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## Nota

# A NEW TRIBE OF SIGMODONTINAE RODENTS (CRICETIDAE)

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**ABSTRACT.** Phylogenetic hypotheses based on molecular markers indicate that the so-called *Reithrodon* group, including the extant genera *Euneomys*, *Neotomys*, and *Reithrodon*, formerly within the tribe Phyllotini, is not monophyletic. In turn, a new clade of tribal rank is recovered constituted by *Euneomys*, *Irenomys*, and *Neotomys*, comprising a small, mostly Andean sigmodontine radiation. Within the new clade, here named and diagnosed, *Irenomys* appears as a taxon with many specialized traits, which suggests an early divergence associated with the exploitation of *Nothofagus* forests. The living members of the new tribe are characterized by several morphological features including grooved upper incisors, narrow and parallel-sided interorbital regions, enlarged interparietals, and simplified and hypsodont molars. This new phylogenetic scenario implies a high degree of craniodental convergence among several lineages of sigmodontine rodents. The tribal position of several high-crowned extinct forms of sigmodontine rodents (e.g., *Panchomys*, *Tafimys*), formerly allocated to the *Reithrodon* group, is in need of revision.

**RESUMEN.** Una nueva tribu de roedores Sigmodontinae (Cricetidae). Hipótesis filogenéticas basadas en marcadores moleculares indican que el denominado grupo *Reithrodon*, incluyendo los géneros vivientes *Euneomys*, *Neotomys* y *Reithrodon*, anteriormente dentro de la tribu Phyllotini, no es monofilético. En cambio, un nuevo clado de rango tribal es recuperado, constituido por *Euneomys*, *Irenomys* y *Neotomys*, comprendiendo una pequeña radiación de sigmodontinos mayormente andinos. Dentro de este nuevo clado, aquí nominado y diagnosticado, *Irenomys* emerge como un taxón con varios rasgos especializados que sugieren una temprana divergencia en el marco de la explotación del bosque de *Nothofagus*. Los miembros vivientes de la nueva tribu están caracterizados por varios rasgos morfológicos, incluyendo incisivos superiores surcados, regiones interorbitarias angostas y de bordes paralelos, interparietales agrandados y molares simplificados e hipsodontes. Este nuevo escenario filogenético implica un alto grado de convergencia en la morfología cráneo-dentaria entre varios linajes de roedores sigmodontinos. La posición tribal de varias formas extintas de roedores sigmodontinos de coronas altas (e.g., *Panchomys*, *Tafimys*), anteriormente ubicadas en el grupo *Reithrodon*, necesita ser revisada.

**Key words:** Andean Region. *Euneomys*. *Irenomys*. *Neotomys*. *Reithrodon*.

**Palabras clave:** *Euneomys*. *Irenomys*. *Neotomys*. Región Andina. *Reithrodon*.

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The advent of DNA sequence methodology has changed earlier systematic hypotheses, mostly based on morphological features, of mammalian classification (e.g., Meredith et al., 2011). While changes within the Mammalia are perhaps not as impressive as those in other groups of vertebrates (e.g., amphibians; see Frost et al., 2006), many unexpected linkages among taxa have been corroborated leading to new classificatory hypotheses based on molecular markers.

Within the amazingly diverse Sigmodontinae radiation (Patton et al., 2015), the case of the *Reithrodon* group, an assemblage of medium-sized, stout-bodied, herbivorous rodents previously grouping the living genera *Euneomys*, *Neotomys*, and *Reithrodon*, emerged as paradigmatic. First recognized by Olds and Anderson (1989) as a clade within the tribe Phyllotini, this group was formally diagnosed and strongly supported by the cladistic morphological analyses conducted by Steppan (1993, 1995; see also Braun, 1993). By this time, several extinct species—including, in order of discovery, *Panchomys steppani*, *Ichthyurodon ameghinoi*, and *Tafimys powelli*—were placed within the *Reithrodon* group, augmenting its known diversity and past distribution (Pardiñas, 1997; Steppan and Pardiñas, 1998; Ortiz et al., 2000). However, only a few years later, several molecular studies questioned both the monophyly of this clade as well as the inclusion of these genera within the tribe Phyllotini. Successive works employing mitochondrial and/or nuclear markers consistently pointed to *Reithrodon* as a unique lineage within Sigmodontinae (e.g., Engel et al., 1998; Smith and Patton, 1999), while *Euneomys* was recovered as neither close to *Reithrodon*, nor Phyllotini (e.g., D'Elía, 2003). As a partial result of this changing scenario, Reithrodontini was expanded to include *Euneomys* and *Neotomys* plus *Reithrodon* (Musser and Carleton, 2005). More refined analyses based on interphotoreceptor-retinoid binding protein sequences (hereafter IRBP) retrieved a close relationship between *Euneomys* and the long-tailed, scansorial mouse *Irenomys*, endemic to the *Nothofagus* forests of southwestern South America (D'Elía et al., 2006; see also Fabre et al., 2012). Finally, the

remaining member of the original *Reithrodon* group (sensu Olds and Anderson, 1989), the Andean rat *Neotomys* was recovered as the sister taxa to the *Euneomys-Irenomys* clade (Martínez et al., 2012; Salazar-Bravo et al., 2013). The close relationship between the terrestrial, stout bodied *Euneomys* and *Neotomys* and the forest specialist *Irenomys* is now well established as a unique branch of the sigmodontine radiation (e.g., Martínez et al., 2012; Salazar-Bravo et al., 2013; Parada et al., 2013; Ventura et al., 2013; Schenk et al., 2013; Pardiñas et al., 2014; see also D'Elía, 2015). This group, however, lacks a formal designation, an issue that we now resolve with the definition and diagnosis of a new tribe of Sigmodontinae (see below).

To assess the definition and diagnosis of the new tribe presented here we follow the concepts portrayed by Reig (1987). In this context we worked based on the extensive morphological revisions produced for several groups of sigmodontine rodents during the last decades (e.g., Voss, 1988; Steppan, 1993, 1995; Pacheco, 2003; Weksler, 2006; Teta, 2013). Several specimens of *Euneomys*, *Irenomys*, and *Neotomys* (see **Appendix I**) were examined for selected anatomical traits (largely following the characters lists compiled by Weksler [2006]). The obtained product is a combination of morphological traits that is unique to this assemblage, although not formally tested with a cladistic approach. This combination is sufficient to conform an intentional meaning of the polythetic concept of the new clade (Reig, 1987:364). This method was successfully employed in the definition of several tribes recently proposed (e.g., Baiomyini, see Musser and Carleton, 2005; Abrotrichini, see D'Elía et al., 2007) and has the aggregate value of allowing a coordinate advancement of classification and nomenclature, abjuring the claim that this feat is only possible by the identification of unequivocal synapomorphies (a task surely desirable but still under construction). The anatomical terminology used in this contribution—regarding osteological, dental, and soft anatomy—follows that employed by the sources previously mentioned, plus Reig (1977), Carleton (1980), and Hume (1994).

Phylogenetic analyses were conducted with Maximum Likelihood (ML) and Bayesian Inference (BI) on a matrix of 4 nuclear (BRAC1, IRBP, GHR and RAG1) and 1 mitochondrial (Cytochrome b gene; Cytb, thereafter) marker for members of the Sigmodontinae and outgroups (**Appendix II**). Because the original datasets (as deposited in GenBank) sampled different species of some genera, our dataset included chimeric sequences for some taxa; the effort was made to include data from closely related (in some instances sister taxa) in our alignments; 4 of the 71 ingroup taxa (Sigmodontinae) were represented by chimeric sequences (see **Appendix II**). Partitioning schemes and substitution models were selected using the Bayesian information criterion in PartitionFinder (Lanfear et al., 2012). The following schemes and substitution models were implemented in the BI analyses: F81+G for GHR\_pos2; GTR+G for BRAC1\_pos1, BRAC1\_pos2 and RAG1\_pos3; GTR+I for GHR\_pos3; GTR+I+G for Cytb\_pos1, Cytb\_pos2, Cytb\_pos3, IRBP\_pos1, IRBP\_pos2, RAG1\_pos1 and RAG1\_pos2; K80+G for BRAC1\_pos3 and SYM+I+G for GHR\_pos1 and IRBP\_pos3. Bayesian analyses (100 million generations) were conducted with MrBayes 3.2.2 (Ronquist et al., 2012) on the CIPRES Science gateway (Miller et al., 2010) and with the concatenated dataset. Convergence of the BI analyses was assessed with Tracer v1.6 (Rambaut et al., 2014) to estimate the effective sample sizes for molecular evolutionary parameters (all reached well above 200), and AWTY (Wilgenbusch et al., 2004) to compare posterior probabilities for independent runs (they were, with a correlation coefficient = 0.997) and to test whether 10 subsamples of the chains sampled trees in proportion to their posterior probabilities with the Slide analysis (clade frequencies were very similar). Maximum Likelihood analyses were run with RAxML (Stamatakis et al., 2008) on CIPRES (Miller et al., 2010) under GTR+G for all partitions identified by PartitionFinder (see above); invariable sites parameter was not included in any of the analyses as per RAxML manual; the number of alternative runs on distinct starting trees was set to 25 in order to avoid entrapment in local maxima.

### Euneomyini, new tribe

**Type genus.**— *Euneomys* Coues, 1874.

**Contents.**— *Euneomys* Coues, 1874, *Irenomys* Thomas, 1919, and *Neotomys* Thomas, 1894

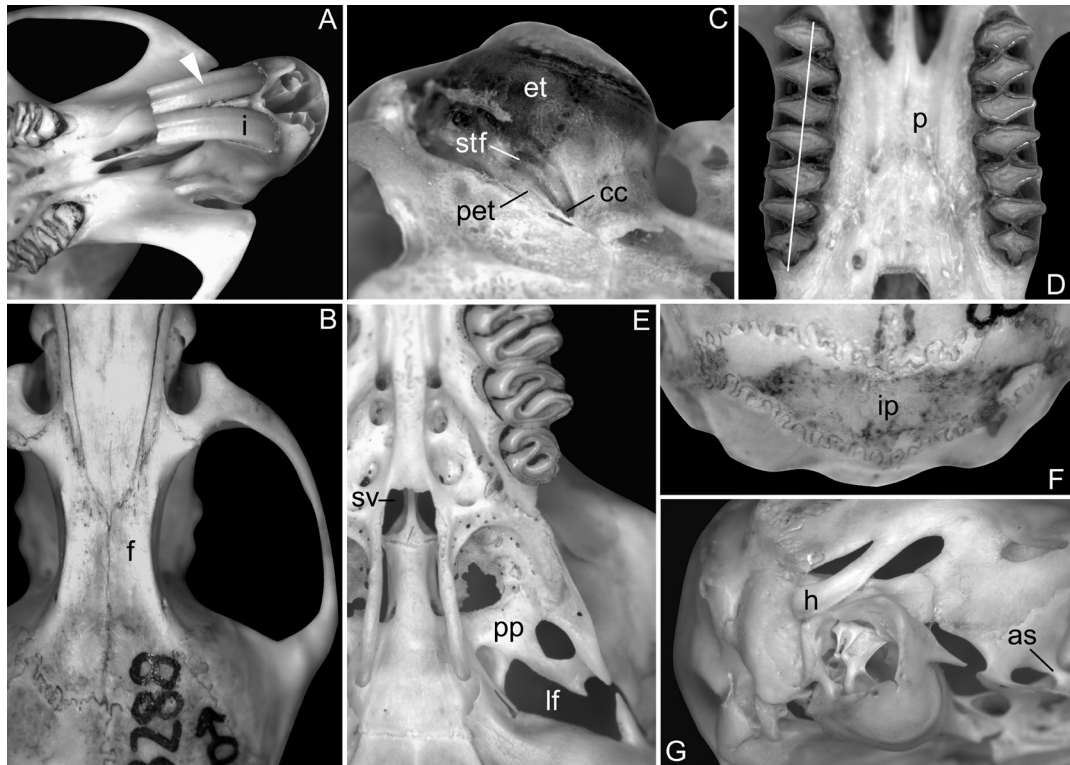
**Definition.**— The clade composed of the last common ancestor of *Euneomys*, *Irenomys*, and *Neotomys* and all of its descendants.

**Diagnosis.**— A tribe of the subfamily Sigmodontinae (sensu Reig, 1980), clade Oryzomyalia (sensu Steppan et al., 2004) grouping medium-sized rodents (head and body length 100–160 mm) characterized by the following combination of characters: narrow and parallel-sided interorbital region; well-developed interparietal; distally spatulated hamular processes directly applied on the auditory bullae dorsal borders; enlarged parapterigoyd plates; well excavated sphenopalatine vacuities; short palates; open lacerate foramina; molar tooththrows posteriorly divergent; upper incisors grooved by folded enamel/dentine; labial root on M1/m1 absent; internal carotid canal entirely bounded (or nearly so) by the petrosal and ectotympanic portions of the auditory bulla; hypsodont and simplified laminated molars; planar coronal surfaces; procingulum of m1 typically isolated from the remainder portion of the molar; gall bladder present; large caecum (after Sanborn, 1947; Hershkovitz, 1962; Olds and Anderson, 1989; Steppan, 1995; Voss, 1991; **Fig. 1** and **2**).

**Etymology.**— The tribal name is formed by adding to the stem of the name of the type genus (ICZN, Article 29.3), *Euneomys*, the suffix ini (Article 29.2); thus, the family-group name becomes Euneomy + ini = Euneomyini.

**Known distribution.**— Euneomyini rodents are distributed along the Andes and peri-Andean ranges, including Puna and adjacent lowlands, from central Perú (ca. 10° S) to southernmost South America, reaching Cape Horn islands (ca. 55° 30' S; Musser and Carleton, 2005). By current understanding, there are no areas of sympatry between the genera of Euneomyini. While the range of *Euneomys* includes both Patagonian lowlands and Andean habitats from southernmost South America to at least 3500 m, *Irenomys* is mainly confined to the *Nothofagus* forest. Although *Neotomys* is also an Andean form (Sanborn, 1947), there is a gap of about 2° in the central Andes where neither *Euneomys* nor *Neotomys* have been recorded (**Fig. 3**).

**Biochron.**— Late Pleistocene (*Euneomys*; see Tammone et al., 2014; *Neotomys*; see Pardifias and Ortiz, 2001) to Recent. The Pleistocene *Euneomys catenatus*, a name combination proposed by Hershkovitz (1962) based on *Bothriomys catenatus*



**Fig. 1.** Views of different morphological traits among representative Euneomyini: A. Groove [marker] on incisors (*Euneomys mordax*; MVZ 183288). B. Narrow and parallel-sided interorbital region (*E. mordax*; MVZ 183288). C. Internal carotid canal bounded by the petrosal and ectotympanic portions of the auditory bulla (*E. chinchilloides*; CNP 3641). D. Molar tooththrow posteriorly divergent and short palate (*Irenomys tarsalis*; UACH 2179). E. Well excavated sphenopalatine vacuities and enlarged parapterygoid plates (*E. mordax*; MVZ 183288). F. Enlarged interparietal (*I. tarsalis*; UACH 2179). G. distally spatulated hamular processes directly applied on the auditory bullae dorsal border (*E. mordax*; MVZ 183288). Abbreviations: as = alisphenoid strut, cc = carotid canal, et = ectotympanic, f = frontal, lf = lacerate foramen, h = hamular process, i = incisor, ip = interparietal, p = palate, pet = petrosal, pp = parapterygoid plate, stf = stapedial foramen, sv = sphenopalatine vacuity.

Ameghino, 1889, is a junior synonym of *Graomys griseoflavus* (cf. Pardiñas, 1995).

**Phylogenetic relationships.**— The monophyletic group that includes *Euneomys*, *Irenomys*, and *Neotomys* has been recovered with high bootstrap and posterior probability values in all analyses to date. These include the combined analyses of single mitochondrial (Cytb) and nuclear (IRBP) genes (e.g., Martínez et al., 2012; Salazar-Bravo et al., 2013; Parada et al., 2013; Ventura et al., 2013) as well as the combined analyses of multiple nuclear (Schenk et al., 2013) and multiple nuclear and mitochondrial loci (J. Salazar-Bravo, unpublished data); in each of these analyses the topology of this clade is the same: (*Irenomys*, (*Euneomys*, *Neotomys*)).

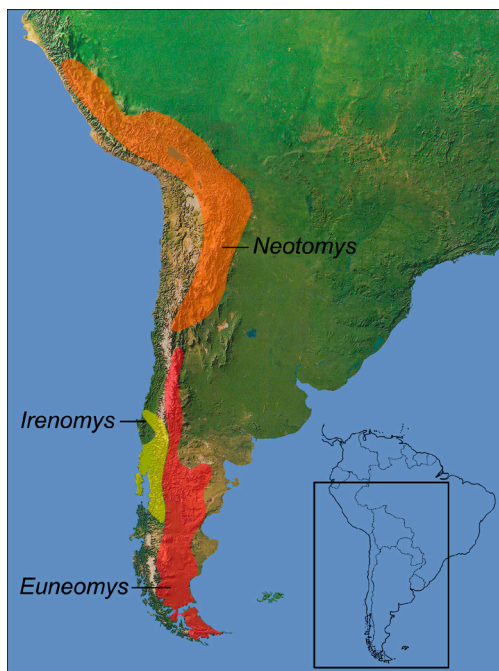
There remains substantial disagreement as to which taxon (or group) is most closely related to

Euneomyini; analyses that include only Cytb and IRBP sequence data tend to suggest that this tribe forms a group (in some cases, with strong Bayesian but poor bootstrap support) with *Chinchillula*, followed by a clade that includes *Andinomys* and *Punomys* (e.g., Salazar-Bravo et al., 2013; Pardiñas et al., 2014) or as a clade within a polytomy that also includes *Chinchillula* and *Reithrodon* (see Carrizo and Catalano, in press). Other analyses recover *Juliomys* as the sister group to Euneomyini (e.g., Ventura et al., 2013: fig. 1), again, often with poor support. Likewise, analyses of 4 nuclear loci suggest that a clade formed by *Andinomys* and *Punomys* is the sister group to Euneomyini, although with very low posterior probability and bootstrap below 50% (Schenk et al., 2013); in this topology *Chinchillula* is recovered as the sister group to the remainder of Oryzomyalia with strong support.



**Fig. 2.** Morphology of upper (above) and lower (below) molar occlusal surfaces in Euneomyini: from left to right, *Irenomys tarsalis* (UACH 2179), *Euneomys chinchilloides* (CNP 3641), and *Neotomys ebriosus* (uncatalogued specimen).

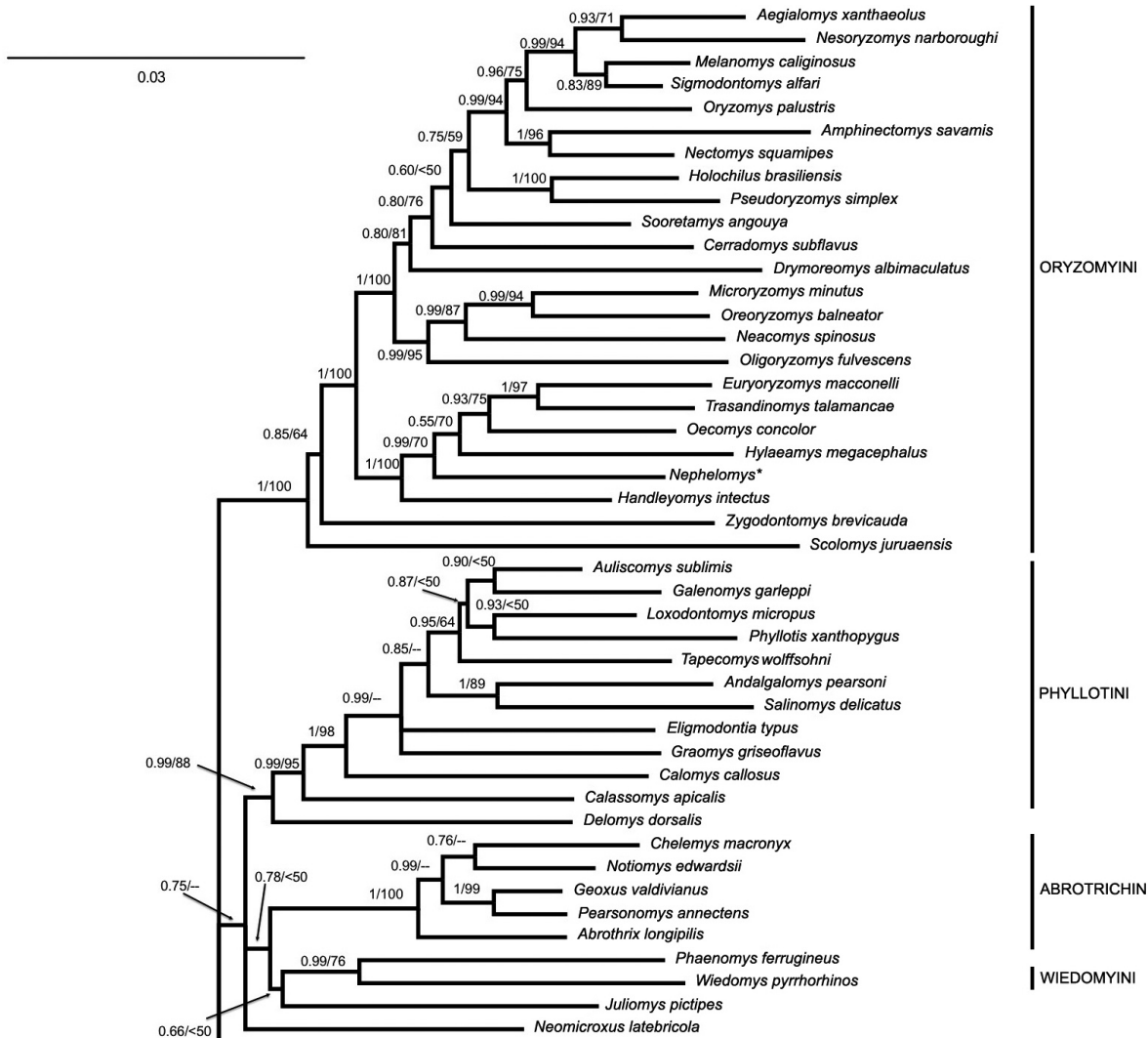
Our own analyses of molecular markers confirm with strong support the position of *Chinchillula* as the sister group to *Oryzomyalia* (Fig. 4). In addition, it recovers a polytomy near the base of the *Oryzomyalia*, with apparent independent origins of the Euneomyini and *Andinomys* + *Punomys* clades. Therefore, it appears that, at least for now, the best course of action is to treat each of these clades as independent from each other. It is important to note that a coordinate treatment of the clade composed by *Andinomys* and *Punomys* regarding Euneomyini promotes the recognition of a new tribe to contain these 2 Andean genera (Salazar-Bravo et al., in preparation).

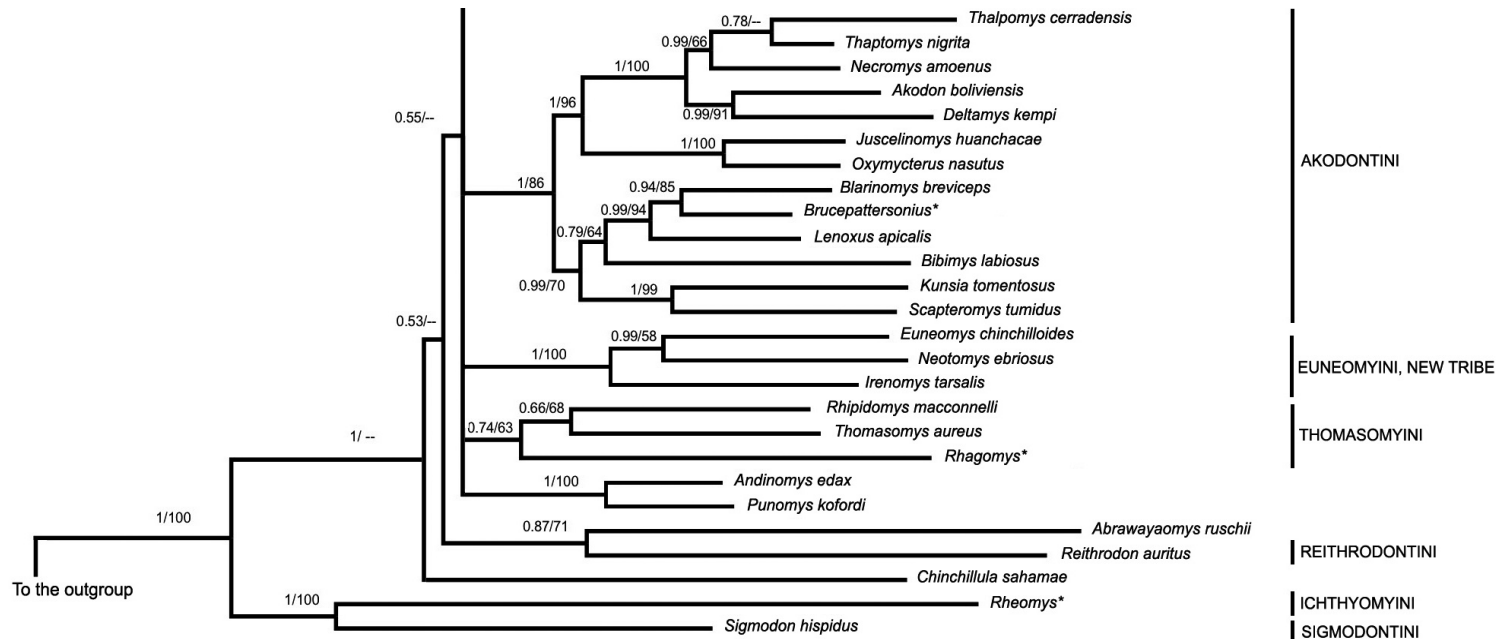


**Fig. 3.** Generalized distributions of the three genera of Euneomyini.

**Remarks.**— The phylogenetic scenario proposed by us and previous workers (e.g., Martínez et al., 2012; Salazar-Bravo et al., 2013; Parada et al., 2013; Schenk et al., 2013) implies a high degree of morphologic convergence among several lineages of sigmodontine rodents. This is particularly evident taking in mind that associations among several of the genera discussed here, including *Euneomys*, *Irenomys*, *Neotomys*, *Reithrodon*, and *Sigmodon*, have been repeatedly advanced or discarded (Sanborn, 1947; Hershkovitz, 1962; Pearson and Patton, 1976; Olds and Anderson, 1989). Molecular-based phylogenies are consistent in identifying that at least 4 major groups of tribal rank are necessary to accommodate these genera (Martínez et al., 2012; Salazar-Bravo et al., 2013). Renewed morphological analyses will be required to place correctly the fossil genera *Panchomys*, *Ichthyurodon*, and *Tafimys*.

Within Euneomyini, the genus *Irenomys* has many specialized traits that appear related to an adaptive exploitation of the *Nothofagus* forest biome. Paleontological data indicate that the expansion of Nothofagaceae and bamboo (*Chusquea*), as well as associated micro- to mesothermal families such as Podocarpaceae





**Fig. 4.** Results of the Bayesian analysis of the combined matrix for members of the Sigmodontinae and outgroups. Numbers indicate posterior probability (left of the diagonal) and ML bootstrap values (right of the diagonal) of adjacent nodes. Dashes indicate nodes that were not recovered in the Maximum Likelihood topology (= -79444.242902). Asterisks represent chimeric sequences (see **Appendix II**).



and Araucariaceae, in Patagonia date from the Middle Eocene-Early Oligocene (cf. Barreda and Palazzesi, 2007). Southern *Nothofagus* forest, currently restricted to a narrow band in the Andean piedmont between 35° to 55°S (Ward, 1965), was in the past well represented across interior Patagonia. In addition, molecular data suggest that the genus *Irenomys* originated between 6.5 Mya (Parada et al., 2013) and 4 Mya (Schenk et al., 2013), which suggests an early and potentially long association with this particular biome. Phenetically, *Irenomys* is quite divergent with respect to *Euneomys* and *Neotomys*. The general bauplan of this *Nothofagus* endemic shows some convergence with both oryzomyine and some thomasomyine representatives, in particular with those specialized for arboreal life (for example, cladistic analyses based solely on postcranial characters placed *Irenomys* in the same clade that the arboreal *Rhipidomys* and *Juliomys* [Carrizo and Catalano, in press]). *Irenomys* is a long-tailed form, a trenchant difference to the short-tailed *Euneomys* and *Neotomys*, although the 3 share thick, well-haired tails (Fig. 5). A contrasting pattern is also observed in the pes morphology, from the long, narrow and covered by protruding plantar pads in *Irenomys* to the powerful broad, densely squamated, and long clawed structure in the remainder Euneomyini. *Irenomys* is an arboreal specialist (Pearson, 1983; Formoso and Sánchez, 2014), although cursoriality is not uncommon in this rat, as the species is readily trapped on the ground (Pearson, 1983). The combined mechanical advantage provided by a long tail and feet covered with fleshy plantar pads to facilitate movements along *Nothofagus* branches appear to be unequivocal (Carrizo et al., 2013). Differences between *Irenomys* and the *Euneomys-Neotomys* pair are not restricted to external traits: the 3 Euneomyini share a well-developed caecum, but that of *Irenomys* has external taeniae and more complex, pouched structure, not the simple caecum of *Euneomys* and *Neotomys*. Cranially, *Irenomys* lacks the premaxillo-maxillary suture with an acutely angled bend that Olds and Anderson (1989:64) and Steppan (1995:91) identified as synapomorphic for the *Reithrodon* group.

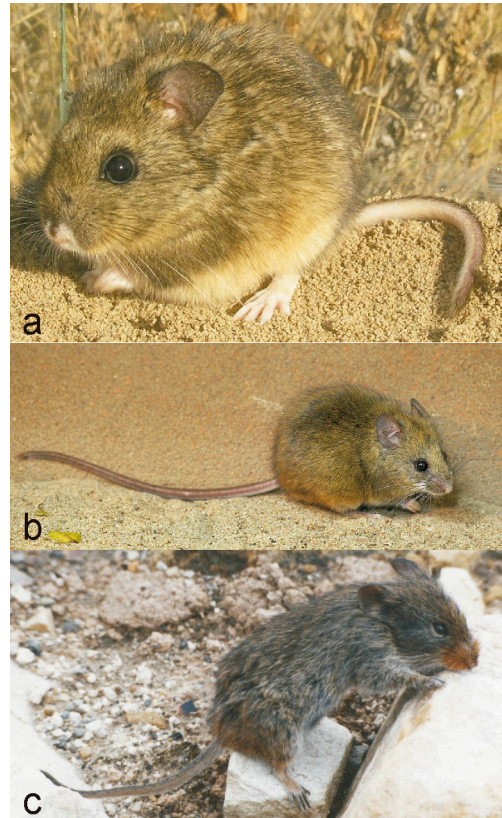


Fig. 5. External views of Euneomyini representatives, from top to bottom: *Euneomys chinchilloides* (photo UFJP), *Irenomys tarsalis* (photo D. Podestá), and *Neotomys ebriosus* (photo H. Zeballos).

There are a number of character states shared by these genera (Table 1); for example: *Irenomys* and *Euneomys* share narrow and high zygomatic plates, which almost completely lack an upper free border, and similar incisive foramina extending to M1 protocones. The “diamond” dental morphology (an example of “transverse lamination” according to Hershkovitz 1962:94) is unique to *Irenomys*, but a persistent posterofossette on M3 (Fig. 2) is one dental trait shared between *Irenomys* and *Euneomys*. An additional dental trait connecting these genera is a lingually displaced anteromedian flexid, notably evident in *Irenomys* and *Neotomys*, on the procingulum of the m1; these structures are typically associated with a persistent anteromedian fossetid in *Euneomys* (Fig. 2). Persistent interfrontal fontanelles

**Table 1**  
Morphological character variation among 3 Euneomyini genera.

Character	<i>Irenomys</i>	<i>Euneomys</i>	<i>Neotomys</i>
Tail length	>HBL	<HBL	<HBL
Palate topography	flat, uncomplicated	ridged, foraminated	ridged, foraminated
Premaxillo-maxillary suture	dorso-ventrally oriented	sharply angled	sharply angled
Spinous process on zygomatic plate	absent	absent	present
Interfrontal fontanelles	present	absent	present
Alisphenoid strut	present	present <sup>a</sup>	absent
Facial circulation	complete	complete	incomplete
Caecum	complex	single	single
Cornified stomach epithelium	extensive	extensive	reduced
2n (FN)	64 (98) <sup>b</sup>	34-36-42 (62 to 66) <sup>c</sup>	70 (68) <sup>d</sup>

<sup>a</sup> Contrary to the condition noted by Stepan (1995:40), we recorded the alisphenoid strut in *Euneomys* as present and bony.

<sup>b</sup> After Ojeda et al. (2004).

<sup>c</sup> After Ojeda et al. (2014).

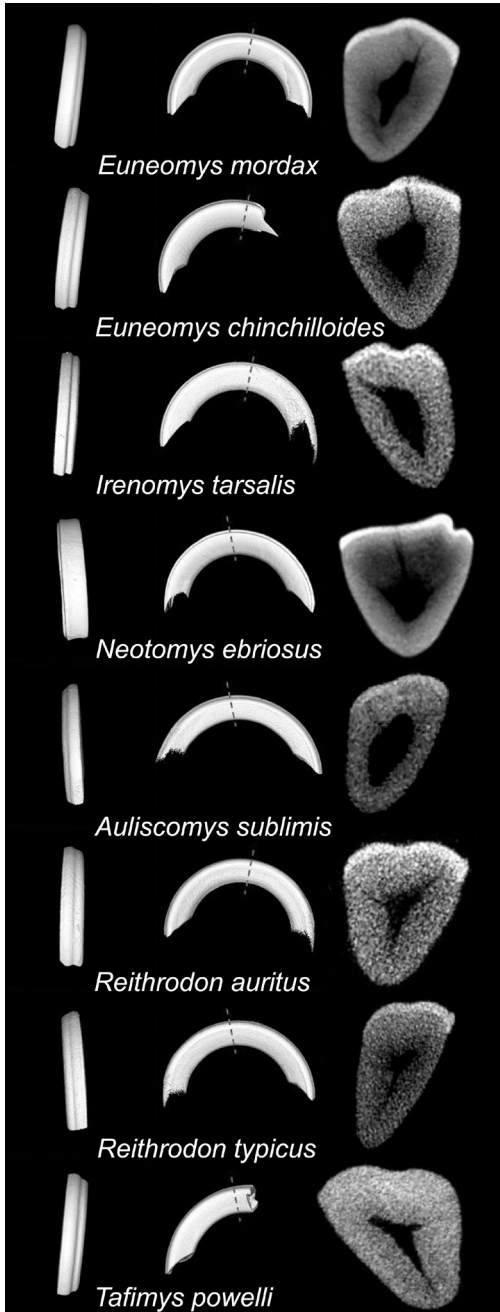
<sup>d</sup> After Pearson and Patton (1976).

have been noted for *Irenomys* and *Neotomys* (Gardner and Anderson, 2001), but not in *Euneomys*. The 3 Euneomyini also share a unilocular-hemiglandular stomach, but this is a widespread condition among sigmodontine rodents (Carleton, 1973). In *Neotomys*, the cornified portion of the stomach is mostly restricted to the fornix ventricularis while in *Irenomys* and *Euneomys* there is more equal distribution between glandular and cornified squamous epithelial portions of the stomach (cf. Carleton, 1973:fig. 3).

With the erection of the tribe Euneomyini, incisor grooves acquire a new significance in sigmodontine systematics. The interpretation of this easily diagnostic character was traditionally hampered by poorly resolved phylogenies. Micro-CT scans of upper incisors in *Euneomys*, *Irenomys* and *Neotomys* (see Ohazama et al., 2010:fig. 3) revealed that grooves are caused by folded enamel/dentine; the same is true for the remainder sigmodontine taxa examined, including living (e.g., *Reithrodon*, *Auliscomys sublimis*) and fossil (e.g., *Tafimys*) representatives (Fig. 6). Although incisor grooves are present in 1 or

a few genera in 3 other sigmodontine tribes (Sigmodontini, Reithrodontini, and Phyllostini), their presence characterizes all 3 members of the Euneomyini. Thus, the retention of this trait appears as a signature of the clade and invites further exploration of a potential adaptive role.

We are at a turning point on the study of the systematics of the Sigmodontinae, as more taxa are incorporated in molecular phylogenetic analyses, although it is also true that key taxa are only recently being included as the result of continuous field work (e.g., Pardiñas et al., 2014). We can expect, therefore, that additional studies will further resolve large parts of the tree, especially with respect to poorly known groups. Nonetheless, we predict that the resolution of the polytomy at the base of the Oryzomyalia will require sequences from many additional loci, perhaps hundreds. This is because gene tree discordance is the expected null when many short branches are combined with large ancestral population sizes (Edwards et al., 2007) such as those that very likely characterized the evolutionary history of the Sigmodontine radiation.



**Fig. 6.** Folding enamel/dentin in sigmodontine rodent incisors: 3-dimensional reconstructions (frontal and lateral views) and cross-section based on micro-CT scans.

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## APPENDIX I

Specimens examined, including dried specimens as well as fluid preserved animals, are housed in the following mammal collections: Colección de Mamíferos del Centro Nacional Patagónico (CNP; Puerto Madryn, Chubut, Argentina), Colección de Material de Egagrópilas y Afines “Elio Massoia” (CNP-E; Puerto Madryn, Chubut, Argentina); Colección Nacional de Mastozoología, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (MACN; Buenos Aires, Argentina), Museum of Vertebrate Zoology (MVZ; Berkeley, California, USA).

*Euneomys chinilloides* (n = 27). Argentina: Chubut, cercanías de Esquel (CNP 4), Cañadón de la Madera, Sierra de Tepuel (CNP 2388, 2422-2424), Altiplanicie del Somuncura, Laguna Blanca (CNP 2406-2421); Establecimiento La Maroma (CNP 4420, 4429, 4621); Santa Cruz, nacimiento río Ecker (CNP 3674), estancia La Ensenada (CNP 2427, 3641).

*Euneomys mordax* (n = 2). Argentina: Neuquén, 1.5 km S Copahue (town) (MVZ 183288, 183289).

*Irenomys tarsalis* (n = 7). Argentina: Depto. Huiliches, Arroyo de las Tierras Coloradas, 1 km E and 2.4 km S Cerro del Chivo (MVZ 163459); Neuquén, Depto. Los Lagos, 3 km NW Confluencia (MVZ 159421), Pilolil (CNP 730) Loma Redonda, Ruca Hué, San Martín de los Andes (CNP 3642); Chubut, lago La Plata (CNP 731); Río Negro, Alto Río Villegas (CNP 778). Chile: Los Lagos, Osorno, Valle de La Picada, 715 m (UACH 2179).

*Neotomys ebriosus* (n = 35). Argentina: Salta, San Antonio de los Cobres (CNP 3639, 3640); San Juan, San Guillermo (30 uncatalogued from owl pellets). Perú, Puno, 13 mi ENE Crucero, Abra Aricoma (MVZ 139590); Arequipa, 2 km W Sumbay (MVZ 174043).

## APPENDIX II

Taxon sampling and access codes for 4 nuclear (BRAC1, GHR, IRBP and RAG1) and 1 mitochondrial (Cytb) markers used in the phylogenetic analyses conducted in this paper.

	BRAC1	GHR	IRBP	RAG1	Cytb
<i>Abrawayomys ruschii</i>			JX949185		JX949189
<i>Abrothrix longipilis</i>	KC953152	KC953233	KC953347	KC953469	U03530
<i>Aegialomys xantheolus</i>		KC953234	KC953349	KC953470	AY163628
<i>Akodon boliviensis</i>		KC953236	KC953351	AY294960	AKOMTCYTBA
<i>Amphinectomys savamis</i>			AY163579		EU579480
<i>Andalgalomys pearsoni</i>	KC953155	KC953241	KC953355	AY963176	JQ434418
<i>Andinomys edax</i>	KC95315	KC953242	KC953356	AY294964	JQ434419
<i>Arvicola terrestris</i>		AM392380	AY277407		AY275106
<i>Auliscomys sublimis</i>	KC953159	KC953244	KC953359	AY294965	JQ434421
<i>Baiomys musculus</i>		KC953245	KC953360	KC953479	EF989933
<i>Bibimys labiosus</i>			AY277436		DQ444329
<i>Blarinomys breviceps</i>			AY277437		AY275112
<i>Brucepattersonius igniventris</i>	KC953162	KC953247	AY277438	KC953482	AY277486 <sup>a</sup>
<i>Calassomys apicalis</i>			JQ434417		JQ434425
<i>Calomys callosus</i>	KC953163	KC953248	AY277440	KC953483	DQ447282
<i>Cerradomys subflavus</i>		KC953251	AY163626	KC953486	AF181274
<i>Chelemys macronyx</i>		KC953252	AY277441		U03533
<i>Chinchillula sahamae</i>			KC953364	KC953487	JQ434422
<i>Clethrionomys gapperi</i>	AY295010A	F540623	AY326080	AY294952	AY309431
<i>Cricetulus migratorius</i>		AY294926	KC953367	AY294956	AY288508
<i>Cricetus cricetus</i>	KC953168	KC953253	AY277410	KC953488	AJ490302
<i>Delomys dorsalis</i>		KC953255	KC953369	KC953491	KF317031
<i>Deltamys kempii</i>			AY277444		AY195862
<i>Drymoreomys albimaculatus</i>			EU649042		EU579487
<i>Eligmodontia typus</i>			AY277445		AF108692
<i>Euneomys chinchilloides</i>	KC953172	KC953259	AY277446	KC953498	AY275115
<i>Euryoryzomys macconnelli</i>			AY163620		GU126538
<i>Galenomys garleppi</i>			JQ434410		JQ434423
<i>Geoxus valdivianus</i>			AY277448		AY275116
<i>Graomys griseoflavus</i>			AY277449		AY275117
<i>Handleyomys intectus</i>			AY163584		EU579490
<i>Holochilus brasiliensis</i>			AY163585		GU126517
<i>Hylaeamys megacephalus</i>			AY163621		AY275124
<i>Irenomys tarsalis</i>	KC953182	KC953268	AY277450	AY294962	ITU03534

(Appendix II cont.)

	BRAC1	GHR	IRBP	RAG1	Cytb
<i>Isthmomyx pirrensis</i>		EF989747	EF989847		DQ836298
<i>Juliomyx pictipes</i>	KC953183	KC953269	KC953385	KC953510	AF108688
<i>Juscelinomys huanchacae</i>			AY277452		AY275119
<i>Kunsia tomentosus</i>			KC953386	KC953511	AY275121
<i>Lenoxus apicalis</i>	KC953185	KC953270	KC953388	KC953512	U03541
<i>Loxodontomys micropus</i>		KC953273	AY277457	AY963183	AY275122
<i>Melanomys caliginosus</i>	KC953191	KC953275	KC953397	KC953521	EU340020
<i>Mesocricetus auratus</i>	AY295013	AF540632	AY163591	AY294955	AM904612
<i>Microrhynchomys minutus</i>		KC953276	AY163592	KC953522	AF108698
<i>Microtus californicus</i>		KC953277	KC953401	KC953523	EF506105
<i>Myospalax palax</i>	KC953192	KC953281	AY326097	KC953525	AF326272
<i>Neacomys spinosus</i>		KC953284	KC953406	KC953528	AF108701
<i>Necomys amoenus</i>	KC953193	KC953285	AY277458	KC953529	AY273911
<i>Nectomys squamipes</i>	KC953194	KC953287	EU273419	KC953531	GU126522
<i>Neomicroxus latebricola</i>			KF437367		KF437365
<i>Neotoma floridana</i>	KC953195	N/A <sup>b</sup>	KC953411	AY294959	AF294344
<i>Neotomys ebriosus</i>		KC953290	KC953413	KC953536	JQ434424
<i>Nephelomys keaysi</i>		KC953291	KC953414	KC953537	EU579505 <sup>c</sup>
<i>Nesomys rufus</i>	KC953197	KC953292	AY326099	KC953539	AF160592
<i>Nesoryzomys narboroughi</i>			AY163600		GU126523
<i>Notiomys edwardsii</i>	KC953200	KC953294	KC953420	KC953542	U03537
<i>Nyctomys sumichrasti</i>	KC953201	KC953296	KC953421		AY195801
<i>Oecomys concolor</i>	KC953203	KC953299	KC953424	KC953545	JF693876
<i>Oligoryzomys fulvescens</i>	KC953204	KC953301	AY163611	KC953547	GU126529
<i>Onychomys leucogaster</i>		KC953303	EF989860	KC953550	EF989959
<i>Oreoryzomys balneator</i>			AY163617		GU126535
<i>Oryzomys palustris</i>	KC953205	KC953304	AY163623	KC953551	GU126539
<i>Ototylomys phyllotis</i>	AY295018	AY294932	KC953429	KC953553	AY009789
<i>Oxymycterus nasutus</i>	KC953206	KC953307	KC953431	KC953555	AF175286
<i>Pearsonomys annectens</i>			AY851749		AF108672
<i>Peromyscus leucopus</i>	AY295014	AY294927	EF989880	AY294957	EF989979
<i>Phaenomys ferruginosus</i>			KM065877		KM065876
<i>Phodopus sungorus</i>	AY295012	AF540640	KC953439	AY294954	AJ973390
<i>Phyllotis xanthopygus</i>	KC953208	KC953314	AY163632	KC953561	U86833
<i>Pseudoryzomys simplex</i>		KC953317	AY163633	KC953564	GU126547
<i>Punomys kofordi</i>	KC953209	KC953318	KC953445	KC953565	JQ434426
<i>Reithrodon auritus</i>	KC953212	AY294930	AY277472	AY294963	EU579474



(Appendix II cont.)

	<b>BRAC1</b>	<b>GHR</b>	<b>IRBP</b>	<b>RAG1</b>	<b>Cytb</b>
<i>Reithrodontomys fulvescens</i>	AY295015	AY294928	EF989904	AY294958	EF990003
<i>Rhagomys longilingua</i>			DQ003723		AY206770 <sup>d</sup>
<i>Rheomys thomasi</i>		KC960491	KC953451		KJ921706 <sup>e</sup>
<i>Rhipidomys macconnelli</i>	KC953213	KC953324	AY277474	KC953573	AY275130
<i>Salinomys delicatus</i>			JQ434415		EU377608
<i>Scapteromys tumidus</i>		KC953326	AY277477	KC953576	AY275133
<i>Scolomys juruaensis</i>		KC953327	KC953454	KC953577	AF108696
<i>Scotinomys teguina</i>	KC953216	KC953328	AY277415	KC953578	AF108705
<i>Sigmodon hispidus</i>	AY295016	AF540641	AY277479	AY241465	AF425227
<i>Sigmodontomys alfari</i>	KC953219	KC953332	AY163641	KC953582	EU074635
<i>Sooretamys angouya</i>		KC953333	KC953456	KC953583	GU126534
<i>Tapecomys wolffsohni</i>	KC953223	KC953336	KC953460	AY963184	U86835
<i>Thalpomys cerradensis</i>			AY277480		AY273916
<i>Thaptomys nigrita</i>	KC953225	KC953337	AY277482	KC953588	AF108666
<i>Thomasomys aureus</i>	KC953226	KC953338	KC953462	KC953589	U03540
<i>Transandinomys talamancae</i>	KC953228	KC953341	KC953465	KC953592	GU126544
<i>Tylomys nudicaudus</i>	AY295019	AY294933	AY163643	KC953593	DQ179812
<i>Wiedomys pyrrhorhinos</i>		KC953342	AY277485	KC953595	EU579477
<i>Zygodontomys brevicauda</i>	KC953230	KC953344	AY163645	KC953596	GU126549

<sup>a</sup> Cytb from *Brucepattersonius soricinus*;

<sup>b</sup> There is no access code for this marker but the sequence was obtained from Schenk et al. 2013 supplementary material deposited with Dryad (<http://datadryad.org,doi:10.5061/dryad.dc34q>). The access code (AY294959) entered in the appendix 1 of Schenk et al. corresponds to the recombination activating gene 1 (RAG1) for the same species;

<sup>c</sup> Cytb from *Nephelomys albigularis*;

<sup>d</sup> Cytb from *Rhagomys rufescens*;

<sup>e</sup> Cytb from *Rheomys raptor*.