, 5 ♀♀, KU 115303–333); 2 km N, 3 km E Mérida (3, 2 ♂♂, 1 ♀, KU 115334–336); Mérida (1 ♂, KU 115337).

Additional records.—Departamento de Rivas: Reserva Natural Volcán Maderas (Medina-Fitoria et al. 2018).

Sciurus variegatoides adolphei (Lesson, 1842)

1842. *Macroxus Adolphei* Lesson, Nouveau Tableau du Règne Animal: Mammifères, Arthus Bertrand, Paris p. 112.

1920. *Sciurus variegatoides adolphei*, Goldman, Smithsonian Miscellaneous Collection 69(5):136.

Lectotype.—MNHN-ZM-MO-2000-611, adult female mounted skin with skull inside, collected by Adolphe Lesson, ship's surgeon of the French ship "La Pylade," prior to 1842.

Type locality.—El Realejo, Departamento de Chinandega, Nicaragua.

Remarks.—These are the largest of the variegated squirrels occurring in Nicaragua. They average the largest of all samples in seven of the nine cranial measurements analyzed (Table 1). This is a distinctive subspecies with a prominent white auricular patch that extends from near the tip of the ear to 10–15 mm posteriorly. Dorsally the overall appearance is a mixture of black or dark agouti and dark silver giving a unique overall dark appearance and that coloration extends down laterally (Fig. 2). The ventrum is strongly countershaded with white in most individuals although some have a mix of white and a light tan–orange color. The dorsal coloration of the hind feet is dark, most approach black although a few specimen are dark brown–agouti. These squirrels occur in extreme northwestern Nicaragua in the departments of Chinandega and León, and

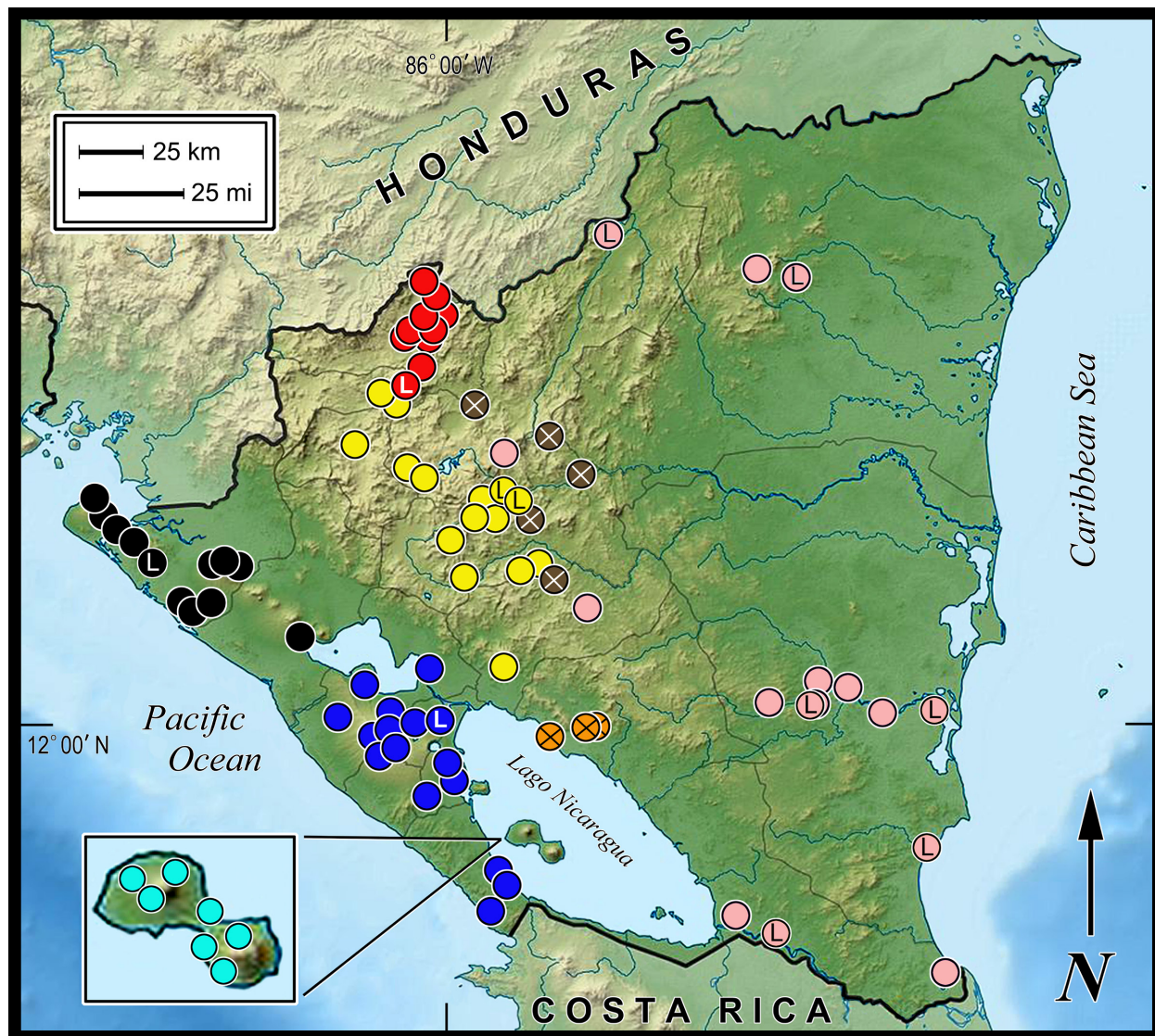


Figure 5. Map of Nicaragua showing the collecting sites and literature records for the six subspecies of *Sciurus variegatoides* in the country. The colors and symbols used on the map are as follows: black closed circles, *S. v. adolphei*; pink closed circles, *S. v. belti*; red closed circles, *S. v. boothiae*; blue closed circles, *S. v. dorsalis*; turquoise closed circles, *S. v. ometepensis*; yellow closed circles, *S. v. underwoodi*; brown symbols with "X", intergrades between *belti* and *boothiae*; orange symbols with "X", intergrades between *belti* and *underwoodi*; symbols marked with "L" indicate records from the literature. See text for details on localities, museum catalog numbers, and our identifications. (Base map courtesy of <http://maplibrary.org>, VMAP0).

are common on the volcanoes of the Cordillera de los Marrabios as far south as the northern end of Lago de Managua and the west in the dry Pacific Lowlands (Fig. 5).

Lesson (1842:112) described *Macroxus adolphei* based on "the male and female were killed by my

brother Adolphe Lesson, in the forests around Realejo in Nicaragua province." Because neither specimen was selected as a holotype, the name was based on syntypes. Cecile Callou, curator in charge of the mammalian types, Muséum national d'histoire naturelle, Paris, France, reports that only the female specimen is present in the collections and they have no information on



Figure 6. Baculum of *Sciurus variegatoides ometepensis* (KU 115312; paratype) from 2 km N Mérida, Isla de Ometepe, Departamento de Rivas, Nicaragua. Total length = 12.8 mm.

the male specimen. The female specimen, therefore, is designated as the lectotype for this taxon and the male will be the paralectotype if found.

Sciurus variegatoides adolphei was obtained at most collecting localities on the Cosigüina Peninsula and was common locally in the taller forests especially along streams on the peninsula. Field collectors noted that higher concentrations occurred in those areas that had tall evergreen trees growing along hot springs; however, in one case, an adult was shot while foraging in a mimosa tree (*Albizia*). The sample from Hacienda Las Colinas is the first record from the Departamento de León and the southernmost record for this subspecies. These squirrels match those from Departamento de Chinandega in overall large size and dorsal and ventral color patterns. There is no discernable evidence of integration of *S. v. adolphei* with *S. v. dorsalis* the subspecies occurring to the south (see account of that subspecies) or with *S. v. underwoodi*, the subspecies occurring directly to the east (see account of that subspecies).

As discussed under Historical Collecting Sites, the San Cristóbal volcanic complex in the Departamento de Chinandega, which is composed of five volcanoes, also has been known historically as Volcán Chinandega and Volcán El Viejo (Rossi et al. 2010). Harris (1937) reported two specimens as *S. v. adolphei* (AMNH 28439, 28443) from Volcán Chinandega and one specimen as *S. v. underwoodi* (AMNH 41231) from Volcán El Viejo. It seems an unlikely situation to have two subspecies occupying this volcanic complex. There is a series of eight squirrels from Hacienda Bellavista on Volcán Casita, which is one of five volcanoes that

make up the San Cristóbal complex. These squirrels are somewhat variable in color, ranging from a dark, nearly black dorsum to dark browns and tans but in general matching those individuals from the coast and the Cosigüina Peninsula in both size and over all color pattern; therefore, all squirrels from San Cristóbal are assigned to *S. v. adolphei*, including AMNH 41231.

On 19 August 1967, two males were collected 7 km S, 1 km E of Cosigüina. The specimens weighed 472.2 and 610 g and had testes lengths of 8 and 27 mm. The smaller individual was judged to be a subadult based on its paler pelage and unfused cranial sutures. Between 1 and 6 March 1968, 12 additional specimens were obtained from the peninsula. Testes measurements and corresponding weights of four males are 20, 30, 31, and 34 mm and 576.4, 615.8, 642.2, and 673.3 g. Six adult females revealed no obvious reproductive activity, although they had enlarged teats, but were not lactating when taken on 2 and 3 March 1968, two on 6 March 1968, and on 14 and 16 July 1966. Lactating adults were taken on 4 and 6 March 1968; they weighed 740.5 and 761.7 g, respectively. Four other females had weights of 490.0, 656.0, 668.8, and 699.9 g. At Hacienda Las Colinas near Lago de Managua, three males and three females collected on 5 and 6 December 1962 had the following weights, respectively: 681, 681, 790; 795, 909, 909 g. Along the northwest coast near El Realejo, a male taken on 29 October 1967 weighed 526 g. A female from San Antonio, also along the coast, evinced no obvious reproductive activity on 9 March 1968.

Squirrels from the Cosigüina Peninsula showed multiple molt lines, which differed in distinctness and regularity, contributing to the variable appearance among individuals. Although molt does not always begin in the same area, it usually begins anteriorly and proceeds posteriorly. Single molt lines usually extend more posteriorly on the dorsum than on the lateral surfaces. No molt lines were observed on the venter (Genoways and Timm 2005). Molt from subadult pelage to adult pelage is evident in a specimen taken on 6 March.

Medina-Fitoria et al. (2018) reported that this subspecies is found from sea level to 800 m. Medina-Fitoria et al. (2018) assigned a photograph of a squirrel from Reserva Silvestre Privada Hato Nuevo,

Departamento de Chinandega to *S. v. underwoodi*. This record is from well within the geographic range of *S. v. adolphei*, to which it is now reassigned, and illustrates some of the problems of identifying mammals from a photograph. Only about half of the color and color pattern of the animal in this photograph is observable and while seemingly somewhat atypical for *S. v. adolphei*, without the specimen in hand, it is best assigned as such based on geographic location.

In a preliminary survey for leptospirosis in Nicaragua, Clark et al. (1966) obtained negative results after examining 18 specimens of *S. v. adolphei* from the vicinity of Puerto Momotombo.

Specimens examined (48).—Departamento de Chinandega: Corinto (1 ♂, AMNH 41229); 6 1/2 km N, 1 km E Cosigüina, 10 m (7, 4 ♂♂, 3 ♀♀, KU 115239–245); 4 1/2 km N Cosigüina, 15 m (2, 1 ♂, 1 ♀, KU 115246–247); 7 km S, 1 km E Cosigüina, 10 m (2 ♂♂, KU 110304–305); El Paraíso, 1 km N Cosigüina, 20 m (3 ♀♀, KU 115248–250); Hacienda Bellavista, Volcán Casita, 720 m (8, 4 ♂♂, 4 ♀♀, KU 106344–351); Hacienda San Isidro, El Realejo (3, 2 ♂♂, 1 ♀, KU 104590, NMNH 337570–571); San Antonio, 35 m (1 ♀, KU 115251); Volcán de Chinandega (2, 1 ♂, 1 ♀ AMNH 28439, 28443); Volcán Viejo (1 ♂, AMNH 41231). Departamento de León: Hacienda Las Colinas; 4 km WNW Puerto Momotombo (18, 11 ♂♂, 7 ♀♀, KU 104372–379, NMNH 334597–598, 337755–762).

Additional record.—Departamento de Chinandega: Reserva Silvestre Privada Hato Nuevo (Medina-Fitoria et al. 2018).

Sciurus variegatoides belti Nelson, 1899

1899. *Sciurus boothiae belti* Nelson, Proceedings of the Washington Academy of Science 1:78.

1937. *Sciurus variegatoides belti*, Harris, Miscellaneous Publications of the Museum of Zoology, University of Michigan 38:13.

Holotype.—NMNH 36477/48847, female adult, skin and skull in good condition, collected by Charles W. Richmond, on 22 November 1892.

Type locality.—Escondido River, 50 miles from Bluefields [= I. P. Plantation, 3 km S, 13 km E Rama], South Caribbean Coast Autonomous Region, Nicaragua.

Remarks.—This subspecies is among the medium-sized variegated squirrels in Nicaragua, but on average, the nasals bones are the shortest in these squirrels (Table 1). These are the darkest of the Nicaraguan variegated squirrels. Dorsally, the three-banded hairs have a 6–7 mm black basal band, a 5–6 mm central silver or tan band, and a short, black terminal tip resulting in the appearance of a dark animal with silver to tan interspersed (Fig. 2). The dark dorsum coloration continues laterally over the sides to the ventrum. The ventrum on most individuals varies from dark orange–chestnut to deep chestnut; a few individuals have small patches of white. The auricular patch is a pale tan to chestnut and extends posteriorly 5–6 mm. The feet are dark agouti to black. A dark, approaching black, phase is present albeit rare in these squirrels.

This is the widest-ranging subspecies of the *S. variegatoides* complex in Nicaragua (Fig. 5), occurring throughout the Caribbean Lowlands east of the lakes between the Río Coco in the north and the Río San Juan in the south and into the eastern slopes and river valleys of the Central Highlands. Medina-Fitoria et al. (2018) reported that *S. v. belti* is found in the Caribbean Lowlands up to 1,500 m.

Specimens collected by Richardson in Nicaragua remain a challenge not only because of their locality data, but also because many come from zones of intergradation between combinations of the taxa *belti*, *boothiae*, and *underwoodi*. Nine specimens taken along the Río Coco in extreme northern Departamento de Jinotega at an altitude of 1,000 feet were assigned by Allen (1910:101) to *boothiae* but he remarked that they graded toward *belti*. However, Harris (1937) placed them with *belti* because the color of the back, ear patches, and the rufous tone the underparts were within the range of variation of that subspecies, and this arrangement is followed here. Both Allen (1908, 1910) and Harris (1937) assigned another group of thirteen specimens taken by Richardson in 1907–1909 at Matagalpa, Uluce, Peña Blanca, Savala, and Chontales to *belti*. These specimens are similar to specimens from Río Coco, but Harris (1937) believed they differ

from these in having more rusty rufous and less white on the underparts. However, as with other specimens from this region, they grade toward *boothiae*, and in agreement with Harris (1937) his assignment to *S. v. belti* is maintained herein. The assignment herein of the three specimens collected in the 1960s from Hacienda La Trampa, in this same region, to *belti* are in agreement with Harris that squirrels of this subspecies from the Caribbean Lowlands are making their way into the eastern slopes of the Central Highlands.

Nine specimens collected by Richardson at “Matagalpa,” which was his home, were examined by Harris (1937) who assigned three of the specimens to *belti* and six to *underwoodi*, which seems an unlikely situation. As Howell (1993, 2010:3) stated: “Many of Richardson’s Nicaraguan collecting localities were small villages not now found on most maps or were given as undelimited geographic features.” Richardson never gave directions or distances from a locality, seldom listed the departments, and his elevations were estimates. Because Matagalpa was his home, he almost certainly collected in several directions from the town and probably listed the town for any sites within a day’s travel from the town (see Historical Collecting Sites above). Harris (1937) surmised that specimens assignable to *belti* came from east of town and those assignable to *underwoodi* came from north or west of Matagalpa. The suggestion by Harris (1937) that the specimens assigned to *belti* were from east of Matagalpa seems less likely given the current sample of *underwoodi* from 3 mi SE San Ramon. The nearest specimen record considered *belti* to the east is from Uluce about 45 km east of Matagalpa and 34 km beyond San Ramon. The other potential direction for the source of these specimens would be to the northeast along the road to El Tuma. There are records of *S. v. belti* in this direction at Peña Blanca and La Trampa, which are at least 50 km to the northeast. These distances from Matagalpa all seem to be too far even for Richardson to have maintained the use of the “Matagalpa” locality designation, but the designation “Matagalpa” may have only been to the department name. Also one cannot discount the possibility that these specimens of *belti* designated as from “Matagalpa” were mislabeled either by Richardson or in the handling and shipping of the specimens to the American Museum of Natural History. Given this degree of uncertainty about the origins of these specimens, they are maintained herein in the list

of specimens here, but not placed on the distribution map.

The single specimen from San Francisco, Departamento de Boaco, is the southern-most example of *S. v. underwoodi* (see account of that subspecies for further discussion). However, three specimens from Hato Grande approximately 42 km south of San Francisco appear to be intergrades between *belti* and *underwoodi*. Their dorsal coloration more closely matches that of *belti* as does the auricular patch; however, the ventrum is not typical of either one, being a dull chestnut and lacking white coloration. The series available from two localities in the vicinity of Villa Sandino, some 75 km southeast of San Francisco, also appear to be intergrades. Based on total evidence for squirrels from these three sites places them among the *S. v. belti* specimens examined. About 45 km northeast of San Francisco, a sample of seven squirrels from Santa Rosa in northeastern Departamento de Boaco is best assigned to *S. v. belti*, which is one of the western-most samples of this subspecies.

All specimens of variegated squirrels from Nicaragua’s Caribbean Lowlands are treated herein as belonging to *S. v. belti*, although clearly additional specimens from throughout the lowlands are needed. Although *S. v. thomasi* has been reported from southeastern Nicaragua (Medina-Fitoria et al. 2018), the specimens of *S. v. thomasi* examined from Costa Rica, including the holotype and those from near the type locality, all differ from Nicaraguan *belti* in being considerably darker dorsally, possessing a bright orange ventrum, dark orange or black (or a combination of both) hind feet dorsally, and with a tan to dark orange auricular patch. The free-ranging individual photographed at Refugio Bartola along the Río San Juan (see Medina-Fitoria et al. 2018:fig. 24) clearly approaches this color pattern of *thomasi* and specimens from this area are needed to more fully access this population. Specimens reported from Departamento Río San Juan, as belonging to *S. v. thomasi* by Medina-Fitoria et al. (2018), are perhaps best considered assigned to *S. v. belti*. Harris (1937) assigned specimens from along the Río San Juan at Sebaco near the lake and from Greytown at the mouth of the river to *S. v. belti*. Because there are few specimens of squirrels (or other mammals) from the Nicaraguan–Costa Rican border region, a more complete understanding of this fauna will only

be possible when additional specimens are available. The few roads extending into Nicaragua's Caribbean Lowlands have clearly contributed to habitats being protected; however, few specimens of any species of mammals are available for study (Martínez-Fonseca et al. 2018).

A female taken at El Recreo (KU 115261) on 26 February 1968 carried three embryos with one in the right horn of the uterus and one in the left measuring 13 mm in crown–rump length and a second embryo in the left horn measuring 8 mm in crown–rump length. Four adult females were judged to be lactating on the following dates: 4 April 1968, 19 June 1967, 11 July 1967, and 4 August 1967. Females evincing no obvious reproductive activity were taken on the following dates: 16 June 1967, 2; 19 June 1967, 1; 22 June 1967, 1; 11 July 1967, 1; 13 July 1967, 2; 24 July 1967, 1; 6 August 1967, 2; and 7 August 1967, 1. Three individuals judged to be juveniles because the third upper molar had not erupted were taken on the following dates: two on 23 April 1963 and one on 28 April 1968. Testes lengths of adult male *S. v. belti* were as follows: 25–26 February 1968—7, 21, 21, 25 mm; 19–25 June 1967—6, 25, 30, 31 mm; 11 July 1967—24, 26 mm; 24 July 1966—23 mm; 4–7 August 1967—23, 24, 24, 26 mm. Adult females taken on 19 March 1963 and 23 April 1963 weighed, respectively, 454 and 577 g, whereas adult males taken on 16 and 23 April 1963 weighed 489.5 and 435 g, respectively.

A total of 394 specimens of *Sciurus variegatoides* from throughout Nicaragua were examined and only three are abnormally black—the specimen from Isla de Ometepe (KU 115308, described above), a young male from the Villa Sandino region (KU 110329), and an adult male from Greytown (NMNH 16412). The latter two localities are approximately 185 km apart. The specimen from Villa Sandino appears nearly black dorsally with a pale orange and white venter. Dorsally, most hairs have a short black basal band, a short agouti middle band, and a long black terminal band. Dorsal agouti-colored hairs with narrow terminal black bands give the overall coloration of a mostly black individual with some agouti interspersed. The adult male from Greytown has generally broad (> 50% length of hair) basal black bands, narrow deep orange middle bands, and broad black terminal bands. The venter and tail hairs are all black. The overall aspect is a black squirrel,

showing orange highlights on close inspection. An additional black variegated squirrel from Refugio Bartola, Río San Juan, including a photograph of a free ranging animal, was reported by Medina-Fitoria et al. (2018). It too has some agouti colored hairs scattered throughout the dorsum. A single adult male from extreme northern Costa Rica (KU) is black dorsally with white and agouti colored hairs ventrally and agouti colored hairs laterally. All of the black-appearing squirrels from this region have some banded hairs and it is the terminal band that is longest and black in color. The *S. variegatoides* of the Caribbean Lowland Evergreen Rainforest are among the most variably colored individuals of the Neotropical variegated squirrel complex and exceeded only by *S. v. ometepensis*.

In a study of the use of dogs by indigenous hunters from Arang Dak in the Bosawas Biosphere Reserve in extreme northeastern Departamento de Jinotega, Koster (2008) presented a list of 20 species of mammals that were harvested among which were five individuals of *S. variegatoides*. Neotropical variegated squirrels were low on the target species list for the hunters, probably because of the low biomass return from the squirrels. Palmer (1945) reported that *butsong* was the Miskito name for the Neotropical variegated squirrel and *tete* was the Sumu name. Jones (1965:354) reported that the Miskito in the Caribbean Lowlands of Nicaragua had two indigenous names for *Sciurus variegatoides*, “*butsong* or *tastas* (the two names evidently are used to distinguish between different color phases of this species).” Clark et al. (1966) examined one Neotropical variegated squirrel from the vicinity of Villa Sandino and 35 from El Recreo for leptospirosis, but had only negative results from these squirrels.

Specimens examined (119).—Departamento de Boaco: Chontales (2 ♀♀, AMNH 28588, 28591); Santa Rosa, 17 km N, 15 km E Boaco (7, 2 ♂♂, 5 ♀♀, KU 110307–312). Departamento de Chontales: Hato Grande, 13 km S, 8 km W Juigalpa (3, 3 ♂♂, KU 115291–293); 1 km N, 2.5 km W Villa Sandino [= Villa Somoza] (10, 6 ♂♂, 4 ♀♀, KU 110327–336); Villa Sandino [= Villa Somoza] (1 ♂, KU 104474). Departamento de Jinotega: Hacienda La Trampa, 5.5 km N, 16 km E Jinotega (3, 2 ♂♂, 1 ♀, KU 99464, NMNH 338824–825); Río Coco (9, 8 ♂♂, 1 ♀, AMNH 29235–238, 29243–244, 29247–248, 29250). Departamento de Matagalpa: Matagalpa (3, 1 ♂, 2 ♀♀, AMNH 28319–321); Peña

Blanca (2, 1 ♂, 1 ♀, AMNH 29810–811); Savala (1 ♂, AMNH 28414); Uluce (5, 4 ♂♂, 1 ♀, AMNH 29805–809). Departamento de Río San Juan: Greytown (1 ♂, NMNH 16412/A23227); Los Sabalos on the Río San Juan (1 ♂, AMNH 41230). North Caribbean Coast Autonomous Region [= Zelaya]: Bonanza (5, 2 ♂♂, 3 ♀♀, KU 96366–367, 99463). South Caribbean Coast Autonomous Region [= Zelaya]: El Recreo (34, 15 ♂♂, 19 ♀♀, KU 104462–463, 104371, 106352–354, 110313–325, 115253–261, NMNH 337738–741, 337746, 337748, 337754); La Esperanza, Río Siguia (19, 13 ♂♂, 6 ♀♀, KU 104464–473); Cara de Mono (2 ♂♂, KU 110326, 115252); 4.5 km NW Rama (5, 1 ♂, 4 ♀♀, TTU 12593–597); Escondido River, 50 mi from Bluefields (6, 3 ♂♂, 3 ♀♀, NMNH 36477/A48847 [holotype], A48873, 51335–338).

Additional records.—Departamento de Jinotega: Arang Dak [14°30'56"N, 85°00'00"W] (Koster 2008). Departamento de Río San Juan: Refugio Bartola (Medina-Fitoria et al. 2018). North Caribbean Coast Autonomous Region: Edén (Harris 1937). South Caribbean Coast Autonomous Region: La Cruz de Río Grande (Medina-Fitoria et al. 2018); Río Sconfra (Medina-Fitoria 2016); Casa Vieja, Río Punta Gorda, Reserva Natural Punta Gorda (Medina-Fitoria et al. 2016).

Sciurus variegatoides boothiae Gray, 1843

1842. *Sciurus richardsoni* Gray, Annals and Magazine of Natural History, series 1, 10:264. Preoccupied by *Sciurus richardsoni* Bachman, 1839, Proceedings of Zoological Society of London, for 1838, p. 100, now considered to be *Tamiasciurus hudsonius richardsoni*.

1843. *Sciurus boothiae* Gray, List of the Specimens of Mammalia in the Collection of the British Museum, Trustee of Museum, London p. 139.

1937. *Sciurus variegatoides boothiae*, Harris, Miscellaneous Publications of the Museum of Zoology, University of Michigan 38:12.

Holotype.—BM(NH) 1842.10.28.43, a juvenile of unknown sex, skin originally a taxidermy mount, but remade into a round museum specimen, with the skull remaining in the skin, received from Mr. Warwick's collection.

Type locality.—"From Honduras," restricted by Nelson (1899) to Honduras: Departamento de Cortés; San Pedro Sula.

Remarks.—These northern Nicaraguan squirrels are on average among the medium-sized variegated squirrels in the country (Table 1); however, as the classification matrix (Table 3) shows this taxon is poorly defined morphometrically. Records of this subspecies in Nicaragua are confined to the mountains of Departamento de Nueva Segovia and an adjacent part of the Departamento de Madriz (Fig. 5) in the extreme north-central part of the country. Harris's specimen from San Juan de Telpaneca, Departamento de Nueva Segovia, was not examined so Harris (1937) was followed in this designation.

This is a dark squirrel in overall in color pattern, with most specimens nearly as dark as *S. v. belti* (Fig. 2). Dorsally, the appearance is black with dark tan-agouti mix. All hairs on the dorsum are three banded having a black base (15–17 mm), an orange-tan middle band approximating 5 mm, and a black, 5–6 mm terminal band. The rusty-tan-cinnamon auricular patch contrasts with the dorsum with the paler color extending only 5–6 mm behind the basal center of the ear. The venter is white, and in many individuals, unicolored bright white. There is usually a sharp contrast between the dark dorsum and the white ventrum producing a strongly contrasting countershading. The hind feet are black with some agouti-tan hairs mixed in.

Harris (1937) described the relationship between *boothiae* and *belti* specimens collected by Richardson in the departments of Jinotega and Matagalpa. He assigned many to *belti*, including material from Río Coco, Matagalpa, Uluce, Peña Blanca, Savala, and Chontales. Although Harris assigned all of these specimens, except six from Matagalpa, to *belti*, he commented twice that these specimens "show intergradation with *boothiae*" and "all of which grade toward *boothiae*." Three specimens collected in the 1960s from Hacienda La Trampa in this region are assigned to *belti*. Therefore, in agreement with Harris, *belti* squirrels from the Caribbean Lowlands occur throughout the eastern side of the Central Highlands. These lowland squirrels perhaps migrated westward along the lowlands associated with major eastward-flowing rivers such as the Río Coco and

the Río Grande de Matagalpa and its major left tributary the Río Tuma. Along these rivers and their tributaries individuals of lowland *belti* encounter individuals of *boothiae* from the uplands thus forming a series of points of intergradation much as described by Howell (1993, 2010) in other groups from this region.

Reproductive data for a series of *S. v. boothiae* from the vicinity of Jalapa were collected between 21 and 27 July 1967. Two adult females were lactating, whereas three others evinced no obvious reproductive activity during this period. A juvenile squirrel with an unerupted upper M3 was taken on 24 July. Nine adult male from this period had a mean testes length of 23.9 (9–35 mm). Medina-Fitoria et al. (2018) reported that this subspecies is found from 500 to 2,000 m.

Specimens examined (35).—Departamento de Nueva Segovia: 7 km N, 4 km E Jalapa (1 ♂, KU 110339); 6.5 km N, 1 km E Jalapa (3, 2 ♂♂, 1 ♀, KU 110359–361); 5 km N, 2.5 km E Jalapa (4, 1 ♂, 3 ♀♀, KU 110340–343); 4.5 km N, 2 km E Jalapa (15, 9 ♂♂, 6 ♀♀, KU 110344–358); 1.5 km N, 1 km E Jalapa (3, 2 ♂♂, 1 ♀, KU 110259–261); Jalapa (4, 3 ♂♂, 1 ♀, AMNH 29241–242, 29273–274); 3.5 km S, 2 km W Jalapa (2, 1 ♂, 1 ♀, KU 110362–363); Jicaro (1 ♀, AMNH 29249); 2.5 km NE Totecacinte (2 ♂♂, KU 110337–338).

Additional record.—Departamento de Madriz: San Juan de Telpaneca (AMNH 29239) (Harris 1937).

Sciurus variegatoides dorsalis Gray, 1849

1849. *Sciurus dorsalis* Gray, Proceedings of the Zoological Society of London [1848] Part 16:138.

1920. *Sciurus variegatoides dorsalis*, Goldman, Smithsonian Miscellaneous Collection 69(5):136.

Holotype.—BM(NH) 1848.10.26.4 (skin) and BM(NH) 1848.11.10.5 (skull), male, skin, originally a taxidermy mount, but remade into a round museum specimen, and skull damaged but some measurements can still be taken, received from M. Sallé via W. Cumming.

Type locality.—Originally given as Caracas, Venezuela (Gray 1848), but later restricted to Costa Rica

by Gray (1867) and finally further restricted to Liberia, Guanacaste Province, Costa Rica by Nelson (1899).

Remarks.—Along with individuals of *S. v. adolphei* to the north, these are the largest variegated squirrels in Nicaragua. The extensive sample of *S. v. dorsalis* averaged the second largest to *adolphei* in seven of the nine cranial measurements and was the widest for postorbital breadth (Table 1). A strongly-marked, generally black, but in some individuals interspersed with brown, or rarely brown dorsal stripe is present in all specimens of this subspecies (Fig. 2; Medina-Fitoria et al. 2018:fig. 22). When the stripe is black, the dorsal hairs forming it are not banded but are black throughout. The overall white appearing sides and venter is formed by two-banded hairs, the basal half being gray and the terminal half white giving sharply contrasting white sides and venter to the black (or brown) dorsal stripe. The auricular patch is white and either consists of unicolor white hairs throughout or hairs with a gray base and white terminal band. There is not as sharp a contrast between the ear patches and body coloration in this subspecies as there is in all other subspecies because the auricular patch tends to be a continuation of the white sides. The interspersal of black and white hairs on the tail trends towards white hairs in this subspecies giving the overall appearance of a paler, whiter tail than in any other subspecies throughout the species' geographic range.

This distinctive subspecies occurs throughout much of the dry forest of western Nicaragua and south to Santa Cruz in Costa Rica's Guanacaste lowlands. In Nicaragua, *S. v. dorsalis* occurs in the area between Lago de Managua and Lago de Nicaragua, and Managua itself. Along the southeastern shore of Lago de Managua, the subspecies occurs as far north as Tipitapa and along the southwestern shore of the lake, as far north as Lago de Jiloa. It occurs from Lago de Managua southward along the western side of Lago de Nicaragua in the departments of Carazo, Granada, Managua, Masaya, and Rivas.

North of Lago de Jiloa along the Pacific coast, the next sample of *S. variegatoides* is from Hacienda Las Colinas near Puerto Momotombo at the northern edge of Lago de Managua in Departamento de León. These squirrels are typical of *S. v. adolphei* and show no characteristics of *S. v. dorsalis*. No samples between Lago

de Jiloa and Las Colinas are available to determine if there is a definable zone of intergradation. If such a zone occurred in the past, it may not be present today because this region has been heavily settled since the colonial period and is under intense agricultural use. From Las Colinas northward, *S. v. adolphei* occurs into the Departamento of Chinandega along the volcanoes of the Cordillera de los Marrabios (Genoways and Timm 2005). To the east of Managua and Tipitapa, the nearest record of variegated squirrels is a specimen from San Francisco, Departamento de Boaco, which are the southern-most *S. v. underwoodi* known. There are no specimens of squirrels in the intervening 45-km gap from Tipitapa to San Francisco and there is no indication of intergradation between these two taxa anywhere throughout the potential contact zones. The intervening area is part of the Central Depression and is under intensive agricultural use. *S. v. dorsalis* is a distinctive subspecies that seems to have a fairly well-defined distribution in the western dry forests of Costa Rica and Nicaragua. In Costa Rica, Harris (1937) noted a zone of integration with *S. v. atrirufus* on the Nicoya Peninsula. McPherson (1971, 1985) wrote that in the Pacific lowlands of Costa Rica “intergrades between *S. v. dorsalis* and *S. v. thomasi* are found ... there is a complex zone of intergradation involving *S. v. rigidus*, *S. v. melania*, and *S. v. dorsalis*. The subspecies *S. v. austini*, described by Harris (1933), is an intergrade between *S. v. rigidus* and *S. v. melania*” (1985:162). However, in a series of 16 specimens obtained by Timm from the Upala area of northern Costa Rica just to the east of known specimens of *S. variegatoides dorsalis*, there is no evidence of integration of these squirrels with *S. v. thomasi*.

Reproductive data for *S. v. dorsalis* are not extensive, but the few data available are as follow. Lactating females were taken on 16 June 1966 and 11 August 1967. Adult females with enlarged teats but not obviously pregnant or lactating were taken on the following dates: 4 March 1956, 1; 31 March 1968, 2; 7 April 1956, 1; 13 June 1966, 2; 16 June 1956, 1; 16 June 1966 1; 26 June 1956, 1; 11 August 1967, 4; 13 August 1967, 1. Testes length for adult males are as follows: 31 March 1968—22, 22, 23, 24, 33 mm; 25 April 1968—23, 25 mm; 13 June 1966—7 mm; 21 June 1966—26 mm; 22 June 1966—27 mm; 11–13 August 1967—8, 9, 10, 24, 26 mm. Weights of two adult males were 681 (1 July 1964) and 596 g (9 July

1964), whereas the weights of two adult females were 900 (8 August 1963) and 455 g (9 October 1964). A juvenile nulliparous female weighing 213.7 g, molting, and with erupting permanent teeth was taken on 11 August 1967. A nulliparous female weighing 232.9 g, also molting, but with all permanent teeth in place, was taken on 31 March 1968.

The collecting site at 3 km N, 4 km W Diriamba was a large coffee finca with an elevation of about 550 m in the highlands of Departamento de Carazo. This was a typical coffee finca having the original large overstory trees remaining in place with the understory trees and bushes removed and replaced by the coffee trees. Neotropical variegated squirrels nested and carried on much of their activities in the tall overstory trees, but they were predatory on the developing coffee beans to the point that they were actively hunted by the managers of the finca. These squirrels also were a pest when the coffee beans were on the drying platforms. At other places in Nicaragua, these squirrels were considered to be pests in the cacao plantations. Medina-Fitoria et al. (2018) reported that *S. v. dorsalis* occurs up to 1,000 m and provided two images of free-ranging individuals of the characteristic color pattern.

Webb and Loomis (1970) described the chigger *Microtrombicula nicaraguae* from a specimen of *S. v. dorsalis* (KU 106357) collected at Finca Santa Cecilia, Departamento de Granada.

Medina-Fitoria et al. (2018:fig. 33) presented a photograph of a squirrel from El Abuelo, Departamento de Rivas, from the southern shore of Lago de Nicaragua. This is an area that would be just to the east of the peripheral geographic range of *S. v. dorsalis* as currently understood, but this individual does not appear to be a *dorsalis* and, in fact, it cannot be placed in any of the currently recognized groups of Nicaraguan squirrels. This individual is not mapped or the locality listed below and the identity of squirrels from this area of Nicaragua and adjacent Costa Rica will not be known until specimens are available for study.

Specimens examined (93).—Departamento de Carazo: 3 km N, 4 km W Diriamba (41, 24 ♂♂, 17 ♀♀, KU 110364–390, 115263–276); 3 mi NNW Diriamba (1 ♀, KU 71550). Departamento de Granada: Finca Santa Cecilia, 6.5 km SE Guanacaste (7, 1 ♂, 6 ♀♀

KU 106355–361); La Calera, 3 mi S, 5 mi W Nandaimé (18, 11 ♂♂, 7 ♀♀, KU 108186–192); Mecatepe (1 ♀, NMNH 339949). Departamento de Managua: Hacienda Azacualpa (2, 1 ♂, 1 ♀ KU 108393; NMNH 361236); 1 mi SSE Las Conchitas (1 ♀, KU 71549); Lake Jiloa (2 ♂♂, AMNH 176694–695); 6 mi WSW Managua (2, 1 ♂, 1 ♀, KU 71545–546); 10 mi SW Managua (1 ♂, KU 71970); Tipitapa (1 ♂, AMNH 41232). Departamento de Masaya: 9 mi NW Masaya (2 ♂♂, KU 71547–548). Departamento de Rivas: Finca Amayo, 13 km S, 14 km E Rivas (11, 7 ♂♂, 4 ♀♀ KU 104701–704, 106362–364); 3 mi SE La Virgen (1 ♂, KU 71551); 8 km NE San Juan del Sur (2, 1 ♂, 1 ♀ KU 106365–366).

Additional record.—Departamento de Masaya: 21 km S Managua “common in the region” (J. Hruska, pers. comm.).

***Sciurus variegatoides underwoodi* Goldman, 1932**

1932. *Sciurus boothiae underwoodi* Goldman, Journal of the Washington Academy of Science 22(10):275.

1937. *Sciurus variegatoides underwoodi*, Harris, Miscellaneous Publications of the Museum of Zoology, University of Michigan 38:9.

Holotype.—NMNH 250219, adult male, skin and skull (left zygomatic arch broken), collected by Cecil F. Underwood on 8 December 1931.

Type locality.—Monte Redondo, about 30 miles NW Tegucigalpa, Departamento de Francisco Morazán, Honduras.

Remarks.—This is the third taxon of medium-sized variegated squirrels occurring in Nicaragua (Table 1). These squirrels average larger than the other medium-sized taxa, *belti* and *boothiae*, but only two-thirds of the specimens in the analyzed sample of *underwoodi* classify correctly in the discriminate function analyses. Five of the 10 misclassified squirrels are classified as *boothiae*, which was a taxon that Harris (1937) believed was influencing some of the specimens of *underwoodi* he examined.

Dorsally the overall appearance is a mixture of black and dark silver giving an overall dark, somewhat mottled appearance. Dorsal coloration extends over the

sides to the ventrum, often extending further ventrally than the lateral coloration in other taxa (Fig. 2). Dorsal hairs are three banded with a black base (ca. 9 mm), dull silver middle band, and short black terminal band. The ventrum is countershaded, but highly variable with a moderate mix of chestnut and white patches or is uniformly dull white. The auricular patch is small, dull white and not contrasting as sharply as in other taxa, and extends back only some 5 mm. The dorsal hind feet are dark, with a mix of dark chestnut or dark silver hairs resulting mostly in an overall mixed agouti pattern.

Harris (1937:10) wrote: “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.” He had only material from San Rafael del Norte and Matagalpa for study, but the material available to us covers a much larger geographic area. In northern Nicaragua, specimens collected by the KU field parties provide new records from the departments of Madriz and Estelí. These sites place *underwoodi* to west and somewhat south of sites where *boothiae* occurs. These two subspecies probably approach each other most closely in eastern Departamento de Madriz at Venecia (*underwoodi*) and San Juan de Telpaneca (*boothiae*). To the south of these sites, there are two localities represented by KU material from near Yali and Richardson’s specimens from San Rafael del Norte examined by Harris (1937).

Harris (1937) had the unusual situation of having Richardson’s specimens labeled as “Matagalpa” that he assigned to *underwoodi* and others to *belti*. The six specimens from Matagalpa were the southernmost representatives of *S. v. underwoodi* that Harris (1937) had available for study and their relationship with *belti* was not readily apparent. With more material now available, the distributions of these taxa can now be refined. About 22 km north of Matagalpa near the border of Jinotega, there is a large sample from Santa María de Ostuma, which is a close match to the description and understanding of *S. v. underwoodi* in Nicaragua presented below. East of Matagalpa at 3 mi SE San Ramon, two specimens appear to be typical *underwoodi*. They are most similar to each other and similar to other specimens identified as *underwoodi*. Dorsal coloration and ear patches are typical of the subspecies, with feet grizzled agouti and ventrum

very light orange, almost tan. There appears to be no influence from the lowland *belti* in this color pattern. Southwest of Matagalpa there is a single specimen from Sebaco, but it is a juvenile and its color pattern is of no real value to this discussion. Between 50 and 60 km to the south of Matagalpa are three localities (11 mi SE Dario and two near Esquipulas) that are assigned to *S. v. underwoodi*.

A single specimen from San Francisco, Departamento de Boaco, at 135 km south of Matagalpa is treated as *S. v. underwoodi*. Dorsally, this specimen's coloration best matches that of *underwoodi* as does the auricular patch; however, the ventrum is a dull chestnut with no interspersed white, which is not typical of any taxon examined herein. This specimen from San Francisco is the southern-most record of *S. v. underwoodi*. As discussed in the *belti* account, the three specimens from Hato Grande approximately 42 km south of San Francisco and the series from the vicinity of Villa Sandino about 75 km southeast of San Francisco, combine color patterns of *belti* and *underwoodi*, but the predominance of evidence places them with *S. v. beltii*, as assigned above. The latter two sites lie west and east, respectively, of the relatively low Cordillera Chontaleña, which forms the divide between rivers that flows directly into Lago de Nicaragua and those that flow eastward into the Caribbean. This small range of mountains represents the southern-most extension of the Central Highlands of Nicaragua and the southern-most topographic feature influencing the distribution of *S. v. underwoodi*.

After this review of the distribution of *S. v. underwoodi*, what can be said about the six specimens of *underwoodi* and the three specimens of *beltii* labeled by Richardson from Matagalpa? In the available material, there are specimens of *underwoodi* in all directions from Matagalpa, which leads to the conclusion that within the environs of Matagalpa, *S. v. underwoodi* should be expected, including these six specimens. The difficulty of determining the source and relationships of the three *beltii* specimens in the account for that subspecies are discussed above.

The distribution map of *S. variegatoides* in Hall and Kelson (1959) and Hall (1981) that shows the distribution of *S. v. underwoodi* extending along the dry forest west of Lago de Nicaragua into extreme

northwestern Costa Rica is in error. This record was based on Goodwin (1946:360) who reported a single specimen from "Prov. Guanacaste: Liberia, Port Parker Bay." The online catalogue of the American Museum of Natural History lists this specimen, which is a skin only, as AMNH 140235, with the locality as "Port Parker Bay," Paquera, Puntarenas Province, collected by C. William Beebe on 23 January 1938. Paquera is located on the extreme southeastern coast of Costa Rica's Nicoya Peninsula, well within the geographic range of *S. v. atrirufus* (Timm et al. 2009). The American Museum's entry is in error when compared with the original handwritten catalogue where the locality for this specimen is given as "Costa Rica: Port Parker Bay?" with the remaining data in agreement with the online information. This brings into question the exact location of Port Parker Bay, Costa Rica. The marine survey in which Beebe was involved places this location at 10°56'N, 85°49'W (Fraser 1943), which is a long abandoned and now washed out port along the north shore of the Santa Elena Peninsula. Goodwin (1946) reported that William Beebe saw several squirrels at Port Parker, but the one he secured was shot in a gully about a mile back of the Port Parker beach. This specimen and the current populations of Santa Elena Peninsula should be reassigned to *S. variegatoides dorsalis* until additional material is available for study.

To the west of populations of *S. v. underwoodi* in Nicaragua are populations of *S. v. adolphei* in the departments of Chinandega and León. These populations are separated by the Central Depression of Nicaragua, which is an area where there are no specimens for study. Historically, there may have been variegated squirrels in this area, but if they occur there today, they are widely dispersed and in low numbers. This is an area of high human population and extensive agricultural crops and ranching operations. The specimens from Matagalpa and San Raphael del Norte, which J. A. Allen (1910) originally identified as the taxon *S. v. variegatoides*, were subsequently assigned to *S. v. underwoodi* by Harris (1937), although he did see some influence of *S. v. boothiae* in them.

Medina-Fitoria et al. (2018) determined that a photographed squirrel from Selva Negra was *S. v. boothiae* and one from Natural Reserve Cerro Arenal was an undetermined taxon. Variegated quirels from northern Departamento de Matagalpa have been as-

signed here to *S. v. underwoodi*. Along with Harris (1937) who noted the influence of *S. v. boothiae* on the population in this part of Nicaragua, these squirrels are best placed with *underwoodi* based on color and over all color pattern.

A female *S. v. underwoodi* was pregnant when obtained on 14 March 1968 at La Danta. A single embryo was implanted in each uterine horn. Lactating females were recorded on 17 March 1968 and 26 June 1964. Females evincing no reproductive activity were taken on the following dates: 15–17 March 1968, 3; 11 April 1968, 1; 10–11 May 1956, 2; 25 June 1964, 1; 29–30 June 1966, 2; 4 July 1967, 1; 3 August 1966, 1. Juvenile individuals with unerupted third upper molars were taken at Sebaco on 26 January 1958 and at San Rafael del Norte on 1 February 1909. Testes length for adult males were as follows: 14–17 March 1968—19, 25, 26, 29, 30, 32 mm; 11 April 1968—5, 28 mm; 20–22 April 1968—8, 22, 25 mm; 29–30 June 1966—23, 25, 25 mm; 1–3 July—12, 26 mm; 4 July 1967—8, 26, 27 mm; 3 August 1966—25 mm. Medina-Fitoria et al. (2018) reported that *S. v. underwoodi* occurs from the lowlands up to 1,200 m.

Specimens examined (49).—Departamento de Boaco: San Francisco, 19 km S, 2 km E Boaco (1 ♀, KU 115262). Departamento de Estelí: 8 mi S Condega (1 ♀, KU 71553). Departamento de Jinotega: San Rafael del Norte (5, 2 ♂♂, 3 ♀♀, AMNH 28438, 29240, 29245–246, 41233); 2 km E Yali (2, 1 ♂, 1 ♀, KU 106335–336). Departamento de Madriz: Daraili, 5 km N, 14 km E Condega (3 ♀♀, KU 97911–913); Venecia, 7 km N, 16 km E Condega (1 ♂, KU 97910). Departamento de Matagalpa: 11 mi SE Dario (1 ♂, KU 71552); Santa Maria de Ostuma (15, 10 ♂♂, 5 ♀♀, KU 106337–343, 110391–395, 115277–279); 3 mi SE San Ramon (2 ♀♀, KU 71554–555); 1 km NE Esquipulas (3, 2 ♂♂, 1 ♀, KU 115288–290); La Danta, 1 km N, 5 km E Esquipulas (8, 4 ♂♂, 4 ♀♀, KU 115280–287); Sebaco (1 ♂, AMNH 176697); Matagalpa (6, 2 ♂♂, 4 ♀♀, AMNH 28411–412, 28444, 30753, 41388–389).

Additional records.—Departamento de Matagalpa: Reserva Natural Cerro Arenal [13°00'25"N, 85°54'16"W] (Medina-Fitoria et al. 2018); Selva Negra (Medina-Fitoria et al. 2018).

CONCLUSIONS AND INSIGHTS

Herein, the systematics, diversity, and distributions of the variegated squirrels of Nicaragua are assessed by critically evaluating historical collecting sites, all published literature, and new morphometric data. To provide insights into the diversity of Nicaragua's fauna, the taxa found in the country are described and mapped. The variegated squirrels found on Isla de Ometepe in Lago de Nicaragua are a here-to-for unrecognized distinctive subspecies that are described as *Sciurus variegatoides ometepensis*. There are now six subspecies of this species found in Nicaragua and 16 throughout the species' geographic range. How and when the small mammal fauna of the volcanic island of Ometepe was colonized from the mainland remains an open question.

Why is the study of subspecific variation valuable? In this modern era, studying subspecific variation, and the description of a population recognized as a subspecies has become controversial. Indeed, some authors have even questioned the value of describing

species new to science. In a recent critique of the subspecies concept in mammalogy, Patton and Conroy (2017) using both morphological and genetic data, provide a valuable review of the history and use of the subspecies concept in mammals. Although morphology and genetic data do at times give somewhat different views of the evolutionary history of populations, both approaches can and do provide valuable insights into phylogenetic relationships.

In modern systematics of mammals, the use of color and color patterns has fallen into disfavor, with the emphasis on higher-level morphometrics, molecular genetics, and now genomics. One of the primary issues of using color as a character is that its genetic control is highly complex and it is not a simple one gene to one color situation (Caro 2005). There has been disagreement as to whether color patterns are adaptive or not (Hershkovitz 1968, 1970) when discussing these patterns' involvement in "social selection" (Lawlor 1969) or "intraspecific communication" (Caro 2005).

However, it is clear that for these diurnal squirrels in the *S. variegatoides* complex their color and color patterns are adaptive and function in social recognition as well as to convey protective value concealing the individual from predators (also see Ancillotto and Mori 2017).

In the variegated squirrels, there is almost certainly selection in coloration and probably intense selection. The color patterns of the Nicaraguan subspecies of *S. variegatoides* are stable over broad geographic areas and, when there is contact between some of the taxa, detectable intergrades are produced indicating a genetic control for the colors and patterns. The color of these squirrels tends to follow Golger's Rule, with the darker form *S. v. belti* occurring in the wetter more humid Caribbean lowlands, the paler colored sandy or reddish animals in some cases having a nearly white dorsum occurring in the western more arid lowlands, and animals with patches of white pelage being found in higher elevations. Neotropical variegated squirrels, as with other closely related squirrels in the genus *Sciurus*, are capable of color vision that is at least dichromatic, giving these squirrels the ability to discriminate among intraspecific colors and color patterns (Arden and Silver 1962; Michels and Shumacher 1968; Jacobs 1974; Yolton et al. 1974). There is no secondary sexual dimorphism in color and color patterns in variegated squirrels as occurs in other diurnal mammals, notable in primates (Caro 2005). As noted by Harris (1937) there is no distinctive seasonal change in pelage color.

Although the bright coloration of some of the subspecies would seemingly make individuals easily spotted by predators, these squirrels can be remarkably difficult to see in tropical forests. In closed canopy forests, often little light penetrates the canopy and it may be quite diffuse, making these dappled squirrels blend into the background (Figs. 2–3). Hayssen (2008) ascribed the distinctive tail coloration in some sciurids as having a role in “tail flagging” behavior, perhaps to induce a predator to strike there or as having a conspecific visual communication function. Throughout the subspecies of *S. variegatoides*, the tail color is remarkably similar despite the extreme variation seen in body color. The tails are long and have a sharply contrasting black and white or rarely black and agouti coloration; the contrasting coloration is dorsal and the ventral view is generally black (see Figs. 2–3).

The newly described *S. v. ometepensis* differs significantly in color from the other subspecies of variegated squirrels occurring in Nicaragua and throughout the geographic range of the species, as well as in cranial and bacular characters. One of the most interesting features in the color pattern of the Ometepe squirrels is the high variability in patterns and colors. Other subspecies do differ widely from each other, but variation within a population is quite limited. In addition, the new subspecies is the most distinct of all of the taxa in Nicaragua in morphometrics. These individuals are small and have unique cranial proportions compared to others subspecies to the point that 41 of 42 specimens examined were correctly identified in a discriminate analysis. The history of this distinctive population is obviously tied to its long isolation on Isla de Ometepe.

Borgia and van Wyk de Vries (2003; van Wyk de Vries 1993) place the origin of Volcán Concepción in the late Quaternary, which would place its origin at least 20,000 to 30,000 years ago. Volcán Concepción lies above a bed of Quaternary mudstone in Lago de Nicaragua, with no indication of earlier volcanic activity in the lake deposits. There is no evidence that the island has ever been in contact with the mainland; therefore, the method of dispersal of terrestrial mammals seems to have been over water. Currently, it is about 6 km west to the mainland of the Departamento de Rivas and 55 km to the east to the mainland of the Departamento de Río San Juan. The prevailing winds are from the west to east or southeast; therefore, the wave action on the lake would move in this same direction. Lago de Nicaragua slowly drains to the southeast to the Río San Juan and then on to Caribbean Sea (Fig. 5). A number of other small terrestrial mammals reported herein from the Isla de Ometepe, such as *Sylvilagus floridanus*, *Oligoryzomys fulvescens*, *Peromyscus nicaraguae*, *Peromyscus stirtoni*, *Sigmodon hirsutus*, and *Liomys salvini* have their affinities to the drier Pacific Coast of Nicaragua. If there truly was no contact between Volcán Concepción and the mainland, then Neotropical variegated squirrels and other small mammals must have reached Isla de Ometepe via over water dispersal from along the western shore of Lago de Nicaragua where currently *S. v. dorsalis* is the dominant form. Although there is no geological evidence for a land connection between the island and the mainland, the presence of arid-adapted rodents and the dry forest cottontail rabbit on the island

might suggest a terrestrial dispersal route. These species of mammals as well as four-eyed opossums and white-tailed deer, are common in disturbed habitats so mature forest would not be a necessary habitat connection. One of the species of *Peromyscus* on Ometepe is black in color, in contrast to the mainland form also attesting to the long isolation of this fauna. For mammals, or any other animals reaching Isla de Ometepe by swimming the water gap, there is always the added danger that Lago de Nicaragua hosts a robust freshwater population of bull sharks (*Carcharhinus leucas*).

One of the major zoogeographic barriers in Middle America is known as the Nicaraguan Gap, which refers to the lowland area in southern Nicaragua that creates a break in the mountainous spine of the region, separating the Central Highlands of Nicaragua and Costa Rica's Cordillera de Guanacaste–Cordillera de Tilarán ranges. In the Pliocene, this gap may have represented the southern terminus of North America, but more recently is seen as an area that terminates or interrupts the distribution of montane taxa both from the north and south. The impact of this “gap” has been studied in the montane sigmodontine rodent, *Scotinomys* (Buchanan and Howell 1967), montane birds (Howell 1969; Weir 2009), and scarabaeid beetles (Ratcliffe and Deloya 1992). In the most recent of these studies, Weir (2009:419) found that in montane birds the genetic differentiation across the Nicaraguan Gap “ranged 1%–9% and had a similar distribution of divergence dates to the Isthmus of Tehuantepec” in Mexico.

The Neotropical variegated squirrels of Nicaragua illustrate some of the impacts of this lowland gap on their distribution. The two montane taxa—*S. v. boothiae* and *S. v. underwoodi*—are confined in their distribution to the Central Highlands of the north-central part of the country east of the Nicaraguan Depression (Fig. 5). The geographic range of *S. v. boothiae* terminates in the mountains of the Departamento de Nueva Segovia and adjacent parts of Madriz in the far north. Populations of *S. v. underwoodi* come further south along the western edge of the Central Highlands to some 50 km east of Managua at San Francisco in the Departamento de Boaco where the highlands are reduced to a few ridges. Finally, some influence of *underwoodi* just east of Lago de Nicaragua along the edges of the

last remnant of highland, the Cordillera Chontaleña is represented in color. Here *underwoodi* is intergrading with *S. v. belti*, the taxon present throughout the eastern Caribbean Lowlands. This brings the eastern taxon to the eastern slopes of Lago de Nicaragua, ending the distribution of the montane forms. The remaining three taxa—*adolphei*, *dorsalis*, and *ometepensis*—are essentially isolated in the arid dry forest of the Pacific Lowlands of western Nicaragua. It is only *dorsalis* that enters Costa Rica and intergrades with other taxa there.

Although nearly 400 variegated squirrels from Nicaragua are now available for study, there is much to learn about the distributions and relationships of these squirrels. More intensive collecting needs to be done between Rama, near the type locality of *belti* and Talamanca in southeastern Costa Rica, which is the type locality of *thomasi*. The relationship of these two taxa occupying the Caribbean Lowlands is poorly understood, but if they represent distinct taxa there should be a zone of intergradation somewhere in this area and currently few specimens are known from Costa Rica. Precise and intensive collecting will be needed along the eastern slopes of Central Highlands and the valleys of the east-flowing rivers to gain a better understanding of the distribution of *belti*, *boothiae*, and *underwoodi* in this region. It would be of interest to learn if there is a zone of intergradation between *adolphei* and *dorsalis* west of Lago de Managua. Additionally, there may be undescribed taxa of variegated squirrels just south of Lago de Nicaragua in Nicaragua and northern Costa Rica.

The hypotheses presented throughout this work on systematic relationships of squirrels clearly need to be tested with genetic data, but herein a groundwork has been laid for additional productive research. The distinctive new variegated squirrel, *S. v. ometepensis*, a large, diurnal, and conspicuous tree squirrel, along with the recent discovery of the southern flying squirrel (*Glaucomys volans*), pygmy squirrel (*Microsciurus alfari*), and rufous tree rat (*Diplomys labilis*) in Nicaragua attests to how much remains to be learned about this interesting fauna (Martínez-Fonseca et al. 2018). Recent efforts by the Nicaraguan conservation community in establishing reserves to protect the country's rich fauna and associated habitats are to be applauded.

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