A new species of *Tanyuromys* Pine, Timm, and Weksler, 2012 (Cricetidae: Oryzomyini), with comments on relationships within the Oryzomyini

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We name and describe a new species of long-tailed sigmodontine rodent of the genus *Tanyuromys*, based on 3 specimens collected from 3 different localities in northern Ecuador, during the period 1953–2008. All 3 localities are at middle elevations on the Pacific Andean slopes and specimens were taken both in intact and disturbed forest areas. *Tanyuromys* previously has been treated as including a single species—*T. aphrastus* (Harris, 1932); however, using morphological and molecular characters (mitochondrial cytochrome *b* [*Cytb*], 1,143 bp), we herein recognize 2 species: *T. aphrastus* proper, which, so far as known, occurs only in Costa Rica and Panama, and a new species known only from Ecuador. The Ecuadoran species, like *T. aphrastus*, is characterized by a long tail (ca. 1.5 × length of head plus body); large, complexly constructed, pentalophodont molars; braincase with beaded supraorbital margins continuous with raised temporal ridges; short, anteriorly constricted incisive foramina; short, narrow palatines; and small auditory bullae. Although similar morphologically, which explains why the 2 species have hitherto been regarded as 1, the few specimens available of each differ in that the new species has, among other traits, a narrower interorbital breadth, narrower zygomatic plate, invariably (thus far) distinct supraorbital bead continuing posteriorly over parietal to lambdoidal crests as a prominent raised ridge, relatively large lateral wing of the parietal, skull with more angular rather than more rounded contours. Molecular and morphological characters confirm that specimens of *T. aphrastus* from Costa Rica and Panama are quite similar; they differ in *Cytb* sequences by 1.2%. The new species from Ecuador, in contrast, differs from the Central American *T. aphrastus* in *Cytb* sequences by 10.2%. The 2 species form a well-supported clade; we infer the genus' phylogenetic associations within the Oryzomyini, based on the complete *Cytb* sequence.

Nombramos y describimos una nueva especie de roedor sigmodontino en el género *Tanyuromys* Pine, Timm y Weksler, 2012, a partir de tres especímenes recolectados entre 1953 y 2008 en tres localidades diferentes en el norte de Ecuador. Las tres localidades se encuentran a altitudes medias en las laderas Andinas del lado Pacífico. Los especímenes fueron recolectados tanto en bosque intacto como perturbado. Hasta el momento, se ha considerado que *Tanyuromys* incluye una sola especie: *T. aphrastus* (Harris, 1932). Sin embargo, mediante datos tanto morfológicos como moleculares (del gen mitocondrial citocromo *b*, [*Cytb*]; de 1,143 pares de bases de longitud), reconocemos en el presente trabajo a dos especies: *T. aphrastus* propiamente dicho, el cual que se sepa solo habita Costa Rica y Panamá, así como una nueva especie que por el momento solo se conoce de Ecuador. La especie ecuatoriana se caracteriza—al igual que *T. aphastus*—por tener la cola extremadamente larga (aproximadamente 1.5 × el largo de la longitud cabeza-cuerpo; molares pentalofodontos grandes, de estructura compleja; caja cefálica con márgenes supraorbitarios rebordeados y continuos con una cresta temporal moderadamente elevada; los forámenes incisivos cortos, con constricción anterior; huesos palatinos cortos y

estrechos y bulla timpánica pequeña. Aunque las dos especies son similares (lo cual explica porque hasta ahora se han considerado una sola), los pocos especímenes de cada una difieren entre sí en que la nueva especie tiene, entre otras características, una anchura interorbitaria más estrecha; la placa cigomática más estrecha; el rebordeado supraorbitario prominentemente elevado, tal marcada cresta (en los especímenes que se conocen hasta el momento), continuando en dirección posterior sobre el hueso parietal hasta las crestas lambdoidales; las alas laterales de los parietales relativamente grandes y los contornos del cráneo más angulares que redondeados. Los análisis moleculares y morfológicos coinciden en que los especímenes de Costa Rica y Panamá difieren poco entre sí: sus secuencias de ADN mitocondrial del citocromo *b* solo se distinguen en un 1.2%. En cambio, la nueva especie de Ecuador difiere de *T. aphrastus* centroamericano en 10.2%. Las dos especies forman un clado bien definido y apoyado. En este trabajo, inferimos las asociaciones filogenéticas del género *Tanyuromys* entre los Oryzomyini con base en secuencias completas del citocromo *b*.

Key words: Andes, biogeography, cytochrome *b*, isthmus closure, molecular phylogeny, morphology, Neotropics, Panamanian land bridge, systematics, trans-Andean

The surprisingly large diversity of South American mammals is well exemplified by rodents, with 14 extant families native to the region. Neotropical rodents range in size from the tiny (ca. 10–13 g) *Calomys laucha* (Fischer, 1814) from the semi-arid Chaco to the world's largest rodent, the 55-kg capybara, *Hydrochoerus hydrochaeris* (Linnaeus, 1766), and they occupy a wide array of niches. The rat and mouse family Cricetidae is the most species-rich family of mammals in the New World, represented by 4 subfamilies—Arvicolinae, Neotominae, Sigmodontinae, and Tylomyinae—and some 111+ extant genera (Jansa and Weksler 2004; Steppan et al. 2004; Musser and Carleton 2005). The most species-rich of these subfamilies is Sigmodontinae; its evolutionary history has been the subject of recent phylogenetic studies resulting in the recognition of at least 86 extant and several extinct genera, including newly recognized genera and species (Pardiñas et al. 2002; Weksler 2003; Weksler et al. 2006; D'Elía et al. 2007; Percequillo et al. 2011; Pine et al. 2012; Salazar-Bravo et al. 2016). Within the subfamily Sigmodontinae, the primarily Neotropical tribe Oryzomyini is a diverse and well-supported clade of 28 extant and 5 extinct currently recognized genera that has been the subject of recent studies by Carleton and Olson (1999), Weksler et al. (2006), Pardiñas (2008), Turvey et al. (2010), Zijlstra et al. (2010), Percequillo et al. (2011), Pine et al. (2012), Machado et al. (2013), Prado and Percequillo (2018), and Hanson and Platt (2018). Using molecular sequence data from 2 nuclear genes evolving at a moderate rate (interphotoreceptor retinoid-binding protein [*Rbp*3] and alcohol dehydrogenase [*Adh*1-I2]) and a rapidly evolving mitochondrial gene (cytochrome *b* [*Cytb*]), Hanson and Platt (2018) reconfirmed the most recent arrangements of the tribe Oryzomyini, and that *Cytb* was quite useful in elucidating taxonomic relationships among genera and among species—the terminal groups—although not the deeper phylogenetic relationships. Unresolved in their multigene phylogenetic analysis was the relationship between *Tanyuromys* and a paraphyletic group composed of *Melanomys* and *Sigmodontomys*. Despite this wealth of research, the diversity of the Oryzomyini is only partially known, with new species and genera regularly being recognized.

Exceptionally long-tailed Oryzomyini from the northern Andes and southeastern Central America, all previously identified as *Sigmodontomys aphrastus* (Harris, 1932), recently were recognized as constituting a distinctive new genus—*Tanyuromys* Pine, Timm, and Weksler, 2012. Previously, the genus *Sigmodontomys* J. A. Allen, 1897, was treated as including 2 species—*S. alfari* (J. A. Allen, 1897) and *S. aphrastus* (see Musser and Carleton 1993, 2005). However, in a study of phylogenetic relationships among the Oryzomyini, using both morphological and molecular data, Weksler (2006) found that *Sigmodontomys* and *Tanyuromys* (the latter still undescribed) were not sister taxa, but rather that *Melanomys* Thomas, 1902, was the sister to *Sigmodontomys*, with the undescribed taxon (*Tanyuromys*) the next group out. Recently, Pine et al. (2012), using additional morphological (98 external, cranial, dental, and postcranial) and molecular (nuclear interphotoreceptor retinoid-binding protein gene, mitochondrial *Cytb* gene, and ribosomal 12S RNA genes) characters, inferred the phylogenetic position of these 2 genera within Oryzomyini, and reconfirmed that *Sigmodontomys* and *Tanyuromys* do not form reciprocally monophyletic groups. *Sigmodontomys* is most closely related to *Melanomys*, with *Tanyuromys* sister to that clade or to the extinct Caribbean genus *Megalomys* Trouessart, 1881.

Despite considerable fieldwork undertaken in the northern Neotropics over the last century, *Tanyuromys* has been reported from only 9 localities, ranging from the Cordillera de Tilarán of northwestern Costa Rica, through the Cordillera de Talamanca of central Costa Rica to western Panama, and then from the western Andean slopes of northern and southern Ecuador (McCain et al. 2007; Pine et al. 2012; Rodríguez-Herrera et al. 2014; Brito and Arguero 2016). McCain et al. (2007) and Pine et al. (2012) recognized that Ecuadoran populations, then represented by 2 and 3 specimens, respectively, differed from those occurring in Costa Rica and Panama. We have now had the opportunity to examine 2 recently obtained specimens, both well-prepared and with fresh tissue samples allowing for molecular comparisons. One specimen is from Ecuador's Volcán Cotacachi (Lee et al. 2010), and 1 from southeastern Costa Rica's Cordillera de Talamanca (Rodríguez-Herrera et al. 2014). These specimens allow us to reassess the status of the Ecuadoran animals and their relationship to those from Central America.

Herein, we make detailed morphological and molecular comparisons among the populations of *T. aphrastus* from Costa Rica

and Panama, and 3 specimens of *Tanyuromys* from Ecuador. The variation among populations shows that more than 1 species is represented over this extensive geographic area. We further restrict the name *T. aphrastus* to the populations that occur in Costa Rica and Panama, with the Ecuadoran specimens representing a species new to science and described below.

MATERIALS AND METHODS

Taxonomic sampling.—We examined all 6 known specimens previously referred to *aphrastus*, from Central America, including the holotype of "*Oryzomys*" *aphrastus* (UMMZ 62875), and the 3 first-collected specimens from northern Ecuador. Specimens from the following institutions were used for molecular and morphological comparisons in this study: Universidad de Costa Rica, San José, Costa Rica (UCR); Museo de Zoología, Pontificia Universidad Católica del Ecuador, Quito, Ecuador (QCAZ); University of Kansas Natural History Museum, Lawrence, Kansas (KU); Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (MCZ); University of Michigan Museum of Zoology, Ann Arbor, Michigan (UMMZ); and National Museum of Natural History, Washington, D.C. (USNM). See McCain et al. (2007), Hanson et al. (2010), and Pine et al. (2012) for specimens used in those studies and that are included here.

Taxon, catalog number, collection depository, locality of collection, and GenBank accession numbers for sequences used in phylogenetic analyses are provided in Appendix I. This project was undertaken with the approval of the University of Kansas Institutional Animal Care and Use Committee. All animal handling protocols are in accordance with the guidelines of the American Society of Mammalogists (Sikes et al. 2016).

Morphological characters.—Terminology for the morphological characters used here, with some modifications, follows Hooper and Musser (1964), Carleton (1973, 1980), Reig (1977), Voss (1988, 1993), Carleton and Musser (1989, 1995), Musser et al. (1998), and Weksler (2006). Cranial measurements follow in part Thomas (1905) and Hershkovitz (1962). All capitalized color terms are from Ridgway (1912).

Molecular techniques.—Genomic DNA was isolated from approximately 0.1 g of liver, muscle, or skin tissue, using a Qiagen extraction kit (Qiagen, Inc., Valencia, California). Skin clips were first rinsed in a 0.5% bleach solution, followed by 2 washes of PBS solution before lysis. The complete *Cytb* gene (1,143 bp) was interrogated using 2 approaches. For fresh tissue the gene was amplified using polymerase chain reaction (PCR) methods with GoTaq (Promega Corp., Madison, Wisconsin), and primers MVZ05 (Smith and Patton 1993) and CB40 (Hanson and Bradley 2008), following a protocol with an initial denaturation at 95°C for 3 min, 35–40 cycles of 95°C for 30 s, 45°C for 1 min, and 72°C for 1 min 30 s, and a final elongation of 72°C for 10 min. Amplicons were purified using the QIAquick PCR purification kit (Qiagen, Inc.) and prepared for sequencing using ABI Prism Big Dye Terminator v3.1 ready reaction mix (Applied Biosystems, Foster City, California). The cycle sequencing reaction was primed with

the PCR amplification primers and additional internal primers (700L—Peppers and Bradley 2000; 400F—Tiemann-Boege et al. 2000; F1—Whiting et al. 2003; and O400R, O700H, O870R—Hanson and Bradley 2008). Following cycle sequencing (1 × 96°C for 1 min, 25 × 96°C for 10 s, 50°C for 5 s, 60°C for 4 min), reactions were precipitated in isopropanol. Purified samples were sequenced using an ABI 3100-*Avant* automated sequencer. Sequencher 4.1 software (Gene Codes Corp., Ann Arbor, Michigan) and MEGA 4.0 (Tamura et al. 2007) were used to proof and align sequences. For skin samples, DNA libraries were made using the KAPA Hyper Prep Kit (KAPA Biosystems, Wilmington, Massachusetts). Libraries were sequenced using the Illumina MiSeq platform, which uses a clonal sequencing process allowing control over DNA degradation (T–C shifts for example) and contamination (see Brace et al. 2015). The entire mitochondrial genome was assembled and annotated to identify the *Cytb* gene sequence.

Phylogenetic analysis.—Sequences for *Tanyuromys* were analyzed within a data set of sequences gathered from GenBank, for individuals representing the 11 currently recognized tribes of Sigmodontinae and 4 non-sigmodontine tribes. Twenty-four genera of the tribe Oryzomyini are represented. Additionally, *Abrawayaomys*, *Juliomys*, and *Neomicroxus* are included because they represent taxa considered incertae sedis and are generally unassigned to tribes (Patton et al. 2015; Salazar-Bravo et al. 2016). Those genera shown to be most closely related to *Tanyuromys* are represented by more than 1 species. Whenever possible, a sequence from the type species of each genus was used. Nucleotide sequence data were evaluated using 2 methods. First, Bayesian inference was used to estimate phylogenetic placement. The software MrModeltest (Nylander 2004) identified the GTR+Γ+I as the best-fit model for Bayesian inference. Bayesian analysis was performed using MrBayes 3.1 software (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003). In the Bayesian inference analysis, sequences were partitioned by codon, and with site-specific gamma distributions and the following options: 4 Markov chains, 10 million generations, and sample frequency every 1,000 generations. The 1st 1,000 trees were discarded as "burn-in" (log probability plateaued before 1,000) and the remaining trees used to estimate a consensus tree. Nodal support for topologies was estimated by using clade probabilities calculated with MrBayes 3.1. Second, mean pairwise genetic distances were estimated using the Kimura 2-parameter (Kimura 1980) model of evolution. A priori groups were established based on geographic clustering, for comparison of genetic distances.

RESULTS

The phylogenetic analysis recovered a monophyletic Sigmodontinae and Oryzomyini (Fig. 1; nodal support is not shown for these groups but was > 95%). Within the Oryzomyini, both *Sigmodontomys* and *Tanyuromys* are recovered within a *Aegialomys* Weksler, Percequillo, and Voss, 2006–*Megalomys*–*Melanomys*–*Nesoryzomys* Heller, 1904–*Sigmodontomys*–*Tanyuromys* grouping, which forms a monophyletic clade of
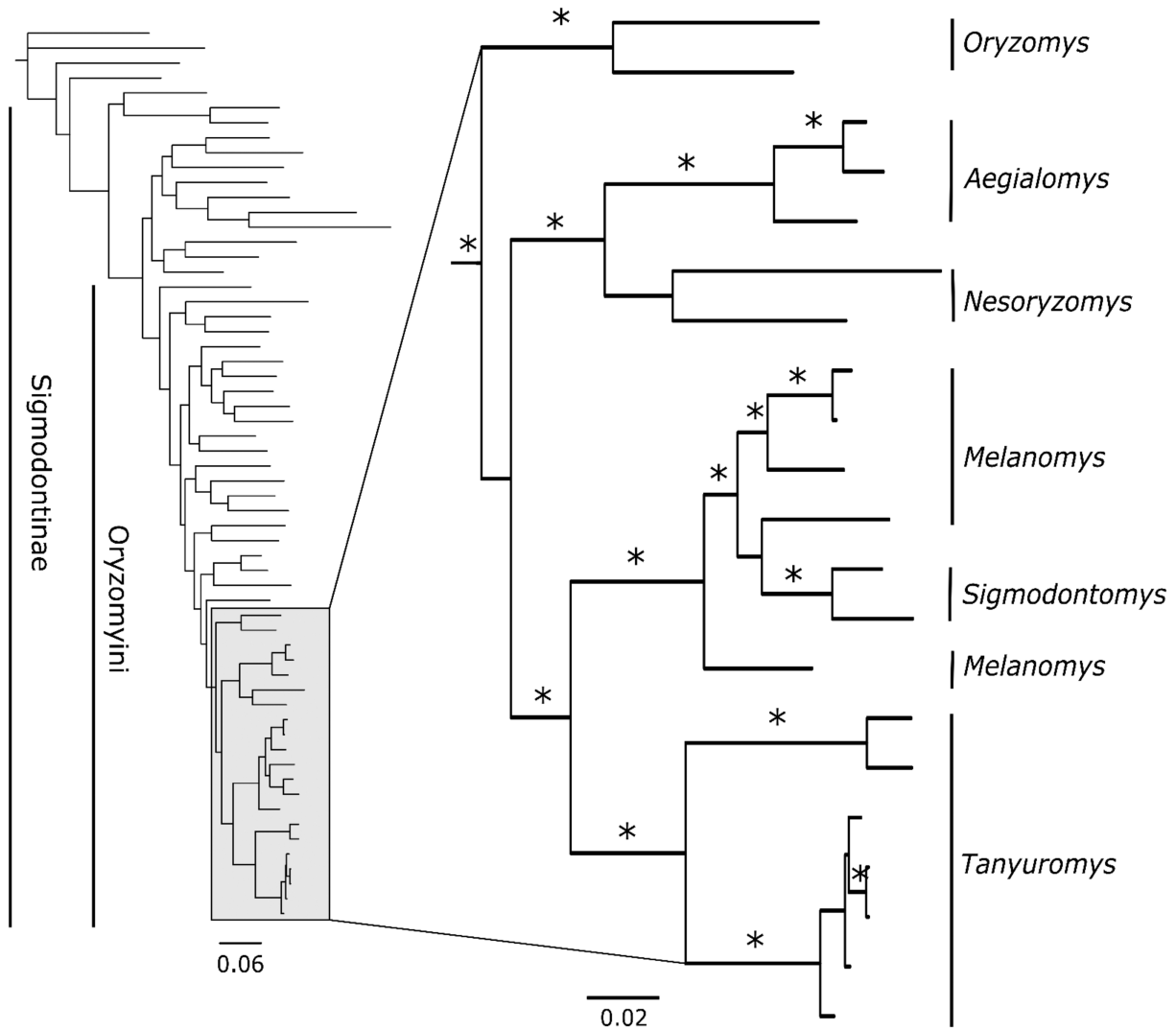
Fig. 1.—Phylogenetic relationships of selected sigmodontine rodents, generated for this paper, based on combined Bayesian analysis of mitochondrial cytochrome *b* (*Cytb*). Tree on the left is overall tree including all outgroup taxa, representing the 11 currently recognized tribes of the subfamily Sigmodontinae (delineated by the outside vertical line) and taxa representing 4 non-sigmodontine tribes (nodal support values not shown). Twenty-four genera of extant Oryzomyini are delineated by the inside vertical line (nodal support values not shown). Subtree enclosed in shaded box is expanded on the right and is based upon the complete mitochondrial *Cytb* gene of the extant genera shown to be most closely related to *Tanyuromys*. Branches labeled with asterisks have posterior probabilities > 0.95. Scale bars represent substitutions/site of corresponding branch lengths.

mainly southeastern Central American and northern South American taxa, and thus corroborates earlier studies of relationships (e.g., Hanson and Bradley 2008; Hanson et al. 2010; Pine et al. 2012; Salazar-Bravo et al. 2016; Steppan and Schenk 2017). In agreement with Pine et al. (2012), *Tanyuromys* is recovered sister to a *Melanomys–Sigmodontomys* clade. These 2 clades are in turn part of a clade sister to a *Aegialomys–Nesoryzomys* clade, with the genus *Oryzomys* Baird, 1857 as sister to all the foregoing. As observed in previous examinations (Hanson and Bradley 2008; Hanson et al. 2010), *Melanomys* appears paraphyletic with respect to *Sigmodontomys*. Within the complex previously known as *aphrastus*, the specimens from Volcán Cotacachi and Pichincha Province in northwestern Ecuador differ from each other by 2.8%, but differ from the Central American samples on average by 10.2% (8.5–11.0%).

The Central American samples differ from each other on average by 0.8% (0.5–1.5%). Genetic distances within other closely related, non-monotypic genera of the Oryzomyini clade are all greater than 5% (*Aegialomys*—5.3%, *Melanomys*—6.6%, *Nectomys*—7.4%, *Nesoryzomys*—12.1%, *Oryzomys*—10.7%) and distances between these groups range between 12.7% and 16.0%.

The molecular variation, over the extensive geographic area where *Tanyuromys* occurs, establishes that there are more than 1 species represented in the genus. Morphologically, the Ecuadoran samples differ significantly from the Central American samples from Costa Rica and Panama, as described below. The specimens that we have examined from the Pacific slopes of Ecuador represent a new species that we describe as follows:

Tanyuromys thomasleei, new species
Lee's Long-tailed Montane Rat
(Figs. 3, 4, 5A, 6, and 7)

Oryzomys aphrastus: Musser and Williams, 1985; part, not *Oryzomys aphrastus* Harris, 1932.

Oryzomys aphrastus: Voss, 1988; not *Oryzomys aphrastus* Harris, 1932.

Sigmodontomys aphrastus: Musser and Carleton, 1993; part, not *Oryzomys aphrastus* Harris, 1932.

S[*igmodontomys*]. *aphrastus*: Musser and Carleton, 2005; part, not *Oryzomys aphrastus* Harris, 1932.

S[*igmodontomys*]. *aphrastus*: Tirira, 2007; not *Oryzomys aphrastus* Harris, 1932.

Sigmodontomys aphrastus: Tirira, 2008; part, not *Oryzomys aphrastus* Harris, 1932.

Sigmodontomys aphrastus: McCain et al., 2008; part, not *Oryzomys aphrastus* Harris, 1932.

Sigmodontomys aphrastus: Lee et al., 2010; not *Oryzomys aphrastus* Harris, 1932.

Tanyuromys aphrastus: Pine et al., 2012; part, not *Oryzomys aphrastus* Harris, 1932.

Sigmodontomys aphrastus: Tirira, 2013; part, not *Oryzomys aphrastus* Harris, 1932. (Previous editions of this checklist of 2011, 2012, also contained this name. Titles of checklists vary).

Tanyuromys aphrastus: Weksler, 2015a; part, not *Oryzomys aphrastus* Harris, 1932.

Tanyuromys aphrastus: Brito and Arguero, 2016; part, not *Oryzomys aphrastus* Harris, 1932.

Tanyuromys aphrastus: Tirira, 2016; part, not *Oryzomys aphrastus* Harris, 1932. (Previous editions of this checklist of 2014, 2015, also contained this name. Titles of checklists vary).

Tanyuromys aphrastus: Ruelas and Pardiñas, 2017; part, not *Oryzomys aphrastus* Harris, 1932.

Tanyuromys aphrastus: Tirira, 2017a; part, not *Oryzomys aphrastus* Harris, 1932.

Tanyuromys aphrastus: Tirira, 2017b; part, not *Oryzomys aphrastus* Harris, 1932.

Tanyuromys aphrastus: Tirira, 2017c; part, not *Oryzomys aphrastus* Harris, 1932. (Previous editions of this checklist also contained this name. Titles of checklists vary).

Holotype.—Dried skin, skeleton, and frozen tissues of an adult male, Museo de Zoología, Pontificia Universidad Católica del Ecuador, Quito, Ecuador (QCAZ 10427), caught 14 July 2008 by Thomas E. Lee, Jr., Tyler J. Cochran, and Daniel Chávez (original number 2033). One aliquot of frozen tissue deposited at Abilene Christian University, Abilene, Texas (TEL 2033). GenBank accession number FJ971254. Condition generally excellent, skin well-made, skull and postcranial skeleton complete. Tip of tail missing on prepared skin.

Type locality.—Ecuador: Imbabura; 10 km E Santa Rosa, lower western slope of Volcán Cotacachi (0°19′51″N, 78°55′55″W), elevation 702 m.

Paratypes.—Ecuador: Pichincha; "Guarumos = Western slope of Mount Pichincha, Pichincha Province, Ecuador Altitude 2000–2500 m" [transcription from original tag] (MCZ 50396); Patton et al. (2015) give the elevation for Guarumos as 2,000 m and coordinates as 00.06667°S, 78.63333°W; Pichincha Province, (near) Mindo, 4,200 feet (1,380 m) (0°03′N, 78°46′W fide Voss 1988) (UMMZ 155808).

Additional records.—In Carchi and Pichincha provinces in northern Ecuador and in southern Ecuador in Azuay Province (see below and Brito and Arguero 2016).

Distribution.—We have examined specimens from Imbabura and Pichincha provinces in northwestern Ecuador and additional specimens of *Tanyuromys* have been reported recently from adjacent Carchi Province in extreme northern Ecuador and from southern Ecuador in Azuay Province (Fig. 2). Members of the genus almost certainly occur discontinuously elsewhere in appropriate habitats at middle elevations of northwestern Ecuador and almost certainly in adjacent Colombia.

Etymology.—Named for Dr. Thomas E. Lee, Jr., Abilene Christian University, Abilene, Texas, in recognition of his contributions to mammalogy; his training of students, both in the United States and Ecuador; and of his capturing the holotype and making it freely available to us for study. The specific epithet is a noun in the genitive case formed by adding "i" to the stem of the name.

Nomenclatural statement.—A life science identifier (LSID) number was obtained for the new species (*Tanyuromys thomasleei*): urn:lsid:zoobank. org:act: 94B3A785-B923-40F8-A4D8-B50731B21DEE.

Diagnosis.—A medium-sized member of the Oryzomyini, with long, glossy, and soft fur dorsally (Fig. 3). Longest mystacial vibrissae when laid back extending well beyond relatively small pinna (16–18 mm). Tail exceptionally long (< 205 mm), ca. 1.5 × head plus body length, appearing nearly naked, with small relatively pale terminal tuft. Two of the prepared skins, including the holotype, have incomplete tail skins. The specimen from Mindo has a 4-mm terminal tuft. Hind foot long (36–37 mm) and narrow, with ungual bristles not extending beyond tips of claws. Dorsal profile of skull little arched; interorbital region relatively narrow anteriorly, with anteriorly convergent margins and prominent beading that continues posteriorly on parietals as a ridge until it dips ventrad to the lambdoidal crest; comparatively narrow zygomatic plate; lateral wing of parietal large; braincase little inflated; contours of skull tending toward angularity rather than being curved; zygomatic arch relatively flaring and with large jugal; carotid circulatory pattern 3 of Voss (1988); bony palate short. Molars complex and lophodont. Capsular process of mandible obsolete or little developed.

Description.—Head plus body length in *T. thomasleei* similar to that of *T. aphrastus*. Dorsal fur long (15 mm on lower back), glossy, and soft. Dorsal coloration of holotype a fine mixture of pale and dark brown-tipped hairs, dull gray basally, giving an overall impression closest to Light Seal Brown of Ridgway (1912), although not matching perfectly with any Ridgway color. The most dorsal and heaviest facial vibrissae black throughout their length, others become pale distally or are pale throughout their length; length of longest mystacial vibrissae up to 60 mm, when laid back reaching well past relatively small pinna. Fur laterally becoming gradually somewhat more
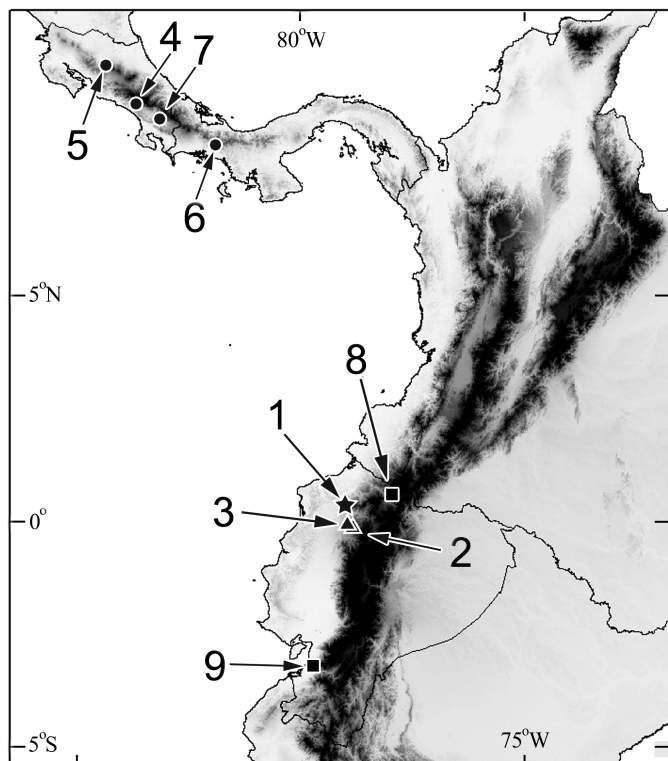
Fig. 2.—Map showing all known localities for *Tanyuromys*. The star and triangles represent the localities for the specimens of *T. thomasleei* examined herein. Locality 1 (star) is the type locality for *T. thomasleei*, at 10 km east of Santa Rosa, Imbabura Province, Ecuador. Locality 2 (triangle) is where the 1st known specimen of *T. thomasleei* was obtained in 1953 at Guarumos on the western slope of Mt. Pichincha, Pichincha Province, Ecuador. Locality 3 (triangle) is where the 2nd known specimen was obtained at Mindo on the Pacific slopes of Volcán Pichincha, Pichincha Province, Ecuador in 1980. The circles represent all known localities for *T. aphrastus*. Locality 4 is where the holotype of *T. aphrastus* was obtained at San Joaquín de Dota in the Cordillera de Talamanca, San José Province, Costa Rica. Locality 5 is Monteverde Cloud Forest Reserve, Monteverde, Alajuela Province, Costa Rica, where 2 specimens of *T. aphrastus* were obtained, 1 in 2000 and 1 in 2002. Locality 6 is where 2 specimens of *T. aphrastus* were obtained at 24 km north-northeast of San Félix, Chiriquí Province, Panamá, in 1980. Locality 7 is where the most recent specimen of *T. aphrastus* was obtained in 2012 in Parque Internacional La Amistad, Puntarenas Province, Costa Rica. The squares represent localities for recent specimens of *T. thomasleei* reported by Brito and Arguero (2016). They reported 3 recently collected specimens of *Tanyuromys* "*aphrastus*," 1 in Carchi Province in northern Ecuador (Locality 8), 1 in Azuay Province in southern Ecuador (Locality 9), and 1 in Pichincha Province (not plotted because essentially identical to Localities 2 and 3). See text and Appendix I for details on localities, museum catalog numbers, and habitats.

buffy. Venter with pale-buff-tipped hairs with drab gray bases showing through. Transition from dorsal coloration to ventral gradual, not abrupt. Tail long, manifestly longer than head plus body, appearing nearly naked, its scales arranged in 15 rings per cm at mid-length in holotype. Scales on dorsal surface of hind foot visible through the hair for a considerable distance proximally. A small hypothenar pad present on plantar surface.

Zygomatic plate relatively narrow, sometimes with small projections on dorsal anterior margin. Braincase not conspicuously inflated, relatively "boxy-looking." Contours of skull generally angular, less rounded. Zygomatic arch comparatively flaring. Mesopterygoid fossa widest anteriorly. Cranial characters given here are based primarily upon the holotype from Volcán Cotacachi, the 1980 specimen from Mindo, and the 1953 specimen from Guarumos. Other characters as given for genus by McCain et al. (2007), Pine et al. (2012), and Weksler (2015a).

Morphological comparisons.—Externally, the 2 species are quite similar. Head plus body length of the holotype of *T. thomasleei* was measured at 139 mm in the field; that length for 4 adult *T. aphrastus* averages 140 mm. Tail length is 207 mm in the holotype of *T. thomasleei* and ranges from > 213 to 235 mm for 4 adult *T. aphrastus*. Length of tail averages ca. $1.5 \times$ length of head plus body in *T. thomasleei* and ca. $1.6 \times$ length of head plus body in *T. aphrastus*. Entire skins of the tail seem to have been preserved in only the specimen of *T. thomasleei* from Mindo. The tail scales are larger in the holotype of *T. thomasleei* than in the adult *T. aphrastus* from Monteverde and they are arranged in a more annular fashion than in *T. aphrastus*. The MCZ specimen of *T. thomasleei*, however, resembles *T. aphrastus* more in this regard than does the holotype. The dorsal fur of the holotype of *T. thomasleei* is somewhat glossier than in the adult Monteverde *T. aphrastus*. The terminal tuft is 4 mm long in the specimen of *T. thomasleei* from Mindo (UMMZ 155808) and is now tan in color (said in an earlier year to be reddish brown by C. M. McCain [in litt.]), whereas it is 6 mm and black in the holotype of *T. aphrastus*. It is also black in the Panamanian immature and white in the immature from Monteverde, Costa Rica. The size of the tail tuft is greatly exaggerated in the figure identified as of *T. aphrastus* (including *T. thomasleei*) in Wilson et al. (2017). Dorsal and heaviest facial vibrissae similar in length in the 2 species; however, they are distinctly darker in *T. thomasleei*, being paler distally or pale throughout their length in *T. aphrastus*. Interorbital breadth relatively narrow compared to that of *T. aphrastus* (4.5, 4.8 mm in *T. thomasleei* versus $\bar{X}$ = 5.4, range = 5.1–5.5, n = 5 in *T. aphrastus*). Zygomatic plate relatively narrow compared to that of *T. aphrastus*, somewhat more projecting anterodorsally than in *T. aphrastus*. Supraorbital beading raised and heavy, usually reaching lambdoidal crest. This ridge appears less prominent in *T. aphrastus*, except in the holotype of *aphrastus*. Lateral wing of parietal comparatively larger than that of *T. aphrastus*. Incisive foramen is relatively shorter in *T. thomasleei* than in *T. aphrastus*, appears constricted anteriorly and posteriorly; whereas margins are more evenly bowed in *T. aphrastus* (see Figs. 4 and 5). Mesopterygoid fossa expanded anteriorly in *T. thomasleei*, but narrows anteriorly in *T. aphrastus*. Palatal bridge is similar in *T. thomasleei* (6.5–7.5 mm) to that of *T. aphrastus* (6.5–7.4 mm), but does not extend as far past molars. Length of upper toothrow (alveolar) is shorter in *T. thomasleei* (5.5–5.8 mm) than in *T. aphrastus* (5.8–6.2 mm; Figs. 6 and 7). Capsular process of mandible less prominent in *T. thomasleei* than in *T. aphrastus*. However, few specimens are available for each species and a range of ages is represented in *T. aphrastus*,

Fig. 3.—Dorsal and ventral views of prepared skin of an adult male *Tanyuromys thomasleei* (holotype; QCAZ 10427). Note that the tip of the tail skin is missing.

Fig. 4.—Dorsal, ventral, and lateral views of the cranium and lateral view of dentary of an adult male *Tanyuromys thomasleei* (holotype; QCAZ 10427); occipitonasal length of skull = 34.4 mm.

thus some distinguishing characters will need to be re-evaluated when additional specimens become available. See Table 1 for selected external and cranial measurements for 3 specimens of *T. thomasleei* and all 6 known specimens of *T. aphrastus*.

Molecular comparisons.—Molecular characters confirm that the *aphrastus* holotype and specimens from Monteverde and Parque Internacional La Amistad, Costa Rica, and a Panamanian population of *T. aphrastus* are quite similar, whereas the specimens from Ecuador form a distinct, separate clade (Fig. 8). The 2 specimens from Monteverde differ from each other by about 0.5%; they were collected in different years and from different elevations, 1 from 1,300 m and 1 from 1,550 m, within continuous habitat. The 2 specimens from Monteverde differ from the *aphrastus* holotype by 0.7%. The 2 specimens from Monteverde and 1 from Parque Internacional La Amistad differ by 0.9%, the specimen from Parque Internacional La Amistad is from a place about midway between the Monteverde population and the Panama locality. The specimen from Parque Internacional La Amistad, the southeasternmost Costa Rican locality, differs by 0.9% from the Panamanian specimen. The 4 Costa Rican samples differ from the Panamanian specimen by 1.2%. Our molecular data span the known range of the species.

The 2 specimens sequenced from Imbabura and Pichincha provinces in northern Ecuador differ from each other by 2.8%. These 2 specimens differ in *Cytb* sequences by 10.2% from specimens representing the Central American populations of *T. aphrastus*.

Habitat.—The 2 specimens from Pichincha Province were from apparently undisturbed forest on the Pacific slopes; 1 from upper montane rainforest between 2,000 and 2,500 m, near Guarumos, and the other from lower montane rainforest near Mindo.

Ecology.—Recently, Lee et al. (2010) reported capturing an adult male, the holotype designated herein for *T. thomasleei*
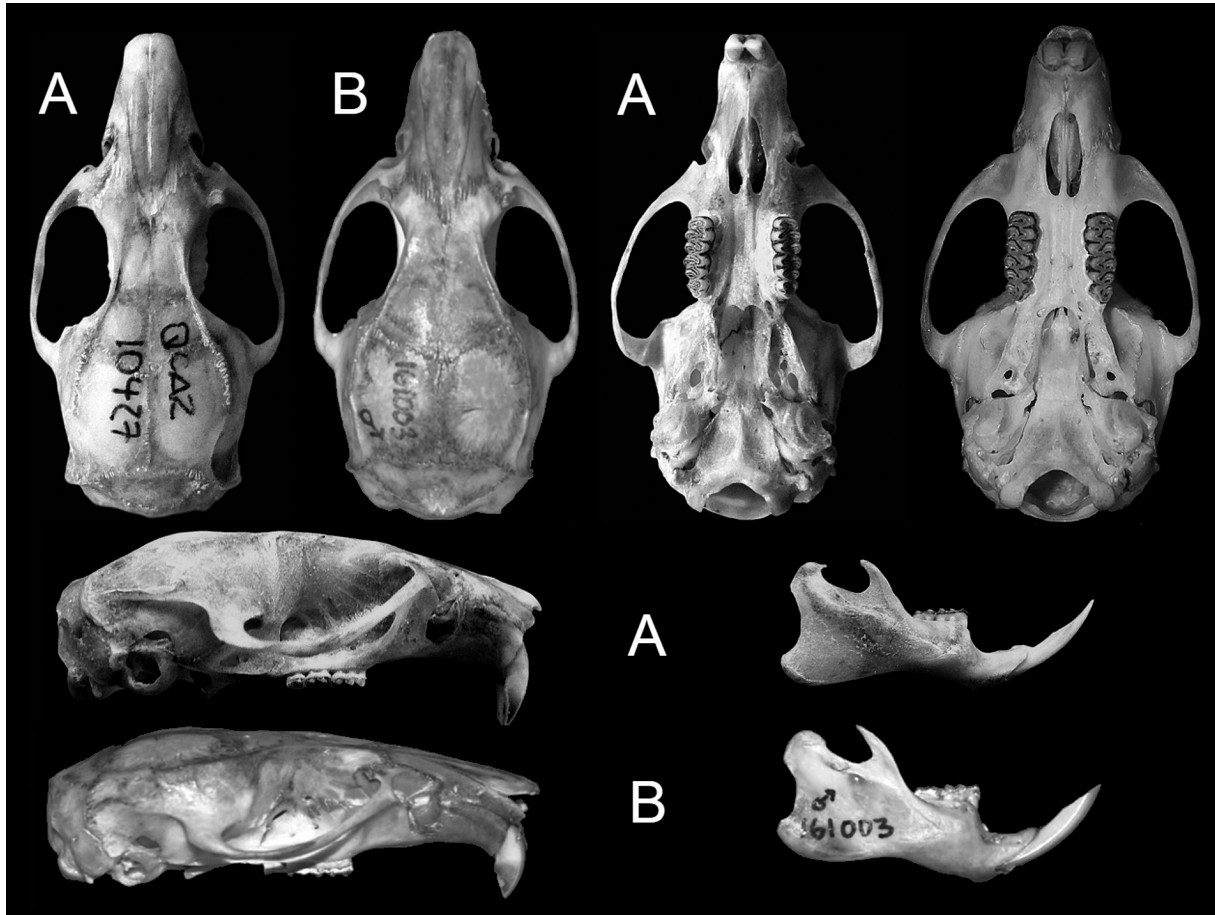
Fig. 5.—Dorsal, ventral, and lateral views of the crania and lateral views of dentaries of adult male *Tanyuromys*: A) *Tanyuromys thomasleei* (QCAZ 10427—holotype, occipitonasal length of skull = 34.4 mm); B) *Tanyuromys aphrastus* (KU 161003; occipitonasal length of skull = 32.9 mm) from Costa Rica.
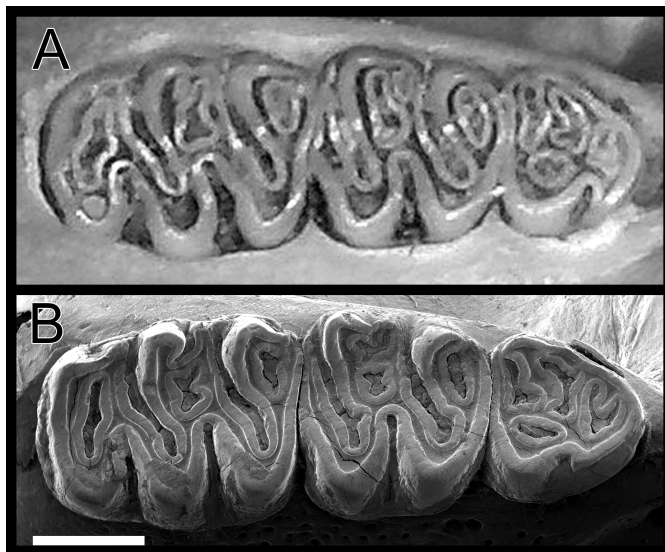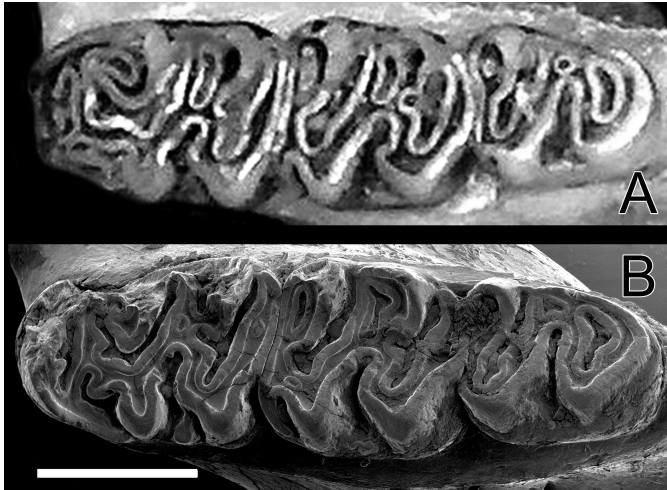

Fig. 6.—Occlusal views of the left maxillary molar rows of *Tanyuromys thomasleei*. A) Adult male (holotype; QCAZ 10427); B) adult female from Mindo, Ecuador (UMMZ 155808). Anterior is to the left. Scale bar represents 1 mm. Bottom image republished from Pine et al. (2012) courtesy of the American Society of Mammalogists.

(QCAZ 10427), in northern Ecuador, at 702 m. This specimen represents the third record for this species and the first from Imbabura. It was caught "in a mixed forest and tall-grass area within 10 m of a stream" (Lee et al. 2010:10). This site is in an area generally characterized as "… within the drainage of the Río Guayllabamba … a mix of mostly secondary forests with some primary riparian and primary upland forests … patches of primary forest have many tall buttressed trees that are covered in epiphytes, most of which are … Bromeliaceae … cleared areas … contained Araceae and Arecaceae (*Iriartea* sp.)" (Lee et al. 2010:2). All localities from Carchi, Imbabura, and Pichincha provinces are at middle elevations on the Pacific versant of northwestern Ecuador. The specimen reported from Azuay Province in southern Ecuador is also on the Pacific slope.

Robert S. Voss (1988:423) reported that "*Oryzomys aphrastus*" [= *T. thomasleei* as herein recognized] was caught along a stream near Mindo (0°03′S, 78°46′W), about 37 km (by air) northwest of Quito, Pichincha Province, in Ecuador's Cordillera Occidental of the western Andes. Voss (1988:420) wrote "The Mindo region, drained by the Ríos Mindo, Canchupi, and Saguambi, is in the foothills of the western Andes (Cordillera Occidental). Hills and ridge tops are covered with cloud forest (Lower Montane Rain

Fig. 7.—Occlusal views of the left mandibular molar rows of *Tanyuromys thomasleei*. A) Adult male (holotype; QCAZ 10427); B) adult female from Mindo, Ecuador (UMMZ 155808). Anterior is to the left. Scale bar represents 1 mm. Bottom image republished from Pine et al. (2012) courtesy of the American Society of Mammalogists.

Forest), but the vegetation of adjacent river valleys more closely resembles Lowland Rain Forest." Voss's specimen (UMMZ 155808), caught in 1980, is of an adult female.

Hershkovitz (1970) regarded *T. aphrastus* as being semiaquatic. Tirira (2008:120), presumably influenced by Hershkovitz's opinion, referred to the animal that he called *Sigmodontomys aphrastus* (including *T. thomasleei*) as the "rata arrocera de agua de cola larga" and the "long-tailed rice water rat." Ruelas and Pardiñas (2017) referred to *T. aphrastus* (including *T. thomasleei*) as "Harris's rice water rat." However, trapping locations and external morphology, including quality of the pelage, show that neither species is semiaquatic (see also Pine et al. 2012), and Ruelas and Pardiñas (2017) stated that *T. aphrastus* (including *T. thomasleei*) is "terrestrial." Neither species has any association with rice. Pine et al. (2012) used the name "long-tailed montane rats" for the members of the genus *Tanyuromys*. We herein use the name Lee's long-tailed montane rat for *T. thomasleei*. "Long-tailed" is appropriate because members of the genus *Tanyuromys* have a tail length ca. 1.5 times the length of head plus body, the longest tails proportionally of any members of the Oryzomyini.

Community composition.—At the type locality on Volcán Cotacachi, Lee et al. (2010) reported *Philander opossum* (Linnaeus, 1758); *Anoura fistulata* Muchhala, Mena V., and Albuja V., 2005; *Glossophaga soricina* (Pallas, 1766); *Micronycteris megalotis* (Gray, 1842); *Carollia brevicauda* (Schinz, 1821); *Carollia castanea* (H. Allen, 1890); *Sturnira bogotensis* Shamel, 1927; *Sturnira ludovici* Anthony, 1924; *Sturnira luisi* Davis, 1980; *Platyrrhinus vittatus* (Peters, 1859); *Eptesicus innoxius* (P. Gervais, 1841); *Melanomys caliginosus* (Tomes, 1860); and *Hoplomys gymnurus* (Thomas, 1897) along with their single specimen of *Tanyuromys*.

At Mindo, where the adult female *T. thomasleei* was obtained, the following species of mammals were observed or collected: the opossums *Caluromys derbianus* (Waterhouse, 1841); *Chironectes minimus* (Zimmermann 1780); *Didelphis*

sp.; *Marmosa phaea* Thomas, 1899; *Marmosa robinsoni* Bangs, 1898; *Marmosops impavidus* (Tschudi, 1845); *Metachirus nudicaudatus* (É. Geoffroy St.-Hilaire, 1803); and *Philander opossum* (Linnaeus, 1758); the rodents *Handleyomys alfaroi* (Allen, 1891); *Ichthyomys tweedii* Anthony, 1921; *Mindomys hammondi* (Thomas, 1913); *Nephelomys moerex* (Thomas, 1914); *Transandinomys bolivaris* (Allen, 1901); and the felid *Herpailurus yagouaroundi* (É. Geoffroy Saint-Hilaire, 1803) (Voss 1988; Gardner 2008; and UMMZ collection).

Comments.—We provide external and cranial measurements for the adult male type in Table 1. Mass was 49 g; descended testes measured 9 × 5 mm. The type locality was not included on the map provided by Pine et al. (2012). We treat *T. thomasleei* as monotypic. The specimen from Guarumos has atypical coloration for any member of the Oryzomyini; it is leucistic with scattered white areas primarily restricted to the anterior half of the dorsum and covering about 5% of the dorsum's area.

The Central American specimens with complete tails have small pencils, a feature that Pine et al. (2012) used as a character for the genus. In the Ecuadoran specimens at hand, aside from the specimen from Mindo, the very tips of the tail are missing, almost certainly postmortem. In the type of *T. thomasleei*, however, it is only the tip of the skin of the tail that is missing—all of the vertebrae are preserved. Because the tails in this extremely long-tailed genus terminate in a very thin tip, it appears that some preparators perhaps attempted to insert a tail wire of larger than serviceable diameter and thereby broke off the tips. Also, the tip might be truncated by the door of a Sherman live trap as seems to be the case with KU 161003.

Tirira (2007, 2008) plotted localities and provided accounts of this species, based on the 1st 2 specimens known. Brito and Arguero (2016) provided images of the plantar surface of a hind foot and a molar toothrow. Tirira (2017a, 2017b) provided a color photograph of a living or dead individual and a map of Ecuador with the potential distribution of *T. thomasleei* shaded.

Both Weksler and Percequillo (2011) and Weksler (2015b) provided a key to the genera of Oryzomyini, based primarily on external characters. Both *T. aphrastus* and *T. thomasleei* are identified in the "*aphrastus* group" by following the character stream of "Dorsal and ventral fur without grooved spines," "Hindfeet with hypothenar pad absent or vestigial," "Hindfeet without natatory fringes – continuous combs of stiff hairs along the plantar margins and sometimes between the digits," and "Hind feet without interdigital webs" (Weksler and Percequillo 2011:287). Villalobos-Chaves et al. (2016) provided a beautifully illustrated key to the rodents of Costa Rica. Their image of the hind footpads of *T. aphrastus* (their figure A1h) provides a useful comparison of cricetines and murines.

Additional specimen of Tanyuromys aphrastus.—David Villalobos-Chaves captured an adult female (field no. DV 024; UCR-1921) in Parque Internacional La Amistad, Sector Pittier, Provincia Puntarenas, Costa Rica [9°01′25.7″N, 82°57′29.3″W], elevation 1,570 m on 11 May 2012 (Rodríguez-Herrera et al. 2014). Timm recently examined this specimen, courtesy of Villalobos-Chaves and Bernal Rodríguez-Herrera. It consists

Table 1.—External and cranial measurements (in mm) of 9 specimens of *Tanyuromys*. The 3 specimens of *T. thomasleei* described here are to the left and the 6 known specimens of *T. aphrastus* from Costa Rica and Panama to the right.[a]

Measurements	*Tanyuromys thomasleei*			*Tanyuromys aphrastus*					
	QCAZ 10427	MCZ 50396	UMMZ 155808	UMMZ 62875	KU 161003	USNM 541200	USNM 541201 (immature)	KU 159021 (immature)	UCR 1921
Head plus body length	139		142	152	133	140	116	84	135
Tail length (tails incomplete in some)	207		205	235	> 213	> 217	176	152	227
Hind foot length (with claw)	36		37	40	37	37	35	31	35
Ear length (from notch)	16		18		18	17	17	13	18
Upper toothrow length (alveolar)	5.5	5.8	5.7	5.8	6.0	5.8	6.2	5.5	6.1
M1 breadth	1.9	2.1	1.9	1.9	2.1	2.1	2.1	1.9	2.0
M2 breadth	1.8	1.9	1.9	2.1	2.0	1.9	1.9	1.8	1.9
M3 breadth	1.4	1.6	1.5	1.8	1.6	1.7	1.6	1.5	1.5
M1–M1 breadth	7.5	7.3	6.8	6.7	7.1	7.1	6.7	5.7	7.4
M3–M3 breadth	7.2	7.1	7.1	6.8	7.1	7.2	6.3	5.9	7.2
Palatal bridge length	7.5	7.1	6.5	6.5	7.4	7.2	7.1	5.5	7.2
Postpalatal length	11.5	10.3	10.4		10.5	9.9	8.8	7.5	
Incisive foramen length	5.1	5.0		5.3	5.3	4.8	4.0	3.8	5.9
Breadth across incisive foramina	2.4	1.9		2.9	2.2	2.1	1.7	1.5	2.8
Upper diastema length	10.4	8.1			8.9	8.7	7.0	5.7	10.1
Zygomatic plate breadth	3.0	2.7	3.1	3.2	3.2	2.8	2.5	2.5	3.5
Occipitonasal length	34.4	31.7			32.9	32.7	29.3	26.1	34.9
Braincase height	10.7		9.6		9.9	10.3	9.8	8.2	
Rostrum breadth	6.9	6.3		6.8	7.1	6.6	5.8	5.4	5.9
Interorbital breadth	4.8	4.5		5.5	5.5	5.1	5.4	4.8	5.4
Zygomatic breadth	18.4				18.6	18.6	16.3	14.4	19.4
Lambdoidal breadth			12.6		13.1	13.3	11.7	10.9	13.5
Rostrum length	10.0	9.0			10.1	9.7	8.5	7.3	9.5

[a] External measurements were taken from the original specimen tags as recorded by the preparer. All cranial measurements taken by Pine except for UCR 1921, which were taken by Timm.
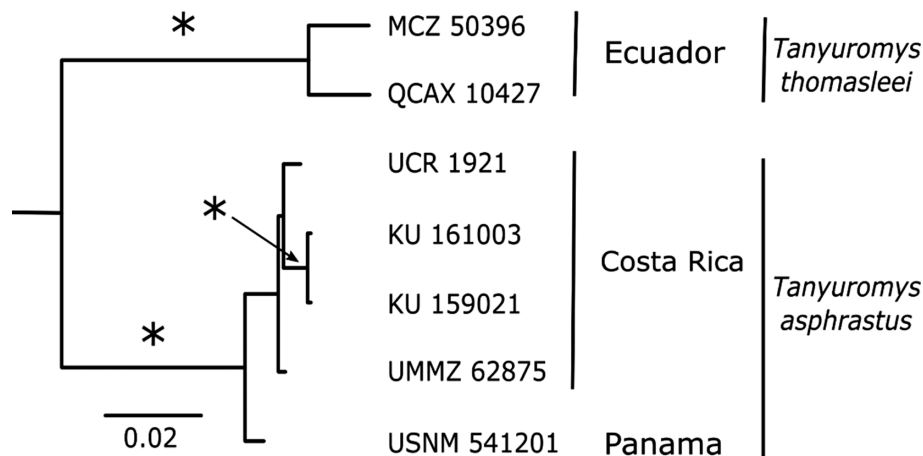
Fig. 8.—Phylogenetic relationships of *Tanyuromys*, based on combined Bayesian analysis of mitochondrial cytochrome *b* (*Cytb*), representing 5 specimens of *Tanyuromys aphrastus* from Central America and 2 specimens of *T. thomasleei* from Ecuador. See text for specific localities.

of a well-made skin, cleaned intact skull and postcranial skeleton, and frozen tissues. Villalobos-Chaves informed us that he captured the animal using chicken meat for bait. The skin and cranial characters conform well with other specimens of *T. aphrastus*. It has a small but obvious tuft at the tip of the tail.

DISCUSSION

Based on combined morphological and molecular data, *Tanyuromys* falls within the *Aegialomys–Megalomys–Melanomys–Nesoryzomys–Oryzomys–Sigmodontomys* clade (Pine et al. 2012; Salazar-Bravo et al. 2016). Based on our analysis of the mitochondrial *Cytb* gene (excluding the extinct *Megalomys*), *Tanyuromys* falls within the *Aegialomys–Melanomys–Nesoryzomys–Oryzomys–Sigmodontomys* clade of the sigmodontine tribe Oryzomyini. As part of the description of the genus *Tanyuromys*, Pine et al. (2012) provided phylogenetic analyses documenting that "*Sigmodontomys*" *aphrastus* and *Sigmodontomys alfari* are not sister taxa but rather that *aphrastus* is a member of a clade that includes *Aegialomys*, *Melanomys*, *Nesoryzomys*, *S. alfari*, and the recently extinct, Caribbean endemic genus *Megalomys*. They stated that

"*Sigmodontomys alfari* is most closely related to *Melanomys*, and *aphrastus* is either the sister to that clade, or to the extinct Caribbean genus *Megalomys*" (Pine et al. 2012:851). In a recent reassessment of the Sigmodontinae, primarily based on genetic data (*Cytb* and a nuclear marker [*Rbp*3]), Salazar-Bravo et al. (2016) reaffirmed that the tribe Oryzomyini was monophyletic. Their combined analysis suggested that *Tanyuromys aphrastus* was a member of a clade that included a grouping of *Aegialomys*; *Megalomys*; *Melanomys*; *Nesoryzomys*; *Pennatomys* Turvey, Weksler, Morris, and Nokkert, 2010; and *Sigmodontomys*; with *T. aphrastus* (based on the adult specimen from Monteverde) as the sister to those genera.

The *Aegialomys–Megalomys–Melanomys–Nesoryzomys–Oryzomys–Sigmodontomys–Tanyuromys* clade found here and in other examinations (Hanson and Bradley 2008; Pine et al. 2012; Salazar-Bravo et al. 2016) is basally well supported by both molecular and morphological data. However, the relationships within the clade vary some, based on data-set examined. The most controversial relationship is that between *Melanomys* and *Sigmodontomys* where *Melanomys* is paraphyletic in regard to *Sigmodontomys*. The branching order leading to paraphyletic *Melanomys* changes based on the gene used (Pine et al. 2012) and is not well supported (though the sister relationship of the 2 genera is well supported). *Melanomys* and *Sigmodontomys* are morphologically distinct with *Melanomys* being one of the most distinct genera in the tribe (Pine et al. 2012). Determining the actual relationships between species assigned to the 2 genera could provide valuable insight on the dispersal and evolution of the clade as a whole.

Elevations of capture for specimens of *T. thomasleei* that we examined range from 702 to 2,000–2,500 m. Elevations of capture for *T. aphrastus* range from 1,220 to 1,550 m.

The distribution of *T. thomasleei* is poorly known, but we do know that *T. aphrastus* occurs in both Costa Rica's Cordillera de Tilarán and Cordillera de Talamanca and the Chiriquí highlands of Panama's Cordillera Central. The Talamanca and the adjacent Chiriquí highlands are primarily tectonic uplift mountains and the Tilarán of volcanic origin. Monteverde, in the Cordillera de Tilarán, is the northernmost locality known for *Tanyuromys* and probably represents the northernmost locality where the genus will be found. The Monteverde region has been of considerable biological interest for decades and is one of the best sampled areas for mammals in Central America (Timm and LaVal 2000, 2018). Several species of small mammals reach their northernmost known distribution there, including the rodents *Nephelomys devius* (Bangs, 1902); *Oligoryzomys vegetus* (Bangs, 1902); *Reithrodontomys creper* Bangs, 1902; and *Rheomys raptor* Goldman, 1912; and the shrew *Cryptotis nigrescens* (Allen, 1895). A shrew, *Cryptotis merriami* Choate, 1970, and a spiny pocket mouse, *Heteromys nubicolens* Anderson and Timm, 2006, reach their southernmost distribution there. One species of shrew—*Cryptotis monteverdensis* Woodman and Timm, 2016—is known only from there.

One or more species of *Tanyuromys* likely occur in the cordilleras of Colombia, however, no specimens currently are known. Based on geography, *T. thomasleei* likely occurs on the Pacific

slopes of the Cordillera Occidental of Colombia. Cadena et al. (1998:11) treated a long-tailed member of the Oryzomyini (Instituto de Ciencias Naturales, Bogotá, specimen 13663), captured on the Pacific Chocoan slopes of Colombia's Andes in the Department of Nariño, as probably belonging to an undescribed species of *Sigmodontomys*. Some of the characters they provided are suggestive of *Tanyuromys*, especially "its extremely long tail" and that it "resembles an *Oryzomys* of the *albigularis* group." However, other characters, especially "a short palate without postpalatal pits, a well-developed alisphenoid strut … and oval (rather than rectangular) molars" clearly exclude inclusion of this specimen from either the genus *Sigmodontomys* or *Tanyuromys*. Cadena et al. (1998) suggested, as did Pine et al. (2012), that this specimen might represent a new taxon phylogenetically close to *Mindomys hammondi* (Thomas, 1913). The identity of this specimen awaits further study.

The Oryzomyini radiated into the diverse array of 33 currently recognized genera and occupy a wide array of niches. Weksler (2006) suggested that the ancestral region for the Oryzomyini was South America prior to the formation of the Panamanian land bridge. The geologic history of the closing of the Isthmus of Panama connecting North and South America is a topic of considerable debate, as well as to when and how mammals (along with other terrestrial taxa) crossed between the continents. Despite numerous studies, the time of the emergence of a permanent Panamanian land bridge is disputed, with a traditional estimate suggesting some 3.5 mya. In contrast however, recent neontological, paleontological, and upgraded geologic mapping in Panama suggests that the isthmus might have been a volcanic chain above sea level from late Eocene until at least late Miocene (Montes et al. 2012a, 2012b, 2015; Bacon et al. 2015; and see references therein, albeit contra O'Dea et al. 2016). Faunal exchanges prior to the complete closure might have been possible, perhaps well before the formation of a permanent land bridge.

The closing of the isthmus caused major climatic changes, which would have had impact on the availability of suitable habitat for many species (Montes et al. 2012b). Although genera such as *Tanyuromys* are currently limited to cooler montane habitats, the climatic changes occurring after the closing of the isthmus could have created cool lowland habitats perhaps conducive to the dispersal and survival of Oryzomyini adapted to cool climates. Recent phylogenetic studies of the Oryzomyini document that this group of rodents possesses marked ability to cross saltwater gaps (Pine et al. 2012; Prado and Percequillo 2018). Hershkovitz (1966) first suggested a nonsynchronous dispersion of the ancestral Oryzomyini between South and Central America. At that time, *Tanyuromys* was known only from the Costa Rican holotype of *T. aphrastus* (then called *Oryzomys aphrastus*) and thus Hershkovitz was uncertain as to where it would fit into his hypotheses of faunal exchange strata. He placed in it stratum III, but with the strange caveat (p. 737) that "Its nearness to *Nectomys* (*Sigmodontomys*) *alfari* suggests that *aphrastus* might belong to faunal stratum IV." On the basis of there being a second species of *Tanyuromys* now known from South America, *T. aphrastus* definitely fits Hershkovitz's

criteria for belonging to faunal stratum III, with dispersal of its ancestral stock from South America into Central America in the Pliocene and over water, as stratum III was characterized in his figure 154. Hershkovitz later (1972:figure 5), however, showed stratum III movement out of South America as occurring during the "Middle–Late Tertiary."

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Appendix I

Specimens included in molecular and descriptive analyses.—Specimens are arranged by genus, species, and locality. Specific identification numbers (museum or collectors' numbers) and GenBank accession numbers (for specimens included in molecular analysis) are listed in parentheses. GenBank numbers presented in bold represent sequences generated in this study. Museum and collectors' initials are as follows: Abilene Christian University Natural History Collections, Abilene, Texas (ACUNHC); Angelo State Natural History Collections, San Angelo, Texas (ASNHC); Departamento de Microbiología, Universidad del Valle, Cali, Colombia (HTC); El Museo de Zoología, Pontificia Universidad Católica del Ecuador, Quito, Ecuador (QCAZ); Field Museum, Chicago, Illinois (FMNH); Instituto de Ciencias Naturales, Bogotá, Colombia (ICN); Michael Valqui (MV; voucher at Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Perú); Museo de Historia Natural La Salle, Caracas, Venezuela (MHNLS); Museu Nacional, Rio de Janeiro, Brazil (MNRJ); Museo Nacional de Historia Natural del Paraguay, San Lorenzo, Paraguay (MNHNP); Museum of Southwestern Biology, Albuquerque, New Mexico (MSB); Museum of Vertebrate Zoology, Berkeley, California (MVZ); Royal Ontario Museum, Toronto, Ontario, Canada (ROM); The Museum of Texas Tech University, Lubbock, Texas (TTU, TK—tissue collection); Thomas E. Lee, Jr. (TEL; vouchers available at ACUNHC and QCAZ); Universidad de Costa Rica, San José, Costa Rica (UCR); University of Kansas Museum of Natural History, Lawrence, Kansas (KU); University of Michigan Museum of Zoology, Ann Arbor, Michigan (UMMZ); Ulysses F. J. Pardiñas (UP). Additional details on some specimens analyzed were listed previously by Weksler (2006), Turvey et al. (2010), and Percequillo et al. (2011).

Abrawayaomys ruschii.—BRAZIL (MNRJ 67557, GenBank AX949189).

Abrothrix longipilis.—CHILE: Araucanía; Fundo Hermanos García (MSB 205660, GenBank GU564083).

Aegialomys galapagoensis.—ECUADOR: Galápagos; Isla Santa Fe (ASNHC 9994, GenBank EU579478).

Aegialomys xanthaeolus.—ECUADOR: Guayas; Bosque Protector Cerro Blanco (TTU 103309, GenBank EU340015).

PERU: Arequipa; 4.5 mi E Acarí (MVZ 145533, GenBank EU579479).

Akodon boliviensis.—BOLIVIA: Tarija; 4.5 km E of Iscayachi (MSB 68571, GenBank KC841367).

Amphinectomys savamis.—PERU: Iquitos; San Pedro (MV 97005, GenBank EU579480).

Andinomys edax.—BOLIVIA: Tarija; 4.3 km E Boyuibe (MSB 67194, GenBank AF159284).

Arvicola terrestris.—SWITZERLAND: 46.83333°N, 8.38333°W (MVZ 155884, GenBank AY275106).

Cerradomys scotti.—PARAGUAY: Canindeyú; Reserva Natural del Bosque Mbaracayú (TK 61881, GenBank EU579482).

Cricetus cricetus.—AUSTRIA: Niederösterreich; 1 km NE Gutramsdorf (MVZ 155880, GenBank AY275109).

Drymoreomys albimaculatus.—BRAZIL: São Paulo; Capão Bonito (MVZ 182088, GenBank EU579487).

Ereoryzomys polius.—PERU: Amazonas; Balsas (FMNH 129243, GenBank EU579483).

Euneomys chinchilloides.—ARGENTINA (UP LB018, GenBank AY275115).

Euryoryzomys macconelli.—PERU: Loreto; Alto Amazonas, Nuevo San Juan, Río Gálvez (AMNH 272678, GenBank EU579484).

Handleyomys alfaroi.—ECUADOR: Esmeraldas; Comuna San Francisco de Bogotá (TTU 102921, GenBank EU579488). NICARAGUA: Matagalpa; Selva Negra (TTU 96983, GenBank EU579489).

Handleyomys intectus.—COLOMBIA: Antioquia; 4 km S El Retiro (ICN 16093, GenBank EU579490).

Holochilus sciureus.—BOLIVIA: Santa Cruz; Estancia San Marcos, 6 km W Ascensión (MSB 99051, GenBank EU579497).

Hylaeamys megacephalus.—VENEZUELA; Bolívar; San Ignacio de Yuruani (MHNLS 8061, GenBank EU579499).

Juliomys pictipes.—PARAGUAY: Alto Paraná; Limoy (TK145073, GenBank FJ026733).

Melanomys caliginosus.—ECUADOR: Esmeraldas; Comuna San Francisco de Bogotá (TTU 102975, GenBank EU340021).

Melanomys chrysomelas.—NICARAGUA: Atlántico Norte; Rosa Grande, Siuna (TTU 100324, GenBank EU340017).

Melanomys columbianus columbianus.—VENEZUELA: Zulia; Misión Tukuko (MHNLS 7698, GenBank EU340022).

Melanomys columbianus idoneus.—PANAMA: Darién; Cana (TTU 39150, GenBank EU340024; ROM 116303, GenBank EU340023).

Microryzomys minutus.—PERU: Cuzco; 32 km NE Paucartambo (MVZ 166666, GenBank EU258535).

Neacomys spinosus.—PERU: Amazonas; Río Cenepa, vicinity of Huampami (MVZ 155014, GenBank EU579504).

Nectomys apicalis.—PERU: Kiteni; Río Urubamba (MVZ 166700, GenBank EU340013).

Nectomys squamipes.—PARAGUAY: Paraguarí; Parque Nacional Ybycui (TTU 108150, GenBank EU074634).

Neomicroxus latebricola.—ECUADOR: Napo; Oyacachi, cantón el Chaco (QCAZ 4160, GenBank KF437365).

Neotoma floridana.—UNITED STATES: Texas; Brazoria County, Peach Point Wildlife Management Area (TK 51632, GenBank AF294343).

Nephelomys albigularis.—PERU: Cajamarca; Las Ashitas (AMNH 268125, GenBank EU579505).

Nesoryzomys fernandinae.—ECUADOR: Galápagos; Isla Fernandina (ASNHC 10580, GenBank EU579506).

Nesoryzomys swarthi.—ECUADOR: Galápagos; Isla Santiago, La Bomba (ASNHC 10003, GenBank EU340014).

Neusticomys monticolus.—ECUADOR: Pichincha; Tandayapa Valley (ACUNHC 900, GenBank KF359515).

Oecomys bicolor.—PERU: Loreto; Nuevo San Juan, Río Gálvez (AMNH 272674, GenBank JF693852).

Oligoryzomys fulvescens.—HONDURAS: Olancho; 4 km E Catacamas, Escuela de Sembrador (TTU 84699, GenBank EU258547).

Oreoryzomys balneator.—ECUADOR: Napa; 12 km NW Cosango (ACUNHC 1204, GenBank EU258534).

Oryzomys palustris.—UNITED STATES: Texas; Galveston County, Virginia Point (TTU 82920, GenBank DQ185382).

Oryzomys couesi.—HONDURAS: Olancho; 4 km E Catacamas, Escuela de Sembrador (TTU 84697, GenBank DQ185383).

Pseudoryzomys simplex.—PARAGUAY: Alto Paraguay; 21°17.93′S, 59°33.87′W (MNHNP, TK 62425, GenBank EU579516).

Phyllotis xanthopygus.—CHILE: Tarapacá; Parinacota; Arica (FMNH 133830, GenBank U86831).

Reithrodon auritus.—ARGENTINA: Río Negro; Las Victorias, 4.2 km E Bariloche (MVZ 182704, GenBank EU579474).

Rheomys raptor.—COSTA RICA: Puntarenas; Monteverde Cloud Forest Reserve, Quebrada Cuecha (KU 159017, GenBank KF359512).

Sigmodon hispidus.—UNITED STATES: Texas; Cameron County, Brownsville (TK 32481, GenBank AF425199).

Sigmodontomys alfari.—ECUADOR: Esmeraldas; Estación Experimental "La Chiquita" (TTU 103047, GenBank EU340016). PANAMA: Bocas del Toro; Isla San Cristobal (USNM 449895, GenBank EU074635).

Sooretamys angouya.—BRAZIL: Rio de Janeiro; Teresópolis (MNRJ 50234, GenBank EU579511).

Tanyuromys aphrastus.—COSTA RICA: Alajuela; Monteverde, Monteverde Cloud Forest Reserve, Sendero Peñas Blancas, 1,300 m [10°18′N, 84°47′W] (KU 161003, GenBank FJ971253); Alajuela/Puntarenas; Monteverde, Monteverde Cloud Forest Reserve, Sendero Brillante, 1,550 m [10°18′N, 84°48′W] (KU 159021, GenBank **MG831951**); Puntarenas; Sector Pittier, Parque Internacional La Amistad Pacífíco, 150 m de la casa de los guardaparques [9°01′25.7″N, 82°57′29.3″W, elevation 1,570 m], (UCR 1921, GenBank **MG831950**); San Joaquín de Dota [holotype; UMMZ 62875, GenBank **MG831953**). PANAMA: Chiriquí; 24 km NNE San Félix (USNM 541200; 541201, GenBank **MG831952**).

Tanyuromys thomasleei.—ECUADOR: Imbabura; 10 km E Santa Rosa, lower western slope of Volcán Cotacachi [holotype] (QCAZ 10427, GenBank **FJ971254**); Pichincha; Guarumos (MCZ 50396, GenBank **MG831949**); Pichincha Province; [near] Mindo, 4,200 feet [1,380 m] [0°03′N, 78°46′W fide Voss (1988)] (UMMZ 155808).

Thomasomys erro.—ECUADOR: Napo; 12 km N Cosanga (ACUNHC 1137, GenBank EU579476).

Transandinomys talamancae.—ECUADOR: El Oro; Puynago (TTU 102637, GenBank EU579514).

Tylomys nudicaudus.—GUATEMALA: Izabal (TK 41551, GenBank DQ179812).

Wiedomys pyrrhorhinos.—BRAZIL: Minas Gerais; Ponte do Colatino (MVZ 197566, GenBank EU579477).

Zygodontomys brevicauda.—VENEZUELA: Sucre; Finca Vuelta Larga, 9.7 km SE, by road from, Guaraunos (AMNH 257321, GenBank EU579521).