# A newly recognized clade of trans-Andean Oryzomyini (Rodentia: Cricetidae), with description of a new genus

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We expand upon recent studies on relationships within the Oryzomyini, in particular, those involving taxa currently assigned to the genus *Sigmodontomys*. In recent years, *Sigmodontomys* has been treated as including 2 species, *alfari* (J. A. Allen, 1897) and *aphrastus* (Harris, 1932), but throughout their complicated taxonomic history both species also have been placed in the genus *Oryzomys*, and *alfari* independently in *Nectomys*. Using morphological (98 external, cranial, dental, and postcranial) and molecular (nuclear interphotoreceptor retinoid–binding protein gene and mitochondrial cytochrome-*b* and ribosomal 12S RNA genes) characters, we infer the phylogenetic position of these 2 species within Oryzomyini. We document that *alfari* and *aphrastus* do not form a monophyletic group. *Sigmodontomys alfari* is most closely related to *Melanomys*, and *aphrastus* is either the sister to that clade, or to the extinct Caribbean genus *Megalomys*. Thus, *aphrastus* is best regarded as representing a new genus, which is described and named herein. This new genus falls within the *Sigmodontomys–Melanomys–Aegialomys–Nesoryzomys* clade, which forms a monophyletic group of mainly southern Central American and northern South American taxa primarily restricted to lowland to midelevation montane trans-Andean habitats and possessing a marked ability to cross expanses of salt water. The new genus occurs at middle elevations from north-central Costa Rica to northwestern Ecuador and along with some populations of *Aegialomys* and *Melanomys* occupies the highest elevations for members of this group.

Key words: cytochrome *b*, 12S gene, interphotoreceptor retinoid–binding protein [IRBP], mitochondrial genes, Neotropics, nuclear gene, phylogeny, Sigmodontinae, *Sigmodontomys*, *Tanyuromys*

The rodent family Cricetidae is one of the most diverse mammalian families, including more than 130 genera divided into 6 subfamilies—Arvicolinae, Cricetinae, Lophiomyinae, Neotominae, Sigmodontinae, and Tylomyinae (Jansa and Weksler 2004; Musser and Carleton 2005; Steppan et al. 2004). The Sigmodontinae, a New World lineage, is the largest cricetid subfamily, both in numbers of described genera and of species, with 83 extant and several extinct genera recognized (D'Elía et al. 2007; Musser and Carleton 2005; Pardiñas et al. 2002; Percequillo et al. 2011; Weksler and Percequillo 2011; Weksler et al. 2006). Within the Sigmodontinae, the tribe Oryzomyini, a well-supported clade consisting of 27 extant and 5 extinct recognized genera, occurs from the northeastern United States through Mexico and Central America to southernmost South America, as well as to Bonaire and Curaçao, the Greater and eastern Lesser Antilles (all extinct), the Fernando de Noronha Archipelago, and the Galapagos Islands (hereafter, Galapagos [Carleton and Olson 1999; Pardiñas 2008; Percequillo et al. 2011; Turvey et al. 2010; Weksler et al. 2006; Zijlstra et al. 2010]). The extinct genera of Oryzomyini currently recognized include *Carletonomys* Pardiñas, 2008 (Argentine pampas; early or middle Pleistocene); *Megalomys* Trouessart, 1881 (Barbuda, Curaçao, Martinique, and Saint Lucia; historic times); *Noronhomys* Carleton and Olson, 1999 (Ilha Fernando de Noronha, Brazil; late Quaternary and perhaps historic times); *Pennatomys* Turvey et al., 2010 (Nevis, St. Eustatius, and St. Kitts, Lesser Antilles; late Holocene and perhaps still extant, see ''Discussion''); and *Agathaeromys* Zijlstra, Madern, and van den Hoek Ostende, 2010 (Bonaire; middle to late Pleistocene).

Among the most poorly known of the currently recognized and extant genera of Oryzomyini is *Sigmodontomys* J. A. Allen, 1897. As presently constituted, *Sigmodontomys* contains 2 species: *alfari* (J. A. Allen, 1897) and *aphrastus* (Harris, 1932). Both species are poorly known and have been the subject of considerable taxonomic debate. The published reports of *aphrastus* are based on only 8 specimens; the holotype from west-central Costa Rica, 2 recently collected specimens from northwestern Costa Rica, 2 specimens from Panama, and 3 from Ecuador (Lee et al. 2010; McCain et al. 2007; Méndez 1993; Musser and Williams 1985; Voss 1988). Harris (1932:5) named *Oryzomys aphrastus* on the basis of a single adult female from Costa Rica, taken by Austin Smith. Especially noteworthy in Harris's brief description is the detailed account of the coloration of the pelage and his observation that the molars have ''prominent cusps and deep re-entrant angles.'' The description contained no comparisons with other species and no skull measurements, and gave merely 3 external measurements taken by Smith in the field. Ellerman (1941:345, 349) assigned *aphrastus* to the subgenus *Oryzomys* Baird, 1857; however, he did not place it in any of the species groups that he recognized. Hershkovitz (1944:73) was the 1st to compare *aphrastus* with *Sigmodontomys alfari* (called *Nectomys alfari* at that time), and noted significant differences, stating:

> The most striking resemblance to *alfari* is noted in the atypical *Oryzomys aphrastus*. Externally, it is distinguished from *alfari* by its darker color, finer pelage, the greater length of its tail (extreme for an oryzomyine rodent), and by the longer fifth hind toe which reaches to base of second phalanx of the fourth toe. Cranially, *aphrastus* is distinguished chiefly by its narrower interorbital region, the greater attenuation of the nasals posteriorly (quite as in *N*[*ectomys*]. *squamipes*), the weaker, narrower zygomatic plate, and, especially, by the even larger size of its cheek teeth, which attain here a maximum in size and complexity among oryzomyine rodents. In *aphrastus*, the greatest width of $m^1$ is nearly equal to the shortest distance across the palate between each of the first molars.

Goodwin (1946:394) provided a brief redescription of Harris's single specimen, gave 5 skull measurements, and was the 1st to note its external resemblance to *Nephelomys devius* (Bangs, 1902), but stated, regarding *aphrastus*, ''its longer tail and larger and broader feet readily distinguish it from the latter [*N. devius*].'' Later, Hershkovitz (1948:56) stated that ''The Costa Rican *Oryzomys aphrastus* … is probably most nearly related to *O*. [now *Mindomys*] *hammondi*.'' Reconsidering, Hershkovitz (1970:792) wrote that *hammondi* ''is not nearly related to the semiaquatic *Oryzomys aphrastus* as I suggested in 1948.'' The habitats recorded for *aphrastus*, along with its external anatomy, show that it is not semiaquatic, contra Hershkovitz (1970:792), and Tirira (2008:120), who called this species the ''Long-tailed Rice Water Rat.'' Hall and Kelson (1959:565) quoted Harris's original description in part and placed *aphrastus* in the subgenus *Oryzomys*, but stated that ''The systematic position of this 'species' is doubtful. Our assignment of it to the '*devius*-group' is provisional.'' Hall (1981:618) amended the

treatment by Hall and Kelson (1959), dispensing altogether with species groups in the subgenus *Oryzomys* and stating ''This 'species' is provisionally placed between *O. albigularis* and *O. capito*.'' Ray (1962:110) stated ''I have compared directly the unique type skull … and find that *O. aphrastus* is an immature *Nectomys*, close to if not conspecific with *Nectomys alfari*.'' Contra Ray (1962), our study of the type proves it to be an adult. Musser and Carleton (1993:748, 2005:1178) provisionally treated *alfari* and *aphrastus* as the sole members of the genus *Sigmodontomys*, stating that the relationships to *Oryzomys* need to be refined and that ''Assignment to *Sigmodontomys* tentative following the observations of Ray … .'' Carleton and Musser (1995:358) suggested that Hershkovitz's initial assessment might be correct; ''*aphrastus* actually may bear closer kinship to another enigmatic, little known species, *Oryzomys* [now *Mindomys*] *hammondi* of northwestern Ecuador'' than it does to *Sigmodontomys alfari*. *Mindomys hammondi* (Thomas, 1913) remains poorly known, is represented in collections by few specimens, and the genus is considered to be monotypic.

Weksler (2006), in a study of phylogenetic relationships among the Oryzomyini, using both morphological and molecular data, found that *alfari* and *aphrastus* were not sister taxa, but rather that *Melanomys* Thomas, 1902, was the sister to *alfari*, with *aphrastus* the next group out. *Nectomys apicalis* Peters, 1861, and *N. squamipes* (Brants, 1827) plus *Amphinectomys* Malygin, 1994, formed the sister group to this clade. At the time of Weksler's study, however, no fresh tissue of *aphrastus* was available for genetic analysis and thus his analyses for that species were based on morphological characters only. Based on this database, Weksler et al. (2006) described 10 new genera from within the polyphyletic genus *Oryzomys*. Independently, based on analysis of nucleotide sequences of the mitochondrial DNA cytochrome-*b* gene (*Cytb*), Hanson and Bradley (2008) found *Sigmodontomys alfari* to be well nested within *Melanomys*, rendering the latter paraphyletic; *aphrastus* was not included in their analysis.

In light of the considerable controversy that has attended the taxonomy of *alfari* and *aphrastus*, and based on our own research on pertinent specimens, we herein: reassess the relationships of *alfari* and *aphrastus*, using morphological and molecular data; incorporate both data sets to evaluate the taxonomic arrangement that best reflects the relationships of these species; and relate our conclusions to the biogeography of this clade. We herein confirm that *alfari* and *aphrastus* are not sister taxa and that *aphrastus* is best regarded as representing a distinct new genus, as described below.

## MATERIALS AND METHODS

*Morphological characters and taxon sampling.*—We examined 7 of the 8 known specimens referred to *aphrastus*. Detailed external and cranial comparisons were made between these and all recognized genera of Oryzomyini (in a very few cases, comparisons were made with published accounts only):

*Aegialomys* Weksler, Percequillo, and Voss, 2006; *Agathaeromys*; *Amphinectomys*; *Carletonomys*; *Cerradomys* Weksler, Percequillo, and Voss, 2006; *Drymoreomys* Percequillo, Weksler, and Costa, 2011; *Eremoryzomys* Weksler, Percequillo, and Voss, 2006; *Euryoryzomys* Weksler, Percequillo, and Voss, 2006; *Handleyomys* Voss, Gómez-Laverde, and Pacheco, 2002; *Holochilus* Brandt, 1835; *Hylaeamys* Weksler, Percequillo, and Voss, 2006; *Lundomys* Voss and Carleton, 1993; *Megalomys*; *Melanomys*; *Microryzomys* Thomas, 1917; *Mindomys* Weksler, Percequillo, and Voss, 2006; *Neacomys* Thomas, 1900; *Nectomys* Peters, 1861; *Nephelomys* Weksler, Percequillo, and Voss, 2006; *Nesoryzomys* Heller, 1904; *Noronhomys*; *Oecomys* Thomas, 1906; *Oligoryzomys* Bangs, 1900; *Oreoryzomys* Weksler, Percequillo, and Voss, 2006; *Oryzomys*; *Pennatomys*; *Pseudoryzomys* Hershkovitz, 1962; *Scolomys* Anthony, 1924; *Sigmodontomys alfari*; *Sooretamys* Weksler, Percequillo, and Voss, 2006; *Transandinomys* Weksler, Percequillo, and Voss, 2006; and *Zygodontomys* J. A. Allen, 1897. New morphological character information for *aphrastus* was combined with that already available for the taxon, and includes phallic and other soft-tissue characters for a total of 98 characters as defined in Weksler (2006) and Percequillo et al. (2011). Reanalysis of certain morphological characters given by Weksler (2006) is provided elsewhere (McCain et al. 2007; Percequillo et al. 2011; Turvey et al. 2010; Voss and Weksler 2009; Weksler et al. 2006). Terminology for and illustrations of the characters described here have been given by Hooper and Musser (1964), Carleton (1973, 1980), Reig (1977), Voss and Linzey (1981), Voss (1988, 1993), Carleton and Musser (1989), Voss and Carleton (1993), Steppan (1995), and Weksler (2006). All capitalized color terms are from Ridgway (1912). We include 6 additional terminal taxa not treated in Weksler's (2006) original analysis. These are *Rhipidomys nitela* Thomas, 1901, as an additional outgroup; *Drymoreomys*, a newly recognized genus of Oryzomyini (Percequillo et al. 2011); 2 species of the extinct Antillean genus *Megalomys*, *M. desmarestii* (Fischer, 1829) and *M. luciae* (Major, 1901), which were found as members of a *Sigmodontomys–Melanomys–Nectomys* clade in a recent cladistic analysis (Turvey et al. 2010); and 2 additional species of *Melanomys*, *M. chrysomelas* (J. A. Allen, 1897) and *M. columbianus* (J. A. Allen, 1899), in order to assess the monophyly of *Melanomys* vis-à-vis *Sigmodontomys alfari* as per Hanson and Bradley's (2008) analyses. The interphotoreceptor retinoid–binding protein [IRBP] sequence data for the specimen identified as *Melanomys caliginosus* (Tomes, 1860) by Weksler (2003), from Venezuela, is treated here as *M. columbianus* (Appendix I), based on the results of morphological analysis of material deposited in the American Museum of Natural History (M. Weksler and S. Loss, Museu Nacional–Universidade Federal do Rio de Janeiro, pers. comm.) and on the molecular results of Hanson and Bradley (2008). The extinct genera *Agathaeromys*, *Carletonomys*, *Noronhomys*, and *Pennatomys* are not included in this analysis because they are represented by very sparse material or are not closely related to the *Sigmodontomys–Melanomys* clade, or

both (Carleton and Olson 1999; Pardiñas 2008; Turvey et al. 2010; Zijlstra et al. 2010).

A detailed list of pertinent species studied and specimens examined can be found in Weksler (2006); additional specimens were listed by McCain et al. (2007), Turvey et al. (2010 [*Megalomys*]), and Percequillo et al. (2011 [*Drymoreomys*]). Specimens of newly analyzed taxa are presented in Appendix I. Specimens from the following institutions were used in this study: American Museum of Natural History, New York, New York (AMNH); Field Museum, Chicago, Illinois (FMNH); Museo Nacional de Costa Rica, San José, Costa Rica (MNCR); Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (MCZ); Museum of Vertebrate Zoology, University of California, Berkeley, California (MVZ); National Museum of Natural History, Washington, D.C. (USNM); Natural History Museum, London, United Kingdom; University of Kansas Natural History Museum, Lawrence, Kansas (KU); and University of Michigan Museum of Zoology, Ann Arbor, Michigan (UMMZ). One specimen of *aphrastus* (KU 159021), obtained at Monteverde, Costa Rica, will be deposited in MNCR.

This project was undertaken with the approval of the University of Kansas Institutional Animal Care and Use Committee. All animal handling protocols were in accordance with guidelines of the American Society of Mammalogists (Sikes et al. 2011).

*Molecular techniques.*—Amplification and sequencing of the nuclear IRBP and mitochondrial (*Cytb*) fragments followed Weksler (2003) and Percequillo et al. (2011), respectively. For ribosomal 12S RNA gene sequences, DNA was isolated from tissue samples preserved in ethanol, using DNeasy and Puregene extraction kits (QIAGEN Inc., Valencia, California). A fragment of the 12S gene was amplified with primers L1091 and H1478 of Kocher et al. (1989), using standard polymerase chain reaction procedures. Amplifications were performed as 20-µl reactions using Amplitaq Gold PCR Mastermix (Perkin-Elmer, Boston, Massachusetts) and recommended concentrations of primers and templates. Reactions were performed for 35 polymerase chain reaction cycles of denaturation at 95°C for 20 s, annealing at 55°C for 15 s, and extension at 72°C for 60 s. After purification, polymerase chain reaction products were sequenced with the same primers used in the polymerase chain reaction amplification. Nucleotide sequences were determined using automated sequencers ABI 3100 or ABI 3130xl (Life Technologies, Grand Island, New York). Fragments of the 12S sequences varied in length from 382 to 391 base pairs (bp) with variation due to 4 insertion–deletion (indel) regions between bases 21 and 31, 197 and 206, 226 and 236, and 297 and 312. The insertion of gaps between these intervals for phylogenetic analyses was ambiguous, and removed prior to all analyses, resulting in a fragment of 349 bp (analyses with fragments did not change any strongly supported node presented here). All resulting new sequences have been deposited in GenBank (accession numbers JF693827–JF693878) and incorporated into a data matrix containing previously published sequences (Appendix II; Bonvicino and Moreira 2001; Percequillo et al.

2011; Weksler 2003, 2006). A Nexus file with complete character matrix used for all analyses is available at http://www. morphobank.org (project id=~~177~~).

*Phylogenetic analysis.*—Morphological characters and DNA sequences were subjected to phylogenetic analyses using maximum parsimony (Farris 1983; Swofford et al. 1996), maximum likelihood (Felsenstein 1981, 2003; Swofford et al. 1996), and Bayesian inference (Huelsenbeck et al. 2001; Yang and Rannala 1997). The data sets were used in combined and separated analyses. Parsimony and Bayesian analyses were employed for the total combined supermatrix and for each individual data set. Maximum-likelihood analyses were used for each gene individually and for the combined molecular supermatrix. In the parsimony analysis, characters were equally weighted. Sequence characters were always treated as unordered, but some multistate morphological characters were ordered as described by Weksler (2006). We employed the ''polymorphic'' coding of Wiens (1995) for characters with intraspecific variation.

The heuristic search algorithm implemented by PAUP* version 4.0b10 (Swofford 2001) was used in all parsimony analyses. Each heuristic search employed 1,000 replicates of random taxon addition with tree-bisection-reconnection branch swapping; clades with at least 1 unambiguous synapomorphy were the only ones retained. Jackknife values (Farris et al. 1996) for the parsimony analyses were calculated using 1,000 pseudoreplicates, with heuristic searches employed within each replicate (36.8% character removal per replicate; 10 random addition replicates, tree-bisection-reconnection branch swapping, and no more than 100 trees saved per replicate). The general time reversible (GTR) model of nucleotide substitution (Rodríguez et al. 1990), corrected for site-specific rate heterogeneity, using the gamma distribution with 4 classes (Yang 1994), was used in all likelihood and Bayesian analyses. Gene-specific unlinked models were employed in the analysis of combined data sets. Base frequencies were empirically estimated from the data. The maximum-likelihood trees were calculated using RAxML (Stamatakis 2006b). Nodal bootstrap values for the likelihood analysis were calculated using 1,000 pseudoreplicates, under the GTRCAT model in RAxML (Felsenstein 1985; Stamatakis 2006a). Bayesian analyses were performed using Markov chain Monte Carlo sampling as implemented in MrBayes 3.1 (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003). Uniform interval priors were assumed for all parameters except base composition, for which we assumed a Dirichlet prior. The parsimony model of Lewis (2001) was used for the morphological characters. We performed 4 independent runs of 10,000,000 generations each, with 2 heated chains sampling for trees and parameters every 10,000 generations. The first 2,500,000 generations were discarded as burn-in, and the remaining trees were used to estimate posterior probabilities for each node. All analyses were checked for convergence by plotting the log-likelihood values against generation time for each run, using Tracer 1.4 (Rambaut and Drummond 2007). All parameters have effective sample sizes greater than 200.

## RESULTS

*Phylogenetic analyses.*—*Sigmodontomys alfari* and ''*S.*'' *aphrastus* are not recovered herein as sister taxa in the analyses of combined data sets, regardless of methodological approach. The concatenated matrix of morphological and molecular data provided 1,177 variable and 856 potentially parsimony-informative characters (morphology, 89; *Cytb*, 476; IRBP, 210; 12S, 81). Bayesian analyses of all combined data resulted in a tree with a high proportion of nodes with high posterior probability ($>$0.95; Fig. 1). The estimated model parameters are: (values for IRBP/12S/*Cytb*): r(A$\leftrightarrow$C): 0.086/0.035/0.013, r(A$\leftrightarrow$G): 0.370/0.278/0.205, r(A$\leftrightarrow$T): 0.043/0.087/0.044, r(C$\leftrightarrow$G): 0.039/0.016/0.009, r(C$\leftrightarrow$T): 0.421/0.555/0.692, r(G$\leftrightarrow$T): 0.041/0.028/0.038; freq: pi(A): 0.227/0.370/0.414, pi(C): 0.268/0.206/0.309, pi(G): 0.275/0.147/0.069, pi(T): 0.231/0.276/0.208; alpha: 0.402/0.180/0.200; alpha (morphology): 1.253. Overall, this tree has similar structure to previous phylogenetic results for the Oryzomyini (Percequillo et al. 2011; Turvey et al. 2010; Voss and Weksler 2009; Weksler 2003, 2006). Thus, the Oryzomyini is reconfirmed as a monophyletic lineage, and 4 major clades are recovered consistently (A–D of Weksler [2006]). Clades B, C, and D have a posterior probability greater than 0.95; however, clade A (containing *Scolomys* and *Zygodontomys*) has a lower posterior probability (0.61). The topological base of the Oryzomyini is unchanged from previous analyses, with clade C (*Microryzomys*, *Oreoryzomys*, *Neacomys*, and *Oligoryzomys*) as sister group to clade D (*Eremoryzomys*, *Drymoreomys*, *Cerradomys*, *Sooretamys*, *Lundomys*, *Holochilus*, *Pseudoryzomys*, *Oryzomys*, *Nectomys*, *Amphinectomys*, *Aegialomys*, *Nesoryzomys*, *Melanomys*, *Sigmodontomys*, *Megalomys*, and *aphrastus*), whereas clade B (*Nephelomys*, *Oecomys*, *Hylaeamys*, *Handleyomys*, *Transandinomys*, *Euryoryzomys*, and *Mindomys*) is basal to C and D. All these deep relationships receive nodal support $>$ 0.95. Relationships of taxa within clade B are still poorly supported, but all intergeneric relationships in clade C and most within clade D have high nodal support. ''*Sigmodontomys*'' *aphrastus* is found as sister to *Megalomys* but with a low posterior probability (0.71), a result similar to that provided by the parsimony analysis of Turvey et al. (2010). As in the analyses of Hanson and Bradley (2008), *Sigmodontomys alfari* is recovered within the *Melanomys* clade, with a moderate posterior probability of 0.87. The 2 clades *S. alfari* + *Melanomys* and ''*S.*'' *aphrastus* + *Megalomys* are in turn sister groups (0.88), in contrast to Turvey et al. (2010), who placed the *aphrastus* + *Megalomys* clade as sister to a clade containing *Nectomys* and *Amphinectomys*.

The maximum-likelihood analysis of the combined molecular partitions (IRBP, *Cytb*, and 12S) recovered a tree (Fig. 2) similar to the total evidence Bayesian tree, except for the nonrecovery of clade A; *Scolomys* is placed as the most basal of the Oryzomyini, but support for this area of the tree is low. The estimated model parameters are: (values for IRBP/12S/*Cytb*): r(A$\leftrightarrow$C): 1.15/2.67/13.6, r(A$\leftrightarrow$G): 5.04/18.1/29.8, r(A$\leftrightarrow$T): 0.597/7.27/12.8, r(C$\leftrightarrow$G): 0.475/0.745/1.1, r(C$\leftrightarrow$T): 5.91/46.0/93.8, r(G$\leftrightarrow$T): 1/1/1; freq: pi(A): 0.218/0.350/0.308, pi(C): 0.278/0.201/0.277, pi(G): 0.288/0.184/0.122, pi(T): 0.216/0.265/0.292; alpha: 0.402/0.188/0.287. The tree likelihood is
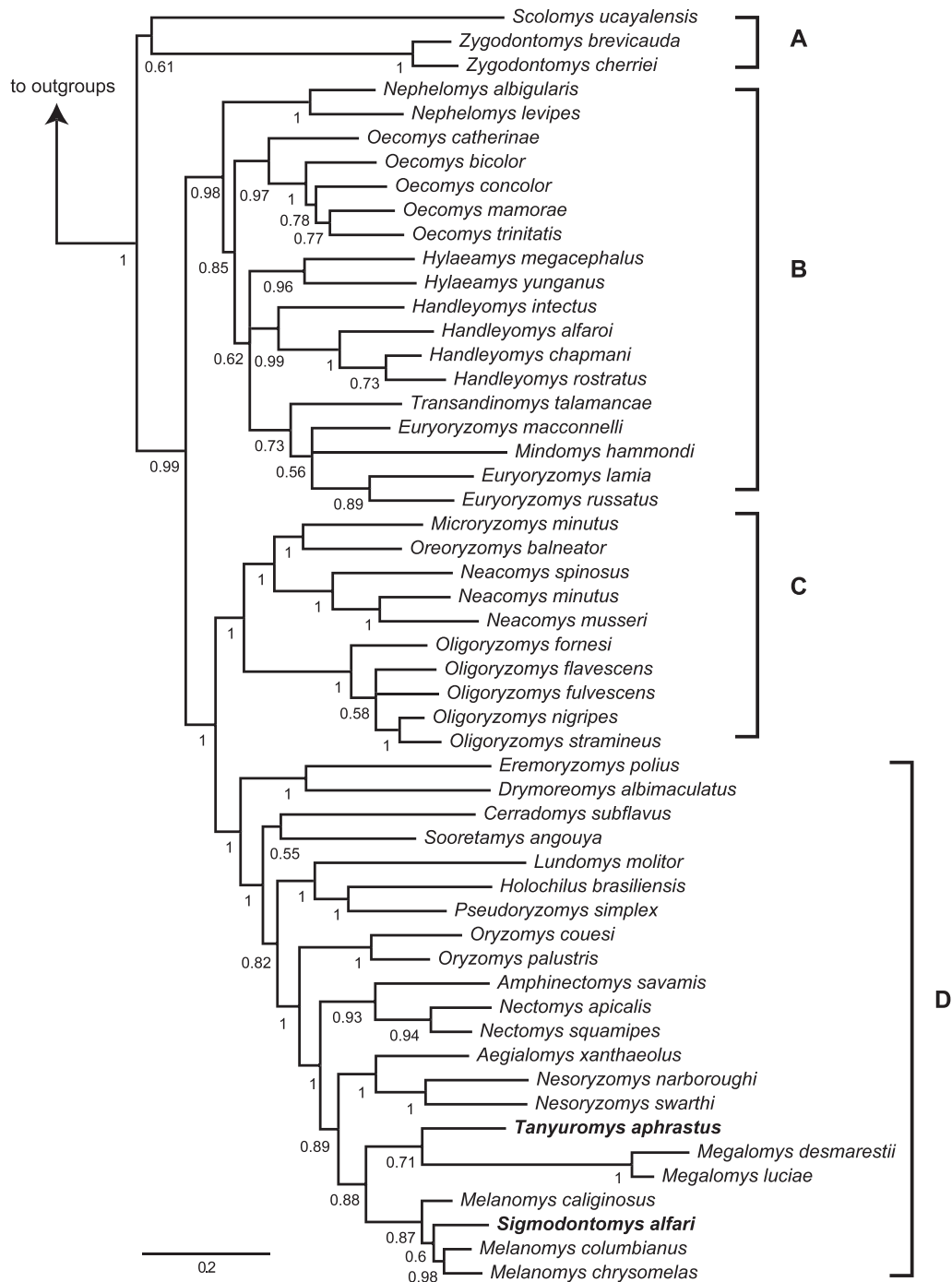
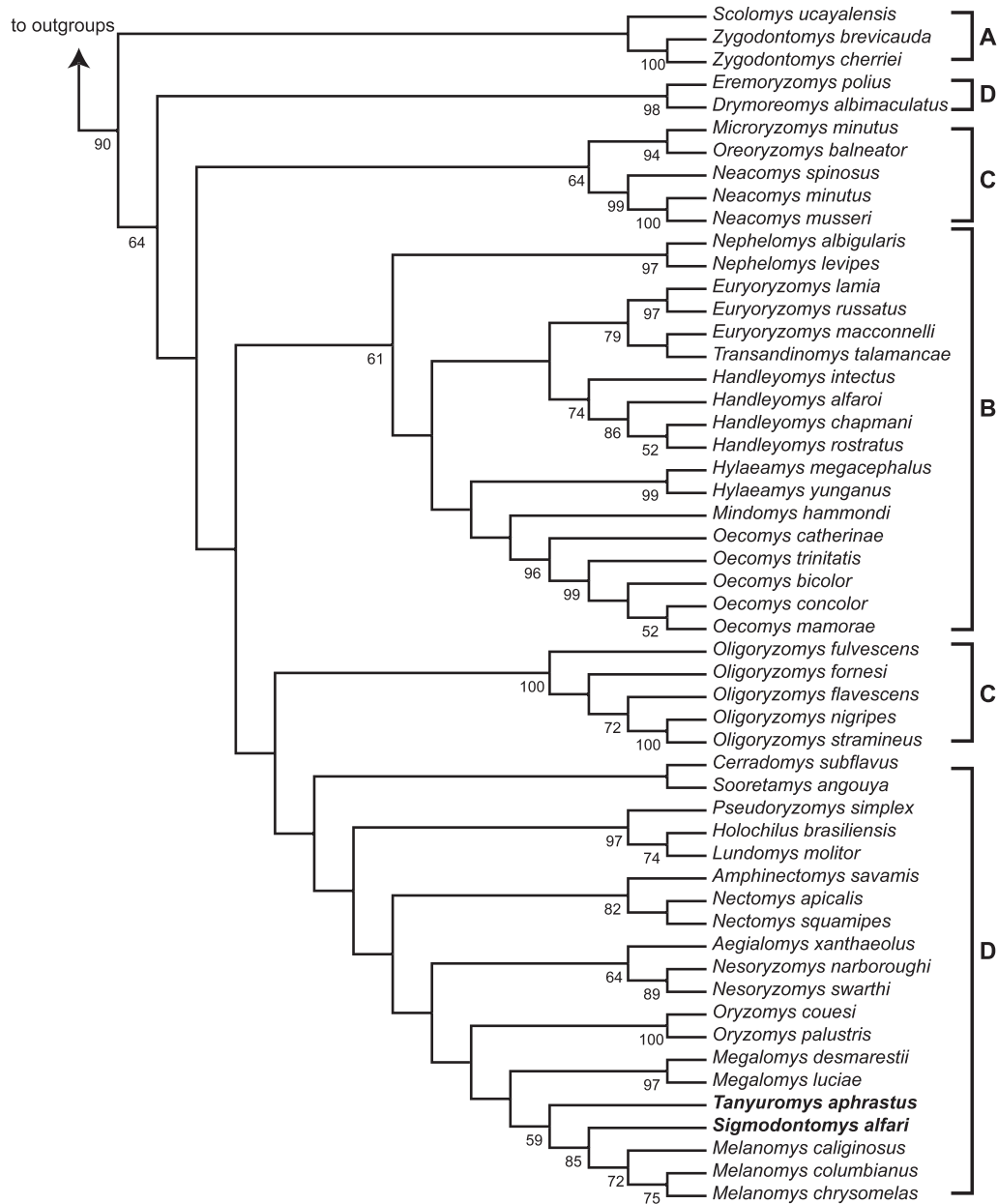**Fig. 1.**—Phylogenetic relationships of Oryzomyini, based on Bayesian analysis of nuclear (interphotoreceptor retinoid–binding protein), mitochondrial (12S and cytochrome-*b*), and morphological characters. Numbers below branches represent posterior probabilities. Outgroups include *Delomys sublineatus*, *Nyctomys sumichrasti*, *Peromyscus maniculatus*, *Rhipidomys nitela*, *Thomasomys baeops*, and *Wiedomys pyrrhorhinos*. Clades referred to as A, B, C, and D are the same as those designated by those letters by Weksler (2006).

($-$Ln): 26,929.81. The maximum-likelihood tree also differs in details of intergeneric relationships, usually involving nodes with low values. An exception is the change in position between the *Oryzomys* and the *Nectomys + Amphinectomys* lineages with respect to the clade including *Melanomys*, *Sigmodontomys alfari*, ''*S.*'' *aphrastus*, *Aegialomys*, and *Nesoryzomys* (termed the *Sigmodontomys* clade). Identical results also are found in the parsimony and Bayesian analyses of molecular data only,

indicating strong morphological signal placing *Nectomys + Amphinectomys* close to the *Sigmodontomys* clade. ''*Sigmodontomys*'' *aphrastus* is recovered as sister group to *Sigmodontomys alfari + Melanomys* with low bootstrap support (62%).

Parsimony analysis of the total supermatrix resulted in 1 tree (6,272 steps, consistency index [CI] = 0.23, retention index [RI] = 0.42; Fig. 3), which has significant changes from
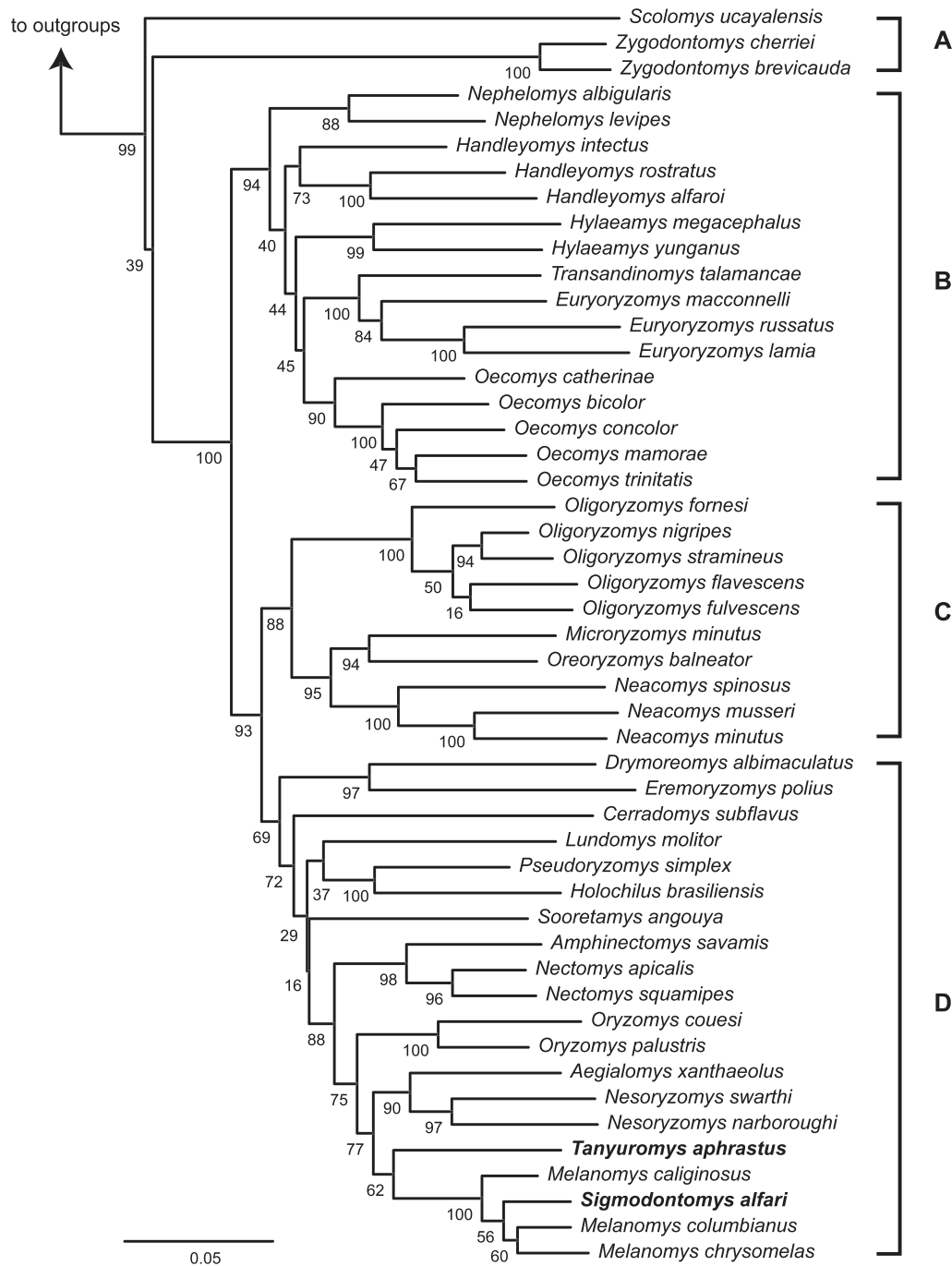
**FIG. 2.**—Phylogenetic relationships of Oryzomyini, based on the maximum-likelihood analysis of combined molecular (interphotoreceptor retinoid–binding protein + cytochrome-*b* + 12S) data sets. See Fig. 1 caption for outgroup taxa used in the analysis. Numbers below branches represent maximum-likelihood bootstrap values. Clades referred to as A, B, C, and D are the same as those designated by those letters by Weksler (2006).

the basal structure of trees recovered in previous cladistic analyses of the tribe (Percequillo et al. 2011; Turvey et al. 2010; Voss and Weksler 2009; Weksler 2003, 2006). Two of the main clades (C and D) are not monophyletic; *Oligoryzomys* does not cluster with *Oreoryzomys*, *Microryzomys*, and *Neacomys*, and *Eremoryzomys* and *Drymoreomys* are not recovered within clade D. This novel structure of relationships is probably due to the phylogenetic signal saturation of

mitochondrial genes (*Cytb* and 12s) in higher-level relationships within Oryzomyini in the parsimony analysis (Weksler 2003), which does not correct for multiple substitutions. In addition, the basal structure of the Oryzomyini in the parsimony analysis has weak nodal support, with all nodes receiving jackknife below 50% (except Oryzomyini proper, with 90%; Oryzomyini minus clade A, with 64%; and clade B, with 61%). ''*Sigmodontomys*'' *aphrastus* is recovered well

FIG. 3.—Phylogenetic relationships of Oryzomyini, based on maximum-parsimony analysis of morphological, nuclear (interphotoreceptor retinoid–binding protein), and mitochondrial (12S and cytochrome-*b*) gene characters (length = 6272, consistency index = 0.23, retention index = 0.42). Jackknife (≥50%) nodal support indexes are shown below branches. Clades referred to as A, B, C, and D are the same as those designated by those letters by Weksler (2006); however, C and D are not monophyletic.

nested in clade D as sister taxon of the *Sigmodontomys alfari* + *Melanomys* clade but with support of only 59%; jackknife support value for the latter clade is 85%. *Megalomys* is in turn placed as the sister taxon to the clade that includes ''*Sigmodontomys*'' *aphrastus* but with jackknife < 50%. *Melanomys* is recovered as monophyletic in the parsimony analysis, with a moderate jackknife value of 72%.

Independent analyses of each data partition produced different hypotheses for the placement of ''*S.*'' *aphrastus* and *S. alfari* (Fig. 4). In the morphology-only parsimony analysis (14 trees; 554 steps, CI = 0.24, RI = 0.63; Fig. 4A), *alfari* and *aphrastus* are recovered as sister taxa (jackknife =

52%), with *Nectomys* as their sister group (<50%); *Melanomys* is recovered as monophyletic with strong nodal support (98%). Analyses of IRBP sequences (Fig. 4B) recovered *aphrastus* as sister group to the clade containing *Melanomys*, *Sigmodontomys*, *Aegialomys*, and *Nesoryzomys* (parsimony jackknife < 50%, likelihood bootstrap = 50%, Bayesian posterior = 0.79) within clade D; *Melanomys* is not recovered as monophyletic, with *Sigmodontomys* as sister group to the clade *Melanomys chrysomelas* (J. A. Allen, 1897) + *M. columbianus* (J. A. Allen, 1899); other overall inferred relationships of Oryzomyini are identical to those of previous IRBP-only analyses (Weksler 2003, 2006). Analyses of *Cytb*
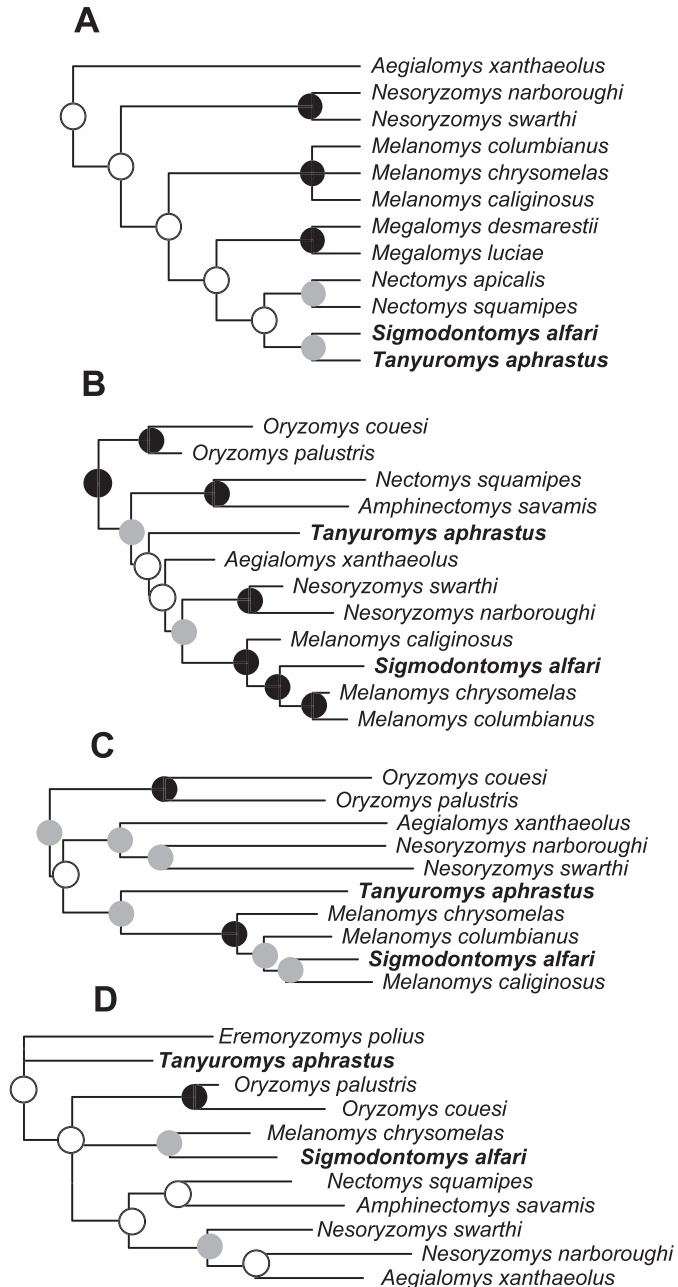
**FIG. 4.**—Relationships among *Tanyuromys*, *Sigmodontomys*, *Melanomys*, and related genera, in the partitioned analyses. Subtrees containing members of clade D phylogenetically close to the *Sigmodontomys* clade as recovered in the A) parsimony analysis of morphological characters, and maximum-likelihood analyses of B) interphotoreceptor retinoid–binding protein, C) cytochrome-*b*, and D) 12S data sets. Circles at each node represent summaries of support values as recovered in cladistic parsimony (CP), maximum-likelihood (ML), and Bayesian inference (BI) analyses (parsimony only for the morphological data sets); black circles are nodes with maximum-likelihood bootstrap and cladistic parsimony jackknife > 85%, and Bayesian inference posterior probability = 1; gray circles are nodes with maximum-likelihood bootstrap and cladistic parsimony jack-knife between 50% and 85%, and Bayesian inference posterior probability between 0.95 and 0.99; and white circles are nodes with maximum-likelihood bootstrap and cladistic parsimony jackknife below 50%, and Bayesian inference posterior probability below 0.95.

sequences (Fig. 4C) place *aphrastus* as sister taxon of the *Sigmodontomys alfari* + *Melanomys* clade (parsimony jackknife = 53%, likelihood bootstrap = 76%, posterior probability = 0.94); *Melanomys* is again not monophyletic, but in this case *S. alfari* is found as sister group to *M. caliginosus*. Analyses of 12S sequences (Fig. 4D) recover ''*S.*'' *aphrastus* as a member of a polytomy including *Eremoryzomys*, and the clade containing *Oryzomys*, *Sigmodontomys alfari*, *Melanomys*, *Nectomys*, *Amphinectomys*, *Aegialomys*, and *Nesoryzomys* with low support; only 1 sequence is available for *Melanomys*, which is found as sister group to *S. alfari*.

These results corroborate earlier studies (Percequillo et al. 2011; Turvey et al. 2010; Weksler 2006), reconfirming that there is no sister relationship between *aphrastus* and *Mindomys hammondi*. The *Sigmodontomys–Melanomys* clade does contain *aphrastus*; however, *aphrastus* and *alfari* are paraphyletic with respect to *Melanomys*. Thus, far from being a dubiously distinct species of *Oryzomys*, as Hall (1981) implied, or a species of *Sigmodontomys*, as it has generally been regarded to be by authors since Musser and Carleton (1993) provisionally treated it as such, *aphrastus* represents a new genus in the Oryzomyini (as defined by Weksler et al. 2006), which may be characterized as follows.

*Tanyuromys*, new genus
Long-tailed Montane Rats
Figs. 5–7

*Oryzomys*: Harris, 1932:5; part; not *Oryzomys* Baird, 1857.
*Sigmodontomys*: Musser and Carleton, 1993:748; part; not *Sigmodontomys* J. A. Allen, 1897.

*Type species.*—*Oryzomys aphrastus* Harris, 1932.
*Included species.*—The type species.
*Known distribution of genus.*—Discontinuously at middle elevations from north-central Costa Rica to northwestern Ecuador (Fig. 8).
*Etymology.*—Long-tailed mouse, from the Greek *tany* (long), *oura* (tail), and *mys* (mouse).
*Diagnosis.*—Oryzomyini with exceptionally long tail with terminal tuft; bony palate short; shallow zygomatic notches; jugal large; stapedial foramen and posterior opening of alisphenoid canal small; squamosal–alisphenoid groove and sphenofrontal foramen absent; molars uniquely complex and lophodont for extant Oryzomyini, with complicated enamel folding pattern of flexi and flexids (Fig. 6). Stomach unilocular–hemiglandular, glandular epithelium extending into corpus; gall bladder absent.
*Description.*—Oryzomyini with body pelage very long, thick, and soft; slate gray basally (approximately 85% of length), tipped with tawny dorsally, more buffy laterally. Mystacial and superciliary vibrissae dark and very long, extending posteriorly beyond posterior margins of pinnae when laid back. Guard hairs on rump up to at least 18 mm in length. Dorsoventral countershading distinct but less so than in many related forms. Fur ventrally less dense than dorsally and a paler gray (plumbeous) liberally washed with buff, described

F‍IG. 5.—Skull of adult *Tanyuromys aphrastus* (KU 161003, male). Greatest length of skull = 33.0 mm.

as ''buffy ochre'' by Reid (1997:208, 2009:212). Juvenile pelage, based on the Panamanian subadult (USNM 541201), markedly different from that of adults (and from that of the even younger Costa Rican subadult, which has more adultlike pelage), being softer, fluffier, and woolly; pale plumbeous, lightly tipped with drab above (overall closest to Hair Brown), more heavily tipped with dull buff below, and small pencil at tip of tail black.

Pinna small, not reaching eye when laid forward, sparsely to moderately covered with short, blackish, dark brown, or
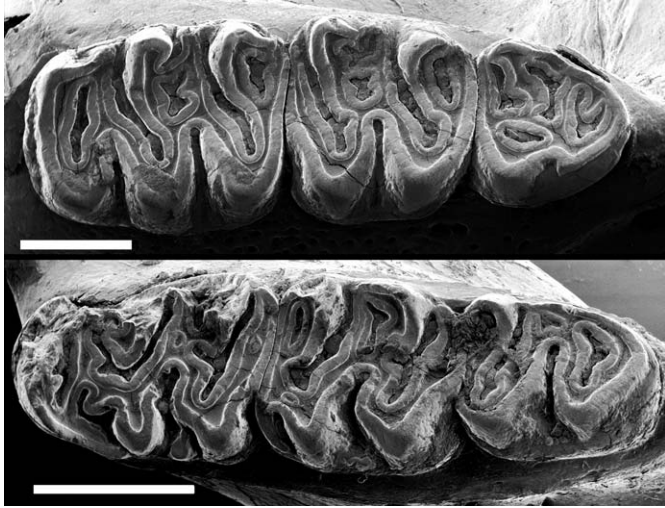
**Fig. 6.**—Molar toothrows of *Tanyuromys aphrastus* (UMMZ 155808). Top) upper left toothrow; bottom) lower left toothrow. Bars represent 1 mm. Anterior is to the left.

reddish brown hairs, both internally and externally. Manual claws small and unkeeled. Hind foot long and slender, adapted for terrestrial life, its skin pale brown; sparsely to moderately covered with short, pale brown to dark brown hairs dorsally; digits 2, 3, and 4 long and subequal in length, with 3 the longest; claws sharp and strongly curved, sometimes with reddish pigmentation at tips; claw of digit 1 extending just beyond base of phalanx 1 of digit 2; claw of digit 5 extending beyond middle of phalanx 2 of digit 4. Pes without natatory fringes. Bristles at base of hind claws variable in length and density, but usually with a moderate number of pale brown to darker brown bristles reaching or almost reaching the tips of the claws. Small, dark squamae visible to naked eye on hind foot both dorsally and ventrally, distinct and dense plantar squamae distal to thenar pad (absent on heel). Hind foot with 4 large and fleshy interdigital pads, with interdigitals 2 and 3 set apart from 1 and 4 as pairs; a thenar pad; and a hypothenar pad absent, vestigial, or moderately well developed. Tail exceptionally long and slender, usually more than 1.5 times length of head plus body; sparsely haired (appearing superficially nearly naked) with short, stout, black or brown hairs, 3 per scale; overall basically brown or blackish concolor or with slight bicoloration except proximally. Small scales arranged in an annular fashion (~14 rows/cm just past outstretched feet in 1 adult specimen) and, because of overlap, exposed portions hexagonal; tail with small terminal tuft. Four pairs of mammae: pectoral, postaxial, abdominal, and inguinal.

Skull (Fig. 5) moderately robust, with profile little arched (essentially flat) from the tips of the nasals to the frontoparietal sutures. Rostrum short, stout, and flanked by very shallow, rounded zygomatic notches; interorbital region anteriorly convergent with strongly beaded supraorbital margins. Braincase broad and slightly inflated, confluent with well-developed and flared temporal crests; lambdoidal and nuchal crests developed in older adults. Large interparietal anteriorly truncated, obtusely angled posteriorly, and with lateral
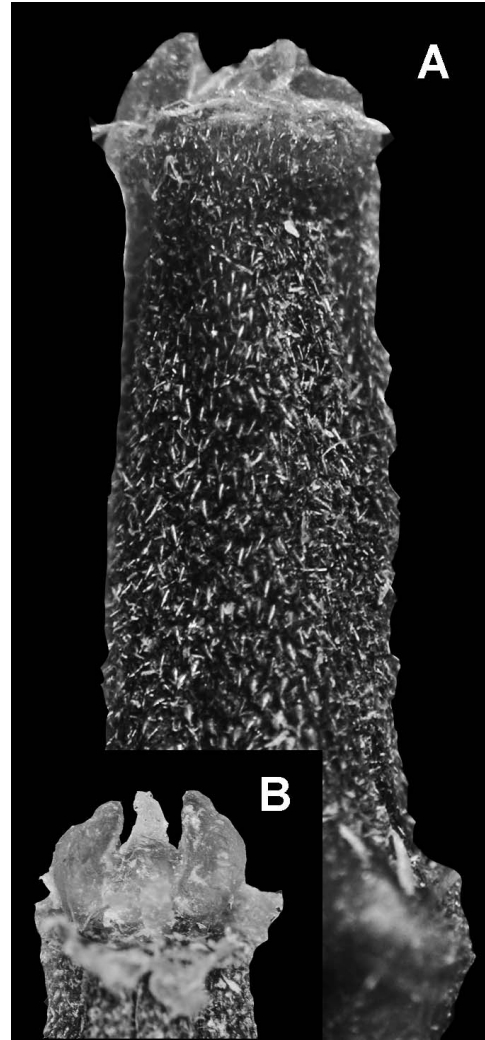


**Fig. 7.**—Glans penis of *Tanyuromys aphrastus* (KU 161003). A) Dorsal view of phallus, showing reduced terminal apparatus and epidermal spines covering entire shaft. B) Ventral view of terminal apparatus, showing the 2 lateral mounds with short digits and the central mound with a reduced cartilaginous component.

extensions. Zygomatic plate of medium width, its anterior edge ranging from slightly convex along its dorsal half to slightly convex along its entire length, its posterior margin anterior to alveolus of M1; anterior margin straight, without anterodorsal spinous process. Zygomatic arches convergent anteriorly, relatively unbowed, widest at squamosal root; jugal present and large (the maxillary and squamosal zygomatic processes widely separated, not overlapping in lateral view). Nasals with acutely angled posterior margins; extending posteriorly beyond premaxillae and behind lacrimals, nearly reaching interorbital constriction. Lacrimals usually with longer maxillary than frontal sutures. Posterior wall of orbit smooth. Frontosquamosal suture anterior to frontoparietal suture (dorsal facet of frontal in broad contact with squamosal). Parietal with broad lateral expansion, a large portion dipping below the temporal ridge posteriorly. Basicranial flexion weakly pronounced, foramen magnum oriented mostly caudad. Incisive foramen short and narrow, not extending posteriorly to level of alveolus of M1,
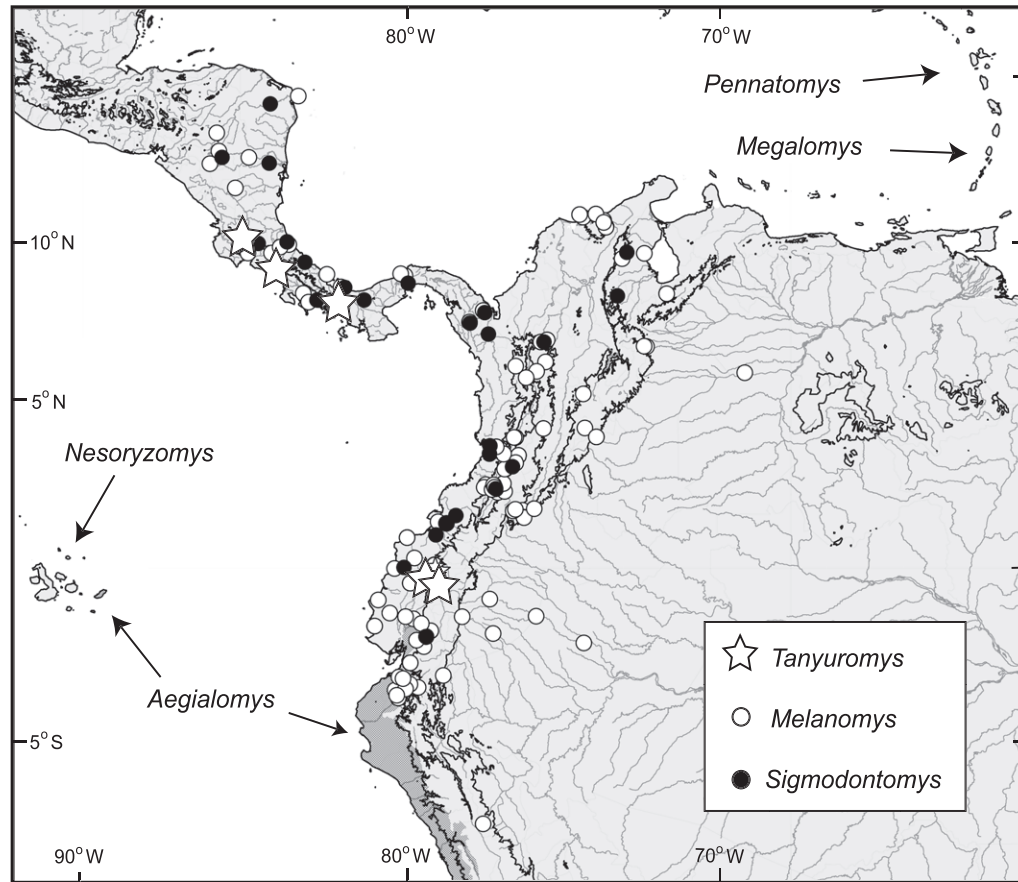
Fɪɢ. 8.—Map of northwestern South America, Central America, the Windward and Leeward Islands, and the Galapagos, showing the distribution of the genera of Oryzomyini discussed in the text. All known localities of *Tanyuromys* are plotted (open stars) as are representative localities for the other mainland taxa of the trans-Andean clade—*Melanomys* (open circle) and *Sigmodontomys* (closed circle)—using locality data from museum records (Appendix I). Arrows indicate the distributions of other members and a putative member (*Pennatomys*) of this clade—*Megalomys* and *Pennatomys* (both extinct) in the Caribbean islands and *Nesoryzomys* and *Aegialomys* in the eastern Galapagos. *Aegialomys* also occurs in mainland western Ecuador and Peru (shaded areas).

widest at midlength and tapering symmetrically anteriorly and posteriorly. Bony palate relatively short as compared with other Oryzomyini, extending just beyond M3s and smooth or weakly sculpted between molar rows. Posterolateral palatal pits simple and small and level with the palatine; mesopterygoid fossa penetrating anteriorly between maxillae; bony roof of mesopterygoid fossa usually perforated by narrow sphenopalatine vacuities (a juvenile specimen has a completely ossified mesopterygoid roof). Alisphenoid strut absent (buccinator–masticatory foramen and accessory foramen ovale confluent); alisphenoid canal with large anterior opening. Stapedial foramen and posterior opening of alisphenoid canal small; squamosal–alisphenoid groove and sphenofrontal foramen absent; secondary anastomosis of internal carotid crosses dorsal surface of pterygoid plate (= carotid circulatory pattern 3 of Voss [1988]). Posterior suspensory process of squamosal absent. Postglenoid foramen large and rounded; subsquamosal fenestra vestigial or absent. Auditory bulla small. Periotic exposed posteromedially between ectotympanic and basioccipital, but usually not extending anteriorly to carotid canal; mastoid unfenestrated and lacerate foramina group absent. Coronoid process long, slender, pointed, posteriorly angled

dorsally, and reaching level of rounded condyloid process. Capsular process of lower incisor alveolus absent or present as a slight, rounded elevation not protruding above level of coronoid–condylar notch, the variable condition of the capsular projection seems to be unrelated to age variation; superior and inferior masseteric ridges conjoined anteriorly as single crest below m1.

Upper incisors ungrooved, slightly opisthodont (Fig. 5), with smoothly rounded enamel bands. Maxillary toothrows straight to slightly bowed outward; when straight, nearly parallel, converging slightly anteriorly. Molars (Fig. 6) large, pentalophodont, and bunodont, with complicated occlusal patterns having extensive, deep, steep-sided flexi and fosseti (enamel islands) with irregular and jagged borders. Anteromedian flexus absent. Lophs and lophids quickly wearing to planar surfaces extending across lingual cones and labial conids; mesolophs on upper molars. Labial and lingual flexi of M1 and M2 deeply interpenetrating; labial flexi convoluted (wrinkled) and enclosed by a cingulum. M1 broadly rectangular, with accessory labial root; anterocone not divided into labial and lingual conules; anteroloph well developed and fused with anterostyle on labial cingulum, fused with anterocone (anteroflexus

reduced or absent). Protostyle absent; paracone usually connected by enamel bridge to posterior moiety of protocone; median mure connected to protocone. Mesoloph well developed, and paralophule forming connection between paracone and mesoloph, isolating lingual portion of mesoflexus into a mesofossette. M2 broad, complex, subcircular; protoflexus absent; mesoflexus present as single internal fossette (a 2nd very small labial fossette is present in the adult from Panama); paracone without accessory loph. M3 broadly triangular or round. M3 smaller than M2, with posteroloph and diminutive hypoflexus that tends to be eliminated through wear. All lower molars (Fig. 6) with anterolabial cingulum and small anterolophid that disappears with wear. Anteroconid of m1 without anteromedian flexid, but with accessory lingual and labial roots. Ectolophid absent on m1 and m2, but mesolophid present and distinct. Posteroflexid present on rectangular m3. (All shapes given of teeth are those of their appearance in occlusal view.)

The adult male from Costa Rica (KU 161003) has the glans penis covered with epidermal spines (Fig. 7). Distal bacular cartilage small and trifid (with a short and slender central digit), bacular mounds not concealed by nonspinous tissue on rim of terminal crater, dorsal papilla spineless, and urethral processes without subapical lobules. Stomach unilocular–hemiglandular, glandular epithelium extending into corpus. Gall bladder absent.

*Comparisons.*—*Tanyuromys* differs from all other extant Oryzomyini (sensu Weksler 2003; Weksler and Percequillo 2011; Weksler et al. 2006) in the degree of lophodonty and complication of the enamel folding pattern of flexi and flexids on the molars (Fig. 6). More specifically, *Tanyuromys* differs from *Neacomys* and *Scolomys* in having soft, rather than spiny, fur. All known species of *Neacomys* and *Scolomys* are considerably smaller than the known species of *Tanyuromys*. From *Oryzomys* (sensu lato), *Oligoryzomys*, *Melanomys*, *Microryzomys*, *Nesoryzomys*, *Oecomys*, and the extinct *Megalomys*, *Tanyuromys* is best distinguished on the basis of dental characters. *Tanyuromys* agrees with *Nectomys* and *Sigmodontomys* in having long nasals; more or less evenly rearwardly diverging, beaded, supraorbital and postorbital shelves; rearwardly diverging zygomata; less elongate, evenly bowed incisive foramina; pitted palate with longitudinal channels; broad, U-shaped mesopterygoid fossa; absence of posterior subsquamosal foramina; small auditory bullae; large molars; small ears; and a distinctive, grayish juvenile pelage. With *Nectomys* (but not *Sigmodontomys*), *Tanyuromys* agrees in having long fur, long secondary folds on the upper molars, and overlapping primary folds. *Tanyuromys* differs from both *Nectomys* and *Sigmodontomys* in having much more complex molar patterns, less-hypsodont molars, a short rostrum; much smaller zygomatic notch; much less-developed temporal ridges; a broad, inflated braincase; and a proportionally longer tail.

*Tanyuromys* has consistently been recovered in a 3-member clade with *Sigmodontomys* and *Melanomys*, and so comparisons among the 3 genera are especially pertinent. The pelage of *Tanyuromys* is somewhat longer and softer than in *Sigmodontomys* and the vibrissae are much longer, extending posteriorly beyond the pinnae. Tail length in *Tanyuromys* usually exceeds 1.5 times the length of the head plus body and there is a terminal tuft, whereas in *Sigmodontomys*, the tail is about the same length as the head plus body and there is no tuft. The hexagonal-appearing caudal scales of *Tanyuromys* are smaller than those in *Sigmodontomys*. Both *Tanyuromys* and *Sigmodontomys* have a small auditory bulla, definite postorbital ridge, subsquamosal fenestra, derived carotid arterial circulation, and well-developed supraorbital crests. *Tanyuromys* has a less-robust but relatively broader skull with a more-inflated braincase than does *Sigmodontomys*. In *Tanyuromys*, the zygomata are more curvilinear and there is less supraorbital beading than in *Sigmodontomys*. *Tanyuromys* has a well-developed jugal, but it is reduced or absent in *Sigmodontomys*. Supraorbital beading in *Tanyuromys* extends dorsally, whereas in *Sigmodontomys* the beading tends to overhang the orbits. *Sigmodontomys* has a broader zygomatic plate than does *Tanyuromys*, and it forms a deeper notch. The temporal ridges are less developed than in *Sigmodontomys*. The nasals taper posteriad manifestly in *Tanyuromys*, whereas their margins are subparallel in *Sigmodontomys*. In *Tanyuromys*, the bony palate is shorter, both absolutely and relatively, reaching the level of posterior edges of M3s only in old animals; whereas in *Sigmodontomys* the palate extends clearly beyond the M3s. The system of palatal pits is more complex in *Sigmodontomys* than in *Tanyuromys*. The capsular processes are much less developed in *Tanyuromys* than in *Sigmodontomys*. Dentally, *Tanyuromys* resembles *Sigmodontomys*. Both have large, complex molars with 4 roots on M1 and 3 on m1. Some of the more noteworthy differences are that in little-worn molars of *Tanyuromys* there are multiple irregular-shaped fissures representing a complicated anteroflexus (or the anterior internal fold of Hershkovitz [1962]) in the 1st upper molar; the paraflexus is undulating instead of being smoothly curved; and the mesostyle is better developed. In the 1st lower molar, there are multiple fissures derived from the protoflexid and anteroflexid. Overall, the fissures are more extensive and more branching, ''dissecting'' the teeth in a ''gnarled branch'' pattern. In general, the upper molars are more lophodont in *Tanyuromys* than in *Sigmodontomys*. *Tanyuromys* possesses an M3 larger, in comparison with the size of the M2, than does *Sigmodontomys*, although, in both, the M2 is larger than the M3. *Tanyuromys* possess an anterolabial cingulum on m2 that is missing in *Sigmodontomys*.

*Tanyuromys* differs from *Melanomys* by its much longer tail, both relatively and absolutely, with terminal tuft. The 2 have different fur color patterns: *Tanyuromys* has medium brown pelage with buffy highlights, whereas the fur in *Melanomys* is very dark brown dorsally and has a less contrastingly pale venter. *Tanyuromys* has much longer vibrissae, extending posteriorly beyond the pinnae. *Melanomys* has an obvious hypothenar pad on the hind foot, whereas it is sometimes absent or vestigial in *Tanyuromys*. The nasal bones of *Tanyuromys* taper acutely posteriorly, whereas in *Melanomys* they terminate bluntly. In *Melanomys*, the zygomatic plate is broader and forms a deeper notch. The jugal in *Tanyuromys* is manifestly

developed, but is reduced or absent in *Melanomys*. *Tanyuromys* also has more opisthodont incisors and lophodont upper molars (the labial and lingual flexi do not interpenetrate deeply on the upper molars of *Melanomys*). The paracone and protocone are connected by the median moiety in *Melanomys* but have a posterior connection in *Tanyuromys*.

Because *Mindomys* occurs sympatrically with *Tanyuromys*, they were previously considered closely related, and their skulls and dentition are superficially similar in appearance, it is useful to contrast the 2. The skull of *Mindomys* has both the rostrum and the braincase more elongate than in *Tanyuromys*, and the interorbital region narrows anteriorly less abruptly. The cranial profile is essentially flat in *Tanyuromys*, from tips of nasals to frontoparietal sutures, but somewhat arched in *Mindomys*. The nasals reach past the lacrimals in *Tanyuromys*, but not in *Mindomys*. The anteriormost portion of the posterior edge of the zygomatic plate in *Tanyuromys* is anterior to M1 but is at the level of anterior edge of M1 in *Mindomys*. Zygomatic arches are more convergent anteriorly in *Tanyuromys* than in *Mindomys*. In *Mindomys*, the incisive foramina are relatively broad and teardrop-shaped and are widest three-fourths of the distance posteriad, whereas in *Tanyuromys* they are more elongate and more evenly bowed. In *Mindomys*, the carotid circulation is pattern 1 (squamosal–alisphenoid groove and sphenofrontal foramen present) of Voss (1988), whereas in *Tanyuromys*, it is pattern 3 (squamosal–alisphenoid groove and sphenofrontal foramen absent, secondary anastomosis of internal carotid crosses dorsal surface of pterygoid plate). Postglenoid foramen is large and rounded in *Tanyuromys*; small and compressed dorsoventrally in *Mindomys*. Superior and inferior masseteric ridges join below m1 to form a single ridge in *Tanyuromys*; in *Mindomys*, they converge anteriorly to form an open chevron below m1. The labial flexi of M1 and M2 in *Tanyuromys* have irregular, convoluted borders, whereas this is not the case in *Mindomys*. In *Tanyuromys*, the anteroloph of M1 is fused with the anterocone, an anteroflexus being reduced or absent. In *Mindomys*, the anteroloph is separated from the anterocone by an anteroflexus. In the M1 of *Tanyuromys*, the labial accessory root is present but it is absent in *Mindomys*. There is no ectolophid on m1 of *Tanyuromys* but there is in *Mindomys*. The m1 of *Tanyuromys* possesses accessory roots, whereas in *Mindomys* they are absent, there being merely 2 large roots, 1 fore and 1 aft. In *Tanyuromys*, glandular epithelium extends into the corpus of the stomach, whereas in *Mindomys* it does not.

Additional characters of the species *Tanyuromys aphrastus* and comparisons between that species and *Melanomys*, *Mindomys hammondi*, *Nephelomys devius*, and *S. alfari*, and a review of what little is known of the ecology of *T. aphrastus* were provided by McCain et al. (2007). Externally, *Tanyuromys* is similar in appearance to the sometimes sympatric *Nephelomys*, although apparently always having a somewhat longer and slightly tufted tail and smaller ears. The muzzle of *Nephelomys* is also more elongated. Collectors should be aware of this because we know of 2 instances in which *Tanyuromys* was mistaken in the field for *Nephelomys*.

*Comments.*—Cadena et al. (1998) reported a single specimen of a ''*Sigmodontomys* sp.'' from Nariño in the Colombian Chocó, and suggested that it was morphologically close to *M. hammondi* and ''*Sigmodontomys*'' *aphrastus*. Our ongoing research suggests that the Nariño rat in fact belongs to a new taxon phylogenetically close to *Mindomys hammondi*, and is not a member of *Sigmodontomys*, *Tanyuromys*, the ''*Sigmodontomys*'' clade, or even clade D of Weksler (2006).

## DISCUSSION

Ellerman (1941:361) was the 1st to compare *Sigmodontomys alfari* with *Melanomys*, which he did based on cusp patterns, stating that in *Nectomys* (in which he included *Sigmodontomys* as a subgenus) ''[C]lear traces of the subsidiary ridges always present. The molars are more hypsodont than [in] *Oryzomys*, and are clearly distinct from the majority in pattern, though they may be approached by the subgenus *Melanomys*.'' Hershkovitz (1944:73), also comparing *S. alfari* with *Melanomys*, wrote ''There is a superficial resemblance between adults in old pelage and juveniles of *alfari* to adults and juveniles, respectively, of *O.* (*Melanomys*) *caliginosus*.'' Weksler (2003), using DNA sequence data, recovered a clade including *Amphinectomys*, *Nectomys*, *Melanomys*, *Sigmodontomys*, *Nesoryzomys*, *Aegialomys xanthaeolus* (Thomas, 1894), *Oryzomys palustris* (Harlan, 1837), and *O. couesi* (Alston, 1877) with *Sigmodontomys alfari* and *Melanomys* being sister groups; *Tanyuromys aphrastus* was not included due to lack of genetic material. Weksler (2006) was the 1st to publish a rationale for a proposed relationship of ''*S.*'' *aphrastus* with any other taxon or taxa, based on a phylogenetic interpretation of morphological characters, despite the various generic assignments and statements as to affinity that had been made concerning *aphrastus* over the past 7 decades.

Our results also corroborate the findings of Hanson and Bradley (2008), which point to a nonmonophyletic status for *Melanomys*. We recovered *Sigmodontomys alfari* as nested within *Melanomys*, in the Bayesian analysis of all data and in the maximum-likelihood analysis of combined genetic data, as well as in the separate analyses of each IRBP and *Cytb* data set. *Melanomys* is recovered as monophyletic in the parsimony analyses of the total data set, and of the morphological data taken in isolation. Nodal support for most of these results, however, is low. Inclusion of *S. alfari* within *Melanomys* has only 0.6 posterior probability in the total Bayesian analysis and 56% bootstrap in the maximum-likelihood analysis (nodal support for the clade including *Melanomys* and *S. alfari*, however, is extremely high, especially in the maximum-likelihood analysis of genetic data, with 100% bootstrap). On the other hand, monophyly of *Melanomys* in the parsimony analysis of morphological characters is high. The latter result is not surprising, because *Melanomys* is clearly one of the most distinctive groups of Oryzomyini (Weksler 2006), possessing several apomorphies, especially its volelike aspect: short tail, lack of countershading, dark pelage, and short pinnae.

What could be causing the nonmonophyly of *Melanomys* in the molecular data set? The possibility of contamination can be discarded because sequences for *Melanomys* and *Sigmodontomys alfari* were generated in 2 different laboratories and using different specimens of *Melanomys* (Hanson and Bradley 2008; Weksler 2003). Because the recovered structure of each gene (*Cytb* and IRBP; Fig. 4) provides different results concerning the position of *S. alfari* within *Melanomys*, we suggest that this could be a case of nonconcordance between gene trees due to retention of ancestral polymorphisms in one of these genes.

Submerging *aphrastus*, *S. alfari*, and *Melanomys* into a single genus (along with *Megalomys*, as based on the combined analyses) would produce a taxonomic arrangement in accord with the recovered phylogenetic structure and could be a means of ''simplifying'' the classification. We think, however, that this option is counterindicated by the sharp morphological differentiation between members of these lineages and it would diminish the heuristic value of the classification in terms of communicating the differences. *Melanomys* is one of the few genera of Oryzomyini that has been recognized since the early 20th century, and is also one of the few such genera maintained continuously throughout the convoluted taxonomic history of the Sigmodontinae as a whole.

We document that *Aegialomys*, *Nesoryzomys*, *Melanomys*, *Megalomys*, *Sigmodontomys*, and *Tanyuromys* form a well-supported, morphologically diverse, and largely trans-Andean clade within the broadly distributed tribe Oryzomyini. The members of this clade occupy (or have occupied) various ranges in southern Central America (especially the highlands and Caribbean versant), northern South America (especially west of the Andes), in the Galapagos, and, up to historic times, in the Lesser Antilles (Turvey et al. 2010). In addition, the ''*Megalomys*'' that occurred on Curaçao and became extinct in the Pleistocene may well have been a member of this clade but it has yet to be critically studied (McFarlane and Lundberg 2002). Members of the clade tend to be relatively large for cricetines and they occur in a variety of habitats. Their insular distributions attest to these animals being excellent dispersers across salt water.

Haffer (1987:123) wrote that the trans-Andean forest region ''comprises the humid lowlands west and north of the Andes, i.e., the Pacific rain forests of Colombia and Ecuador, the humid portions of Caribbean Colombia, the humid middle Magdalena Valley and the forested lowlands of Middle America.'' Using this definition, Musser et al. (1998:174) discussed, at length, the trans-Andean distribution of what was then called *Oryzomys bolivaris* (now *Transandinomys bolivaris* (J. A. Allen, 1901)), including ''Its geographic range in the trans-Andean region is closely tied to ever wet and humid tropical evergreen forests extending from coastal lowlands to midmontane elevations and is concordant with the distributions of other rodents tied to the same forest environments.'' Other species that Musser et al. (1998) treated as having a trans-Andean distribution are *Sigmodontomys alfari* and ''*Sigmodontomys*'' *aphrastus*. They further stated that future

revisionary studies may reveal a trans-Andean distribution for *Melanomys caliginosus*. Weksler (2003:345) also treated *Sigmodontomys* (encompassing both *alfari* and *aphrastus*) as trans-Andean in distribution.

*Tanyuromys* is the 1 genus in the clade recovered herein that is not primarily restricted to the lowlands; it occurs at middle and higher elevations in mountainous regions of Costa Rica, Panama, Colombia (presumably), and Ecuador. *Melanomys* occurs in a wide array of lowland and middle-elevation habitats, and is especially abundant in highly disturbed forests. *Melanomys* is broadly distributed in the Caribbean lowlands of Central America and ranges down (mostly) the Pacific lowlands of tropical South America, occurring up to 2,300 m, and may include as many as 6 species (Hanson and Bradley 2008). *Sigmodontomys*, with 1 recognized lowland species, also occurs in the Caribbean lowlands of southern Central America and into the Pacific lowlands of northern South America.

*Nesoryzomys* occurred on at least 6 Galapagos islands (Steadman and Zousmer 1988). Reaching the Galapagos constitutes the greatest overwater dispersal distance for terrestrial mammals. *Aegialomys* is known from a single extant species that occurred on 2 islands in the Galapagos and 1 or more extant species from the mainland's Pacific lowlands of Ecuador and Peru (where it also ranges up to about 2,500 m). Although *Nesoryzomys* and *Aegialomys* are not trans-Andean in the sense of typically being found in wet forests, they are trans-Andean in the purely spatial sense, being found west of the Andes on the mainland or the Galapagos, or both. Therefore, it seems that there must have been at least 2 invasions of the Galapagos by members of this clade—by an ancestor of present-day and extinct *Nesoryzomys* and (presumably more recently) by the present-day genus *Aegialomys*.

In Patton and Hafner's (1983:557) phenetic cluster analysis based both on distance and correlation matrices of 23 qualitative characters, *Nesoryzomys* was linked with the 2 species of *Aegialomys*, forming ''a definite unit relative to other oryzomyines, not joining any of the latter until fairly far out in the dendrogram.'' Other phenograms based on using different methods and character states, however, gave different configurations and their factor analysis showed (p. 557) ''… strong separation of *Nesoryzomys* from the other oryzomyines [including *Aegialomys*].'' Nonetheless, on the basis of penis morphology and ''the clustering pattern based on … skin and skull characters which link *Nesoryzomys* with *O.* [*Aegialomys*] *xantheolus* [sic] and *O.* [*Aegialomys*] *bauri* [= *A. galapagoensis*],'' Patton and Hafner (1983:560) hypothesized that *Nesoryzomys* arose from a ''*xantheolus*-like [sic] ancestral stock inhabiting the xeric coastal regions of Peru and Chile.'' Unaccountably, although Patton and Hafner (1983:560) gave Peru and Chile as having housed the ancestral stock, and the Galapagos, the entirety of Peru, and northernmost Chile are all in the tropics, they discounted the origins of any of the Galapagos rats ''among tropical representatives of the oryzomyine complex.''

The sister relationship between the mainland *Aegialomys* and the Galapagoan *Nesoryzomys* that was inferred by Patton

and Hafner (1983) and that we have consistently found is quite remarkable and intriguing. Both *Aegialomys* and *Nesoryzomys* occur on the Galapagos, an island group some 970 km west of the South American mainland. *Nesoryzomys* is quite distinct from all other Oryzomyini, including *Aegialomys*, karyologically (Gardner and Patton 1976), morphologically, phenetically, and electrophoretically (Patton and Hafner 1983). Galapagoan and mainland *Aegialomys* are extremely similar to each other karyologically (Gardner and Patton 1976), morphologically, phenetically, and electrophoretically (Patton and Hafner 1983). Sequence information for Galapagoan *Aegialomys* would be most welcome, although the close affinity between the insular and mainland species assigned to *Aegialomys* seems unassailable based on the other types of data. This close affinity between mainland and insular *Aegialomys* even led Patton and Hafner (1983) to hypothesize colonization of the Galapagos via pre-Columbian human transport.

*Megalomys* is the only genus shown, as a member of this clade, that does not have a trans-Andean distribution. Two species of *Megalomys* still occurred in the Lesser Antilles at least until the 1800s. Four named species (1 from Curaçao) are now recognized (Turvey et al. 2010). Regardless of the affinities of *Megalomys*, its supposed occurrence both in the eastern Lesser Antilles and on Curaçao is biogeographically anomalous and we concur with McFarlane and Lundberg (2002:280) that ''the *Megalomys* spp. of the eastern Lesser Antilles are likely to have evolved from [a] mainland oryzomyine ancestor or ancestors independently of events on Curaçao, in which case the genus *Megalomys* as currently recognized would have to be regarded as a polyphyletic construct.'' Also, as noted by Turvey et al. (2010), the animal known as *Megalomys audreyae* Hopwood, 1926, from Barbuda, may not belong in *Megalomys*.

Another potential member of this clade is *Pennatomys*, as based in the analyses of Turvey et al. (2010). The single described species of *Pennatomys* (*P. nivalis* Turvey et al., 2010) occurred on Nevis, St. Eustatius, and St. Kitts in the Lesser Antilles at least until historic times, but there is now what is claimed to be evidence for the existence of a living species of native muroid on Nevis. The late James W. Johnson, a resident naturalist and nature guide on Nevis, provided color photographs, said to have been taken on Nevis, of a long-tailed rodent that could conceivably belong to the newly described genus *Pennatomys* or else to some other but as yet undescribed taxon (see text and photographs at Nevis Historical and Conservation Society [2010]). In the photographs provided, the animal has a pale gray dorsum, white venter, and a black, naked tail considerably longer than head plus body. We have examined specimens of *Rattus rattus* (Linnaeus, 1758) that approach this animal in coloration, and are not convinced that the rodent photographed could not belong to that species. Greater and Lesser Antillean species of Oryzomyini other than of *Pennatomys* have been placed in *Megalomys*, *Oryzomys*, and *Oligoryzomys*, but the Nevis animal looks like a member of none of these genera. Turvey

et al. (2010:764) noted that Johnson had reported to them that there have been reports of ''unusual-looking rats occurring on Nevis into recent times'' and that they had been eaten by people there at least until the 1930s. An attempt to collect this mysterious rodent in 2009, however, recovered only the invasive *R. rattus* (S. T. Turvey, Zoological Society of London, pers. comm.).

The resolution of relationships among a number of genera and species that have not yet been studied in detail will shed further light on the biogeography and diversity of this interesting clade. In addition to individual mammalian species that have trans-Andean distributions, it is now becoming apparent that there are more supraspecific trans-Andean clades than had been previously recognized (e.g., this paper; Gutiérrez et al. 2010; Rossi et al. 2010).

## RESUMEN

A partir de estudios recientes, profundizamos acerca de las relaciones filogenéticas dentro de Oryzomyini, en particular aquellas que involucran taxa actualmente atribuidos al género *Sigmodontomys*. Recientemente se ha considerado que *Sigmodontomys* incluye 2 especies, *alfari* (J. A. Allen, 1897) y *aphrastus* (Harris, 1932), sin embargo, a través de su complicada historia taxonómica, ambas especies también han sido incluidas dentro del género *Oryzomys*, y *alfari* independientemente dentro del género *Nectomys*. Usando caracteres morfológicos (98 externos, craneales, dentales y postcraneales) y moleculares (citocromo *b*, 12S y IRBP), inferimos la posición filogenética de estas 2 especies dentro de Oryzomyini. Documentamos que *alfari* y *aphrastus* no forman un grupo monofilético. *Sigmodontomys alfari* es el taxón hermano de *Melanomys*, mientras *aphrastus* es hermano de dicho grupo, o del género caribeño extinto *Megalomys*. Por consiguiente, consideramos a *aphrastus* como un nuevo género que describimos y nombramos a continuación. Este nuevo género está incluido dentro del clado formado por *Sigmodontomys–Melanomys–Aegialomys–Nesoryzomys*, el cual representa un grupo monofilético bien sustentado principalmente del sur de Centroamérica y norte de Sudamérica, restringido principalmente a hábitats de tierras bajas a elevaciones intermedias trasandinas, y caracterizado por su habilidad de cruzar barreras de agua salada. El nuevo género se encuentra en elevaciones medianas y altas desde el centro y norte de Costa Rica hasta el noroeste de Ecuador y, junto con algunas poblaciones de *Aegialomys* y *Melanomys*, ocupa las localidades más altas de cualquier miembro de este grupo.

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## APPENDIX I

List of newly analyzed specimens of taxa included in phylogenetic analyses. Other specimens analyzed were listed previously by Weksler (2006), Turvey et al. (2010), and Percequillo et al. (2011).

*Tanyuromys aphrastus.*—COSTA RICA: Alajuela/Puntarenas; Monteverde Cloud Forest Reserve (KU 159021, 161003). San José; San Joaquín de Dota (UMMZ 62875). ECUADOR: Pichincha; Guarumos (MCZ 50396); Pichincha; Mindo (UMMZ 155808). PANAMA: Chiriquí, 24 km NNE San Félix (USNM 541200, 541201).

*Rhipidomys nitela.*—VENEZUELA: Bolívar; 12 km SW San Ignacio de Yuruani (AMNH 257273–257275). FRENCH GUIANA: Sinnamary; Paracou (AMNH 267021, 267582, 267583, 267594); Les Nouragues (AMMH 269821).

*Melanomys caliginosus.*—ECUADOR: Esmeraldas; Esmeraldas (AMNH 33216, 33219, 33220); Manabí; Cuaque (AMNH 66331, 66333, 66335, 66338, 66340); Pichincha; Gualea (AMNH 46689, 46691, 46696); Pichincha; Las Maquinas (AMNH 66326, 66327, 66329, 66330); Guayas; Río Pescado (AMNH 61967).

*Melanomys chrysomelas.*—COSTA RICA: Limón; Suerre (AMNH 10777); Puntarenas; Palmar (AMNH 139412, 139416, 139419, 139421, 139423); San José; San Geronimo Pieris (AMNH 123559–123561). NICARAGUA: Río Tuma (AMNH 28394, 28404, 29529, 29532); Chontales (AMNH 28556, 28557). PANAMA: Bocas del Toro (USNM 464387, 464388, 464390, 464391, 464877, 464878, 464880, 464883, 503716, 575658, 575660, 578384, 578385).

## APPENDIX II

Taxa and specimens sequenced for interphotoreceptor retinoid–binding protein (IRBP), cytochrome-b (Cytb), and 12S genes. Species names, localities, GenBank accession numbers, and voucher numbers are provided for all taxa included in the phylogenetic analyses.

| Species | Country | State or province | Locality | IRBP GenBank accession no.[a] | Cytb GenBank accession no.[a] | 12S GenBank accession no.[a] | Museum catalog or collector's no.[b] |
|---|---|---|---|---|---|---|---|
| Aegialomys xanthaeolus | Peru | Arequipa | 4.5 miles E Acari | AY163628 | GU126545 | JF693827 | MVZ 145533 |
| Amphinectomys savamis | Peru | Iquitos | San Pedro | AY163579 | | JF693828 | MV 970045 |
| Cerradomys subflavus | Brazil | Minas Gerais | Fazenda Canoas | AY163626 | GU126543 | JF693829 | MNRJ 61665 |
| Delomys sublineatus | Brazil | São Paulo | Estação Biológica Boracéia | AY163582 | AF108687 | JF693830 | FMNH 141628 (IRBP, 12S), MVZ 183075 (Cytb) |
| Drymoreomys albimaculatus | Brazil | São Paulo | Parque Estadual Intervales | GU126515 | GU126516 | | MVZ 182088 (IRBP), MVZ 182089 (Cytb) |
| Eremoryzomys polius | Peru | Amazonas | Balsas | AY163624 | GU126540 | JF693831 | FMNH 129243 |
| Euryoryzomys lamia | Brazil | Goiás | Parque Nacional Chapada dos Veadeiros | AY163619 | GU126537 | JF693832 | MNRJ 46654 (IRBP), CRB 983 (Cytb, 12S) |
| Euryoryzomys macconnelli | Peru | Loreto | Río Gálvez | AY163620 | GU126538 | JF693833 | AMNH 272678 (IRBP), AMNH 272669 (Cytb, 12S) |
| Euryoryzomys russatus | Brazil | Rio de Janeiro | Guapimirim | AY163625 | GU126542 | JF693834 | ORG 67 (IRBP), MNRJ 50230 (Cytb, 12S) |
| Handleyomys alfaroi | El Salvador | Santa Ana | Parque Nacional Montecristo | AY163615 | GU126533 | JF693835 | ROM 101537 |
| Handleyomys intectus | Colombia | Antioquia | 4 km S El Retiro | AY163584 | | JF693836 | ICN 16093 |
| Handleyomys rostratus | El Salvador | Ahuachapán | El Imposible | AY163622 | GU126541 | JF693837 | ROM 101843 |
| Holochilus brasiliensis | Paraguay | Ñeembucú | Estancia Santa Teresa | AY163585 | GU126517 | JF693838 | GD 81 |
| Hylaeamys megacephalus | Venezuela | Bolívar | San Ignacio de Yuruaní | AY163621 | | JF693839 | MHNLS 8061 |
| | Brazil | Pará | 52 km SSW Altamira | | AF108695 | | USNM 549548 |
| Hylaeamys yunganus | Suriname | Saramacca | Tafelberg | AY163629 | GU126546 | JF693840 | CMNH 76926 |
| Lundomys molitor | Uruguay | Colonia | Arroyo Cufre | AY163589 | | JF693841 | MNHN 4292 |
| Melanomys caliginosus | Ecuador | Esmeraldas | Comuna San Franscico de Bogotá | EU649052 | EU340020 | | TTU 102819 |
| Melanomys chrysomelas | Nicaragua | Atlantico Norte | Rosa Grande | EU649053 | EU340017 | JF693842 | TTU 100324 |
| | Costa Rica | Heredia | La Flaminea | | | | RMT 4658 |
| Melanomys columbianus | Venezuela | Zulia | Misión Tukuko | AY163590 | EU340022 | | MHNLS 7698 |
| Microryzomys minutus | Peru | Cuzco | 32 km NE Paucartambo | AY163592 | | JF693843 | MVZ 166666 |
| | Peru | Cuzco | 3 km E Amaybamba | | AF108698 | | MVZ 173975 |
| Neacomys minutus | Peru | Loreto | Río Gálvez | AY163595 | GU126519 | JF693844 | AMNH 272867 |
| Neacomys musseri | Peru | Loreto | Río Gálvez | AY163596 | GU126520 | JF693845 | AMNH 272676 |
| Neacomys spinosus | Peru | Amazonas | Río Cenepa | AY163597 | GU126521 | JF693846 | MVZ 155014 |
| Nectomys apicalis | Peru | Cuzco | Kiteni, Río Urubamba | | U03539 | JF693847 | MVZ 166700 |
| Nectomys squamipes | Brazil | São Paulo | Ilha do Cardoso | AY163598 | GU126522 | JF693848 | FMNH 141632 |
| Nephelomys albigularis | Peru | Cajamarca | Las Ashitas | AY163614 | GU126532 | | AMNH 268125 |
| Nephelomys levipes | Peru | Cuzco | 54 km NE Paucartambo | | JF693875 | | MVZ 171468 |
| Nesoryzomys narboroughi | Ecuador | Galapagos | Isla Fernandina | AY163600 | GU126523 | JF693849 | ASNHC 8675 |
| Nesoryzomys swarthi | Ecuador | Galapagos | Isla Santiago | AY163601 | GU126524 | JF693850 | ASNHC 10003 |
| Nyctomys sumichrasti | El Salvador | Santa Ana | Parque Nacional Montecristo | AY163603 | | JF693851 | ROM 101531 |
| | Honduras | Atlantida | Lancetilla Botanical Garden | | AY195801 | | TTU 84484 |
| Oecomys bicolor | Peru | Loreto | Río Gálvez | AY163604 | | JF693852 | AMNH 272674 |
| | Peru | Amazonas | Aguaruna, Río Cenepa | | AF108699 | | MVZ 154999 |
| Oecomys catherinae | Brazil | Espírito Santo | Reserva Florestal da Cia. Vale do Rio Doce | AY163605 | GU126525 | JF693853 | MF 29 |
| Oecomys concolor | Peru | Amazonas | Río Cenepa | AY163606 | JF693876 | JF693854 | MVZ 155005 |

**APPENDIX II.—Continued.**

| Species | Country | State or province | Locality | IRBP GenBank accession no.[a] | Cytb GenBank accession no.[a] | 12S GenBank accession no.[a] | Museum catalog or collector's no.[b] |
|---|---|---|---|---|---|---|---|
| *Oecomys mamorae* | Brazil | Mato Grosso do Sul | Rio Vermelho | AY163607 | GU126526 | JF693855 | MVZ 198026 |
| *Oecomys trinitatis* | Peru | Loreto | Río Gálvez | AY163608 | GU126527 | JF693856 | MUSM 13320 |
| *Oligoryzomys flavescens* | Brazil | São Paulo | Pedreira | AY163609 | GU126528 | JF693857 | MNRJ 53276 (IRBP), CRB 1430 (*Cytb*, 12S) |
| *Oligoryzomys fornesi* | Brazil | Goiás | Terezina de Goiás | AY163610 | GU126529 | JF693858 | CRB 747 (IRBP), CRB 757 (12S) |
| *Oligoryzomys fulvescens* | Venezuela | Sucre | Finca Vuelta Larga | AY163611 | GU126530 | JF693859 | AMNH 257262 |
| *Oligoryzomys nigripes* | Brazil | São Paulo | Pedreira | AY163612 | GU126531 | JF693860 | MNRJ 66222 |
| *Oligoryzomys stramineus* | Brazil | Goiás | Terezina de Goiás | AY163613 | | JF693861 | MNRJ 46406 (IRBP), MNRJ 46873 (*Cytb*, 12S) |
| *Oreoryzomys balneator* | Peru | Cajamarca | 4 km W Chaupe | AY163617 | GU126535 | JF693862 | AMNH 268144 |
| *Oryzomys couesi* | Mexico | Jalisco | Chamela | AY163618 | GU126536 | JF693863 | TTU 37749 |
| *Oryzomys palustris* | United States | Texas | Freesto | AY163623 | GU126539 | JF693864 | TTU 75311 |
| *Peromyscus maniculatus* | Mexico | Durango | Hacienda Coyotes | AY163630 | | | TTU 81622 |
| | United States | Michigan | High Island | | AY322508 | JF693865 | UMMZ 165752 |
| *Pseudoryzomys simplex* | Paraguay | Ñeembucú | Estancia Yacaré | AY163633 | GU126547 | JF693866 | GD 65 |
| *Rhipidomys nitela* | Venezuela | Bolívar | San Ignacio de Yuruaní | AY163636 | | | MHNLS 7820 |
| | Brazil | Pará | Rio Xingú | | AF108682 | | MZUSP 21316 |
| *Scolomys ucayalensis* | Peru | Loreto | Río Gálvez | AY163638 | | JF693867 | AMNH 272721 |
| | Brazil | Amazonas | Barro Vermelho | | AF108696 | | INPA 2489 |
| *Sigmodontomys alfari* | Panama | Bocas del Toro | Isla San Cristobal | AY163641 | GU126548 | JF693868 | USNM 449895 |
| *Sooretamys angouya* | Brazil | Rio de Janeiro | Teresópolis | AY163616 | GU126534 | JF693869 | MNRJ 50234 |
| *Tanyuromys aphrastus* | Costa Rica | Alajuela | Monteverde Cloud Forest Reserve | JF693878 | JF693877 | JF693870 | KU 161003 |
| *Thomasomys baeops* | Peru | Cajamarca | Las Ashitas | AY163642 | | JF693871 | AMNH 268146 |
| | Ecuador | Bolívar | Río Tatahuazo | | DQ914654 | | MSB 70704 |
| *Transandinomys talamancae* | Panama | Bocas del Toro | Tierra Oscura | AY163627 | GU126544 | JF693872 | USNM 449894 |
| *Wiedomys pyrrhorhinos* | Brazil | Bahia | Jaborandi | AY163644 | | | MNRJ 67023 |
| | Brazil | Bahia | Fazenda Massapê | | AY275134 | | MVZ 197567 |
| *Zygodontomys brevicauda* | Venezuela | Sucre | Finca Vuelta Larga | AY163645 | GU126549 | JF693873 | AMNH 257321 |
| *Zygodontomys cherriei* | Venezuela | Zulia | Misión Tukuko | AY163646 | GU126550 | JF693874 | USNM 448665 |

[a] Voucher sources for GenBank sequences: AY322———, AY195———, Bradley et al. 2004; AY275———, D'Elía 2003; EU649———, J. D. Hanson, in litt.; EU340——, Hanson and Bradley 2008; GU———————, Percequillo et al. 2011; DQ————, Salazar-Bravo and Yates 2007; U————, Smith and Patton 1993; AF—————, Smith and Patton 1999; AY163———, Weksler 2003; JF—————, present study.

[b] Initials for institutions other than those listed in the ''Materials and Methods'' are: ASNHC = Angelo State Natural History Collections, San Angelo, Texas; CMNH = Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; ICN = Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia; INPA = Instituto Nacional de Pesquisas da Amazonia, Manaus, Brazil; MHNLS = Museo de Historia, Natural La Salle, Caracas, Venezuela; MNHN = Museo Nacional de Historia Natural, Montevideo, Uruguay; MNRJ = Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; MSB = Museum of Southwestern Biology, University of New Mexico, Albuquerque, New Mexico; MUSM = Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru; MZUSP = Museu de Zoología, Universidade de São Paulo, São Paulo, Brazil; ORG = Laboratorio de Vertebrados, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil (voucher at MNRJ); ROM = Royal Ontario Museum, Toronto, Ontario, Canada; TTU = The Museum, Texas Tech University, Lubbock, Texas. Collectors' initials and names for field numbers are: CRB = Cibele R. Bonvícino (voucher at MNRJ); GD = Guillermo D'Elía (voucher at MNRJ); MF = Monica Fonseca (voucher at Universidade Federal de Minas Gerais, Minas Gerais, Brazil); MV = Michael Valqui (voucher at MUSM); RMT = Robert M. Timm (voucher at KU).