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Small Mammals of Guandera Biological Reserve, Carchi Province, Ecuador and Comparative Andean Small Mammal Ecology

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Abstract

In 2014, a mammal survey was conducted in an ecotone region (including páramo and temperate forest) on the Eastern Versant of the Andes in Carchi province, Ecuador. Sherman traps, Tomahawk traps, pitfall traps, and mist nets were used to collect mammal specimens at two sites (3,340 m elevation and 3,650 m elevation). A total of 142 specimens representing 14 species were collected from the survey area. Species collected include: *Didelphis pernigra*, *Microryzomys altissimus*, *M. minutus*, *Nephelomys albigularis*, *Neusticomys monticolus*, *Reithrodontomys mexicanus soderstromi*, *Thomasomys baeops*, *T. cinnameus*, *T. vulcani*, *T. ucucha*, *Sturnira bidens*, *S. erythromos*, and *Myotis keaysi*. One additional species (*Mazama rufina*) was documented by a partial skull salvaged from the forest near the biological station. A comparison of the effects of elevation on Ecuadorian rodent diversity was conducted by examining previous collections from this region. This comparison revealed an ecological gradient and turnover of cricetid rodent diversity (at the taxonomic level of tribe) that occurs between 2,070 m and 2,500 m. Furthermore, a reexamination of the taxonomy of *Thomasomys* was warranted based on the results of *Cyt*b analyses (this study) and more comprehensive descriptions of *Thomasomys* species in the recent literature.

Key words: Carchi Province, distribution range, ecology, Ecuador, elevation gradient, mammals

Resumen

En 2014 se llevó a cabo un inventario de mamíferos en una región de ecotono (incluyendo páramo y bosques temperados) en las estribaciones orientales de los Andes en la provincia del Carchi, Ecuador. Se usaron trampas Sherman, trampas Tomahawk, trampas de caída y redes de neblina para recolectar especímenes de mamíferos en dos localidades (a 3340 y 3650 m de elevación). Un total de 142 especímenes fueron recolectados representando 14 especies. Las especies registradas incluyen: *Didelphis pernigra*, *Microryzomys altissimus*, *M. minutus*, *Nephelomys albigularis*, *Neusticomys monticolus*, *Reithrodontomys mexicanus soderstromi,*

Thomasomys baeops, *T. cinnameus*, *T. vulcani*, *T. ucucha*, *Sturnira bidens*, *S. erythromos* y *Myotis keaysi*. Una especies adicional (*Mazama rufina*) fue documentada por una porción de cráneo recuperada del bosque cercano a la estación biológica. Una comparación de los efectos de la elevación en los roedores ecuatorianos se llevó a cabo al revisar colecciones previas de esta región. Esta comparación reveló un gradiente ecológico y recambio en la diversidad de roedores cricétidos (al nivel taxonómico de tribu) que ocurren entre los 2070 y los 2500 m de elevación. Además, una reexaminación de la taxonomía de *Thomasomys* fue confirmada en base a los resultados de análisis de citocromo *b* (este estudio) y una revisión más completa de las especies de *Thomasomys* en literatura reciente.

Palabras clave: Carchi, ecología, Ecuador, gradiente altitudinal, mamíferos, rango de vida

INTRODUCTION

The Guandera Biological Reserve is part of the Ceja Andean forest or Evergreen high mountain forest of the Northern Andes in Ecuador, transitioning to páramo (Ministerio del Ambiente del Ecuador 2013). This area was the subject of a previous survey (Tirira and Boada 2009). This study compares the results of the two surveys at Guandera, and the results are further compared to those of several similar collecting efforts within the region.

Multiple surveys of an area may be necessary to fully reveal species diversity, especially if sampling occurs in different seasons. With these surveys, a picture of the ecological differences between Oryzomyine and Thomasomyine rodents is beginning to emerge (Lee et al. 2006a, 2006b, 2008, 2010, 2011; Tirira and Boada 2009).

MATERIALS AND METHODS

Study area and survey sampling.—This study was conducted from 18 July to 5 August 2014 at sites in the temperate cloud forest (Site 1; 3,340 m) and Eastern páramo (Site 2; 3,650 m) in Guandera Biological Reserve, located in Carchi province, Ecuador, on the Eastern slope of the Andes (Fig. 1). The majority of time and effort was focused on the temperate forest at 3,340 m located at 0°35'21"N, 77°42'19"W. Trees were surprisingly tall (about 18 m) for such a high elevation site. For the most part, trapping efforts occurred in or near the riparian habitat of the Río Quebrada Mirador. Tree families (including arboreal fern) that were observed in the temperate forest were: Araliaceae, Brunelliaceae, Chloranthaceae, Clusiaceae, Cunoniaceae, Dicksoniaceae, Lauraceae, Rosaceae, Rubiaceae. Other plant families observed in the temperate forest were: Araceae, Bromeliaceae, Equisetaceae, Onagraceae, Orchidaceae and Scrophulariaceae (Patzelt 2004). The páramo habitat of the second site primarily was alpine grassland dominated by *Puya* (Bromeliaceae).

Five Tomahawk and 200 Sherman traps were set daily in grasslands, on forest floors, in trees, in streams, and on stream banks for 3,600 trap nights. Bats were caught with 9, 12, and 18 m mist nets at the 3,340 m site; nets were set in forests, fields, and in riparian habitats (for about 5 hours per night). Pitfall traps were set in forests and along stream banks and logs. Only 42 trap nights were conducted at 3,650 m because of the difficulty of reaching that site for daily trapping. All voucher specimens (skins, skulls, skeletons, and frozen liver tissue) were deposited in the Abilene Christian University Natural History Collection (ACUNHC) and at the Museo de Zoología Sección de Mastozoología at Pontificia Universidad Católica del Ecuador (QCAZ-M). Specimens were treated in accordance with the guidelines of the American Society of Mammalogists for the use of wild mammals in research (Sikes et al. 2011).

Voucher specimens from this study were compared to specimens in the collections of ACUNHC and QCAZ-M to confirm species identity. Some specimens of questionable identification were examined by other researchers, named in the acknowledgments, to corroborate species identifications. A number of

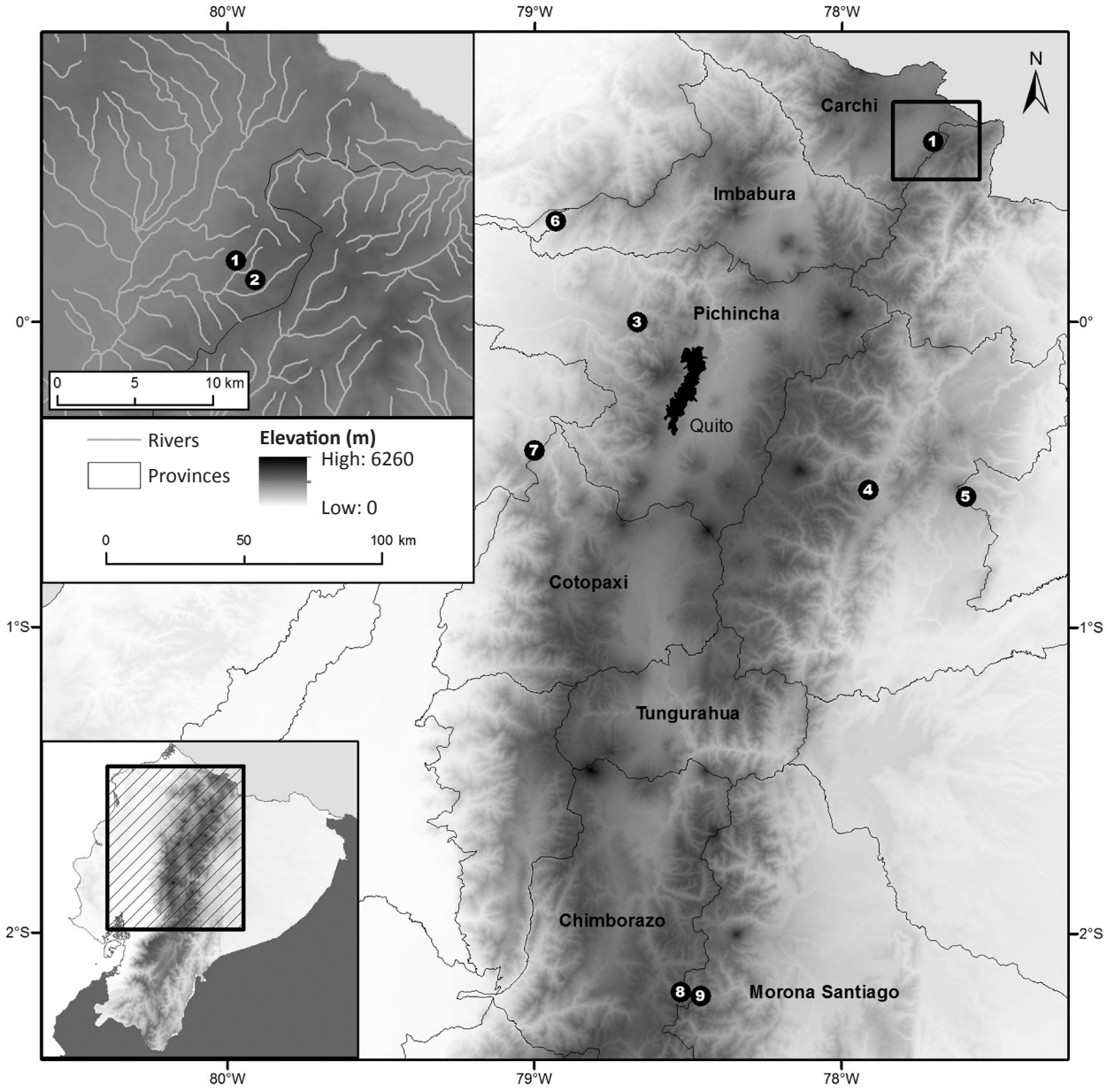

Figure 1. The location of the study sites in Guandera Biological Reserve are designated by the numbers 1 (3,340 m elevation, 0°35'21"N, 77°42'19"W) and 2 (3,650 m elevation, 0°37'10.09"N, 77°40'9.71"W) (also see inset map). The other study sites used for comparison are: location 3, the Tandayapa Valley (0°00'13"N, 78°40'70"W) (Lee et al. 2006a); location 4, the Cosanga River Valley sites (0°33'00"S, 77°55'00"W and 0°31'70"S, 77°52'99"W) (Lee et al. 2006b); location 5, the eastern slope of Volcán Sumaco (0°34'19"S, 77°35'64"W) (Lee et al. 2008); location 6, Santa Rosa (0°19'51"N, 78°55'55"W and 0°17'33"N, 78°57'38"W) (Lee et al. 2010); location 7, Otonga (0°25'11"S, 79°0'11"W) (Jarrín and Fonseca 2001; T. Lee, unpublished data); location 8, Sangay National Park Atillo Lagoons (2°11'33.4"S, 78°31'29.38"W to 2°10'55.99"S, 78°29'57.36"W) (Lee et al. 2011); and location 9, just east of Sangay National Park (2°12'17.87"S, 78°27'30.92"W) (Lee et al. 2011). Not shown: Guajalito (Jarrín and Fonseca 2001).

taxonomic identifications were further corroborated by sequencing the cytochrome-*b* gene (*Cyt*b) and comparing those sequences with those of previously identified specimens. Voucher specimens that were sequenced include *Myotis keaysi* (R. Neal Platt, pers com.) and all of the *Thomasomys* taxa (see below). Nomenclature used in this study follows Wilson and Reeder (2005) for marsupials, deer, and rodents, except for the Oryzomyine rodents, which follows Weksler et al. (2006), and bats, which follows Gardner (2007). A Shannon Index value (Shannon 1948) was calculated for each site and compared to diversity values from similar studies (Jarrín and Fonseca 2001; Lee et al. 2006a, 2006b, 2008, 2010, 2011; T. Lee, unpublished data; sites 3–9, Fig. 1).

Taxon sampling for DNA extraction and sequencing.—Tissues from the genus *Thomasomys* were sampled from specimens housed in the Abilene Christian University Natural History Collection (ACUNHC) and The Museum of Vertebrate Zoology at Berkeley (MVZ), the Museo de Zoología Sección de Mastozoología Pontificia Universidad Católica del Ecuador (QCAZ-M) and supplemented with sequences from GenBank (Appendix). Total genomic DNA was isolated from vouchered museum specimens using approximately 0.1 g of EtOH−preserved liver tissue with an EZNA Tissue DNA Kit (Omega Bio-Tek, Norcross, GA) following the manufacturer's instructions.

The entire *Cyt*b gene was amplified using polymerase chain reaction (PCR) with the primers P484 and P485 (Steppan et al. 1999) for 32 samples. The PCR protocol for *Cyt*b consisted of a 20 µL sample containing 15.25 µL H_2O, 2.0 µL 10X Thermopol Reaction Buffer with 20 mM Mg^{2+} (New England Biolabs, Ipswich, MA), 1.0 µL of each 5 µM primer, 0.25 µL 2.5 mM dNTP, 0.2 µL 5 U/µL Taq polymerase (New England Biolabs), and 2.0 µL diluted DNA template of unknown concentration. PCR conditions in a Biometra thermocycler (Whatman, Göttingen, Germany) included initial denaturation at 95°C for 2 min; followed by 35 cycles at 95°C for 0.75 min, 46°C for 0.75 min, and 72°C for 1.5 min; with a final extension at 72°C for 8 min.

All PCR products were visualized by 1% agarose gel electrophoresis and purified with an EZNA Cycle-Pure Kit (Omega Bio-Tek, Norcross, GA) following the manufacturer's instructions. Sanger sequencing of the purified product was conducted at the DNA Analysis Facility on Science Hill at Yale University. Sequences were assembled and edited using the program Sequencher version 5.2.4 (Gene Codes Corporation, Ann Arbor, MI). Alignments were assembled using MEGA v6.0.2 software (Tamura et al. 2013) with the codon structure as a guide. DNA sequences were deposited in GenBank and accession numbers are listed in the Appendix.

Phylogenetic analyses.—Phylogenetic analyses were conducted using maximum likelihood (ML; Felsenstein 1981) and Bayesian inference (BI; Huelsenbeck and Ronquist 2001). The DNA substitution model (GTR+I+G) was identified by ModelTest as the most appropriate model for analysis (Posada and Crandall 1998), and each codon position was treated as a separate partition. Maximum liklihood searches were implemented in RAxML v7.2.7 (Stamatakis 2006) as implemented through the CIPRES web portal (http://www.phylo.org/). The ML tree was selected based on the combined results of 1,000 replicated searches. Clade support for the concatenated data was assessed with nonparametric bootstrapping (BS) and Bayesian posterior probabilities (PP). Bootstrap support values were estimated by 1,000 ML bootstrap searches in RAxML using search procedures above. The resulting trees from BS were summarized with a 50% majority rule consensus tree (not shown) in Mesquite v3.02 (Maddison and Maddison 2015). Bayesian inference analyses to obtain PP were conducted in MrBayes v3.2.3 (Ronquist et al. 2012) through the CIPRES web portal with the following options: 4 Markov chains, 10 million generations, and sample frequency every 1,000th generation. The first 1,000 trees were discarded as burn-in based on stabilization of likelihood scores.

In addition, pairwise genetic distances were estimated using *Cyt*b data under the Kimura 2-parameter model of evolution (Kimura 1980). Average genetic distances were estimated for selected clades, and values were used to infer levels of genetic divergence between taxonomic groups. Comparisons of genetic distances between recognized sister species pairs within the closely related genus *Rhipidomys* (Costa et al. 2011; Schenk et al. 2013) were used as benchmarks for evaluating levels of genetic divergence between and within clades in *Thomasomys* following the rationale outlined in Bradley and Baker (2001), Baker and Bradley (2006), and Salazar-Bravo and Yates (2007).

RESULTS

Survey results.—In total, 142 specimens of 14 species of small mammals were collected. Thirteen species were collected at 3,340 m and three species at 3,650 m (Table 1). Four rodent species, *Microryzomys altissimus*, *Neusticomys monticolus*, *Thomasomys vulcani*, and *T. ucucha*, as well as the cervid *Mazama rufina*, represent new range records. Additionally, *Myotis keaysi* and *T. ucucha* represent elevation records.

ORDER DIDELPHIMORPHIA
Family Didelphidae
***Didelphis pernigra* Allen, 1900**
Andean White-eared Opossum

One male specimen (QCAZ 15034) was collected in a grassy field next to the biological station's structure located in the temperate forest. The specimen shows white ears and a black stripe on the mid-dorsum of the otherwise white head. The rest of the specimen's body is black. The tail was proximally black and distally white. Tirira and Boada (2009) recorded this species as present in Guandera, but no specimen was used to document this species in their study. Instead they reported the presence of footprints as evidence of the species occurrence.

ORDER CHIROPTERA
Family Phyllostomidae
***Sturnira bidens* Thomas, 1915**
Bidentate Andean Fruit Bat

Thirteen specimens (QCAZ 15035-15047) were collected in the temperate forest. All individuals were males. This species can be distinguished by two lower incisors instead of the typical four for the genus (Giannini and Barquez 2003). These specimens were

Table 1. Presented are range status, collecting site, and measurements (mm) of mammal specimens collected in or near Guandera Biological Reserve, Ecuador. Range designations are as follows: R = major range records (species not recorded previously in Guandera or within 70 km of the study sites); E = elevation distribution record for the eastern Ecuadorean Andes; Known = species previously documented from Guandera Biological Reserve.

Species	Range	Site	Total length	Tail length	Hind foot length	Ear length	Forearm length
Didelphis pernigra	Known	1	764	411	56	45	N/A
Sturnira bidens	Known	1	59-71	0	10-18	15-20	42.1-44.9
Sturnira erythromos	Known	1	56-62	0	11	13-17	33.2
Myotis keaysi	E	1	96	41	8	10	43.4
Mazama rufina	R	1	N/A	N/A	N/A	N/A	N/A
Microryzomys altissimus	R	2	194	110	22	15	N/A
Microryzomys minutus	Known	1	169-179	100-109	20-21	14	N/A
Nephelomys albigularis	Known	1	292-306	153-163	34-35	22-24	N/A
Neusticomys monticolus	R	1	223	110	27	11	N/A
Reithrodontomys mexicanus	Known	1	164-192	94-123	16-21	13-22	N/A
Thomasomys baeops	Known	1	240-245	135-140	25	13-16	N/A
Thomasomys cinnameus	Known	1 and 2	195-227	114-128	22-25	12-18	N/A
Thomasomys vulcani	R	1	222-258	111-135	26-32	16-22	N/A
Thomasomys ucucha	R, E	1 and 2	260-266	150-151	25-31	17-18	N/A

collected well within the documented range (Gardner 2007; Tirira and Boada 2009).

***Sturnira erythromos* (Tschudi, 1844)**
Hairy Yellow-shouldered Bat

Two specimens (QCAZ 15051 and 15052) were collected in the temperate forest. The mastoidal breadth (11.33 mm) and the mandibular toothrow (6.90 mm) are indicative of *S. erythromos*. However, the specimens possessed a forearm length >42 mm, were all gray in color with no shoulder spots, and the condylobasal length of one specimen was 19.74 mm. These characters indicate that it is morphologically similar to *S. bogotensis* (Giannini and Barquez 2003). These specimens were collected well within the documented geographic range for *S. erythromos* (Tirira 2007; Gardner 2007), and the species previously was documented from Guandera (Tirira and Boada 2009).

Family Vespertilionidae
***Myotis keaysi* Allen, 1914**
Hairy-legged Myotis

One male specimen (QCAZ 15032) was collected in a mist net set at the edge of a secondary forest and a small agricultural field near the temperate forest. This specimen represents an elevation record at 3,340 m for Ecuador. The previous record was 2,950 m (Tirira 2007).

ORDER ARTIODACTYLA
Family Cervidae
***Mazama rufina* (Pucheran, 1851)**
Ecuador Red Brocket

The occurrence of a male *Mazama rufina* (QCAZ 15053) was documented by the presence of a partial skull with antlers that was salvaged from the temperate forest at the 3,340 m site. The identification was consistent with descriptions given by Hershkovitz (1982) and confirmed by Eliécer E. Gutiérrez (pers. comm.). No other cervids are known from this area (Tirira 2007) and this is the first physical record from the site. Previously, this species was thought to occur at Guandera based on interviews with people from the area (Tirira and Boada 2009).

ORDER RODENTIA
Family Cricetidae
***Microryzomys altissimus* (Osgood, 1933)**
Highland Small Rice Rat

One male (QCAZ 15050) was collected in the páramo at the 3,650 m site. The incisor tubercle of this specimen was shorter when compared with *M. minutus* (QCAZ 11931, 11935, 11936, from Atillo Lagoons, Chimborazo, and QCAZ 15048 from San Francisco, Carchi). The cranial pelage was hispid and grizzled brownish gray and the dorsum was grizzled brown. These characters separate this species from *M. minutus* (Carleton and Musser 1989). The tail in this specimen is bicolored, and the feet have long white hair. The ventral fur is a cream color. This species has not been recorded in Guandera but has been found in another location in Carchi Province (Carleton and Musser 1989; Tirira 2007; Tirira and Boada 2009).

***Microryzomys minutus* (Tomes, 1860)**
Montane Small Rice Mouse

One male and one female (QCAZ 15048 and 15049) were collected in the temperate forest site. These specimens conform to published descriptions. For example, the tail is monocolored, the dorsoventral pelage does not contrast, and the feet are brown with short hair (Carleton and Musser 1989).

***Nephelomys albigularis* (Tomes, 1860)**
White-throated Rice Rat

Two *Nephelomys albigularis*, one male and one female (QCAZ 14932 and 14933), were collected at the 3,340 m site. The alisphenoid strut was absent in both specimens, which separates this species from the morphologically similar species, *N. moerex* (Weksler and Percequillo 2011). Further, the throat was white in these specimens, a character that is absent in *N. moerex*. This species was documented by Tirira and Boada (2009) at Guandera.

***Neusticomys monticolus* Anthony, 1921**
Montane Ichthyomyine

One *Neusticomys monticolus* (QCAZ 15033) was collected in a small muddy bottom stream that was only

8 cm wide. The hindfeet had weakly developed fringing hair that is typical of this species and distinguishes it from other Icthyomyine species in Ecuador (Voss 1988). There are no previous records of *N. monticolus* from Carchi Province (Packer and Lee 2007; Tirira and Boada 2009; Voss 1988). The most proximate record is from Imbabura (Voss 1988; Tirira 2007).

***Reithrodontomys mexicanus soderstromi* Thomas, 1898**
Ecuadorian Harvest mouse

Fifteen male and 17 female harvest mice (QCAZ 14934–14965) were collected in the temperate forest site. These specimens have dark hindfeet with white toes, in contrast to another collection of *R. m. soderstromi* from Pichincha that has white hind feet. All specimens had grooved upper incisors that distinguishes this species from most other Ecuadorean rodents.

***Thomasomys baeops* Osgood, 1914**
Short-faced Thomasomys

One male, one female, and one juvenile were collected (QCAZ 14931, 14966, and 14967). The identification of this species was confirmed by characters presented by Voss (2003) and Pacheco (2015). These characters include: length of hind foot <25 mm, auditory bullae small and uninflated, maxillary molar row ≥4.2 mm, and no white tipped tail (Voss 2003). Furthermore, *Cyt*b haplotypes from these specimens clustered with specimens we considered to be *T. baeops* and those identified as such on GenBank (see *DNA sequence analysis*).

***Thomasomys cinnameus* Anthony, 1924**
Cinnamon-colored Thomasomys

Six females and three males were collected from the temperate forest and one from the páramo (QCAZ 14913–14922). Color of the fur and skeletal characteristics were used to distinguish this species. *Thomasomys cinnameus* is similar in external appearance to *T. paramorum*; however, *T. cinnameus* is smaller in total length and is a more uniform cinnamon brown color than *T. paramorum*. Furthermore, the color is consistent with that described by Anthony (1924). *Thomasomys cinnameus* can be separated from *T. paramorum* by cranial characters such as uninflated auditory bullae in *T. cinnameus* (Voss 2003). Other characters used to identify the specimens of *T. cinnameus* are: the presence of primitive carotid circulation pattern, an alisphenoid strut, and long incisive foramina (Voss 2003). The Guandera specimens are larger overall and lighter in color than the specimens from Sangay (Lee et al. 2011). Both samples were identified as *T. cinnameus* according to a key and descriptions presented by Pacheco (2015). Pacheco (2015) suggests that there is more than one taxon currently recognized in this group. This assertion of two taxa is supported by the *Cyt*b data (see *DNA sequence analysis*).

***Thomasomys ucucha* Voss, 2003**
Ucucha Thomasomys

Two individuals of *T. ucucha* were collected, one male and one female (QCAZ 14930 and 14968). This is the first record of this species from Guandera and only the second outside of Papallacta, which is 120 km southeast of Guandera (Voss 2003). Other specimens from Carchi are from Los Encinos and Ipuerán (Arcos et al. 2007). These specimens were collected from both the páramo and the temperate forest. These specimens represent a slight elevation record because they were collected lower (at 3,340 m) than those previously reported (Arcos et al. 2007; Voss 2003). The characters used to distinguish this animal from other *Thomasomys* are: distinct capsular process of the lower incisor alveolus, primitive carotid circulation pattern, presence of an alisphenoid strut, and very short incisive foramina (Voss 2003). The specimens present a light gray tip of the tail fur and dark gray ventral pelage. These specimens are similar to *T. hylophilus*, but the Carchi specimens have a distinct capsular process which distinguishes *T. ucucha* from *T. hylophilus* (Pacheco 2015; Voss 2003). A third juvenile specimen (QCAC 14929) also was collected with some morphological affinities with *T. ucucha*. However, analysis of *Cyt*b sequence indicated a very divergent *Thomasomys* lineage from *T. ucucha* (see *DNA sequence analysis*). This specimen clustered with *T. ladewii* and it has morphological similarities with that taxon according to Pacheco (2015). Additional genetic and comparative morphological analysis will be required before the taxonomic status of QCAZ 14929 is determined.

***Thomasomys vulcani* (Thomas, 1898)**
Pichincha Thomasomys

This was the most numerous species (n = 66) collected during the 2014 trip (QCAZ 14924, 14928, 14970–15031, 15054, and 15055). Notably, Tirira and Boada (2009) did not collect this species in their survey of Guandera, and the species had never been recorded in Carchi province (Tirira 2007). This species was not captured in the páramo, but it was by far the most common mammal collected in the temperate forest. Some of the characteristics used to distinguish this species were: color, head and body length, relatively short tail length, presence of an alisphenoid strut, auditory bullae small and uninflated, a primitive carotid circulation pattern, and a capsular process that is indistinct or absent (Voss 2003). The color of these specimens seems to be consistent with the original description of *T. rhoadsi* by Stone (1914), and is regarded as a synonym of *T. vulcani* by Pacheco (2015).

DNA sequence analyses.—Phylogenetic reconstructions based on *Cyt*b sequences generally provided strong to moderate support for clades representing species and sister species pairs. No clades containing more than two species, including the clade of *Thomasomys* as a whole, had greater than 50% BS or greater than 0.95 Bayesian PP (Fig. 2). Most clades containing only one species had greater than 70% BS and 0.95 PP with the following exceptions: the *T. baeops* clade had 0.98 PP but less than 50% BS; the *T. cinnameus* clade had 0.96 PP but less than 50% BS; and a clade containing *T. silvestris* and a *Cyt*b haplotype identified on GenBank as *T. caudivarius* (see discussion below) had 0.96 PP but less than 50% BS (Fig. 2). Similarly, most clades containing two sister species in this study had greater than 70% BS and 0.95 PP with the following exceptions: the clade containing *T. caudivarius* and *T. paramorum* had less than 50% BS and less than 0.95 PP; the clade containing *T. silvestris* and *T. ucucha* had 91% BS but less than 0.95 PP; the clade containing *T. oreas* and *T. andersoni* had less than 70% BS and less than 0.95 PP (Fig. 2); and the clade containing *T. ladewi* and the unidentified juvenile with morphology similar to *T. ucucha* had less than 50% BS and less than 0.95 PP (Fig. 2).

Mean genetic distances for *Cyt*b were estimated using the Kimura 2-parameter model of evolution (Kimura 1980). The mean genetic distances within intraspecific clades were less than 5.00% with the following exceptions: two *Cyt*b haplotypes of *T. oreas* (AF108677 and DQ914651) gathered from GenBank had a distance of 7.50%; a haplotype from *T. silvestris* (KR818900) and a haplotype from the voucher identified as *T. caudivarius* on GenBank (DQ914648) had a distance of 6.40% (see discussion below); and two well supported clades containing haplotypes of *T. cinnameus* had an average distance of 11.08% (Fig. 2). In contrast, all average distance values between sister species clades sampled in this study were greater than 5.00% and ranged from 6.80% to 11.55% (Fig. 2).

DISCUSSION

Results of this study are directly comparable to an earlier small mammal survey of Guandera Biological Reserve (Tirira and Boada 2009). Both surveys reported 14 small mammal species. Tirira and Boada (2009) collected seven bat species as opposed to three reported herein; however, the current survey reports more rodent species (nine to their six). Both surveys report one marsupial species each and the recent survey collected a *Mazama* skull. Perhaps the most defining difference between the surveys is that the current survey reports the most common animal sampled (n = 66) was *T. vulcani*, whereas Tirira and Boada (2009) reported none from their 2003 survey. The most common animal in the Tirira and Boada (2009) survey was *T. baeops* (n = 32). It is difficult to determine why *T. vulcani* was not caught in the 2003 survey. Some points to consider: first, eleven years separate the two surveys; the amplitude of rodent population dynamics from year to year can be great. Second, the Tirira and Boada (2009) study was conducted in October, whereas our study was conducted in July and August. The possibility of seasonal changes in the ecosystem may explain the differences.

Elevational patterns of species diversity remain unclear in many places around the world (Wen et al.

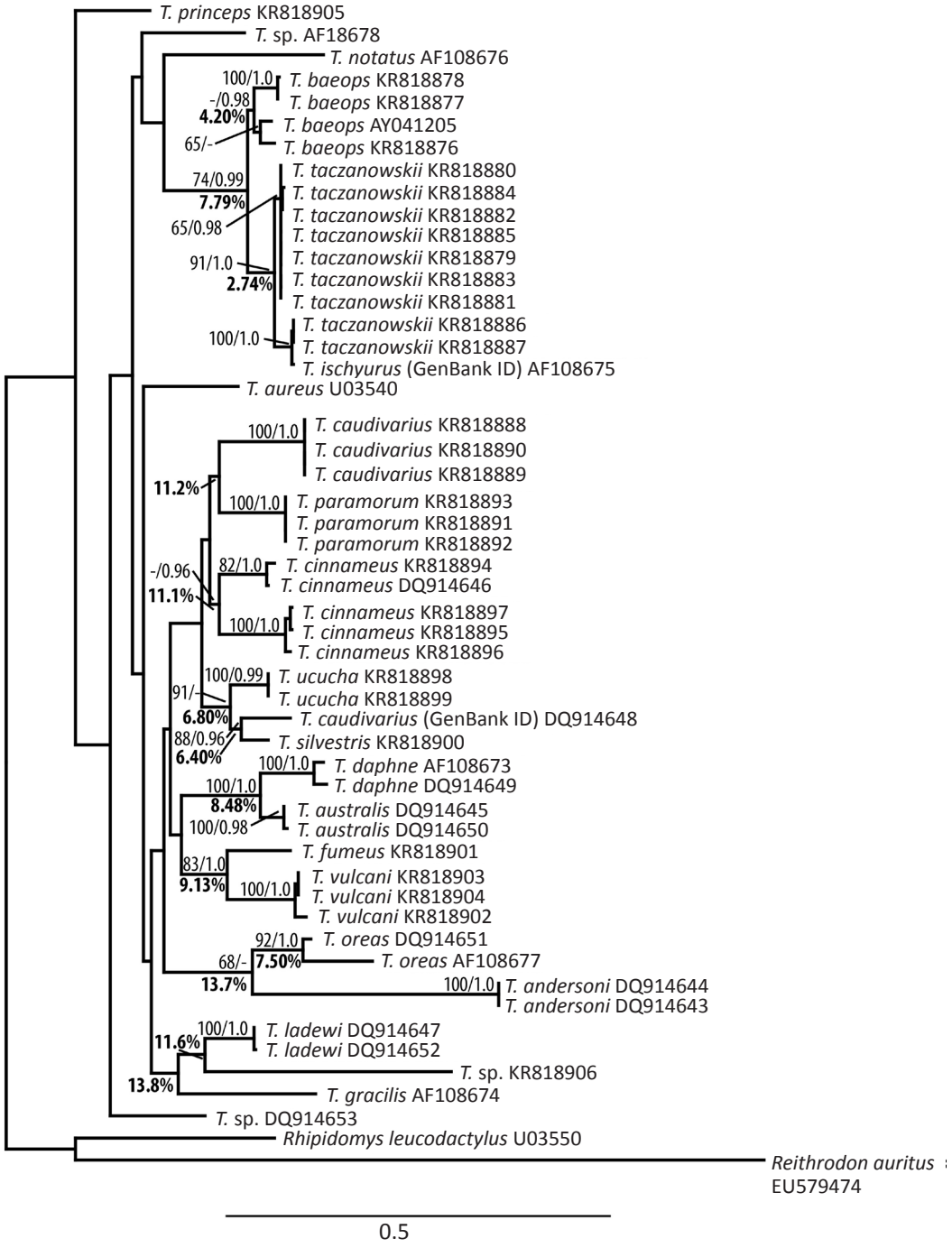

Figure 2. Maximum likelihood tree from analysis of *Cyt*b sequences, the scale bar represents nucleotide substitutions per site. Numbers at branch tips are GenBank accession numbers; numbers above branches are maximum likelihood bootstrap proportions/Bayesian inference posterior probabilities, respectively. Bootstrap proportions less than 50% and posterior probabilities less than 0.95 are not shown or are designated by a dash. Bold numbers below selected branches are average Kimura 2-parameter genetic distances between the two sister clades subtended by the branch. If GenBank accessions from previous studies designate a taxon name that conflicts with taxonomy in this study, "(GenBank ID)" is included following the taxon name.

2014). Most of these studies focus on species richness and diversity (McCain 2005); whereas, few provide data of the abundance of animals at various elevation points. A comparison of the effect of elevation on Ecuadorian rodents can be made by looking at past studies (Table 2). In general, the collection effort, sampling techniques, and the time of year that the surveys took place were the same in studies conducted by Lee et al. (2006a, 2006b, 2008, 2010, 2011). These studies reveal an ecological gradient and turnover of cricetid rodents (at the taxonomic level of tribe) that occurs between 2,070 m and 2,500 m (Fig. 3). Between these two elevation points, Oryzomyini and Thomasomyini rodents shift, or turnover, in total abundance (Fig. 3). Patterns like these are sometimes missed because of the concentration of effort to document range records (records on a flat map) and elevation records. If, instead of range, the focus is on abundance, then another pattern emerges (Fig. 3). Many studies have examined change due to elevation in mammalian diversity (Patterson et al. 1989, 1996; McCain 2005; Wen et al. 2014). These studies demonstrate that diversity peaks for non-volant mammals at mid-elevations and they reveal patterns, such as decline in bat diversity and increase in cricetid rodent diversity, with increased elevation. These data are further supported by Lee et al. (2006a, 2006b, 2008, 2010, 2011) (Table 2).

At low elevations, 450–700 m, there are very few cricetid rodents in terms of abundance, although the number of species is high and these are mostly of the tribe Oryzomyini (Fig. 3). Furthermore, a large percentage of the low elevation rodents are non-cricetid species. From 1,500 to 2,100 m, the number of cricetid rodents increases, and most are Oryzomyini rodents. Most Oryzomyini rodents are in the genera *Nephelomys* and *Oreoryzomys* from 1,500 to 2,100 m. Above 2,500 m, Thomasomyini rodents are in the majority in terms of diversity (numbers of species) and numbers of individuals. Oryzomyini rodents above 2,500 m are usually in the genera *Microryzomys* and *Nephelomys* (Fig. 3, Table 2). A few species of *Thomasomys* are found as low as 1,200 m (Tirira 2007). However, it seems that *Thomasomys* is the majority (in numbers and diversity) only above 2,500 m, and about half the species in Ecuador have no record of occurrence below 2,500 m (Tirira 2007). More surveys are needed from both sides of the Andes to further confirm these observations.

In light of remarks made by Pacheco (2015), we need to address some of the taxonomic decisions with regard to this study and two past publications (Lee et al. 2008, 2011). We used information from keys and descriptions in Pacheco (2015), in conjunction with *Cyt*b sequence data, to identify all *Thomasomys* specimens presented in this study. Following criteria in Bradley and Baker (2001), Baker and Bradley (2006), and Salazar-Bravo and Yates (2007), sister species pairs within a closely related genus were used as benchmarks for evaluating levels of genetic divergence between and within species in *Thomasomys*. Genetic distances between sister species pairs in *Rhipidomys* reported by Costa et al. (2011) were 4.11%, 6.10%, and 8.27%, which are in close agreement with the 5% rule of thumb proposed by Baker and Bradley (2006).

With both morphological characters, using Pacheco's (2015) key, and *Cyt*b comparison with *T. vulcani*, we can further confirm that this taxon from Volcán Sumaco is *T. fumeus*. *Cyt*b sequence data suggest that *T. vulcani* and *T. fumeus* are sister taxa but that they are likely distinct species with an average genetic distance of 9.13% (Fig. 2). These data conform to the understanding of the relationship between these two species (Pacheco 2015).

Specimens identified as *T. praetor* by Lee et al. (2011) are *T. princeps* according to description by Pacheco (2015). The specimens of *T. princeps* particularly are similar with regard to the description of the hind foot and dorsal coloration (Pacheco 2015). *Thomasomys princeps* previously have been recorded only from the eastern slope of the Andes in Colombia (Pacheco 2015).

Specimens attributed to *T. silvestris* in Lee et al. (2011) conform more closely with descriptions of *T. caudivarius* (Pacheco 2015). These specimens of *T. caudivarius* were collected in Sangay National Park. They are similar in morphology to *T. silvestris* except for the ventral coloration, which is a brown-orange in *T. caudivarius* compared with the silver-gray ventral surface of *T. silvestris*. Similarly, a voucher specimen of *T. silvestris* seems to have been misidentified as *T. caudivarius* on GenBank (*Cyt*b accession DQ914648). This haplotype was grouped with our *T. silvestris* haplotype (0.96 PP). However, the genetic distance between these two haplotypes was moderately high (6.40%),

Table 2. Comparison of bat, rodent, and overall mammalian species composition between this study and previously conducted studies in Ecuador. Data are presented in order from lowest to highest elevation. H^p represents Shannon (1948) values.

Location	Elevation	Site Number (see Fig. 1)	Bat species recorded	H^p for bats	Rodent species recorded	H^p for rodents	Total mammal species recorded	H^p for mammals
Santa Rosa (Lee et al. 2010)	450 m	6	16	1.10	5	0.61	23	1.23
Santa Rosa (Lee et al. 2010)	702 m	6	10	0.86	4	0.60	15	1.03
Santa Rosa (Lee et al. 2010)	450–702 m	6	22	1.19	8	0.79	32	1.31
Otonga (Jarrín and Fonseca 2001)	1,300–2,300 m	7	18	1.02	N/A	N/A	N/A	N/A
Tandayapa (Lee et al. 2006a)	1,500–2,000 m	3	13	0.88	3	0.23	19	0.99
Guajalito (Jarrín and Fonseca 2001)	1,800–2,000 m	Not shown	16	1.03	N/A	N/A	N/A	N/A
Cosanga (Lee et al. 2006b)	1,900–2,100 m	4	15	0.82	3	0.12	20	0.91
Otonga (T. Lee, unpublished)	2,072 m	7	8	0.83	7	0.34	20	0.75
Volcan Sumaco (Lee et al. 2008)	2,500 m	5	8	0.58	4	0.48	12	0.84
Sangay National Park (Lee et al. 2011)	2,962 m	9	4	0.50	5	0.67	10	0.84
Sangay National Park (Lee et al. 2011)	3,400 m	8	0	N/A	8	0.66	10	0.75
Sangay National Park (Lee et al. 2011)	2,962–3,400 m	8 and 9	4	0.50	8	0.73	15	0.88
Guandera Biological Reserve (Tirira and Boada 2009)	3,340–3,650 m	1 and 2	7	0.76	6	0.61	14	0.99
Guandera Biological Reserve (this study)	3,340–3,650 m	1 and 2	3	0.26	9	1.07	14	1.15

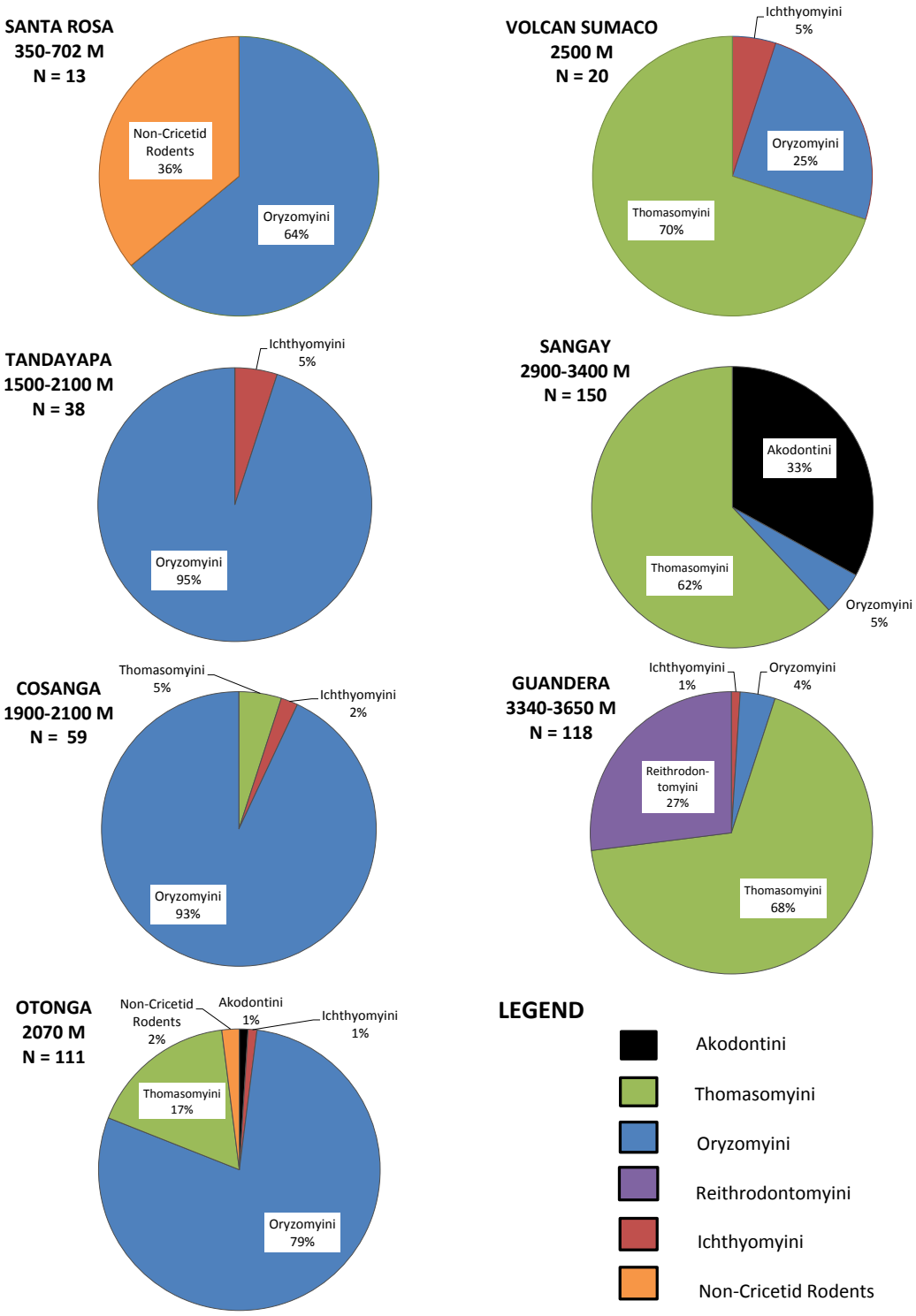

Figure 3. Comparative ecological sample data of Cricetid rodents from seven locations surveyed in Ecuador (see Fig. 1 for survey locations). The pie charts are arranged from lowest to highest elevation, and each chart is arranged at the taxonomic level of Cricetid tribe.

suggesting that the haplotypes were sampled from distantly related populations if not separate species. Together, the haplotypes in this clade were strongly supported as sister to *T. ucucha* (Fig. 2). In contrast, the vouchers currently identified as *T. caudivarius* are weakly supported as sister to *T. paramorum* and have an average genetic distance of 11.70% from *T. sylvestris* (Fig. 2).

Finally, specimens identified as *T. baeops* from Sangay National Park (Lee et al. 2011) cluster more closely with *T. taczanowskii* in reconstructions based on *Cyt*b (Fig. 2). This clade of Sangay haplotypes had an average genetic distance of only 2.74% from *T. taczanowskii* haplotypes sampled from Peru. Together, haplotypes in the *T. taczanowskii* clade had an average genetic distance of 7.79% from *T. baeops*, suggesting that *T. baeops* and *T. taczanowskii* identified in this study are distinct species (Fig. 2). However, some characters presented by Pacheco (2015), such as the length of the incisive foramina, are more similar to that of *T. baeops* with regard to the Sangay specimens. All of the Sangay specimens have a white tipped tail and very few of our specimens that we assigned to *T. baeops* from localities other than Sangay share this character. In agreement with *Cyt*b results, the white tipped tail is more closely associated with *T. taczanowskii* than with *T. baeops* (Pacheco 2015).

Two species sampled for *Cyt*b haplotypes exhibited unusually large intraspecific genetic distances, prompting further investigation. Haplotypes of *T. oreas* had a distance of 7.50%, and two clades of *T. cinnameus* haplotypes had an average distance of 11.08% (Fig. 2). Although these data suggest that the *T. oreas* haplotypes represent different species, 7.50% genetic divergence is still lower than between many sister species in *Thomasomys*. In contrast, the clades within *T. cinnameus* differ more than most sister species within the genus, suggesting that *T. cinnameus* is very likely composed of two species (Fig. 2). Pacheco has suggested that *T. cinnameus* could represent more than one taxon (Pacheco 2015), and the status of *T. cinnameus* has become a priority in the ongoing investigation of species boundaries and phylogenetic relationships within the genus *Thomasomys* through increased taxonomic and molecular sampling.

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APPENDIX

Specimens examined.—Specimens used for molecular analysis in this study are listed below by locality. Museum accession numbers and GenBank accession numbers for *Cyt*b sequences are listed in parentheses, respectively. Museum acronyms follow Hafner et al. (1997), and abbreviations for identification numbers are as follows: Abilene Christian University Natural History Collections (ACUNHC); Museum of Vertebrate Zoology (MVZ); Museo de Zoología de la Pontificia Universidad Católica del Ecuador (QCAZ).

Thomasomys baeops (3).—ECUADOR: Carchi, Guandera Biological Reserve (ACUNHC 1866, KR818878; ACUNHC 1892, KR818877); Napo, Volcan Sumaco (ACUNHC 1355, KR818876).

Thomasomys caudivarius (3).—ECUADOR: Chimborazo, Sangay National Park (ACUNHC 1592, KR818888); Morona Santiago, Sangay National Park (ACUNHC 1554, KR818890; ACUNHC 1557, KR818889).

Thomasomys cinnameus (4).—ECUADOR: Carchi, Guandera Biological Reserve (ACUNHC 1898, KR818895; ACUNHC 1899, KR818896; QCAZ 14913, KR818897); Chimborazo, Sangay National Park (ACUNHC 1564, KR818894).

Thomasomys fumeus (1).—ECUADOR: Napo, Volcan Sumaco (ACUNHC 1339, KR818901).

Thomasomys paramorum (3).—ECUADOR: Chimborazo, Sangay National Park (ACUNHC 1549, KR818893; ACUNHC 1600, KR818891; ACUNHC 2247, KR818892).

Thomasomys princeps (1).—ECUADOR: Morona Santiago, Sangay National Park (ACUNHC 1560, KR818905).

Thomasomys silvestris (1).—ECUADOR: Cotopaxi, Otonga Nature Reserve (QCAZ 13067, KR818900).

Thomasomys sp. (1).—ECUADOR: Carchi, Guandera Biological Reserve (ACUNHC 1893, KR818906).

Thomasomys taczanowskii (9).—ECUADOR: Chimborazo, Sangay National Park (ACUNHC 1570, KR818881; ACUNHC 1598, KR818879; ACUNHC 1609, KR818880); Morona Santiago, Sangay National Park (ACUNHC 1594, KR818883; ACUNHC 1614, KR818882; QCAZ 11945, KR818884; QCAZ 11947, KR818885); PERU: Cajamarca; Rio Zana, 2.5 km NE Monte Seco on trail to Chorro Blanco (MVZ 181999, KR818886; MVZ 182003, KR818887).

Thomasomys ucucha (2).—ECUADOR: Carchi, Guandera Biological Reserve (ACUNHC 1890, KR818899; QCAZ 14969, KR818898).

Thomasomys vulcani (3).—ECUADOR: Carchi, Guandera Biological Reserve (ACUNHC 1908, KR818903; QCAZ 14925, KR818902; QCAZ 14926, KR818904).

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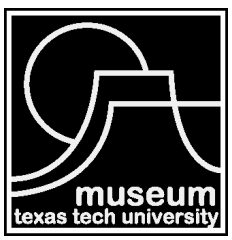

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