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DESCRIPTION OF A NEW TRIBE OF SIGMODONTINE RODENTS (CRICETIDAE: SIGMODONTINAE) WITH AN UPDATED SUMMARY OF VALID TRIBES AND THEIR GENERIC CONTENTS

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ABSTRACT

We provide a formal recognition to a tribal level clade composed of *Andinomys* and *Punomys*, two extant sigmodontine genera consistently and repeatedly recovered in the phylogenetic analyses of molecular and morphological data. As currently recognized, this tribe is distributed in middle to high elevations in the Andes of Bolivia, Peru, northern Chile, and northwestern Argentina in habitats that range from high elevation grasslands and ecotonal areas to dry Puna. Within this new clade, *Punomys* appears as the more specialized member as it is fully restricted to rocky outcrops and their immediate surrounding areas at elevations above 4400 m on both sides of the Altiplano. In contrast, *Andinomys* occupies a broad elevational range (500–4000 m) and multiple habitats, from subtropical mountain forests and semiarid Puna and Prepuna to high altitudinal grasslands. Both taxa share a number of possible synapomorphies (e.g., presence of caudal enlargement of the post-zygapophysis in the second and eighth thoracic vertebrates, unilocular-hemiglandular stomachs with a large corpus and deep incisura angularis, and very similar chromosomal complements) and other diagnostic morphological features. The supratribal phylogenetic relationships of the taxon here named are not resolved even with the moderate amount of molecular data now available. In addition, we present a revised classification for the Sigmodontinae and comment on the content and context of this unique radiation of the Cricetidae.

Key words: Altiplano, Andinomyini, *Andinomys*, *Oryzomyia*, *Punomys*

RESUMEN

En este trabajo reconocemos formalmente un clado de nivel tribal compuesto por los géneros de roedores sigmodontinos *Andinomys* y *Punomys*, el que es consistentemente recuperado en el análisis filogenético de datos moleculares y morfológicos. Los miembros de esta tribu se distribuyen en los Andes de Perú, Bolivia, norte de Chile y el noroeste de Argentina en hábitats que van desde praderas altoandinas y hábitats ecotonales hasta la Puna seca. Dentro de este nuevo clado *Punomys* parece ser el miembro más especializado, ya que está totalmente restringido a afloramientos rocosos y sus áreas aledañas en elevaciones superiores a 4400 m

en ambos lados del Altiplano. En contraste, *Andinomys* ocupa múltiples ambientes en elevaciones que van desde 500–4000 m y que incluyen bosques subtropicales de montaña, Puna y pre-Puna semiáridas y pastizales de altura. *Andinomys* y *Punomys* comparten una serie de posibles sinapomorfías (por ejemplo, ampliación caudal de la postzigapófisis de la segunda y octava vertebras torácicas, estómagos uniloculares y hemiglandulares con incisura y corpus especialmente prominentes y complementos cromosómicos muy similares) entre otras características morfológicas diagnósticas. Las relaciones filogenéticas supratribales del taxón aquí nombrado no se resuelven incluso con una cantidad moderada de datos moleculares. Por último, se presenta una clasificación actualizada para la subfamilia Sigmodontinae y se ofrecen comentarios sobre el contenido y el contexto de esta singular radiación de los Cricetidae.

Palabras clave: Altiplano, Andinomyini, *Andinomys*, *Oryzomyia*, *Punomys*

INTRODUCTION

The systematics of the Sigmodontinae, the largest subfamily of living cricetids, has seen a renaissance in the last 30 years with the incorporation of DNA sequence methodology for phylogenetic inference, and with the integration of cladistic methodology in the study of morphological characters (see the literature synthesis in D'Elía and Pardiñas 2015a). As a direct result, traditional suprageneric groups recognized in the subfamily (e.g., Vorontsov 1959; Hershkovitz 1962, 1966; Reig 1980) have in many cases changed dramatically in content and composition (e.g., Akodontini; see D'Elía and Pardiñas 2015b), have remained without substantive modifications (e.g., Ichthyomyini; see Voss 1988), or have been recognized only recently as new and formally diagnosed (e.g., Euneomyini; see Pardiñas et al. 2015).

With the exception of the Akodontini, the Phyllotini is the sigmodontine tribe that has experienced the most changes in context and composition since the diagnosis made by Olds and Anderson (1989). First, cladistic analyses of morphological data (e.g., Stepan 1993, 1995; but see Braun 1993) and later a succession of molecular-based phylogenetic studies suggested the removal of several genera from the tribal contents envisioned by Olds and Anderson (1989); as a result, the following genera have been excluded from Phyllotini: *Punomys*, *Andinomys*, *Euneomys*, *Irenomys*, *Neotomys*, *Chinchillula*, and *Reithrodon* (e.g., Engel et al. 1998; Smith and Patton 1999; D'Elía 2003; Martínez et al. 2012; Salazar-Bravo et al. 2013). In addition, fieldwork

in previously poorly sampled areas of South America revealed high levels of genetic and morphological diversity leading to the recognition of three new genera belonging to the Phyllotini in the last 20 years: *Salinomys*, *Tapecomys*, and *Calassomys* (Braun and Mares 1995; Anderson and Yates 2000; Pardiñas et al. 2014a).

Among the unexpected results from advances in molecular phylogenetics and systematics in the Sigmodontinae is the recognition of previously unsuspected suprageneric assemblages (i.e., tribes). For example, based on the phylogenetic analysis of a mitochondrial gene (cytochrome *b*), the pioneering work of Smith and Patton (1999) first identified an “Andean clade” composed of several taxa (*Abrothrix*, *Chelemys*, *Geoxus*, *Notiomys*, and *Pearsonomys*) previously subsumed under Akodontini. This group was later formally described as the tribe Abrotrichini (see D'Elía et al. 2007) and characterized by a combination of characters, none uniquely synapomorphic (but see Carrizo and Catalano 2015; Teta et al. 2016). Likewise, phylogenetic analyses of multilocus markers confirmed the existence of a clade of seemingly disparate taxa (*Euneomys*, *Irenomys*, and *Neotomys*) distinguished by a series of morphological characters (i.e., narrow interorbital regions, grooved incisors, etc.); this clade was recently named as the tribe Euneomyini (Pardiñas et al. 2015). Remarkably, some trenchant morphological characters present in this clade appear also in other recent and extant taxa, suggesting previously unappreciated levels of morphological convergence among groups of sigmodontine rodents.

Andinomys and *Punomys*, two genera of Andean sigmodontines with previously uncertain phylogenetic associations, are consistently and repeatedly recovered as a distinctive branch in the sigmodontine radiation based on molecular data. Starting with Zeballos (2009), based on cytochrome *b* gene sequence data, several authors have confirmed this relationship with multilocus datasets (Salazar-Bravo et al. 2013; Schenk et al.

2013; Machado et al. 2015; Parada et al. 2015). This clade lacks a formal tribal designation, an issue that we resolve herein based on karyological and morphological data. In addition, we update the tribal classification of Sigmodontinae to encapsulate relatively recent changes in its systematics and consider the processes that resulted in this extraordinary radiation.

METHODS

DNA sequences and phylogenetic analyses.—DNA sequences for a mitochondrial (cytochrome *b*) and a nuclear marker (IRBP) were either obtained by us or retrieved from GenBank for representatives of the Sigmodontinae and several outgroup taxa. With the exception of three currently recognized genera in the Ichthyomyini (*Anotomys*, *Ichthyomys*, and *Chibchanomys*), one in the Akodontini (*Gyldenstolpia*), and one in the Oryzomyini (*Mindomys*), all remaining genera of the recognized tribes and *incertae sedis* taxa in the Sigmodontinae were included in this study (Table 1). In addition, our sampling also included representative sequences for two genera of extinct sigmodontines (*Megalomys* and *Pennatomys*). For the samples processed by us, amplification and sequencing followed protocols in D'Elia (2003) and Salazar-Bravo et al. (2013).

DNA sequences were subjected to phylogenetic analyses using maximum likelihood (ML; Felsenstein 1981), and Bayesian inference (BI; Huelsenbeck et al. 2001). The data sets were used in combined and separated analyses using partitioning schemes and substitution models identified by PartitionFinder (Lanfear et al. 2012). Bayesian Inference were conducted on the CIPRES Science gateway (Miller et al. 2010) and included gene-specific unlinked models in the analysis of combined data sets; uniform interval priors were assumed for all parameters except base composition and SYM+I+G (for cytochrome *b*, codon positions 1 and 2, and IRBP, codon positions 1, 2, and 3) and GTR+I+G (for cytochrome *b*, codon position 3) parameters, which assumed a Dirichlet process prior. Runs consisting of two independent runs, each with three heated and one cold Markov chains, were allowed to proceed for six million generations and were sampled every 1,000 generations. The analyses were repeated

three times. The first 25% of trees were discarded as “burn-in” and the remaining trees were used to compute a 50% majority rule consensus tree and obtain posterior probability (PP) estimates for each clade. All analyses were checked for convergence by plotting the log-likelihood values against generation time for each run, using Tracer 1.6 (Rambaut et al. 2014). All parameters had effective sample sizes greater than 200. Additionally, convergence was assessed in the BI analyses by testing whether or not BI chains sampled trees in proportion to their posterior probabilities (AWTY; Wilgenbusch et al. 2008). The maximum-likelihood trees were calculated using RAxML-GUI (Silvestro and Michalak 2012); nodal bootstrap values (Felsenstein 1985) for the likelihood analysis were calculated using autoMRE, under the GTRCAT model. Branches with posterior probability [PP] ≥ 0.95 were considered well supported. Because Bayesian PP values tend to be a less conservative estimate of node reliability than nonparametric bootstrap values [BS] (Alfaro et al. 2003), inclusion of both support values on our trees represents the upper and lower bounds, respectively, of node reliability (Douady et al. 2003).

Karyotypic data.—The chromosomes of *Andinomys edax* were reported by Pearson and Patton (1976) for a female from Jujuy (Argentina), by Spotorno et al. (1994, 2001) for a male and a female from northern Chile, and by Peurach (1994) for one male and one female from southern Bolivian populations. For comparison, we obtained the karyotype of a male *Punomys kofordi* (from La Paz, Bolivia) following protocols outlined in Baker et al. (2003). Briefly, karyotypes were obtained from bone marrow after 45 minutes of in vivo incubation with the mitotic inhibitor Velban (Sigma-Aldrich, St. Louis, Missouri), followed by fixation in 3:1 methanol: glacial acetic acid mix. Cell spreads

Table 1. Taxon sampling and GenBank accession numbers for one nuclear (IRBP) and one mitochondrial (cytochrome *b*) marker used in the phylogenetic analyses conducted in this paper. n/a: not available.

Species	Cytochrome <i>b</i>	IRBP
<i>Abrawayomys ruschii</i>	JX949189	JX949185
<i>Abrothrix hirta</i>	U03530	KC953347
<i>Aegialomys xantheolus</i>	EU074632	EU273420
<i>Aepeomys lugens</i>	n/a	DQ003722
<i>Akodon boliviensis</i>	M35691	KC953351
" <i>Akodon</i> " <i>serrensis</i>	EF622508	KF815411
<i>Amphinectomys savamis</i>	EU579480	AY163579
<i>Andalgalomys pearsoni</i>	JQ434418	JQ434398
<i>Andinomys edax</i>	JQ434419	JQ434399
<i>Arvicola terrestris</i>	AY275106	AY277407
<i>Auliscomys sublimis</i>	JQ434421	JQ434402
<i>Baiomys musculus</i>	EF989933	KC953360
<i>Bibimys labiosus</i>	DQ444329	AY277436
<i>Blarinomys breviceps</i>	AY275112	AY277437
<i>Brucepattersonius</i> sp.	AY277486	AY277438
<i>Calassomys apicalis</i>	JQ434425	KX431561
<i>Calomys laucha</i>	AY033190	JQ434404
<i>Cerradomys subflavus</i>	EU579481	AY163626
<i>Chelemys megalonyx</i>	DQ309559	EU091259
<i>Chinchillula sahamae</i>	JQ434422	JQ434409
<i>Chilomys instans</i>	AF108679	n/a
<i>Clethrionomys gapperi</i>	AY309431	AY326080
<i>Cricetulus longicaudatus</i>	KM067270	AY326082
<i>Cricetus cricetus</i>	AJ490302	AY277410
<i>Delomys</i> sp.	KF317031	KC953369
<i>Deltamys kempfi</i>	AY195862	AY277444
<i>Drymoreomys albimaculatus</i>	EU579487	EU649042
<i>Eligmodontia typus</i>	AF108692	AY277445
<i>Eremoryzomys polious</i>	EU579483	AY163624
<i>Euneomys chinchilloides</i>	AY275115	AY277446
<i>Euryoryzomys macconnelli</i>	GU126538	AY163620
<i>Galenomys garleppi</i>	JQ434423	JQ434410
<i>Geoxus valdivianus</i>	AY275116	AY277448
<i>Graomys griseoflavus</i>	AY275117	AY277449
" <i>Handleyomys</i> " <i>alfaroi</i>	EU579489	EU649044

Table 1. (cont.)

Species	Cytochrome <i>b</i>	IRBP
<i>Handleyomys intectus</i>	EU579490	AY163584
<i>Holochilus brasiliensis</i>	GU126517	AY163585
<i>Hylaeamys megacephalus</i>	EU579499	AY163621
<i>Irenomys tarsalis</i>	U03534	AY277450
<i>Isthmomyomys pirrensis</i>	DQ836298	EF989847
<i>Juliomys pictipes</i>	FJ026733	KC953385
<i>Juscelinomys huanchacae</i>	AY275119	AY277452
<i>Kunsia tomentosus</i>	AY275121	KC953386
<i>Lenoxus apicalis</i>	U03541	KC953388
<i>Loxodontomys micropus</i>	AY275122	AY277457
<i>Lundomys molitor</i>	JQ966241	JQ966805
<i>Megalomys desmarestii</i>	LN810053	n/a
<i>Melanomys caliginosus</i>	EU340020	KC953397
<i>Mesocricetus auratus</i>	AM904612	AY163591
<i>Microakodontomys transitorius</i>	n/a	EU649054
<i>Microryzomys minutus</i>	AF108698	AY163592
<i>Microtus californicus</i>	EF506105	KC953401
<i>Myospalax aspalax</i>	AF326272	AY326097
<i>Neacomys spinosus</i>	EU579504	AY163597
<i>Necomys amoenus</i>	AY273911	AY277458
<i>Nectomys squamipes</i>	GU126522	EU273419
<i>Neomicroxus latebricola</i>	KF437365	KF437367
<i>Neotoma floridana</i>	AF294344	KC953411
<i>Neotomys ebriosus</i>	JQ434424	JQ434413
<i>Nephelomys albigularis</i>	EU579505	AY163614
<i>Nesomys rufus</i>	AF160592	AY326099
<i>Nesoryzomys swarthi</i>	EU340014	AY163601
<i>Neusticomys monticolus</i>	KF359515	KR105605
<i>Nyctomys sumichrasti</i>	AY195801	KC953421
<i>Oecomys concolor</i>	JF693876	KC953424
<i>Oligoryzomys fulvescens</i>	GU126529	AY163611
<i>Onychomys leucogaster</i>	EF989959	EF989860
<i>Oreoryzomys balneator</i>	EU579510	AY163617
<i>Oryzomys palustris</i>	GU126539	AY163623
<i>Ototylomys phyllotis</i>	AY009789	KC953429
<i>Oxymycterus nasutus</i>	EF661854	AY277468

Table 1. (cont.)

Species	Cytochrome <i>b</i>	IRBP
<i>Paynomys macronyx</i>	U03533	AY277441
<i>Pennatomys nivalis</i>	LN810055	n/a
<i>Peromyscus leucopus</i>	EF989979	EF989880
<i>Phaenomys ferrugineus</i>	KM065876	KM065877
<i>Phodopus sungorus</i>	AJ973390	KC953439
<i>Phyllotis xanthopygus</i>	U86833	AY163632
<i>Podoxymys roraimae</i>	KM816650	KM816650
<i>Pseudoryzomys simplex</i>	GU126547	AY163633
<i>Punomys kofordi</i>	JQ434426	JQ434414
<i>Reithrodon auritus</i>	EU579474	AY163634
<i>Reithrodontomys fulvescens</i>	EF990003	EF989904
<i>Rhagomys longilingua</i>	KX423691	DQ003723
<i>Rheomys</i> sp.	KJ921706	KC953451
<i>Rhipidomys macconnelli</i>	AY275130	AY277474
<i>Salinomys delicatus</i>	EU377608	JQ434415
<i>Scapteromys tumidus</i>	AY275133	AY277477
<i>Scolomys ucayalensis</i>	EU579518	AY163638
<i>Scotinomys teguina</i>	AF108705	AY277415
<i>Sigmodon hispidus</i>	AF425227	AY277479
<i>Sigmodontomys alfari</i>	EU074635	AY163641
<i>Sooretamys angouya</i>	GU126534	KC953456
<i>Tanyuromys aphrastus</i>	JF693877	JF693878
<i>Tapecomys wolffsohni</i>	U86834	KC953460
<i>Thalpomys cerradensis</i>	AY273916	AY277480
<i>Thaptomys nigrata</i>	AF108666	AY277482
<i>Thomasomys aureus</i>	U03540	AY277483
<i>Transandinomys talamancae</i>	GU126544	KC953465
<i>Tylomys nudicaudus</i>	DQ179812	AY163643
<i>Wiedomys pyrrhorhinos</i>	EU579477	AY277485
<i>Wilfredomys oenax</i>	KJ663726	KJ663727
<i>Zygodontomys brevicauda</i>	GU126549	AY163645

were visualized using an Olympus BX51 microscope; ten good-quality spreads were scanned and counted. Images were photographed using an Applied Imaging Systems (San Jose, California).

Morphological data.—We follow a polythetic approach (Mayr and Ashlock 1991) to identify morphological features useful to characterize the new tribe; by the very nature of this approach, some combination of characters, some likely plesiomorphic and some

probably derived, is unique to this group. We suggest, nonetheless, that our approach be further tested on a quantitative phyletic framework when data on most of the other tribes in the Sigmodontinae become available. We observe, however, that Carrizo and Catalano (2015) identified some diagnostic characters for the group of interest, after a cladistic analysis of the Phyllotini s.l., although their analyses did not include all the characters we used here (e.g., chromosomes, stomach and penial morphology) or did not include all pertinent taxa (e.g., *Calassomys*). In order to identify diagnostic charac-

ters, we relied on extensive morphological revisions and cladistic analyses produced for several groups of sigmodontine rodents during the last several decades (e.g., Hershkovitz 1962; Carleton 1973, 1980; Voss 1988; Stepan 1993, 1995; Braun 1993; Pacheco 2003; Weksler 2006; Teta 2013; Carrizo and Catalano 2015), augmented by our own study of several specimens of *Andinomys* and *Punomys* (see Appendix). Throughout the text, we use the abbreviations M1-3 or m1-m3 to individually reference the upper (maxillary) and lower (dentary) molars, respectively.

RESULTS

Based on the combination of karyotypic and morphological characters, and informed by the results of the phylogenetic analyses of molecular data, we recognize a new tribe of sigmodontine rodents (Rodentia: Cricetidae), as follows:

Andinomyini, new tribe

Type genus.—*Andinomys* Thomas, 1902.

Contents.—*Andinomys* Thomas, 1902 and *Punomys* Osgood, 1943.

Definition.—The clade, as disclosed by analyses of IRBP and cytochrome *b*, composed of the last common ancestor of *Andinomys*, and *Punomys* and all of its descendants.

Diagnosis.—A tribe in the Sigmodontinae (sensu Reig 1980), member of the Oryzomyalia (sensu Stepan et al. 2004), composed of medium-sized (adult head and body length 130–180 mm), heavy-bodied rodents; dorsal pelage long (above 17 mm on back), dense and lax, upper parts and sides drab, underparts whitish with hairs basally gray or a hint of buff; tails sharply bicolored without terminal brush; pinnae equal to or larger than 22 mm; front and hind feet white covered dorsally with short silver and white hairs; full complement of six fleshy plantar pads, including four interdigitals, a thenar, and a large hypothenar; ungual tufts present, silvery white, and extending well beyond claws.

Skulls heavy, interorbital region parallel-sided, with supraorbital edges squared and somewhat raised;

rostra heavy with well-developed nasals expanded in its anterior half and broader than their interorbital regions; interfrontal fontanelles present (Gardner and Anderson 2001); braincase squared; zygomatic plate broad (always above 10% of condyloincisive length) with deep dorsal notch; carotid arterial circulation characterized by an enlarged carotid canal and stapedia foramen, a squamosal-alisphenoid groove, sphenofrontal foramen, and a groove on the posterolateral margin of the parapterygoid plates (pattern 1 of Voss 1988); incisive foramina long; maxillary septum reaching about half way of the incisive foramina; palate long and narrow (sensu Hershkovitz 1962), marked by two deep long sulci containing enlarged posterior palatine foramina (Fig. 1); parapterygoid fossae shallow, slightly wider than mesopterygoid fossa; postglenoid foramen on the same plane, but anterior to subsquamosal fenestra; alisphenoid strut absent; incisors opisthodont (contra Patton 2015, who reported *Punomys* with orthodont incisors) and specialized with the cutting edge acutely angular (also true for the lower incisors); molar tooththrows hypsodont, posteriorly divergent; first upper molar with anteroloph, mesoloph, and enteroloph; first lower molar with two-roots. Mandibles robust, with poorly developed capsular projections; anterior margin of the masseteric ridge at the same level with protoconid of the m1.

Stomachs unilocular-hemiglandular, with enlarged corpuses and deep incisura angularis (Spotorno 1976); internal morphology of the stomach distinct in that the bordering fold circumscribes a small area of the glandular epithelium near the proximal portion of corpus and close to the esophageal opening (Fig. 2); gall bladder present.

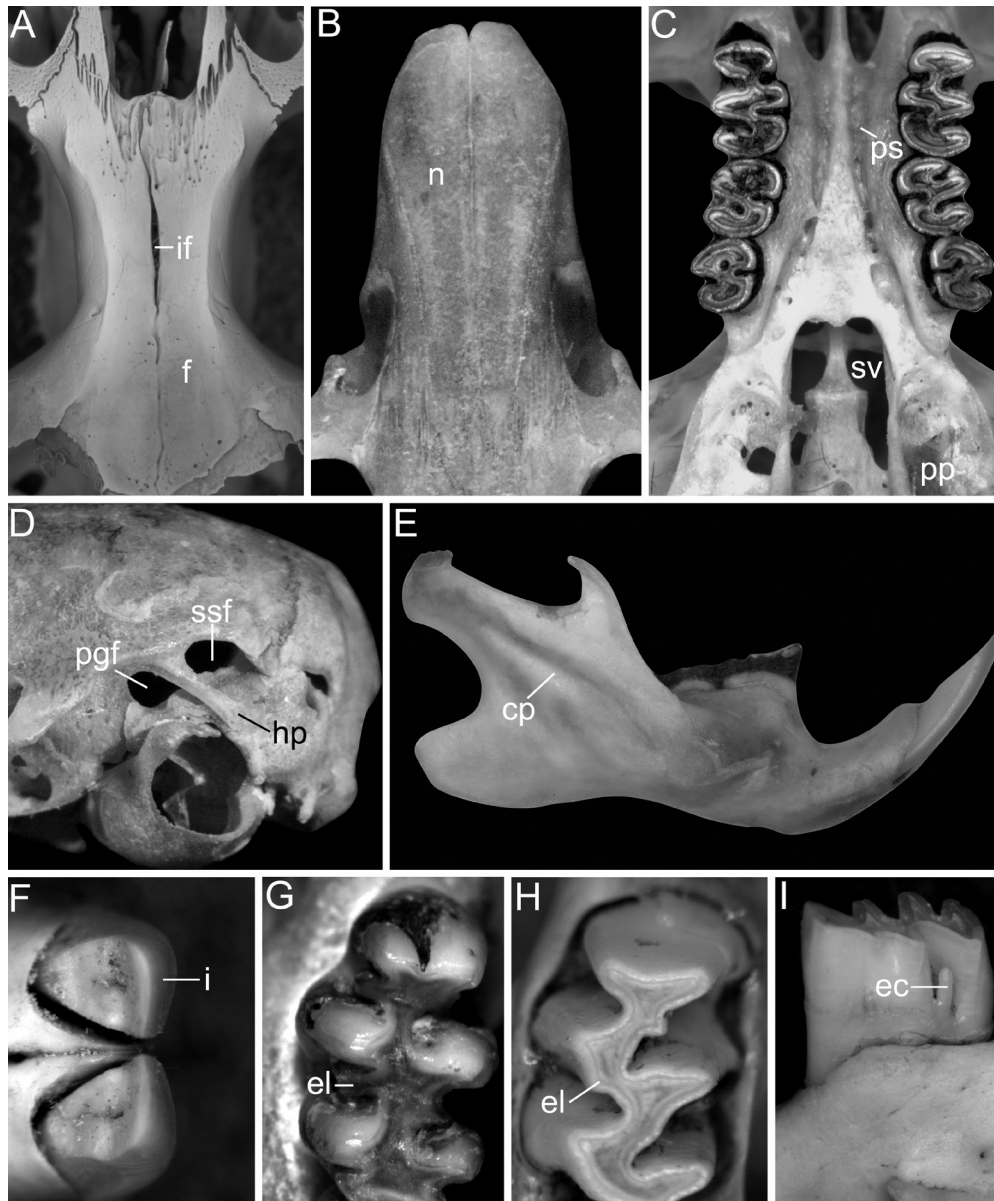


Figure 1. Views of key morphological characters in representatives of the Andinomyini. A. Parallel-sided supraorbital regions, with squared edges (*Andinomys edax*: CNP-E 809-1). B. Heavy rostra with well-developed nasals expanded anteriorly, broader than their interorbital regions (*Punomys kofordi*: TTU-M 125722). C. Molar tooththrows posteriorly divergent, long palate, well-developed palatal sulci, well-developed sphenopalatine vacuities, and shallow parapterygoid plates about as wide as mesopterygoid fossae (*Andinomys edax*: CNP 2364). D. Postglenoid foramen on the same plane, but anterior to subsquamosal fenestra (*Punomys kofordi*: TTU-M 125722). E. Mandibles robust, with poorly developed capsular projections (*Andinomys edax*: CNP 2364). F. Upper incisors, ventral view (*Andinomys edax*: CNP-E 809-1). G-H. First upper molars (G, *Punomys kofordi*: TTU-M 125722; H, *Andinomys edax*: CNP-E 810-1). I. First lower molar (*Andinomys edax*: CNP-E 810-1). Abbreviations: cp = capsular projection; ec = ectostylid; el = enteroloph; f = frontal; hp = hamular process; i = incisor; if = interfrontal fontanelle; n = nasal; pp = parapterygoid plate; ps = palatal sulci; sv = sphenopalatine vacuities.

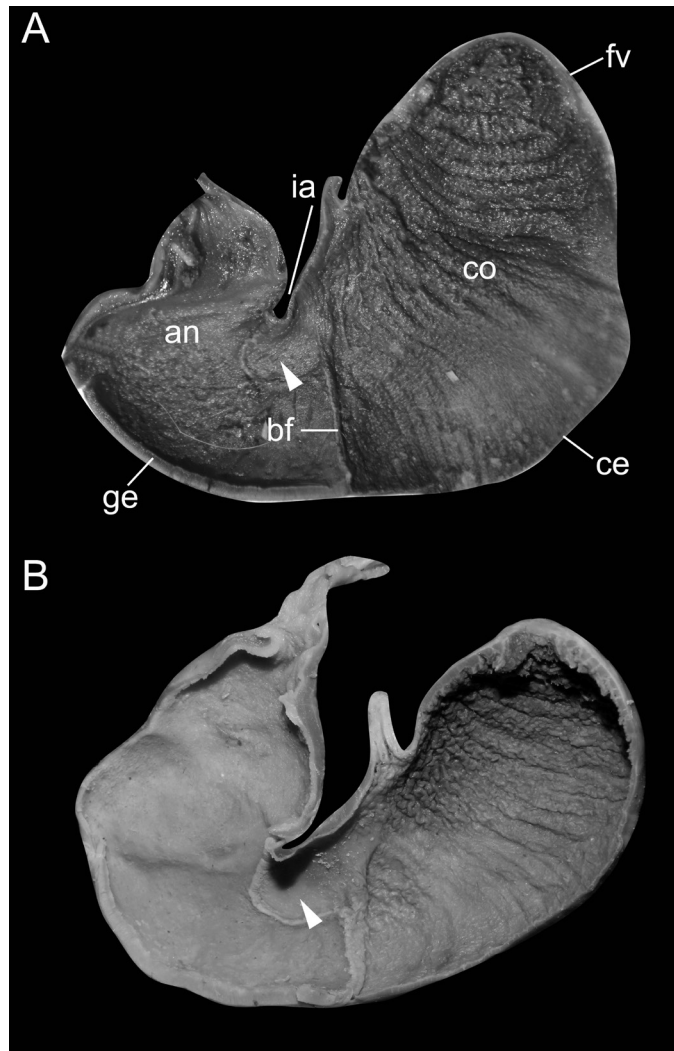


Figure 2. Views of the internal stomach morphology in representatives of the Andinomyini. A. *Andinomys edax* (CNP 5401); B. *Punomys kofordi* (MUSA 4692). The arrow depicts an area of the epithelium encapsulated by the bordering fold. Abbreviations: an = antrum; ce = cornified epithelium; bf = bordering fold; co = corpus; fv = fornix ventricularis; ge = glandular epithelium; ia = incisura angularis. Figures are scaled to the same length.

Phalli robust and barrel-shaped, with a slightly ventrally placed crater and robust proximal bacula.

Chromosomal complements composed of one pair of metacentric and 26 pairs of acrocentric chromosomes for a total of $2N=56$, $FN=56$; Y-chromosomes small and acrocentric, X-chromosomes large and submetacentric.

Mammæ, 2-2=8.

Etymology.—The tribal name is formed following Articles 29.2 and 29.3 of the ICZN (ICZN 1999), by adding the suffix *ini* to the stem of the name of the type genus, *Andinomys*; therefore, Andinomy + *ini* = Andinomyini. Implicitly, Thomas (1902) used *Andinomys* to highlight the Andes (or Cordillera de los Andes), the general area of distribution inhabited by the genus.

Known distribution.—The two rodent genera composing the Andinomyini are distributed in the Andes of extreme southern Perú, northernmost Chile, Bolivia, and north-western Argentina, in habitats that include subtropical mountain forests to pre-Puna and semiarid Puna (Yepes 1935; Pearson and Pearson-Ralph 1978; Patton 2015; Salazar-Bravo and Jayat 2015) (Fig. 3). Sympatry between members of these two genera (*Andinomys* and *Punomys*) has not been recorded, but at several localities (e.g., Valle de La Paz, Bolivia) they occur in neighboring localities, although separated by elevation and habitat types: *Andinomys* prefers the semi-arid portions of the valley up to 3600 m, whereas *Punomys* occupies the barren, broken rock areas at elevations above 4500 m (Pacheco and Patton 1995; Salazar-Bravo et al. 2011); *Punomys* is the genus with the highest elevational range of any species of mammals in the Neotropics. *Andinomys* ranges broadly from 500 to 4000 m, occupying a variety of habitat types along this broad expanse of terrain (Salazar-Bravo and Jayat 2015 and Fig. 3).

Biochron.—Middle-Upper Pleistocene of Argentina (Ortiz and Jayat 2007) to Recent for *Andinomys*; currently, no fossils are known for *Punomys*.

Remarks.—In addition to the characters identified in the formal diagnosis presented above, cladistic analyses of morphological characters identified the following putative synapomorphies for the tribe described herein: presence of caudal enlargement of the postzygapophysis in thoracic vertebrae T2–T8, and distinctly shaped neural processes (low but elongated) in last lumbar and first sacral vertebrae (Carrizo and Catalano 2015).

Nevertheless, *Andinomys* and *Punomys* are quite distinct on a multitude of traits. Some noteworthy differences in character states include: tail to head and body ratio (much less than 50% in *Punomys*, but between ca. 70% and 100% in *Andinomys*); soles of feet (black and covered with small round scales in *Punomys*, pink and naked in appearance in *Andinomys*); shape of the zygomatic plate (with upper border projecting as a short spine in *Andinomys*, but less so in *Punomys*); topography and plication of molars (pentalophodont and crested in *Punomys*, highly hypsodont, tetralophodont and planar in *Andinomys*) (Fig. 4); shape of the mandibular processes (coronoid extending dorsally to

the same level as the articular condyle in *Punomys*, but projecting above it in *Andinomys*); size of the hamular process of squamosal (thick in *Punomys*, narrow in *Andinomys*). In addition, although the baculum in each genus is unique among the Sigmodontinae, they differ markedly from each other: in *Punomys* the distal process of the baculum is reduced to a triangular mass of, apparently uncalcified, hard tissue, whereas in *Andinomys* the distal process of the baculum is complex, with a central element short and broad and flanked by longer, wing-shaped lateral digits (Spotorno 1987).

Phylogenetic relationships.—The general phylogenetic topology that we recovered for the Sigmodontinae is congruent with previous studies (e.g., Smith and Patton 1999; Fabre et al. 2012; Parada et al. 2013, 2015; Salazar-Bravo et al. 2013; Schenk et al. 2013; Leite et al. 2014; Pardiñas et al. 2014a, b; Machado et al. 2015). In particular, we retrieved a monophyletic Sigmodontinae (posterior probability [PP]=1 and bootstrap support values [BS]=99) that splits at the base into two major clades: one, the Sigmodontalia (sensu Leite et al. 2014) composed of *Sigmodon* and the ichthyomyine genera *Rheomys* and *Neusticomys*, and a second group, the Oryzomyalia (sensu Steppan et al. 2004), also with strong support (PP = 1, BS=100). Within the latter, the majority of the tribes currently recognized in the Sigmodontinae (Abrothrichini, Akodontini, Euneomyini, Phyllotini, Oryzomyini, etc.) are resolved with moderate to strong support (Fig. 5).

Andinomys and *Punomys* consistently are recovered as sister genera, with the highest PP and BS values. However, as in previous analyses, the relationships of these two genera to the remaining Sigmodontinae are unresolved; the same is true for most tribes recognized within Oryzomyalia. In combination, these results support the recognition of *Andinomys* and *Punomys* as members of a distinct tribe within the Sigmodontinae.

Previous analyses that included only cytochrome *b* and IRBP sequence data indicated that the Andinomyini grouped with Chinchillula + Euneomyini, in some cases with strong Bayesian but poor bootstrap support (e.g., Salazar-Bravo et al. 2013). Likewise, analyses of four nuclear loci revealed a clade formed by *Andinomys* and *Punomys* as the sister-group to Euneomyini, although with very low PP and BS below 50% (Schenk et al. 2013). The study of Pardiñas et al. (2015), com-

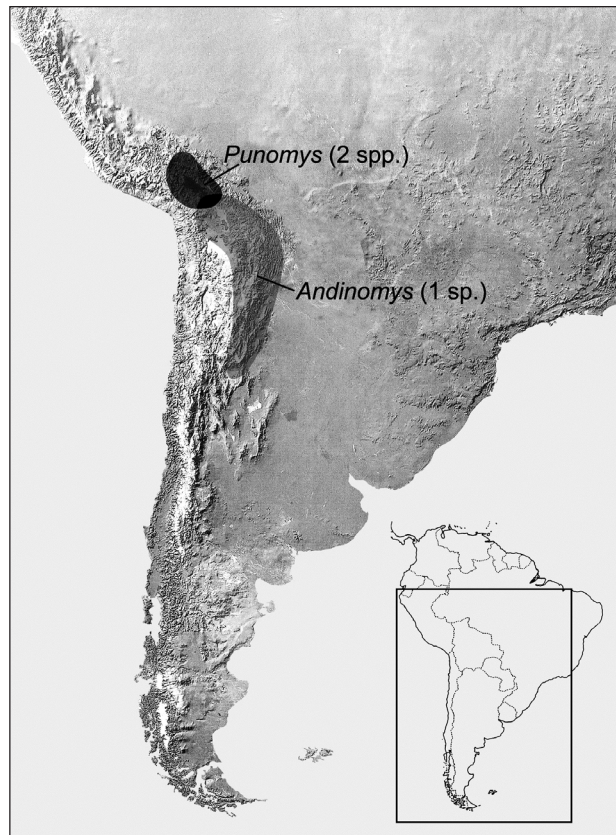


Figure 3. Schematic geographic distributions of the Andinomyini in South America.

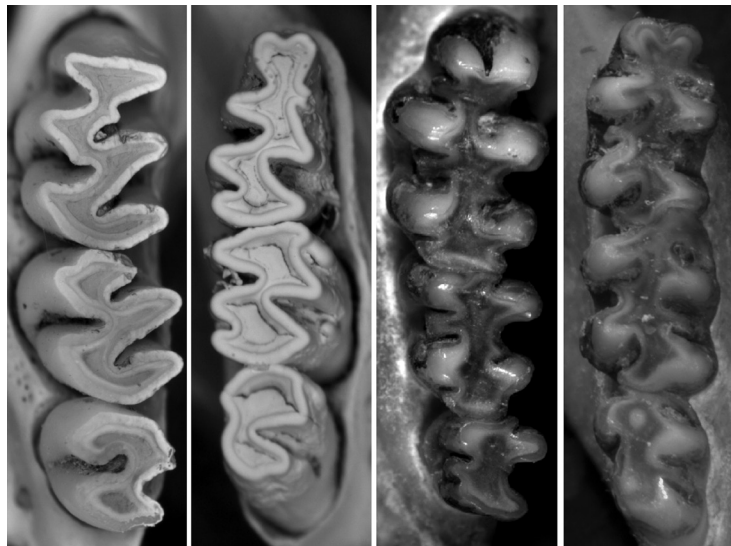


Figure 4. Morphology of upper and lower molar occlusal surfaces in Andinomyini. Left, *Andinomys edax* (CNP-E 809-1); right, *Punomys kofordi* (TTU-M 125722).

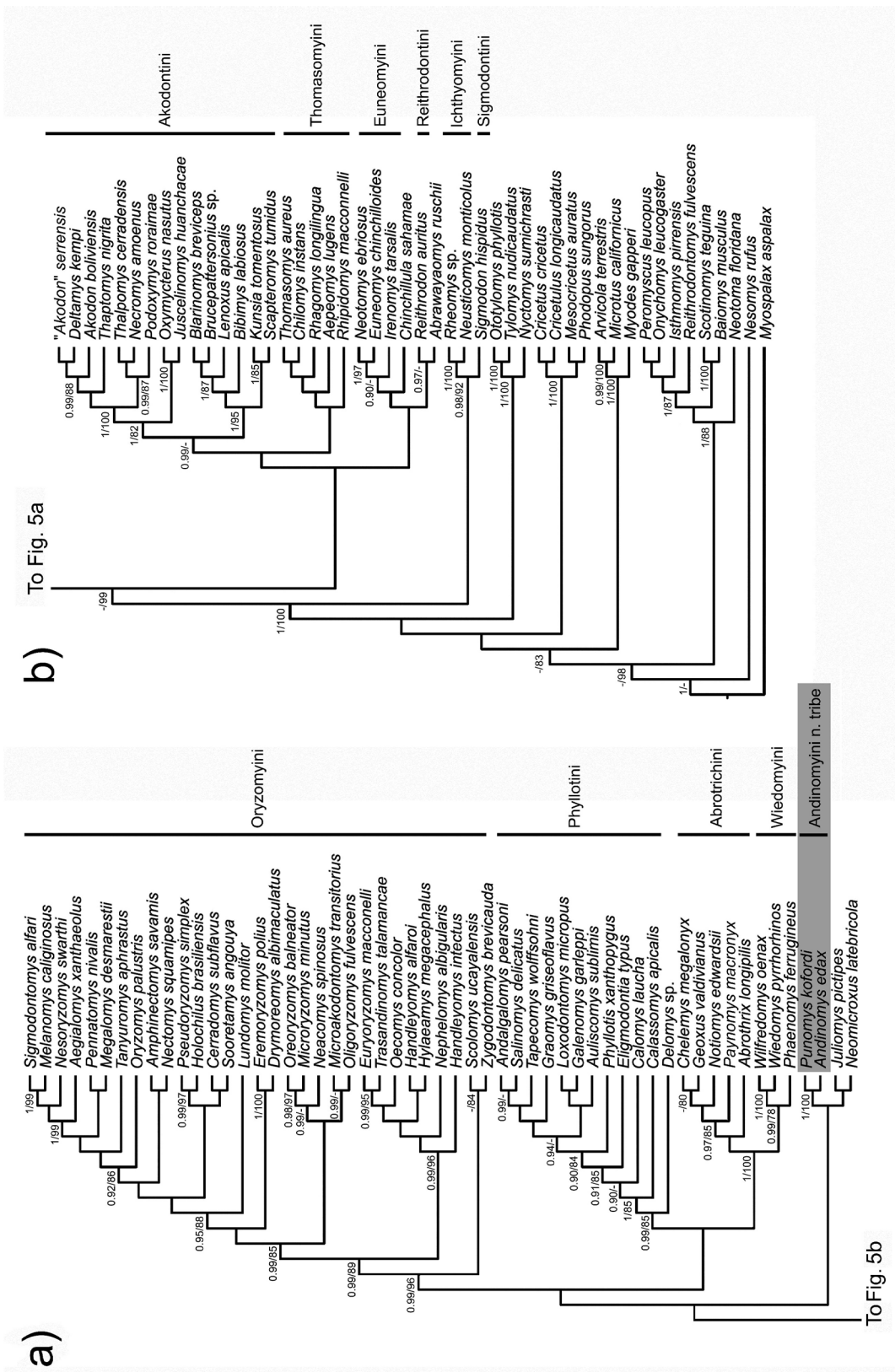


Figure 5. Results of the ML analysis of the combined matrix of one nuclear (IRBP) and one mitochondrial (cytochrome *b* gene) marker for members of the Sigmodontinae and outgroups. Numbers indicate posterior probability (PP, left of the diagonal) identified in the Bayesian analyses (see text for details) and maximum likelihood bootstrap values (BS, right of the diagonal) of adjacent nodes; dashes indicate nodes that were not recovered in the Maximum Likelihood topology (= -53354.390449), or whose support values were < 0.85 (PP) or < 80% (ML bootstraps).

binning analyses of four nuclear and one mitochondrial marker, mirrored the topology recovered by Schenk et al. (2013) with regards to the position of *Chinchillula* as sister-group to the remainder of Oryzomyalia.

In summary, *Andinomys* and *Punomys* are consistently resolved as sister genera, regardless of the taxonomic sampling, the number of characters analyzed

(e.g., single mitochondrial vs. multiple nuclear markers or morphological and molecular data in combination), or the analytical method employed. Notwithstanding the modest amounts of molecular data now available (e.g., Schenk et al. 2013; Pardiñas et al. 2015), the closest relatives to the tribe Andinomyini (*Andinomys* and *Punomys*) remain unclear.

DISCUSSION

Taxonomy of the Sigmodontinae.—Our analyses and interpretations support a view of the Sigmodontinae that is, at best, incompletely reflected by the current taxonomy of the subfamily. We argue that the recognition of groups of genera (i.e., tribes) provides substantial information on patterns of phenotypic evolution and the geographic and ecological context under which they evolved, and thus, ought to be incorporated in a formal taxonomic treatment. As discussed by many authors (see literature synthesis in D'Elía and Pardiñas 2015a and below), some of these groups differ in internal diversity and in amplitude of distribution and are arranged in coherent morphotypes with sharp distinctions from other such groups (e.g., Akodontini vs. Oryzomyini). In other tribes, however, the internal morphological coherence is only identifiable after detailed scrutiny within the framework of a molecular-based phylogeny (e.g., Euneomyini, Andinomyini). We recognize that notions of rank equivalency are biased by interpretations of levels of divergence, age, or content that are bound to fail for a number of theoretical or empirical reasons (see Frost et al. 2006 for a clear discussion of this issue). But, we submit that taxonomies are constructions for verbal and written communication representing sets of hypotheses of relationships that must be further tested as data becomes available.

Phylogenetic structure within the Sigmodontinae.—Sigmodontine rodents (Cricetidae, Sigmodontinae) are an exceptional group among Neotropical mammals. With 86 recognized genera and ~432 living species, mostly restricted to South America, they represent the most diversified group of mammals in the region (Patton et al. 2015).

Approximately 200 years of taxonomic studies, aided by molecular analyses in the last three decades,

have converged on a moderately strong hypothesis on sigmodontine phylogenetics, supporting many previously accepted suprageneric arrangements, while modifying and identifying new ones (e.g., Smith and Patton 1999; Jansa and Weksler 2004; D'Elía et al. 2006; Fabre et al. 2012; Martínez et al. 2012; Salazar-Bravo et al. 2013; Schenk et al. 2013; Leite et al. 2014; Machado et al. 2015; Pardiñas et al. 2014a, b, 2015). All these studies agree on a few major points; for example, Sigmodontinae includes two major groups, one composed of mostly North and Central American forms in the genus *Sigmodon* + Ichthyomyini (the Sigmodontalia), and a second group, composed of mostly South American forms (the Oryzomyalia) that in a relatively short span of time (< 5 MA) diversified in several tribal-level lineages; currently most of the relationships among tribes are best represented by a basal polytomy.

One of the most interesting contributions from molecular-based studies of the Sigmodontinae is the phylogenetic refinement of several of its constituting tribes. For example, the Phyllotini, once considered one of the best-characterized tribes in the subfamily (e.g., Pearson 1958; Hershkovitz 1962; Olds and Anderson 1989; Steppan 1995), is now revealed as a polyphyletic composite of four tribal-level clades of tetralophodont rodents (Andinomyini, Euneomyini, Phyllotini, and Reithrodontini, see below), hinting at several instances of putative morphological convergence among distinct sigmodontine lineages.

In summary, although the basic cladistic structure of the sigmodontine radiation appears to be relatively well defined, there are many areas that require much work, including: a) ascertaining the phylogenetic context of the Sigmodontinae; b) resolving the basal radiation of the Oryzomyalia; and c) increasing taxo-

nomic sampling within the Thomasomyini and the Ichthyomyini, the two tribes currently most poorly sampled. We note, in particular, the weak nature of support for Thomasomyini as currently understood. In the last assessment of the contents of the tribe, Pacheco et al. (2015) included the genera *Aepeomys*, *Chilomys*, *Rhagomys*, *Rhipidomys*, and *Thomasomys*; although no molecular-based phylogenetic analysis has rigorously tested their hypothesis, we emphasize the long-branches that appear to characterize this tribe and the somewhat unstable position of some of their purported generic members (e.g., *Rhagomys*) (Fig. 5). Data for the remaining members of the tribe are urgently needed to assess the nature and content of the tribe.

Two pulses of diversification.—Two important questions in sigmodontine systematics are associated with parts of the tree that lack resolution: the phylogenetic relationships of the Sigmodontinae with other subfamilies in the Cricetidae and the basal diversification of the Oryzomyalia. They represent pulses of diversification in the evolution of the Cricetidae that are responsible for a large proportion of the current diversity of the family, yet there is very little consensus on the underlining environmental or ecological factors that may have triggered them.

Ascertaining the phylogenetic context of the Sigmodontinae requires identification of its sister-group relationships within the Cricetidae. Currently, two hypotheses are advanced on this regard, both hinging on the position of the Tylomyinae. One involves the Tylomyinae as sister-group to the Sigmodontinae. Five recent comprehensive studies (Fabre et al. 2012; Leite et al. 2014; Salazar-Bravo et al. 2013; Schenk et al. 2013; Vilela et al. 2013) lend credence to the Tylomyinae and Sigmodontinae as sister taxa, although in all cases this relationship was supported by low maximum-likelihood bootstrap values and low to medium posterior probability values. A second hypothesis views the Tylomyinae and Neotominae as sister groups to each other, which together form a polytomy with Sigmodontinae, Cricetinae and Arvicolinae. This topology, which has not been recovered in the analyses of single or combined nucleotide markers to date, was the hypothesis favored by Dickerman's (1992) analysis of DNA:DNA hybridization. The use of genomic approaches, such as those recently called for by Lessa et al. (2014) should help determine whether these

and related questions (e.g., the diversification of the Oryzomyalia) resulted from an explosive radiation or whether the patterns we currently see reflect a lack of resolution based on the few loci employed.

Tempo and mode of diversification in the Sigmodontinae.—Although most species of Sigmodontinae are endemic to South America, there is strong consensus that the subfamily's ancestors likely invaded the continent from either Central or North America, probably as late as the Late Miocene or Early Pliocene (Nasif et al. 2009; Prevosti and Pardiñas 2009), although it is unclear how many lineages invaded South America and the timing of the invasion(s) (e.g., Leite et al. 2014).

Predicated on the closure of Panama bridge at 3.5 Mya, recent studies have uniformly favored the hypothesis of the arrival of one or few lineages of early sigmodontines into South America via waif dispersal through a proto-Caribbean sea. However, new evidence now suggests that the Isthmus of Panama, and by extension, the closure of the Central American Seaway, occurred in the middle Miocene (13–15 Mya), about 10 million years earlier than previously thought (Montes et al. 2015); this marks a substantial shift in our understanding of the merger between North and South America and suggests that now it is not necessary to invoke waif dispersal into South America for the ancestral stock of Sigmodontinae (Parada et al. 2013; Schenk et al. 2013; Vilela et al. 2013; Leite et al. 2014). However, sigmodontines are absent from the middle Miocene (13 mybp) Honda group of La Venta, the richest Miocene tropical fossil deposit in South America (Kay and Madden 1997). The same is true for the fossiliferous and well-sampled deposits of the late Miocene (about 6 mybp), Cerro Azul Formation in Central Argentina (with the exception of the controversial locality of Caleúfu; see Verzi and Montalvo 2008; Prevosti and Pardiñas 2009).

In light of the new dates and geological evidence, recent analyses of molecular and fossil data designed to evaluate the tempo of biotic exchange have suggested at least two main waves of terrestrial dispersal across the Panamá Isthmus: one at about 20 Mya and a second one at about 6 Mya (Bacon et al. 2015). How did these waves of dispersal affect the patterns of diversification in the Sigmodontinae? To satisfactorily answer this question, we will need better calibrated,

more comprehensive, trees for the group of interest, a hope that currently rest on the promise of genomic data. Moreover, incorporating fossil material in explicit phylogenetic hypotheses, including those purported to be primitive sigmodontine rodents (e.g., *Cordimus*, Zijlstra et al. 2014) in addition to recent and extinct Sigmodontinae will help reconcile these two sources of information (genomes and fossils) and will illuminate the processes by which this group diversified. In fact, we are facing a paradox regarding the origin of Sigmodontinae because most hypotheses advanced in the last two decades were constructed without fossils. Therefore, the plausible existence of totally fossil groups (including tribes) and past diversity for the recognized extinct suprageneric assemblages could be a crucial factor to really understand this radiation and its geographic origins (Barbieri et al. 2016).

Tempo, mode and place of diversification of the Andinomyini.—The absolute chronology of Neotropical muroid evolution is unlikely to be established in the absence of convincing fossil evidence, critically missing—or, in the best of cases, unstudied—for most of the groups and areas of interest (Pardiñas, et al. 2002; Ortiz et al. 2011). The fossil record for *Andinomys* extends from the middle-upper Pleistocene of Argentina to the Recent and though informative on the paleodistribution of this genus it is too recent to shed light on its place or time of origin (Ortiz and Jayat 2007). Based on current distribution of these genera it is parsimonious to suggest that the ancestor was probably Andean in distribution and likely occupied the area around the Titicaca Lake basin, where both genera overlap their distributions.

Two recent studies have assessed the divergence time between *Andinomys* and *Punomys* at about 4 Mya (HDP 2.2–5.8); these studies differed only on the number of taxa analyzed, but used the same three fossil calibrations, thus it is not surprising they estimated very similar times of divergence for these two genera (Parada et al. 2013, 2015). A third study estimated the divergence between *Punomys* and *Andinomys* at 2.17 Mya (HDP 1.4–2.94); this study used a denser sampling of muroid groups, four nuclear markers and 13 calibration points, five of which were based on sigmodontine fossils (Schenk et al. 2013). Three additional studies have estimated times of divergence for the Sigmodontinae, or at least portions of the subfamily, although *Andinomys* or *Punomys* were not included in

their analyses (Leite et al. 2014; Machado et al. 2014; Vilela et al. 2014).

Only one of the fossil calibration points used by Parada et al. (2013, 2015) was also used by Schenk et al. (2013), that for *Auliscomys formosus* from the Monte Hermoso Formation of Buenos Aires, Argentina. Parada et al. (2013) used this fossil to calibrate the entire crown clade of Phyllotini, whereas Schenk et al. (2013) adopted a conservative approach and used it to calibrate the most recent common ancestor of *Phyllotis*, *Loxodontomys*, *Tapecomys*, and *Andalgalomys*. Although small, these inconsistencies, in combination with the number of fossil calibrations and the number of markers used, resulted as expected on theoretical grounds (Edwards and Beerli 2000; Loss-Oliveira et al. 2012) in the differences in estimated dates between these studies.

Despite these caveats, the ancestor to *Punomys* and *Andinomys* likely occupied the area around the basin of the Titicaca Lake between 2 and 5 mya (the approximate points of overlap of the credibility intervals for the studies mentioned above). Regrettably, these dates bracket the onset of major environmental changes in the region driven either by global-scale glacial events (Zachos et al. 2001), or some geomorphological and geological event (e.g., Andes achieved at that time their present morphology and for the most part their current elevation, Garzzone et al. 2008). This combination of events likely produced subsequent vegetational changes, such as the rapid expansion of plants using the C4 photosynthetic pathway at the Miocene/Pliocene boundary (Hynek et al. 2012), and are potentially responsible for the diversification of the *Andinomys* + *Punomys* clade among other taxa with hysodont, tetralophodont molars.

An updated classification of the extant Sigmodontinae.—In a recent contribution, Fabre et al. (2015) outlined a higher-level classification for extant Rodentia, based almost solely on the evidence retrieved from molecular markers. Despite the need for adjustment to recent taxonomic changes (e.g., the description of *Euneomyini*), these authors' contribution includes several inaccuracies, including the use of non-existent nominal taxa (e.g., “*Abrawayaomyini*,” “*Abrothrixi*” [sic]) or several improbable relationships (e.g., *Rhagomys* or *Wilfredomys* as members of Phyllotini); therefore, a

more accurate and current picture of the Sigmodontinae is needed.

Current data indicates that the subfamily includes at least eleven tribes, which in alphabetic order are: Abrotrichini, Andinomyini, Akodontini, Euneomyini, Ichthyomyini, Oryzomyini, Phyllotini, Reithrodontini, Sigmodontini, Thomasomyini, and Wiedomyini. In addition, several genera (e.g., *Abrawayaomys*) should still

be considered Sigmodontinae incertae sedis, although further work will probably indicate the existence of single-genus tribes (for example, *Delomys*). We are aware that some forthcoming taxonomic changes will include, among others, the description of new genus for “*Akodon*” *serrensis* (Pardiñas et al., in press). Therefore, the valid tribes and member genera of the extant Sigmodontinae are presented in Table 2.

Table 2. An updated summary of valid tribes and their generic contents in the Sigmodontinae.

Subfamily Sigmodontinae Wagner, 1843	
Incertae sedis	
	<i>Abrawayaomys</i> Souza Cunha and Cruz, 1979
	<i>Chinchillula</i> Thomas, 1898
	<i>Delomys</i> Thomas, 1917
	<i>Juliomys</i> González, 2000
	<i>Neomicroxus</i> Alvarado-Serrano and D’Elía, 2013
Tribe Abrotrichini D’Elía, Pardiñas, Teta and Patton, 2007	
	<i>Abrothrix</i> Waterhouse, 1837
	<i>Chelemys</i> Thomas, 1903
	<i>Geoxus</i> Thomas, 1919
	<i>Notiomys</i> Thomas, 1890
	<i>Paynomys</i> Teta, Cañon, Patterson and Pardiñas, 2016
Tribe Andinomyini Salazar-Bravo, Pardiñas, Zeballos and Teta (this paper)	
	<i>Andinomyis</i> Thomas, 1902
	<i>Punomys</i> Osgood, 1943
Tribe Akodontini Vorontsov, 1959	
	<i>Akodon</i> Meyen, 1833
	<i>Bibimys</i> Massoia, 1979
	<i>Blarinomys</i> Thomas, 1896
	<i>Brucepattersonius</i> Hershkovitz, 1998
	<i>Deltamys</i> Thomas, 1917
	<i>Gyldenstolpia</i> Pardiñas, D’Elía and Teta, 2009
	<i>Juscelinomys</i> Moojen, 1965
	<i>Kunsia</i> Hershkovitz, 1966
	<i>Lenoxus</i> Thomas, 1909
	<i>Necromys</i> Ameghino, 1889
	<i>Oxymycterus</i> Waterhouse, 1837
	<i>Podoxymys</i> Anthony, 1929
	<i>Scapteromys</i> Waterhouse, 1837
	<i>Thalpomys</i> Thomas, 1916
	<i>Thaptomys</i> Thomas, 1916
Tribe Euneomyini Pardiñas, Teta, and Salazar-Bravo, 2015	
	<i>Euneomys</i> Coues, 1874
	<i>Irenomys</i> Thomas, 1919
	<i>Neotomys</i> Thomas, 1894

Table 2. (cont.)

Tribe Ichthyomyini Vorontsov, 1959
<i>Anotomys</i> Thomas, 1906
<i>Chibchanomys</i> Voss, 1988
<i>Ichthyomys</i> Thomas, 1893
<i>Neusticomys</i> Anthony, 1921
<i>Rheomys</i> Thomas, 1906
Tribe Oryzomyini Vorontsov, 1959
<i>Aegialomys</i> Weksler, Percequillo and Voss, 2006
<i>Amphinectomys</i> Malygin, 1994
<i>Cerradomys</i> Weksler, Percequillo, and Voss, 2006
<i>Drymoreomys</i> Percequillo, Weksler, and Costa, 2011
<i>Eremoryzomys</i> Weksler, Percequillo, and Voss, 2006
<i>Euryoryzomys</i> Weksler, Percequillo, and Voss, 2006
<i>Handleyomys</i> Voss, Gómez-Laverde, and Pacheco, 2002
<i>Holochilus</i> Brandt, 1835
<i>Hylaeamys</i> Weksler, Percequillo, and Voss, 2006
<i>Lundomys</i> Voss and Carleton, 1993
<i>Melanomys</i> Thomas, 1902
<i>Microakodontomys</i> Hershkovitz, 1993
<i>Microryzomys</i> Thomas, 1917
<i>Mindomys</i> Weksler, Percequillo, and Voss, 2006
<i>Neacomys</i> Thomas, 1900
<i>Nectomys</i> Peters, 1861
<i>Nephelomys</i> Weksler, Percequillo, and Voss, 2006
<i>Nesoryzomys</i> Heller, 1904
<i>Oecomys</i> Thomas, 1906
<i>Oligoryzomys</i> Bangs, 1900
<i>Oreoryzomys</i> Weksler, Percequillo, and Voss, 2006
<i>Oryzomys</i> Baird, 1857
<i>Pseudoryzomys</i> Hershkovitz, 1962
<i>Scolomys</i> Anthony, 1924
<i>Sigmodontomys</i> J. A. Allen, 1897
<i>Sooretamys</i> Weksler, Percequillo, and Voss, 2006
<i>Tanyuromys</i> Pine, Timm, and Weksler, 2012
<i>Transandinomys</i> Weksler, Percequillo, and Voss, 2006
<i>Zygodontomys</i> J. A. Allen, 1897
Tribe Phyllotini Vorontsov, 1959
<i>Andalgalomys</i> Williams and Mares, 1978
<i>Auliscomys</i> Osgood, 1915
<i>Calassomys</i> Pardiñas, Lessa, Teta, Salazar-Bravo, and Câmara, 2014
<i>Calomys</i> Waterhouse, 1837
<i>Eligmodontia</i> F. Cuvier, 1837
<i>Galenomys</i> Thomas, 1916
<i>Graomys</i> Thomas, 1916
<i>Loxodontomys</i> Osgood, 1947
<i>Phyllotis</i> Waterhouse, 1837

Table 2. (cont.)

	<i>Salinomys</i> Braun and Mares, 1995
	<i>Tapecomys</i> Anderson and Yates, 2000
Tribe Reithrodontini Vorontsov, 1959	
	<i>Reithrodon</i> Waterhouse, 1837
Tribe Sigmodontini Wagner, 1843	
	<i>Sigmodon</i> Say and Ord, 1825
Tribe Thomasomyini Steadman and Ray, 1982	
	<i>Aepeomys</i> Thomas, 1898
	<i>Chilomys</i> Thomas, 1897
	<i>Rhagomys</i> Thomas, 1917
	<i>Rhipidomys</i> Tschudi, 1845
	<i>Thomasomys</i> Coues, 1884
Tribe Wiedomyini Reig, 1980	
	<i>Phaenomys</i> Thomas, 1917
	<i>Wiedomys</i> Hershkovitz, 1959
	<i>Wilfredomys</i> Ávila-Pires, 1960

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APPENDIX

Specimens examined are housed in the following collections (organized alphabetically by collection's acronym): Colección Boliviana de Fauna (CBF; La Paz, Bolivia); Colección de Mamíferos del Centro Nacional Patagónico (CNP; Puerto Madryn, Chubut, Argentina); Colección de Material de Egagrópilas y Afines “Elio Massoia” del Centro Nacional Patagónico (CNP-E; Puerto Madryn, Chubut, Argentina); Colección Nacional de Mastozoología, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (MACN; Buenos Aires, Argentina); mammal collection of the Museum of Southwestern Biology (MSB; University of New Mexico, Albuquerque, NM); Colección científica asociada al Museo de Historia Natural de la Universidad Nacional de San Agustín (MUSA; Arequipa, Peru); and the Natural Science Research Laboratory (TTU; Museum of Texas Tech University, Lubbock).

Andinomys edax (n = 32).—ARGENTINA, Catamarca, Quebrada Seca (CNP-E 810), Belén, Río Vallecito (MACN 50.422); Jujuy, Quebrada Alumbrijo, aprox. 8 km al NE de Santa Ana, 2900 m (CNP 2364), Humahuaca, Pucará (CNP 5401), Tilcara (MACN 17563); Salta, Parque Nacional Los Cardones, Valle Encantado (CNP-E 809-1), Quijano (MACN 17565); Tucumán, El Infiernillo (MACN 17566), Chicligasta, Sierra del Aconquija (MACN 29.253). BOLIVIA, Chuquisaca: 9 km. N Padilla (CBF 1063), El Palmar (CBF 4719); Cochabamba: 16.5 km NW Colomi (MSB 70545, CBF 3662), Curubamba, 7.5 km SE Rodeo (CBF 3473, MSB 70544); La Paz: Ananta (CBF 7172, CBF 7177 and CBF 7191), Collana (CBF 783), Khañuma (CBF 894), Ovejuyo (CBF 895), Valencia (CBF 1201, CBF 1205, CBF 1206); Potosí: 28km W de Acacio (by rd, CBF 4889); Tarija: 4.5 km E Iscayachi (MSB 67192); Rancho Tambo, 61 km (by rd) E Tarija (MSB 57099); Patanca (CBF 7506, CBF 7507, CBF 7508). PERU, Puno: Chucuito, Hda. Ventilla, entre Pichupichuni y Huacullani (MUSA 4544, MUSA 4545, MUSA 4618).

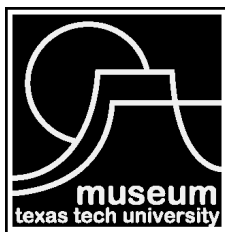
Punomys kofordi (n = 6).—BOLIVIA, La Paz: cumbre del camino a Yungas (CBF 858, TTU-M 125722). PERU, Puno: Hacienda Aricoma, Sandia (MUSA 4333, MUSA 4677, MUSA 4692, MUSA 4693).

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