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A phylogenetic appraisal of Sigmodontinae (Rodentia, Cricetidae) with emphasis on phyllotine genera: systematics and biogeography

Jorge Salazar-Bravo, Ulyses F. J. Pardiñas & Guillermo D'Elía

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Here, we present a comprehensive phylogenetic analysis based on nuclear and mitochondrial DNA sequences of rodents of the subfamily Sigmodontinae. The emphasis is placed on the large tribe Phyllotini; sampling includes for the first time in any molecular-based phylogenetic analysis representatives of several genera traditionally considered to be phyllotines. Given the broad taxonomic sampling, results provide substantial improvements in our knowledge on both the structure of the sigmodontine radiation and of phyllotine phylogenetic relationships. For instance, the tribe Ichthyomyini was not recovered monophyletic. Similarly, in a novel hypothesis on the contents of the tribe Phyllotini, it is shown that unlike *Galenomys*, the genera *Chinchillula*, *Neotomys* and *Punomys* are not phyllotines. The later genera together with *Andinomys*, *Euneomys*, *Irenomys* and *Juliomys* form part of novel generic clades of mostly Andean sigmodontine rodents. More in general, results strongly suggest the occurrence of several instances of putative morphological convergence among distinct sigmodontine lineages (e.g. among now considered to be ichthyomyines; between Phyllotini and some Andean taxa; among *Euneomys-Neotomys* and *Reithrodon*). Finally, we suggest that the historical biogeography of the sigmodontine rodents is far more complex than earlier envisioned.

Corresponding author: *Guillermo D'Elía, Instituto de Ciencias Ambientales y Evolutivas, Universidad Austral de Chile, Valdivia, Chile. E-mail guille.delia@gmail.com*
Jorge Salazar-Bravo, Department of Biological Sciences, Texas Tech University, Lubbock, TX 79409, USA. E-mail: j.salazar-bravo@ttu.edu
Ulyses F. J. Pardiñas, Unidad de Investigación Diversidad, Sistemática y Evolución, Centro Nacional Patagónico, Puerto Madryn, Argentina. E-mail: ulyses@cenpat.edu.ar
Guillermo D'Elía, Instituto de Ciencias Ambientales y Evolutivas, Universidad Austral de Chile, Valdivia, Chile. E-mail: guille.delia@gmail.com

Introduction

Rodents of the subfamily Sigmodontinae (Myomorpha: Cricetidae) compose one of the most diverse and widely distributed group of mammals of the Western Hemisphere (ca. 400 living species in some 85 genera). The monophyly of the subfamily Sigmodontinae is strongly supported by the analysis of molecular data (Sarich 1985; Catzeflis *et al.* 1992, 1993; Dickerman 1992; Engel *et al.* 1998; Steppan *et al.* 2004), although the few attempts at diagnosing it based on morphological characters have been hindered by the impressive morphological heterogeneity of the group (but see Pacheco 2003).

Traditionally, sigmodontine genera have been united in groups, most of which are properly recognized at the tribal level (D'Elía *et al.* 2007); one of the largest components of the Sigmodontinae is the tribe Phyllotini (sensu Steppan 1995), with about 50 living species grouped into 12 genera. Phyllotines are ubiquitous in pastoral habitats of the Andes, from central Ecuador to the northern margin of the Strait of Magellan and from the Pacific coast of Peru and Chile

east through Patagonia to southeastern Brazil and to northwestern Venezuela, Curaçao and Trinidad and Tobago. They reach their maximum species diversity in the Puna habitats (Reig 1986). Species boundaries, relationships among species and the content of the tribe have been studied by several authors (Pearson 1958; Hershkovitz 1962; Pearson & Patton 1976; Olds & Anderson 1989; Braun 1993; Steppan 1993, 1995), yet over 50 years of systematic work has not converged on a fully established taxonomy and classification for the tribe. In fact, three major issues still remain to be resolved: (i) the content of the tribe, (ii) the relationships among species members and (iii) the relationship of the phyllotines to other sigmodontine rodents.

Although various authors had commented on its contents, Olds & Anderson (1989) were the first authors to provide a formal diagnosis for the Phyllotini where they included the following 14 genera: *Andalgalomys*, *Andinomys*, *Auliscomys*, *Calomys*, *Chinchillula*, *Eligmodontia*, *Euneomys*, *Galenomys*, *Graomys*, *Irenomys*, *Neotomys*, *Phyllotis*, *Punomys* and *Reithrodon*. In addition, these authors suggested a '*Reithrodon*-group' composed of *Euneomys*, *Neotomys* and *Reithrodon*, which was later enlarged with the description of several extinct genera (Steppan & Pardiñas 1998; Ortiz *et al.* 2000). Adding to the diversity of the tribe, two new genera of living phyllotines were described in the last two decades, *Salinomys* (Braun & Mares 1995) and *Tapecomys* (Anderson & Yates 2000). Also, some important contributions to our understanding of the composition of the Phyllotini include the finding that *Andinomys*, *Euneomys*, *Irenomys*, *Neotomys* and *Reithrodon* do not belong to the tribe (Engel *et al.* 1998; Smith & Patton 1999; D'Elía 2003; Martínez *et al.* 2012) and that the '*Reithrodon*-group' is polyphyletic (D'Elía 2003). Finally, the analysis of morphological characters allowed removing *Punomys* from the content of the tribe (Steppan 1993, 1995). Given these results, in the last formal classification of Sigmodontinae (D'Elía *et al.* 2007), the tribe Phyllotini is thought to include only 10 living genera; while, among others, *Andinomys*, *Chinchillula*, *Euneomys*, *Irenomys*, *Neotomys* and *Punomys* are considered as Sigmodontinae *incertae sedis*.

Understanding the evolution of the Phyllotini is important in the context of South American landscapes and fauna: for one, the large majority of members of the Phyllotini are central Andean in distribution, and thus, a robust phylogeny may shed light on the complex and still poorly understood biogeographic history of this region. In addition, the Phyllotini has the distinction of including some of the oldest cricetid fossils in the continent with elements dated to the Lower Pliocene of Argentina (Pardiñas & Tonni 1998; Prevosti & Pardiñas 2009); therefore, developing strong hypotheses of relationships is important to understand the timeframe of the radiation. Thus, the objectives of this work are threefold. First, we test with molecular data the composition and structure of the tribe Phyllotini including for the first time several taxa for which no nuclear data were available previously or for which no molecular data existed. In addition, we include several endemic taxa to the high Andes (*Chinchillula* and *Punomys*), currently considered as *incertae sedis* but that earlier were considered as phyllotines, as well as an undescribed genus from southeastern Brazil to provide a more inclusive view to the structure of the Sigmodontinae. Finally, we provide a nuclear DNA-based phylogenetic hypothesis for the genus *Calomys*, one of the most diverse of the Phyllotini.

Methods

Taxonomic sampling

We analysed two data sets, one including 86 taxa (82 belonging to the ingroup), each represented by DNA sequences of the interphotoreceptor retinoid-binding protein (IRBP) nuclear gene and another covering 72 taxa (68 belonging to the ingroup), each represented by mitochondrial (cytochrome *b* gene sequences) and nuclear (IRBP) data. For the later matrix, mitochondrial and nuclear sequences were obtained from the same specimen, in most cases. In both data sets, the outgroup was formed by representatives of the remainder subfamilies of the Cricetidae: Arvicolinae (*Arvicola terrestris*), Cricetinae (*Cricetus cricetus*), Neotominae (*Neotoma albigula*) and Tylomyinae (*Tylomys nudicaudatus*). Differences in taxonomic sampling among data sets referred to the ingroup; none of the 12 missing taxa from the second data set belonged to the Phyllotini (see supporting information). Our sampling includes representatives of all sigmodontine tribes; additionally, and for the first time in any molecular phylogeny, we include data for the genera *Chinchillula*, *Galenomys*, *Punomys* and Phyllotini n. gen. and nuclear data for the genus *Andinomys*.

DNA extraction, PCR amplification and Sequencing

Sequences gathered in this study were obtained from specimens (see supporting information) housed at the following collections: American Museum of Natural History, New York, USA (AMNH), Field Museum of Natural History, Chicago, USA (FMNH), Museo de Historia Nacional de la Universidad de San Marcos, Lima, Peru (VPT), Museo de la Estación Biológica de Rancho Grande, El Limón, Venezuela (AMV), Museu de Ciências Naturais da Pontifícia Universidade Católica de Minas Gerais, Belo Horizonte, Brazil (DG), Museum of Southwestern Biology, University of New Mexico, Albuquerque, USA (MSB and RE), Museum of Texas Tech University, Lubbock, USA (TTU), and Sam Noble Oklahoma Museum of Natural History, Norman, USA (OMNH). Total genomic DNA was extracted from either frozen or alcohol-preserved tissues with standard methods

(e.g. Salazar-Bravo *et al.* 2001). Double-stranded symmetrical amplification of the loci of interest was accomplished following the methods of Anderson & Yates (2000) for cytochrome *b* and D'Elía (2003) for the IRBP.

Prior to sequencing, amplified products were cleaned using the QIAquick PCR Purification Kit protocol (QIAGEN, Inc., Valencia, CA, USA) or ExoSAP-IT (USB Corporation, Cleveland, OH, USA), with methods recommended by the manufacturers and visualized on 1% agarose gels. Amplicons were cycle-sequenced with the amplification primers and Big Dye® Terminator v3.1 chemistry (Applied Biosystems, Inc., Foster City, CA, USA) at either Macrogen USA Corp. (Rockville, MD, USA) or at the Center for Biotechnology and Genomics of Texas Tech University (Lubbock, TX). In all cases, both heavy and light DNA strands were sequenced and compared. Sequences were visualized, reconciled and translated to proteins to proof for stop codons using SeqMan (DNASTAR 2003). All sequences were deposited in GenBank (accession numbers JQ434398-JQ434426).

Phylogenetic analyses

As we used protein-coding genes, alignment was non-problematic and was done with Opal (Wheeler & Kececioglu 2007) in Mesquite v2.74 (Maddison & Maddison 2010) using the default values for all alignment parameters.

For the first analysis (only IRBP sequences), aligned sequences were subjected to maximum-parsimony (MP; Farris 1982), likelihood (ML; Felsenstein 1981) and Bayesian (BA; Rannala & Yang 1996) analyses. In the MP analysis, characters were treated as unordered and equally weighted. PAUP* (Swofford 2002) was used to perform 5000 replicates of heuristic searches with 10 random addition of sequences each, tree bisection-reconnection branch swapping and a time limit of 5 s per addition-sequence replicate. One thousand bootstrap (BP) replications with 3 addition-sequence replicate each and MAXTREE set to 3000 were performed using PAUP*. ML analysis was conducted in Treefinder (Jobb *et al.* 2004; Jobb 2008). The best-fitting model of nucleotide substitution per codon position (1st J3(Optimum,Empirical):G(Optimum):5; 2nd TN[Optimum,Empirical):G[Optimum):5; 3rd TVM(Optimum,Empirical):G(Optimum):5; see Jobb 2008) was selected with the Akaike information criterion in Treefinder using the 'propose model' routine. We estimated the best tree under the model of nucleotide substitution previously selected using the search algorithm 2 as implemented in Treefinder version March 2011; nodal support was estimated with 1000 Bootstrap pseudoreplicates (BL). Bayesian analysis was conducted in MrBayes 3.1.2 (Ronquist & Huelsenbeck 2003) by means of two independent runs with three heated and one cold Markov chains each. The best-fitting model of sequence evolution was selected using MrModeltest2 (Nylander 2004) and the Akaike Information Criterion (AIC). A model with equal base frequencies, six categories of base substitution, a proportion of invariant sites and a gamma-distributed rate parameter (SYM + I + G) was specified with all model parameters estimated in MrBayes; data were partitioned attending to codon position. Runs were allowed to proceed for 10 million generations, and trees were sampled every 1000 generations. Log-likelihood values were plotted against generation time to check that the runs converged on a stable log-likelihood value. The first 25% of the sampled trees were discarded as burn-in; the remaining trees were used to compute a 50% majority rule consensus tree and obtain posterior probability (PP) estimates for each clade.

For the second matrix (smaller data set, but including IRBP and cytochrome *b*), we concatenated data partitions using SequenceMatrix (Meier *et al.* 2011) and analysed it with model-based methods. ML analysis was conducted in Treefinder with the same protocol used for the IRBP solo matrix specifying for the cyt *b* partition the following models also selected in Treefinder: 1st GTR(Optimum, Empirical):G(Optimum):5, 2nd TVM(Optimum,Empirical): G(Optimum):5, 3rd TVM(Optimum,Empirical):GI(Optimum):5; see Jobb 2008). Similarly, Bayesian analysis was conducted in MrBayes 3.1.2 with the same search strategy used for the IBRP solo matrix using the best-fitting models selected using MrModeltest2: GTR + I + G and SYM + I + G for the cytochrome *b* and IRBP gene, respectively.

Results

Analyses of the IRBP data set

Phylogenetic analyses of this data set using parsimony (27 446 trees of 1235 steps, consistency index = 0.543 and Retention index = 0.652), likelihood (lnL = −8724.4407), and Bayesian inference produced three topologies with several areas of congruence (Figs 1 and 2). For example, analyses recovered a monophyletic Sigmodontinae (BP = 100; BL = 100; PP = 1), showed the lack of monophyly of Ichthyomyini, and a monophyletic Oryzomyalia (BP = 55; BL = 61; PP = 0.99). In general, there was agreement on the major grouping within the latter: the clade corresponding to Oryzomyini (BP = 90; BL = 91; PP = 1); a clade (BP = 77; BL = 82; PP = 1) formed by Phyllotini (BP = 88; BL = 84; PP = 1) and *Delomys*; the clade of Abrotrichini (BP = 98; BL = 100; PP = 1); Wiedomyini; the clade of the tribe Akodontini (BP = 84; BL = 88; PP = 1); that of Thomasomyini (BP < 50; BL = 57; PP = 1); a clade (BP = 50; BL < 50; PP = 0.76) formed by

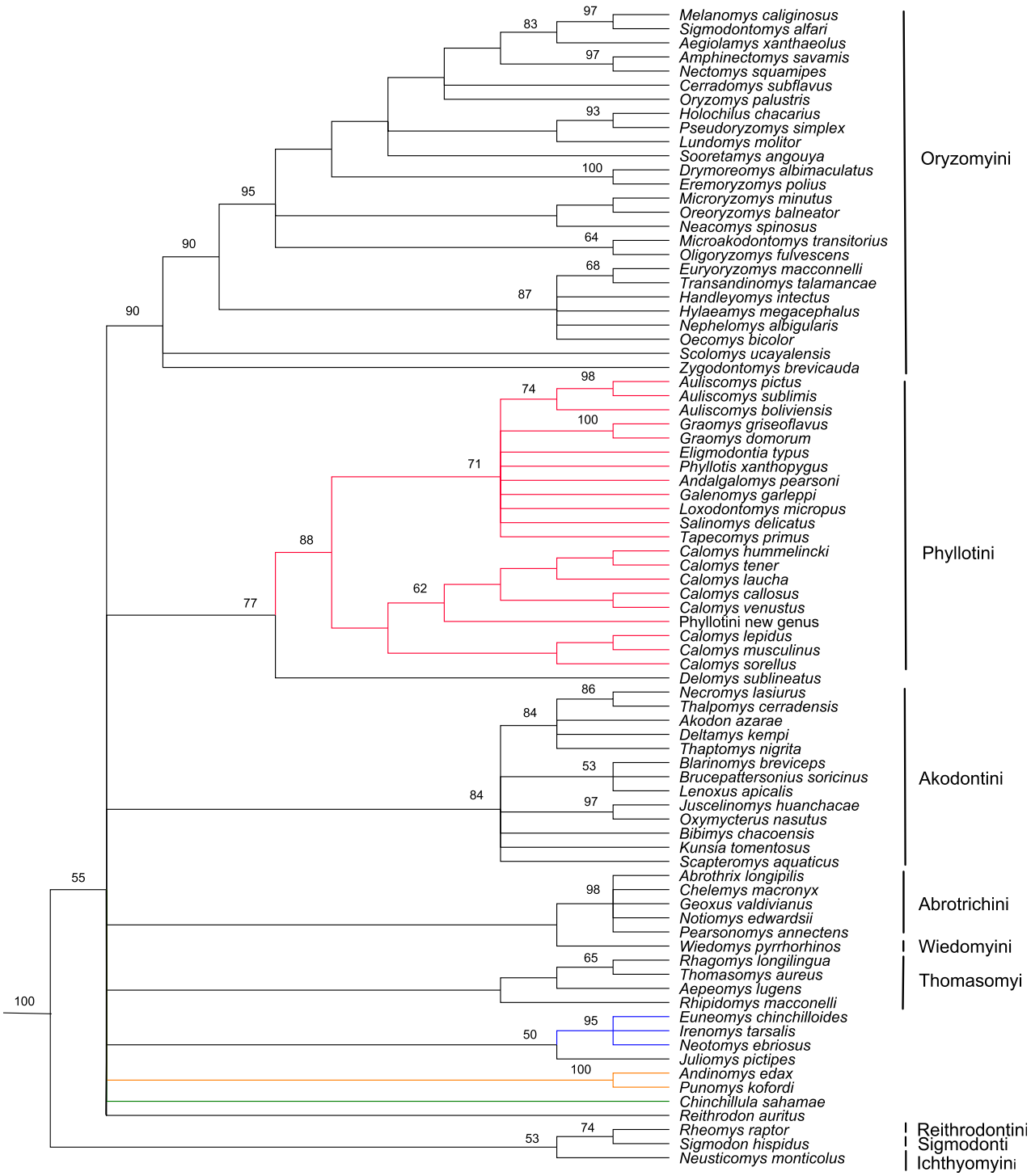

Fig. 1 Strict consensus tree obtained in the maximum-parsimony analysis of IRBP gene sequences of sigmodontine rodents. The topology is the strict consensus of 27 446 shortest trees of 1235 steps, consistency index = 0.543 and Retention index = 0.652. Numbers indicate Bootstrap support values of the adjacent nodes. Only Bootstrap values above 50% are shown.

Juliomys and a strongly supported clade (BP = 95; BL = 97; PP = 1) formed by the hypsodont and incisor-grooved taxa *Euneomys*, *Neotomys* and *Irenomys*; another clade composed of the mostly high Andean Puna *Andinomys* and *Punomys* (BP = 100; BL = 100; PP = 1); and finally *Chinchillula* that in the MP analysis falls to a polytomy at the base of

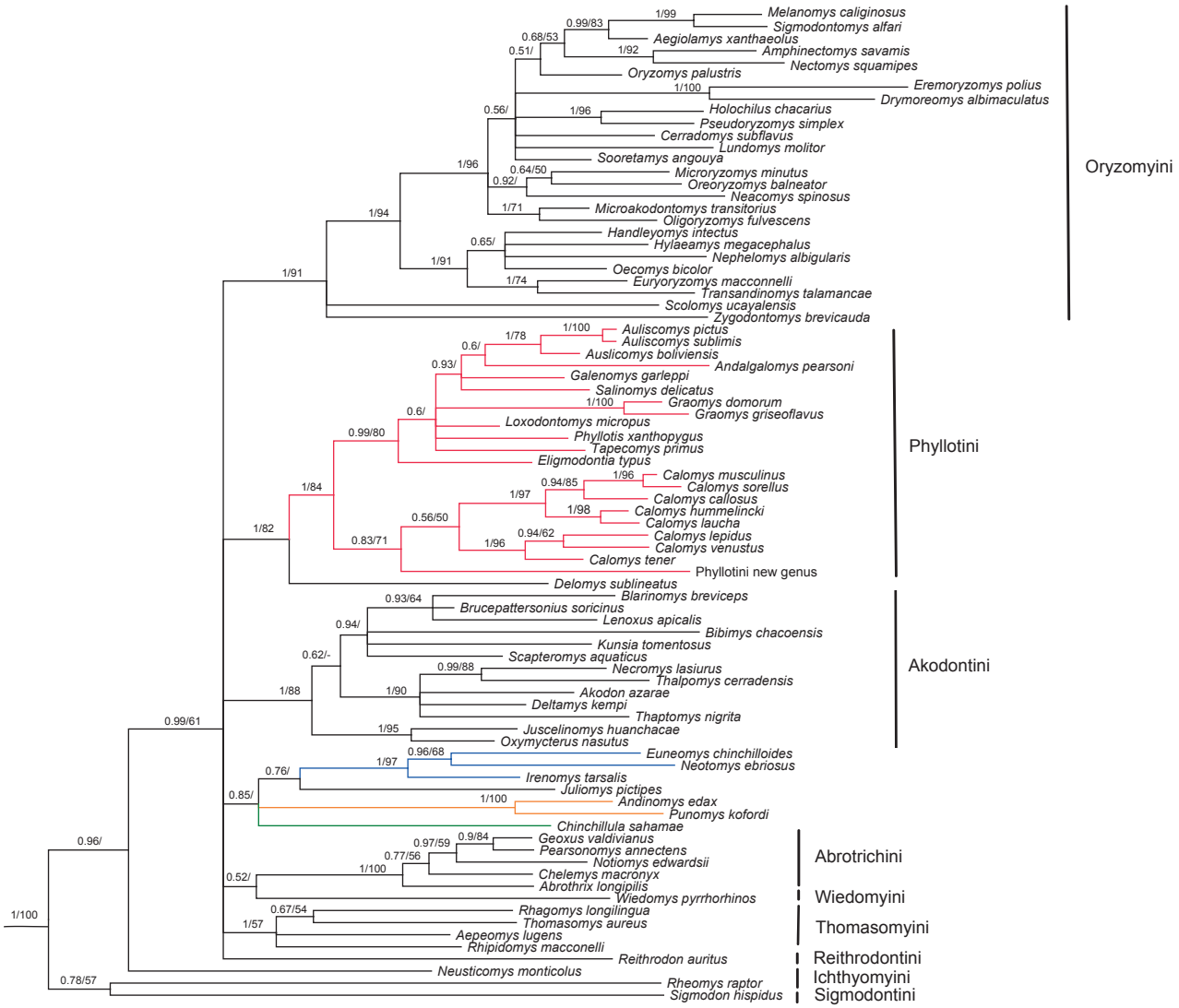

Fig. 2 Majority rule consensus obtained in the Bayesian analysis of IRBP gene sequences of sigmodontine rodents. Numbers indicate posterior probability (left to the diagonal) and maximum-likelihood Bootstrap (right to the diagonal) values of the adjacent nodes. Only Bootstrap values above 50% are shown. An '-' indicates that the signalled node was not recovered in the most likely tree (ln = −8724.4407)

Oryzomyalia and in the ML and Bayesian analyses forms part of a weakly supported clade (BL < 50; PP = 0.85) together with the clade formed by *Euneomys*, *Neotomys*, *Irenomys* and *Juliomys* and the clade formed by *Andinomys* and *Punomys*.

In addition, differences between the topologies recovered in these analyses are noteworthy: in the ML and Bayesian analyses, *Neusticomys* is sister (BL > 50; PP = 0.96) to Oryzomyalia, whereas in the MP is sister in a weakly supported relationship (BP = 53) to a clade (BP = 74) formed by *Rheomys* and *Sigmodon*. Other differences are found in the structure of the tribe Phyllotini; for example, in the MP analysis Phyllotini n. gen. is embedded within *Calomys* (BP < 50), whereas in the ML and Bayesian analyses, it is resolved as the sister group (BL = 71; PP=0.93) to *Calomys* (BL = 50; PP = 0.56). Similarly, relationships among phyllotine genera are less resolved in the MP tree than in the ML and BA topologies.

Analysis of the concatenated data set

The results of the concatenated analysis were, for the most part, congruent with those of the previous analyses (Fig. 3). Sigmodontinae appears strongly supported (BL = 100; PP = 1); the dichotomy at its base leads in one hand to a clade formed by *Sigmodon* and in the other to the large clade of Oryzomyalia (BL < 50; PP = 1).

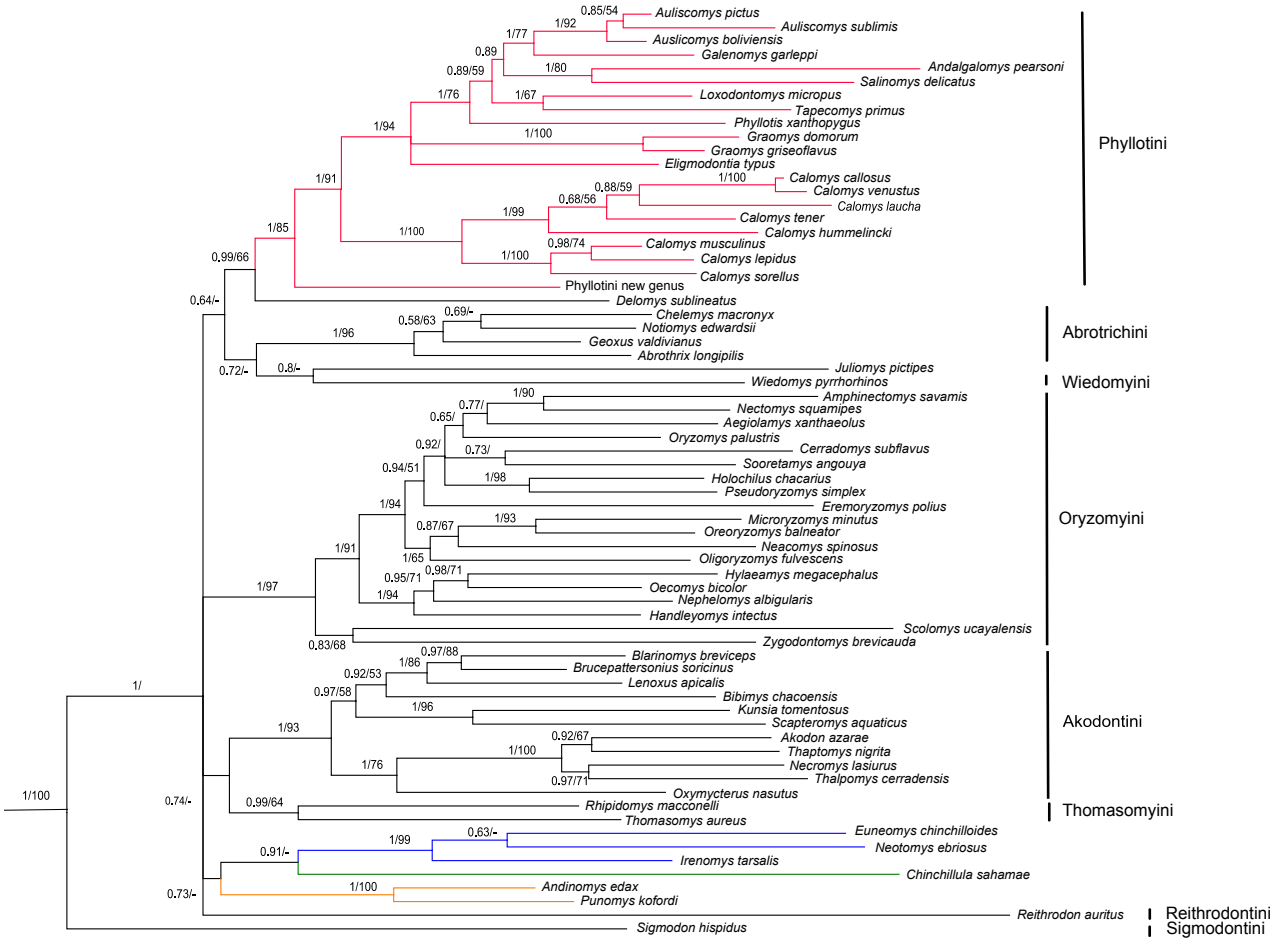

Fig. 3 Majority rule consensus obtained in the Bayesian analysis of the combined matrix of cytochrome *b* and IRBP gene sequences of sigmodontine rodents. Numbers indicate posterior probability (left to the diagonal) and maximum-likelihood bootstrap (right to the diagonal) values of the adjacent nodes. Only Bootstrap values above 50% are shown. An '-' indicates that the signalled node was not recovered in the most likely tree (ln = −36 245.076)

Within the latter, most of the main groups seen in the IRBP solo analyses are also recovered: Abrotrichini (BL = 96; PP = 1); the clade (BL = 66; PP = 0.99) formed by Phyllotini (BL = 85; PP = 1) and *Delomys*; Oryzomyini (BL = 97; PP = 1); Akodontini (BL = 93; PP = 1); the clade (BL=100; PP=1) formed by *Punomys* and *Andinomys*; and the clade (BL = 99; PP = 1) formed by *Euneomys*, *Neotomys* and *Irenomys*. In addition, *Calomys* is recovered monophyletic (BL = 100; PP = 1), and Phyllotini n. gen. is recovered as sister to the remaining Phyllotini (BL = 91; PP = 1). A difference between the combined and IRBP solo topologies is that in the former *Juliomys* does not appears related to the clade *Irenomys*, *Neotomys* and *Euneomys* but to *Wiedomys* in the Bayesian analysis (PP = 0.8) or as sister to *Chinchillula* in the ML analysis (BL < 50); as such in the combined analyses Abrotrichini does not appear sister to *Wiedomys*.

Discussion

This study includes for the first time sequence data for four sigmodontine genera (i.e. *Chinchillula*, *Galenomys*, *Punomys*, Phyllotini n. gen.) and nuclear data for the majority of the phyllotine genera. In consequence, several aspects of the results of this study represent novel hypotheses of relationships and corroborate hypotheses presented in other studies. Below, we discuss our results in the light of the main objectives of our analyses.

The general structure of the radiation of the Sigmodontinae

Our analyses support, for the most part, previous claims about the overall phylogenetic structure of the sigmodontine, with some important differences. In particular, like Weksler (2003) and Steppan *et al.* (2004), our analyses suggest that the basal cladogenetic split within Sigmodontinae

separated the ancestor of *Sigmodon* and *Rheomys*, in one branch, from the ancestor of the rest of the sigmodontines in the other. Given that *Sigmodon* and *Rheomys*, respectively, belong to the tribes Sigmodontini and Ichthyomyini, it was then derived that these two tribes were sister to each other and together sister to Oryzomyalia (e.g. D'Elía *et al.* 2006a). However, the inclusion of a second representative of the tribe Ichthyomyini, *Neusticomys*, in the IRBP-based analyses performed here, portrays this tribe as non-monophyletic because *Neusticomys* and *Rheomys* are not sister to each other (see also Martínez *et al.* 2012). The nature of the non-monophyly of Ichthyomyini varies depending on the phylogenetic method, but is always found. The ML and Bayesian analyses recover (BL < 50; PP = 0.96) *Neusticomys* sister to Oryzomyalia, while the MP analysis places *Neusticomys* sister (BP = 53) to the clade formed by *Rheomys* and *Sigmodon* (BP = 74; BL = 57; PP = 0.78).

The Ichthyomyini was the first tribe of sigmodontine rodents to receive a modern and thorough systematic revision (Voss 1988). The monophyly of the tribe is supported by a number of morphological characters (e.g. the disposition of the mystacial vibrissae, well-developed masseteric tubercles, the contents of the infraorbital foramen and the attachment of the nuchal ligament to the third thoracic vertebra), which were considered uniquely derived among the Sigmodontinae. Our results intimate that depending on the topology considered, it is equally parsimonious to suggest that these features would have independently evolved more than once (i.e. in the lines leading to *Neusticomys* and *Rheomys* either in the Bayesian or MP analyses) or that while appearing in a single line (i.e. the last common ancestor or the clade (*Neusticomys* (*Rheomys*, *Sigmodon*)) in the MP analysis) would have been lost in the line leading to *Sigmodon*. We summit that these alternatives and the polyphyly of Ichthyomyini must be tested with further data, especially with a broader ichthyomyine sampling (i.e. *Anotomys*, *Chibchanomys*, *Ichthyomys*) and the analyses of additional loci.

Like in other published studies (Weksler 2003, 2006; D'Elia *et al.* 2006a), we also recovered a strongly supported monophyletic Oryzomyalia (*sensu* Steppan *et al.* 2004), formed by 11 main lineages: seven corresponding to named tribes (Abrotrichini, Akodontini, Oryzomyini, Phyllotini *s.s.*, Reithrodontini, Thomasomyini and Wiedomyini), one leading to a clade formed by the Andean genera *Andinomys* and *Punomys*, another corresponding to a clade composed by the genera *Juliomys*, *Irenomys*, *Euneomys* and *Neotomys*, and the last two corresponding to the genera *Chinchillula* and *Delomys*. Relationships among these 11 main lineages are incompletely resolved, and for the most part lack any appreciable level of support (except in the case of the clade *Delomys* – Phyllotini *s.s.*). This pattern of incomplete resolution involving most main lineages of Oryzomyalia has been uncovered in previous phylogenetic studies of sigmodontine relationships characterized by narrower taxonomic coverage than the one used here (mitochondrial: Smith & Patton 1999; D'Elía 2003; IRBP: Weksler 2003; mitochondrial and IRBP: D'Elía 2003; and growth hormone receptor, breast cancer gene 1, recombination activating gene 1 and the protooncogene c-myc: Steppan *et al.* 2004). The lack, or at least paucity, of synapomorphies relating most of these 11 lineages may be indicative of the rapid burst of diversification of the Oryzomyalia, which would have occurred with 7.68 and 13.67 Ma (Parada *et al.* 2013). The fact that relationships were not resolved by the analyses of the above-mentioned loci is suggestive that this is in fact a hard polytomy. The analysis of additional loci may help resolve this polytomy as happened with the basal polytomy found in the first molecular-based phylogenetic analyses of Echimyidae (Galewski *et al.* 2005).

Phyllotine Systematics

Our analyses were designed to test the structure of the Phyllotini and the position of several taxa previously associated to this tribe. We corroborated previous results (e.g. Steppan 1995; Smith & Patton 1999; D'Elía 2003) showing that *Andinomys*, *Euneomys*, *Irenomys*, *Punomys* and *Reithrodon* are not part of the tribe Phyllotini; similarly, we expanded these results to *Chinchillula* and *Neotomys*, while showing that *Galenomys* is a phyllotine. According to the topologies recovered in our analyses, the tribe Phyllotini is composed by the following living genera: *Auliscomys*, *Andalgalomys*, *Galenomys*, *Salinomys*, *Graomys*, *Loxodontomys*, *Phyllotis*, *Tapecomys*, *Eligmodontia*, *Calomys* and Phyllotini n. gen. In addition, the genus *Delomys* is the sister taxon to the Phyllotini.

Within the Phyllotini, *Calomys* with 13 species is one of the two most diverse members of Phyllotini, and certainly, the one with the broadest geographic and ecological distribution. Despite renovated interest (Salazar-Bravo *et al.* 2001; Almeida *et al.* 2007; Cordeiro-Estrela *et al.* 2008; Bonvicino *et al.* 2010), two issues still deserve attention with regard to the systematics of the genus: its monophyletic status and the species limits among its constituent species. Our data somehow diminish support for the monophyly of *Calomys*. MP and ML recovered a paraphyletic *Calomys* respect to Phyllotini n. gen.; while the BA topology shows a monophyletic *Calomys*, but lacking significant support. Removing Phyllotini n.gen. from the analyses increases the support for the monophyly of *Calomys* (results not shown). In the combined analysis of both IRBP and cytochrome *b* gene data, Phyllotini n.gen. is resolved as the sister group to all the remaining phyllotines (PP = 1; BL = 91) and the monophyly of *Calomys* is strongly supported (PP = 1; BL = 100). The morphological characters

of Phyllotini n. gen. clearly indicate that it represents an heretofore unknown phyllotine, but molecular data at hand do not adequately resolve its position with respect to *Calomys* or the remaining phyllotines, and thus, further discussion with regard to this issue would require new molecular characters. The nature of the incongruence between IRBP solo-based topologies and that including cytochrome *b* gene characters (e.g. Feijoo *et al.* 2010) is unclear, but it may have several causes. We discard this incongruence is due to the presence of nuclear insertions of mitochondrial sequences (i.e. NuMts; Lopez *et al.* 1994) or pseudogenes in our data set given that there were no shifts in the reading frame and translation of DNA sequences resulted in protein sequences without internal stop codons. The acquisition of sequences of additional loci will hopefully clarify this issue.

Our data show that relationships within the clade composed by all phyllotines except *Calomys* and Phyllotini n. gen. are in general unresolved. Steppan *et al.* (2007) using cytochrome *b* and RAG1 DNA gene sequences data recovered a *Phyllotis* group composed of *Auliscomys*, *Loxodontomys*, *Phyllotis*, *Tapecomys*, and –they suggested– possibly the *Andalgalomys/Salinomys* clade. Our results do not agree with this hypothesis; our BA analyses recovers (IRBP solo, PP = 0.93; combined data set, PP = 0.90) the clade composed by *Andalgalomys*, *Auliscomys*, *Galenomys* and *Salinomys*. All other genera have ambiguous relationships. Therefore, our analyses did not support an *Andalgalomys* and *Graomys* clade, contrary to the morphological results of Braun (1993) and Steppan (1993, 1995) nor a restricted *Auliscomys* group (*sensu* Steppan 1993) composed of *Auliscomys* and *Galenomys*. Clearly, there is a need to reassess the patterns of morphological variation within the phyllotine and to incorporate additional sequences to the analysis.

The non-phyllotine condition of some Andean taxa

Analyses recovered two well-supported clades of taxa with marked Andean distributions that, at some point in taxonomic history, were considered to be phyllotines (e.g. Cabrera 1961; Hershkovitz 1962; Olds & Anderson 1989; Steppan 1995); *Euneomys*, *Neotomys* and *Irenomys* form a strongly supported clade (IRBP: BP = 95; BL = 97; PP = 1; combined: PP = 1; BL = 99) at the time that *Andinomys* and *Punomys* are always recovered in a separate strongly supported clade (IRBP: BP = 100; BL = 100; PP = 1; combined: PP = 1; BL = 100). These two clades are never recovered as sister to each other; more important, they do not form part of the phyllotine radiation and neither are sister to it. As stated above, Phyllotini is sister to *Delomys*. Similarly, the *Euneomys-Neotomys-Irenomys* clade appears in the IRBP analyses, although with low support, sister to the non-Andean genus *Juliomys*. The clade *Andinomys-Punomys* falls to a polytomy at the base of the oryzomyalid clade in the IRBP MP analysis, or form a clade together with the *Euneomys-Neotomys-Irenomys-Juliomys* clade and *Chinchillula* (considered a phyllotine previously) in the model-based analyses of both data sets,

Punomys is an enigmatic taxon with poorly understood phylogenetic relationships; Vorontsov (1979) referred it without justification to the Phyllotini, disregarding the observation of the original describer of the genus (Osgood 1943), who had refrained from allying *Punomys* to any of the then known groups of sigmodontine genera. Based on its peculiar skull and dental morphology, some authors have assigned an *incertae sedis* status to *Punomys* (Reig 1980), while others followed Vorontsov (1979) in including it within the Phyllotini (Olds & Anderson 1989; Braun 1993). Steppan (1993) conducting a comprehensive analysis of the phylogenetic relationships of ca. 50 taxa of phyllotine rodents and outgroup taxa, recovered *Punomys* as a Sigmodontinae with uncertain phylogenetic position as in most of his most fundamental trees, *Punomys* was recovered outside the Phyllotini. Remarkably, in 32 of the 121 most parsimonious trees recovered, *Punomys* formed a clade with other Andean taxa (i.e. *Irenomys* and *Andinomys*), and thus, at least in part, some of these trees mirrored the set of relationships depicted by the IRBP solo and the combined analyses. As noted above, in all of our analyses, *Andinomys* and *Punomys* are sister to each other (IRBP: BP = 100; BL = 100; PP = 1; combined: PP = 1; BL = 100). These two genera are only superficially similar; in fact, only 59% of 96 morphological characters surveyed by Steppan (1995) showed character states shared by *Andinomys* and *Punomys*, and most were symplesiomorphies shared with other taxa either in the Phyllotini or more generally within Sigmodontinae (Steppan 1993). A reassessment of the morphology of *Andinomys* and *Punomys* is much needed to test the topology found in this study.

The robust clade formed by Andean *Euneomys*, *Neotomys* and *Irenomys* (IRBP: BP = 95; BL = 97; PP = 1; combined: PP = 1; BL = 99; see also Martínez *et al.* 2012) is characterized by the presence of highly hypsodont molars and grooved upper incisors. These and other characters (e.g. the shape and position of the premaxillo-maxillary suture) led various authors (Olds & Anderson 1989; Steppan 1995) to suggest a close phylogenetic relationship between *Euneomys*, *Neotomys* and *Reithrodon*; this assemblage was then informally referred to as to the '*Reithrodon*-group'. In contrast, the phylogenetic scenario proposed by all our analyses suggests that highly hypsodont molars (and likely other craniodental characters) evolved independently at least twice among the taxa studied. Our analyses resolved a strongly supported clade composed by ((*Euneomys*, *Neoto-*

mys) *Irenomys*) distantly related to *Reithrodon*, which is another sigmodontine genus with highly hypsodont molars, sigmoidal molars, etc. Climatic fluctuations of the late Cenozoic, associated with the rise of the Andes (e.g. Klein *et al.* 1999; Baker *et al.* 2001; Garzione *et al.* 2008) favored the development of Puna grasslands, which could have in turn selected for an increment of hypsodonty in unrelated sigmodontines inhabiting these open, more arid habitats. Whether the evolution of hypsodonty is correlated with other characters observed in these lineages, such as the shape and position of the premaxillo-maxillary suture and the shape of the zygomatic plate, is a matter that requires further study. It is also important to note that several extinct sigmodontine taxa sharing some characters with *Reithrodon* and similar forms have been described (e.g. Pardiñas 1997; Ortiz *et al.* 2000). None of these fossils have been included in dense phylogenetic analyses.

Biogeographic considerations

The evolution of the Phyllotini s.s. is thought to be strongly associated with the Andean Altiplano and, therefore, to the landscape evolution of Andean ranges (e.g. Reig 1984, 1986; Smith & Patton 1993, 1999). As such, the distribution of phyllotines in non-Andean areas was thought to be the result of dispersal events from the Andean highlands (e.g. Reig 1984; Almeida *et al.* 2007). These simplistic scenarios were swayed by the influential concept of areas of original differentiation (AOD) advanced for the Sigmodontinae (Reig 1984, 1986). Briefly, 'an AOD is the geographic space within which a given taxon experienced the main differentiation of its component taxa of subordinate rank' (Reig 1986:411). As most genera considered to be phyllotines by Reig (1986) distribute in the South Central Andes, he suggested the tribal AOD to be located in that area (Fig. 4A) and that latter phyllotines spread towards the northern and southern Andes and the eastern lowlands. Available evidence indicates that the historical biogeography of Phyllotini is much more complex than early envisioned. The analysis of the known distributions of extant phyllotines shows (Fig. 4A–B) that only six of 11 genera (*Auliscomys*, *Calomys*, *Galenomys*, *Loxodontomys*, *Phyllotis* and *Eligmodontia*) distribute in high Andean areas, that only two of these (*Auliscomys* and *Galenomys*) are restricted to the Andean highlands, while the other four are also widely distributed–or even richer in species-–at intermediate and/or low elevations. In addition, two genera, *Tapecomys* and *Graomys*, inhabit intermediate elevations, although the latter mostly ranges below 1000 m (Hershkovitz 1962). Finally, three genera, *Andalgalomys*, *Salinomys* and Phyllotini n. gen. are restricted to lowland areas (Braun & Mares 1995). Therefore, phyllotines are not a clear highland group, as previously considered. Another remarkable fact is that in all our analysis, the Phyllotini s.s. is sister to the Atlantic forest genus *Delomys* (Fig. 4A); all of these lines of evidence suggest that the ancestor to the crown group Phyllotini ranged mostly outside the Andes. The fossil record supports this scenario given that the oldest known phyllotine, *Auliscomys formosus*, comes from the Atlantic coast of Buenos Aires province, Argentina (Fig. 4A). Studies including all phyllotine species, in particular for those genera with large range of altitudinal distribution, are needed to assess with certainty the place of the basal phyl-

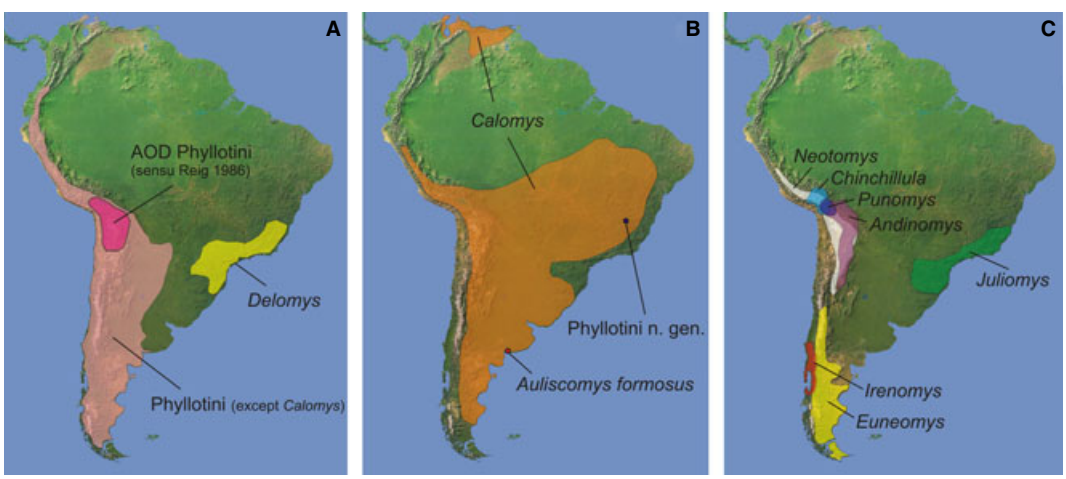

Fig. 4 Geographic distributions of selected sigmodontine taxa. —A) Current distribution of the tribe Phyllotini (except *Calomys* and Phyllotini new genus) as delimited in this study. The geographic location of the tribal Area of Original Differentiation as suggested by Reig (1984, 1986) and that of the sister group of the tribe Phyllotini, the genus *Delomys*, are also indicated. —B) Distributions of the phyllotine genera *Calomys* and Phyllotini new genus, and recording locality of the oldest known phyllotine, *Auliscomys formosus*. —C) Distribution of *Juliomys* and genera previously considered as belonging to the tribe Phyllotini and that at the light of phylogenetic results are now regarded as Sigmodontinae incertae sedis (see text).

lotine radiation. Recently, Parada *et al.* (2013) estimated for the phyllotine crown group an age of 5.75–7.75 Ma. The global-scale glacial event of the late Miocene resulted in southern South America in an arid and cold pulse (Shackleton 1995), which may have been amplified by the fact that the Andes achieved at that time their present morphology and for the most part their current elevation (Rabassa 2008). The subsequent vegetational changes, including the rapid replacement of Miocene subtropical savannas by drier steppes (Rabassa 2008; see also Ortiz-Jaureguizar & Cladera 2006), may have triggered, among other faunal changes, the basal diversification of the phyllotines, a group of mostly herbivorous rodents inhabiting arid and semiarid areas of South America.

Further, our study suggests a closer relationship between taxa who currently occur in the Atlantic Rainforest and the Andes. This pattern is found in different sigmodontine clades identified in this and other analyses: for example (Fig. 4C), *Juliomys* and the clade formed by *Euneomys*, *Neotomys* and *Irenomys*, the sister relationship between *Wiedomys* and Abrotrichini (D'Elía *et al.* 2006b), the clade formed by *Brucepattersonius* and *Lenoxus* (D'Elía 2003), and the sister group relationship between *Drymoreomys* and *Eremoryzomys* (Percequillo *et al.* 2011a). These paired examples of groups of Andean and Atlantic Forest endemics suggest historical connections between these distant South American biomes. Interestingly, Nores (1992; but see Da Silva 1994), suggested historical connections between the Yungas forest of the eastern flanks of the Andes and the Atlantic forests, which are now separated by the ca. 700 km of xerophytic Chaco. These past connections, likely driven by Quaternary climatic changes, may explain the observed pattern of sister bird species presently distributed at both forests. Even when some of the sigmodontine disjunctions here listed may be artefacts of deficient sampling efforts (see below), the fact that the pattern emerges in different parts of the sigmodontine tree invites to further explore its causes.

A caveat that requires consideration is that some of these currently disjunct distributions may be artefacts of poor sampling; for example, Percequillo *et al.* (2011a) recently reported *Rhagomys* in the middle of Amazonia, which was previously known only from the Atlantic forest and in the Andes.

In conclusion, the phylogenetic analyses presented herein provide substantial improvements in our knowledge of phyllotine phylogenetic relationships and on the structure of the sigmodontine radiation, by providing a hypothesis on the contents of the tribe Phyllotini as well as identifying novel generic clades of sigmodontine rodents. Similarly, the study suggests the occurrence of several instances of putative morphological convergence among distinct sigmodontine lineages (e.g. among now considered to be ichthyomyines; between Phyllotini and some Andean taxa; among *Euneomys-Neotomys* and *Reithrodon*). Finally, as expected, this study emphatically shows that much work (e.g. broader taxonomic sampling, analysis of new loci, integration of morphological evidence) still remains to be conducted before a deeper understanding of the evolutionary history of this important integrant of the South American fauna can be reached.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1 Genbank accession numbers of the DNA sequences (IRBP and cyt *b* genes) analysed in the phylogenetic analyses of Sigmodontinae.