Phylogeny of the tribe Abrotrichini (Cricetidae, Sigmodontinae): integrating morphological and molecular evidence into a new classification

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Abstract

The tribe Abrotrichini (five genera and 14 living species) is a small clade within the speciose subfamily Sigmodontinae (Rodentia, Cricetidae), representing one of the extant successful radiations of mammals at southern high latitudes of the Neotropics. Its distribution is mostly Andean, reaching its greatest diversity in southern Argentina and Chile. We evaluate the phylogenetic relationships within this tribe through parsimony and Bayesian approaches based on 99 morphological characters (including 19 integumental characters, 38 skull characters, 31 dental characters, three postcranial skeletal characters, seven from the male accessory glands and phallus and one from the digestive system) and six molecular markers (one mitochondrial and five nuclear). We include representatives of all, except one, of the currently recognized species of living Abrotrichini plus one fossil form. Based on total evidence, we recovered a primary division between the genus *Abrothrix* and a group including the long-clawed Abrotrichini, *Chelemys*, *Geoxus*, *Notiomys* and *Pearsonomys*. Both clades are recognized and named here as subtribes. The large degree of morphological variation observed within *Abrothrix* suggests that species in the genus fall into four groups, which we recognize as subgenera. In addition, the two known species of *Chelemys* do not form a monophyletic group, and *Geoxus* was recovered as paraphyletic with respect to *Pearsonomys*. To reconcile classification and phylogenetics, we describe a new genus for *Chelemys macronyx* and include *Pearsonomys* as a junior synonym of *Geoxus*. Our results highlight the importance of both morphology and molecules in resolving the phylogenetic relationships within this tribe. Based on biogeographical analyses, we hypothesize that Abrotrichini originated in south-western South America by vicariance and then diversified mostly by successive dispersal events.

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The tribe Abrotrichini, which includes the genera *Abrothrix* Waterhouse, 1837, *Chelemys* Thomas, 1903, *Geoxus* Thomas, 1919, *Notiomys* Thomas, 1890, and *Pearsonomys* Patterson, 1992, represents a small clade (14 species) within the speciose subfamily Sigmodontinae (> 400 species; see Patton et al., 2015). From a morphological and ecological viewpoint, Abrotrichini is a diverse group including cursorial/scansorial (e.g. *Abrothrix*) to fossorial (e.g. *Geoxus*) forms with insectivorous (e.g. *Notiomys*) to herbivorous (e.g. *Chelemys*) food habits, which vary in size from ~20 g (e.g. *Abrothrix andina*) to ~55 g (e.g. *Chelemys macronyx*). The species of this tribe occupy a variety of habitats, from humid–cold and forested areas (e.g. *Geoxus*) to open herbaceous or shrubby steppes (e.g. *Abrothrix*, *Notiomys*). The Plio-Pleistocene fossil record of this tribe includes only a single form, referred to as aff. *Abrothrix* by Ortiz et al. (2012), from north-western Argentina. Other two Pliocene species referred to *Abrothrix* by Reig (1978, 1987), †"*Ab.*" *kermacki* and

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†"*Ab.*" *magna*, do not fit the diagnosis of the tribe Abrotrichini and were recently reassigned to the tribe Akodontini (Teta et al., 2014). Fossil remains of living species are known from Patagonia, central and southern Chile and north-western Argentina and are restricted to the Late Pleistocene–Holocene (e.g. Pardiñas et al., 2002; Ortiz et al., 2011; Tammone et al., 2014).

Abrotrichini possesses some peculiarities which make it unique within the Sigmodontinae (Rodríguez-Serrano et al., 2008a). Its distribution is mostly Andean, reaching its greatest diversity in southern Argentina and Chile (see Patton et al., 2015); indeed, Abrotrichini could be considered as one of the few successful radiations of Recent Neotropical mammals at high latitudes (e.g. Pardiñas et al., 2011; Cañón et al., 2014). Additionally, four of its five genera (i.e. *Chelemys*, *Geoxus*, *Notiomys* and *Pearsonomys*) have adaptations for subterranean life and are considered fossorial, an unusual lifestyle within Sigmodontinae (e.g. Pearson, 1984).

The taxonomic history of the Abrotrichini was closely linked to that of the tribe Akodontini, in which its members were included during most of the 20th century (e.g. Reig, 1987). Although several authors had noted the connection among the long-clawed mice of the genera *Chelemys*, *Geoxus*, *Notiomys* and *Pearsonomys* (e.g. Osgood, 1925; Pearson, 1984; Reig, 1987; Patterson, 1992), the close relationship between this group and *Abrothrix* was not envisaged until the 1990s (see Table 1). According to Reig (1987, who included *Abrothrix* as a subgenus of *Akodon*), *Abrothrix*, *Chelemys*, *Geoxus* and *Notiomys* (*Pearsonomys* was described later) comprised a southern radiation of the tribe Akodontini. Moreover, some forms now included within *Abrothrix* (e.g. *Ab. andina*, *Ab. olivacea*) were treated by Reig (1987) as members of the subgenus *Akodon* (*Akodon*) (Table 1). Reig (1987) also considered as valid the genus *Chroeomys* Thomas, 1916, a taxon that others had included as a subgenus (e.g. Cabrera, 1961) or even as a full synonym of *Akodon* (e.g. Voss and Linzey, 1981). Subsequent analyses based on allozymes provided additional information on the relationships between these genera (e.g. Patton et al., 1989; Spotorno et al., 1990; Dickerman, 1992; Barrantes et al., 1993), but it was not until the late 1990s when this clade was recognized as a separate entity (see also Engel et al., 1998; Smith and Patton, 1999). Initially designated as the "Andean Clade" by Smith and Patton (1993, 1999), the tribe Abrotrichini was formally diagnosed and defined by D'Elía et al. (2007).

During the last decade, molecular evidence has clarified the interrelationships among the members of this tribe (e.g. D'Elía et al., 2003, 2006; Rodríguez-Serrano et al., 2008a; Feijoo et al., 2010). One of the main conclusions was that Abrotrichini comprises two principal clades, one encompassing the mostly long-clawed forms *Chelemys*, *Geoxus*, *Notiomys* and *Pearsonomys*, and the other restricted to the cursorial/scansorial taxa of the genus *Abrothrix*. Within this context, Spotorno et al. (1990) and D'Elía (2003) needed to include *Chroeomys* within *Abrothrix* in order to maintain the monophyly of the genus. However, the relationships among species and even genera within this clade are not completely resolved; in fact, trees obtained from the analysis of different genes are usually contradictory (e.g. Teta et al., 2011; Cañón, 2012; Cañón et al., 2014). In the case of *Abrothrix*, the topologies inferred from unlinked loci show different phylogenetic relationships among species (Cañón, 2012; Cañón et al., 2014). At the generic level, while *Abrothrix* is recovered as a monophyletic group, some authors suggest that patterns of morphological variation within this clade are better reflected by its division into two or more genera (Teta et al., 2011; Patterson et al., 2015). A different situation is evident within the clade of long-clawed Abrotrichini, where the analysis of molecular markers rejects the monophyly of *Chelemys* and *Geoxus*, at least as they are currently understood (D'Elía et al., 2006; Rodríguez-Serrano et al., 2008a; Teta et al., 2011; Cañón, 2012).

The geographical range of Abrotrichini extends from the west central altiplano of Peru and the western mountain ranges of Argentina and Bolivia to the southernmost parts of Argentina and Chile, including several austral islands and the Patagonian steppe (Patton et al., 2015). To better understand the biogeographical history of Sigmodontinae, Reig (1972, 1984, 1986a,b) used the concept of Area of Original Differentiation (AOD) to discuss the geographical origin and dispersion of different groups in this subfamily. In his conception, taxa now grouped in Abrotrichini were the southern Andean component of the Akodontini. Reig (1986a,b) postulated that the zone between the south-central and the north-southern Andes was the AOD for Akodontini, specifically in the southern Puna region which extends from central Peru southward to north-western Argentina. From this area, the southern Andean component would have dispersed southward and then differentiated at higher latitudes. Reig (1986a,b) considered the southern Andes as a focal point or secondary area of differentiation for the genera now included in Abrotrichini.

As was summarized above, several unresolved questions related to the phylogeny of the Abrotrichini highlight the importance of a phylogenetic analysis that integrates the available data together with new character systems. In this work, we propose a new phylogenetic hypothesis for the tribe, including all but one of the currently recognized species and the only known fossil representative, based on the cladistic analysis of combined morphological and molecular

Table 1
Main taxonomic hypotheses for the genera now referred to Abrotrichini

Thomas (1916, 1927) Akodonts	Ellerman (1941) Akodonts	Osgood (1943) Akodonts	Cabrera (1961) Akodonts
Abrothrix	*Akodon* (*Abrothrix*)	*Akodon* (*Abrothrix*)	*Akodon* (*Abrothrix*)
*Akodon**	*Akodon* (*Akodon*)*	*Akodon* (*Akodon*)*	*Akodon* (*Akodon*)*
Chroeomys	*Akodon* (*Chroeomys*)	*Chroeomys*	*Akodon* (*Chroeomys*)
Chelemys	*Notiomys*[†]	*Notiomys*	*Notiomys*
Geoxus	*Notiomys*	*Notiomys*	*Notiomys*
Notiomys	*Notiomys*	*Notiomys*	*Notiomys*

Voss and Linzey (1981) Akodonts	Reig (1987) Akodontini[§]	Smith and Patton (1999) Andean Clade	D'Elía et al. (2007) Abrotrichini
Abrothrix[‡]	*Akodon* (*Abrothrix*)	*Abrothrix*	*Abrothrix*
Akodon	*Akodon* (*Akodon*)	*Abrothrix*	*Abrothrix*
Chroeomys	*Chroeomys*	*Chroeomys*	*Abrothrix*
Notiomys[¶]	*Chelemys*	*Chelemys*	*Chelemys*
Notiomys	*Geoxus*	*Geoxus*	*Geoxus*
Notiomys	*Notiomys*	*Notiomys*	*Notiomys*
		*Pearsonomys***	*Pearsonomys*

[*]This name was applied to species currently included under *Angelomys* subgen. nov.

[†]Ellerman (1941) recognized three species groups within *Notiomys*: "edwardsii Group", "valdivianus Group" and "megalonyx Group", which coincide with modern concepts of the genera *Notiomys*, *Geoxus* and *Chelemys*, respectively.

[‡]Genus treated as belonging to the "oxymycterine group," which was regarded as outside of akodonts, *sensu stricto*.

[§]In part; this list does not include all the genera of Akodontini recognized by Reig (1987).

Including *Chelemys* and *Geoxus* as synonyms.

[**]Genus and species not described until 1992 (Patterson, 1992).

data. In addition, we tested via parsimony and Bayesian approaches the biogeographical hypothesis advanced by Reig (1986a,b). This is the first combined-evidence phylogenetic analysis for this tribe, based on the widest taxon and character sampling to date. In addition, it is the first attempt to assess relationships within Abrotrichini that includes morphological features in an explicit phylogenetic context. These sources of evidence (morphological and molecular) are first considered separately and then in combination. Based on the results, a new taxonomic classification is proposed.

Materials and methods

Taxonomic sampling

We studied 291 specimens of sigmodontine rodents (see Data S1 for a complete list of specimens examined), including representatives of all but one of the currently recognized species of Abrotrichini (see Patton et al., 2015), as well as six outgroups. *Abrothrix hershkovitzi*, a species that some consider a synonym of *Ab. xanthorhina* (see Abud, 2011), was the only form omitted from our analyses. In addition, we included a fossil form, designated as aff. *Abrothrix* by Ortiz et al. (2012) and here called †*Abrothrix* sp. nov. This fossil comes from the Uquía Formation (Middle Pleistocene), Jujuy, Argentina, and is the only known extinct species of tribe Abrotrichini (see Teta et al., 2014). Whenever possible, we examined at least ten specimens per taxon. Species were identified by comparisons with reference materials and original descriptions. Taxonomy follows Patton et al. (2015), with modifications (justifications for our taxonomic usages appear in Data S2). The outgroups we chose for this study include representatives of the tribes Akodontini (*Akodon azarae*), Oryzomyini (*Holochilus brasiliensis*), Phyllotini (*Phyllotis xanthopygus*), Reithrodontini (*Reithrodon auritus*), Sigmodontini (*Sigmodon hispidus*) and Wiedomyini (*Wiedomys pyrrhorhinos*). We chose these taxa because they were used as outgroups by Cañón et al. (2014) and broadly represent the diversity of other lineages within Oryzomyalia, the sigmodontine clade that includes the Abrotrichini together with Akodontini, Euneomyini, Oryzomyini, Phyllotini, Reithrodontini, Thomasomyini, Wiedomyini and several *incertae sedis* genera (Steppan et al., 2004). Monophyly of Abrotrichini was not tested, as it has been strongly and consistently supported by previous studies using molecular markers (e.g. Parada et al., 2013; Salazar-Bravo et al., 2013; Schenk et al., 2013; Cañón et al., 2014; Pardiñas et al., 2015). *Sigmodon hispidus* was used to root the trees, because it is the sister group to Oryzomyalia within Sigmodontinae (e.g. Engel et al., 1998; Steppan et al., 2004; Schenk et al., 2013).

Character sampling

Morphology dataset. The morphological data matrix included 19 integumental characters, 38 skull characters, 31 dental characters, three postcranial characters, seven characters from the male accessory glands and phallus, and one character from the digestive system. Integumental and skull characters were scored from adult individuals in age-classes 3–6 (*sensu* Patterson, 1992), whereas dental characters were evaluated in specimens aged 2–4. Anatomical descriptions for each character are included in Appendix 1. Anatomical terminology follows Carleton (1980), Carleton and Musser (1989), Steppan (1995), Pacheco (2003) and Weksler (2006). Dental structures were designated following Reig (1977) and O'Leary et al. (2013). Scoring of male accessory gland, phallus and digestive system traits was based on the descriptions of Hooper and Musser (1964), Carleton (1973), and Voss and Linzey (1981), respectively. Nevertheless, we verified these characters through direct examination of specimens whenever suitable material was available.

Morphological characters were defined using a reductive approach, focusing on their logical independence (Wilkinson, 1995; Strong and Lipscomb, 1999). Discrete characters (i.e. features with explicitly defined and distinctly different character states) were prioritized in the analysis; continuous characters, those describing relative position, distance, shape or colour, were included only if discontinuous differences between states could be established. Because characters were primarily selected to resolve Abrotrichini relationships, the non-molecular dataset does not include autapomorphic characters for outgroup taxa; it does, however, include autapomorphies for ingroup taxa that might plausibly serve as synapomorphies for clades in this analysis (see Weksler, 2006, for a similar approach). Multistate characters were coded as non-additive (Prevosti, 2010). Polymorphisms were coded as such (coded as 0–1 if both states were represented by different specimens of a taxon; Campbell and Frost, 1993). With this method, the most parsimonious state is chosen from among the alternatives for polymorphic characters/taxa during parsimony searches.

Molecular dataset. We used the same molecular dataset employed by Cañón et al. (2014; sequences available at Genbank: http://www.ncbi.nlm.nih.gov/), which included one mitochondrial locus and five nuclear loci (Data S3). The mitochondrial fragment corresponds to the first portion of the protein-coding cytochrome b gene (cytb); and the nuclear loci are: (i) exon 6 of the gene coding for the dentin matrix (DMP1), (ii) first exon of the gene coding for 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 the gene encoding preproinsulin 1 (Ins). The number of studied specimens, primers used, and methods for the editing and alignment of sequences are detailed by Cañón et al. (2014).

Phylogenetic analyses

Phylogenetic analyses were conducted under a maximum-parsimony criterion using the software TNT 1.1 (Goloboff et al., 2008) for the morphological matrix and for the combined dataset. Parsimony searches were conducted using TNT's default treatments of multistate taxa and branch collapse, and running new technology searches (xmult: 10 rounds of ratchet, 10 of drifting, in addition to program defaults for sectorial searches and fusing). We specified 20 hits on the shortest-length tree and performed subsequent traditional searches using bbreak, followed by 250 replications of a traditional search (mult command, with defaults except for numbers of replications). The information contained in the most parsimonious trees was synthesized through strict consensus (Bremer, 1990). For each tree, we calculated the length and the consistency (CI) and retention (RI) indices. The non-molecular data matrix was analysed with equal weights for all characters.

To evaluate the support of the branches, we used the option of symmetric resampling, which is not distorted by character weighting (Goloboff, 1993; Goloboff et al., 2003), and Bremer support values (Bremer, 1994). Symmetric resampling was expressed by group frequencies (SR) and group differences (GC), which assess the contradiction between the characters (Goloboff et al., 2003); both measures were calculated by performing 1000 pseudoreplicates, each consisting of ten random addition searches. In addition, we calculated partitioned Bremer support (PBS; Baker and De Salle, 1997) values in the simultaneous analysis. PBS provides a measure of the positive or negative contribution of each partition to nodal support. PBS was calculated using two sets of partitions: (i) morphological vs. molecular data, and (ii) internal partitions for each dataset: six partitions for the morphological characters (i.e. integumental, cranial, dental, postcranial, reproductive, digestive) and five for the molecular characters (cytb, IRBP, DMP1, βfbg, Adh, Ins).

Bayesian phylogenetic reconstructions were carried out using MrBayes 3.2 (Ronquist and Huelsenbeck, 2003) on the morphological and combined dataset (morphology and DNA characters; for phylogenetic molecular analyses, see Cañón et al., 2014). We implemented Bayesian analyses to compare results obtained by parsimony (a method that produces point

estimates, i.e. single trees) with an approach that instead produces a probability distribution (Bayesian); we could also compare results obtained under parametric (Bayesian) and non-parametric (parsimony) methods. For the simultaneous analysis, we used two character partitions, morphology and DNA. We ran the standard partition (characters 1–99) using the Mk model, set by default in MrBayes for morphological characters, which assumes no constant characters are present (Mkv model; Lewis, 2001). This was done using the standard model for unordered characters with a standard gamma distribution to accommodate rate variation across sites. The DNA partition (100–4540) was run using the GTR+G+I model determined using the Akaike information criterion (AIC) in jModeltest (Posada, 2008). All analyses were run for a total of 1×10^7 generations. Trees were sampled every 1000 generations resulting in 10 000 saved trees, the first 25% of which were discarded as burn-in. The remaining trees were used to construct a majority-rule consensus tree and obtain *a posteriori* probability values.

Biogeographical analysis

To analyse ancestral areas, two different methods were used: Fitch optimization (FP, Ronquist, 1994), originally developed for character-state reconstructions, and dispersal-vicariance analysis (DIVA), developed specifically for ancestral range reconstructions. The Fitch optimization was performed with TNT 1.1 (Goloboff et al., 2008), constructing a matrix based on the total-evidence parsimony tree, and a matrix of distributional characters representing the geographical distribution of the terminals. The geographical matrix was constructed by assigning the distribution of each species to one or more of 13 biogeographical provinces proposed by Morrone (2014, 2015) for the Neotropical and Andean regions: Atacama, Chacoan, Coquimban, Prepuna, Puna, Magellanic forest, Maule, Monte, Patagonian, Rondonia, Santiagan, Valdivian forest and Yungas (for a map and details see Morrone, 2014, 2015). Dispersal-vicariance analysis (S-DIVA) was implemented in RASP software (Reconstruct Ancestral State in Phylogenies; Yu et al., 2011). For this analysis, we used the Bayesian combined trees obtained with MrBayes and the same geographical distribution data. Frequencies of an ancestral range at a node in the reconstructions are averaged over all trees, and each alternative ancestral range at a node is weighted by the frequency with which the node occurs or by some other measure of nodal support (Yu et al., 2011). Terminals present in more than one area were coded as multistate. Four chains were run simultaneously for 5×10^5 generations, sampling every 1000, and the temperature for heating the chains was 0.1.

Results

Phylogenetic analyses

The morphological data matrix has $99 \times 26 = 2574$ cells, of which 146 (5.6%) were scored as missing ("?"), two (0.1%) were scored as inapplicable ("-") and 48 (1.9%) were scored as polymorphic (Data S4). Data completeness for most terminal taxa ranged from 88 to 100%, except for †*Abrothrix* sp. nov., which could be scored for only 19 (19%) characters. The molecular data matrix consists of 4441 bp of which 1490 sites were variable. Cytochrome b shows the highest levels of variation, whereas the nuclear locus for Ins shows the lowest (Data S5).

The analysis of the combined matrix, including morphological data and six molecular markers, produced two most parsimonious trees, each with 3102 steps (CI = 0.605; RI = 0.554). The strict consensus is shown in Fig. 1. The analysis recovered a major dichotomy between *Abrothrix* and the long-clawed Abrotrichini. Some relationships within these clades were incompletely resolved. One polytomy involved *Chelemys megalonyx*, *Notiomys* and [*Geoxus* (*Geoxus-Pearsonomys*)], and a second polytomy occurred within *Abrothrix*, involving *Ab. jelskii cruceri*, *Ab. jelski sodalis* and the fossil form †*Abrothrix* sp. nov. A total of 17 nodes were recovered in the combined parsimony analysis (Fig. 1). PBS indicate that morphological and DNA characters supported 13 and nine clades, respectively (see tables S6.1 and S6.2 in Data S6). Only five clades are supported by characters of both datasets. The main clades of our topology (i.e. Abrotrichini, *Abrothrix* and long-clawed Abrotrichini) are uniquely defined by positive contributions of morphology relating to the dentition (tables 6.1s and 6.2s in Data S6). In order of importance, dental, skull and integumental characters were the morphological partitions with the largest contributions, whereas βfbg, cytb and Ins were the molecular sequences with the largest positive participation (tables 6.1s and 6.2s in Data S6). Similarly, the Bayesian combined topology recovered the main division between *Abrothrix* (with two internal clades) and the remaining genera (Fig. S1a). All relationships within the tribe are resolved and well supported.

A heuristic search of the morphological data produced a single most-parsimonious tree of 280 steps (CI = 0.475; RI = 0.754). The topology of this tree indicated a major dichotomy between a clade containing *Abrothrix* taxa and another with the long-clawed Abrotrichini, *Chelemys*, *Geoxus*, *Notiomys* and *Pearsonomys* (Fig. 2). Overall, the supporting values were higher for the latter group than for *Abrothrix*. Synapomorphies and autapomorphies are listed in Appendix 2. Bayesian analysis also recovered the major dichotomy between *Abrothrix* and the long-clawed Abrotrichini
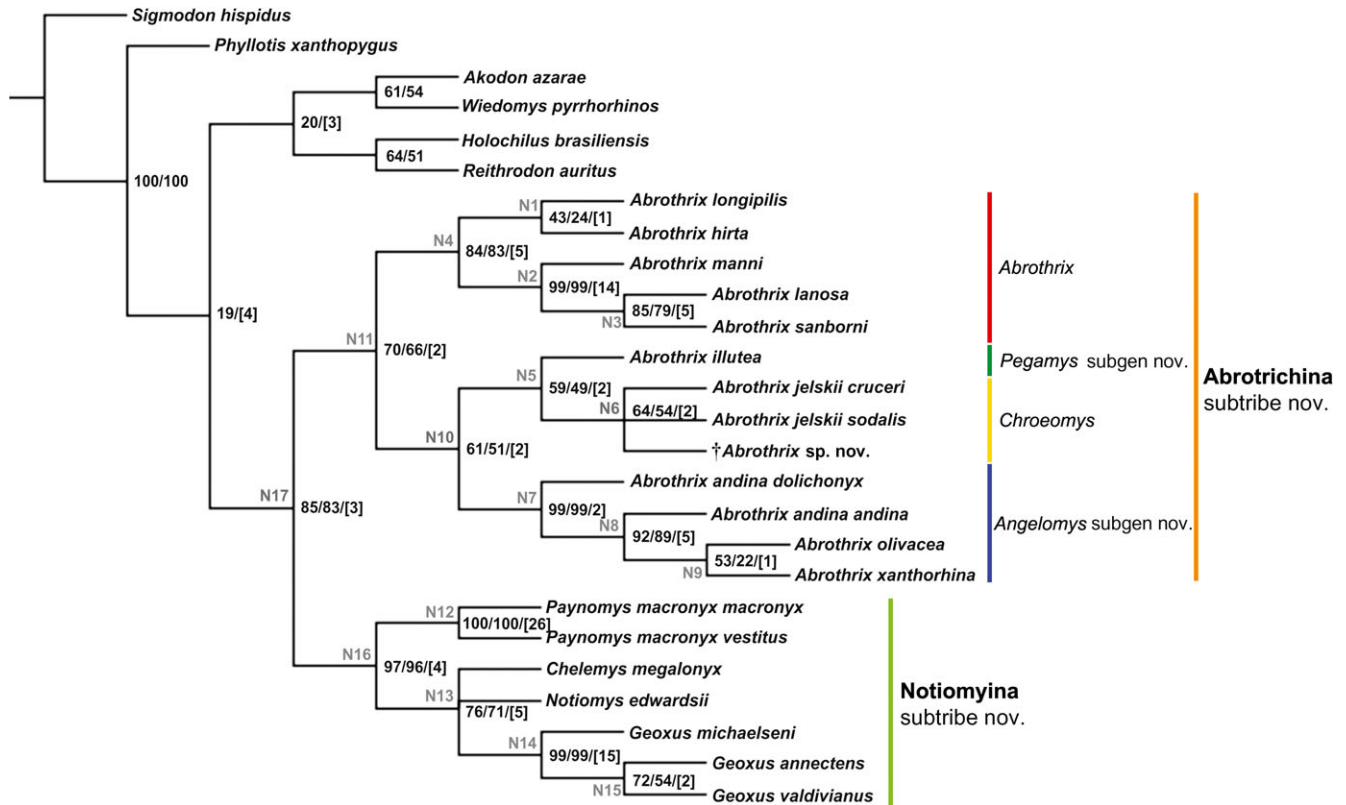
Fig. 1. Strict consensus of two most parsimonious trees resulting from cladistic parsimony analysis of 99 morphological characters and six molecular markers (tree length = 3102 steps; CI = 0.605; RI = 0.554); support values are indicated on each branch and are expressed as group frequencies (SR)/group differences (GC), and Bremer support [BR]. Grey numbers associated with the branches identify the nodes at their right, and they are associated with the PBS values (Data S6).

(Fig. S2b), and similarly, support was higher for the long-clawed group. The Bayesian topology differed from that obtained by parsimony in two major ways: (i) *Ab. jelskii* spp. plus †*Abrothrix* sp. nov. form a large clade with *Ab. olivacea*, *Ab. xanthorhina*, *Ab. andina andina* and *Ab. andina dolichonyx*; and (ii) *Akodon azarae* (Akodontini) falls within Abrotrichini as sister of *Abrothrix*. This latter result can be attributed to the small number of outgroups, including only one Akodontini and due to strong morphological similarities between these genera (cf. Patterson et al., 1984; Reig, 1987).

The main points of agreement among trees, besides the major dichotomy between *Abrothrix* and the long-clawed Abrotrichini, included: (i) a clade containing *Abrothrix hirta*, *Ab. lanosa*, *Ab. longipilis*, *Ab. manni* and *Ab. sanborni* (= *Abrothrix s.s.*); (ii) a clade including *Ab. andina*, *Ab. olivacea* and *Ab. xanthorhina*; (iii) a clade restricted to *Ab. jelskii* ssp. plus † *Abrothrix* sp. nov. (= *Chroeomys*); (iv) a clade including *Ab. illutea* (sometimes found as sister of *Abrothrix s.s.*, sometimes as sister of *Chroeomys*); (v) the non-monophyly of *Chelemys*; and (vi) the paraphyly of *Geoxus* with respect to *Pearsonomys* (Table 2).

Biogeographical analysis

Biogeographical reconstructions show different ancestral areas for Abrotrichini depending on the method used. Parsimony (Fitch) results favour a northern widespread ancestral range for the tribe, assigning high probabilities to Atacama, Chacoan, Rondonia and Yungas provinces (Fig. S2). On the other hand, the S-DIVA analysis (maxarea = 2) identified the southern Andean region, more specifically the Valdivian forest and Patagonian provinces, as the range of the most recent common ancestor of Abrotrichini (Fig. S3). Similar results are obtained for both the long-clawed Abrotrichini and the clade that comprises *Ab. hirta*, *Ab. lanosa*, *Ab. longipilis*, *Ab. manni* and *Ab. sanborni*. However, the hypothetical ancestral range of the second main clade of *Abrothrix* (*Ab. andina*, *Ab. illutea*, *Ab. jelskii*, *Ab. olivacea*, *Ab. xanthorhina* and †*Ab.* sp. nov.) lies to the north, in the Chacoan, Prepuna and Puna provinces. For the same internal nodes mentioned above, the FP analysis assigns other provinces or more restricted ranges as the ancestral areas. In contrast with S-DIVA results, ambiguous results point to Maule and Patagonian
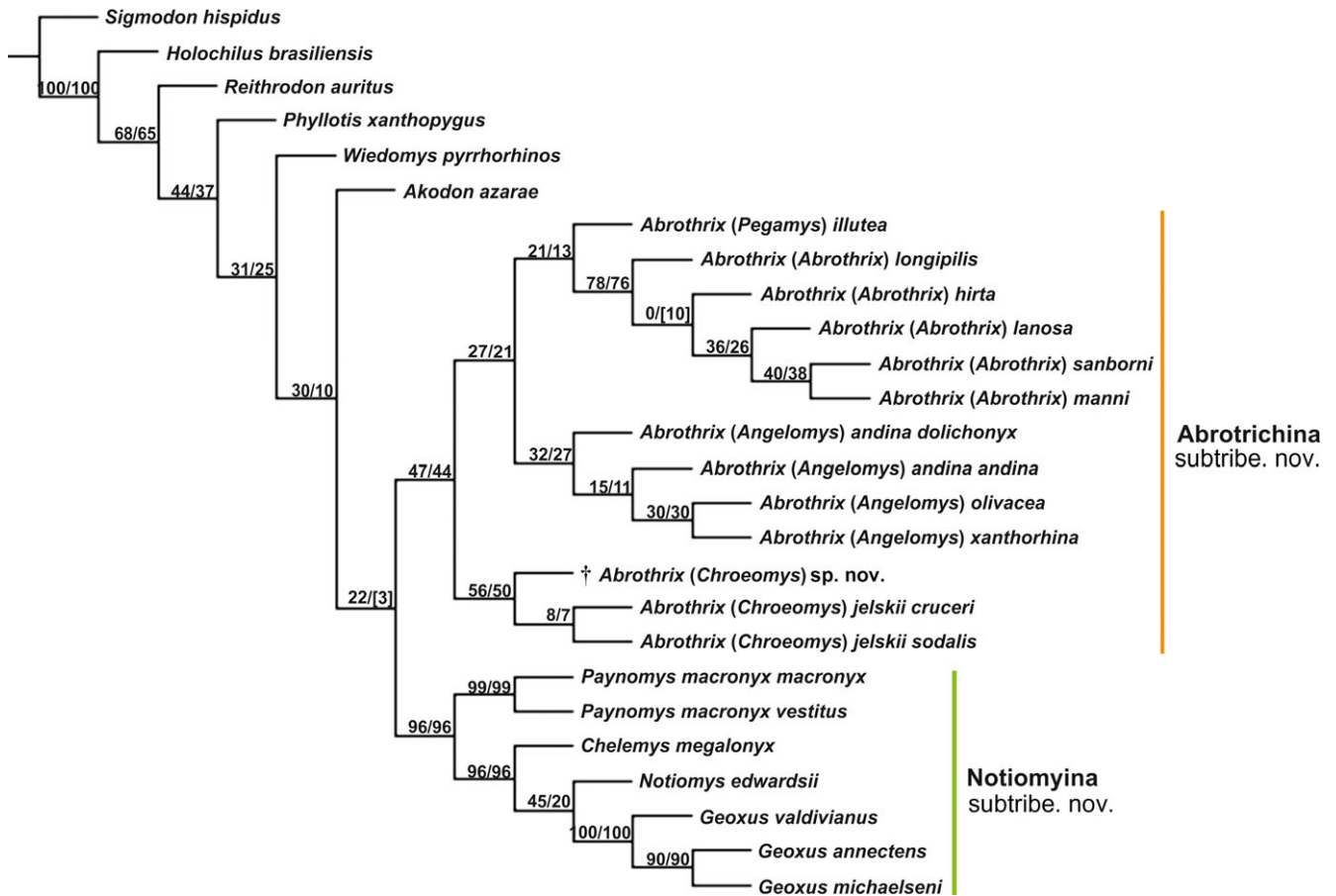
Fig. 2. Single most parsimonious tree resulting from cladistic parsimony analysis of 99 morphological characters (tree length = 280; CI = 0.475; RI = 0.754); support values are indicated on each branch and are expressed as group frequencies (SR)/group differences (GC).

Table 2
Main points of agreement between the different methodological approaches used in this work

	Parsimony		Bayesian	
	Morphology alone	Morphology + molecular markers	Morphology alone	Morphology + molecular markers
A clade including *A. hirta*, *A. lanosa*, *A. longipilis*, *A. manni* and *A. sanborni*	Yes	Yes	Yes	Yes
A clade including *A. andina*, *A. olivacea* and *A. xanthorhina*	Yes*	Yes	No	Yes
A clade including *A. jelskii* spp. + †*Abrothrix* sp. nov.	Yes*	Yes	Yes	Yes
Abrothrix illutea	Sister to *Abrothrix* s.s.*	Sister to *Chroeomys*	Sister to *Abrothrix* s.s.*	Sister to *Chroeomys*
Paraphyly of *Geoxus* regarding *Pearsonomys*	Yes	Yes	Yes	Yes
Monophyly of *Chelemys macronyx* and *C. megalonyx*	No	No	No	No

*With low support values.

provinces as the ancestral area for the long-clawed clade. Maule, Valdivian and Magellanic forest provinces are recovered as the ancestral area for the clade including *Ab. manni*, *Ab. lanosa* and *Ab. sanborni*, and the Puna province for the clade containing the living *Ab. andina*, *Ab. illutea*, *Ab. jelski*, *Ab. olivacea* and *Ab. xanthorhina* and the fossil †*Ab.* sp. nov.

Discussion

Revised taxonomy based on combined data

Phylogenetic relationships of the tribe Abrotrichini have been evaluated chiefly with molecular markers (e.g. D'Elía, 2003; D'Elía et al., 2006; Rodríguez-Serrano

et al., 2008b; Feijoo et al., 2010; Teta et al., 2011; Cañón et al., 2014). These studies confirmed tribal monophyly as well as a major division between cursorial forms of the genus *Abrothrix* and the fossorial long-clawed Abrotrichini, consisting of the genera *Chelemys*, *Geoxus*, *Notiomys* and *Pearsonomys*. Relationships recovered within each of these clades have varied, in most cases with the taxonomic sampling in different analyses. To date, the most comprehensive study was carried out by Cañón et al. (2014; see also Cañón, 2012), who evaluated five nuclear markers and one mitochondrial marker. Based on those results, and with the objective to avoid informal names such as "long-clawed abrotrichine" or "fossorial clade" (see the prior discussion), we propose a subtribal arrangement for Abrotrichini. Under this scheme, the clade of *Abrothrix* is formally designated as Abrotrichina subtribe nov. and the long-clawed Abrotrichini are recognized as Notiomyina subtribe nov. (see Appendix 3).

Consistency between the species groupings identified in past studies of *Abrothrix* (e.g. Teta et al., 2011; Teta, 2013; Cañón et al., 2014; D'Elia et al., 2015a,b; Patterson et al., 2015) and in this study robustly supported groupings, offering insights on how to sensibly subdivide *Abrothrix*. Two main alternatives to its current classification have been proposed: (i) restrict *Abrothrix* (as a genus or subgenus) to *Ab. longipilis* and related species (i.e. *Ab. hirta*, *Ab. lanosa*, *Ab. manni*, *Ab. sanborni*) and revalidate *Chroeomys* to encompass *jelskii*, *illutea*, *andina*, *olivacea* and *xanthorhina* (Cañón et al., 2014), or (ii) restrict *Abrothrix* to *longipilis* and its allied forms and *Chroeomys* to *jelskii*, and erect a new taxon for the group of *Ab. andina*, *Ab. olivacea* and *Ab. xanthorhina* and another for *Ab. illutea* (Teta et al., 2011; Teta, 2013). The first option is the most economical in terms of taxonomy, because names are available and recognizable for both clades. However, for the reasons detailed in the next paragraph, we adopt the second option (Table 3). We chose a subgeneric arrangement to subdivide *Abrothrix* because this category usefully serves to label clades of closely related species while retaining traditional binomial usage (e.g. Voss et al., 2014).

A taxonomic arrangement that includes four subgenera within *Abrothrix* makes sense for several reasons: (i) All four subgenera can be diagnosed morphologically and are monophyletic in the combined data parsimony tree (see Tables 2 and 3 and the taxonomic accounts below). (ii) Subsequent studies on *Abrothrix* could benefit from the formal recognition of well-supported and diagnosable clades, avoiding the use of informal names (e.g. "olivacea group", "longipilis group"; see Cañón et al., 2014). As explained by Voss et al. (2014), informal names (such as "sections" or "groups") have two disadvantages: hierarchical relationships are unapparent (e.g. do sections contain groups or do groups contain sections?), and informal names are not regulated by widely accepted conventions, and so lack rules to mediate alternative usage [in contrast, subgenera are regulated by the ICZN (1999), so usage is constrained by typification and priority]. (iii) To subsume a variety of morphotypes and distinctive evolutionary and ecological variants under a single name is less useful to research on adaptation, biogeography, diversification and other topics, producing a classification with less heuristic value (Wheeler, 2004; Ford, 2006). For example, two of the better known species of *Abrothrix*, *Ab. hirta* and *Ab. olivacea*, have strongly contrasting life histories (see Spotorno et al., 1990: table 3), a situation clouded by the current nomenclature. (iv) Estimated times of divergence among subgenera of *Abrothrix* are comparable to those documented for groupings of the long-clawed Abrotrichini (Cañón et al., 2014; see also Patterson and Upham, 2014; Patterson and Norris, 2015).

Regarding Notiomyina subtribe nov., two nomenclatural issues are apparent: (i) morphological analysis highlights numerous differences between *Chelemys megalonyx* (the type species of *Chelemys*) and *Chelemys macronyx*, which were not recovered as sister taxa in molecular or combined analyses of molecular and morphological data; and (ii) both morphological and molecular evidence suggests that *Geoxus* is paraphyletic with respect to *Pearsonomys*. To modify the Abrotrichini classification to the phylogenetic hypothesis presented here, we could: (i) name a new genus to accommodate *Chelemys macronyx* and another for the southern populations of *Geoxus*; (ii) name a new genus to include *Chelemys macronyx* and synonymize *Pearsonomys* with *Geoxus*; or (iii) return to the classification of Osgood (1925), who considered all these forms as synonyms of *Notiomys*. The final option can be ruled out, because a single polymorphic genus that includes such divergent taxa as *Chelemys* and *Geoxus* is difficult to reconcile with the current sigmodontine systematic paradigm (e.g. Weksler et al., 2006). Of the remaining scenarios, option 2 seems better supported by our data, as the morphological differences between *Pearsonomys* and both species of *Geoxus* are slight, and the link between *annectens* and *valdivianus* is strongly supported in all analysis.

Morphology and molecular markers

The combined analysis of morphological and molecular evidence helps to resolve some of the questions previously raised in the study of molecular markers, providing the basis for a revised tribal classification. The contribution of morphology was crucial, because it provided stronger and more explicit context for formalizing taxonomic changes.

Within Abrotrichini, different genes provide a mixture of signals that, analysed separately, fail to recover

Table 3
Morphological comparisons using selected traits among the four proposed subgenera for *Abrothrix*

	Abrothrix	*Angelomys* subgen. nov.	*Chroeomys*	*Pegamys* subgen. nov.
Coloration	Dorsally dark, sometimes with a reddish band on the midline; venter whitish to nearly dark as dorsum	Dorsally olivaceous to brownish, paler on venter; sometimes with reddish marks on nose, feet and tail	Sharply demarked, including rufous markings on nose, periocular and tail and white postauricular patches	Dorsally greyish brown, paler on venter
Claws on manus	Claws moderately long, keeled for about one-third to half of their length	Claws small to medium, not keeled	Claws moderately long, keeled for about one-third to half of their length	Claws moderately long, keeled for about one-third to half of their length
Rostrum	Long and narrow	Short and narrow	Short and broad	Short and broad
Nasals and premaxillae	Projecting well in front of the incisors as a tube	Extending slightly to moderately in front of the incisors	Extending slightly in front of the incisors	Extending slightly in front of the incisors
Shape of nasals	Outer margins nearly straight.	Slightly widened in its anterior third	Slightly widened in its anterior third	Slightly widened in its anterior third
Lacrimals	Equal contact with maxillary and frontal bones	Contacting mainly maxillary	Equal contact with maxillary and frontal bones	Equal contact with maxillary and frontal bones
Palate	Long	Long	Short or long	Short
Tympanic bullae	Not inflated	Variable inflated	Inflated	Not inflated
Maxillary septum length	No more than half of the length of incisive foramina	No more than half of the length of incisive foramina	No more than half of the length of incisive foramina	Larger than half of the length of incisive foramina
Molars	Mesodont	Mesodont	Slightly hypsodont	Mesodont
Anteroflexus on M1	Well developed	Well developed	Slightly marked	Well developed
Anteroloph length on M2	Long	Long	Short	Long
Protostylid on m1	Present	Present	Absent	Present
Ectostylid on m1	Present or not	Present or not	Absent	Absent
Mesolophid on m1–2	Present	Present	Absent	Present
Cartilaginous digits of the baculum	Absent or indistinct	1 medial and 2 laterals, reduced	1 medial and 2 laterals, reduced	2 laterals, reduced

the monophyly of clades that are resolved in the combined approaches (cf. Cañón et al., 2014). When morphological data are incorporated into these analyses, the monophyly of most of these groups (e.g. the group of *Ab. Andina–Ab. olivacea*) is well supported, and the relationships recovered are better resolved (Teta, 2013). In fact, especially for Notiomyina subtribe nov., the combined analysis is supported mostly by the morphological partition, determining the topology of the preferred hypothesis. This situation is not unique; other cases exist in which molecular data do not override the morphological partition, especially when different molecular markers are incongruent (as is true here; see also O'Leary et al., 2013; Cañón et al., 2014). A different scenario is seen within *Abrothrix*, where the tree topology is mostly dictated by the molecular partition. As discussed by previous authors, discrepancies in phylogenetic signal between morphological and molecular partitions, or even between different molecular markers, are not uncommon in various animal groups, including mammals (see Lopardo et al., 2011, and references therein).

Morphological differentiation within the long-clawed Abrotrichini is impressive, especially for a small radiation of fossorial forms. Despite sharing several integumental characteristics (see the taxonomic summary below) involved in their fossorial mode of life (Pearson, 1984), this is an ecomorphologically diverse group, including herbivorous species with robust skulls, broad zygomatic plates and moderately hypsodont molars (e.g. *Chelemys macronyx*) and more insectivorous or specialized forms with delicate skulls, narrow zygomatic plates and minute, brachyodont teeth (e.g. *Geoxus*, *Notiomys*). By comparison, morphological differentiation within *Abrothrix* is more limited, at least judging from skeletal and soft-part anatomy. Even so, some of the taxa here recognized, such as *Abrothrix* (*Chroeomys*), were long considered as valid and distinct from typical *Abrothrix* (e.g. Gyldenstolpe, 1932; Reig, 1987; Steppan, 1995). Other forms [e.g. *Abrothrix* (*Angelomys*) subgen. nov.] were also distinguished in prior analyses, although they lacked explicit taxonomic proposals (e.g. Patterson et al., 1989; Smith and Patton, 1999). In sum, morphology together with other traits (e.g. molecules, ecology, biogeography) provides a more solid framework for recognizing the four subgenera here proposed.

PBS values emphasize the importance of morphology in solving the phylogenetic relationships within the tribe Abrotrichini. Some molecular markers (i.e. βfbg, Ins) also help to resolve groups, highlighting the value of total-evidence approaches. Among morphological characters, dental traits make major contributions to tree topology. This is a welcome result, as most of the fossil forms of Sigmodontinae are known mostly or entirely from dental remains (e.g. Reig, 1972; Pardiñas et al.,

2002; Zijlstra, 2012). Detailed analysis of dental data is much needed to better define and/or describe some structures (e.g. see the discussion concerning the mesoloph in Pardiñas, 2008), beyond their simple presence–absence. Homoplasy and non-independence of characters, partially as a result of the atomization of numerous dental traits during analysis, have been pivotal points in criticisms of morphology-based phylogenies (e.g. Koepfli et al., 2007; see also the exchange between Naylor and Adams, 2001 and O'Leary et al., 2003). However, even when teeth are regarded as integrated structures ("character complexes") that are both developmentally and functionally correlated, this should not disqualify the utility of detailed analyses of dentition or any other complex morphology (see also Prevosti, 2010). Further studies about the phylogenetic position of some crucial fossil forms (e.g. *Prosigmodon*) would surely benefit from this kind of approach, providing a more complete framework to study the origin, early diversification and evolution of Sigmodontinae.

An important difference between our hypothesis and others recently proposed (e.g. Parada et al., 2013; Cañón et al., 2014) is the position of *Wiedomys*, an enigmatic genus often recovered as the sister group of the Abrotrichini (but see Machado et al., 2015). In contrast, our parsimony analysis recovered this genus within a clade comprising exemplars from several tribes: [(*Akodon azarae* + *Wiedomys pyrrhorhynos*) (*Reithrodon auritus*+*Holochilus brasiliensis*)], and this clade as the sister of Abrotrichini. Although *Wiedomys* and Abrotrichini are united in molecular analyses, these clades possess numerous trenchant morphological differences that refute a sister-group relationship. Replicating this pattern of bizarre and unexpected relationships emerging from recent molecular analyses, the Atlantic Forest endemic *Delomys* appears as sister to the widespread Phyllotini (Salazar-Bravo et al., 2013), and the bizarre spiny mouse *Abrawayaomys* appears as sister to the disjointly distributed Reithrodontini (Ventura et al., 2013). We argue that inclusion of morphological traits in phylogenetic analyses could alter some relationships that have been recovered based solely on molecular analyses that are difficult to reconcile with phenotypic evidence. In fact, despite our limited outgroup sampling and inability to establish it conclusively, a sister relationship between Abrotrichini and Akodontini emerges as the most rational hypothesis in view of a wide array of data, including morphology, karyology and geographical distribution (cf. Reig, 1987).

Biogeography and timing of diversification

Parsimony and Bayesian analysis differ drastically in the location of the most recent common ancestor of the extant Abrotrichini. Results of the parsimony

approach agree partially with the hypothesis developed by Reig (1986a,b) for his concept of Akodontini, placing the main area of differentiation of Abrotrichini as a disjoint ancestral area in the northern part of the current distribution of the tribe. In contrast, the S-DIVA analysis recovered the southern portion of the Andean region (i.e. Valdivian forest and Patagonian provinces) as the most likely ancestral area for the tribe. This result would support the secondary area of differentiation proposed by Reig (1984). Ambiguities and low resolution to the more basal nodes in the FP analysis suggest the need to be cautious with these results.

According to Cañón et al. (2014), the timing of the initial diversification of the crown group of this tribe was relatively recent, and occurred during the Early Pliocene (a minimum of 4.4 Myr; 2.35–6.65 Ma). During the Late Miocene and the Early Pliocene, the Patagonian Andean Cordillera was successively uplifted, progressively developing a barrier to moisture-laden winds off the South Pacific. The resulting rain-shadow effect on eastern Patagonian landscapes and the opening of the Drake Passage initiated the differentiation of biogeographical subregions in southern South America (Pascual et al., 1996). In addition, the areas inundated by marine transgressions were later covered by large areas of open steppes, extending from northern Patagonia to central and northern Argentina, Uruguay, along the eastern slopes of the rising Andes, and also in the upper Amazon basin (Pascual et al., 1996; Donato et al., 2003; Ortiz Jaureguizar and Cladera, 2006), creating new habitats.

Under this scenario, we hypothesize that the Abrotrichini lineage was isolated from an ancestral sigmodontine stock by vicariance west of the Andes and its evolution then continued mostly through successive dispersal events. From the Latest Miocene onwards into the Pliocene, the initial populations of the southern Andes would have expanded their ranges in at least two directions: (i) northward, into Chile, northwestern Argentina, central-south Peru and south-western Bolivia, and (ii) south-eastward, across Patagonia. Rodríguez-Serrano et al. (2008a) suggested that the ancestor of the Abrotrichini was a fossorial form that inhabited forested environments in south-western South America. According to these authors, the major division within Abrotrichini occurred as a result of the formation of the hyperarid Atacama Desert and the Arid South American Diagonal as a consequence of the progressive uplift of the Andes Mountains. This event initiated the confinement of the Temperate Forests in southern South America and augured the formation of open environments, such as Patagonia and Puna.

Abrotrichini are the most diverse tribe west of the southern Andes. On the other hand, the two most speciose and widely distributed tribes in the Neotropics, Akodontini and Oryzomyini, are virtually absent from this region (Pardiñas et al., 2011). Two hypotheses could explain this scenario: (i) other tribes were unable to colonize the Pacific lowlands over the emerging Andean chain due to ecological restrictions; and/or (ii) the resident Abrotrichini were successful competitors, excluding would-be colonists of other taxa to southern latitudes, especially in the case of morphologically similar Akodontini. Both hypotheses suggest that the various sigmodontine clades differentiated in multiple areas separated by geographical barriers rather than in a single place. Integrative approaches, like the one presented here, indicate that we are close to developing more rigorous analyses to improve simplistic scenarios proposed to explain the origin and early diversification of sigmodontine rodents (e.g. Parada et al., 2013; Leite et al., 2014).

Final remarks

Combined analysis of morphological traits and molecular markers resulted in a better resolved phylogeny of the tribe Abrotrichini. As in previous studies, combined analyses show a major dichotomy within the tribe between a clade of cursorial forms and another comprising fossorial taxa. Morphological analyses also contributed to a new taxonomic arrangement that agrees with the proposed phylogenetic hypothesis. Within this context, we showed that certain character systems considered only partially informative (e.g. dental traits) can contribute importantly to resolve phylogenetic relationships within the Sigmodontinae.

It is interesting to note that the *Abrothrix* problem (i.e. the substantial morphological heterogeneity of this genus) has been apparent for at least three decades (see Patterson et al., 1984), although we have not appreciated the taxonomic problems with *Chelemys* and *Geoxus* until recent molecular phylogenies and the capture of new specimens (e.g. of *G. michaelseni*).

As a final note, combined analyses, employing both morphological characters and molecular markers, are to be preferred, as they represent the best approach to phylogenetic inference in terms of maximizing explanatory power and providing the framework for assessing incongruence (Lopardo et al., 2011). In addition, morphology-based phylogenies are mandatory to determine the position of fossil forms, which in turn are key to dating biological radiations. Within this context, additional data, especially from other character systems (e.g. postcranial, digestive apparatus), are needed to advance a better phylogenetic hypothesis than our present one. Traditional anatomical studies, despite being descriptive, are still greatly needed in biology.

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References

Abud, C., 2011. Variación genética y estructura filogeográfica de *Abrothrix olivaceus* en la Patagonia argentina y el sur chileno. Masters dissertation. Facultad de Ciencias, Universidad de la República, Montevideo, Uruguay.

Baker, R.H., De Salle, R., 1997. Multiple sources of character information and the phylogeny of Hawaiian drosophilids. Syst. Biol. 46, 654–673.

Barrantes, G.E., Ortells, M.O., Reig, O.A., 1993. New studies on allozyme genetic distance and variability in akodontine rodents (Cricetidae) and their systematic implications. Biol. J. Linnean Soc. 48, 283–298.

Bremer, K., 1990. Combinable component consensus. Cladistics 6, 369–372.

Bremer, K., 1994. Branch support and tree stability. Cladistics 10, 295–304.

Cabrera, A., 1961. Catálogo de los mamíferos de América del Sur. Parte II. Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia". Cien. Zool. 4, 309–732.

Campbell, J.A., Frost, D.R., 1993. Anguid lizards of the genus *Abronia*: revisionary notes, descriptions of four new species, phylogenetic analysis, and key. Bull. Am. Mus. Nat. Hist. 216, 1–121.

Cañón, C., 2012. Sistemática molecular de los roedores de la tribu Abrotrichini (Cricetidae: Sigmodontinae). Tesis de Maestría. Facultad de Ciencias Naturales y Oceanográficas, Universidad de Concepción, Concepción, Chile.

Cañón, C., Mir, D., Pardiñas, U.F.J., Lessa, E., D'Elía, G., 2014. A multilocus perspective on the phylogenetic relationships and diversification of rodents of the tribe Abrotrichini (Cricetidae: Sigmodontinae). Zool. Scrip. 43, 443–454.

Carleton, M.D., 1973. A survey of gross stomach morphology in New World Cricetinae (Rodentia, Muroidea), with comments on functional interpretations. Misc. Publ. Mus. Zool. Univ. Mich. 146, 1–43.

Carleton, M.D., 1980. Phylogenetic relationships in neotomine-peromyscine rodents (Muroidea) and a reappraisal of the dichotomy within New World Cricetinae. Misc. Publ. Mus. Zool. Univ. Mich. 157, 1–146.

Carleton, M.D., Musser, G.G., 1989. Systematic studies of oryzomyine rodents (Muridae, Sigmodontinae): a synopsis of *Microryzomys*. Bull. Am. Mus. Nat. Hist. 191, 1–83.

Carrizo, L.V., Catalano, S.A., 2015. First phylogenetic analysis of the tribe Phyllotini (Rodentia: Sigmodontinae) combining morphological and molecular data. Cladistics 31, 593–620.

D'Elía, G., 2003. Phylogenetics of Sigmodontinae (Rodentia, Muroidea, Cricetidae), with special reference to the akodont group, and with additional comments on historical biogeography. Cladistics 19, 307–323.

D'Elía, G., 2015. Genus *Pearsonomys* Patterson, 1992. In: Patton, J.L., Pardiñas, U.F.J., D'Elía, G. (Eds.), Mammals of South America. Volume 2 – Rodents. University of Chicago Press, Chicago, pp. 138–140.

D'Elia, G., Pardiñas, U.F.J., Teta, P., 2015a. Tribe Abrotrichini D'Elía, Pardiñas, Teta and Patton, 2007. In: Patton, J., Pardiñas, U.F.J., D'Elía, G. (Eds.), Mammals of South America. Volume 2 – Rodentia. University of Chicago Press, Chicago, pp. 107–109.

D'Elia, G., Teta, P., Upham, N.S., Pardiñas, U.F.J., Patterson, B.D., 2015b. Description of a new soft-haired mouse, genus *Abrothrix* (Sigmodontinae), from the temperate Valdivian rainforest. J. Mammal. 96, 839–853.

D'Elía, G., González, E.M., Pardiñas, U.F.J., 2003. Phylogenetic analysis of sigmodontine rodents (Muroidea), with special reference to the akodont genus *Deltamys*. Mamm. Biol. 68, 351–364.

D'Elía, G., Ojeda, A., Mondaca, F., Gallardo, M.H., 2006. New data of the long-clawed mouse *Pearsonomys annectens* (Cricetidae, Sigmodontinae) and additional comments on the distinctiveness of *Pearsonomys*. Mamm. Biol. 71, 39–51.

D'Elía, G., Pardiñas, U.F.J., Teta, P., Patton, J.L., 2007. Definition and diagnosis of a new tribe of sigmodontine rodents (Cricetidae: Sigmodontinae), and a revised classification of the subfamily. Gayana 71, 187–194.

Dickerman, A.W., 1992. Molecular systematics of some New World muroid rodents. Unpublished doctoral dissertation. University of Wisconsin-Madison, USA.

Donato, M., Posadas, P., Miranda-Esquivel, D., Ortiz Jaureguizar, E., Cladera, G., 2003. Historical biogeography of the Andean region: evidence from *Listroderina* (Coleoptera: Curculionidae: Rhytirrhinini) in the context of the South American geobiotic scenario. Biol. J. Linnean Soc. 80, 339–352.

Ellerman, J.R., 1941. The Families and Genera of Living Rodents. Vol. 2. Muridae. British Museum (Natural History), London.

Engel, S.R., Hogan, K.M., Taylor, J.F., Davis, S.K., 1998. Molecular systematics and paleobiogeography of the South American sigmodontine rodents. Mol. Biol. Evol. 15, 35–49.

Feijoo, M., D'Elía, G., Pardiñas, U.F.J., Lessa, E.P., 2010. Systematics of the southern Patagonian-Fueguian endemic *Abrothrix lanosus* (Rodentia: Sigmodontinae): phylogenetic position, karyotypic and morphological data. Mamm. Biol. 75, 122–137.

Ford, F., 2006. A splitting headache: relationships and generic boundaries among Australian murids. Biol. J. Linnean Soc. 89, 117–138.

Gallardo, M.H., Aguilar, G., Goicoechea, O., 1988. Systematics of sympatric cricetid *Akodon* (*Abrothrix*) rodents and their taxonomic implications. Medio Ambiente. 9, 65–74.

Goloboff, P.A., 1993. Estimating character weights during tree search. Cladistics 9, 83–91.

Goloboff, P.A., Farris, J.S., Källersjö, M., Oxelman, B., Ramírez, M., Szumik, C., 2003. Improvements to resampling measures of group support. Cladistics 19, 324–332.

Goloboff, P.A., Carpenter, J.M., Arias, J.S., Miranda-Esquivel, D.R., 2008. Weighting against homoplasy improves phylogenetic analysis of morphological data sets. Cladistics 24, 1–16.

Gyldenstolpe, N., 1932. A manual of neotropical sigmodont rodents. Kungliga Svenska Vetenskapsakademiens Handlingar. 11, 1–164.

Hershkovitz, P., 1962. Evolution of Neotropical cricetine rodents (Muridae) with special reference to the phyllotine group. Fieldiana Zool. 46, 1–524.

Hooper, E.T., Musser, G.G., 1964. The glans penis in Neotropical cricetines (family Muridae) with comments on classification of muroid rodents. Misc. Publ. Mus. Zool. Univ. Mich. 123, 1–57.

ICZN, 1999. International Code of Zoological Nomenclature, 40th edn. International Trust for Zoological Nomenclature, London.

Kelt, D.A., 1994. The natural history of small mammals from Aisen Region, southern Chile. Rev. Chil. Hist. Nat. 67, 183–207.

Koepfli, K.P., Gompper, M.E., Eizirik, E., Ho, C.C., Linden, L., Maldonado, J.E., Wayne, R.K., 2007. Phylogeny of the Procyonidae (Mammalia: Carnivora): molecules, morphology and the Great American Interchange. Mol. Phylogenet. Evol. 43, 1076–1095.

Leite, R.N., Kolokotronis, S.O., Almeida, F.C., Werneck, F.P., Rogers, D.S., Weksler, M., 2014. In the wake of invasion: tracing the historical biogeography of the South American cricetid radiation (Rodentia, Sigmodontinae). PLoS ONE 6, 1–12.

Lewis, P.O., 2001. A likelihood approach to estimating phylogeny from discrete morphological character data. Syst. Biol. 50, 913–925.

Lopardo, L., Giribet, G., Hormiga, G., 2011. Morphology to the rescue: molecular data and the signal of morphological characters in combined phylogenetic analyses – a case study from mysmenid spiders (Araneae, Mysmenidae), with comments on the evolution of web architecture. Cladistics 27, 278–330.

Machado, L., Passaia, M.H., Pacheco Rodrigues, F., Bortolotto Peters, F., Sponchiado, J., Valiati, V.H., Christoff, A.U., 2015. Molecular phylogenetic position of endangered *Wilfredomys* within Sigmodontinae (Cricetidae) based on mitochondrial and nuclear DNA sequences and comments on Wiedomyini. Zootaxa 3986, 421–434.

Morrone, J.J., 2014. Biogeographical regionalization of the Neotropical region. Zootaxa 3782, 1–110.

Morrone, J.J., 2015. Biogeographical regionalization of the Andean region. Zootaxa 3936, 207–236.

Naylor, G.J.P., Adams, D.C., 2001. Are the fossil data really at odds with the molecular data? Morphological evidence for Cetartiodactyla phylogeny reexamined. Syst. Biol. 50, 444–453.

Ojeda, A.A., D'Elía, G., Ojeda, R.A., 2005. Taxonomía alfa de *Chelemys* y *Euneomys* (Rodentia, Cricetidae): el número diploide de ejemplares topotípicos de *C. macronyx* y *E. mordax*. Mastozool. Neotrop. 12, 79–82.

O'Leary, M., Gatesy, J., Novacek, M., 2003. Are the dental data really at odds with the molecular data? Morphological evidence for whale phylogeny (re)reexamined. Syst. Biol. 52, 853–864.

O'Leary, M.A., Bloch, J.I., Flynn, J.J., Gaudin, T.J., Giallombardo, A., Giannini, N.P., Goldberg, S.L., Kraatz, B.P., Luo, Z., Meng, J., Ni, X., Novacek, M.J., Perini, F.A., Randall, Z.S., Rougier, G.W., Sargis, E.J., Silcox, M.T., Simmons, N.B., Spaulding, M., Velazco, P.M., Weksler, M., Wible, J.R., Cirranello, A.L., 2013. The placental mammal ancestor and the post-K-Pg radiation of placentals. Science 339, 662–667.

Ortiz Jaureguizar, E., Cladera, G.A., 2006. Paleoenvironmental evolution of southern South America during the Cenozoic. J. Arid Environ. 66, 498–532.

Ortiz, P.E., Jayat, J.P., Pardiñas, U.F.J., 2011. Fossil sigmodontine rodents of Northwestern Argentina: taxonomy and paleoenvironmental meaning. In: Salfity, J.A., Marquillas, R.A. (Eds.), Cenozoic Geology of the Central Andes of Argentina. SCS Publisher, London, pp. 301–316.

Ortiz, P.E., García López, D.A., Babot, M.J., Pardiñas, U.F.J., Alonso Muruaga, P.J., Jayat, J.P., 2012. Exceptional Late Pliocene microvertebrate diversity in northwestern Argentina reveals a marked small mammal turnover. Palaeogeogr. Palaeoclimatol. Palaeoecol. 361-362, 21–37.

Osgood, W.H., 1925. The long-clawed South American rodents of the genus *Notiomys*. Field Mus. Nat. Hist. Zool. Series. 12, 112–125.

Osgood, W.H., 1943. The mammals of Chile. Field Mus. Nat. Hist. Zool. Series. 30, 1–268.

Pacheco, V., 2003. Phylogenetic analyses of the Thomasomyini (Muroidea: Sigmodontinae) based on morphological data. Unpublished doctoral dissertation. City University of New York, New York, USA.

Parada, A., Pardiñas, U.F.J., Salazar-Bravo, J., D'Elía, G., Palma, R.E., 2013. Dating an impressive Neotropical radiation: molecular time estimates for the Sigmodontinae (Rodentia) provide insights into its historical biogeography. Mol. Phylogenet. Evol. 66, 960–968.

Pardiñas, U.F.J., 2008. A new genus of Oryzomyini rodent (Cricetidae: Sigmodontinae) from the Pleistocene of Argentina. J. Mammal. 89, 1270–1278.

Pardiñas, U.F.J., D'Elía, G., Ortiz, P., 2002. Sigmodontinos fósiles (Rodentia, Muroidea, Sigmodontinae) de América del Sur: Estado actual de su conocimiento y prospectiva. Mastozool. Neotrop. 9, 209–252.

Pardiñas, U.F.J., Udrizar-Sauthier, D.E., Teta, P., D'Elía, G., 2008. New data on the endemic Patagonian long-clawed mouse *Notiomys edwardsii* (Rodentia: Cricetidae). Mammalia 72, 273–285.

Pardiñas, U.F.J., Teta, P., D'Elía, G., Lessa, E., 2011. The evolutionary history of sigmodontine rodents in Patagonia and Tierra del Fuego. Biol. J. Linnean Soc. 103, 495–513.

Pardiñas, U.F.J., Teta, P., Salazar-Bravo, J., 2015. A new tribe of Sigmodontinae rodents (Cricetidae). Mastozool. Neotrop. 22, 171–186.

Pascual, R., Ortiz-Jaureguizar, E., Prado, J.L., 1996. Land mammals: paradigm of Cenozoic South American geobiotic evolution. In: Arratia, G. (Ed.), Contribution of Southern South America to Vertebrate Paleontology. Müncher Geowissenschaftliche Abhandlungen (A), München, Germany, pp. 265–319.

Patterson, B.D., 1992. A new genus and species of long-clawed mouse (Rodentia: Muridae) from temperate rainforests of Chile. Zool. J. Linnean Soc. 106, 127–145.

Patterson, B.D., Norris, R.W., 2015. Towards a uniform nomenclature for ground squirrels: the status of the Holarctic chipmunks. Mammalia: doi: 10.1515/mammalia-2015-0004.

Patterson, B.D., Upham, N.S., 2014. A newly recognized family from the Horn of Africa, the Heterocephalidae (Rodentia: Ctenohystrica). Zool. J. Linnean Soc. 172, 942–963.

Patterson, B.D., Gallardo, M.H., Freas, K.E., 1984. Systematics of mice of the subgenus *Akodon* (Rodentia: Cricetidae) in southern South America, with the description of a new species. Fieldiana Zool. New Ser. 23, 1–16.

Patterson, B.D., Meserve, P.L., Lang, B.K., 1989. Distribution and abundance of small mammals along an elevational transect in temperate rainforests of Chile. J. Mammal. 70, 67–78.

Patterson, B.D., Smith, M., Teta, P., 2015. Genus *Abrothrix* Waterhouse, 1837. In: Patton, J.L., Pardiñas, U.F.J., D'Elía, G. (Eds.), Mammals of South America. Volume 2 – Rodents. University of Chicago Press, Chicago, pp. 109–127.

Patton, J.L., Myers, P., Smith, M.F., 1989. Electromorphic variation in selected South American akodontine rodents (Muridae: Sigmodontinae), with comments on systematic implications. Z. Sauget. 54, 347–359.

Patton, J.L., Pardiñas, U.F.J., D'Elía, G., (Eds). 2015. Mammals of South America. Volume 2, Rodents. The University of Chicago Press, Chicago, IL.

Pearson, O.P., 1983. Characteristics of a mammalian fauna from forests in Patagonia, southern Argentina. J. Mammal. 64, 476–492.

Pearson, O.P., 1984. Taxonomy and natural history of some fossorial rodents of Patagonia, southern Argentina. J. Zool. (Lond.) 202, 225–237.

Pearson, O.P., 1995. Annotated keys for identifying small mammals living in or near Nahuel Huapi National Park or Lanin National Park, southern Argentina. Mastozool. Neotrop. 2, 99–148.

Posada, D., 2008. jModelTest: phylogenetic model averaging. Mol. Biol. Evol. 25, 1253–1256.

Prevosti, F.J., 2010. Phylogeny of the large extinct South American canids (Mammalia, Carnivora, Canidae) using a "total evidence" approach. Cladistics 26, 456–481.

Reig, O.A., 1972. The evolutionary history of the South American cricetid rodents. Unpublished doctoral dissertation. Unpublished doctoral dissertation. University of London, London, England.

Reig, O.A., 1977. A proposed unified nomenclature for the enamelled components of the molar teeth of the Cricetidae (Rodentia). J. Zool. Lond. 181, 227–241.

Reig, O.A., 1978. Roedores cricétidos del Plioceno superior de la provincia de Buenos Aires (Argentina). Publ. Mus. Munic. Cienc. Nat. Mar del Plata "Lorenzo Scaglia" 2, 164–190.

Reig, O.A., 1980. A new fossil genus of South American cricetid rodents allied to *Wiedomys*, with an assessment of the Sigmodontinae. J. Zool. (Lond.) 192, 257–281.

Reig, O.A., 1984. Distribuição geográphica e história evolutiva dos roedores muroideos sudamericanos (Cricetidae: Sigmodontinae). Rev. Bras. Gen. 7, 333–365.

Reig, O.A., 1986a. Diversity patterns and differentiation of high Andean rodents. In: Vuilleumier, F., Monasterio, M. (Eds.), High Altitude Tropical Biogeography. Oxford University Press, London, pp. 404–439.

Reig, O.A., 1986b. Diversity patterns and differentiation of high Andean rodents. In: Vuilleumier, F., Monasterio, M. (Eds.), High Altitude Tropical Biogeography. Oxford University Press, Oxford, pp. 404–440.

Reig, O.A., 1987. An assessment of the systematics and evolution of the Akodontini, with the description of new fossil species of *Akodon* (Cricetidae: Sigmodontinae). In: Patterson, B.D., Timm, R.M. (Eds.), Studies in Neotropical Mammalogy: Essays in honor of Philip Hershkovitz. Zool. New. Ser. 39. Field Museum of Natural History, Fieldiana, pp. 347–400.

Rodríguez, V.A., Theiler, G.R., 2007. Micromamíferos de la región de Comodoro Rivadavia (Chubut, Argentina). Mastozool. Neotrop. 14, 97–100.

Rodríguez-Serrano, E., Hernández, C.E., Palma, R.E., 2008a. A new record and an evaluation of the phylogenetic relationships of *Abrothrix olivaceus markhami* (Rodentia: Sigmodontinae). Mammal. Biol. 73, 307–317.

Rodríguez-Serrano, E., Palma, R.E., Hernández, C.E., 2008b. The evolution of ecomorphological traits within the Abrothrichini (Rodentia: Sigmodontinae): a Bayesian phylogenetics approach. Mol. Phylogen. Evol. 48, 473–480.

Ronquist, F., 1994. Ancestral areas and parsimony. Syst. Biol. 43, 267–274.

Ronquist, F., Huelsenbeck, J.P., 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19, 1572–1574.

Salazar-Bravo, J., Pardiñas, U.F.J., D'Elía, G., 2013. A phylogenetic appraisal of Sigmodontinae (Rodentia, Cricetidae) with emphasis on phyllotine genera: systematics and biogeography. Zool. Scrip. 42, 250–261.

Sanborn, C.C., 1947. Geographical races of the rodent *Akodon jelskii* Thomas. Fieldiana Zool. 31, 133–142.

Schenk, J.J., Rowe, K.C., Steppan, S.J., 2013. Ecological opportunity and incumbency in the diversification of repeated continental colonizations by muroid rodents. Syst. Biol. 62, 837–864.

Smith, M.F., Patton, J.L., 1993. The diversification of South American murid rodents: evidence from mitochondrial DNA sequence data for the akodontine tribe. Biol. J. Linn. Soc. 50, 149–177.

Smith, M.F., Patton, J.L., 1999. Phylogenetic relationships and the radiation of sigmodontine rodents in South America: evidence from cytochrome b. J. Mammal. Evol. 6, 89–128.

Spotorno, A.E., 1986. Systematics and evolutionary relationships of Andean phyllotine and akodontine rodents. Doctoral dissertation. University of California at Berkeley, California, USA.

Spotorno, A.E., 1992. Parallel evolution and ontogeny of simple penis among New World cricetid rodents. J. Mammal. 73, 504–514.

Spotorno, A.E., Zuleta, C., Cortés, A., 1990. Evolutionary systematics and heterochrony in *Abrothrix* species (Rodentia, Cricetidae). Evol. Biol. 4, 37–62.

Steppan, S.J., 1995. Revision of the tribe Phyllotini (Rodentia: Sigmodontinae), with a phylogenetic hypothesis for the Sigmodontinae. Fieldiana Zool. New Ser. 80, 1–112.

Steppan, S.J., Adkins, R.M., Anderson, J., 2004. Phylogeny and divergence-date estimates of rapid radiations in muroid rodents based on multiple nuclear genes. Syst. Biol. 53, 533–553.

Strong, E.E., Lipscomb, D., 1999. Character coding and inapplicable data. Cladistics 11, 363–371.

Tammone, M.N., Hajduk, A., Arias, P., Teta, P., Lacey, E.A., Pardiñas, U.F.J., 2014. Last Glacial Maximum environments in northwestern Patagonia revealed by fossil small mammals. Quat. Res. 82, 198–208.

Teta, P., 2013. Relaciones filogenéticas de la tribu Abrotrichini (Rodentia, Cricetidae): análisis separados y combinados de evidencias morfológicas y moleculares. Unpublished doctoral dissertation. Fac. Cienc. Nat. y Museo. Univ. Nac. La Plata, La Plata, Argentina.

Teta, P., Pardiñas, U.F.J., 2015. Genus *Notiomys* Thomas, 1890. In: Patton, J.L., Pardiñas, U.F.J., D'Elía, G. (Eds.), Mammals of South America. Volume 2 – Rodents. University of Chicago Press, Chicago, pp. 135–138.

Teta, P., Pardiñas, U.F.J., D'Elía, G., 2006. "Abrotrichinos". In: Bárquez, R.M., Díaz, M.D., Ojeda, R.A. (Eds.), Mamíferos de Argentina: Sistemática y Distribución. Sociedad Argentina para el Estudio de los Mamíferos, Tucumán, Argentina, pp. 192–197.

Teta, P., D'Elía, G., Pardiñas, U.F.J., Jayat, P., Ortiz, P., 2011. Phylogenetic position and morphology of *Abrothrix illutea* Thomas, 1925, with comments on the incongruence between gene trees of *Abrothrix* (Rodentia, Cricetidae) and their implications for the delimitation of the genus. Zoosyst. Evol. 87, 227–241.

Teta, P., Pardiñas, U.F.J., Ortiz, P.E., 2014. Posición sistemática de *Akodon* (*Abrothrix*) *kermacki* y *A.* (*Ab.*) *magnus* (Rodentia, Cricetidae) del Plio-Pleistoceno del sudeste de Buenos Aires, Argentina. Rev. Bras. Paleont. 17, 405–416.

Teta, P., Pardiñas, U.F.J., D'Elía, G., 2015a. Genus *Chelemys* Thomas, 1903. In: Patton, J.L., Pardiñas, U.F.J., D'Elía, G. (Eds.), Mammals of South America. Volume 2 – Rodents. University of Chicago Press, Chicago, pp. 127–132.

Teta, P., Pardiñas, U.F.J., D'Elía, G., 2015b. Genus *Geoxus* Thomas, 1919. In: Patton, J.L., Pardiñas, U.F.J., D'Elía, G. (Eds.), Mammals of South America. Volume 2 – Rodents. University of Chicago Press, Chicago, pp. 132–135.

Thomas, O., 1916. The grouping of the South-American Muridae commonly referred to *Akodon*. Anna. Mag. Nat. Hist. Ser. 8, 336–340.

Thomas, O., 1927. On a further collection of mammals made by Sr. E. Budin in Neuquen, Patagonia. Anna. Mag. Nat. Hist. Ser. 19, 650–658.

Ventura, K., Silva, M.J., Geise, L., Leite, Y., Pardiñas, U.F.J., Yonenaga-Yassuda, Y., D'Elía, G., 2013. The phylogenetic position of the enigmatic Atlantic forest-endemic spiny mouse *Abrawayaomys* (Rodentia: Sigmodontinae). Zool. Stud. 52, 1–10.

Voss, R.S., Linzey, A.V., 1981. Comparative gross morphology of male accessory glands among Neotropical Muridae (Mammalia: Rodentia) with comments on systematic implications. Misc. Publ. Mus. Zool. Univ. Mich. 159, 1–41.

Voss, R.S., Gutiérrez, E.E., Solari, S., Rossi, R.V., Jansa, S.A., 2014. Phylogenetic relationships of mouse opossums (Didelphidae, *Marmosa*) with a revised subgeneric classification and notes on sympatric diversity. Am. Mus. Novit. 3817, 1–27.

Weksler, M., 2006. Phylogenetic relationships of oryzomine rodents (Muroidea: Sigmodontinae): separate and combined analyses of morphological and molecular data. Bull. Amer. Mus. Nat. Hist. 296, 1–149.

Weksler, M., Percequillo, A.R., Voss, R.S., 2006. Ten new genera of oryzomyine rodents (Cricetidae: Sigmodontinae). Am. Mus. Novit. 3537, 1–29.

Wheeler, Q.D., 2004. Taxonomic triage and the poverty of phylogeny. Philos. Trans. R. Soc. Lond. [Biol.] 359, 571–583.

Wilkinson, M., 1995. A comparison of two methods of character construction. Cladistics 11, 297–308.

Yu, Y., Harris, A.J., He, X.J., 2011. RASP (Reconstruct Ancestral State in Phylogenies) 2.0 beta. http://mnh.scu.edu.cn/soft/blog/RASP

Zijlstra, J., 2012. A new oryzomyine (Rodentia: Sigmodontinae) from the Quaternary of Curaçao (West Indies). Zootaxa 3534, 61–68.

Supporting Information

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

Appendix 1

List of the morphological characters used in the phylogenetic analysis

External morphology

1 Nose coloration: non-reddish (0); or reddish and sharply contrasting with the rest of head (1). The description and coding of this character follows Pacheco (2003, ch. 16).

2 Body pelage pattern: dorsal and ventral colours sharply delimited, dorsum darker than pale ventral surface, resulting in conspicuous countershading (0); dorsal and ventral colours subtly delimited, dorsum slightly darker than ventral surface, resulting in weak countershading (1); or limits of dorsal and ventral colours indistinct, ventral surface dark, countershading absent (2). The description and coding of this character follows Weksler (2006, ch. 15).

3 External ear size: ears with extremely thin and small pinnae, mostly hidden in the fur of the head (0); ears small to medium, but pinnae externally visible and semicircular (1); or ears large and ovate (2).

4 Genal 1 vibrissae: absent (0); or present (1). The description and coding of this character follows Pacheco (2003).

5 Tail furring: tail densely furred, scales not visible even at higher magnification (0); or tail sparsely furred, scales macroscopically obvious (1). The description and coding of this character follows Weksler (2006).

6 Tail coloration: indistinctly bicoloured (0); or sharply bicoloured, darker above and paler below (1).

7 Tail length: < 55% of the head and body length (0); or 60–85% of the head and body length (1); or > 90% of the head and body length (2).

8 Pollex: ending in a rounded nail (0); or ending in a small claw (1) (Fig. 3a,b).

9 Relative length of the second digit on manus: second digit slightly shorter to equal to the fourth (0); or second digit much shorter than the fourth (1) (Fig. 3a,b).

10 Margins of the hindfeet: without a fringe of hairs (0); with a dense fringe of hairs extended slightly beyond the plantar surface (1) (Fig. 3d); or with a shaggy fringe of hairs extended well beyond the plantar surface (2) [see Pardiñas et al. (2008: fig. 3)].

11 Relative length of hallux: hallux distinctly shorter than the fifth digit (0); or hallux slightly shorter than the fifth (1) (Fig. 3c,d).

12 Ungual tufts on pes: abundant, longer than claws (0); or sparse, shorter than claws (1) (Fig. 3c,d).

13 Relative position of the first interdigital pad on manus: nearly in the same line of the second (0); or placed posterior to the second (1) (Fig. 3a,b).

14 Relative position of the first interdigital pad on pes: nearly in the same line of the fourth (0); or placed anterior to the fourth interdigital (1) (Fig. 3c,d).

15 Relative position of the second interdigital pad on pes: nearly in the same line of the third (0); or placed anterior to the third (1) (Fig. 3c,d).

16 Position of hypothenar pad in relation to thenar: gap between hypothenar and thenar pads (0); or gap absent, the hypothenar and thenar pads level or overlap (1) (Fig. 3c,d).

17 Claws on manus: claws small to medium, not keeled (0); claws moderately long, keeled for about one-third to half of their length (1); or claws very long, subequal to digit or longer, keeled for about half or more of their length (2). This character was modified from Pacheco (2003).

18 Base of claws (manus): the base of each claw covers almost entirely the respective finger (1); or claw narrower, its base covering only the central part of the finger (1).

19 Mammae pairs: 6 mammae in inguinal, abdominal and postaxial pairs (0); or 8 mammae in inguinal, abdominal, postaxial and pectoral pairs (1); or 10 or more mammae; if 10, arranged in inguinal, abdominal, thoracic, postaxial and pectoral pairs. This character was modified from Pacheco (2003, ch. 13–15) and Weksler (2006).

Skull

20 Nasals and premaxillae: ending at the plane of the anterior face of the incisors (0); extending slightly to moderately in front of the incisors (1); or projecting well in front of the incisors as a tube (2) (Fig. 4a–c).

21 Posterior end of nasals: posterior margin bluntly, rounded to squared (0); or forming a sharp angle, with acutely pointed terminus (1). The description and coding of this character follows Weksler (2006) (Fig. 4d,e).

22 Length of nasals: short, not extending posteriorly beyond the triple-point suture between the maxillary, frontal and lacrimal (0); or long, extending posteriorly well beyond the maxillary–frontal–lacrimal suture (1). The description and coding of this character follows Weksler (2006) (Fig. 4e,f).

23 Lacrimals: equally contacting maxillary and frontal bones (0); or contacting mainly maxillary (1). The description and coding of this character follows Weksler (2006) (Fig. 5).

24 Interorbital shape: anteriorly divergent, narrowest region in posterior half (0); or narrowest point centrally situated, as bounded by the frontals (1); or posteriorly divergent, narrowest region anterior (2). The description and coding of this character follows Steppan (1995, ch. 49P) (Fig. 5).

25 Zygomatic notches: indistinct (0); or moderate to deep (1).

26 Frontal sinuses: not inflated (0); or inflated (1) (Fig. 4g).

27 Interparietal length: long, > 1/3 of the parietal length (0); or short, < 1/3 of the parietal length (1). The description and coding of this character follows Pacheco (2003).
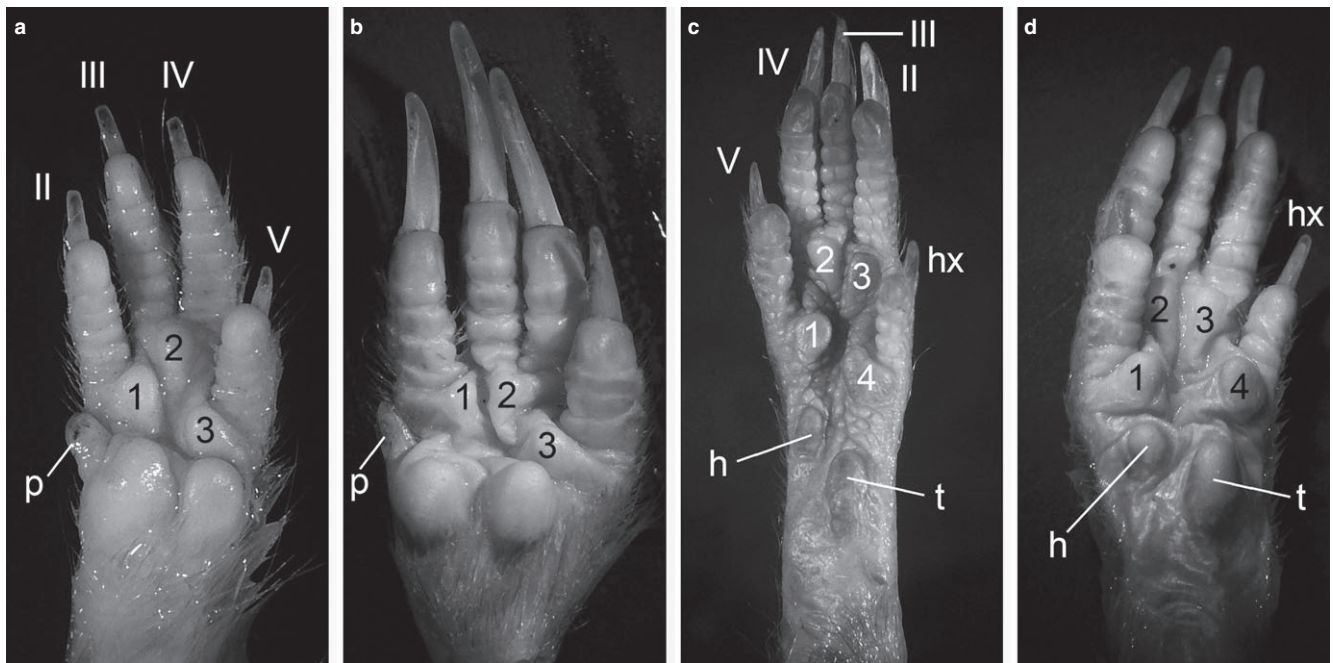
Fig. 3. Palmar (a, b) and plantar (c, d) views of left fore foot and right hind foot of *Abrothrix* (*Angelomys*) *andina* (a; CNP w/n), *Ab.* (*Abrothrix*) *lanosa* (c; CNP 1385) and *Paynomys macronyx vestitus* (b, d; CNP uncatalogued). I–V, digits; 1–5, interdigital pads; h, hypothenar; hx, hallux; p, pollex; t, thenar.

28   Nasolacrimal capsules: medially located on rostrum at the level of the incisive capsules (0); or placed below the incisive capsules (1) (Fig. 5).

29   Zygomatic plate slope: vertical (0); or slanted backward from the base (see Pacheco, 2003: ch. 24). We consider as inclined plates where the anterior border forms an angle > 115° with the longitudinal axis of the skull.

30   Upper free border of zygomatic plate: absent (0); present and rounded (1); or produced as a sharp corner or spinous process (2) (Fig. 4a–c).

31   Infraorbital foramen: lumen narrow to moderately open and compressed at its base, nearly piriform in shape (0); or lumen wide and nearly ovate in shape (1) (Fig. 6a,b).

32   Scar for the origination of the superficial masseteric muscle: indicated as a rounded rough area (0); or as an osseous prominence, rounded and elevated (1). This structure is found at the base of the zygomatic plate, near its anterior border (Fig. 6a).

33   Ethmoid foramen: dorsal to M1 (0); dorsal to M2 or M2/M3 contact (1); dorsal to M3 (2); or posterior to M3 (3). This character was modified from Pacheco (2003) (Fig. 6c–e).

34   Maxillary knob dorsal to M2: absent (0); or present (1) (Fig. 6c).

35   Anterior border of alisphenoid: not projected forward (0); or projected anteriorly as a free osseous flake (1) (Fig. 6f–h).

36   Sphenofrontal foramen: absent (0); or present and laterally visible (1); or present, sometimes incomplete, placed behind the osseous flake of the alisphenoid and not visible laterally (2). The sphenofrontal foramen is located at the end of the squamosal–alisphenoid channel. Patterson (1992:136) indicated that "a sphenofrontal foramen, obsolete or entirely lacking in the remaining long-clawed genera [*Geoxus, Notiomys, Pearsonomys*], is present in *Chelemys* [which then included *Paynomys* gen. nov.]; as in those groups, however, the main course of the supraorbital branch of the stapedial artery passes through a ventral sphenoid foramen, and the squamosal–alisphenoid groove is fenestrated". Our revision of materials indicates that the sphenofrontal foramen is always present in Abrotrichini, although sometimes is not completely surrounded by bone or open to the anterior lacerate foramen (Fig. 6f–h).

37   Alisphenoid strut: absent (0); or present (1).

38   Bullae inflation: not inflated (0); or moderately inflated, Eustachian tube small (1); or inflated, Eustachian tube indistinct (2). The description and coding of this character follows Pacheco (2003) (Fig. 7a–c).

39   Anterodorsal portion of the ectotympanic: rounded to subcuadrangular, well separated from the mastoid (0); or narrow and acuminated and close to the mastoid (1).

40   Stapedial process of bulla: short and wide and distally rounded (0); or long and "spine" shaped (1). According to Patterson (1992: 136), who had access only to the holotype, the stapedial process of *Pearsonomys* is short, ending at the lacerate foramen, while in *Geoxus* this structure contacts the parapterygoid. Our review of a large series of *Pearsonomys* suggests that this condition, present in the holotype, is infrequent within this taxon, being registered in three of 14 specimens; in the remaining ones, the spine reaches the parapterygoid.

41   Orbicular apophysis of the malleus: peduncle proportionally wide, ending in a distal rounded button slightly larger in diameter than the base (0); or peduncle proportionally narrow and long, ending in a bulbous button (1) (Fig. 8c,d).

42   Length of incisive foramina: short, not extending or just reaching the anterior face of the molar series (0); or long, extending between the protocones of the first upper molar (1) (Fig. 4h–k).

43   Shape of incisive foramina: external borders nearly straight and parallel (0); borders nearly parallel, with a widening in its anterior third (1); parenthesis-shaped, without constrictions (2); or parenthesis-shaped, with a constriction between the middle and the posterior third (3) (Fig. 4h–k).

44   Maxillary septum length: short, subequal to or less than half the length of incisive foramina (0); or larger than half the length of incisive foramina (1). This character was modified from Pacheco (2003) (Fig. 4h–k).

45   Posterolateral palatal pits: simple and small (1); simple, moderate to large (1); or large with internal divisions (2). *Notiomys*

Fig. 4. Selected cranial traits of Abrotrichini. (a–c) Anterior projection of nasals and premaxillae: (a) ending at the anterior plane of the incisors [*Chelemys megalonyx* (UACh 1462)]; (b) extending slightly in front of the incisors [*Notiomys edwardsii* (MVZ 163067)]; (c) projecting well in front of the incisors in the form of a tube [*Abrothrix* (*Abrothrix*) *manni* (GD 1190)], white arrow indicates the free upper border of zygomatic plate (absent in a and b; present and rounded in c). (d–f) Morphology of nasals: (d) posterior margin blunt [*C. megalonyx*]; (e, f) posterior margin sharply angled, with acutely pointed terminus [E, *Ab.* (*Chroeomys*) *jelskii cruceri* (MVZ 173063)]; F, *Ab.* (*Ab.*) *manni*], nasal widened over the anterior third of its length is indicated by the white arrow. (g) Inflated frontal sinuses [*Ab.* (*Ab.*) *manni*]. (h–k) Shape of incisive foramina and maxillary septum length: (h) parenthesis-shaped, without constrictions; maxillary septum more than half the length of incisive foramina [*Ab.* (*Pegamys*) *illutea* (CNP 1489)]; (i) parenthesis-shaped, with a constriction between the middle and the posterior third; maxillary septum short, half or less of the length of incisive foramina [*Ab.* (*Chroeomys*) *jelskii cruceri*]; (j, k) borders nearly parallel and widened over its anterior third; maxillary septum exceeds half the length of incisive foramina [J, *N. edwardsii*; K, *C. megalonyx*]. if = incisive foramina; zn = zygomatic notch; n = nasal; pm = premaxillae; zp = zygomatic plate; fs = frontal sinus; ms = maxillary septum. The figures are not to scale.

edwardsii is the only Abrotrichini that includes populations with large, internally divided, posterolateral palatal pits (Pardiñas et al., 2008: fig. 7) (Fig. 8a,b).

46 Palatal length: short, its posterior border is nearly in line with the posterior plane of the last molars (0); or long, its posterior border is behind the posterior plane of the last molars (1) (Fig. 8a,b).
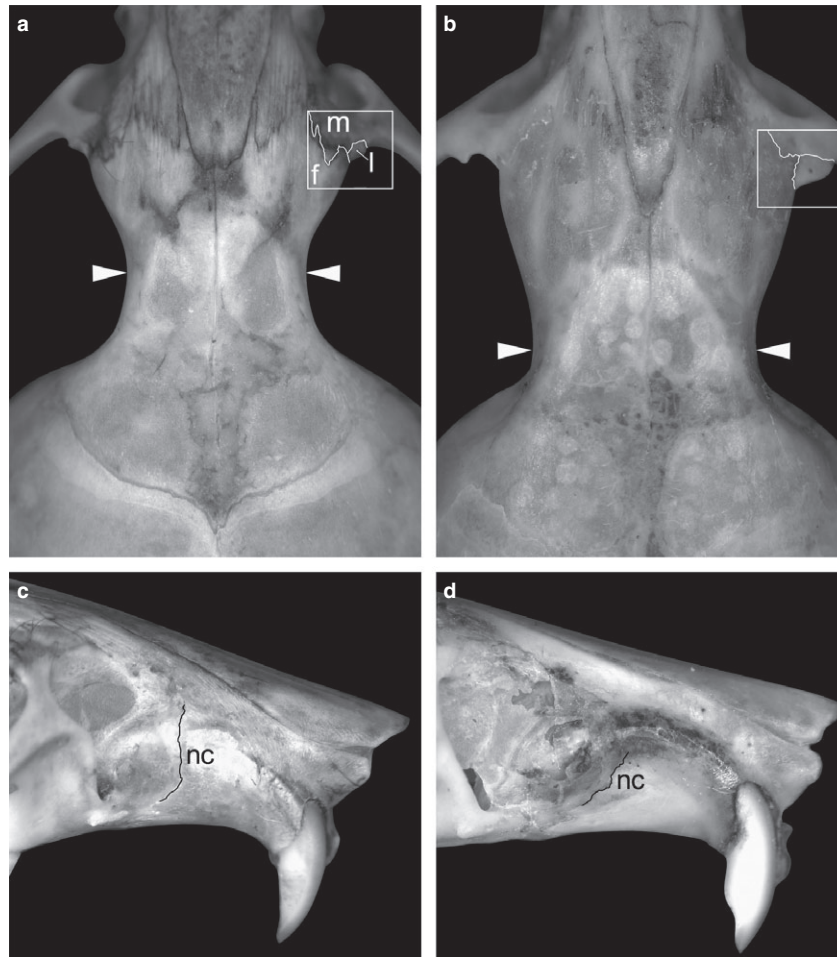
Fig. 5. Selected cranial traits of Abrotrichini. (a, b) Interorbital region: (a) interorbital region narrowest centrally, bounded by the frontals (f); lacrimals (l) mainly in contact with the maxillary (mx); (b) interorbital region anteriorly divergent and narrowest posteriorly; l in equal contact with m and f bones. (c, d) Nasolacrimal capsules (nc): (c) placed at middle height on rostrum, superficial to the incisive capsules; (d) placed below the incisive capsules [a, c: *Abrothrix* (*Angelomys*) *olivacea* (CNP 2580); b, d: *Geoxus annectens* (UACh 1064)].

47 Sphenopalatine vacuities: present as large apertures along the presphenoid, reaching basisphenoid (0); or present, but reduced to narrow slits mostly along the presphenoid (1) (Fig. 8a,b).

48 Parapterygoid fossa deep: at the same level as palate (0); excavated but not reaching level of mesopterigoid roof (1); or deeply excavated, reaching level of mesopterygoid roof (2). For description and coding of this character we follow Weksler (2006).

49 Relative width of parapterygoid fossa: subequal to slightly narrower than adjoining mesopterygoid fossa (0); or distinctly broader than mesopterygoid fossa (1). This character was modified from Steppan (1995).

50 Shape of mesopterygoid fossa: posteriorly convergent, "horseshoe"-shaped (0); paralell sided "U"-shaped (1); or posteriorly divergent, "V"-shaped (2). For description and coding of this character we follow Steppan (1995).

51 Presphenoid–basisphenoid suture: located anterior to the middle portion of the mesopterygoid fossa (0); located towards the middle portion of mesopterygoid fossa (1); or located posteriorly to the middle portion of the mesopterygoid fossa (2). Even when this is a continuous character, discontinuities between character states are sufficiently obvious as to not present coding ambiguities. Mesopterygoid length was taken between the posterior palatal border and the distal extreme of pterygoids (Fig. 8a,b).

52 Diastema shape: slightly excavated, smoothly concave all along (0); or deeply to moderately excavated (0) (Fig. 9).

53 Diastema length: short, subequal to the combined m1–m2 length (0); or long, subequal or larger than the combined m1–m3 length (1) (Fig. 9).

54 Capsular projection of the incisive: placed below the coronoid process (0); or placed towards the condyle (1) (Fig. 9).

55 Lower teeth concealed by coronoid process in lateral view: none (0); or posterior part of m3 (1); or anterior part of m3 (2) (Fig. 9).

56 Height of coronoid process: above maximun height of mandibular condyle (0); subequal (1); below mandibular condyle (2). The description and coding of this character follows Steppan (1995) (Fig. 9).

57 Shelf bearing lower molars: not continuing behind the last molar (0); or well formed, continuing behind the last molar (1).

Dentition

58 Incisor procumbency: opisthodont (0); or orthodont (1); or proodont (2) (see Hershkovitz, 1962: 101–103) (Fig. 4a,b).

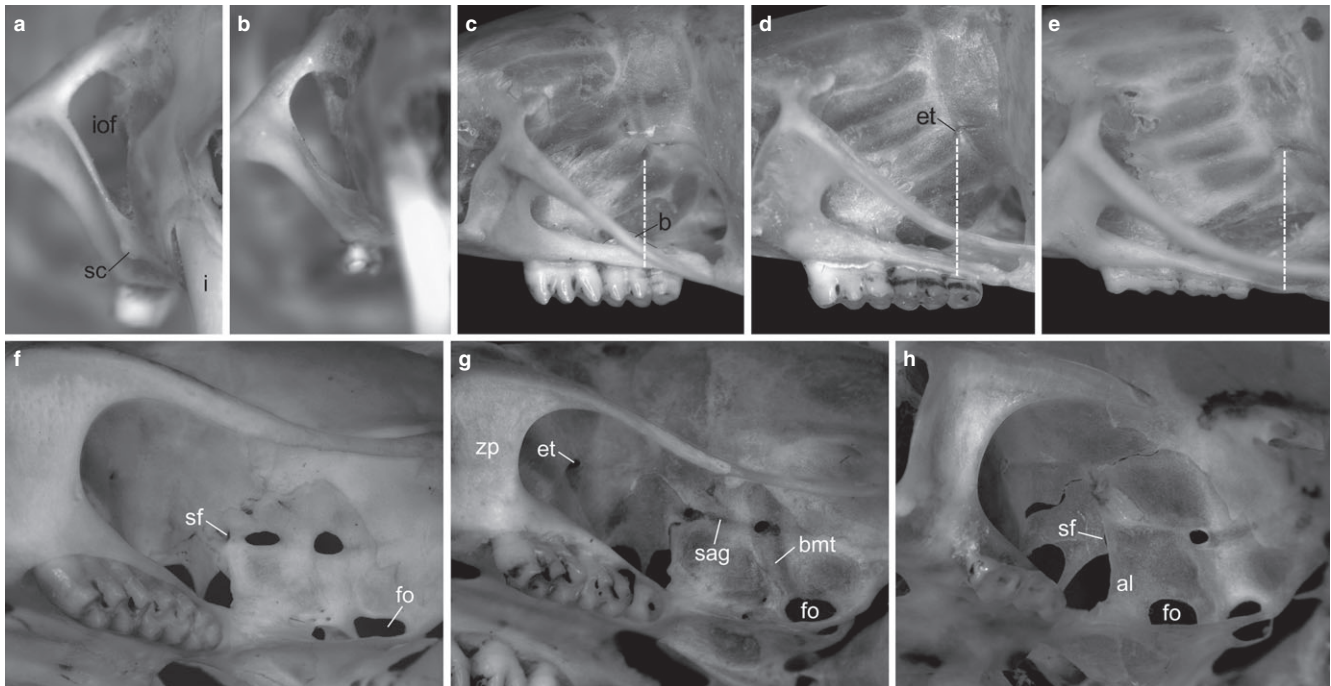59 Enamel on incisors: pale yellow to pale orangish (0); or bright orange (1).

Fig. 6. Selected cranial traits of Abrotrichini. (a, b) Infraorbital foramen [iof]: (a) lumen narrow to moderately open and compressed at its base, nearly piriform in shape [*Chelemys megalonyx* (UACh 1462)]; (b) lumen wide and nearly ovate in shape [*Geoxus valdivianus* (UACh 2170)]. (c–e) Relative position of the ethmoid foramen [et]: dorsal to M2/M3 [*Abrothrix* (*Abrothrix*) *hirta* (UACh 1867)]; (d) dorsal to M3 [*Ab.* (*Ab.*) *sanborni* (GD 1165)]; (e) posterior to M3 [*Geoxus annectens* (UACh 1064)]. (f–h) Alisphenoid region: (f) *Paynomys macronyx* (GD 931); (g) *Ab.* (*Ab.*) *hirta* (CNP 2339); (h) *Geoxus valdivianus* (CNP 812); the sphenofrontal foramen [ef] in *Geoxus* is hidden, in lateral view, by an osseous flake of the alisphenoid [al]. b = maxillary knob dorsal to M2; bmt = trough for masticatory-buccinator nerve; sf = sphenofrontal foramen; fo = foramen ovale; I = upper incisors; zp = zygomatic plate; sag = squamosal–alisphenoid groove; sc = scar for the origin of the superficial masseteric muscle. The figures are not to scale.

60 Molar occlusal topography: brachyodont (0); or mesodont (1); or hypsodont (2). We follow Hershkovitz (1962) and Reig (1987) in the definition of these categories (Figs 10 and 11).

61 Crown topography: planate (0); or crested (1); or terraced (2). The description and coding of this character follows Hershkovitz (1962: 101–103) (Figs 10 and 11).

62 Labial flexi on M1: relatively deep and narrow, transversely to posteriorly orientated (0); or relatively deep and narrow, transversely orientated in its first portion and turning backwards in its posterior part (1); or widely open, shallow and transversally disposed (2) (Fig. 12b).

63 Anteromedian flexus on M1: absent (0); or present and shallow (1); or present and deep (2) (Fig. 12a).

64 Procingulum shape: anterior–posteriorly compressed, nearly as inverted triangle in general shape (0); or laterally expanded, in some cases "fan"-shaped (1) (Figs 10–12).

65 Anteroflexus on M1: absent (0); or present but slightly evident (1); or present and well developed (2). The degree of development of the anteroflexus, present as a fold between the protocone and the anteroloph plus parastyle, is linked to the expression of this latter structure and its degree of fusion with the protocone. *Abrothrix* and *Paynomys* typically show an intact anteroloph + parastyle and a shallow anteroflexus. The anteroflexus is completely lost in adult specimens of *Chelemys*, *Notiomys*, *Geoxus* and *Paynomys* gen. nov. (Fig. 12a).

66 Anteroloph on M1: absent or minute (0); or present and well developed (1) (Fig. 12b).

67 Orientation of paracone and metacone on M1: anteriorly orientated (0); or transversely orientated (1) (Fig. 12a).

68 Mesoloph on M1: present but small in young individuals, coalesced in adult ones (0); or present but small in all ages (1); or present and well expressed in all ages (2). The mesoloph of Abrotrichini tends to merge with a paralophule and mesostyle. The study of young individuals suggests that this sequence of fusions usually begins with the paralophule + mesostyle and ends with the mesoloph. The final result is a structure that extends labially from the median wall, and together with the paracone usually encloses an island of enamel that corresponds to the position of the mesoflexus (Fig. 12a,b).

69 Mesostyle on M1: absent (0); or present (1) (Fig. 12a).

70 Anteroloph length on M2: short, reaching half of the length of the paracone (0); or long, reaching or surpassing 3/4 of the length of the paracone (1) (Fig. 12c).

71 Paraflexus on M2: present as an indentation on the labial side of the tooth (0); or present and deep (1) (Fig. 12c).

72 Mesofossette on M1–M2 of young individuals: absent (0); or present as an enamel island (1) (Fig. 12b).

73 Mesoloph on M2: present but small in young individuals, coalesced in adults (0); or present in all ages (1) (Fig. 12c).

74 Size of anterior cusps relative to posterior ones on M2: paracone and protocone broader than metacone and hypocone (0); or subequal (1). In *Abrothrix*, the surface of the metacone and hypocone in occlusal view are subequal to that of the paracone and protocone, giving the tooth a subquadrangular contour. By contrast, in the fossorial forms the metacone and hypocone are markedly smaller than the paracone and protocone, so that the tooth tapers posteriorly (Figs 10 and 11).

75 Hypocone on M3: absent or indistinct (0); or present (1). The third upper molar in Abrotrichini is small and subcircular in outline.
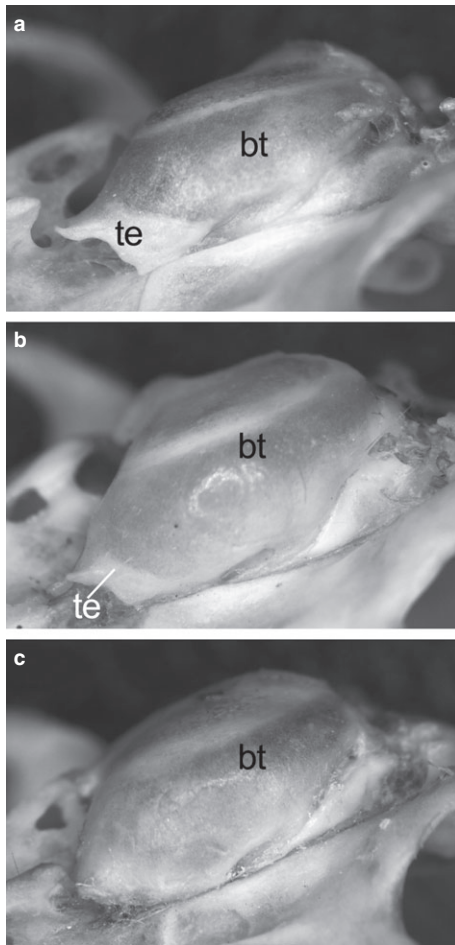
Fig. 7. Bullae (bt) inflation in Abrotrichini. (a) Not inflated [*Abrothrix* (*Abrothrix*) *hirta* (UACh 1867)]; (b) moderately inflated, Eustachian tube (te) small [*Chelemys megalonyx* (UACh 1462)]; (c) inflated, Eustachian tube indistinct [*Ab.* (*Angelomys*) *andina andina*, C-3501]. The figures are not to scale.

The paracone and protocone are well developed, like the metacone, which occupies most of the posterior half of the tooth; in turn, the hypocone is mostly absent. The only exception to this pattern is *Paynomys macronyx*, which has both a moderately deep hypoflexus and a small hypocone (Fig. 12c).

76 Mesofossette on M3: absent (0); or present (1). The third lower molar of some Abrotrichini is characterized by the presence of a centrally placed circular enamel island, which appears after the close of the mesoflexus and persists even in old adult specimens (Fig. 12c).

77 Relative length of M3: short, less than half of the M2 measured antero-posteriorly (0); or clearly larger than half of the M2 (1) (Figs 10 and 11).

78 Roots on M3: 1 (0); 2 (1); or 3 (2).

79 Anteromedian flexid on m1: absent (0); or present and shallow (1); or present and deep (2) (Fig. 12d).

80 Procingulum shape on m1: wider than large (0); or larger than wide (1) (Figs 10 and 11).

81 Protostylid on m1: absent or indistinct (0); or present (1) (Fig. 12d).

82 Mesolophid on m1: absent (0); or present (1). This structure is only present on the genus *Abrothrix*, with the exception of *A.* (*Chroeomys*) (Fig. 12d).

83 Ectostylid on m1: absent (0); or present (1) (Fig. 12d).

84 Size of anterior cusps relative to the posterior ones on m2: metaconid and protoconid broader than entoconid and hypoconid (0); or subequal (1) (Figs 10 and 11).

85 Mesolophid on m2: absent (0); or present (1). This structure is only present on the genus *Abrothrix*, with the exception of *A.* (*Chroeomys*) (Fig. 12e).

86 Posterolophid on m2: absent (0); or present and transversely orientated (0); or present and posteriorly orientated (1) (Fig. 12e,f).

87 Protostylid on m2: absent or indistinct (0); or present (1) (Fig. 12e).

88 Shape of m3: m3 "T"-shaped, with the hypoconid and entoconid much reduced (0); or m3 "S"- or "Z"-shaped (1) (Figs 10 and 11).

Postcranial skeleton

89 Lateral supracondylar crest of the humerus: slightly developed (0); moderately developed (1); or wide and well extended laterally (2) (Fig. 13).

90 Medial epicondyle of the humerus: much shorter than the combined length of capitulum and trochlea (0); or subequal or longer than the combined length of capitulum and trochlea (1) (Fig. 13).

91 Medial extension of olecranon process of the ulna: absent (0); or present (1).

Phallus and accessory reproductive glands

92 Size of ampullary glands: normal (0); or larger than the typical condition (1). Voss and Linzey (1981) give a detailed description of these character states (Fig. 14).

93 Size of bulbo-urethral glands: normal (0); or larger than the typical condition (1). See Voss and Linzey (1981) for a detailed character description (Fig. 14).

94 Central digit of distal baculum: absent (0); reduced (1); or well developed (2). See Gallardo et al. (1988) and Spotorno (1992) (Fig. 15).

95 Lateral digits of distal baculum: absent (0); reduced (1); or well developed (2). See Gallardo et al. (1988) and Spotorno (1992) (Fig. 15).

96 Central bacular mound: absent (0); reduced (1); or well developed (2). See Spotorno (1992) (Fig. 15).

97 Lateral bacular mound: absent (0); reduced (1); or well developed (2). See Spotorno (1992).

98 Dorsal hood on phallus: absent (0); present (1). See Spotorno (1992).

Stomach

99 Stomach morphology: gastric glandular epithelium of stomach limited to antrum, not extending beyond incisura angularis (0); or gastric glandular epithelium covers antrum and proximal portion of corpus near oesophageal opening (1). Carleton (1973: 13, 14) reported that *Ab.* (*Abrothrix*) *longipilis* [= *Ab.* (*Ab.*) *hirta*], *Ab.* (*Angelomys*) *olivacea* and *Ab.* (*Chroeomys*) *jelskii* had the gastric glandular epithelium limited to the antrum; however, our analysis of specimens indicated that at least in *longipilis* and *olivacea* the gastric glandular epithelium covers both the antrum and the proximal portion of corpus near esophageal opening (Fig. 16).
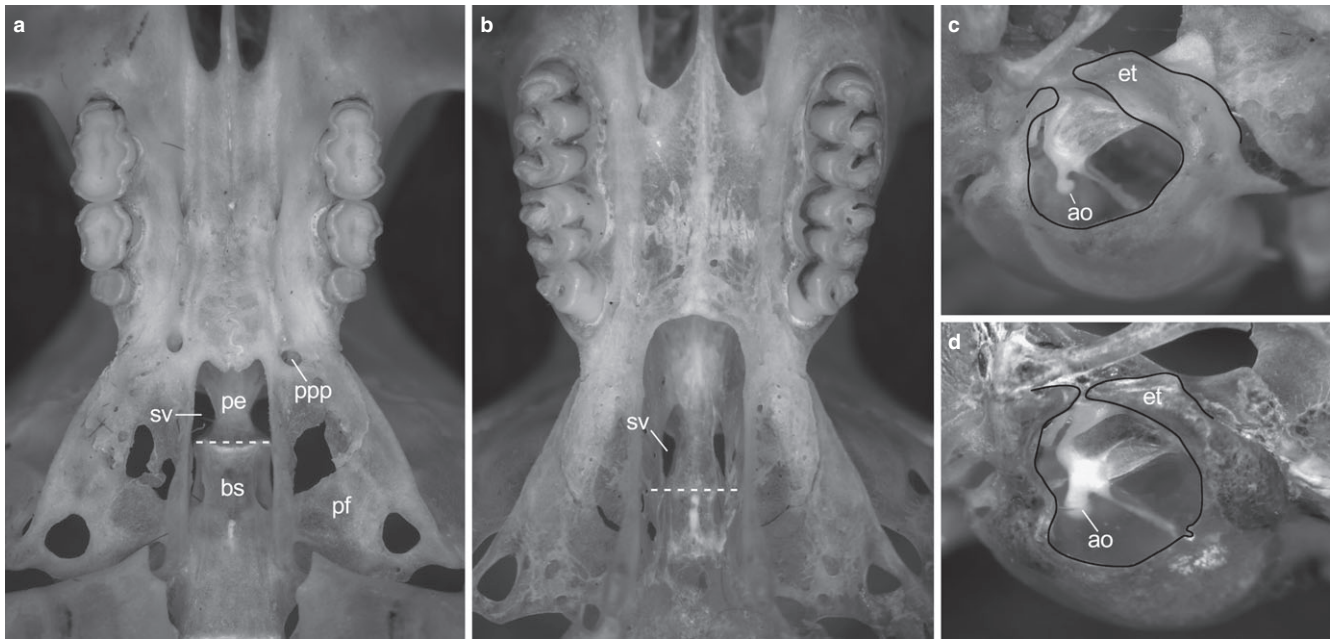
Fig. 8. Selected cranial traits of Abrotrichini. (a, b) Palate, roof of mesopterygoid fossa and relative position of the presphenoid–basisphenoid suture (white line): (a) palate long, with large and internally divided posterolateral palatal pits (ppp) and roof of mesopterygoid fossa with sphenopalatine vacuities (sv) present as large apertures along the presphenoid, reaching basisphenoid [*Notiomys edwardsii* (MVZ 163067)]; (b) palate short, with simple and small ppp and roof of mesopterygoid fossa with sphenopalatine vacuities (sv) reduced to narrow slits mostly along the presphenoid [*Abrothrix* (*Pegamys*) *illutea* (CNP 1489)]. (c, d) Lateral view of auditory region: (c) anterodorsal portion of the ectotympanic (et) rounded to subquadrate, well separated from the mastoid and orbicular apophysis of the malleus (ao) with the peduncle proportionally narrow and long, ending in a bulbous button [*Geoxus valdivianus* (UACh 2170)]; (d) anterodorsal portion of the et narrow and acuminate, close to the mastoid and ao with the peduncle proportionally wide, ending in a distal rounded button slightly larger in diameter than the base [*Ab.* (*P.*) *illutea* (CNP 1489)].

Appendix 2

List of synapomorphies and autapomorphies from the tree obtained by cladistic parsimony analysis of 99 morphological characters. Character numbers and states as in character analysis (Appendix 1).

Sigmodon hispidus: no autapomorphies

Akodon azarae: ch. 46: 1→0; ch. 60: 2→1; ch. 62: 1→0; ch. 65: 1→2; ch. 68: 01→2; ch. 82: 0→1; ch. 85: 0→1

Phyllotis xanthopygus: ch. 38: 0→1; ch. 64: 1→0; ch. 70: 1→0; ch. 84: 1→0; ch. 86: 1→0; ch. 87: 1→0

Holochilus brasiliensis: ch. 12: 0→1; ch. 33: 1→0; ch. 37: 0→1; ch. 40: 1→0; ch. 68: 0→1; ch. 73: 0→1; ch. 82: 0→1; ch. 85: 0→1

Reithrodon auritus: ch. 4: 1→0; ch. 50: 1→2

Wiedomys pyrrhorhinos: ch. 1: 0→1; ch. 2: 1→0; ch. 24: 1→2; ch. 38: 0→2; ch. 44: 0→1; ch. 60: 2→0

Abrothrix (*Abrothrix*) *longipilis*: no autapomorphies

Abrothrix (*Abrothrix*) *hirta*: no autapomorphies

Abrothrix (*Abrothrix*) *lanosa*: ch. 59: 1→0; ch. 94: 0→1; ch. 95: 0→1

Abrothrix (*Abrothrix*) *sanborni*: no autapomorphies

Abrothrix (*Abrothrix*) *manni*: ch. 47: 0→1; ch. 58: 0→1

Abrothrix (*Angelomys*) *olivacea*: no autapomorphies

Abrothrix (*Angelomys*) *xanthorhina*: no autapomorphies

Abrothrix (*Angelomys*) *andina dolichonyx*: no autapomorphies

Abrothrix (*Angelomys*) *andina andina*: ch. 51: 1→2

Abrothrix (*Chroeomys*) *jelskii cruceri*: ch. 40: 1→0; ch. 46: 1→0; ch. 57: 1→0; ch. 79: 1→0

Abrothrix (*Chroeomys*) *jelskii sodalis*: no autapomorphies

†*Abrothrix* (*Chroeomys*) sp. nov.: ch. 66: 0→1

Abrothrix (*Pegamys*) *illutea*: ch. 22: 1→0; ch. 43: 3→2; ch. 44: 0→1; ch. 46: 1→0; ch. 47: 0→1; ch. 63: 1→0

Paynomys macronyx macronyx: no autapomorphies

Paynomys macronyx vestitus: no autapomorphies

Chelemys megalonyx: ch. 20: 1→0; ch. 54: 0→1; ch. 57: 1→0; ch. 63: 1→0; ch. 86: 2→0

Notiomys edwardsii: ch. 1: 0→1; ch. 2: 1→0; ch. 3: 1→0; ch. 10: 0→2; ch. 23: 0→1; ch. 25: 1→0; ch. 27: 0→1; ch. 49: 0→1; ch. 55: 0→2; ch. 78: 1→0

Geoxus annectens: ch. 7: 0→1; ch. 38: 1→2; ch. 55: 0→1

Geoxus valdivianus: no autapomorphies

Geoxus michaelseni: ch. 59: 1→0

Node 1: ch. 94: 1→0; ch. 96: 1→0

Node 2: ch. 20: 1→2; ch. 55: 1→0; ch. 95: 1→0; ch. 97: 1→0

Node 3: no synapomorphies

Node 4: ch. 32: 0→1; ch. 33: 1→2

Node 5: ch. 46: 1→0

Node 6: ch. 23: 0→1

Node 7: ch. 49: 0→1

Node 8: ch. 38: 2→1; ch. 55: 1→2

Node 9: ch. 60: 2→1; ch. 65: 1→2; ch. 72: 0→1; ch. 82: 0→1; ch. 85: 0→1

Node 10: ch. 63: 1→0; ch. 70: 1→0

Node 11: no synapomorphies

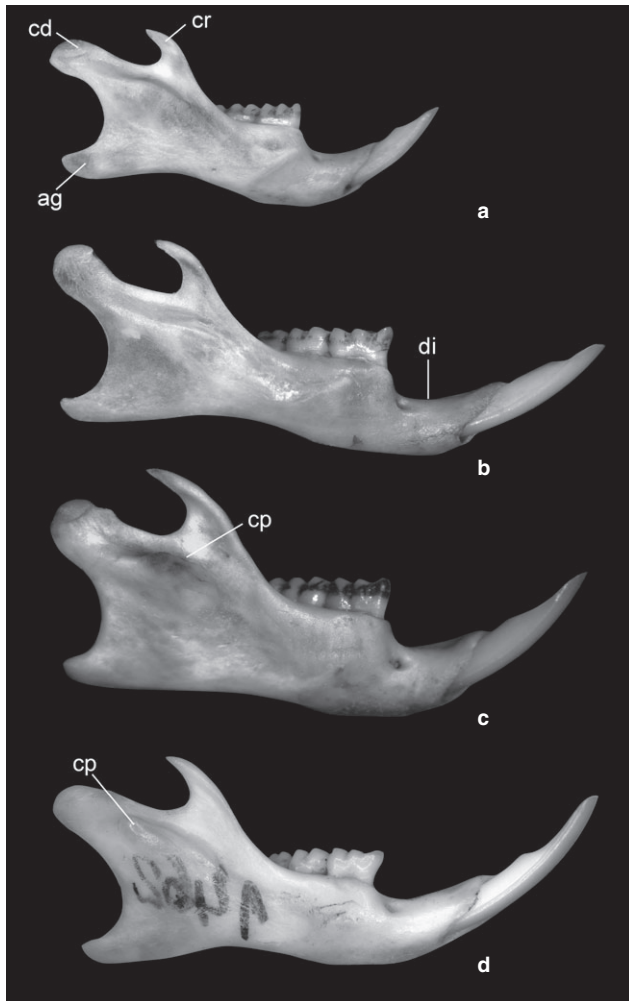Node 12: ch. 94: 2→1; ch. 95: 2→1; ch. 96: 2→1; ch. 97: 2→1

Fig. 9. Dentary morphology in Abrotrichini. Right mandibles (except D, which has been flipped) of some Abrotrichini: (a) *Abrothrix* (*Angelomys*) *olivacea* (CNP 2154); (b) *Ab.* (*Ab.*) *sanborni* (GD 1165); (c) *Paynomys macronyx* (CNP 1896); (d) *Chelemys megalonyx* (CNP 1896) ag = angular process; cd = condylar process; cr = coronoid process; di = diastema; cp = capsular projection of the lower incisor.

Node 13: ch. 10: 0→1; ch. 23: 0→1; ch. 26: 1→0; ch. 46: 1→0; ch. 50: 1→0

Node 14: ch. 38: 0→1; ch. 42: 1→0; ch. 45: 0→1; ch. 52: 0→1; ch. 55: 1→0; ch. 60: 2→0; ch. 62: 1→2; ch. 65: 1→0; ch. 66: 1→0; ch. 67: 0→1; ch. 74: 1→0; ch. 88: 1→0

Node 15: ch. 31: 0→1; ch. 70: 1→0; ch. 71: 1→0; ch. 76: 1→0; ch. 77: 1→0; ch. 80: 1→0

Node 16: ch. 20: 1→2; ch. 28: 0→1; ch. 29: 1→0; ch. 33: 1→3; ch. 34: 0→1; ch. 35: 1→0; ch. 36: 1→2; ch. 39: 1→0; ch. 40: 0→1; ch. 41: 0→1; ch. 43: 1→3; ch. 48: 1→0; ch. 61: 2→1; ch. 79: 1→0; ch. 84: 1→0; ch. 89: 1→2; ch. 98: 0→1

Node 17: ch. 44: 1→0; ch. 47: 0→1

Node 18: ch. 5: 1→0; ch. 7: 1→0; ch. 8: 0→1; ch. 9: 1→0; ch. 11: 1→0; ch. 12: 0→1; ch. 13: 1→0; ch. 14: 1→0; ch. 15: 1→0; ch. 16: 1→0; ch. 18: 1→0; ch. 30: 1→0; ch. 40: 1→0; ch. 43: 3→1; ch. 44: 0→1; ch. 64: 1→0; ch. 69: 1→0; ch. 86: 1→2; ch. 89: 0→1; ch. 90: 0→1; ch. 91: 0→1

Node 19: ch. 4: 1→0; ch. 34: 1→0; ch. 57: 0→1; ch. 76: 0→1; ch. 79: 2→1

Node 20: ch. 3: 2→1; ch. 26: 0→1; ch. 45: 1→0; ch. 49: 1→0; ch. 51: 0→1; ch. 66: 0→1; ch. 67: 1→0

Node 21: ch. 65: 0→1; ch. 69: 0→1; ch. 73: 0→1; ch. 79: 0→2

Node 22: ch. 22: 0→1; ch. 30: 2→1; ch. 39: 0→1; ch. 81: 0→1; ch. 99: 1→0

Node 23: ch. 3: 1→2; ch. 24: 2→1; ch. 42: 0→1; ch. 44: 1→0; ch. 46: 0→1; ch. 48: 2→1; ch. 58: 1→0; ch. 62: 0→1

Node 24: no synapomorphies.

Appendix 3

Taxonomic summary

Tribe Abrotrichini D'Elía et al., 2007

Type genus: *Abrothrix* Waterhouse, 1837.

Contents: *Abrothrix* Waterhouse, 1837; *Chelemys* Thomas, 1903; *Geoxus* Thomas, 1919; *Notiomys* Thomas, 1890; *Paynomys* gen. nov.

Emended morphological diagnosis: rodents of the subfamily Sigmodontinae (*sensu* Reig, 1980) including species of small to medium size (from ~20 g in *Abrothrix andina* to ~55 g in *Paynomys macronyx*), with the following combination of characters: pelage long and soft; tail shorter than the combined length of head and body; genal vibrissae absent; claws equally robust on manus and pes; pes broad with naked palms; skull usually enlarged and with a rounded braincase; interorbital region "amphora-shaped", with rounded supraorbital borders; nasals and premaxillae slightly projected in front of the anterior plane of the upper incisors or forming a noteable tube; nasals longer than frontals; zygomatic plate narrow, with short or absent upper free border; frontal sinus moderately to well developed; anterior border of mesopterygoid fossa rounded to quadrate; posterior suspensory process of squamosal present and connected to the tegmen tympani; stapedial foramen and posterior opening of alisphenoid canal small to relatively large, squamosal-alisphenoid groove and sphenofrontal foramen present; horizontal ramus of mandible gracile and enlarged, except in *Paynomys*; upper incisors ungrooved; molars brachyodont to relatively hypsodont, with main cusps in opposite pairs or slightly alternated; procingulum of M1/m1 reduced and usually fan-shaped; anteromedian flexus/id usually present but shallow; anteroflexus absent or present but faint; para- and metaflexus transversely to posteriorly orientated; mesoloph/id poorly to moderately, usually fused to paracone; M3 small and subcylindrical in outline and usually with a subcentral and circular enamel island. Axial skeleton includes 13 ribs, 13 thoracic vertebrae, 6 lumbar vertebrae, 4 sacral vertebrae and 18–29 caudal vertebrae Stomach is unilocular–hemiglandular. Gall bleader is absent (Gyldenstolpe, 1932; Osgood, 1943; Carleton, 1973; Reig, 1987; Steppan, 1995; D'Elía et al., 2007; D'Elia et al., 2015a).

Karyotypes: most of the species of *Abrothrix* shared a 2*n* = 52, except for some populations of *Ab. olivacea* of southern Argentina that have a 2*n* = 44 (Rodríguez and Theiler, 2007). Diploid complement of long-clawed Abrotrichini varies between 52 and 56 (Pearson, 1984; Ojeda et al., 2005; D'Elía et al., 2006; Gallardo, in litt.).

Distribution: from central Peru, along the highlands of western south America to the Island of Tierra del Fuego and the Cape Horn archipelago. Elevational range in Chile and Argentine Patagonia extend from sea level to 3500 m (Osgood, 1943; Patterson et al., 1984; Teta et al., 2006).

Biochron: Late Pliocene to Early Pleistocene (Uquía Formation, Jujuy Province, north-western Argentina) to Recent (Teta et al., 2014).

Remarks: Carrizo and Catalano (2015), in a combined phylogenetic analysis of the tribe Phyllotini, defined 20 morphological
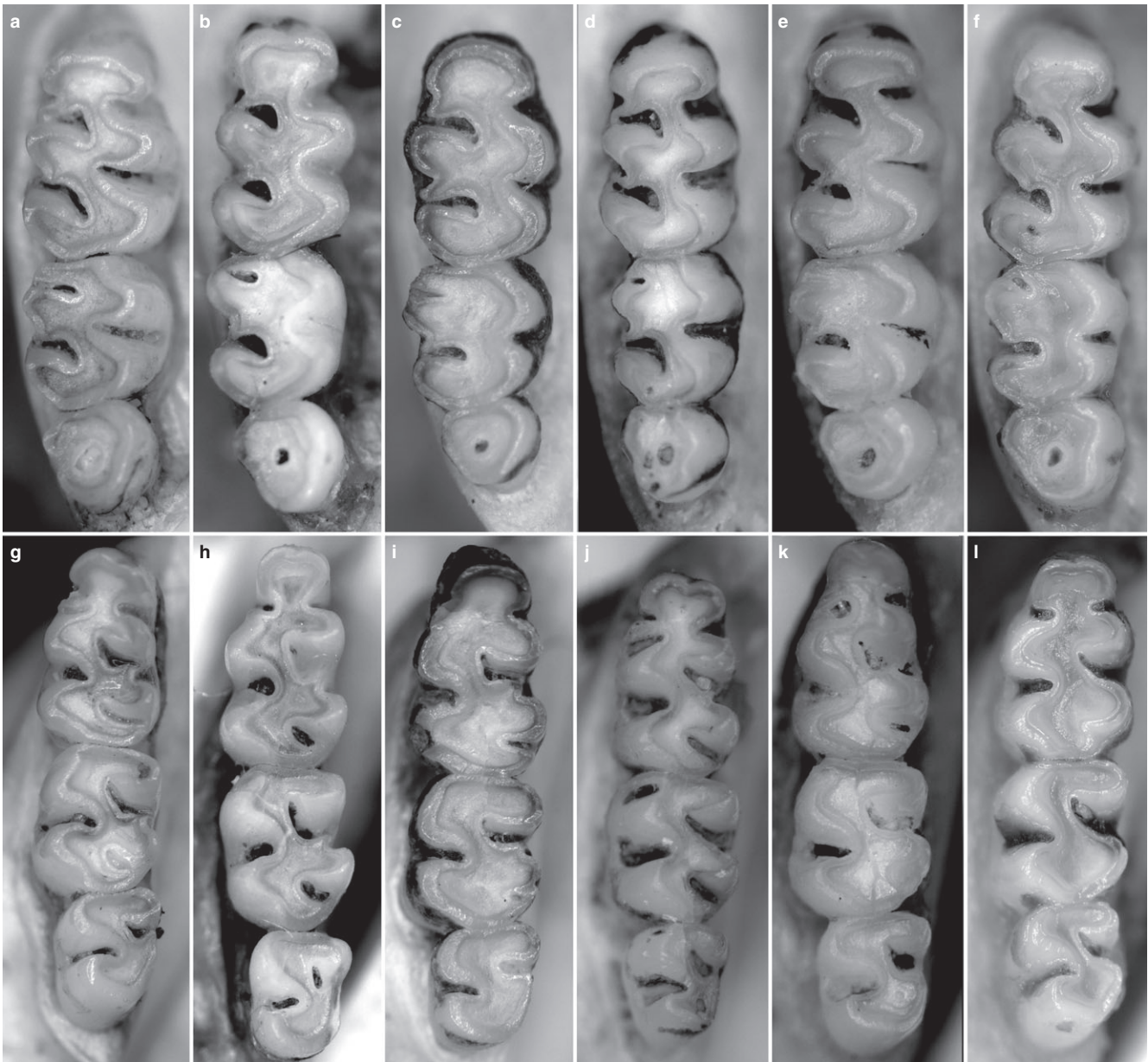
Fig. 10. Right upper molars (above) and left lower molars in *Abrothrix*. (a–g) *Ab. (Abrothrix) longipilis* (UACh 1159); (b-h) *Ab. (Ab.) lanosa* (CNP 1377); (c–i) *Ab. (Pegamys) illutea* (CNP 1483); (d–j) *Ab. (Angelomys) olivacea* (CNP 2560); (e–k) *Ab. (An.) andina dolichonyx* (UACh 3587); (f–l) *Ab. (Chroeomys) jelski sodalis* (MACN 2775). The figures are not to scale.

synapomorphies for this tribe (11 postcranial, 8 craniodental and 1 of external morphology), against the four recovered by us. Carrizo and Catalano (2015) include four of the five genera here recognized and only five species of Abrotrichini. A more accurate definition of the synapomorphies of this tribe is still pending an analysis of a more adequate sample including a larger representation of other sigmodontine genera. Dorsal, ventral and lateral views of the skull, and lateral views of the mandible, for all Abrotrichini species included in this work are available on Data S7.

Abrotrichina subtribe nov.

Type genus: *Abrothrix* Waterhouse, 1837.

Contents: *Abrothrix* Waterhouse, 1837.

Morphological diagnosis: As for the genus *Abrothrix* (see below).

Genus *Abrothrix* Waterhouse, 1837

Type species: *Mus longipilis* Waterhouse, 1837.

Contents: four subgenera, as diagnosed below.

Emended morphological diagnosis: rodents of the subfamily Sigmodontinae, tribe Abrotrichini (*sensu* D'Elía et al., 2007), with the following combination of characters: size small to medium in the context of the tribe (head and body length < 120 mm; tail length < 90 mm; weight ~20 to ~38 g); pelage dense and soft; dorsal and ventral colours sharply to indistinctly delimited; ears small to medium, pinnae externally visible and semicircular; tail sparsely furred, scales macroscopically obvious; claws small to medium, not keeled
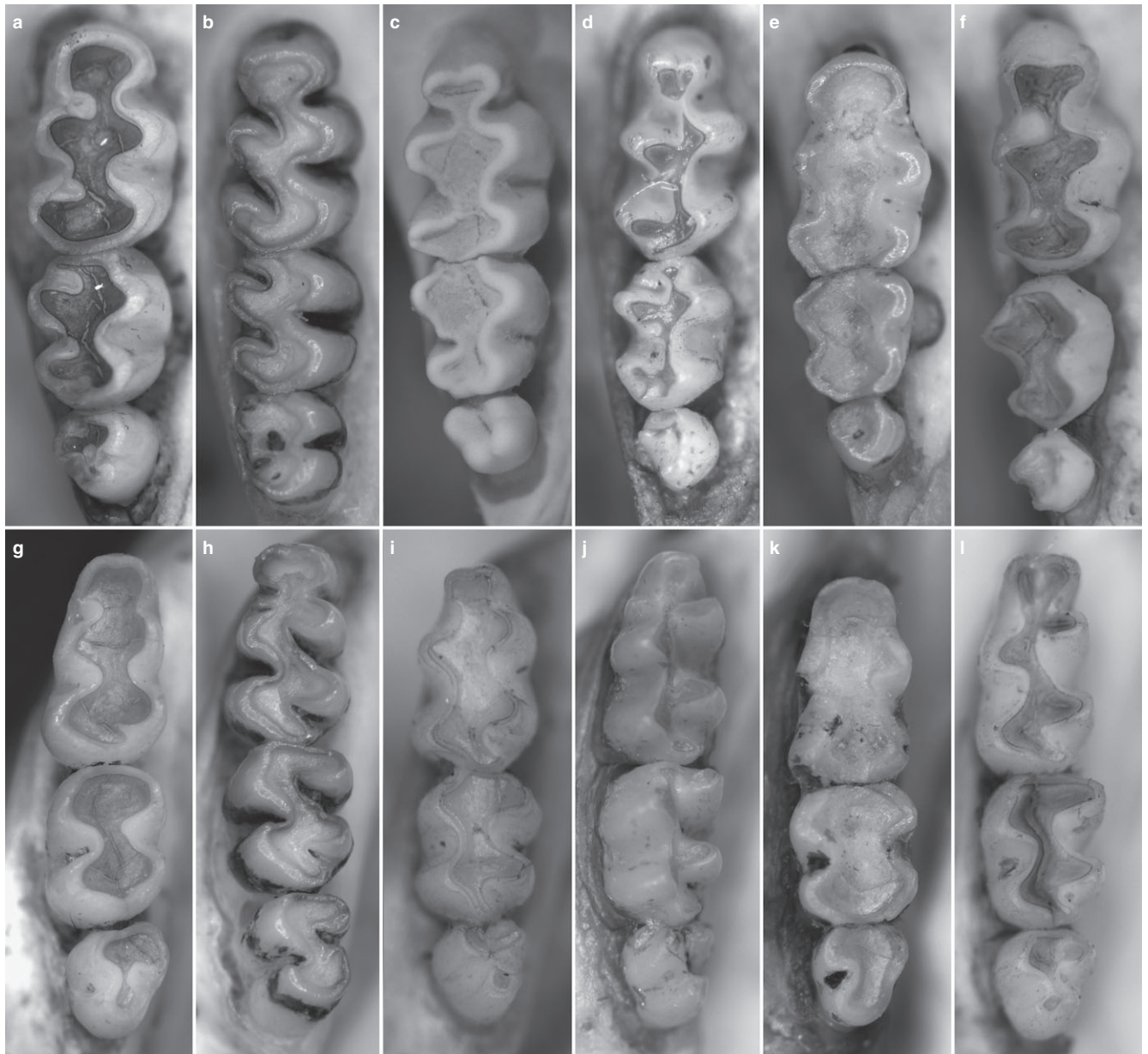
Fig. 11. Right upper molars (above) and left lower molars in long-clawed Abrotrichini. (a–g) *Chelemys megalonyx* [UACh 1462]; (b–h) *Paynomys macronyx* [CNP 2373]; (c–i) *Notiomys edwardsii*; (d–j) *Geoxus valdivianus* [UACh 2173]; (e–k) *G. michaelseni* [CNP 437]; (f–l) *G. annectens* [UACh 4478]. The figures are not to scale.

to moderately long, keeled for about one-third to half of their length; ungual tufts on pes abundant and longer than claws; skull gracile, with globose braincase, rostrum short to long and delicate zygomatic arches; interorbital constriction amphora-shaped, with well-developed frontal sinus; nasals and premaxillae moderately projected in front of the anterior plane of the upper incisors or forming a distinct tube ("trumpet"); zygomatic plate narrow, with the anterior border straight and nearly vertical; infraorbital foramen with its lumen narrow to moderately open and compressed at its base, nearly piriform in shape; incisive foramina long, extending to the level of the protocones of the M1; palate short to long; horizontal ramus of mandible gracile and enlarged, with a moderately deep diastema; upper incisors ophistodont to proodont; molars mesodont to hypsodont, usually terraced; procingulum of M1/m1 fan-shaped; anteroloph and parastyle on M1 well developed; para- and metacone on M1–2 transversally orientated; mesoflexus reabsorbed by the fusion of the para- and mesoloph, usually persisting as an enamel island; M3 cylindrical, with a circular enamel island centrally placed; m1 with a conspicuous protostylid (except in *A. jelskii*); metaconid and entoconid of m1–2 orientated backwards; mesolophid on m1–2 well developed (except in *A. jelskii*); m3 "S"- or "Z"-shaped; distal digits of the baculum and bacular mounds absent or reduced.

Distribution: as for the tribe.

Remarks: based on the results of the combined analysis, we recognize four subgenera, diagnosable on morphological grounds, within *Abrothrix* (main differences between them are depicted in Fig. 17).
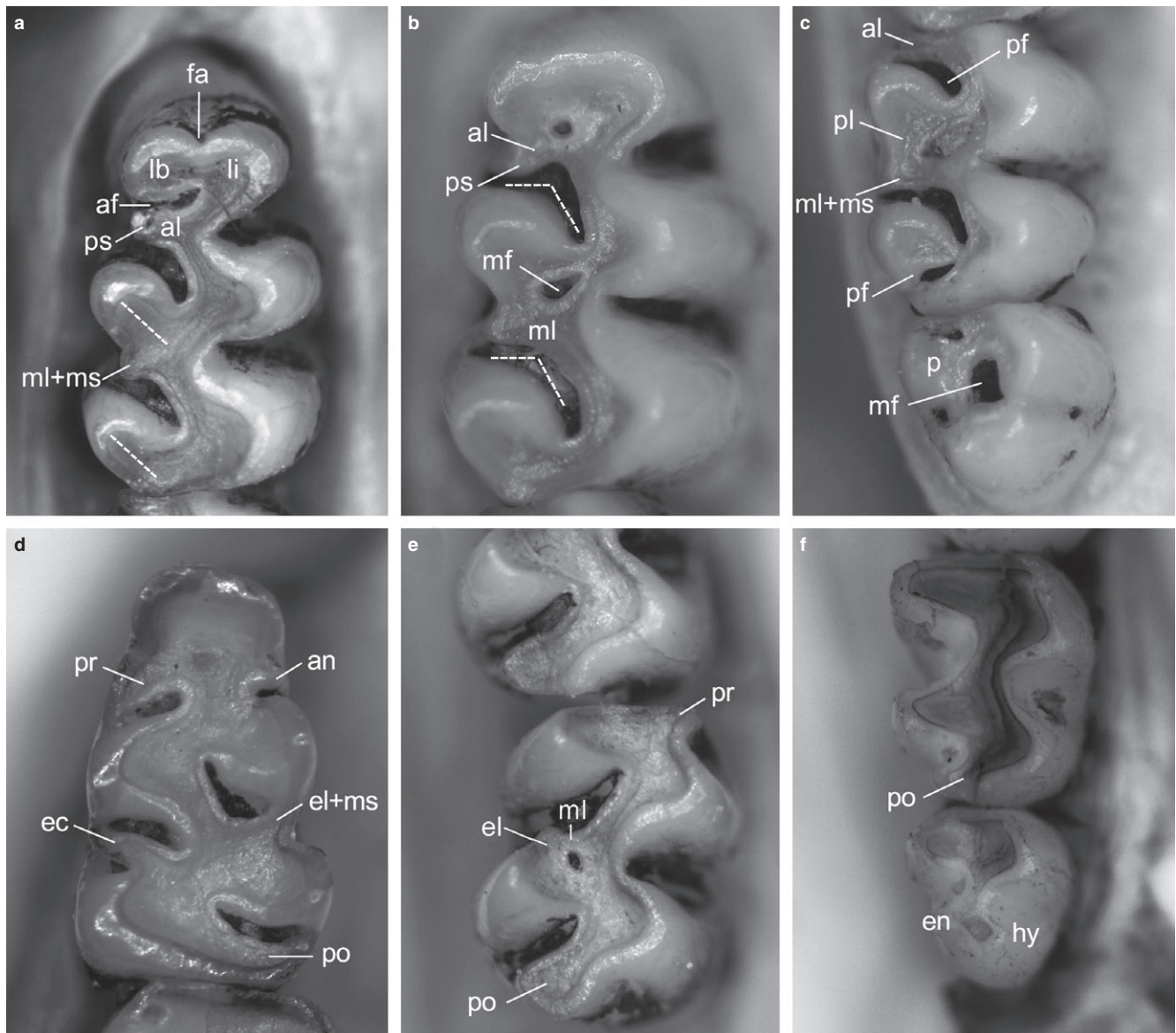
Fig. 12. Molar structures in Abrotrichini. Dental details on right M1 (a, b), right M2–3 (c), left m1 (d), right m2 (e) and right m2– (f) of *Paynomys macronyx* (a) and *Abrothrix* (*Abrothrix*) *hirta* (b, c, e), *Ab*. (*Ab*.) *manni* (d), and *Geoxus annectens* (f). af = anteroflexus; al = anteroloph; an = anterolophid; ec = ectolophid; el = entolophulid; en = entoconid; fa = anteromedian flexus; hy = hypoconid; lb = labial conule; li = lingual conule; mf = mesofossette; ml = mesoloph/lophid; ms = mesostyle/stylid; p = paracone; pf = posterolophule; pl = paralophule; po = posterolophid; pr = protostylid; ps = parastyle. The discontinuous line indicates the orientation of the paracone and metacone (a) and the labial flexi of M1 (b). The figures are not to scale.

Subgenus *Abrothrix* Waterhouse, 1837

Type species: *Mus longipilis* Waterhouse, 1837

Content: *hirta* Thomas, 1895 (including *suffusus* Thomas, 1903; *francei* Thomas, 1908; *modestior* Thomas, 1919; *moerens* Thomas, 1919; *angustus* Thomas, 1927; *nubila* Thomas, 1929; *apta* Osgood, 1943; *castaneus* Osgood, 1943); *lanosa* Thomas, 1897; *longipilis* Waterhouse, 1837 (including *porcinus* Philippi, 1858; *brachytarsus* Philippi, 1900; *fusco-ater* Philippi, 1900; *melampus* Philippi, 1900); *manni* D'Elía, Teta, Upham, Pardiñas and Patterson, 2015; *sanborni* Osgood, 1943.

Emended morphological diagnosis: size small to medium in the context of the tribe; dorsal coloration dark, sometimes with a median reddish band; venter whitish to nearly as dark as dorsum; claws moderately long, keeled for about one-third to half of their length; rostrum long and narrow; nasals and premaxillae projecting well in front of the incisors as a tube; nasal outer margins nearly straight; lacrimals equally contacting maxillary and frontal bones; palate long; tympanic bullae not inflated; maxillary septum subequal to or less than half of the length of incisive foramina; molars mesodont; anteroflexus on M1 well developed; anteroloph on M2 long, reaching or surpasing 3/4 of the length of the paracone; anteromedian flexid on m1 present; protostylid on m1 present; ectostylid on m1 present or not; mesolophid on m1–2 present; baculum arched along its length; cartilaginous digits of the baculum absent or indistinct.

Distribution: from central–northern Chile and central–western Argentina to the Island of Tierra del Fuego. Elevational range in
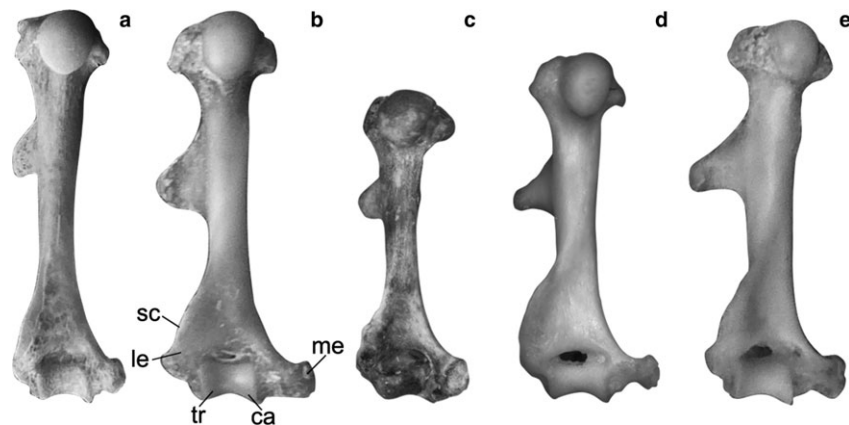
Fig. 13. Posterior view of the left humera in some Abrotrichini. (a) *Abrothrix* (*Pegamys*) *illutea* [CNP 1484]; (b) *Chelemys megalonyx* [UACh 1462]; (c) *Notiomys edwardsii* [CNP 3241]; (d) *Geoxus valdivianus* [UACh 2170]; (e) *Geoxus annectens* [UACh 1064]. ca = capitulum; sc = lateral supracondilar crest; le = lateral epicomdyle; me = medial epicondyle; tr = trochlea.
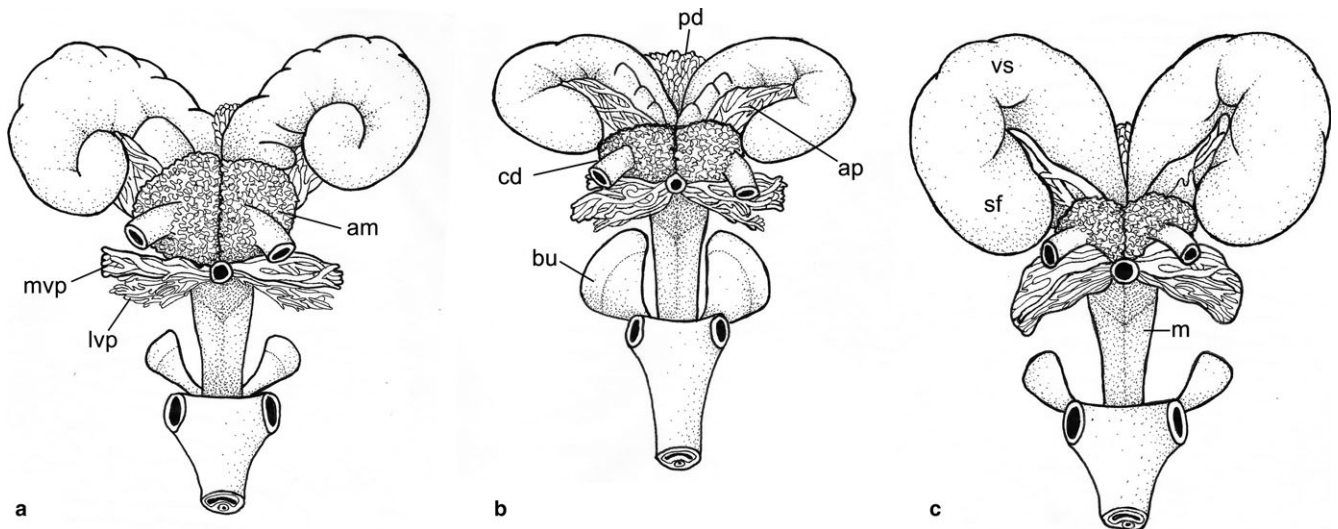

Fig. 14. Ventral view of the male reproductive tract in some Abrotrichini. (a) *Abrothrix* (*Abrothrix*) *hirta*; (b) *Geoxus valdivianus*; (c) *Paynomys macronyx*. am = ampullary glands; ap = anterior prostate; bu = bulbourethral glands; cd = deferent duct; lvp = lateral ventral prostate; m = m. compressor urethrae; mvp = medial ventral prostate; pd = dorsal prostate; sf = subterminal flexure of the vesicular gland; vs = vesicular gland [redrawn from Voss and Linzey (1981) and CNP 2373].

Chile and southern Argentina from sea level to 3000 m (Patterson et al., 2015).

Angelomys subgen. nov.

Type species: *Mus olivaceus* Waterhouse, 1837.

Content: *andina* Philippi, 1858 (including *dolichonyx* Philippi, 1896; *cinnamomea* Philippi, 1896; *jucundus* Thomas, 1913; *gossei* Thomas, 1920; *polius* Osgood, 1944); *hershkovitzi* Patterson et al., 1984; *olivacea* Waterhouse, 1837 (including *brachiotis* Waterhouse, 1837; *canescens* Waterhouse, 1837; *renggeri* Waterhouse, 1839; *atratus* Philippi, 1900; *brevicaudatus* Philippi, 1872; *chonoticus* Philippi, 1900; *foncki* Philippi, 1900; *germaini* Philippi, 1900; *infans* Philippi, 1900; *landbecki* Philippi, 1900; *lepturus* Philippi, 1900; *longibarbu*s Philippi, 1900; *macronychos* Philippi, 1900; *mochae* Philippi, 1900; *nasica* Philippi, 1900; *nemoralis* Philippi, 1900; *pencanus* Philippi, 1900; *psilurus* Philippi, 1900; *ruficaudus* Philippi, 1900; *senilis* Philippi, 1900; *trichotis* Philippi, 1900; *vinealis* Philippi, 1900; *xanthopus* Philippi, 1900; *beatus* Thomas, 1919; *markhami* Pine, 1973;

*mansoensi*s De Santis and Justo, 1980); *xanthorhina* Waterhouse, 1837 (including *llanoi* Pine, 1976).

Etymology: we dedicate this name in honour of Ángel E. Spotorno, for his contributions to the systematics of South American mammals, especially rodents, including important contributions to the anatomy of the genus *Abrothrix*. Ángel also contributed much to our understanding of the diversity, relationships and biogeography of Abrotrichini, Akodontini and Phyllotini rodents.

Morphological diagnosis: size small in the context of the tribe; dorsal coloration olivaceous to brownish, lighter on venter; sometimes with reddish marks on nose, feet and tail; claws small to medium, not keeled; rostrum short and narrow; nasals and premaxillae extending slightly to moderately in front of the incisors; nasals slightly widened over their anterior third; lacrimals contacting mostly maxillary; palate long; tympanic bullae inflated or not; maxillary septum subequal to or less than half of the length of incisive foramina; molars mesodont; anteroflexus on M1 well developed; anteroloph on M2 long, reaching or surpassing 3/4 of
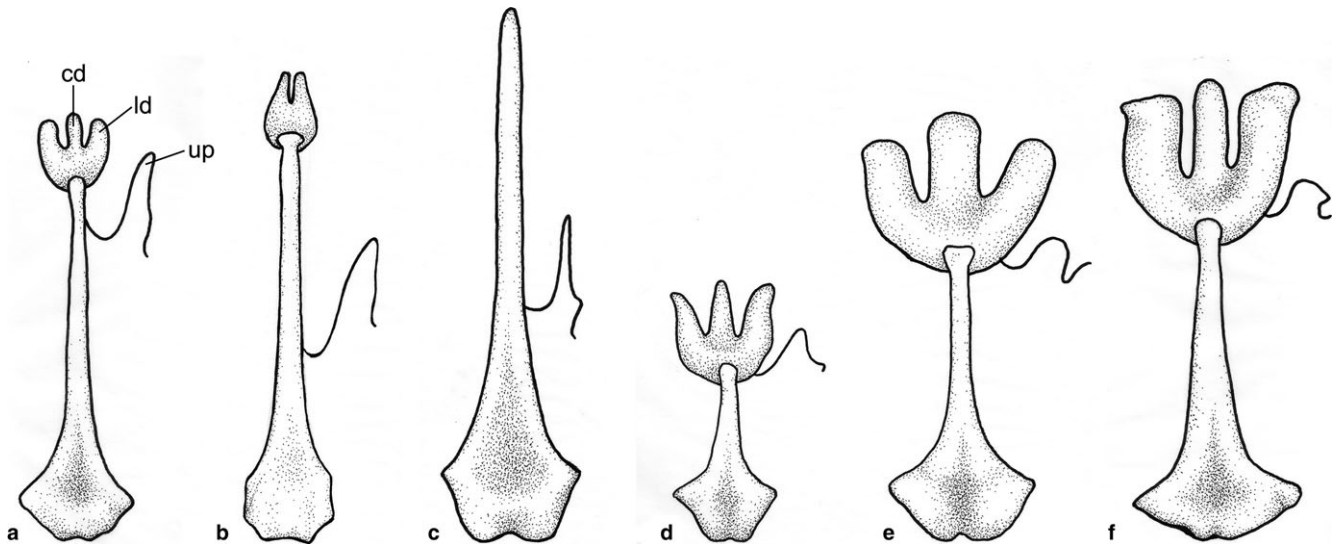
Fig. 15. Morphology (ventral view) of baculum, cartilaginous digits [cd = central digit; ld, lateral digit] and urethral processes [up] of some Abrotrichini. (a) *Abrothrix* (*Angelomys*) *olivacea*; (b) *Ab.* (*Pegamys*) *illutea*; (C) *Ab.* (*Ab.*) *hirta*; (d) *Notiomys edwardsii*; (e) *Geoxus valdivianus*; (f) *Paynomys macronyx* [redrawn from Spotorno (1986) and Teta et al. (2011)].
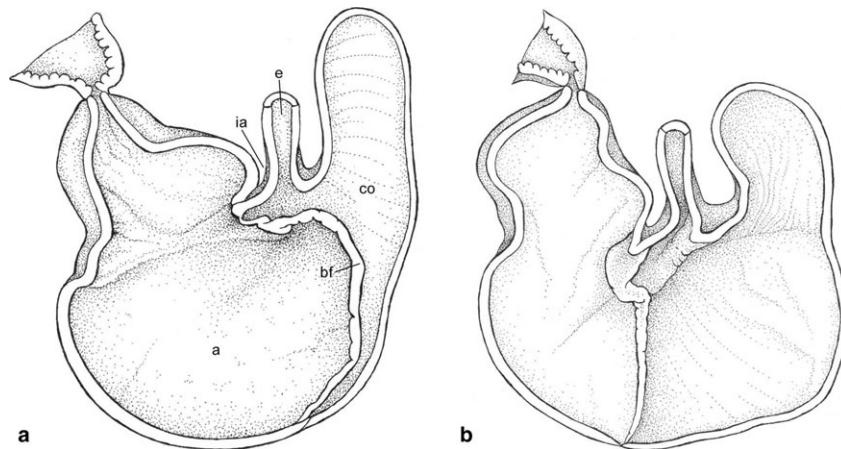

Fig. 16. Stomach morphology in Abrotrichini. (a) Stomach unilocular–hemiglandular, with the gastric glandular epithelium covering the antrum and proximal portion of corpus near oesophageal opening [*Notiomys edwardsii* (CNP 1); redrawn from Pardiñas et al. (2008)]; (b) stomach unilocular–hemiglandular, with the gastric glandular epithelium limited to antrum, not extending beyond incisura angularis [*Abrothrix* (*Pegamys*) *illutea*; redrawn from Teta et al. (2011)]. a = antrum; bf = bordering fold; ce = cornified epithelium; co = corpus; e = oesophagus; ge = glandular epithelium; ia = angular incisure; p = pilorous.

the length of the paracone; anteromedian flexid on m1 present; protostylid on m1 present; ectostylid on m1 present or not; mesolophid on m1–2 present; baculum relatively straight and rod-like; cartilaginous baculum reduced, including one medial and two lateral digits.

Distribution: from southern Peru, along the Andean highlands to the Isla Grande de Tierra del Fuego and southern Pacific and Atlantic outer islands from sea level to 3000 m (Patterson et al., 2015).

Subgenus *Chroeomys* Thomas, 1916

Type species: *Akodon pulcherrimus* Thomas 1897.

Content: *jelskii* (including *pyrrhotis* Thomas, 1894; *pulcherrimus* Thomas 1897; *cayllomae* Thomas, 1901; *inambarii* Thomas, 1901; *cruceri* Thomas, 1901; *bacchante* Thomas, 1902; *sodalis* Thomas, 1913; *inornatus* Thomas, 1917; *ochrotis* Sanborn, 1947).

Emended morphological diagnosis: size small in the context of the tribe; coloration sharply demarked, including reddish marks on nose, periocular and tail and white postauricular patches; palmar and plantar pads large and fleshy; claws moderately long, keeled for about one-third to half of their length; rostrum short and broad; nasals and premaxillae extending slightly in front of the incisors; nasals slightly widened in its anterior third; lacrimals equally contacting maxillary and frontal bones; palate short to long; tympanic bullae inflated; maxillary septum subequal to or less than half of the length of incisive foramina; molars relatively hypsodont; anteroflexus on M1 faint but present; anteroloph on M2 short, extending half of the length of the paracone; anteromedian flexid on m1 present; protostylid on m1 absent; ectostylid on m1 absent; mesolophid on m1–2 present; cartilaginous baculum reduced, including one medial and two lateral digits.
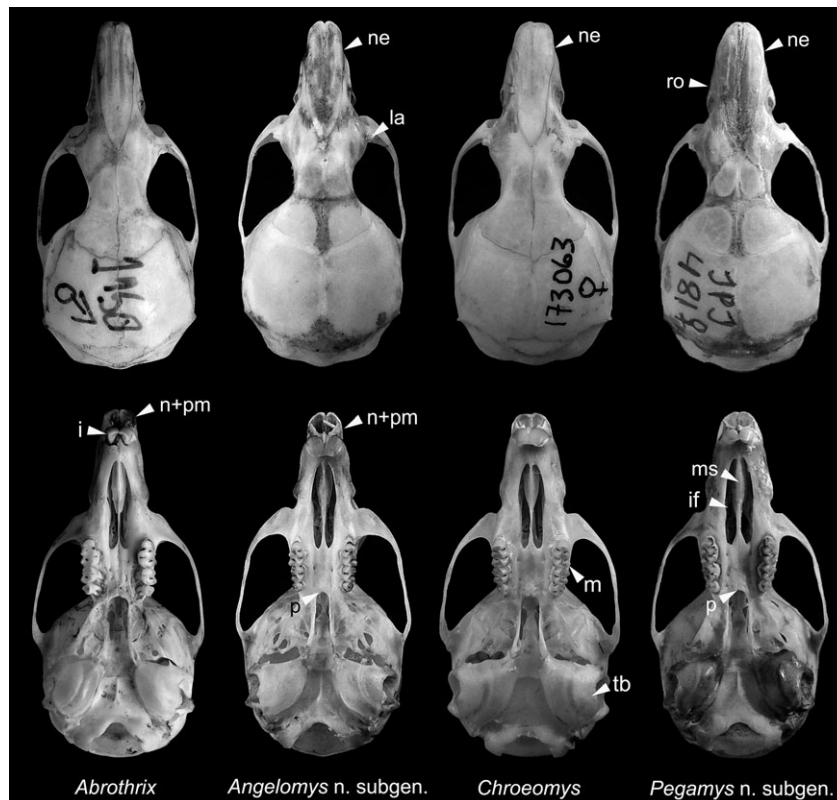
Fig. 17. Selected differences in the qualitative cranial anatomy among the subgenera of *Abrothrix*: *Abrothrix* (*Abrothrix*) *longipilis* (type species of the genus), *Ab.* (*Angelomys*) *olivacea*, *Ab.* (*Chroeomys*) *jelskii* and *Ab.* (*Pegamys*) *illutea*. Nasals and premaxillae (n+pm) extend well beyond the anterior face of the incisors (i) in *longipilis* and moderately beyond in *olivacea*; nasals are anteriorly expanded (ne) and upper incisors are proportionally robust in *olivacea*, *illutea* and *jelskii*; rostrum (ro) is proportionally broad and short in *illutea* and *jelskii*; incisive foramina (if) has its external borders nearly straight and parallel and the maxillary septum length (ms) is larger than half of the length of incisive foramina in *illutea*; molars (m) are relatively hypsodont and tympanic bullae (tb) are inflated in *jelskii*. The figures are scaled to the same length.

Distribution: Altiplano, about 2200–5000 m, from central and southern Peru, western Bolivia and north-western Argentina (Sanborn, 1947; Patterson et al., 2015).

Pegamys subgen. nov.

Type species: *Abrothrix illutea* Thomas, 1925.

Content: *illutea* Thomas, 1925

Etymology: we dedicate this name in honour of Margaret "Peg" Smith, for her contributions to the taxonomy of the Cricetidae. Together with J. L. Patton, Peg was a pioneer in the use of molecular sequences to understand the phylogenetic relationships of this family of rodents and highlighted the distinctiveness of the tribe Abrotrichini within the Sigmodontinae radiation.

Morphological diagnosis: size medium in the context of the tribe; dorsal coloration greyish brown, paler on venter; claws moderately long, keeled for about one-third to half of their length; rostrum short and broad; nasals and premaxillae extending slightly anterior to the incisors; nasals slightly widened over their anterior third; lacrimals in equal contact with the maxillary and frontal bones; palate short; tympanic bullae not inflated; maxillary septum extends more than half the length of incisive foramina; molars mesodont; anteroflexus on M1 well developed; anteroloph on M2 long, reaching or surpassing 3/4 of the length of the paracone; anteromedian flexid on m1 present; protostylid on m1 present; ectostylid on m1 absent; mesolophid on m1–2 present; cartilaginous baculum reduced, including only the lateral digits.

Distribution: restricted to a small hilly area in the provinces of Catamarca and Tucumán, northern Argentina, between 700 and 2500 m (Teta et al., 2011).

Notiomyina subtribe nov.

Type genus: *Notiomys* Thomas, 1890.

Contents: *Chelemys* Thomas, 1903; *Geoxus* Thomas, 1919; *Notiomys* Thomas, 1890; *Paynomys* gen. nov.

Morphological diagnosis: rodents of the subfamily Sigmodontinae, tribe Abrotrichini, with the following combination of characters: size small to large; tail densely furred, scales not visible even with magnification; pollex ending in a small claw; second digit of the manus slightly shorter to equal to the fourth; hallux slightly shorter than the fifth digit; ungual tufts on pes sparse, shorter than claws; first interdigital pad on manus nearly in line with the second; first interdigital pad on pes nearly in line with the fourth; second interdigital pad on pes nearly in line with the third; hypothenar and thenar pads level or overlap; base of manual claws covering almost entirely the respective phalange; upper free border of zygomatic plate absent; incisive foramina with outer borders nearly parallel, slightly broadened over its anterior third; procingulum on M1 antero-posteriorly compressed, nearly as an inverted triangle in shape; mesostyle on M1 absent; posterolophid on m2 present and posteriorly orientated; lateral supracondylar crest of the humerus moderately to well developed; medial epicondyle of the humerus subequal or longer than the combined length of capitulum and trochlea; medial extension of olecranon process of the ulna present.

Remarks: based on the results of the combined analysis, we include *Pearsonomys* in the synonymy of *Geoxus* and describe a new genus to contain *Chelemys macronyx*.

Genus *Chelemys* Thomas, 1903.

Type species: *Hesperomys megalonyx* Waterhouse, 1844.

Content: *megalonyx* Waterhouse, 1844 (including *scalops* Gay, 1847; *microtis* Philippi, 1900).

Emended morphological diagnosis: rodents of the subfamily Sigmodontinae, tribe Abrotrichini, with the following combination of characters: size medium to large in the context of the tribe (head and body length ~120 mm; tail length ~55 mm; weight ~50 g); pelage dense and short; dorsally brownish and grey on the venter; pinnae externally visible and semicircular; manual claws well developed and with a ventral keel that runs nearly half of their length; skull elongated and moderately robust with a relatively globose braincase and expanded zygomatic arches; nasals and premaxillae short, not extending anterior to the plane of upper incisors; interorbital region wide, amphora-shaped, with inflated frontal sinus; lacrimals in equal contact with maxillary and frontal bones; zygomatic plate proportionately narrow and high; infraorbital foramen compressed basally; incisive foramina narrow, with its outer borders nearly parallel and widened in its anterior third; palate long; mesopterygoid fossa "U"-shaped, with its anterior border rounded to subquadrate; roof of mesopterygoid fossa completely ossified or with small sphenopalatine vacuities; tympanic bullae moderately inflated, Eustachian tube small; dentary moderately robust, proportionally long and low; diastema slightly excavated, smoothly concave all along; capsular projection placed towards the condyloid process; shelf bearing lower molars does not extend behind the last molar; upper incisors orthodont to slightly proodont; molars small, brachyodont and terraced; procingulum of M1 rounded, without anteromedian flexus; anteroloph and parastyle indistinct; paracone and metacone of M1–M2 transversally orientated; mesoflexus reabsorbed by the fusion of para- and mesoloph; M3 medium-sized, with lingual and labial flexi well expressed and with a centrally positioned subcircular enamel island; procingulum of m1 subquadrate with a conspicuous protostylid; meta- and entoconid transversally orientated; mesolophid of m1–m2 absent; m3 with small hypo- and entoconid.

Distribution: *C. megalonyx* is endemic to central Chile, where it is known from a few localities in shrubby to forested coastal areas from near Santiago de Chile (ca. 30°S) and the vicinities of Valparaíso and Concepción to near Valdivia (39°S) (Osgood, 1943; Teta et al., 2015a).

Remarks: principal morphological differences between *Chelemys* and *Paynomys* gen. nov. are depicted on Fig. 18.

Genus *Geoxus* Thomas, 1919

Type species: *Oxymycterus valdivianus* Philippi, 1858.

Contents: *annectens* Patterson, 1992; *valdivianus* Philippi, 1858 (including *fossor* Thomas, 1919; *araucanus* Osgood, 1925; *chiloensis* Osgood, 1925; *bullocki* Osgood, 1943); *michaelseni* Matschie, 1898 (including *microtis* J. A. Allen, 1903, *bicolour* Osgood, 1943, and possibly *delfini* Cabrera, 1905).

Emended morphological diagnosis: rodents of the subfamily Sigmodontinae, tribe Abrotrichini, with the following combination of characters: size small to medium in the context of the tribe (head and body length < 120 mm; tail length < 80 mm; weight ~25 to 42 g); pelage long, thick and somewhat hispid (*annectens*) to dense and short (*michaelseni*, *valdivianus*); dorsally blackish to brown, typically paler on the venter; pinnae small to large, externally visible and semicircular; manual claws well developed and with a ventral keel that runs nearly half of their length; skull delicate, with a rounded braincase and moderately to scarcely expanded zygomatic arches; rostrum proportionally large and narrow, with nasals and premaxillae projecting well in front of the incisors as a tube; frontal sinuses well inflated; interorbital region anteriorly divergent, narrowest in its posterior half; nasolacrimal capsules located below the incisive capsules; ethmoid foramen dorsal or posterior to M3; anterior border of alisphenoid well projected anteriorly as a free osseous flake; zygomatic plate proportionately narrow and low and slanted backward from the base; infraorbital foramen with its lumen wide and nearly ovate in shape; incisive foramina parenthesis-shaped, with a constriction between the middle and the posterior third; palate long; mesopterygoid fossa parallel sided and "U"-shaped; parapterygoid fossa at the same level of palate; sphenopalatine vacuities large; tympanic bullae moderately to well inflated; anterodorsal portion of the ectotympanic rounded to subquadrate and well separated from the
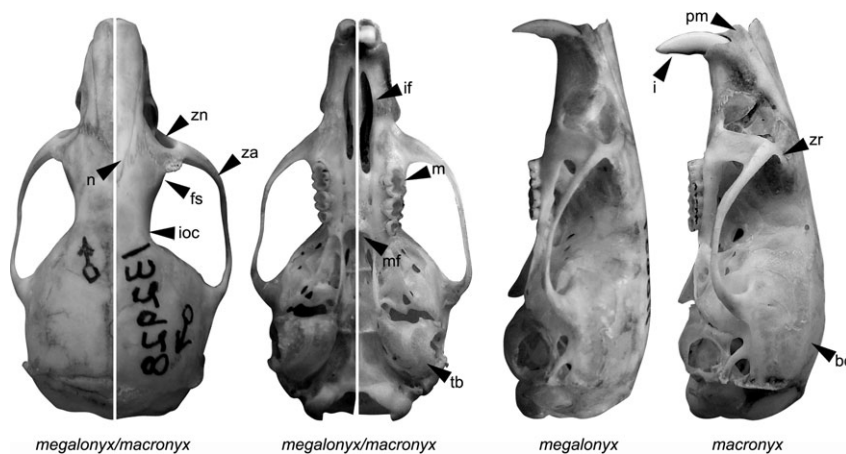

Fig. 18. Selected differences in the qualitative cranial anatomy of *Chelemys megalonyx* and *Paynomys macronyx*. The figure portrays characteristic contrasts between both taxa, including, in *P. macronyx*, deeply excavated zygomatic notches (mz); nasals (n) extending posteriorly well beyond the maxillary–frontal–lacrimal suture; more strongly flaring zygomatic arches (az); frontal sinuses not inflated (fs); interorbital contriction (ioc) posteriorly placed; incisive foramina (if) extended between the molar series; molars (m) robust and hipsodont; anterior border of the mesopterygoid fossa (mf) placed at the plane defined by the posterior border of the third upper molars; tympanic bullae (tb) not inflated; premaxillae (pm) extended moderately in front of the anterior face of the upper incisors; upper incisors (i) orthodont to ophistodont; upper zygomatic root (zr) narrower and braincase (bc) quadrate and more robust. The figures are scaled to the same length.

mastoid; orbicular apophysis of the malleus with its peduncle proportionally narrow and long and ending in a bulbous button; dentary proportionally long and low with a small capsular projection; diastema slightly excavated, smoothly concave throughout; coronoid process short; incisors orthodont; molars simple and small, brachyodont and crested; procingulum of M1 small; mesoloph on M1 present but small in young individuals, coalesced in adults; M3 strongly reduced and rounded in outline; mesoloph on m1–2 absent; procingulum on m1 "fan"-shaped and without anteromedian flexid; metaconid and protoconid broader than entoconid and hypoconid; stomach unilocular–hemiglandular with the glandular epithelium covering both the antrum and proximal portion of corpus near oesophageal opening; phallus with a dorsal hood usually present; baculum with three well-developed cartilaginous digits; ampullary and bulbourethral glands present and larger than is typical for Abrotrichini.

Distribution: *G. annectens* is endemic to south-central Chile, with its populations restricted to Valdivian forests of the Coastal Cordillera (D'Elía, 2015; Teta et al., 2015b). *Geoxus valdivianus* is distributed from the vicinities of Concepción, Chile, and west-central Neuquén, Argentina, including the islands of the Pacific litoral to ca. 46°S, where it is replaced by *G. michaelseni*. This latter species occurs south as far as Fuerte Bulnes, Magallanes, Chile. Both taxa are mostly restricted to a narrow fringe of *Nothofagus* and *Araucaria* forests (Pearson, 1983; Patterson et al., 1989), although they are not infrequent in shrubby ecotonal areas and high Andean prairies mixed with low bushes and scattered trees (Kelt, 1994; Pearson, 1995).

Genus *Notiomys* Thomas, 1890

Type species: *Hesperomys* (*Notiomys*) *edwardsii* Thomas, 1890.

Content: *edwardsii* Thomas, 1890.

Emended morphological diagnosis: rodents of the subfamily Sigmodontinae, tribe Abrotrichini, with the following combination of characters: size small in the context of the tribe (head and body length ~86 mm; tail length ~40 mm; weight ~21 g); pelage dense and soft; head with bright rufous spots on the sides of the rostrum; ears with extremely thin and small pinnae, hidden in the fur of the head and showing a tuft of contrasting white hairs; manus and pes dorsally covered by orangish to white hairs; manual claws well developed and with a ventral keel that runs nearly half of their length; pes with conspicuous inner and outer fringes of white hairs; skull delicate, with a rounded braincase, broad interorbital region and flared zygomatic arches; rostrum proportionally short, with nasals and premaxillae somewhat projecting in front of the incisors; frontal sinuses well inflated; inconspicuous zygomatic notches; zygomatic plate narrow and tall without a free upper border and strongly flared with respect to the sagittal plane, producing a wide infraorbital foramen; incisive foramina short; palate long; mesopterygoid fossa parallel sided "U"-shaped; sphenopalatine vacuities large; tympanic bullae moderately inflated, Eustachian tube small; dentary proportionally long and low; diastema slightly excavated, smoothly concave along its length; upper incisors orthodont; molars simple and small, brachyodont and crested; M1 trilophodont with fan-shaped procingulum indented anteriorly by a shallow anteromedian flexus; M2 bilophodont with area of the proto- and paracone clearly broader than that of the hypo- and metacone; M3 small and cylindrical in outline; M3/m3 with a single root; caecum moderately developed; stomach unilocular–hemiglandular with the glandular epithelium covering the antrum and proximal portion of corpus near oesophageal opening; baculum with three well-developed cartilaginous digits; dorsal hood absent.

Distribution: *N. edwardsii* is endemic to Argentina; its distribution extends from southern Santa Cruz north to north-western Río Negro, occupying shrubby and herbaceous steppes in arid to semi-arid environments of Patagonia (Pardiñas et al., 2008; Teta and Pardiñas, 2015).

Paynomys gen. nov.

Type species: *Acodon macronyx* Thomas, 1894.

Content: *macronyx* Thomas, 1894 (including *vestitus* Thomas, 1903; *connectens* Osgood, 1925; *alleni* Osgood, 1925; *fumosus* Thomas, 1927).

Morphological diagnosis: rodents of the subfamily Sigmodontinae, tribe Abrotrichini, with the following combination of characters: size medium to large in the context of the tribe (head and body length ~125 mm; tail length ~52 mm; weight ~55 g); pelage dense and short; dorsally yellowish brown to dark brown, lighter on the venter; pinnae externally visible and semicircular; manual claws well developed and with a ventral keel that runs nearly half of their length; skull robust with a subquadrate braincase and strongly flaring zygomatic arches; rostrum proportionally short and wide; nasals slightly expanded in its anterior third; lacrimals contacting mainly maxillary; frontal sinuses not inflated; interorbital constriction centrally situated, as bounded by the frontals; zygomatic plate proportionally narrow and high; infraorbital foramen compressed basally; incisive foramina wide, with its outer borders nearly parallel and opened over its anterior third; palate short, with its posterior border nearly in line with the posterior plane of the last molars; mesopterygoid fossa "horseshoe"-shaped, with its anterior border rounded to subquadrangular; sphenopalatine vacuities large; tympanic bullae not inflated; dentary robust, proportionally short and high; diastema deeply excavated; mental foramen laterally positioned; capsular projection placed towards the coronoid process; coronoid high and inflected backward; incisors orthodont to slightly ophistodont; molars proportionally large, relatively hypsodont and terraced; anteroloph of M1 well developed; paracone and metacone of M1–M2 anteriorly orientated; mesoflexus reabsorbed by the fusion of para- and mesoloph; M3 large (~2/3 M2), with a complex occlusal surface and well-developed metacone and hypocone; procingulum on m1 "fan"-shaped; m1 with obvious protostylid; metaconid, posterolophid and entoconid posteriorly orientated; mesolophid on M1–2 indistinct; m3 with sigmoid appearance; stomach unilocular–hemiglandular with a glandular epithelium does not cross the lesser curvature; baculum with three well-developed cartilaginous digits; ampullary and bulbourethral glands present and "normal" in size.

Etymology: we dedicate this name in memory of Oliver Payne Pearson (1915–2003), "Paynie" to many, for his many incisive contributions to the biology of South American mammals, including numerous outstanding works on the ecology and taxonomy of several Abrotrichini species.

Distribution: from central Chile (33°S) and west-central Argentina (34°S) south to 51°S. *Paynomys* is mostly restricted to high Andean prairies, *Nothofagus* forests and ecotonal areas; some scattered, isolated populations occur through central Patagonia in suitable environments (Teta et al., 2015a,b).