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Rodents of the eastern and western slopes of the Tropical Andes: phylogenetic and taxonomic insights using DNA barcodes

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The Andes Mountains particularly the forests along the mid-elevations of their eastern and western slopes, are a hotspot of biodiversity (high numbers of species and endemics). Among mammals, rodents are a priority group for study in the Tropical Andes given their high diversity and often relatively small geographic ranges. Here, we use DNA barcoding as a tool to help in the identification, and preliminary analysis of the phylogenetic relationships, of rodents from two natural reserves: Otonga, a private forest reserve, located on the western slopes, and Sangay National Park, located on the eastern slopes of the Ecuadorian Andes. We sequenced 657 bp of the mitochondrial Cytochrome Oxidase I (COI) gene for 201 tissue samples of sigmodontine and echimyid rodents collected primarily in Otonga and Sangay. We conducted phylogenetic analyses using maximum-likelihood and Poisson tree processes (PTP) species delimitation analyses. Three sets of data were analyzed: 1) our newly generated sequences, 2) our *Mesomys* sequence plus DNA sequences of Echimyidae available in GenBank, and 3) all of our sequences (all Sigmodontinae and one Echimyidae) together with relevant DNA sequences of Sigmodontinae available in GenBank. Our samples consisted of 24 species; the molecular data indicated that only one species—*Microryzomys minutus*—was shared between both eastern and western localities. Contrary to the currently recognized distributions of *Akodon mollis* and *Chilomys instans,* our species delimitation analysis suggests that these species are not shared between Otonga and Sangay, and may actually represent two species each. The sample of *Mesomys* from the eastern slopes of the Andes differs minimally from that from the lowlands of the Ecuadorian Amazon, suggesting that both populations would correspond to the same species, *Mesomys hispidus*. Both *Mindomys hammondi* and an undescribed *Mindomys* from Otonga do not form a reciprocally monophyletic group with relation to *Nephelomys*. The *Nephelomys* of Sangay might correspond to two different species. The eastern and western slopes of the Tropical Andes harbor different species of rodents, with only one of our study species shared between both localities, implying that other cases of shared species between the eastern and the western slopes of the Andes need further assessment. Several lineages represented in our sample may require formal taxonomic description, highlighting the need for further systematic research. The new genetic data generated in our study could speed taxonomic discovery in the Andes and help to illuminate interesting evolutionary patterns, such as the radiation of *Thomasomys*.

Los Andes particularmente los bosques de las elevaciones medias de las estribaciones occidentales y orientales, son un punto caliente de biodiversidad (alto número de especies y de endemismo). Entre los mamíferos andinos, los roedores son un grupo prioritario a ser estudiado dada su alta biodiversidad y sus rangos de distribución que por lo general son pequeños. En esta contribución, usamos códigos de barras de ADN como una herramienta para la identificación y generación de hipótesis filogenéticas preliminares de los roedores colectados principalmente en dos reservas naturales: Otonga, ubicada en las estribaciones occidentales, y Sangay, localizada en las estribaciones orientales de los Andes ecuatorianos. Secuenciamos 657 pares de base del gen mitocondrial Citocromo Oxidasa I (COI) en 201 muestras de tejido de roedores sigmodontinos y echimyidos colectados principalmente en Otonga y Sangay. Hicimos análisis filogenéticos usando máxima verosimilitud, y análisis de delimitación de especies mediante el proceso de árboles de Poisson (PTP). Tres grupos de datos fueron analizados: 1) todas nuestras nuevas secuencias generadas, 2) nuestra secuencia de *Mesomys* más las secuencias de ADN de Echimiydae disponibles en GenBank, y 3) todas nuestras secuencias (mayoritariamente Sigmodontinae) junto con secuencias de ADN de Sigmodontinae disponibles en GenBank. Nuestra muestra contiene 24 especies; los datos moleculares demuestran que solo una especie—*Microryzomys minutus*—es compartida entre ambas localidades del este y oeste. Mientras que nuestro análisis de delimitación de especies sugiere que *Akodon mollis* y *Chilomys instans* no son compartidas entre Otonga y Sangay, y representan dos especies cada una. La muestra de *Mesomys* de la vertiente oriental de los Andes es mínimamente diferente de secuencias de las tierras bajas de la Amazonia ecuatoriana; recomendando que ambas poblaciones podrían corresponder a la misma especie, *Mesomys hispidus*. *Mindomys hammondi* y una especie no descrita de *Mindomys* de Otonga no forman un grupo monofilético en relación a *Nephelomys*.

Los *Nephelomys* de Sangay corresponderían a dos especies diferentes. Las vertientes occidental y oriental de los Andes tropicales albergan especies diferentes de roedores, con una sola especie compartida entre ambas indicando que otros casos de especies compartidas entre el este y occidente necesitan ser investigadas con mayor detalle. Múltiples especies de nuestra muestra necesitarían descripción formal, lo que revela que se requiere más investigación sistemática en la región. Los nuevos datos genéticos aquí presentados podrían acelerar los descubrimientos taxonómicos en los Andes y ayudar a explorar patrones volutivos interesantes, como la radiación de los *Thomasomys*.

Key words: *Akodon*, Andes, *Chilomys*, Echimyidae, Ecuador, *Microryzomys*, *Oligoryzomys*, *Sigmodontinae*, species delimitation, *Thomasomys*.

Introduction

The Andes Mountains encompass diverse environments along their slopes, ranging from lowland forests to glacier-covered peaks at over 6,000 meters above the sea level (masl). These different environments harbor high levels of species diversity and endemism, and together they make the Andean region one of the most important diversity hotspots on the planet (Myers *et al.* 2000). The Andean rodent fauna is no exception to these environmental trends. Recent analyses have detected several hotspots of rodent diversity along the Andes, such as the eastern slopes in Ecuador and Peru (Prado *et al.* 2015; Maestri and Patterson 2016).

The systematics of Neotropical rodents is in a phase of rapid update and improvement, triggered especially by active efforts in Latin American countries to train taxonomic specialists (Voss 2009) and by the recent availability of a synthetic treatment of the entire rodent fauna of South America (Patton *et al.* 2015). However, many systematic relationships remain to be clarified, especially in clades of Andean rodents such as akodontines and thomasomyines, as well as some oryzomyines and echimyids. Such studies have been difficult to perform due to various limitations in past collecting and inventory work (Patterson 2002), and the logistic difficulties of visiting natural history museums in foreign countries to undertake revisionary work. These difficulties are evidenced, for example, in the data gaps for rodent sampling in various areas, such as in middle elevation forests near Papallacta in eastern Ecuador (Voss 2003).

The rodent fauna of the Andean slopes of northwestern South America is rich in species of *Thomasomys*. It is not uncommon to find large (e. g., *T. aureus*), medium (e. g., *T. silvestris*), small (e. g., *T. baeops*), and very small (e. g., *T. cinnameus*) species of the genus living in sympatry (Jarrín 2001; Pacheco 2003, 2015; Lee *et al.* 2011). Other components of the rodent fauna of the Andean forests include oryzomyines such as *Microryzomys, Nephelomys*, *Oreoryzomys,* and the enigmatic *Mindomys hammondi*, which is known from few specimens (Carleton and Musser 1989; Weksler 2006; Weksler *et al.* 2006).

The usage of molecular markers has been pivotal to accelerate and improve taxonomic work. One common approach has been the use of DNA barcodes—sequences of the mitochondrial gene COI—which have been applied successfully for facilitating identifications of specimens in Neotropical faunal surveys (Clare *et al.* 2007; Borisenko *et al.* 2008); however, this approach has not been used exhaustively with Andean mammals. Here, we use DNA barcoding as evidence to identify and conduct preliminary phylogenetic analysis of rodents from two natural reserves: Otonga, located in the western slopes of the Andes (cis-Andean), and Sangay National Park, located in the eastern slopes of the Andes (trans-Andean). Also, we explore whether populations shared between the eastern and western slopes of the Andes are likely to be conspecific, or alternately whether they represent divergent lineages that may not be recognized under current taxonomic classifications.

Materials and Methods

Sampling. We used selected samples of 21 species of rodents, primarily identified on the basis of morphological characters, collected in two Andean forests: Otonga, a private forest reserve located in the western slopes of the Andes in the province of Cotopaxi in northern Ecuador (Jarrín 2001), and Sangay National Park located in the eastern slopes of the Andes in the provinces of Chimborazo, Morona Santiago and Tungurahua in south-central Ecuador (Armstrong and Macey 1979; Fonseca *et al.* 2003; Figure 1). Three different field parties collected voucher specimens with tissues during 2006 in Otonga, and during 2010 and 2012 in Sangay. Morphological identifications of all specimens were conducted using specialized taxonomic literature (*e. g.*, Carleton and Musser 1989; Weksler 2006; Patton *et al.* 2015), and by side-by-side comparisons with voucher specimens from the following collections: Abilene Christian University (ACUNHC) in Abilene, Texas, USA; American Museum of Natural History (AMNH) in New York, New York, USA; Escuela Politécnica Nacional (MEPN) in Quito, Ecuador; Museo Ecuatoriano de Ciencias Naturales (MECN) in Quito, Ecuador; National Museum of Natural History (NMNH) in Washington DC, USA; and Pontificia Universidad Católica del Ecuador (QCAZ) in Quito, Ecuador. Some previous findings of the mammals collected by these parties have been reported elsewhere (Lee *et al.* 2011; Helgen *et al.* 2013; Ojala-Barbour *et al.* 2013; Brito and Ojala-Barbour 2014; Brito *et al.* 2014; Brito *et al.* 2017). Examined specimens are housed at different mammal collections as indicated in Appendix 1.

Laboratory work. We used the DNeasy kit (Qiagen, Valencia, California, USA), following the manufacturer´s protocol, to extract DNA of 201 samples of either liver or muscle from rodents collected in Otonga and Sangay. We performed PCR amplifications with the Illustra puReTaq Ready-To-Go PCR beads (GE Healthcare, Little Chalfont, Buckinghamshire, UK) to amplify a fragment of the mitochondrial COI gene using the "cocktail 2"—an M13-tailed primer cocktail optimized for mammals—with the primer ratios and thermal cycle conditions of Clare *et al.* (2007). We

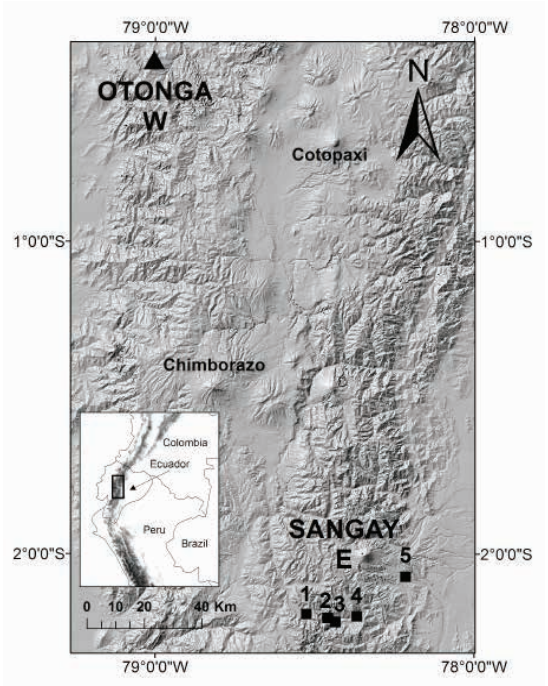

Figure 1. Otonga Reserve and Sangay National Park, localities of the rodent specimens analyzed in this study. Otonga samples were collected by Helgen *et al.* (2013). For Sangay, points 1 and 2 correspond to localities near the Atillo Lagoon sampled by Lee *et al.* (2011); and points 3 to 5 correspond to localities sampled by J. Brito and R. Ojala-Barbour (Ojala-Barbour *et al.* 2013; Brito *et al.* 2014). Chimborazo and Cotopaxi volcanoes are labeled as points of reference. Inset: map of northwestern South America indicating in a black rectangle the expanded map.

cleaned the PCR products with ExoSAP-IT (Affymetrix Inc., Santa Clara, California, USA), and conducted sequencing reactions with the ABI Big Dye chemistry (Applied Biosystems, Inc., Foster City, California, USA), using the primers M13F and M13R (Messing 1983). We sequenced the products on an ABI 3730xl DNA Analyzer automatic sequencer (Applied Biosystems, Inc., Foster City, California, USA). New sequences were deposited in GenBank (accession numbers: MF806172 – MF806372).

Phylogenetic analyses. We constructed three alignments: (A) an alignment containing our 201 newly generated sequences; (B) an alignment including our sample of *Mesomys,* a COI sequence of *Chinchilla lanigera*, and 614 sequences of the COI gene of members of the family Echimyidae (retrieved from the nucleotide database of GenBank searching for "Echimyidae COI"); C) an alignment including our 201 newly generated sequences plus 1,775 sequences of sigmodontinae rodents retrieved from GenBank with the search terms "Sigmodontinae COI". To align the sequences we used the MUSCLE (Edgar 2004) plugin in Geneious Pro v8.1.5 with default parameters. We checked the alignments manually for obvious misplacements, and trimmed all alignments to a length of 657 bp.

For each alignment we conducted phylogenetic analyses using maximum likelihood in RAxML v8 (Stamatakis 2014). We used the model GTRGAMMA for alignment A—tree A—(Figure 2) and the model GTRCAT for alignments B—tree B—(Figure 3) and C—tree C—(Figures 4 to 7). For each analysis support values were estimated using 1,000 nonparametric bootstrap pseudo replicates. For analyses A and C we used as outgroup our sequence of *Mesomys*, and of *Chinchilla lanigera* for analysis B. For each RAxML analysis, we started with a complete alignment as described above to obtain the reduced alignment (a matrix without redundant haplotypes); later, we resumed the analysis with the reduced alignment and let it finish.

Species delimitation. We performed species delimitation analyses for the best maximum likelihood trees using the Poisson tree processes (PTP) method in the bPTP web server (Zhang *et al.* 2013). The PTP method was built as an operational criterion of the Phylogenetic Species Concept (Eldredge and Cracraft 1980). PTP is a fast and accurate species delimitation method that uses as input a non-ultrametric tree; PTP models speciation rates from the number of substitutions in a phylogeny, and expects to find statistically significant differences from intra and inter specific relationships (Zhang *et al.* 2013). PTP has been successfully applied to mammals and other organism such as trypanosome parasites (Cottontail *et al.* 2014; Ermakov *et al.* 2015; Bernal and Pinto 2016), and this method has been found to be more robust than the popular GMYC method that uses time divergences from ultrametric trees which are error prone and computationally expensive to estimate (Zhang *et al.* 2013; Tang *et al.* 2014). We ran the PTP analyses for 100,000 MCMC generations for tree A, 200,000 MCMC generations for tree B, and 400,000 generations for tree C. For all analyses we set the thinning value at 100, a burn-in of 0.1, and removed outgroups to improve species delimitation.

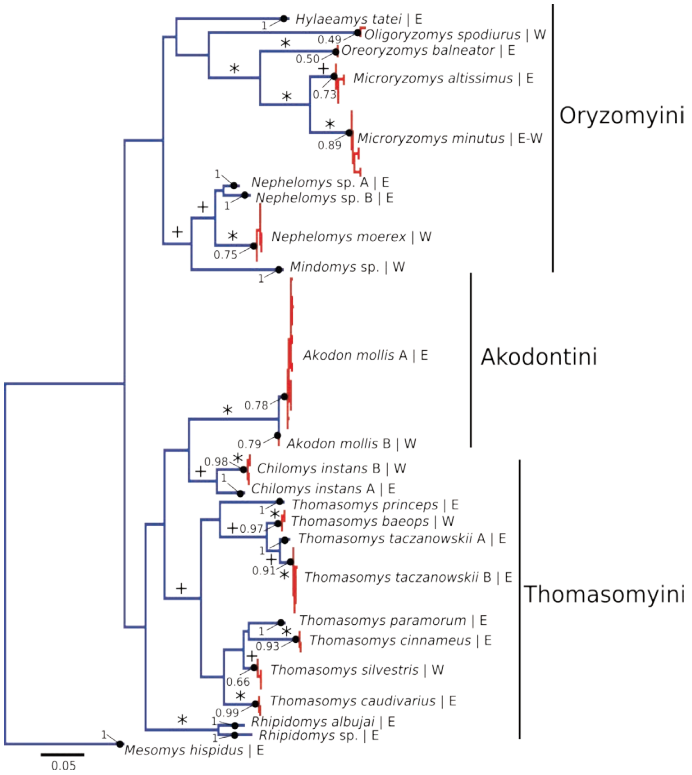

Figure 2. Maximum likelihood gene tree (tree A; see text) of unique haplotypes of the COI gene of the rodents collected in Otonga (West, W) and Sangay (East, E). Color of the branches indicates the results of the PTP species delimitation analysis: monophyletic groups in red indicate a single putative species as well as terminal branches in blue. Numbers associated with each putative species are supporting values of the PTP species delimitation; values of 1 indicate the highest possible support. Single plus symbols indicate main branches with moderate ML bootstrap values ≥75 %, and asterisks indicate main branches with strong ML bootstrap values ≥95 %.

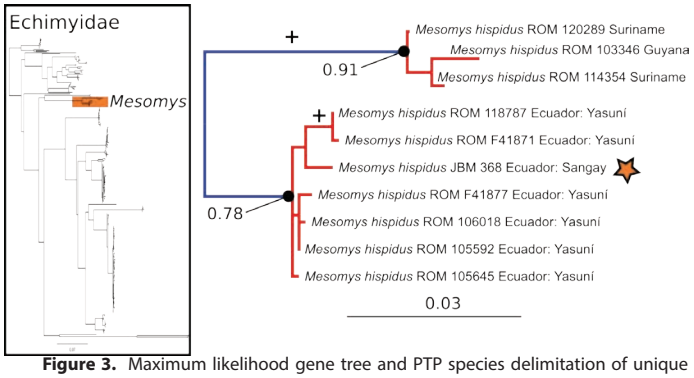

Figure 3. Maximum likelihood gene tree and PTP species delimitation of unique haplotypes of the COI gene of the rodents of the family Echimyidae available in GenBank plus the sample of *Mesomys* collected at Sangay in the eastern slopes of the Ecuadorian Andes (inset); main figure panel is a zoom-out of tree to depict only the genus *Mesomys*, showing two putative species within *M. hispidus*. Colors, symbols and support values correspond to the same as in Figure 2. Names of terminals indicate sample codes and geographic origin of the samples; sequences retrieved from GeneBank keep their original identifications. Star indicates the sample of *Mesomys hispidus* from Sangay.

Results

Our maximum likelihood gene tree A (Figure 2) recovered a paraphyletic tribe Thomasomyini (represented in our sample by *Thomasomys*, *Chilomys*, and *Rhipidomys*) relative to *Akodon mollis*; however, the members of the Oryzomyini were recovered as a monophyletic group (Figure 2). The maximum likelihood species delimitation analysis in PTP of tree A returned 24 candidate species. Even though we expected three shared species between both sides of the Andes (Figure 1), the molecular data supported that only one species—*Microryzomys minutus*—was shared between both eastern and western localities. In contrast, *Akodon mollis*, and *Chilomys instans* show structured variation, with percentage of difference >1.4 % between both putative species of *Akodon* and 7 % between the putative species of *Chilomys*. Also, our species delimitation suggests that *Thomasomys taczanowskii* is comprised of two putative species, both distributed in the Eastern slopes of the Andes; the divergence between both is 3 % (Figure 2).

The maximum likelihood gene tree of the family Echimyidae — tree B — (Figure 3) contained 281 unique terminals, and the maximum likelihood PTP analysis of species delimitation returned 42 candidate species. The sample of *Mesomys* from the eastern slopes of the Andes is nested with sequences of Yasuní National Park from the lowlands of the Ecuadorian Amazonia, confirming that both populations likely correspond to the same species (Figure 3).

The COI gene tree of the subfamily Sigmodontinae (tree C; Figures 4 to 7) consisted of 1,020 unique sequences, and the maximum likelihood species delimitation returned 153 candidate species. The genus *Oligoryzomys* was recovered as polyphyletic. The Otonga samples of *Oligoryzomys destructor* are sister to a clade of *Oligoryzomys* species including 6 candidate species within *O. fulvescens* and a sample identified as *O. nigripes* (Figure 4). The genera *Mindomys* and *Nephelomys* form a monophyletic group. However, the genus *Mindomys* (*M. hammondi* and an undescribed *Mindomys* from Otonga) was not recovered monophyletic (Figure 5). The specimens of *Nephelomys* from Sangay National Park might correspond to two different species, with a divergence of 5.6 %, and *Nephelomys moerex* from Otonga is sister to two *Nephelomys* species from Central America (Figure 5). The genus *Hylaeamys* was recovered as monophyletic and *H. tatei* was nested well inside the genus, as sister to a clade comprised of 6 candidate species currently identified within *H. yunganus* (Figure 6). Both species of *Rhipidomys* from Ecuador form a monophyletic group sister to a clade formed by *R. scandens*, *R. leucodactylus* (2 putative species), and *R. nitela* (Figure 7).

Discussion

The DNA barcoding initiative was established as a fast and universal approach to speed the discovery and identification of species (e. g., Hebert *et al.* 2003; Hebert and Gregory 2005; Harris and Bellino 2013). However, using the mito-

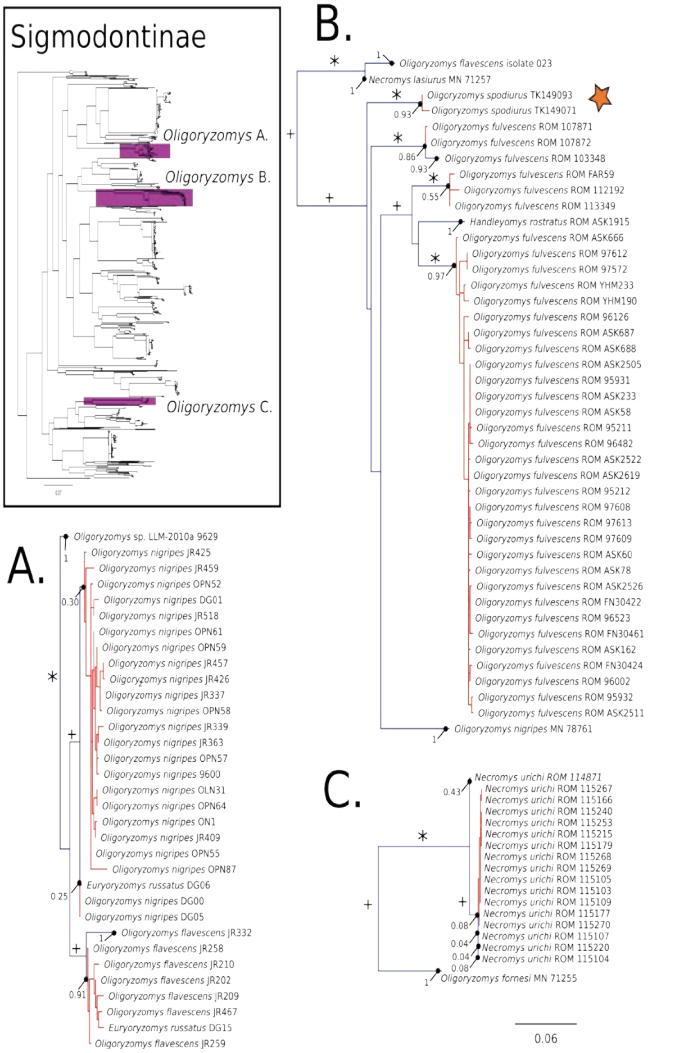

Figure 4. Maximum likelihood gene tree and PTP species delimitation of unique haplotypes of the COI gene of the rodents of the subfamily Sigmodontinae available in GenBank plus our sample (Appendix 1) collected in Otonga Reserve and Sangay National Park (inset). Main figure panels are zoom-outs of the three clades were appear representatives of *Oligoryzomys*. Colors, symbols and support values correspond to the same as in Figure 2. Names of terminals indicate sample codes; sequences retrieved from GeneBank keep their original identifications. Star indicates the samples of *Oligoryzomys spodiurus* from Ontonga. *Oligoryzomys* is depicted as a paraphyletic genus; this is regarded as a spurious result (see text). True *Oligoryzomys* is depicted in clade B.

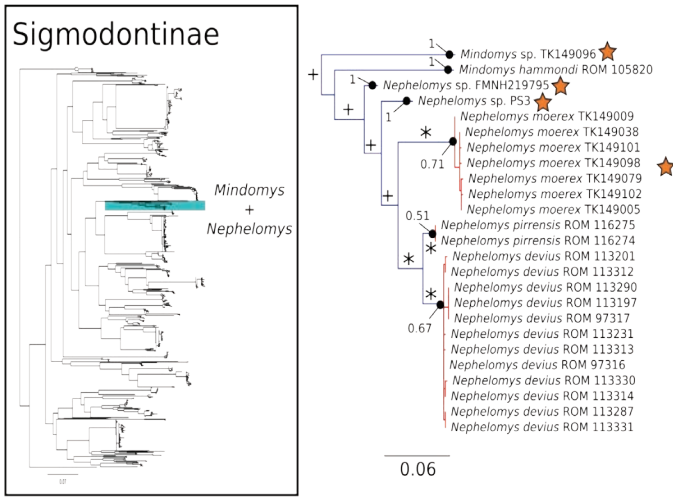

Figure 5. Maximum likelihood gene tree and PTP species delimitation of unique haplotypes of the COI gene of the rodents of the subfamily Sigmodontinae available in GenBank plus our sample (Appendix 1) collected at Otonga Reserve and Sangay National Park (inset). Main figure panel is a zoom-out of the *Mindomys* + *Nepehelomys* clade. Colors, symbols and support values correspond to the same as in Figure 2. Names of terminals indicate sample codes; sequences retrieved from GeneBank originally identified as *N. albigularis* were reclassified as *N. devius* and *N. pirrensis* based on their geographic origins. Stars indicate the species of *Mindomys* and *Nephelomys* sequenced for this study.

chondrial COI gene as the marker of choice for mammals has faced resistance from researchers used to working mainly with the CYTB gene; this is shown by the asymmetric number of sequences for the two markers deposited in GenBank (as of December 31st, 2016 there are 37,101 and 136,965 sequences of the mammalian COI and CYTB genes, respectively). Also it has been argued that CYTB gene performs better in deeper nodes of phylogenies, and it seems more informative for discriminating species (Tobe *et al.* 2010); however, this stance has faced criticism, as it has been demonstrated that COI gene behaves similarly to CYTB gene (Nicolas *et al.* 2012), and various studies have successfully made use of COI gene for species identifications (e. g., Clare *et al.* 2007; Borisenko *et al.* 2008). Although, we are aware that single locus phylogenies are substandard, and well-accepted phylogenetic inferences in mammals are increasingly made with larger, even genomic scale datasets (e. g., Meredith *et al.* 2011; Foley *et al.* 2016). In this study we found the COI gene to be a useful marker for species identification; however, more taxa and loci are needed to obtain robust phylogenies of these rodent taxa.

Along the Andes there are three main patterns of allopatric distributions: (1) a latitudinal pattern is evidenced when a pair of sister species are distributed one to the north and the other to the south, e. g., *Hippocamelus antisensis* (north) vs. *H. bisulcus* (south), and *Nasuella meridensis* (north) vs. *N. olivacea* (south) (Helgen *et al.* 2009; Pinto *et al.* 2016); (2) a cross Andean pattern is evidenced when a pair of sister species are distributed with one in the eastern slopes and another in the western slopes of the Andes, e. g., *Bassaricyon alleni* (east) vs. *B. medius* (west) (Helgen *et al.* 2013); and (3) altitudinal pattern is evidenced when one species is in higher elevations and its close relatives are in lower elevations, e. g., *Bassaricyon neblina* and *Dactylomys peruanus* vs. the rest of the species in their respective genera (Helgen *et al.* 2013; Upham *et al.* 2013). In this work, we highlight further possible examples of the cross Andean pattern of distributions: of the three species supposedly shared between the eastern and western slopes of the Andes, two (*Chilomys instans* and *Akodon mollis*) may represent multiple species. However, suggestion of two species within *Akodon mollis* in particular should be interpreted with caution; the scant genetic differentiation between the Otonga and Sangay specimens (< 2 %) and the fact that *A. mollis* is a widespread Andean species might suggest that intermediate lineages in the inter-Andean valleys are yet to be found, and we may have only one — not multiple — species level clades (Lee *et al.* 2011). Further sampling, and the analysis of additional morphological and genetic data will elucidate whether *A. mollis* is one or multiple species (Alvarado-Serrano *et al.* 2013). Our results from DNA barcoding provide preliminary views into biodiversity within these lineages which can be explored with other datasets, approaches, and sampling.

As noted, our results indicate that the interpretations of rodent species being widely distributed across both the eastern and western slopes of the tropical Andes should be viewed with certain caution. Of the species that we sampled in our comparisons, only *Microryzomys minutus* can be considered to indeed occupy both Andean slopes in light of our barcode data. Potentially, this Andean species is well adapted to different environments such as high elevation grasslands (páramos), Andean forests, and inter-Andean valleys. This tolerance to multiple environments would facilitate the colonization of both Andean slopes, but at the same time this may suggest that forest specialists (e. g., *Chi-*

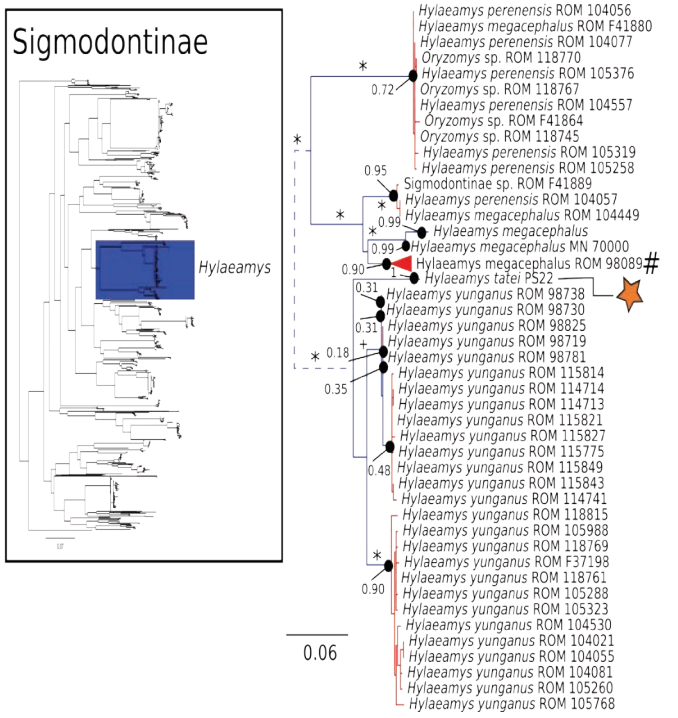

Figure 6. Maximum likelihood gene tree and PTP species delimitation of unique haplotypes of the COI gene of the rodents of the subfamily Sigmodontinae available in GenBank plus all our samples included in Figure 2 collected in Otonga Reserve and Sangay National Park (inset); main figure panel is a zoom-out of the *Hylaeamys* clade. Colors, symbols and support values correspond to the same as in Figure 2. Names of terminals indicate sample codes; sequences retrieved from GeneBank keep their original identifications. Star indicates the sample of *Hylaemays tatei* from Sangay. Pound symbol indicates a very large clade of *Hylaeamys megacephalus* that was collapsed to obtain a clearer representation of this figure. Doted lines indicate branch lengths were reduced.

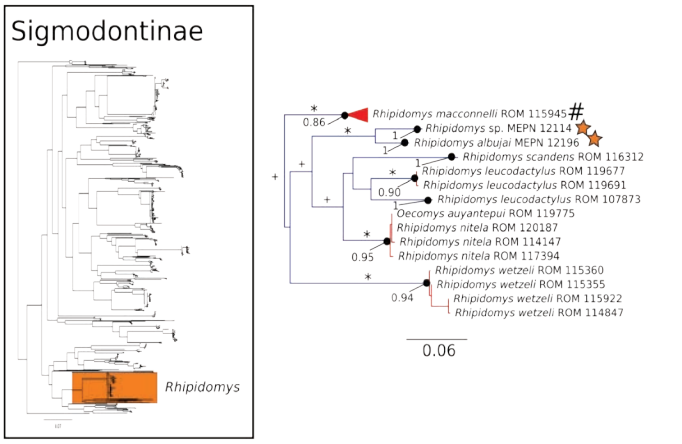

Figure 7. Maximum likelihood gene tree and PTP species delimitation of unique haplotypes of the COI gene of the rodents of the subfamily Sigmodontinae available in GenBank plus all our samples included in Figure 2 collected in Otonga Reserve and Sangay National Park (inset); main figure panel is a zoom-out of the *Rhipidomys* clade. Colors, symbols and support values correspond to the same as in Figure 2. Names of terminals indicate sample codes; sequences retrieved from GeneBank keep their original identifications. Stars indicate the two species of unnamed *Rhipidomys* reported in this study. Pound symbol indicates a very large clade of *Rhipidomys macconnelli* that was collapsed to obtain a clearer representation of this figure.

lomys) would be less likely to colonize both Andean slopes.

Species delimitation methods, such as PTP and GMYC, are useful as an initial approach to delimit species using DNA sequences (Pons *et al*. 2006; Zhang *et al.* 2013). While these inferences are useful, there are also several pitfalls associated with these analyses and the results should be taken with caution, particularly when only one method and locus are used (Carstens *et al.* 2013). In our results, the splitting of *Akodon mollis* could very well represent a false positive associated with shallow genetic differentiation; however, the deep divergence between both clades within *Chilomys instans* indicates that the delimitation results might reflect real species-level diversity (Figure 2). In the case of species delimitation of the subfamily Sigmodontinae (Tree C), it is possible that there was an over-splitting of species by the PTP analysis; for example, there was a potential over splitting of *Hylaeamys yunganus* in multiple species (Figure 6). Further systematic research will clarify the species limits of these taxa.

Following the analyses of González-Ittig *et al.* (2014) we preliminarily recognize the *Oligoryzomys* of the western slopes of the Ecuadorian Andes as *O. spodiurus*; these populations were traditionally regarded as part of the widespread *O. destructor* (Weksler and Bonvicino 2015). We also recovered *Oligoryzomys* as paraphyletic, but we propose that this may be due to two artifacts: incorrect identifications of various voucher specimens associated with sequences available in GenBank (sequences of specimen MN71255 [GenBank accession number: KF815407] (Figure 4C) actually belongs to *Necromys lasiurus*, based on the analysis of CYTB of the same specimen,results not shown); and putative pseudogenes (Numts; Bensasson *et al.* 2001) in sequences generated by Müller *et al.* (2013) [GenBank accession numbers: GU938877, GU938878, GU938886-GU938890, GU938892-GU938894, GU938898, GU938899, GU938953, GU938969-GU938988] (Figure 4A), based on the position of these sequences in an analyses of a larger dataset of *Oligoryzomys* barcodes (M. Weksler *et al.*, in prep.). Traditionally, the genus *Oligorzomys* has been a hard group to study because of the availability of a large number of taxonomic names and various difficulties inherent in assessing patterns of morphological variation. Fortunately, there have been new efforts to generate a more comprehensive understanding of the diversity in the genus (Weksler and Bonvicino 2005, 2015; González-Ittig *et al.* 2014; Weksler *et al.* 2017). Our barcode data corroborate the sister relationship of *Oreoryzomys*, a poorly studied Andean genus, and *Microryzomys* (Weksler 2006).

Even though our phylogenetic analysis of the COI gene did not recover the two species of *Mindomys* as monophyletic (Figure 5), further analysis with the IRBP and CYTB gene do indeed recover these two species as a monophyletic lineage (C. M. Pinto and M. Weksler in prep.), a good example of the marked limitation of DNA barcoding for providing accurate insight into species-level phylogenetics. *Mindomys* form a monophyletic group with *Nephelomys*; both of these genera are mostly Andean, with two species of *Nephelomys*, *N. devius* and *N. pirrensis*, distributed in the mountain areas of Central America (Percequillo 2003, 2015). Our barcode data suggest that *N. moerex* of the western slopes of the Andes may be most closely related to Central American species (Figure 5). Without further systematic study we are not yet confident in assigning species names to the two candidate species of the eastern slopes of the Andes; potential names for these candidate species include *N. albigularis, N. auriventer,* and *N. nimbosus* (Brito *et al.* 2015; Percequillo 2015; Tinoco López 2015).

The tribe Thomasomyini was not recovered as monophyletic in our Maximum Likelihood analyses (Figure 2). This result is not surprising for several reasons: 1) Monophyly of this tribe is not strongly supported in studies using additional molecular data — CYTB and IRBP genes — (Salazar-Bravo *et al.* 2016). 2) The COI marker is problematic for unveiling deep nodes in phylogenies; a recent example of this limitation is the utility of this marker to in the phylogeny of bats, without using constraints (Amador *et al.* in press). 3) The taxonomic sampling of the analysis was very limited with only 24 species; it is known that phylogenetic accuracy increases with taxon sampling (Zwickl and Hillis 2002).

Currently, specimens of *Thomasomys* from Sangay are assigned to *T. caudivarius*, *T. cinnameus, T. paramorum, T. princeps* and *T. taczanowskii* (Lee *et al.* 2011, 2015). Our phylogenetic analyses show that true *T. silvestris*, from Otonga, are sister to a clade formed by *T. paramorum* and *T. cinnameus*; also the large species *T. princeps* is closely related to small sized species *T. baeops* and *T. taczanowskii*. These relationships differ from previous phylogenetic hypotheses based solely on morphological or CYTB data (Pacheco 2003; Lee *et al.* 2011, 2015); the single relationship that is constant across phylogenies is the sister relationship of *T. baeops* and *T. taczanowskii*. Two putative species were recovered within *T. taczanowskii* (Figure 2); however, it is possible that they correspond to a single species given the scant genetic divergence with the COI gene (3 %). The puzzling pattern showing that large species of *Thomasomys* do not

form a clade (Lee *et al.* 2015) potentially indicates multiple origins of the large body-size phenotype, suggesting that the evolution of body size in *Thomasomys* is more complex than previously suggested by discrete grouping of species by body-size (Pacheco 2003, 2015). Detailed exploration of the radiation of thomasomyine rodents along the Andes is much needed, and will likely provide exciting results about diversification patterns along the Andes, as have emerged from studies of plants (e. g., Monasterio and Sarmiento 1991; Hughes and Eastwood 2006; Nürk *et al.* 2013).

The results for Echimyidae show that the analyzed sequences of *Mesomys hispidus* contain two putative species with divergences in the range of 6.9- 7.2 % (Figure 3). One of these putative species is distributed in the Guiana Shield, and the other in the western Amazon of Ecuador. These results are in line with the findings of five relatively deep mitochondrial clades within *M. hispidus*, with mean divergence 4.6 % (Patton *et al.* 1994, 2000). Also, our results suggest that the *Mesomys* sample (JBM 368) from the Andes is conspecific with the *Mesomys* from Yasuní in the western Amazonian lowlands (genetic divergence ranging from 1.2 to 1.4 %). These results contrast with a previous analysis, in which the sample JBM 368 was assigned as a different species from the lowland samples (Upham *et al.* 2013). Additional work on the morphology and genetics of *M. hispidus* will be needed to clarify its taxonomy.

Our results indicate that the alpha taxonomy of the tropical Andean rodents is still not fully resolved, for example with respect to delineation of species in the genera *Chilomys* and *Mindomys*. Also, COI sequences that we have obtained for the genera *Thomasomys* and *Chilomys* provide the first data from this marker for these genera, and may be useful for onward rodent barcoding efforts and for efforts toward a comprehensive multilocus phylogeny of thomasomyines, which remains an outstanding goal in Neotropical mammalogy (Salazar-Bravo and Yates 2007; Lee *et al.* 2011, 2015). While acknowledging its limitations, we encourage research teams studying Neotropical rodents to provide DNA barcoding data whenever possible, which may help to speed new species discoveries and taxonomic reviews in a highly diverse order in which many lines of basic taxonomic and inventory research remain open, active, and fruitful.

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Appendix

List of the 201 samples of mammals from Otonga Reserve and Sangay National Park sequenced for this study. List includes collector numbers, museum numbers, collection locality, and GenBank accession numbers.

Species	Field number	Tissue number	Museum number	Locality	GenBank Accession
Akodon mollis A	PS14	--	FMNH 219797	Sangay	MF806219
Akodon mollis A	PS4	--	FMNH 219798	Sangay	MF806236
Akodon mollis A	PS17	--	FMNH 219804	Sangay	MF806257
Akodon mollis A	PS26	--	FMNH 219805	Sangay	MF806260
Akodon mollis A	PS6	--	MEPN 12135	Sangay	MF806212
Akodon mollis A	PS10	--	MEPN 12138	Sangay	MF806220
Akodon mollis A	PS34	--	MEPN 12156	Sangay	MF806223
Akodon mollis A	PS39	--	MEPN 12161	Sangay	MF806238
Akodon mollis A	TEL2235	ACUNHC1618	QCAZ 11880	Sangay	MF806242
Akodon mollis A	TEL2242	--	QCAZ 11881	Sangay	MF806261
Akodon mollis A	TEL2256	ACUNHC1595	QCAZ 11882	Sangay	MF806234
Akodon mollis A	TEL2257	ACUNHC1586	QCAZ 11883	Sangay	MF806226
Akodon mollis A	TEL2321	ACUNHC1583	QCAZ 11884	Sangay	MF806254
Akodon mollis A	TEL2328	ACUNHC1585	QCAZ 11885	Sangay	MF806256
Akodon mollis A	TEL2346	--	QCAZ 11888	Sangay	MF806252

Akodon mollis A	TEL2363	--	QCAZ 11889	Sangay	MF806240
Akodon mollis A	TEL2237	ACUNHC1587	QCAZ 11890	Sangay	MF806245
Akodon mollis A	TEL2238	ACUNHC1575	QCAZ 11891	Sangay	MF806239
Akodon mollis A	TEL2240	ACUNHC1620	QCAZ 11892	Sangay	MF806248
Akodon mollis A	TEL2253	ACUNHC1619	QCAZ 11893	Sangay	MF806224
Akodon mollis A	TEL2259	--	QCAZ 11894	Sangay	MF806225
Akodon mollis A	TEL2268	--	QCAZ 11895	Sangay	MF806216
Akodon mollis A	TEL2269	ACUNHC1603	QCAZ 11896	Sangay	MF806235
Akodon mollis A	TEL2272	ACUNHC1616	QCAZ 11897	Sangay	MF806221
Akodon mollis A	TEL2273	ACUNHC1604	QCAZ 11898	Sangay	MF806217
Akodon mollis A	TEL2276	ACUNHC1628	QCAZ 11899	Sangay	MF806262
Akodon mollis A	TEL2277	ACUNHC1577	QCAZ 11900	Sangay	MF806258
Akodon mollis A	TEL2280	ACUNHC1579	QCAZ 11901	Sangay	MF806222
Akodon mollis A	TEL2281	--	QCAZ 11902	Sangay	MF806218
Akodon mollis A	TEL2282	ACUNHC1584	QCAZ 11903	Sangay	MF806237
Akodon mollis A	TEL2286	--	QCAZ 11904	Sangay	MF806249
Akodon mollis A	TEL2289	--	QCAZ 11905	Sangay	MF806263
Akodon mollis A	TEL2297	ACUNHC1591	QCAZ 11906	Sangay	MF806227
Akodon mollis A	TEL2299	--	QCAZ 11907	Sangay	MF806255
Akodon mollis A	TEL2302	--	QCAZ 11908	Sangay	MF806228
Akodon mollis A	TEL2314	ACUNHC1576	QCAZ 11910	Sangay	MF806229
Akodon mollis A	TEL2317	ACUNHC1596	QCAZ 11911	Sangay	MF806230
Akodon mollis A	TEL2350	--	QCAZ 11913	Sangay	MF806259
Akodon mollis A	TEL2352	--	QCAZ 11914	Sangay	MF806253
Akodon mollis A	TEL2356	--	QCAZ 11915	Sangay	MF806243
Akodon mollis A	TEL2370	ACUNHC1581	QCAZ 11916	Sangay	MF806250
Akodon mollis A	TEL2376	--	QCAZ 11917	Sangay	MF806241
Akodon mollis A	TEL2379	--	QCAZ 11918	Sangay	MF806246
Akodon mollis A	TEL2385	--	QCAZ 11919	Sangay	MF806244
Akodon mollis A	TEL2389	ACUNHC1580	QCAZ 11920	Sangay	MF806247
Akodon mollis A	TEL2390	--	QCAZ 11921	Sangay	MF806214
Akodon mollis A	TEL2391	--	QCAZ 11922	Sangay	MF806231
Akodon mollis A	TEL2392	--	QCAZ 11923	Sangay	MF806213
Akodon mollis A	TEL2396	--	QCAZ 11924	Sangay	MF806232
Akodon mollis A	TEL2397	--	QCAZ 11925	Sangay	MF806215
Akodon mollis A	TEL2399	--	QCAZ 11926	Sangay	MF806211
Akodon mollis A	TEL2400	--	QCAZ 11927	Sangay	MF806251
Akodon mollis A	TEL2401	--	QCAZ 11928	Sangay	MF806233
Akodon mollis B	KMH2227	TK149044	QCAZ 8634	Otonga	MF806209
Akodon mollis B	MP74	TK149070	QCAZ 8635	Otonga	MF806210
Chilomys instans A	PS24	--	MEPN 12149	Sangay	MF806264
Chilomys instans B	MP62	TK149051	QCAZ 8691	Otonga	MF806266
Chilomys instans B	MP64	TK149053	QCAZ 8693	Otonga	MF806269
Chilomys instans B	MP69	TK149058	QCAZ 8694	Otonga	MF806265
Chilomys instans B	MP91	TK149099	QCAZ 8695	Otonga	MF806267
Chilomys instans B	KMH2241	TK149080	QCAZ 8740	Otonga	MF806268
Hylaeamys tatei	PS22	--	MEPN 12147	Sangay	MF806196
Mesomys hispidus	JBM368	--	MEPN 12212	Kutukú	MF806172
Microryzomys altissimus	TEL2298	--	QCAZ 11929	Sangay	MF806185
Microryzomys altissimus	TEL2347	ACUNHC1553	QCAZ 11930	Sangay	MF806183
Microryzomys altissimus	TEL2278	ACUNHC1605	QCAZ 11931	Sangay	MF806182
Microryzomys altissimus	TEL2279	--	QCAZ 11932	Sangay	MF806179
Microryzomys altissimus	TEL2322	--	QCAZ 11933	Sangay	MF806181

Microryzomys altissimus	TEL2327	--	QCAZ 11934	Sangay	MF806180
Microryzomys altissimus	TEL2258	--	QCAZ 11973	Sangay	MF806184
Microryzomys minutus	KMH2235	TK149063	QCAZ 8673	Otonga	MF806186
Microryzomys minutus	KMH2236	TK149064	QCAZ 8674	Otonga	MF806187
Microryzomys minutus	KMH2257	TK149106	QCAZ 8675	Otonga	MF806189
Microryzomys minutus	KMH2258	TK149107	QCAZ 8676	Otonga	MF806188
Microryzomys minutus	MP53	TK149026	QCAZ 8677	Otonga	MF806195
Microryzomys minutus	PS9	--	FMNH 219796	Sangay	MF806194
Microryzomys minutus	PS35	--	MEPN 12158	Sangay	MF806191
Microryzomys minutus	PS69	--	MEPN 12190	Sangay	MF806190
Microryzomys minutus	TEL2362	ACUNHC1556	QCAZ 11935	Sangay	MF806193
Microryzomys minutus	TEL2371	ACUNHC1571	QCAZ 11936	Sangay	MF806192
Mindomys sp.	MP88	TK149096	QCAZ 8720	Otonga	MF806197
Nephelomys moerex	KMH2204	TK149005	QCAZ 8696	Otonga	MF806204
Nephelomys moerex	KMH2210	TK149009	QCAZ 8697	Otonga	MF806198
Nephelomys moerex	KMH2221	TK149038	QCAZ 8700	Otonga	MF806201
Nephelomys moerex	KMH2253	TK149102	QCAZ 8709	Otonga	MF806202
Nephelomys moerex	MP83	TK149079	QCAZ 8717	Otonga	MF806203
Nephelomys moerex	MP90	TK149098	QCAZ 8718	Otonga	MF806200
Nephelomys moerex	MP93	TK149101	QCAZ 8719	Otonga	MF806199
Nephelomys sp. A	PS2	--	FMNH 219795	Sangay	MF806205
Nephelomys sp. B	PS3	--	MEPN 12133	Sangay	MF806206
Oligoryzomys spodiurus	MP75	TK149071	QCAZ 8678	Otonga	MF806174
Oligoryzomys spodiurus	MP85	TK149093	QCAZ 8681	Otonga	MF806173
Oreoryzomys balneator	--	--	MEPN 12226	Cordillera del Cóndor	MF806175
Oreoryzomys balneator	PS66	--	MEPN 12187	Sangay	MF806178
Oreoryzomys balneator	PS57	--	MEPN 12189	Sangay	MF806177
Oreoryzomys balneator	PS56	--	MEPN 12197	Sangay	MF806176
Rhipidomys albujai	PS75	--	MEPN 12196	Sangay	MF806208
Rhipidomys sp.	--	--	MEPN 12114	Cordillera del Cóndor	MF806207
Thomasomys baeops	MP92	TK149100	QCAZ 8746	Otonga	MF806276
Thomasomys baeops	KMH2225	TK149042	QCAZ 8692	Otonga	MF806275
Thomasomys baeops	KMH2209	TK149010	QCAZ 8739	Otonga	MF806274
Thomasomys caudivarius	PS28	--	MEPN 12151	Sangay	MF806307
Thomasomys caudivarius	PS29	--	MEPN 12152	Sangay	MF806323
Thomasomys caudivarius	PS36	--	MEPN 12159	Sangay	MF806309
Thomasomys caudivarius	TEL2345	ACUNHC1602	QCAZ 11912	Sangay	MF806325
Thomasomys caudivarius	TEL2270	ACUNHC1572	QCAZ 11949	Sangay	MF806310
Thomasomys caudivarius	TEL2271	ACUNHC1592	QCAZ 11950	Sangay	MF806312
Thomasomys caudivarius	TEL2285	ACUNHC1563	QCAZ 11951	Sangay	MF806313
Thomasomys caudivarius	TEL2287	--	QCAZ 11952	Sangay	MF806314
Thomasomys caudivarius	TEL2293	ACUNHC1557	QCAZ 11953	Sangay	MF806322
Thomasomys caudivarius	TEL2301	ACUNHC1562	QCAZ 11954	Sangay	MF806315
Thomasomys caudivarius	TEL2318	--	QCAZ 11955	Sangay	MF806311
Thomasomys caudivarius	TEL2319	--	QCAZ 11956	Sangay	MF806316
Thomasomys caudivarius	TEL2343	ACUNHC1567	QCAZ 11959	Sangay	MF806324
Thomasomys caudivarius	TEL2344	--	QCAZ 11960	Sangay	MF806308
Thomasomys caudivarius	TEL2354	ACUNHC1554	QCAZ 11961	Sangay	MF806321
Thomasomys caudivarius	TEL2355	ACUNHC1573	QCAZ 11962	Sangay	MF806317
Thomasomys caudivarius	TEL2377	--	QCAZ 11964	Sangay	MF806320
Thomasomys caudivarius	TEL2393	--	QCAZ 11965	Sangay	MF806326
Thomasomys caudivarius	TEL2398	--	QCAZ 11966	Sangay	MF806319
Thomasomys caudivarius	TEL2402	--	QCAZ 11967	Sangay	MF806318

Thomasomys cinnameus	PS40	--	MEPN 12163	Sangay	MF806291
Thomasomys cinnameus	TEL2236	ACUNHC1601	QCAZ 11968	Sangay	MF806299
Thomasomys cinnameus	TEL2243	ACUNHC1564	QCAZ 11969	Sangay	MF806293
Thomasomys cinnameus	TEL2246	--	QCAZ 11970	Sangay	MF806298
Thomasomys cinnameus	TEL2250	--	QCAZ 11971	Sangay	MF806297
Thomasomys cinnameus	TEL2252	--	QCAZ 11972	Sangay	MF806292
Thomasomys cinnameus	TEL2291	ACUNHC1559	QCAZ 11975	Sangay	MF806303
Thomasomys cinnameus	TEL2292	ACUNHC1627	QCAZ 11976	Sangay	MF806300
Thomasomys cinnameus	TEL2296	ACUNHC1610	QCAZ 11977	Sangay	MF806301
Thomasomys cinnameus	TEL2307	ACUNHC1611	QCAZ 11978	Sangay	MF806295
Thomasomys cinnameus	TEL2308	--	QCAZ 11979	Sangay	MF806294
Thomasomys cinnameus	TEL2310	ACUNHC1582	QCAZ 11980	Sangay	MF806305
Thomasomys cinnameus	TEL2311	--	QCAZ 11981	Sangay	MF806302
Thomasomys cinnameus	TEL2329	--	QCAZ 11982	Sangay	MF806306
Thomasomys cinnameus	TEL2274	--	QCAZ 11983	Sangay	MF806296
Thomasomys cinnameus	TEL2365	--	QCAZ 12018	Sangay	MF806337
Thomasomys paramorum	TEL2233	ACUNHC1624	QCAZ 11984	Sangay	MF806359
Thomasomys paramorum	TEL2234	ACUNHC1593	QCAZ 11985	Sangay	MF806360
Thomasomys paramorum	TEL2239	ACUNHC1626	QCAZ 11986	Sangay	MF806361
Thomasomys paramorum	TEL2241	ACUNHC1590	QCAZ 11987	Sangay	MF806362
Thomasomys paramorum	TEL2244	ACUNHC1600	QCAZ 11988	Sangay	MF806358
Thomasomys paramorum	TEL2245	ACUNHC1625	QCAZ 11989	Sangay	MF806357
Thomasomys paramorum	TEL2247	ACUNHC1597	QCAZ 11990	Sangay	MF806329
Thomasomys paramorum	TEL2248	ACUNHC1574	QCAZ 11991	Sangay	MF806363
Thomasomys paramorum	TEL2249	ACUNHC1607	QCAZ 11992	Sangay	MF806364
Thomasomys paramorum	TEL2251	ACUNHC1589	QCAZ 11993	Sangay	MF806356
Thomasomys paramorum	TEL2255	ACUNHC1612	QCAZ 11994	Sangay	MF806334
Thomasomys paramorum	TEL2262	ACUNHC1599	QCAZ 11996	Sangay	MF806333
Thomasomys paramorum	TEL2263	ACUNHC1606	QCAZ 11997	Sangay	MF806354
Thomasomys paramorum	TEL2264	ACUNHC1608	QCAZ 11998	Sangay	MF806353
Thomasomys paramorum	TEL2300	ACUNHC1615	QCAZ 11999	Sangay	MF806352
Thomasomys paramorum	TEL2309	ACUNHC1569	QCAZ 12000	Sangay	MF806340
Thomasomys paramorum	TEL2312	ACUNHC1622	QCAZ 12001	Sangay	MF806327
Thomasomys paramorum	TEL2320	--	QCAZ 12002	Sangay	MF806355
Thomasomys paramorum	TEL2323	ACUNHC1568	QCAZ 12003	Sangay	MF806335
Thomasomys paramorum	TEL2324	--	QCAZ 12004	Sangay	MF806330
Thomasomys paramorum	TEL2325	ACUNHC1613	QCAZ 12005	Sangay	MF806304
Thomasomys paramorum	TEL2326	--	QCAZ 12006	Sangay	MF806341
Thomasomys paramorum	TEL2348	--	QCAZ 12011	Sangay	MF806338
Thomasomys paramorum	TEL2349	ACUNHC1558	QCAZ 12012	Sangay	MF806346
Thomasomys paramorum	TEL2351	--	QCAZ 12013	Sangay	MF806336
Thomasomys paramorum	TEL2353	--	QCAZ 12014	Sangay	MF806344
Thomasomys paramorum	TEL2357	--	QCAZ 12015	Sangay	MF806339
Thomasomys paramorum	TEL2358	--	QCAZ 12016	Sangay	MF806342
Thomasomys paramorum	TEL2364	--	QCAZ 12017	Sangay	MF806331
Thomasomys paramorum	TEL2366	--	QCAZ 12019	Sangay	MF806347
Thomasomys paramorum	TEL2367	--	QCAZ 12020	Sangay	MF806343
Thomasomys paramorum	TEL2368	--	QCAZ 12021	Sangay	MF806366
Thomasomys paramorum	TEL2369	--	QCAZ 12022	Sangay	MF806349
Thomasomys paramorum	TEL2374	--	QCAZ 12023	Sangay	MF806332
Thomasomys paramorum	TEL2375	--	QCAZ 12024	Sangay	MF806348
Thomasomys paramorum	TEL2380	ACUNHC1549	QCAZ 12025	Sangay	MF806365
Thomasomys paramorum	TEL2381	--	QCAZ 12026	Sangay	MF806345

Thomasomys paramorum	TEL2383	--	QCAZ 12027	Sangay	MF806351
Thomasomys paramorum	TEL2384	--	QCAZ 12028	Sangay	MF806350
Thomasomys paramorum	TEL2275	ACUNHC1623	QCAZ 12029	Sangay	MF806328
Thomasomys princeps	TEL2288	--	QCAZ 11937	Sangay	MF806271
Thomasomys princeps	TEL2295	--	QCAZ 11938	Sangay	MF806273
Thomasomys princeps	TEL2378	ACUNHC1560	QCAZ 11939	Sangay	MF806272
Thomasomys princeps	TEL2394	ACUNHC1548	QCAZ 11940	Sangay	MF806270
Thomasomys silvestris	KMH2237	TK149065	QCAZ 8741	Otonga	MF806371
Thomasomys silvestris	MP66	TK149055	QCAZ 8742	Otonga	MF806367
Thomasomys silvestris	MP68	TK149057	QCAZ 8743	Otonga	MF806369
Thomasomys silvestris	MP70	TK149059	QCAZ 8744	Otonga	MF806372
Thomasomys silvestris	KMH2231	TK149048	QCAZ 8747	Otonga	MF806370
Thomasomys silvestris	MP82	TK149078	QCAZ 8749	Otonga	MF806368
Thomasomys taczanowskii A	PS56	--	FMNH 219801	Sangay	MF806277
Thomasomys taczanowskii A	PS25	--	FMNH 219803	Sangay	MF806278
Thomasomys taczanowskii B	--	--	MEPN 12224	Cordillera del Cóndor	MF806282
Thomasomys taczanowskii B	PS1	--	MEPN 12132	Sangay	MF806285
Thomasomys taczanowskii B	PS64	--	MEPN 12185	Sangay	MF806281
Thomasomys taczanowskii B	TEL2254	ACUNHC1598	QCAZ 11941	Sangay	MF806286
Thomasomys taczanowskii B	TEL2290	ACUNHC1570	QCAZ 11942	Sangay	MF806287
Thomasomys taczanowskii B	TEL2306	ACUNHC1614	QCAZ 11943	Sangay	MF806288
Thomasomys taczanowskii B	TEL2386	--	QCAZ 11945	Sangay	MF806290
Thomasomys taczanowskii B	TEL2387	--	QCAZ 11946	Sangay	MF806289
Thomasomys taczanowskii B	TEL2388	--	QCAZ 11947	Sangay	MF806280
Thomasomys taczanowskii B	TEL2395	--	QCAZ 11948	Sangay	MF806279
Thomasomys taczanowskii B	TEL2372	--	QCAZ 11963	Sangay	MF806283
Thomasomys taczanowskii B	TEL2261	ACUNHC1609	QCAZ 11995	Sangay	MF806284