ORIGINAL INVESTIGATION

Systematics of the southern Patagonian-Fueguian endemic *Abrothrix lanosus* (Rodentia: Sigmodontinae): Phylogenetic position, karyotypic and morphological data

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Abstract

Abrothrix lanosus (Thomas, 1897) is morphologically redescribed on the basis of new specimens collected in Tierra del Fuego (Argentina). Cranial, mandibular, skeletal, penile, and chromosomal characteristics are described and compared with other species of *Abrothrix*, especially those of the Patagonian-Fueguian region. Its phylogenetic position within Abrotrichini is explored using DNA sequences of the mitochondrial cytochrome *b* (cyt *b*) and the nuclear Interphotoreceptor Retinoid Binding Protein (IRBP) genes. Phylogenetically, cyt *b* places *A. lanosus* as sister of *A. jelskii*, whereas IRBP groups *A. lanosus* and *A. longipilis*. The latter topology is most consistent with morphological data and taxonomic history. Several cranial and mandibular characters distinguish *A. lanosus* from the other species of the genus, including *A. longipilis*, which is its most similar species. *A. lanosus* shares with other congeners a $2n = 52$ karyotype and differs from other species of *Abrothrix* by at least 10% (*p*-distances) sequence divergence in cyt *b*. In conclusion, *A. lanosus* is a valid species, readily distinguishable from other *Abrothrix* in the southern Patagonian-Fueguian region. Although many data, including penile and skull morphology, suggest that *A. longipilis* is its closest living relative, *A. jelskii* is retained as a viable alternative until additional data are obtained.
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Introduction

Abrothrix together with *Chelemys*, *Geoxus*, *Notiomys* and *Pearsonomys* compose the recently diagnosed tribe of sigmodontine rodents Abrotrichini (D'Elía et al. 2007). Solid evidence shows that the abrotrichines represent one of the main lineages of Sigmodontinae (Dickerman 1992; Barrantes et al. 1993; Smith and Patton 1993, 1999; D'Elía 2003; D'Elía et al. 2006a, b). Among abrotrichines, *Abrothrix* is the most diverse genus and the one with the largest geographic distribution, from Perú to Tierra del Fuego and the Cape Horn islands.

Abrothrix lanosus (Thomas, 1897) is one of the least studied species of *Abrothrix*. With a restricted distribution in southern Argentina and Chile, it is one of the few native terrestrial mammals that currently inhabit Tierra

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del Fuego. The taxonomic history of this form, despite the handful of studies have focused on it, is relatively complex. It was originally described as *Oxymycterus lanosus* but later transferred by Thomas (1909) to *Microxus* (now considered a synonym of *Akodon*; see D'Elía 2003). Osgood (1943) allocated *lanosus* in *Abrothrix* and considered it as a subgenus of *Akodon*; whereas Reig (1978, 1987) considered *Abrothrix* to be a synonym of *Akodon*. Mann (1978) regarded *lanosus* as a subspecies of *A. longipilis*, a proposition that did not find many followers, since most researchers kept recognizing *lanosus* as a full species (e.g., Yáñez et al. 1978; Tamayo and Frassinetti 1980; Reise and Venegas 1987; Tamayo et al. 1987; Galliari and Pardiñas 1999; Musser and Carleton 2005; Teta et al. 2006).

Not much is known about the natural history of *A. lanosus*. It has been trapped in or near deep forest, preferably in cool and damp habitats (Osgood 1943; Reise and Venegas 1987). Jaksic et al. (1978) reported that in Magallanes, southern continental Chile, *A. lanosus* is preyed upon by the horned owl *Bubo magellanicus*.

The main goal of this work is to present new information to contribute to the knowledge of *A. lanosus*. We report for the first time information on its karyotype, and penis and stomach morphology; in addition, we further describe its external and craniodental morphology. This information is interpreted in light of the topology resulting from the first molecular-based phylogenetic analysis that includes *A. lanosus*, using both mitochondrial and nuclear DNA sequences.

Materials and methods

Specimens and distribution

This study was based on 27 specimens of *Abrothrix lanosus* recently collected at three Argentinean localities on the Island of Tierra del Fuego: Bahía Zaratiegui (CNP 1374–CNP 1376, CNP 1384–CNP 1387), CADIC, Ushuaia (CNP 1388–CNP 1400), Laguna Verde (CNP 1378–CNP 1383). All specimens are housed at the Colección de Mamíferos del Centro Nacional Patagónico (CENPAT, Puerto Madryn, Chubut, Argentina). The animals were trapped using Sherman-type traps baited with rolled oats mixed with vanilla and animal fat and prepared following standard techniques as museum specimens. Data from previous reported specimens of *A. lanosus* were obtained from the literature. The holotype of *Oxymycterus lanosus* (BM 80.7.28.11), housed at The Natural History Museum (London, UK), was studied through the analysis of digital pictures kindly sent by Louise Tomsett. Additionally, two individuals (USNM 482121 and USNM 482123)

trapped at Bahía Buen Suceso (Tierra del Fuego; Pine et al. 1978) and housed at National Museum of Natural History (Washington, DC) were assessed through digital pictures kindly sent by D. Wilson. The following specimens reported by Osgood (1943) and housed at the Field Museum of Natural History (Chicago) were also studied: ARGENTINA, Tierra del Fuego, Lago Fagnano: FMNH 50379 FMNH 50380, FMNH 50382, FMNH 50383, FMNH 50384, FMNH 50385, FMNH 50386, FMNH 50387, FMNH 50388, FMNH 50392; CHILE, XII Región, Magallanes, Punta Arenas: FMNH 50396, FMNH 50397, FMNH 50399, FMNH 50400, FMNH 50401, FMNH 50402, FMNH 50403, FMNH 50404, FMNH 50405, FMNH 50406, FMNH 50407. A gazetteer of collecting localities for *A. lanosus* (including the ones reported here) was compiled using all published records for the species (Table 1). In addition, the type locality of *A. lanosus* was unequivocally located on the basis of historical sources and nautical charts

Morphology

Cranial and mandibular descriptions followed Carleton (1980), Voss (1988), Carleton and Musser (1989), and Patterson (1992); whereas dental description followed Reig (1977). Standard external measurements were taken from specimen labels and field catalogs. Craniodental measurements were taken with digital calipers and followed the definitions provided by Patterson (1992). The studied specimens were age-classified using the tooth-wear criteria also described by Patterson (1992). For comparative purposes we studied series of *Abrothrix jelskii* (2; ARGENTINA, Jujuy, Sierra de Zenta: MACN 27.75, MACN 27.76); *Abrothrix longipilis* (13; ARGENTINA, Chubut: Epuyén: MACN 21472; Estancia Leleque, La Potrada: CNP 46, CNP 459; Laguna Larga: CNP 50, CNP 192, CNP 232, CNP 480; El Maitén: CNP 53, CNP 67, CNP 355, CNP 499; WSW end Lago Blanco: CNP 378; CHILE, VIII Región, Ñuble, Fundo La Madera: IEEUACH 2981); *Abrothrix markhami* (2; CHILE, XII Región, Última Esperanza, Isla Wellington, about 1.2 km NW Puerto Eden: USNM 501220 [paratype], USNM 501221 [holotype]); *Abrothrix olivaceus* (10; ARGENTINA: Chubut, Piedra Parada: CNP 52, CNP 336; Estancia Los Manantiales: CNP 55, CNP 62; Estancia Leleque: CNP 90, CNP 93; Estancia La Madrugada: CNP 127, CNP 144; El Maitén: CNP 331, CNP 509); *Abrothrix sanborni* (3; CHILE, XI Región, Coyhaique, Reserva Nacional Coyhaique; FMNH 134236; X Región, Parque Nacional Vicente Perez Rosales: FMNH 130138; X Región, Osorno, Valle de la Picada IEEUACH 2083). Acronyms for collections and institutions were these specimens are housed are as

Table 1. Gazetteer of recording localities for *Abrothrix lanosus*.

Number	Locality	Country	Lat S	Long W	Alt (m)	Voucher[a]	Reference	Remarks
1	Cerro Casa de Piedra, NP Perito Moreno	Argentina	47°57′	72°05′		MLP 5.X.99.3	Galliari and Pardiñas (1999)	Specimens from owl pellets
2	"Upper Rio Chico de Santa Cruz, in the Cordilleras" [río Tucu-Tucu valley]	Argentina	48°24′	71°49′		USNM 84211	Allen (1905)	Trapped specimens
3	Monteith Bay (Anafur Island)	Chile	50°22′	75°02′		BM 80.7.28.11	Thomas (1897)	Holotype
4	PN Torres del Paine [near headquarters according to Johnson et al. 1990]	Chile	51°00′	72°47′		Unknown	Rau et al. (1978)	Specimens from owl pellets
5	Vicinity of Punta Arenas	Chile	53°08′	70°55′		FMNH 50396	Osgood (1943)	Trapped specimens
6	Lago Fagnano [near E end according to C. Sanborn field notes]	Argentina	54°32′	67°13′		FMNH 50379	Osgood (1943)	Trapped specimens
7	Bahía Parry	Chile	54°37′	69°22′		IPAT 68	Yáñez et al. (1978)	Trapped specimens
8	Bahía Buen Suceso	Argentina	54°47′	65°15′		USNM 482121	Pine et al. (1978)	Trapped specimens
9	Cerro Cóndor	Argentina	54°47′	68°34′	300	DR 761	Reise and Venegas (1987)	Trapped specimens
10	CADIC, Ushuaia	Argentina	54°49′	68°19′	1	CNP 1394	This paper	Trapped specimens
11	Bahía Zaratiegui (= Bahía Ensenada), PN Tierra del Fuego	Argentina	54°50′	68°28′	1	CNP 1374	This paper	Trapped specimens
12	Laguna Verde, PN Tierra del Fuego	Argentina	54°50′	68°34′	6	CNP 1377	This paper	Trapped specimens
13	Lapataia, 20 km W Ushuaia, 3 km E Chilean border	Argentina	54°51′	68°34′	20	DR 742	Reise and Venegas (1987)	Trapped specimens

Acronyms for institutions or collections are: BM, the Natural History Museum, London, UK; CNP, Centro Nacional Patagónico, Puerto Madryn, Argentina; DR, D. Reise personal collection; FMNH, Field Museum of Natural History, Chicago, USA; IPAT, Instituto de la Patagonia, Punta Arenas, Chile; MLP, Museo de La Plata, La Plata, Argentina; and USNM, National Museum of Natural History, Washington D.C., USA.

[a] A single specimen per locality is listed for reference.

follows: CNP, Centro Nacional Patagónico, Puerto Madryn, Argentina; FMNH, Field Museum of Natural History, Chicago, USA; IEEUACH, Instituto de Ecología y Evolución de la Universidad Austral de Chile, Valdivia, Chile; MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina. Penis description followed Hooper and Musser (1964) and Spotorno (1992) and was based on an excised phallus from one formalin-preserved specimen (CNP 1396). A ventral cut exposed the urethral processes and the anterior mounds of the baculum; a second cut exposed the baculum and its anterior processes. For bacular analysis, skeletal staining with Alcian Blue and Alizarin Red (for cartilaginous and osseous tissue, respectively) was carried out together with tissue clearing in 2% KOH solution (Lidicker 1968). Stomach description followed Carleton (1973) and was based on two specimens (CNP 1389 and CNP 1393). Excised stomachs were bisected along the horizontal plane with respect to the longitudinal body axis using the dorsal half for descriptions.

Karyotype

Mitotic metaphase chromosomes were described from bone-marrow cell suspensions obtained in the field from two specimens (CNP 1399, female; CNP 1400, male) of *A. lanosus*, following Verma and Babu (1995). Marrow was first incubated in 0.1 ml (0.05%) colchicine plus 9.9 ml KCl (0.075 M) solution for 40 min at 37 °C and then fixed in 3:1 methanol/glacial acetic acid. Karyotypic analysis was performing by non-differential staining of chromosomes in phosphate-buffered Giemsa (pH = 6.8). Ten metaphase spreads were counted for each specimen.

Phylogeny

Phylogenetic analyses were based on complete cytochrome-*b* gene (hereafter cyt *b*) sequences and a 759 bp fragment of the first exon of the nuclear gene Interphotoreceptor Retinoid Binding Protein (hereafter IRBP) of the following specimens: both genes: *A. lanosus*, CNP 1396 and CNP 1399; cyt *b*: *A. longipilis*, CNP 174 and *A. olivaceus*, CNP 584; additional sequences were downloaded from GenBank. The ingroup was completed with abrotrichine representatives. When available, more than one representative per species was included. Representatives of the remaining sigmodontine tribes and some of the sigmodontine genera that have not clear phylogenetic relationships were used as outgroup taxa (see Results and discussion).

Total DNA was extracted following Miller et al. (1988). The cyt *b* sequences were gathered using primers MVZ 05 and MVZ 16 and MVZ 103 and MVZ 14 as in Pardiñas et al. (2003). IRPB sequences were gathered using primers A1 and F1 as in D'Elía et al. (2006b) following the conditions outlined in Jansa and Voss (2000). Amplification products were purified and sequenced in both directions by Macrogen Inc. DNA sequences were edited using Proseq3 (Filatov 2002). Resulting sequences were deposited in GenBank (EU683430–EU683435). Sequence alignment was done using Clustal X (Thompson et al. 1997) using default parameter values. Sigmodontine sequences of cyt *b* differ in length (see D'Elía et al. 2003, p. 353); from the alignment it became clear that the position of the indel/s responsible for such difference are at the very end of the sequence. We therefore limited our analyses to the first 1137 bases of cyt *b*. A set of partial and complete sequences were used for both gene analyses. Due to the different taxonomic coverage available for each gene, aligned sequences of both regions were separately analyzed by Maximum Parsimony (MP) (Farris 1982) and Bayesian analyses (Rannala and Yang 1996). MP analyses were carried out in PAUP*4 (Swofford 2000) with characters treated as unordered and equally weighted, 200 replicates of heuristic searches with random addition of sequences and tree bisection reconnection (TBR) branch swapping. Relative support of the recovered clades was assessed by performing 1000 bootstrap replications (BS). Bayesian analyses were done using Mr.Bayes 3.1 (Ronquist and Huelsenbeck 2003), by means of two independent runs, each with 3 heated and 1 cold Markov chains. A model with six categories of base substitution, a gamma-distributed rate parameter, and a proportion of invariant sites was specified; all model parameters were estimated in MrBayes. Uniform-interval priors were assumed for all parameters except base composition and GTR parameters, which assumed a Dirichlet process prior. Runs were allowed to proceed for 1 million generations; trees were sampled every 100 generations for each chain. To check that the runs converged on a stable log-likelihood value, we plotted the log-likelihood values against generation time for each. The first 25% of the trees were discarded as burn-in and the remaining trees were used to compute a 50% majority rule consensus tree and obtain posterior probability (PP) estimates for each clade.

Results and discussion

Rodentia Bowdich, 1821

Cricetidae Fischer, 1817

Sigmodontinae Wagner, 1843

Abrotrichini D'Elía et al. 2007

Abrothrix lanosus (Thomas, 1897)

Hesperomys (*Habrothrix*) *xanthorhinus* (sensu Thomas, 1881, p. 5, part)

Oxymycterus lanosus Thomas, 1897, p. 218

Oxymycterus lanosus (sensu Allen, 1905, p. 83)

Microxus lanosus (sensu Thomas, 1909, p. 237)

Akodon (*Abrothrix*) *lanosus* (sensu Osgood, 1943, p. 197)

Abrothrix lanosus (sensu Pine et al. 1978, p. 106)

Holotype: BM 80.7.28.11, male, skin and skull, collected by R.W. Coppinger.

Type locality: ''Monteith Bay, Straits of Magellan'' (Thomas, 1897, p. 218). The holotype was obtained during the naval mission of HMS Alert. O. Thomas described the mammals obtained by this expedition and gave the key to find the placement of Monteith Bay, ''The specimens were obtained, with few exceptions, in the western portion of the Magellan region, and in the immediate neighbourhood of the Madre de Dios archipelago, off the west coast of Patagonia'' (Thomas, 1881, p. 3). A nautical chart of this region (British Chart 1826, Concepción Channel to Castillo Channel, 1964) reveals that Monteith Bay is a small bay on the south coast of Anafur Island (50°23′S, 75°01′W, Fig. 1) just opposite to Caracciolo Island (part of the Madre de Dios Archipelago). Most researchers have looked for this locality in the southern portion of the Strait of Magellan, obviously without success (Gyldenstolpe
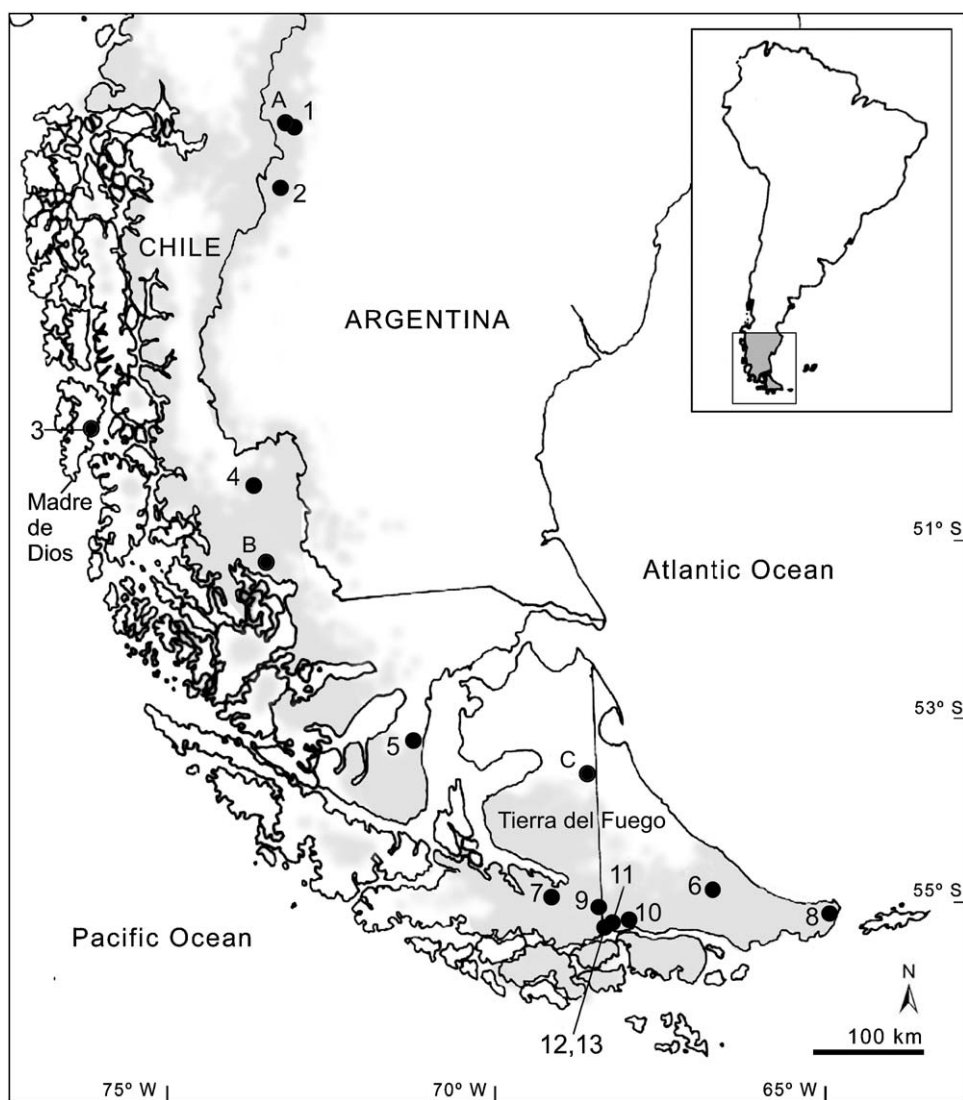

Fig. 1. Recording localities for *Abrothrix lanosus* (compiled from several sources; see Table 1). Numbers specify current localities; letters indicate fossil occurrences (A: Cerro Casa de Piedra 5; B: Cueva del Milodón; C: rockshelter Tres Arroyos 1). Anafur Island, where the type locality of *Abrothrix lanosus* lies, is part of the Madre de Dios Archipelago. Grey shadow indicates the distribution of the Magellan forest.

Table 2.   External measurements (in mm) and weights (in grams) of *Abrothrix lanosus* specimens obtained in southern Tierra del Fuego (Argentina).

	Sex	TL	HBL	T	F(wc)	F(c)	E	W
CNP 1374	Male	170	107	63	21	23	13	30
CNP 1375	Female	174	106	68	19	21	12.5	28
CNP 1376	Female	176	106	70	20	22	12.5	26
CNP 1377	Female	172	102	70	21	23	12.5	23
CNP 1378	Female	154	92	62	20	22	13	16
CNP 1379	Female	124	73	51	18	20	10.5	9
CNP 1380	Female	154	92	62	20	22	12	16
CNP 1381	Female	142	85	57	18	20	12	14
CNP 1382	Female	163	96	67	20	22	13	24
CNP 1383	Male	137	79	58	19	21	12.5	11
CNP 1384	Female	165	97	68	20	22	13	20
CNP 1385	Male	167	102	65	19	21	12.5	22
CNP 1386	Female	166	103	63	20	22	13	22
CNP 1387	Male	140	83	57	19	21	12	13
CNP 1394	Female	161	97	64	19	20	12	31
CNP 1395	Male	165	103	62	21	23	13	23
CNP 1396	Male	171	111	60	20	22	12	37
CNP 1397	Male	165	107	58	20	22	13	24
CNP 1398	Male	138	79	59	20	21	12	13
CNP 1399	Female	164	98	66	19	21	12	28
CNP 1400	Male	164	96	68	21	22	13	–
Mean		158.67	95.90	62.76	19.71	21.57	12.43	21.50
SD		14.29	10.66	4.98	0.90	0.93	2.78	7.45
Min		124	73	51	18	20	10.5	9
Max		176	111	70	21	23	13	37

Abbreviations: TL = total length, HBL = head and body length, T = tail length, F(wc) = foot length without claw, F(c) = foot length with claw, E = ear length, and W = weight.

1932; Osgood 1943; Cabrera 1961). Two corollaries can be retrieved from knowing the true geographic position of Monteith Bay: (a) it is an insular locality and the westernmost record for the species; (b) neither topotypes nor specimens collected moderately close to the type locality have been studied since the original description.

Distribution: Voucher specimens of *A. lanosus* are only known from 12 localities (Fig. 1 and Table 1). These localities suggest that the species occurs in a narrow western strip from ca. 48° to 55°S, both in Argentinean and Chilean territories. A single recording locality, the type locality, is on a Chilean Pacific island. Localities on the mainland (four in total) comprise two near the Argentina–Chile border of western Santa Cruz province (Argentina), and two in southern Chile (Magallanes Region). The remaining records are in the southern portion of the Island of Tierra del Fuego. The scattered distributional pattern displayed by *A. lanosus* appears to be, especially in the continent, a result of the rarity of this form (as observed from trapping and owl pellets analyses; UFJP pers. obs.), coupled with limited trapping efforts in suitable habitats.

Measurements: External and craniodental individual measurements are given in Tables 2 and 3, respectively.

Description: *Abrothrix lanosus* is one of the smallest representatives of the genus, characterized by its reduced eyes and ears and a tail of about 65% of head and body length combined (Fig. 2). Dorsal and ventral body contrast is markedly less conspicuous than in the syntopic congeneric species *A. olivaceus*, a difference that is useful for field discrimination. External appearance resembles that of a small *Oxymycterus* or *Brucepattersonius*, especially in terms of the pointed rostrum, semi-hidden ears, small eyes, and somewhat hispid aspect. This similarity is reinforced by the presence of sharp and moderately developed claws on the manus. The dorsal pelage is dense, soft and woolly; it is composed by almost entirely grey hairs with an ochraceous tip, giving a general yellowish-olive colouration; the belly is also grey but with whitish hair tips producing a somewhat frosted aspect. Adult specimens have the rhinarium and lips covered by extremely short, thin and delicate hairs; a small dirty-white spot is located on the nose. The ears are short, with rounded

Table 3.   Skull and mandible measurements of selected specimens of *Abrothrix lanosus* from southern Tierra del Fuego (Argentina).

	CNP 1384	CNP 1374	CNP 1376	CNP 1377	CNP 1380
Skull length	26.25	26.45	26.44	26.47	25.22
Condylobasal length	24.73	25.32	25.48	25.09	23.47
Basal length	22.08	22.62	22.44	22.19	20.77
Zygomatic breadth	11.99	12.31	12.25	11.89	11.68
Braincase breadth	11.28	11.47	11.44	11.51	11.66
Mastoid breadth	7.61	7.67	7.83	7.70	7.40
Palatilar length	10.52	10.60	10.50	10.55	9.85
Incisive length	6.00	5.90	6.10	5.98	5.50
Incisive width	2.12	2.28	2.10	2.20	1.97
Diastema length	6.73	6.87	6.94	6.92	6.16
Toothrow length	3.52	3.65	3.48	3.54	3.53
Palatal width at M1	4.90	5.07	5.14	4.98	4.88
Palatal width at M3	4.56	4.52	4.59	4.00	4.23
Zygomatic plate width	1.61	1.60	1.60	1.65	1.31
Nasal length	10.44	11.18	10.71	10.25	9.50
Nasal width	3.04	3.08	2.95	2.77	2.83
Rostrum width	4.75	4.50	4.92	4.68	4.82
Incisor width	1.40	1.51	1.45	1.46	1.24
Frontal sinus width	6.08	6.23	6.09	6.03	5.82
Interorbital breadth	4.50	4.72	4.67	4.62	4.68
Frontal length	8.32	7.64	8.32	8.08	8.04
Parietal length	6.04	6.01	6.38	5.76	6.05
Interparietal length	0.48	0.54	0.35	0.74	0.96
Interparietal width	2.35	4.20	3.46	4.92	5.51
Mandibular length	13.21	13.39	13.35	13.33	12.62
Condylar length	6.73	6.62	6.34	6.42	5.23
Process height	4.80	4.48	4.80	4.68	4.15
Ramus depth	2.45	2.55	2.53	2.57	2.31
Age class	5	5	6	5	4

Fig. 2. A young adult specimen of *Abrothrix lanosus* trapped in Laguna Verde (Tierra del Fuego, Argentina). Note the small ears and the whitish feet.

pinnae that are internally and externally covered by delicate agouti hairs. Mystacial vibrissae, abundant in number, are bright, and moderately long, but do not surpass the ears when laid back alongside the head. The tail is strongly bicoloured, dorsally darker and ventrally much paler, and conspicuously haired with long and partially rigid hairs. The dorsal surface of manus and pes is covered by short and thin white to cream hairs; the minute scales under these hairs produce a finely mottled aspect. Ungual tufts are pure white and shorter than claws. Plantar pads are six: a short but blunt thenar pad, a well developed circular hypothenar pad, and four large interdigital pads. Fingers present well expressed calluses. Palmar and plantar surfaces are covered by minute scales.

The skull of *A. lanosus* is delicate with an enlarged and pointed rostrum, inflated sinuses, gracile zygomatic arches, and rounded and well inflated braincase (Fig. 3). The anterior portion of the nasal bones is moderately
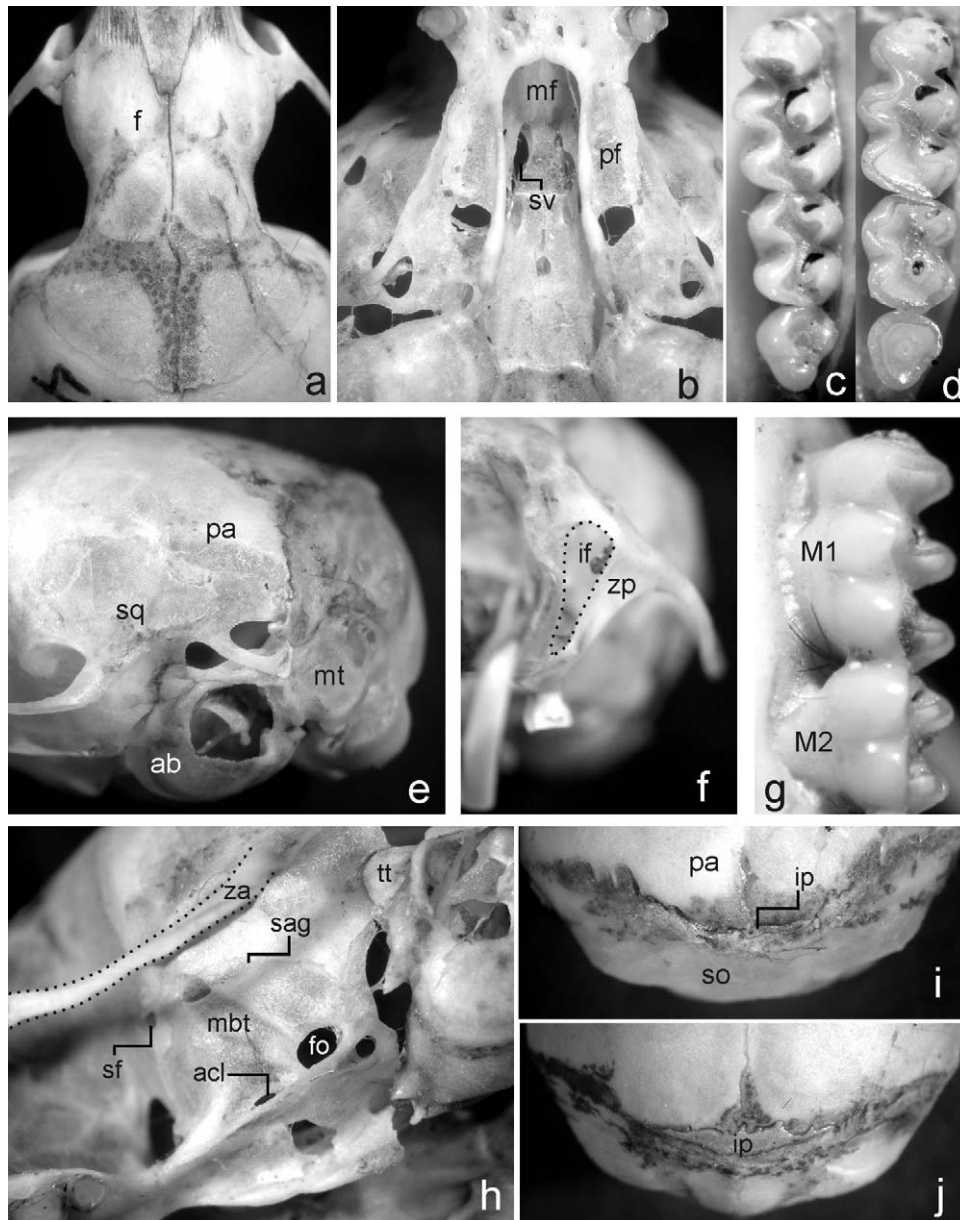
Fig. 3. Selected craniodental traits for *Abrothrix lanosus*: (a) Interorbital region in dorsal view (CNP 1380); (b) Mesopterygoid region (CNP 1376); (c, d) Left upper molar rows in *Abrothrix lanosus* through increasing wear (CNP 1380 and CNP 1377); (e) Temporal region (CNP 1374); (f) Skull in frontal view showing the large infraorbital foramen (CNP 1374); (g) Left M1-M2 in lingual view showing the morphology of the crested corona in a young individual (CNP 1383); (h) Squamosal-alisphenoid region (CNP 1374); (i, j) Posterior portion of the braincase showing variable expression of the interparietal bone from virtually absent (CNP 1376) to filiform (CNP 1380). *Abbreviations*: ab = auditory bulla, acl = anterior opening of alisphenoid canal, f = frontal, fo = foramen ovale, if = infraorbital foramen, ip = interparietal, M1 = upper first molar, M2 = upper second molar, mbt = trough for masticatory-buccinator nerve, mf = mesopterygoid fossa, mt = mastoid, pa = parietal, pf = parapterygoid fossa, sag = squamosal-alisphenoid groove, sf = sphenofrontal foramen, so = supraoccipital, sq = squamosal, sv = sphenopalatine vacuities, tt = tegmen tympani, za = zygomatic arch, zp = zygomatic plate.

bent upwards and, with the premaxillaries, produces a somewhat trumpet-like effect. The nasals are divergent forward, although they run in parallel during the anterior one third and almost cover the entire rostrum in dorsal view. The naso-frontal suture is markedly acute (V-shaped) reaching a line between the small lacrimal bones (Fig. 3a). The interorbital region is rounded, smooth, and with frontal sinuses well expressed. The coronal suture is U-shaped (Fig. 3a). The interparietal is present although typically reduced to a very narrow strip (Figs. 3i, j). The occipital region is well inflated and without ridges. The zygomatic plates are
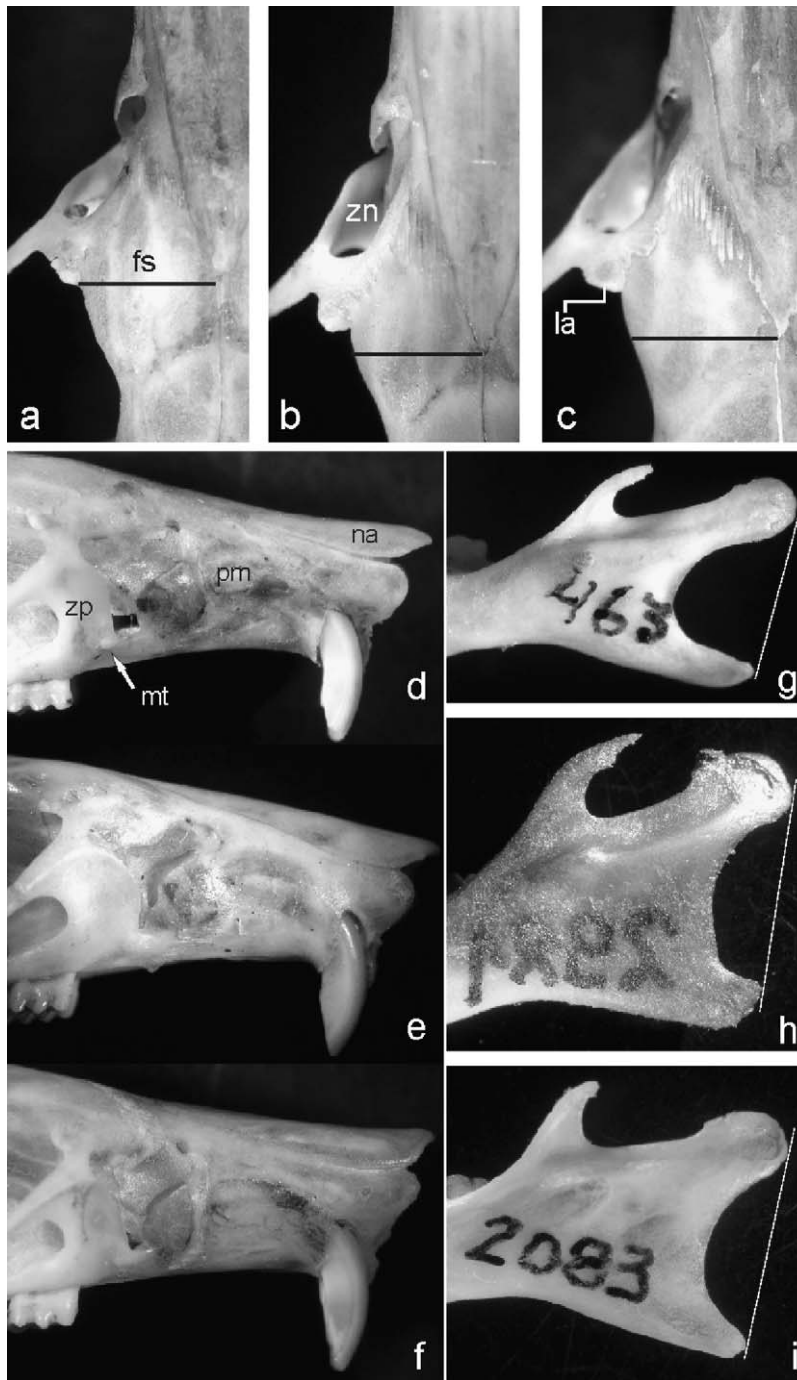
Fig. 4. Skull and mandibles of *A. lanosus* (CNP 1374), *A. longipilis* (IEEUACH 2981), and *A. sanborni* (IEEUACH 2083). Frontal morphology: (a) *Abrothrix lanosus*, (b) *A. longipilis*, and (c) *A. sanborni*; the line highlights the posteriormost point reached by the nasals in relation to the lacrimal position. Rostral morphology, in lateral view, (d) *Abrothrix lanosus* (a, CNP 1374; b, CNP 1376), (e) *A. longipilis*, and (f) *A. sanborni*. Vertical rami, in labial views, of (g) *Abrothrix lanosus*, (h) *A. longipilis*, and (i) *A. sanborni*. *Abbreviations*: fs = frontal sinus, la = lacrimal, zn = zygomatic notch, mt = masseteric tubercle, na = nasal, pm = premaxillary, zp = zygomatic plate.

medium in height, narrow, with the anterior border partially slanted, and the upper root broad. A visible masseteric tubercle is present. The inclination of the zygomatic plate with respect to the sagital plane of the skull produces a well developed, basally expanded infraorbital foramen (Fig. 3f). The zygomatic plates (although narrow) coupled with conspicuous nasolacrimal capsules determinate well expressed zygomatic

notches. The subsquamosal fenestra and the postglenoid foramen, subequal in size, are crossed by a broad hamular process of the squamosal (Fig. 3e). Cranial foramina associated with the cephalic arterial pattern and other osteological traits of the alisphenoid region include a large foramen ovale, a more reduced anterior opening of the alisphenoid canal, a deep and broad trough for the masticatory-buccinator nerve, and a squamosal-alisphenoid groove that connects anteriorly to a sphenofrontal foramen (Fig. 3h). In the conjunction between the trough for masticatory-buccinator nerve and the squamosal-alisphenoid groove there is a large perforation consistently present. The alisphenoid strut is absent. All these traits plus a large stapedial foramen indicate that the cephalic blood supply in *A. lanosus* is similar to the presumably primitive muroid pattern (Carleton 1980). The palatal region is characterized by broad and large incisive foramina that terminate by the anterolingual M1 conules. The palate is broad and smooth, and the U-shaped anterior border of the mesopterygoid fossa typically terminates just posterior to the third molars (Fig. 3b). The mesopterygoid fossa is broader than the parapterygoid fossae, and the mesopterygoid roof is excised by moderately large sphenopalatine vacuities. Auditory bullae are medium in size and leave the petrosal bone partially exposed. Mastoids are characterized by a large fenestra (Fig. 3e).

Abrothrix lanosus has a morphologically distinctive mandible characterized by its slender constitution, a marked constriction of the horizontal ramus below m3, and a deeply excavated angular notch (Fig. 4g). The anterior point of the diastema is slightly below the alveolar plane. The masseteric crest conforms a single well expressed ridge. The angular and condyloid processes are thick and markedly forward projected, while the coronoid process is comparatively short and distally spatulated. The capsular projection of the lower incisor alveolus is smooth. Internally and behind m3, the mandible displays a well developed squared-shaped platform.

As pointed out by Thomas (1897), the ungrooved upper incisors are slightly opisthodont and very pale yellow in colour, while lower ones are white. Upper and lower molars display typical the *Abrothrix* pattern (Fig. 3c and d; see Reig 1987).

Postcranial skeletal characters obtained from three specimens (CNP 1374, CNP 1377, and CNP 1384) include 7 cervical, 13 thoracic, 6 lumbar, and 25/26 caudal vertebrae, and 13 ribs (2 free). The articulation of the first rib is double. The humerus lacks an entepicondylar foramen.

The penis is elongated (9.0 mm), curved ventrally, and exhibits a deep terminal crater that extends about 45% of the total length of the glans penis (Fig. 5). Urethral processes are long (2.7 mm) and inserted near the middle of the glans penis. The glans penis also has very small soft-bacular mounds. Inside, the proximal baculum narrows distally; no distal baculum was found even after staining and clearing of tissue (Fig. 5).

The stomach conforms to the unilocular hemiglandular type defined and illustrated by Carleton (1973). As in other congeneric species, in *A. lanosus* the gastric glandular epithelium covers the antrum and the proximal portion of corpus near the esophageal
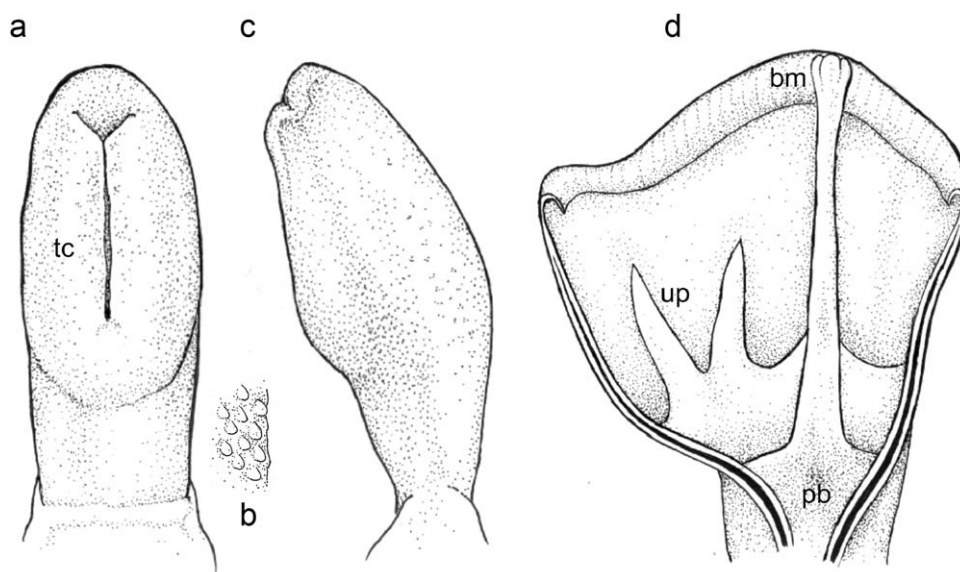

Fig. 5. Morphology of the glans penis of *Abrothrix lanosus*: schema based on CNP 1396 (CADIC, Tierra del Fuego, Argentina). (a) Ventral view. (b) Close up of the external surface showing spines. (c) Lateral view. (d) Internal view: bm, bacular mounds; up, urethral processes; pb, proximal baculum.

opening. In addition, the *incisura angularis* is very shallow.

Karyotype: The diploid complement of *A. lanosus* is $2n = 52$ (FN = 56), including 23 pairs of acrocentric chromosomes (medium to small), one pair of large subtelocentrics, and one pair of medium-sized meta-centrics. The sex chromosomes were identified as a medium-sized X and a small subtelocentric Y.

DNA sequences and phylogenetic analysis: The cyt *b* sequences of *A. lanosus* differed by 0.107 (*p*-distance) from *A. jelskii* and by 0.110 from *A. longipilis*; in turn, *A. jelskii* and *A. longipilis* differed by 0.103. The divergences between these three species and other taxa were all greater than 0.117, 0114, and 0.106 for *A. jelskii*, *A. lanosus*, and *A. longipilis*, respectively. Except for two ambiguous sites in the reported IRBP sequence of *A. longipilis*, the sequences of *A. lanosus* were identical to the former in the 759 bp that can be compared directly. In the same region, *A. lanosus* and *A. longipilis* differed from *A. jelskii* in four unambiguous sites. These three species differed from other species of *Abrothrix* in at least five sites.

Both of the phylogenetic methods that we employed resulted in similar topologies for each gene analyzed; therefore, here we just present those derived from the MP analyses (Bayesian results are available upon request). The IRPB data set has 244 variable sites of which 72 are parsimony informative. A total of 90 shortest trees (length: 325; CI: 0.80; RI: 0.79) were found; their strict consensus is portrayed in Fig. 6a. The cyt *b* matrix has 531 variable sites of which 431 are parsimony informative. MP analysis of this matrix produced five shortest trees (length: 2168; CI: 0.38; RI: 0.52); their consensus is portrayed in Fig. 6b.

Analysis of both genes supports the monophyly of the tribe Abrotrichini (cyt *b*: BS = 60, BY = 0.80; IRBP: BS = 99, BY = 1.0) as early evidenced by D'Elía (2003), D'Elía et al. (2006a, b), Dickerman (1992), and Smith and Patton (1993, 1999). Within Abrotrichini, as the referred studies already found, the first dichotomy leaves *Abrothrix* as sister to the remaining abrotrichines. As the focus of the present study is *A. lanosus*, here we will not discuss further the non-*Abrothrix* clade. *Abrothrix* was always recovered as monophyletic and with strong support (IRBP: BS = 71, BY = 1.0; cyt *b*: BS = 96, BY = 0.99). Differences resolving the closest relation-ships of *A. lanosus* were found between the inferred phylogenies based on cyt *b* and IRBP genes. In the cyt *b* analyses *A. lanosus* appears sister to *A. jelskii* (BS = 74, BY = 0.99). Meanwhile, in the IRBP analyses *A. lanosus* forms a clade together with *A. longipilis* (BS = 57; BY = 0.95). Moreover, within this clade both *A. lanosus* sequences do not form a clade; i.e., there is a basal polytomy formed by both *A. lanosus* sequences and that

of *A. longipilis*. As explained by Pamilo and Nei (1988), different topologies may result from the different evolutionary histories of each gene used; however, it must be remembered that the analyses are based on slightly different taxonomic sampling.

The IRBP topology is easier to reconcile with distributional and morphological data, as well as with the taxonomic history of *Abrothrix* than the one arising from the analyses of cyt *b* sequences. The distributions of *A. lanosus* and *A. longipilis* overlap in southern South America (including Tierra del Fuego). Meanwhile *A. jelskii* is found in the central Andes (northern Argentina, Bolivia and Peru). There is a gap of about 2500 km between the known distributions of *A. lanosus* and *A. jelskii*. However, sigmodontine distribu-tions may have suffered important fluctuations, even dramatic ones in short periods of time (e.g., Pardiñas 1999; D'Elía et al. 2005). On the basis of morphological variation, Mann (1978) synonymized *A. lanosus* under *A. longipilis*. Analysis of a third gene may help in clarifying the nature of the differences between the cyt *b*- and IRBP-based topologies. Similarly, the inclusion in future phylogenetic analyses of additional species of *Abrothrix*, especially *A. illuteus*, would be welcome. Below we present data that supports the relationship of *A. longipilis* as the closest species to *A. lanosus*.

Comparisons: Both craniodental and soft-anatomical characters suggest a close phenetic relationship between *Abrothrix lanosus* and *A. longipilis* and to a lesser extent also with *A. sanborni*. At the same time, *A. lanosus* clearly differs from *A. jelskii*. Externally the latter markedly departs from the remaining *Abrothrix*. Its colouration is conspicuous, generally markedly counter-coloured: the venter is whitish or grayish, while there are contrasting patches of white or buff hair behind the ears and of fulvous or ochraceous hairs on the muzzle, feet, tail dorsum, flanks, and back. In addition, the skull of *A. jelskii* clearly departs from that of *A. lanosus* and *A. longipilis*. In *A. jelskii* the palate ends about level of the posterior side of the M3, while in *A. lanosus* and *A. longipilis* the palate extends beyond the plane of the molar rows. Also, the nasals and premaxillae of *A. jelskii* do not form a trumpet-like tube as in *A. lanosus* and *A. longipilis*, and *A. jelskii* has larger tympanic bullae than either *A. lanosus* or *A. longipilis*. Finally, the incisors of *A. jelskii* are unusually slender and with their anterior surfaces pale yellow. External appearance readily distinguishes *A. longipilis* from *A. sanborni*, the former exhibiting sharply delimited dorsal and ventral colours, larger ears, less pointed muzzle, and more powerful anterior claws, whereas the latter is markedly darker. Cranially, and regarding the variation displayed by *A. longipilis* along its wide distribution, *A. lanosus* might appear to be a minute example of the former. However several differences can be indicated (Fig. 4), including larger lacrimal bones and
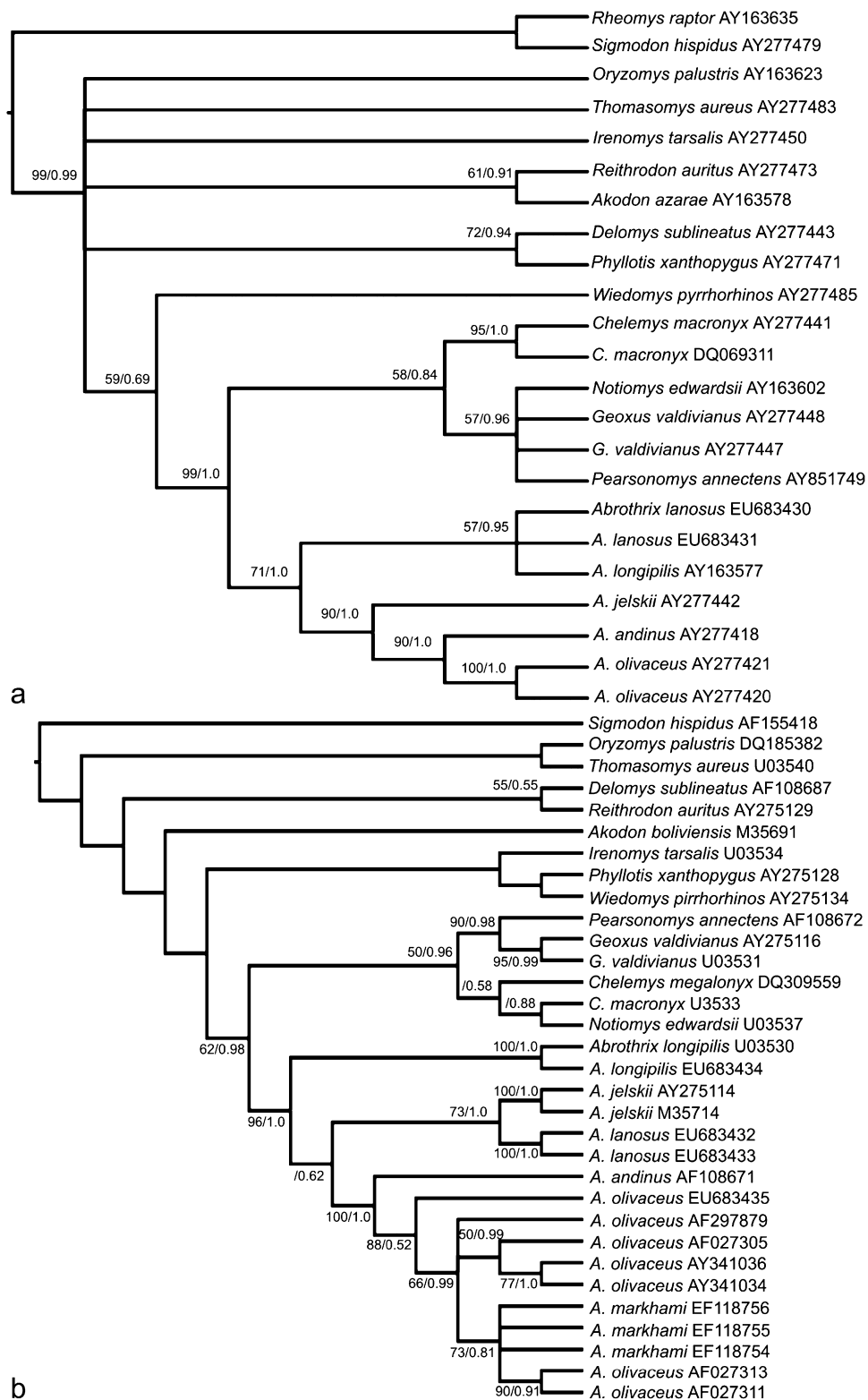
Fig. 6. (a) Strict consensus tree of the 90 most-parsimonious trees (length: 325; CI: 0.80; RI: 0.79) obtained in the maximum-parsimony analysis of IRBP gene sequences. (b) Strict consensus tree of the five most-parsimonious trees (length: 2168; CI: 0.38; RI: 0.52) obtained in the maximum-parsimony analysis of cyt *b* gene sequences. Numbers on branches indicate bootstrap (left to the diagonal) and posterior probability (right to the diagonal) values of the adjacent node. Only Bootstrap values above 50% are shown. Genbank accession numbers of analyzed sequences are included at terminal labels.

interparietal; opisthodont, orange-coloured upper incisors; broader zygomatic plate; and large sphenopalatine vacuities, among others. *Abrothrix sanborni* differs somewhat in gross cranial morphology by having larger lacrimals; a more acute naso-frontal suture that surpasses the lacrimal line; nasal bones more divergent anteriorly that, together with the premaxillaries, form a closed tube (Fig. 4); gnathic process more developed; orthodont, rich-coloured upper incisors; narrow incisive foramina; larger parapterygoid fossae than the mesopterygoid fossa; narrower sphenopalatine vacuities; and flatter mastoid capsules. The mandible among these three species also exhibit contrasting morphological traits (Fig. 4), especially in the ascending ramus: *A. longipilis* and *A. sanborni* have shallowly excised semilunar notches, shorter angular and condyloid processes, and a horizontal ramus that is less constricted below m3.

Results obtained by Spotorno (1992) on penis morphology also show the phenetic proximity among the *Abrothrix* species discussed. However, the presence of reduced bacular mounds in *A. lanosus* is not found in *A. longipilis*. In that regard, the phallus of *A. lanosus* might represent an intermediate stage between complex and simple forms, as described in Carleton (1980) and Spotorno (1992).

To date, several species of *Abrothrix* have been analyzed cytogenetically, and several populations have been studied within some widely distributed species. These studies indicate that the genus is karyotypically conservative: *A. andinus*, *A. jelskii*, *A. longipilis*, *A. illuteus*, *A. olivaceus* (including *xanthorhinus*), and *A. sanborni* all share, together with *A. lanosus*, the same $2n = 52$ karyotype (Spotorno and Fernández 1976; Gallardo 1982; Rodríguez et al. 1983; Patterson et al. 1984; Reig 1987; Liascovich et al. 1989; Spotorno et al. 1990). The only marked departure from this pattern so far is the recent documentation of a population of *Abrothrix olivaceus* with a $2n = 44$ (Rodríguez and Theiler 2007). Therefore, the available cytogenetic evidence does not help clarify the phylogenetic position of *A. lanosus* within *Abrothrix*.

Natural history and environments: Captive individuals are docile and easy to manage with bare hands. Times of capture in February and December reveal that the species is basically nocturnal, but also exhibits some diurnal activity. All specimens trapped by us were obtained from coastal localities with well developed soils and dense vegetation cover of "Mata negra" (*Junielia tridens*), outside, although very close to the edge of nearby Fueguian forest. In this type of environment and in the mentioned months, two other sigmodontine species were dominant, *A. olivaceus* and *Oligoryzomys longicaudatus*, whereas *A. lanosus* was a subsidiary component of this assemblage. It is important to note

however, that *A. lanosus* has also been captured in dense *Nothofagus* forest. Osgood (1943, p. 197) mentioned that *A. lanosus* "was found sparingly in or near deep forest on Tierra del Fuego and in the vicinity of Punta Arenas where it shows preference for cool, damp habitat." Based on our field experience in southern Argentina and a complete analysis of available literature, we suppose that *A. lanosus* basically occurs in open-habitats, mainly shrublands or shrubland–grassland steppes, associated with, or very close, to forest, but not actually inside it.

Fossil record: Fossil remains of *Abrothrix lanosus* have been recovered from three archaeological deposits in the Fuego-Patagonia region (Fig. 1). The first and oldest record comes from Late Pleistocene beds at the classical locality Cueva del Milodón (51°35′S, 72°36′W, Magallanes, Chile; Simonetti and Rau 1989). A still-unpublished Late Holocene record is from Rockshelter 1 in Tres Arroyos (53°23′S, 68°47′W, Tierra del Fuego, Chile; U. Pardiñas, pers. obs.). Finally, also from the Late Holocene, some remains have been recovered in the rich sequence of Cerro Casa de Piedra 5 (47°57′S, 72°05′W, Santa Cruz, Argentina; Pardiñas 1998). It is interesting to note that Tres Arroyos is located on the Sierra de Carmen Sylva in the northern steppe portion of Tierra del Fuego, about 150 km north to the nearest recent record (Lago Fagnano) for the species, which lies in a forested area.

Final considerations

After the original description of *A. lanosus* by Thomas (1897), the second reference to this species was made by Allen (1905, p. 83) based on two fresh specimens collected in western Santa Cruz, Argentina. In fact, these two specimens were classified by Thomas himself (cf. Allen, 1905, p. 84) and the external description gave by Allen is coincident in all the traits with those made by Thomas in 1897. Osgood (1943, p. 197) was the first to study and refer to this species specimens from the southern tip of the continent ("vicinity of Punta Arenas") and the first Fueguian individuals (Lake Fagnano). The characterization offered by Osgood also fits the original description of *lanosus* from Monteith Bay. The specimens inspected by Osgood that are deposited in the Field Museum of Natural History fit our morphological characterization of *A. lanosus* (Table 1). However, we remark that we have not directly studied the type material of *A. lanosus* and as such we were not able to assess the degree of differentiation of our material and that of the type locality. Moreover, to our knowledge nobody has captured additional specimens at the type locality of *A. lanosus*.

Abrothrix lanosus is one of the six extant species of Sigmodontinae that inhabits Tierra del Fuego (the

remaining five are *Abrothrix olivaceus*, *A. longipilis*, *Reithrodon auritus*, *Euneomys chinchilloides*, and *Oligoryzomys longicaudatus*). All six species also occur in the continent, and *A. lanosus* is the one with the smallest geographic distribution, most of which was covered by ice during the last glaciation (McCulloch et al. 2000; Glasser et al. 2004). Therefore, we hypothesize that limited geographic structure would be found across all *A. lanosus* distribution. However, the possibility that extant *A. lanosus* diversity comes from more than one refugium cannot be ruled out without data from continental populations of the species.

From a systematic point of view, both morphology and nuclear DNA-based phylogenetic analysis support a close relationship between *A. lanosus* and *A. longipilis*; their IRBP sequences are identical, whereas the two species differ by 11.4% (observed differences) in their mitochondrial cyt *b* gene. Mann (1978) recognized the close similarity between the species, and our data concur, while supporting a species level distinction between these two forms. *Abrothrix sanborni* (Osgood, 1943) is another species that, according to phylogenetic evidence (Spotorno et al. 2000), is closely related to *A. longipilis*, as suggested by its simple type penis morphology and several craniodental features (Spotorno 1992). These three species depart in several features from the remaining species traditionally included in *Abrothrix* (i.e., *A. andinus*, *A. jelskii*, *A. hershkovitzi*, *A. olivaceus*; Musser and Carleton 2005). The evidence at hand suggests that the genus as is currently understood has a broad range of morphological variation; therefore, although monophyletic, it may be worth of be divided into more than one genus.

In the last decade, several contributions improved our systematic understanding of the Abrotrichini (e.g., Pearson and Smith 1999; Smith et al. 2001; D'Elía et al. 2007; Rodríguez-Serrano et al. 2008); clearly, however, additional issues need to be explored. In particular, additional southern species are in need of reappraisal. For example, *A. llanoi*, early proposed as an Isla de los Estados endemic form (Pine 1976), was later briefly subsumed under the *A. olivaceus* complex (Patterson et al. 1984). Similarly, *A. hershkovitzi* or *A. mansoensis*, both known only from few specimens collected decades ago, would warrant additional studies. The clarification of these and other taxonomic problems is needed to better understand the evolutionary diversification of small mammals in southern South America.

Acknowledgements

References

Allen, J.A., 1905. I. The Mammalia of Southern Patagonia. Reports of the Princeton University Expeditions to Patagonia 1896–1899, 3(1) Zoology, 210pp., 29 láminas.

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. Linn. Soc. 48, 283–298.

Cabrera, A., 1961. Catálogo de los mamíferos de América del Sur. Parte II. Rev. Mus. Argent. Cs. Nat. ''B. Rivadavia'' Cs. Zool. 4, 309–732.

Carleton, M.D., 1973. A survey of gross stomach morphology in New World Cricetine (Rodentia, Muroidea) with comments on functional interpretations. Misc. Pub. Mus. Zool. Univ. Michigan 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. Pub. Mus. Zool., Univ. Michigan 157, l–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.

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., 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., Pardiñas, U.F.J., Myers, P., 2005. An introduction to the genus *Bibimys* (Rodentia: Sigmodontinae): phylogenetic position and alpha taxonomy. In: Lacey, E., Myers, P. (Eds.), Mammalian Diversification: From Chromosomes to Phylo-

geography. University of California Publications in Zoology, Berkeley, pp. 211–246.

D'Elía, G., Luna, L., González, E.M., Patterson, B.D., 2006a. On the Sigmodontinae radiation (Rodentia, Cricetidae): an appraisal of the phylogenetic position of *Rhagomys*. Mol. Phyl. Evol. 38, 558–564.

D'Elía, G., Ojeda, A.A., Mondaca, F., Gallardo, M.H., 2006b. New data of 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. Ph.D. Dissertation, University of Wisconsin-Madison.

Farris, J.S., 1982. The logical basis for phylogenetic analysis. In: Platnick, I., Funk, V.A. (Eds.), Advances in Cladistics. Proceedings of the Second Meeting. Willi Henning Society, vol. 2. Columbia University Press, New York, pp. 1–36.

Filatov, D.A., 2002. ProSeq: a software for preparation and evolutionary analysis of DNA sequence data sets. Mol. Ecol. Notes 2, 621–624.

Gallardo, M.H., 1982. Chromosomal homology in southern *Akodon*. Experientia 38, 1485–1487.

Galliari, C.A., Pardiñas, U.F.J., 1999. *Abrothrix lanosus* (Rodentia: Muridae) en la Patagonia continental argentina. Neotrópica 45 (113–114), 119–120.

Glasser, N.F., Harrison, S., Winchester, V., Aniya, M., 2004. Late Pleistocene and Holocene palaeoclimate and glacier fluctuations in Patagonia. Glob. Plann. Change 43, 79–101.

Gyldenstolpe, N., 1932. A manual of Neotropical sigmodont rodents. Kungl. Svenska Vetensk. Handl. 3, 1–164.

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.Michigan 123, 1–57.

Jaksic, F., Rau, J., Yáñez, J., 1978. Oferta de presas y predación por *Bubo virginianus* (Strigidae) en el Parque Nacional "Torres del Paine. An. Inst. Patagonia (Chile) 9, 199–202.

Jansa, S.A., Voss, R.S., 2000. Phylogenetic studies on didelphid marsupials, I: introductions and preliminary results from nuclear IRBP gene sequences. J. Mamm. Evol. 7, 43–77.

Johnson, W.E., Franklin, W.L., Iriarte, J.A., 1990. The mammalian fauna of the northern Chilean Patagonia: a biogeographical dilemma. Mammalia 54, 457–469.

Liascovich, R.C., Barquez, R.M., Reig, O.A., 1989. A karyological and morphological reassessment of *Akodon* (*Abrothrix*) *illuteus* Thomas. J. Mamm. 70, 386–391.

Lidicker, W.Z., 1968. A phylogeny of New Guinea rodent genera based on phallic morphology. J. Mamm. 49, 609–643.

Mann, G., 1978. Los pequeños mamíferos de Chile. Gayana, Zoología 40, 40–105.

McCulloch, R.D., Bentley, M.J., Purves, R.S., Hulton, N.R.J., Sugden, D.E., Clapperton, C.M., 2000. Climatic inferences from glacial and palaeoecological evidence at the last glacial termination, southern South America. J. Q. Sci. 15, 409–417.

Miller, S., Dikes, D., Polesky, H., 1988. A simple salting out procedure for extracting DNA for human nucleated cells. Nucleic Acid Res. 16, 215.

Musser, G.M., Carleton, M.D., 2005. Superfamily Muroidea. In: Wilson, D.E., Reeder, D.M. (Eds.), Mammal Species of the World: A Taxonomic and Geographic Reference, third ed. Johns Hopkins University Press, Baltimore, pp. 894–1531.

Osgood, W.H., 1943. Field museum of natural history. Zool. Ser. 30, 1–268.

Pamilo, P., Nei, M., 1988. Relationships between gene trees and species trees. Mol. Biol. Evol. 5, 568–583.

Pardiñas, U.F.J., 1998. Roedores holocénicos del sitio Cerro Casa de Piedra 5 (Santa Cruz, Argentina): tafonomía y paleoambientes. Palimpsesto 5, 66–90.

Pardiñas, U.F.J., 1999. Los roedores muroideos del Pleistoceno tardío-Holoceno en la Región Pampeana (sector Este) y Patagonia (República Argentina): aspectos taxonómicos, importancia bioestratigráfica y significación paleoambiental. Unpublished. Ph.D. Thesis, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata.

Pardiñas, U.F.J., D'Elía, G., Cirignoli, S., 2003. The genus *Akodon* (Muroidea: Sigmodontinae) in Misiones, Argentina. Mamm. Biol. 68, 129–143.

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

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. Field Zool., n.s 23, 1–16.

Pearson, O.P., Smith, M.F., 1999. Genetic similarity between *Akodon olivaceus* and *Akodon xanthorhinus* (Rodentia: Muridae) in Argentina. J. Zool. 247, 43–52.

Pine, R., 1976. A new species of *Akodon* (Mammalia: Rodentia: Muridae: Cricetinae) from Isla de los Estados, Argentina. Mammalia 40, 63–68.

Pine, R., Angle, J.P., Bridge, D., 1978. Mammals from the sea, mainland and islands at the southern tip of South America. Mammalia 42, 105–114.

Rannala, B., Yang, Z., 1996. Probability distribution of molecular evolutionary trees: a new method of phylogenetic inference. J. Mol. Evol. 43, 304–311.

Rau, J., Yánez, J., Jaksic, F., 1978. Confirmación de *Notiomys macronyx alleni* O. y *Eligmodontia typus typus* C., y primer registro de *Akodon* (*Abrothrix*) *lanosus* T. (Rodentia: Cricetidae) en la zona de Ultima Esperanza (XII Región, Magallanes). An. Inst. Patagonia (Chile) 9, 203–204.

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

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

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. Field Zool., n.s. pp. 347–399.

Reise, D., Venegas, W., 1987. Catalogue of records, localities and biotopes from research work on small mammals in Chile and Argentina. Gayana, Zoología 51, 103–130.

Rodríguez, M., Montoya, R., Venegas, W., 1983. Cytogenetic analysis of some Chilean species of the genus *Akodon* Meyen (Rodentia, Cricetidae). Caryologia 36, 129–138.

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

Rodríguez-Serrano, E., Hernández, C.E., Palma, R.E., 2008. A new record and an evaluation of the phylogenetic relationships of *Abrothrix olivaceus markhami* (Rodentia: Sigmodontinae). Mamm. Biol. 73, 309–317.

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

Simonetti, J.A., Rau, J.R., 1989. Roedores del Holoceno temprano de la cueva del Milodón, Magallanes, Chile. Not. Men. Mus. Nac. Hist. Nat. (Chile) 315, 3–5.

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. Mamm. Evol. 6, 89–128.

Smith, M.F., Kelt, D.A., Patton, J.L., 2001. Testing models of diversification in mice in the *Abrothrix olivaceus/xanthorhinus* complex in Chile and Argentina. Mol. Ecol. 10, 397–405.

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

Spotorno, A., Fernández, R., 1976. Chromosome stability in southern *Akodon* (Rodentia, Cricetidae). Mamm. Chrom. Newsletter 17, 13–14.

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

Spotorno, A., Palma, E.R., Valladares, P.J., 2000. Biología de roedores reservorios de hantavirus en Chile. Rev. Chil. Enfectología 17, 197–210.

Swofford, D.L., 2000. PAUP*. Phylogenetic Analysis using Parsimony (* and other methods). Sinauer Associates, Sunderland, MA.

Tamayo, M., Frassinetti, D., 1980. Catálogo de los mamíferos fósiles y vivientes de Chile. Bol. Mus. Nac. Hist. Nat. (Chile) 37, 323–399.

Tamayo, M., Núñez, H., Yáñez, J., 1987. Lista sistemática actualizada de los mamíferos vivientes en Chile y sus nombres comunes. Not. Men. Mus. Nac. Hist. Nat. (Chile) 312, 1–13.

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

Thomas, O., 1881. 1. Account of the zoological collections made during the survey of H.M.S. 'Alert' in the Straits of Magellan and on the coast of Patagonia. I. Mammalia Proc. Zool. Soc. London 1881, 3–6.

Thomas, O., 1897. Descriptions of four new South-American mammals. Ann. Mag. Nat. Hist. (London) 20 (6), 218–221.

Thomas, O., 1909. Notes on some South-American mammals, with descriptions of new species. Ann. Mag. Nat. Hist. (London) 4 (8), 230–242.

Thompson, J.D., Gibson, T.J., Plewniak, F., Jeanmougin, F., Higgins, D.G., 1997. The CLUSTAL X windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. Nucleic Acid Res. 25, 4876.

Verma, R.S., Babu, A., 1995. Human Chromosomes, Principles and Techniques. McGraw-Hill, New York.

Voss, R., 1988. Systematics and ecology of ichthyomyine rodents (Muroidea): patterns of morphological evolution in a small adaptative radiation. Bull. Am. Mus. Nat. His. 188, 259–493.

Yáñez, J., Sielfeld, W., Valencia, J., Jaksic, F., 1978. Relaciones entre la sistemática y la morfometría del subgénero *Abrothrix* (Rodentia: Cricetidae) en Chile. An. Inst Patagonia (Chile) 9, 185–197.