A multilocus perspective on the phylogenetic relationships and diversification of rodents of the tribe Abrotrichini (Cricetidae: Sigmodontinae)

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Abrotrichini is a recently defined and diagnosed tribe of Sigmodontinae with a complex taxonomy. Abrotrichine genera, *Abrothrix* (including *Chroeomys*), *Chelemys*, *Geoxus*, *Notiomys* and *Pearsonomys*, are mostly distributed in the central and southern Andes and adjacent lowlands and show terrestrial and fossorial habits. Recent studies have evidenced some incongruence between current taxonomy and abrotrichine phylogeny, such as the polyphyly of *Chelemys* and paraphyly of *Geoxus* respect to *Pearsonomys*. We used DNA sequence data of six loci (one mitochondrial and five nuclear) to resolve the relationships within the tribe. Independent and combined analyses of these loci were carried out using parsimony, maximum likelihood and Bayesian inference. Estimates of divergence time of the main lineages of abrotrichines were calculated with a molecular clock using as calibration, a fossil recently found. The concatenated data set increased the resolution and defined the relationships within the tribe. Our phylogenetic analyses corroborate that *Abrothrix* is sister of a clade containing the long-clawed abrotrichines. We recovered two main clades within *Abrothrix* that match morphologic variation and geographic distribution of its species. In addition, we corroborated the lack of monophyly of *Chelemys* and the lack of monophyly of *Geoxus*. We discuss different taxonomic scenarios to abrotrichine classification reflects the phylogenetic relationships obtained in this study. Our molecular clock estimated the Abrotrichini crown age to be around the early Pliocene (4.4 Ma) and suggest that the tribe diversified over a short period of time.

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Introduction

About one half of the living South American rodents belong to the subfamily Sigmodontinae, which constitutes one of the most diverse and complex groups of New World mammals. Currently, it contains nine groups distinguished with the formal rank of tribe: Abrotrichini, Akodontini, Ichthyomyini, Oryzomyini, Phyllotini, Reithrodontini, Sigmodontini, Thomasomyini, and Wiedomyini; in addition, 12 genera are considered as *incertae sedis* (Alvarado-Serrano & D'Elía 2013; Salazar-Bravo *et al.* 2013). Phylogenetic

studies based on morphological and molecular data have defined and refined the generic content of each of these tribes as well as the relationships within them (Steppan 1995; Smith & Patton 1999; D'Elía 2003; Pacheco 2003; Weksler 2006; Coyner et al. 2013; Salazar-Bravo et al. 2013; Ventura et al. 2013; Pardiñas et al. 2014).

Abrotrichini, formerly referred in the literature as the "Andean clade," was the last sigmodontine tribe to be identified and named. It includes the genera Abrothrix (including Chroeomys), Chelemys, Geoxus, Notiomys, and Pearsonomys and is distributed in the central and southern Andes and nearby lowlands reaching the Atlantic in southern Patagonia and Tierra del Fuego. Relationships among abrotrichine genera and their specific diversity have not been free of conflicts and changes. Traditionally, and based on morphological characters, abrotrichines were considered to be typical akodontines (Reig 1987) or oxymycterines (Hershkovitz 1966; an assemblage of taxa, including the nominotypical genus Oxymycterus, now firmly placed within the Akodontini). Suggestion that abrotrichines constituted a distinct group came from allozyme studies (Patton et al. 1989; Spotorno et al. 1990; Dickerman 1992; Barrantes et al. 1993) as well as from the initial mtDNA gene sequence analysis carried out by Smith & Patton (1991). However, the taxonomic coverage of these studies did not allow a clear distinction between abrotrichines and akodontines. More recent cytochrome b DNA sequence studies (Smith & Patton 1993, 1999) provided evidence that abrotrichines are not part of akodontine radiation. Additional research allowed the corroboration of their distinction from Akodontini and helped delimit two main abrotrichine groups: Abrothrix in one hand and the remaining genera, which are long-clawed, in the other (D'Elía 2003; D'Elía et al. 2006; Rodríguez-Serrano et al. 2008; see the formal proposal of the tribe in D'Elía et al. 2007).

Specific diversity is not equally distributed among abrotrichine genera. The genus Abrothrix contains eight species (Patterson et al. in press) distributed along the central and southern Andes. Two species, inhabitants of forest and steppe environments, are recognized for Chelemys: C. macronyx and C. megalonyx (Teta et al. in press). Finally, the remaining long-clawed genera Geoxus, Notiomys, and Pearsonomys are considered to be monospecific (Patterson 1992; Musser & Carleton 2005; Pardiñas et al. 2008). Phylogeographic studies have raised questions about the accepted specific diversity of most abrotrichine genera (Lessa et al. 2010; Palma et al. 2010; Sierra 2010; Alarcón et al. 2011). In addition, neither Chelemys (Rodríguez-Serrano et al. 2008) nor Geoxus (Lessa et al. 2010) appear to be monophyletic. Finally, Feijoo et al. (2010) and Teta et al. (2011) have shown that the tree topologies gathered on the basis of mitochondrial and nuclear DNA sequences are incongruent in regard to the phylogenetic relations within Abrothrix. In both cases, the nuclear-based trees seem to be easier to reconcile with distributional and morphological data.

Understanding the evolution of Abrotrichini is important in the context of South American landscapes and fauna. Abrotrichini is one of the most diverse and abundant sigmodontine groups in Patagonia, and thus, a robust phylogeny of the tribe may shed light on the complex and still poorly understood biogeographic history of this region (Pardiñas et al. 2011). Herein, we present a systematic study of Abrotrichini based on one mitochondrial and five nuclear loci aimed to generate a phylogenetic hypothesis to evaluate the content of each genus, relationships among genera, and the timing of the main cladogenetic events within the tribe.

Materials and methods

Taxonomic sampling
Taxonomic coverage is wide, spanning representatives of all abrotrichine genera and of 12 of 13 recognized living species. In addition, for Abrothrix longipilis, A. olivacea, Chelemys macronyx, and Geoxus valdivianus sampling includes representatives of the main phylogeographic units recovered in Lessa et al. (2010), Palma et al. (2010), Alarcón et al. (2011) and Abud et al. (in litt.). As such, sampling includes 28 abrotrichine terminals (Table 1); the corresponding specimens are deposited in the following collections: CNP, Centro Nacional Patagónico, Puerto Madryn, Argentina; UACh, Colección de Mamíferos, Universidad Austral de Chile, Valdivia, Chile; MSB, Museum of Southwestern Biology, Albuquerque, New Mexico, USA; MVZ, Museum of Vertebrate Zoology, University of California, Berkeley, USA; UWBM, Burke Museum of Natural History and Culture, Washington University, Washington, USA; and field catalogues of Jonathan Guzmán (JG; Universidad de Concepción, Concepción, Chile) and Jorge Pablo Jayat (JPJ, Universidad Nacional de Tucumán, Tucumán, Argentina). Sequences recovered from representatives of the remaining sigmodontine tribes as well as some incertae sedis sigmodontine genera were used to conform the outgroup (Table 1).

Sequence acquisition
A few DNA sequences were downloaded from Genbank (Table S1). Most of the sequences were generated by us with the following protocol. We extracted genomic DNA using the protocol of Wizard Genomic DNA Purification System of Promega. We amplified and sequenced one mitochondrial and five nuclear loci. The mitochondrial fragment corresponds to the first portion of the protein coding cytochrome b gene (cytb). Nuclear loci are: (i) exon 6 of the gene coding for the dentin matrix (DMP1), (ii)

Table 1 List of specimens used in the phylogenetic analysis of relationships among rodents of the tribe Abrotrichini. See text for collection acronyms

Taxon	Voucher	Country	Locality
Ingroup			
Abrothrix andina	UWBM 49048	Chile	Farellones, Valle Nevado
Abrothrix illutea	JPJ 1411	Argentina	Trancas, Tucumán
Abrothrix illutea	JPJ 1479	Argentina	Monteros, Tucumán
Abrothrix jelskii	MVZ 173076	Peru	Ollachea, Puno
Abrothrix lanosa	CNP 1377	Argentina	Laguna Verde, Tierra del Fuego
Abrothrix lanosa	CNP 1396	Argentina	Ushuaia, Tierra del Fuego
Abrothrix lanosa	CNP 1399	Argentina	Ushuaia, Tierra del Fuego
Abrothrix longipilis	UACH 7257	Chile	Chile Chico, Aysén
Abrothrix longipilis	UACH 7258	Chile	Malalcahuello, Araucanía
Abrothrix longipilis	UACH 7259	Chile	Altos del Lircay, Talca
Abrothrix longipilis	CNP 2831	Argentina	Laguna Varvarco Tapia, Neuquén
Abrothrix olivacea	CNP 1750	Argentina	La Valenciana, Mendoza
Abrothrix olivacea	UACH 7255	Chile	Puerto Vagabundo, Aysén
Abrothrix olivacea	UACH 7256	Chile	Valle Shagrila, Ñuble
Abrothrix olivacea	CNP 994	Argentina	Ea. Talagapa, Chubut
Abrothrix olivacea	CNP 1424	Argentina	Puerto Beta, Tierra del Fuego
Abrothrix sanborni	UACH 7260	Chile	Parque Katalapi, Pichiquillaipe
Abrothrix sanborni	UACH 7261	Chile	Parque Tantauco, Chiloé
Chelemys macronyx	JG 101	Chile	Torres del Paine, Magallanes
Chelemys macronyx	CNP 1249	Argentina	Ea. Talagapa, Chubut
Chelemys macronyx	CNP 446	Argentina	Ea. La Ensenada, Santa Cruz
Chelemys megalonyx	MSB 205852	Chile	Parque Nacional Fray Jorge, Coquimbo
Geoxus valdivianus	UACH 7262	Chile	Ruta Futrono-Llifen
Geoxus valdivianus	CNP 438	Argentina	Pla. Quetrihué, Neuquén
Geoxus valdivianus	CNP 437	Argentina	Ea. La Ensenada, Santa Cruz
Notiomys edwardsii	G5T01	Argentina	Ea. Lag. Manantiales, Santa Cruz
Notiomys edwardsii	CNP 1	Argentina	Laguna Blanca, Río Negro
Pearsonomys annectens	UACH 7056	Chile	Fundo San Martín, Valdivia
Outgroup			
Akodon azarae	CNP 3172	Argentina	Ea. Sta Ana de Carpinchorí, Entre Ríos
Akodon azarae	CNP 751	Argentina	Punta Indio, Buenos Aires
Holochilus brasiliensis	UACH 7263	Paraguay	Estancia Yacaré, Ñeembucu
Irenomys tarsalis	MVZ 155839	Argentina	Puerto Blest, Río Negro
Reithrodon auritus	CNP 2304	Argentina	Pico Salamanca, Chubut
Thomasomys aureus	MVZ 170076	Peru	Paucartambo, Cusco
Thomasomys ischyurus	MVZ 181999	Peru	Río Zana, Cajamarca
Sigmodon hispidus	MSB 75587	Mexico	Veracruz
Wiedomys pyrrhorhinos	MVZ 197567	Brazil	Fazenda Massapé, 15 km SW Serrinha

first exon of the interphotoreceptor retinoid binding protein (IRBP), (iii) second intron of alcohol dehydrogenase gene 1 (Adh), (iv) seventh intron of β-fibrinogen gene (βfbg), and (v) second intron of preproinsulin 1 (Ins). In general, for each terminal, DNA sequences of the six genes analysed were gathered from a single specimen; however, composite terminals were constructed in a few cases (Table S1). Primers used (including newly developed primers for Ins) are listed in Table S2 of the Supplemental Material. Amplification conditions are given by Da Silva & Patton (1993) for the cytb gene, Amman *et al.* (2006) for the Adh, Matocq *et al.* (2007) for βfbg, Jansa & Voss (2000) for the IRBP and Reeder & Bradley (2004) for DMP1. For the Ins locus (reported in this study), we used the same conditions as for βfbg. All reactions included negative controls. Amplicons were purified and sequenced at the external service of Macrogen, Inc. (Seoul, Korea). Sequences were edited with CodonCode Aligner (CodonCode, Dedham, MA, USA) and submitted to GenBank (KJ614571–KJ614668).

Phylogenetic analysis

DNA sequence alignment was performed with Clustal X (Thompson *et al.* 1997) using the default settings. Phylogenetic analyses were performed using maximum parsimony (MP), maximum likelihood (ML) and Bayesian inference (BI). Analyses were conducted for each locus independently and for a matrix with all six genes concatenated. In the concatenated analysis (4441 characters) for those terminals that miss a locus, we completed the matrix with ambiguous state characters (i.e. N; see Table S1).

MP analyses were carried out in PAUP*4 (Swofford 2000) with characters treated as unordered and equally weighted, 200 replicates of heuristic searches with random addition of sequences and tree bisection reconnection (TBR) branch swapping. Two measures of nodal support were computed. First, we assessed the support by 1000 bootstrap replicates (BP) with five replicates of sequence addition each. Second, we calculated the Bremer support values (BS, Bremer 1994). In the concatenated analysis, we also computed partitioned Bremer support values (PBS) as a measure of the positive or negative contribution of each partition to a particular node. Bremer support values (regular or partitioned) were calculated using command files written in TREEROT v3 (Sorenson & Franzosa 2007).

ML analyses were conducted in Treefinder (Jobb *et al.* 2004; Jobb 2008). The best fitting model of nucleotide substitution for each gene (cytb: J2[Optimum, Empirical]:G[Optimum]:5; Adh: TVM[Optimum,Empirical]:G[Optimum]:5; bfbg: HK[{3,1,1,1,1,3}, Empirical]:G[Optimum]:5; DMP1: TN[Optimum,Empirical]:G[Optimum]:5; Ins: HKY[Optimum,Empirical]:G[Optimum]:5; IRBP: J3[Optimum, Empirical]:G[Optimum]:5;) see Jobb 2008) was selected with the Akaike information criterion (Akaike 1974) 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). The concatenated matrix was analysed as in the solo ML analyses using the selected substitution model for each gene partition.

Bayesian inference was conducted in the software BAYES-PHYLOGENIES (Pagel & Meade 2004). A general likelihood-based mixture model of gene sequence evolution (Pagel & Meade 2004), implemented in a Bayesian Markov Chain Monte Carlo framework, was used to estimate the posterior probability of the phylogenetic trees. The Reversible-Jump Markov Chain Monte Carlo procedure (Pagel & Meade 2005) was used to find the best mixture model summarizing sequence evolution. This approach accommodates heterogeneity across sites without the need of a priori partitioning and allows more than one model to be applied to each gene in the alignment. Two runs consisting of 1×10^7 generations and four Markov chains were conducted. Trees were sampled every 1000 generations resulting in 10 000 saved trees; convergence and effective sample size (ESS) were assessed in TRACER v.1.5 (Rambaut & Drummond 2007). The first 25% of the saved trees were removed to avoid the inclusion of trees sampled before the convergence of the Markov Chain. The remaining trees were used to construct a majority-rule consensus tree and obtain a posteriori probability values (PP).

Divergence time estimation

Divergence time estimation was conducted in BEAST v1.7.1. (Drummond et al. 2012), with the combined data set and the following parameters: a nucleotide substitution model GTR+Γ+I; relaxed molecular clock (uncorrelated lognormal) that takes into account variation in substitution rate over time, speciation Yule Process, and an initial random tree. Four independent runs of 10 million generations and log parameter estimates sampled every 1000 generations with an initial burn-in of the 30% of the generations were performed. Log and trees files were combined and summarized using LogCombiner v1.7.1 and TreeAnnotator v1.7.1 (BEAST package) after verifying the credibility of each parameter estimate by means of effective sample size (ESS) values in TRACER v1.5 (Rambaut & Drummond 2007). The estimated divergence times on each node were summarized as mean heights on the maximum clade credibility tree and displayed on FIGTREE v1.4.0 (http://tree.bio.ed.ac.uk/software/figtree/).

To calibrate the molecular clock, we used the fossil record related to Abrothrix reported by Ortiz et al. (2012). Maxillary and mandible remains recovered at the Uquía Formation, San Roque, 4 km SSW of Humahuaca, Humahuaca department, Jujuy, Argentina, belong to four specimens (PVL 6251, 6252, 6256, 6360) now housed in the fossil Vertebrate Collection of the Instituto Miguel Lillo, San Miguel de Tucumán, Argentina. According to Ortiz et al. (2012), the Uquía Formation contains tuff horizons, which has been dated at Esquina Blanca to 3.54 Ma. In the same locality, Walther et al. (1998) determined an age of 2.5 Ma for a second horizon about 180 m above the local base (Reguero et al. 2007). Evidence indicates that the average age of Uquía Formation is 3.02 Ma. After studying these fossils, Teta (2013) concluded that they belong to an undescribed species related to the living A. jelskii. We used these records to constrain the node leading to A. illutea and A. jelskii in the form of a normal prior distribution with mean of 3.02 and standard deviation of 0.52.

Results

Nucleotide sequence characteristics

The entire data set consist of 4441 bp of which 33.5% were variable. All nuclear genes display similar levels of variation and base composition (Table 2). The mitochondrial locus shows higher level of variation and compositional bias (Table 2).

Phylogenetic relationships

Parsimony, likelihood, and Bayesian single locus analyses recovered mostly resolved topologies except for some polytomies at the base of a few clades (Figs S2–S7). The monophyly of Abrotrichini was corroborated by all loci and reconstruction methods; in most cases abrotrichine monophyly was recovered with high support (BP/BS/BL/PP: cytb: 100/3/84/0.99, Adh: 100/11/92/1.0, βfbg: 99/7/99/1.0, DMP1: 87/5/64/1.0, Ins: 100/5/100/1.0 and IRBP: 98/8/100/1.0). Within the tribe, all loci recovered a clade formed by the long-clawed genera Chelemys, Geoxus, Notiomys, and Pearsonomys (cytb: 77/6/86/1.0, Adh: 92/3/80/0.86, βfbg: 59/1/67/0.75, DMP1: 81/3/76/1.0, Ins: 91/2/93/1.0 and IRBP: 69/1/72/0.95). Relationships within the long-clawed clade vary among loci; however, all analyses displayed the lack of monophyly of Chelemys and Geoxus.

The genus Abrothrix was recovered monophyletic, and as such sister to the long-clawed clade in the topologies of four of the six genes analysed independently: cytb (95/8/98/1.0), βfbg (82/2/89/1.0), DMP1 (69/2/67/1.0), and Ins (62/1/57/0.63). Within Abrothrix, it was possible to differentiate two main groups. The first group (hereafter 'olivacea group'), composed by A. andina, A. illutea, A. jelskii, and A. olivacea, was recovered with moderate to high support by the analysis of five loci (Adh: 52/1/58/0.98; βfbg only ML: 54; DMP1: 74/1/76/0.95; Ins: 77/2/81/1.0; IRBP ML and BI: 78/0.96). In most cases within this clade, A. andina and A. olivacea form a clade sister to a clade form by A. illutea and A. jelskii. The other main group of Abrothrix

Table 2 Variable sites, nucleotide contents, and sequence divergence within different groups of rodents of the tribe Abrotrichini

	Variable sites	A	C	G	T	% GC	Divergence (p distance)				
							Abrotrichini	Abrothrix	A. illutea	Long-clawed	G. valdivianus
Cytb	293	28.1	28.3	13.3	30.2	41.2	12.36	10.07	0.370	10.70	10.78
Adh	49	23.2	26.8	28.0	22.0	36.1	1.77	1.11	0.16	1.21	1.32
βfbg	74	30.2	23.7	31.8	14.3	39.2	2.40	1.43	0.00	2.52	1.37
DMP1	90	29.2	17.9	21.6	31.3	55.2	1.92	1.52	0.11	1.62	1.34
Ins	49	20.3	23.7	30.8	25.2	51.3	1.64	1.36	0.00	0.76	0.77
IRBP	86	32.0	19.4	16.9	31.6	54.2	1.71	1.50	0.00	1.09	0.54

Intraspecific comparisons of *Abrothrix illutea* and *Geoxus valdivianus* were between the specimens JPJ 1411 and 1479, and UACH 7262 and CNP 438, respectively.

(hereafter 'longipilis group') contains the species *A. lanosa*, *A. longipilis*, and *A. sanborni* and was recovered by the analysis of three loci (βfbg: -/1/72/1.0; DMP1: 56/1/51/0.92; Ins: 77/2/87/0.94). Within the *longipilis* group, *A. lanosa* and *A. sanborni* are sisters in most topologies.

The concatenated analyses of the six loci showed similar results to those of the individual analyses (Fig. 1 and Fig. S1). Topologies of MP, ML and BI were highly congruent, well resolved, and with high support for most clades. These topologies recovered the following main clades: Abrotrichini (100/42/100/1.0), long-clawed abrotrichines (100/15/100/1.0), *Abrothrix* (100/19/100/1.0), and within it the *olivacea* group (89/6/100/1.0) and *longipilis* group (55/6/94/1.0). MP, ML, and BI topologies recovered *A. olivacea* paraphyletic to *A. andina*. The three reconstruction methods differ in the position of *C. megalonyx* and *N. edwardsii*.

Twenty four abrotrichine nodes are identified in the concatenated ML and Bayesian trees (numbers in Fig. 1). Support for the main clades of the concatenated analyses is
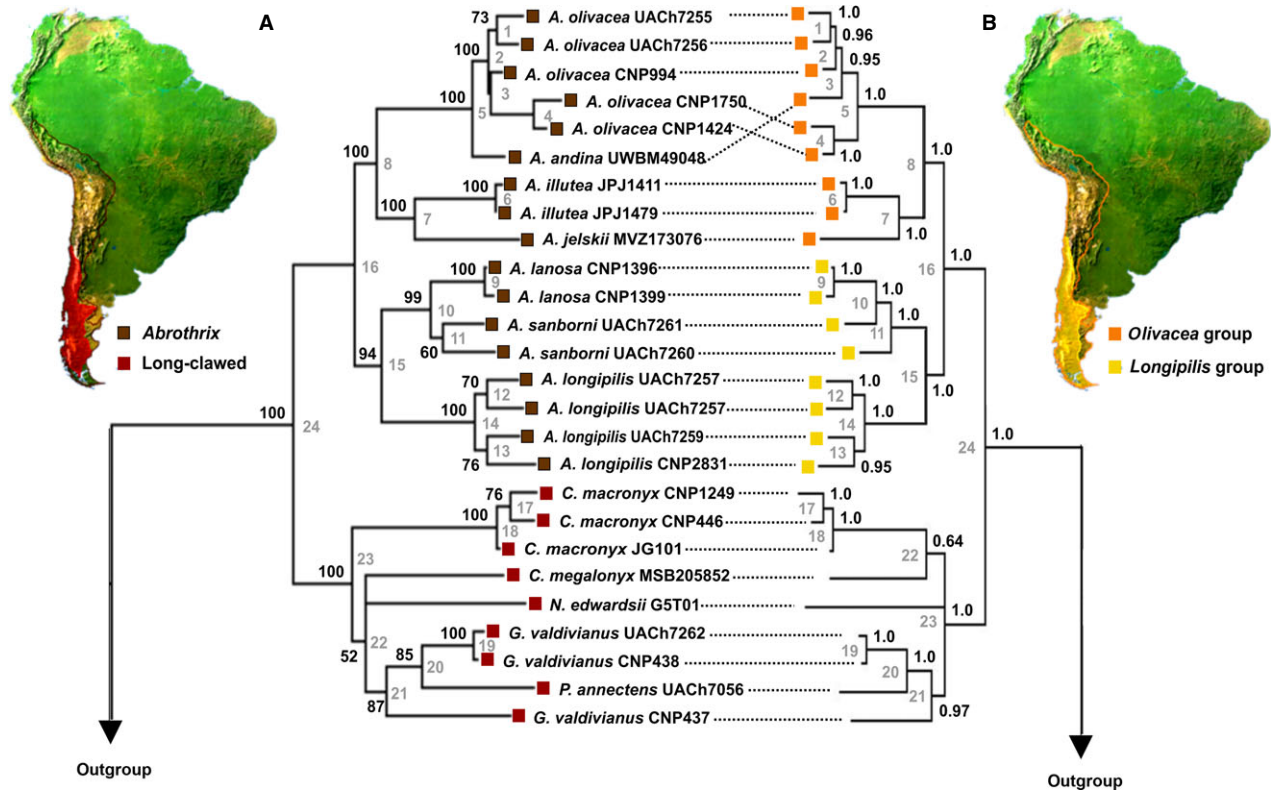

Fig. 1 Phylogenetic trees of abrotrichine rodents based on a concatenated matrix of six genes, and geographic distribution of the main clades recovered (left side: *Abrothrix* (brown) and long-clawed (red); right side: *olivacea* group (orange) and *longipilis* group (yellow). —A. maximum likelihood tree. Bootstrap values are indicated left of nodes. —B. Majority-rule consensus obtained in a Bayesian analysis. Posterior probabilities are indicated next to nodes. Specimen CNP437 of *Geoxus* corresponds to the southern clade of *Geoxus* (see text for details).

variable among gene partitions (Table S3). Meanwhile 25 abrotrichine nodes are identified in the concatenated MP tree (Fig S1, Table S4; values of partitioned Bremer support index are shown in Table S5).

Divergence dating

Molecular clock analysis estimated an age for the stem Abrotrichini of 7.01 Ma (95% HPD: 3.68–11.09) and for the abrotrichine crown group of 4.4 Ma (2.35–6.65). The long-clawed clade radiated at an estimated 3.12 Ma (1.66–4.94) and *Abrothrix* at 3.24 Ma (1.03–4.69). Finally, crown ages for the *olivacea* and *longipilis* groups were 2.71 Ma (1.61–3.78) and 2.61 Ma (1.35–3.95), respectively (Table 3).

Discussion

Current diversity of Abrotrichini is reviewed by Teta (2013) and D'Elía et al. (in press), whereas molecular phylogenetics of the tribe has been examined by Teta et al. (2011, and references therein). Our study of abrotrichine relationships provides strong support for the monophyly of the Abrotrichini, with an expanded representation of species within the group and, most importantly, with the addition of four new nuclear loci to the commonly used cytb and IRBP. Expanded taxon and gene sampling corroborate some hypotheses advanced in previous studies and provide new insights into the diversification of abrotrichines. Below, we first discuss the systematics of each of the two main clades within the tribe; then, we address the timing of abrotrichine diversification.

Systematics of Abrothrix

Abrothrix is a moderately diverse genus (i.e. 8 spp, Patterson et al. in press), but still the most diverse and widely distributed of Abrotrichini. It is also the one displaying the

Table 3 Divergence age estimates for the main clades of the tribe Abrotrichini based on a matrix combining of six genes. Ages (Ma) are mean node heights from HPD and intervals at 95% (upper–lower)

Main clade (N°)	Mean (Ma)	95% HPD (Ma)
Abrotrichini	4.4	2.35–6.65
Abrothrix	3.24	1.03–4.69
olivacea group	2.71	1.61–3.78
A. andina + A. olivacea	1.13	0.54–1.81
A. illutea + A. jelskii	1.81	0.88–2.81
longipilis group	2.61	1.35–3.95
A. lanosa + A. sanborni	1.38	0.58–2.36
A. longipilis	1.09	0.51–1.87
Long-clawed	3.12	1.66–4.94
C. macronyx + N. edwardsii	2.48	1.20–4.01
G. valdivianus + P. annectens	2.36	1.14–3.91

largest morphologic variation of the tribe. In addition, species within the genus have complex taxonomic histories (Tate 1932; Osgood 1943; Mann 1978; reviewed in Patterson et al. in press) and those that have been studied with a phylogeographic approach show intricate demographic histories (Palma et al. 2005, 2010; Rodríguez-Serrano et al. 2006; Lessa et al. 2010). Another relevant result of previous phylogenetic analyses based on mitochondrial and nuclear DNA sequences centred on *Abrothrix* was the fact that the topologies resulting from each locus were incongruent (Feijoo et al. 2010; Teta et al. 2011). These authors, after mentioning possible causes behind the incongruence seen, stated that the IRBP trees reflect better than the cytb trees the observed pattern of morphological variation and are more congruent with species distributions.

Species of *Abrothrix* fall into two monophyletic groups, which are highly supported by parsimony, likelihood, and Bayesian analyses of the concatenated matrix and show distinctive morphologies and species distributions. One of these clades is formed by *A. olivacea*, *A. andina*, *A. illutea*, and *A. jelskii*, whereas the other contains *A. longipilis*, *A. lanosa*, and *A. sanborni*; we refer them as the *olivacea* and *longipilis* groups, respectively.

Species of the *olivacea* group are primarily in the northernmost areas occupied by the tribe and are mostly distributed in open areas (Patterson et al. in press). *Abrothrix jelskii* is the abrotrichine with the northernmost distribution, reaching central Peru in the north (Arana-Cardó & Ascorra 1994; Jayat et al. 2013) and western of Bolivia and northern Argentina in the south. *Abrothrix illutea* has the most restricted range of the genus being found in northwestern Argentina (Teta et al. 2011). *Abrothrix andina* inhabits highlands from southern Peru to central Argentina and Chile (Osgood 1943). *Abrothrix olivacea* has the largest geographic distribution of the tribe ranging from the Peruvian-Chilean border west of the Andes and central Argentina (Mendoza) in the eastern side of the Andes towards the south where it reaches the Cape Horn in southernmost South America; in addition, in southern Patagonia and Tierra del Fuego it reaches the Atlantic (Musser & Carleton 2005). *Abrothrix hershkovitzi* is known from Aracena Island of Tierra del Fuego Archipelago as well as from islands in the Cape Horn group (Patterson et al. 1984). Only two cytb sequences attributed to this species are available in Genbank (EU840992 and EU840993); these sequences were retrieved from specimens (housed at the Museum of South-western Biology with numbers MSB 224744 and MSB 223869) collected at Aracena Island, the island where the type locality of *A. hershkovitzi* is placed. Both haplotypes fall within the clade of Fueguian *A. olivacea* (Abud 2011). As such, an assessment of the distinction of *A. hershkovitzi* requires additional sampling and multilocus data.

Species of the *longipilis* group are of southern distribution (Patterson *et al.* in press) and mostly associated to forested areas; *A. longipilis* is the most widely distributed species of the group, ranging from northern Tierra del Fuego in the south to central Argentina (Mendoza) and north-central Chile (Coquimbo) in the north. Meanwhile, *A. lanosa* and *A. sanborni* have bounded ranges predominantly associated to Valdivian and Magellan forest in southern South America (Osgood 1943; Feijoo *et al.* 2010).

Morphologically, species of the *olivacea* and *longipilis* groups are easily told apart (Teta *et al.* 2011). Species of the *olivacea* group are smaller than those of the *longipilis* group, with short pelage and dorsal coloration from dark brown or olive brown to grey or pale ochre. Further, they have slender skulls with nasals moderately extended, which result in a short and narrow rostrum. Meanwhile, species of the *longipilis* group are dark brown coloration or blackish and have nasals and premaxillae slightly projected anterior to the incisors forming a distinctive a trumpet-like tube. Species groups also differentiate in their gland penis morphology (Spotorno 1986; Gallardo *et al.* 1988; Feijoo *et al.* 2010; Teta *et al.* 2011). *Abrothrix andina*, *A. jelskii*, *A. illutea*, and *A. olivacea* show a complex baculum consisting of a reduced distal baculum with two lateral and one median cartilaginous mound. By the contrary, a simple baculum characterized by lacking cartilaginous digits on its extreme is present in *Abrothrix longipilis*, and *A. sanborni*, although that of *A. lanosa* shows reduced cartilaginous digits. As the complex type is also present in almost all other sigmodontines, it is considered the plesiomorphic character state for the tribe (i.e. the simple gland penis may be considered a synapomorphy of *longipilis* group).

The taxonomic history of *Abrothrix* is complex (see Patterson *et al.* in press for detailed synonymic list that includes early placement of some species in *Chelemys*, *Bolomys*, *Microxus*, *Oxymycterus*), but can be summarized as follows. The species *longipilis* and related forms (such as *sanborni*) were placed in *Abrothrix*, which depending on the authority was considered as a subgenus of *Akodon* (Reig 1987; Musser & Carleton 1993) or granted generic status (Hershkovitz 1966). Meanwhile, *illutea*, *olivacea* and related forms (e.g. *hershkovitzi*) were considered to be forms of *Akodon s.s.* (Reig 1987; Smith & Patton 1991). *Chroeomys*, encompassing its type species *jelskii*, was considered as a distinct genus (Musser & Carleton 1993). Finally, *andina* was considered as an *Akodon* (Honacki *et al.* 1982) or placed in *Chroeomys* (Musser & Carleton 1993). In addition, some authors considered these genera, *Abrothrix*, *Akodon* and *Chroeomys*, not to be closely related (e.g. Hershkovitz 1966 considered *Abrothrix* to be an oxymycterine and not an akodontine). The allozyme-based study of Spotorno *et al.* (1990) and the cytb-based studies of Smith & Patton (1991, 1993, 1999)

discovered the phylogenetic closeness of species currently placed in *Abrothrix*; however, even when Spotorno *et al.* (1990) suggested placing all these species in *Abrothrix*, most authors kept allocating them in the three mentioned genera or subgenera (Smith & Patton 1991, 1993; Musser & Carleton 1993). D'Elía (2003) found similar results to those of Smith & Patton (1999) and after considering three classificatory schemes, suggested formally placing all of them, including *jelskii*, in *Abrothrix*. This usage of *Abrothrix* is currently in use (Patterson *et al.* in press).

Our phylogenetic results, congruent with morphological variation and geographic distribution, bring up the possibility of splitting the genus *Abrothrix*. Even when *Abrothrix* as currently understood is monophyletic, and as such the current classificatory scheme is fully congruent with the more robust available phylogeny, different authors have discussed the issue of split the now allegedly morphologically diverse *Abrothrix* (Teta *et al.* 2011; Teta 2013; Patterson *et al.* in press). One possibility may be to (i) restrict *Abrothrix* to the *longipilis* group, which contains *longipilis*, type species of the genus (thereby, *Abrothrix* will include *A. lanosa*, *A. longipilis*, and *A. sanborni*) and (ii) use the available epithet *Chroeomys* for the *olivacea* group, which contains *jelskii* type species of the genus (this way, *Chroeomys* will include *andina*, *illutea*, *jelskii* and *olivacea* and related forms). An alternative option considered and disregarded by D'Elía (2003; see also Patterson *et al.* in press) is to (i) restrict *Abrothrix* to *longipilis* and associated forms (i.e. the *longipilis* group), (ii) delimit *Chroeomys* to include its type species *jelskii* and eventually *illutea*, which is sister to *jelskii*, and (iii) nominate a new genus to *A. andina*, *A. olivacea* and associated forms. Acknowledging that *Abrothrix* is morphologically heterogeneous and that splitting would be useful if resulting genera are confidently diagnosed, we defer nomenclatural action until resulting genera be morphologically diagnosed (Teta 2013). Finally, our results showing the paraphyly of *A. olivacea* with respect to *A. andina* suggest that species limits within *Abrothrix* should be further evaluated.

Systematics of the long-clawed abrotrichines

Four of the five abrotrichine genera have semi-fossorial and fossorial habits. Fossorial rodents are characterized by reduced eyes and ears, short tails and pelage, long claws (Shimer 1903; Prout 1964; Nevo 1979; Reig *et al.* 1990; Yates & Moore 1990), and characteristic skeletal, muscular and physiologic changes (Shimer 1903; Stein 2000). Several of these features are found in a mosaic pattern among long-clawed abrotrichines (Pearson 1984).

The taxonomic history of long-clawed abrotrichines is contorted. *Chelemys* and *Geoxus* were described as subgenera of *Akodon* (Thomas 1903). Osgood (1925) transferred them to *Notiomys*, a position followed by some authorities

(Ellerman 1941; Osgood 1943; Cabrera 1961) but not by others, who ranked then as distinct genera (Thomas 1927; Gyldenstolpe 1932). Latter, Pearson (1984) consolidated the current view that considers these taxa as distinct genera, given the degree of morphological differentiation among them (see also Reig 1987). Finally, Patterson (1992) described a fourth genus of long-clawed abrotrichines, the monospecific *Pearsonomys*, and identified five external and 12 cranial and dental state characters that it shares with *Geoxus* to the exclusion of *Chelemys*. In general, genera of long-clawed abrotrichines are poorly known. Most of this knowledge comes from taxonomic revisions, range extensions and the collection of basic natural history data (Pearson 1984; Martin & Archangelsky 2004; D'Elía *et al.* 2006; Pardiñas *et al.* 2008; Figueroa *et al.* 2012).

In line with previous studies (D'Elía *et al.* 2006; Rodríguez-Serrano *et al.* 2008; Feijoo *et al.* 2010; Teta *et al.* 2011), the monophyly of the fossorial clade is well supported by our data. Relationships within this clade vary across analyses. Nevertheless, results of concatenated analysis are robust in relation to two important issues of fossorial abrotrichine systematics.

The first of these issues relates to *Chelemys*. Rodríguez-Serrano *et al.* (2008) showed the lack of monophyly of *Chelemys*, as *C. macronyx* is not sister to *C. megalonyx* in their analyses. Our results, with much denser taxonomic sampling and additional loci, corroborate this finding. However, it is worth noting that for *C. megalonyx*, we have analysed sequences of only two genes retrieved from two distinct specimens (MSB 205807 and MSB 205852; Table S1) but collected at the same area, Parque Nacional Fray Jorge, Coquimbo, Chile, were no other long-clawed abrotrichine species has been reported. No analysis recovered *C. megalonyx* as sister to *C. macronyx*. There is no less inclusive clade than the entire long-clawed clade that includes *megalonyx* and *macronyx*; therefore, if both species are to be kept in the same genus, the only option is to return to the all inclusive *Notiomys*, as in Osgood (1925). Under this scheme, *Chelemys*, *Geoxus* and *Pearsonomys* would be junior synonyms of *Notiomys*. As stated above, this conception has been rejected in the light of the large degree of morphological variability that such genus would encompass. Therefore, the simplest option for a classification consistent with the phylogeny is to restrict *Chelemys* to its type species, *megalonyx*, and to describe a new genus for *macronyx*. This action should be formally undertaken only after a morphological diagnosis of the new genus is available. Similarly, the analysis of additional sequence data for *C. megalonyx* is also desirable.

The second issue of fossorial abrotrichine systematics to which our results shed new light pertains to the distinction of *Geoxus* and *Pearsonomys*. When describing *Pearsonomys*, Patterson (1992) highlighted both its distinctive traits and

its closer similarity to *Geoxus* than to *Chelemys*. Even so, the paraphyly of *Geoxus* relative to *Pearsonomys* reported by Lessa *et al.* (2010) on the basis of cytb sequences was unexpected. It was found that *Geoxus* is composed of two highly divergent (10.9% observed divergence in the cytb gene, Table 2) clades that latitudinally replace each other and that are not sister to each other. The northern clade was recovered as sister to *Pearsonomys*, and the southern *Geoxus* clade was, in general and with varying degree of support, sister to the clade of northern *Geoxus* plus *Pearsonomys*. Observed divergence at the cytb gene between *Pearsonomys* and northern *Geoxus* is 8.5% and between *Pearsonomys* and southern *Geoxus* is 10.6%. Our multilocus analysis confirms that *Geoxus valdivianus* is not monophyletic (Fig. 1), corroborating the finding of Lessa *et al.* (2010). This implies that classificatory changes are needed at two levels. At the generic level, one option is to consider *Pearsonomys* a junior synonym of *Geoxus*. This way, *Geoxus* would comprise three species, *annectens* and the two currently encompassed in *valdivianus*. Another option, less compatible with the degree of morphological variation displayed by both forms currently placed under *valdivianus*, is to name a new genus for the southern form. In any case, the formal proposition of a new classificatory scheme needs to be backed by a detailed morphological assessment (Teta 2013). At the species level, our results imply that the name *valdivianus* should be restricted to northern *Geoxus*, given that the geographic location of these specimens is near to type locality described by Philippi (1858) for *Oxymycterus valdivianus*. Similarly, for the southern clade of *Geoxus* the name *bicolor* Osgood (1943) is available; a morphological evaluation of this taxonomic form in the context of a larger geographic coverage would clarify if this name corresponds to southern *Geoxus*. In this line, it is worth expanding the geographic coverage to the area of Punta Arenas, in the northern shore of the Strait of Magellan, to include representatives of the form *michaelseni* Matschie (1898), and as such clarify if the southern clade reaches that latitude (i.e. in which case the name *michaelseni* would apply) or if southernmost populations of the genus belong to a distinct species of *Geoxus* as suggested by Reig (1987).

Timing of the abrotrichine diversification

Estimations of divergence times are an important exercise to learn about the process of differentiation. In this sense, calibration is a critical step in this type of analysis because it is necessary to have reliable data for a correct estimate. Fossil evidence and biogeographic events constitute invaluable elements to infer divergence times of their respective living lineages (Warnock *et al.* 2012). The oldest taxa traditionally considered to be related to *Abrothrix* are *Abrothrix kermacki* and *A. magna*; two forms found almost 1000 km eastward

of the current generic distribution. Both forms are from the upper Pliocene and early Pleistocene of near Mar del Plata, Buenos Aires, Argentina (Reig 1987). However, the generic allocation of these forms has been questioned by Pardiñas (1999) and Teta (2013). Recently, Ortiz *et al.* (2012) reported a new extinct species related to *Abrothrix* derived from Uquía Formation, Jujuy Province, Argentina. Fossil horizons of Uquía Formation have been dated between 3.54 Ma (Marshall *et al.* 1982) and 2.5 Ma (for more details see Reguero *et al.* 2007). Mandible and molar descriptions emphasize the closeness of this record with *A. jelskii* (Teta 2013). We used this record from Uquía to calibrate the relaxed molecular clock analysis.

As happens with several other animal clades, including that of the subfamily Sigmodontinae (Parada *et al.* 2013), molecular estimates indicate the tribe Abrotrichini radiated well before the earliest fossil record found so far for the tribe. Our calibration based on multilocus data estimated the crown age of Abrotrichini around the early Pliocene (4.4 Ma, Zanclean Age). Broadly, our estimation is slightly younger but still in line with those obtained on the basis of other calibration points and data sets by Rodríguez-Serrano *et al.* (2008; 5 Ma) and Parada *et al.* (2013; 4.9 Ma). As such, Abrotrichini and Sigmodontini are the two sigmodontine tribes that radiated more recently; the only ones whose crown groups entirely diversified in the Pliocene. The successive bouts of Andean uplift during the Pliocene favored the differentiation of biogeographic subregions and the creation of new habitats (Ortiz-Jaureguizar & Cladera 2006). Similarly, the marked climatic changes occurring during the Pliocene/Pleistocene transition (e.g. cyclical advancew and retreats of glaciers), which affected species geographic ranges (Pascual *et al.* 1996; Ortiz-Jaureguizar & Cladera 2006; Tonni & Carlini 2008), may have prompted the diversification of the abrotrichines.

In this regard, it is of interest to note that, even though crown ages of both main abrotrichine clades are about the same (Table 3), the long-clawed clade attained a larger degree of external and cranial morphological variation than *Abrothrix*, perhaps as a result of fossoriality. We expect that results of the present study, including both the phylogenetic relationships and divergence time estimations, would constitute the basis for future studies on the evolutionary biology of abrotrichine rodents.

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Supporting Information

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

Table S1. List of specimens of the tribe Abrotrichini used per locus in the phylogenetic analysis.

Table S2. Primers (forward and reverse) used to amplify and sequence one mitochondrial and five nuclear genes for selected abrotrichine rodents.

Table S3. Congruence of the different solo partition analyses with the concatenated analyses (ML: Maximum Likelihood; BI: Bayesian inference) of abrotrichine DNA sequences (see text for gene abbreviations).

Table S4. Descriptive values for the Maximum Parsimony analysis of abrotrichine relationships per locus and for the combined matrix.

Table S5. Partitioned Bremer support values obtained in the analysis of one mitochondrial and five nuclear loci of abrotrichine relationships.

Fig. S1. Phylogenetic tree obtained in the concatenated maximum parsimony analysis of abrotrichine DNA sequences.

Fig. S2. Phylogenetic trees of relationships among abrotrichines obtained from the cytb gene solo analysis.

Fig. S3. Phylogenetic trees of relationships among abrotrichines obtained from the Adh gene solo analysis.

Fig. S4. Phylogenetic trees of relationships among abrotrichines obtained from the βfbg gene solo analysis.

Fig. S5. Phylogenetic trees of relationships among abrotrichines obtained from the DMP1 gene solo analysis.

Fig. S6. Phylogenetic trees of relationships among abrotrichines obtained from the Ins gene solo analysis.

Fig. S7. Phylogenetic trees of relationships among abrotrichines obtained from the IRBP gene solo analysis.