



# Description of a new soft-haired mouse, genus *Abrothrix* (Sigmodontinae), from the temperate Valdivian rainforest

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Analyses of morphological and molecular data indicate the existence of an unrecognized and unnamed species of soft-haired mouse, genus *Abrothrix*. Here, we name and describe this new species, which inhabits the Valdivian ecoregion, from the north of Chiloé Island onto the mainland in the Chilean regions of Los Lagos and Los Ríos; it also occurs at a single locality in the Argentinean province of Neuquén. Long confused with A. sanborni, the new species presents a unique combination of characters that differentiate it in external, cranial, phallic, and dental terms from its congeners. Phylogenetic analysis, based on cytochrome-*b* gene sequences, indicates that the new species is sister to a clade formed by the austral species *A. lanosa* and *A. sanborni* and differs on average from the mby 5.7% and 5.2%, respectively. Results based on the nuclear *Fgb*-I7 locus are less conclusive regarding the phylogenetic position of the new species but also show its distinction. We comment on the conservation significance of our findings, considering that forests of the Valdivian ecoregion are suffering substantial human disturbance through intensive logging.

Análisis de datos morfológicos y moleculares indican la existencia de una especie nueva e innominada de ratones del género Abrothrix. En este trabajo nominamos y describimos esta nueva especie que habita la ecorregión Valdiviana, desde el norte de la Isla de Chiloé hasta áreas continentales adyacentes de las regiones chilenas de Los Lagos y Los Ríos; la especie también ha sido registrada en una localidad de la provincia argentina del Neuquén. Largamente confundida con A. sanborni, la nueva especie presenta una combinación única de caracteres, incluyendo: coloración dorsal negruzca marrón oscuro a marrón-oliva; coloración ventral marrón grisácea a grisácea; cráneo delicado, con la constricción interorbital en forma de reloj de arena y caja craneana redondeada; rostro angosto y largo; nasales y premaxilares proyectados más anteriormente que los incisivos; placa cigomática estrecha; paladar extendiéndose apenas más allá del plano definido por el margen posterior de los M3; molares mesodontes; en adultos M1 sin flexo anteromedio; parastilo y mesolofo presentes; estómago unilocular-hemiglandular; cráter terminal del pene dirigido ventralmente; elementos apicales cartilaginosos ausentes. Análisis filogenéticos basados en secuencias del gen del citocromo b indican que la nueva especie es hermana de un clado formado por las especies australes A. lanosa y A. sanborni y que difiere de éstas en promedio 5.7 % y 5.2 %, respectivamente. Resultados basados en el locus nuclear beta fibrinógeno son menos conclusivos en relación a la posición filogenética de la nueva especie, aunque también muestran su distinción. Considerando que la ecorregión Valdiviana está sufriendo un impacto antrópico substancial, finalizamos el trabajo comentando sobre la relevancia de nuestro hallazgo para la biología de la conservación.

Key words: Abrothrix sanborni, Abrotrichini, Argentina, Chile, Cricetidae, Muroidea, taxonomy, temperate rainforest, Valdivian forest

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The Valdivian forests of southern Chile and nearby Argentina harbor a diverse mammal assemblage that is distinctive for its large proportion of endemics, as well as its phylogenetic diversity (e.g., the single living microbiothere, *Dromiciops gliroides*; one of the 7 living paucituberculates, *Rhyncholestes raphanurus*; the world's smallest deer, *Pudu puda*; the most endangered canid in the world, *Lycalopex fulvipes*; as well as distinctive sigmodontine rodents, including the monotypic *Irenomys* and several species of the tribe Abrotrichini).

Of the 5 genera in the tribe Abrotrichini, Abrothrix has the largest geographic distribution and is the most diverse, both in terms of morphological variation and species richness (Teta 2013; D'Elía et al. 2015). The taxonomic history of Abrothrix is complex; various forms now referred to as Abrothrix were earlier placed in Akodon, Chelemys, Bolomys, Microxus, and Oxymycterus (see synonymic list in Patterson et al. 2015). Recently, based on morphological evidence and the molecular phylogeographic analysis presented by Palma et al. (2010), Teta and Pardiñas (2014) showed the distinction of A. hirta (Thomas 1895) from Abrothrix longipilis (Waterhouse 1837), the type species of the genus. Both species are regarded as monotypic; the former is now restricted to populations of north-central Chile, whereas the latter includes populations in southern Chile and Argentina (Teta and Pardiñas 2014). In addition, Abud (2011; see also Cañón et al. 2014:448) raised doubts concerning the distinction of A. hershkovitzi (Patterson et al. 1984) from A. olivacea (Waterhouse 1837). Presently 9 species are recognized within the genus Abrothrix (Teta and Pardiñas 2014; Patterson et al. 2015). Analyses of a concatenated matrix of 6 loci recover 2 main clades that are morphologically distinct; the olivacea group includes A. olivacea, A. andina, A. hershkovitzi, A. illutea, and A. jelskii, whereas the longipilis group contains A. longipilis, A. hirta, A. lanosa, and A. sanborni (Cañón et al. 2014; Patterson et al. 2015). However, cladistic analysis of morphological data does not recover the monophyly of the olivacea group; species of Abrothrix fall into 4 main groups, the *longipilis* group, a restricted *olivacea* group (formed by A. olivacea plus A. andina), and the monotypic groups of A. jelskii and A. illutea (Teta 2013).

Abrothrix sanborni was described by Osgood (1943) based on small, dark specimens collected in southernmost Chiloé, a large island in southern Chile (42°S latitude), and the nearby mainland, for which none of the numerous taxa named by Philippi (1990) apply (Osgood 1943:195). Distinguished by its small size and uniformly blackish pelage, A. sanborni is considered endemic to temperate Valdivian forest at lower elevations (Patterson et al. 1989). It has been recorded in Chile at several localities of Los Ríos and Los Lagos regions (Mann 1978; Iriarte 2008), and at a single Argentinean locality in Neuquén province (Pearson 1995). Across its distributional range, A. sanborni is sympatric with the congeners A. olivacea and A. hirta. Distinguishing A. sanborni from A. olivacea, both in the field and on the basis of voucher specimens, is straightforward, given the more brownish pelage of the latter and marked cranial and penile differences (Osgood 1943; Mann 1978; Spotorno 1992). However, the distinction of A. sanborni

and A. hirta (until 2014 considered a synonym of A. longipilis) has been far less clear-cut, and as a result, several authors have considered A. sanborni as a synomym of "A. longipilis" (e.g., Mann 1978; Gallardo et al. 1988; Spotorno et al. 2000). In addition, on purely morphological grounds, there have been reports of putative hybrids between these 2 forms (Pine et al. 1979; Gallardo et al. 1988; Patterson et al. 1989; Pearson 1995). Based on analyses of cytochrome-b gene sequences of specimens collected in northern Chiloé Island and on the adjacent mainland, Palma et al. (2010) suggested that A. sanborni is distinct from A. hirta (as those populations are now understood). However, as shown below, A. sanborni as currently delimited encompasses 2 distinct lineages that each rank as species. Populations from northern Chiloé and the adjacent mainland do not represent A. sanborni but rather an undescribed species that is named and described below.

#### MATERIALS AND METHODS

The specimens studied in this work are deposited in systematic collections (see Appendix I). Specimens recently collected were secured in accordance with Sikes et al. 2011.

Genetic and phylogenetic analyses.—Genetic comparisons and phylogenetic analyses were based on DNA sequences of 2 loci, the mitochondrial cytochrome-b gene (hereafter Cytb; the first 801 base pairs [bp]) and the nuclear beta-fibrinogen, intron 7 (hereafter Fgb-I7; 621 bp). Analyses based on Cytb included 85 sequences gathered from specimens of 8 of the 9 species of Abrothrix currently considered valid (Teta and Pardiñas 2014; Patterson et al. 2015; but see Cañón et al. 2014 about the distinction between A. hershkovitzi, which our sampling lacks, and A. olivacea). Sampling is both geographically and genealogically extensive for species of the A. longipilis group, particularly for A. hirta, which is sympatric with the new species and has strong phylogeographic structure (Lessa et al. 2010; Palma et al. 2010). Of the Cytb sequences analyzed, 19 belong to a new species described below and were gathered from specimens collected at 3 Chilean localities (Fig. 1; Appendix I). The Cytb sampling includes sequences derived from the dried tissues of museum specimens, including one of the paratypes of A. sanborni (FMNH 22724), and 4 other individuals (A. sanborni: FMNH 127565, FMNH 130197, FMNH 132269; A. n. sp.: FMNH 130713; see Appendix I). In addition, our sample includes a topotype of A. lanosa (MZUC-UCCC32943).

Sample size for the *Fgb*-I7 locus was slightly smaller than for *Cytb*, including 62 sequences from 9 species of *Abrothrix*; 7 sequences belonged to the new species and were gathered from specimens collected at 3 Chilean localities (Fig. 1; Appendix I). *Abrothrix* is sister to the clade of long-clawed rodents (Smith and Patton 1999; Cañón et al. 2014), and sequences from representatives of *Chelemys*, *Geoxus*, *Notiomys*, and *Pearsonomys* were used to form the outgroup. As such, the *Cytb* and *Fgb*-I7 matrices included 89 and 66 sequences, respectively (Appendix I).

Most DNA sequences were generated by us, but a number were also downloaded from GenBank. Fresh tissue sequences of *Cytb* 



**Fig. 1.**—A: map of southern South America depicting, as shadow areas, the known distribution of *Abrothrix lanosa*, *A. sanborni*, and *A. manni* n. sp. B: map of part of southern Chile and southwestern Argentina showing the collection localities of specimens of *A. lanosa* (squares) and *A. manni* n. sp. (circles) studied here. Locality numbers corresponds to those in Appendix I.

were amplified using primers MVZ 05 and MVZ 16 as outlined in Cañón et al. (2010). For dried tissue specimens, a whole toe was removed from the pes, ground using a Qiagen TissueLyser (Qiagen, Germantown, Maryland) and metal bead, and then rehydrated in 70% ethanol for 48h. Samples were then centrifuged, decanted, and the pellet soaked in sodium chloride-tris-EDTA (STE) buffer (5 M NaCl, 1 M Tris-HCl, 0.2 M ethylenediaminetetraacetic acid [EDTA]) for 3-6h. After another round of pelleting, tissue digestion and extraction were performed according to the Qiagen DNeasy protocol, yielding > 70 ng/µL of DNA from each sample. Primers MVZ 45 and MVZ 16 (Smith and Patton 1993) were used to amplify and sequence 413-bp fragments of Cytb from each specimen at the Field Museum of Natural History, as described in Upham et al. (2013). Fgb-I7 sequences generated in this study were obtained using primers FGB\_F and FGB\_R (Wickliffe et al. 2003) with the following protocol: initial denaturation at 94°C per 10min, 33 cycles of denaturation at 94°C per 1 min, annealing at 60°C per 1 min and extension at 72°C per 1 min; followed by a final extension at 72°C during 7 min. Amplicons were sequenced using an external sequencing service (Macrogen, Inc., Seoul, South Korea). DNA sequences were edited using CodonCode (Codon-Code, Dedham, Massachusetts); all new sequences were deposited in GenBank (KP665988-KP666030).

Sequences were aligned in Clustal X (Thompson et al. 1997) using the default parameter values. Observed genetic distances (p) were calculated in MEGA 6 (Tamura et al. 2013). Phylogenetic analyses were based on matrices limited to a single sequence per haplotype or allele (Cytb: 60; Fgb-I7: 30). Phylogenetic relationships were inferred via Bayesian analyses using MrBayes 3.1 (Ronquist and Huelsenbeck 2003). Analysis of each matrix consisted of 2 independent runs, each with 5 heated and 1 cold Markov chains. Substitutions models, HKY+I+G for Cytb and HKY+G for Fgb-I7 were selected using jModelTest (Darriba et al. 2012). All model parameters were estimated in MrBayes. Uniform-interval priors were assumed for all parameters except base composition and substitution model parameters, which assumed a Dirichlet prior. Runs were allowed to proceed for 20 million generations with trees sampled every 1,000 generations per chain. To check for convergence 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 to obtain posterior probability (PP) estimates for each clade.

*Divergence time estimation.*—Dating of the events of diversification was done using the *Cytb* data set analyzed phylogenetically (60 terminals of which 56 correspond to *Abrothrix*) and the Bayesian relaxed-clock model implemented in BEAST 1.8.0 (Drummond et al. 2012). BEAST analyses were run using

the XSEDE online computing cluster on the CIPRES Science Gateway (Miller et al. 2010). The HKY+I+G substitution model was used, including 4 gamma categories and estimated base frequencies, and branch lengths were estimated using independent draws from a lognormal distribution. Clock means were set to a uniform prior with a large upper bound, and a Yule (pure-birth) process was assumed for the tree prior. As in the abrotrichine centered study of Cañón et al. (2014), an undescribed fossil species from the Uquía Formation (San Roque, 4 km south-southwest of Humahuaca, Humahuaca department, Jujuy, Argentina) that is most closely related to the living A. jelskii (Teta 2013) was used to constrain the split of A. illutea and A. jelskii by means of a lognormal distribution with an offset to 2.5 Ma, mean (in real space) of 0.331, SD of 1. This resulted in a minimum age of 2.5 Ma with a soft maximum (upper 95% of prior) at 3.54 Ma. The Markov Chain Monte Carlo (MCMC) was run for 40 million generations and parameters sampled every 10,000 generations, yielding 3,600 trees after a 10% burn-in (final log-likelihood of 5,322.48). After checking for stable posterior distributions for all parameters (estimated sample size [ESS] > 200) in Tracer v1.6 (Rambaut and Drummond 2007), a maximum clade credibility tree was constructed using TreeAnnotator (Drummond et al. 2012). The resulting timetree containing mean divergence times and error bars for each node (95% highest posterior density intervals) was plotted in R using the ape and phyloch packages (Paradis et al. 2004; R Core Team 2013).

Morphological analyses.-Descriptions of anatomical traits followed Reig (1977) for dental features, and Carleton (1980), Carleton and Musser (1989), and Patterson (1992) for external and skull morphology. Morphological analysis and description of stomachs followed Carleton (1973). Standard external measurements (in mm) were recorded from specimen tags or field catalogs: total length (TL), tail length (T), hindfoot length (HF), ear length (E), and weight (W, in g). Nineteen craniodental measurements were obtained with digital calipers and recorded to the nearest 0.01 mm following the definitions provided by Patterson (1992): skull length (SL), condylo-basal length (CIL), basal length (BL), zygomatic breadth (ZB), braincase breadth (BB), palatilar length (PL), incisive foramina length (IL), incisive foramina width (IW), diastema length (DL), maxillary toothrow length (TL), zygomatic plate width (ZW), nasal width (NW), rostrum width (RW), frontal sinus width (FSW), interorbital breadth (IB), mandibular length (ML), condylar length (CL), condylar height (CH), and mandibular ramus depth (RD).

Morphometric analyses were performed on a set of 89 adult specimens (age classes 3–5; see the tooth-wear criteria defined by Patterson 1992) that included representatives of *A. lanosa*, *A. sanborni*, and the new species. Sexual dimorphism in cranial morphometric variables was evaluated in a multivariate analysis of variance on the largest population sample of the new species (La Picada, Chile). Because no significant differences (P >0.05) between males and females were detected, individuals of both sexes were pooled for the remaining morphometric analyses. Multivariate analyses using principal components and canonical variates were used to explore the patterns of phenetic differentiation. All analyses were run on the log-transformed data set of craniodental measurements using the software InfoStat (Di Rienzo et al. 2008).

## RESULTS

Phylogenetic analyses.—The Cytb matrix had 304 variable characters. The resulting tree from MrBayes (Supporting Information S1) resembles that generated using BEAST (Fig. 2). Only a single salient difference between these topologies was found (see below); minor differences pertain to intraspecific relationships among haplotypes. Analyses show a monophyletic Abrothrix (here and afterwards PP values are those gathered with MrBayes and BEAST; PP = 1; PP = 0.9). The A. olivacea species group is recovered as monophyletic, although without support (PP = 0.68; PP = 0.62); within this group, A. illutea and A. jelskii are sister to each other (PP = 0.96; PP = 0.97), and sister to a clade (PP = 1; PP = 1) formed by A. olivacea and A. andina. A. olivacea is not recovered as monophyletic in the tree generated by MrBayes but its monophyly is recovered with BEAST although without support (PP = 0.67); this is the single important difference between topologies. Species of the A. longipilis group fall into 2 clades, which are not sister to each other. One of these clades (PP = 0.98; PP = 1) is composed of A. hirta (PP = 1; PP = 1) and A. longipilis (PP = 1; PP = 1), whereas the other is formed by A. lanosa (PP = 1; PP = 1) and haplotypes recovered from specimens currently assigned to A. sanborni, which in turn do not form a monophyletic group, but fall into 2 allopatric clades that are not sister to each other. One of these clades (PP = 0.88; PP = 0.91) is formed by haplotypes recovered from specimens collected in southern Chiloé Island, including the haplotype recovered from a paratype of A. sanborni. This clade, which represents true A. sanborni, is sister to A. lanosa in a strongly supported relationship (PP = 1; PP = 1). The remaining haplotypes of specimens currently assigned to A. sanborni, collected in northern Chiloé and on the mainland in the Chilean regions of Los Lagos and Los Ríos, form a species-level clade that is marginally (PP = 0.91) and strongly supported (PP = 1) by the MrBayes and BEAST analyses, respectively. The northern Chiloé-mainland clade is sister to the A. sanborni plus A. lanosa clade and differs on average by 5.2% and 5.7% from A. sanborni and A. lanosa, respectively (Supporting Information S2). The observed average divergence between A. sanborni and A. lanosa is 4.6%.

The analyzed *Fgb*-I7 matrix had 71 variable characters. The resulting Bayesian tree (Supporting Information S1) is less resolved than that produced from the *Cytb* matrix. *Abrothrix* is recovered as monophyletic (PP = 1). Sequences of *Abrothrix* fall into 3 well-supported clades. One (PP = 1) is formed by sequences of *A. illutea* and *A. jelskii*, but the latter is not recovered as monophyletic. The 2nd clade (PP = 0.99) is comprised of sequences of *A. andina* and *A. olivacea*, but the latter does not appear to be monophyletic. Finally, the 3rd clade (PP = 1) corresponds to sequences of the *A. longipilis* group. Within this clade, the only species analyzed with more than a single sequence, *A. sanborni* s.s., was recovered as monophyletic (PP



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**Fig. 2.**—Chronogram illustrating the diversification of the genus *Abrothrix* obtained from the Bayesian analysis of a matrix of *Cytb* gene sequences. Ages are represented as mean node height for a maximum clade credibility tree compiled from postburning trees topologies obtained in BEAST. Bars at the nodes represent the 95% highest posterior density credibility interval of the node's age. Dots signal nodes with a posteriori probability of 0.95 or greater. Numbers signaled with arrows correspond to a posteriori probability values found in Bayesian analysis conducted in MrBayes for selected nodes (for further details see Supporting Information S1). Terminal labels are as follow: haplotype number; locality number; number of specimens sharing the given haplotype. Locality numbers are those of Appendix I and Fig. 1. Haplotype numbers are also given in Appendix I next to GenBank accession numbers. Delimitation of geologic epochs follows Gradstein et al. (2012).

= 0.99), but *A. hirta* and the northern Chiloé-mainland form are not. Despite the lack of resolution of the nuclear *Fgb*-I7 gene tree, it is noteworthy that this topology lends additional support to ranking at the species level, the northern Chiloé-mainland lineage; no allele is shared between this form and any other species of *Abrothrix*, including *A. sanborni* (i.e., the southern Chiloé clade).

*Divergence time.*—Molecular clock analysis estimated an age for crown *Abrothrix* of 5.1 Ma (95% HPD: 3.1–7.5). The stem age of the Chiloé-mainland lineage is 1.9 Ma (0.9–3.1)

and the crown age of the group is 0.6 Ma (0.2-1.0). Crown ages for other species of *Abrothrix* and multispecies clades are provided in Table 2.

*Morphometric analyses.*—Principal components I and II accounted for 48.3% and 9.82% of the total variance. Bivariate plots show that specimens from southern Chiloé (including the holotype of *A. sanborni*) and those from northern Chiloé-mainland scarcely overlap in multivariate space (Fig. 3). In turn, *A. lanosa* from the Magellanic region is well separated from the other 2 forms. Specimens referred to *A. sanborni* mostly



**Fig. 3.**—Specimen scores of adult individuals of *Abrothrix* for principal components (PC) 1 and 2, extracted from the variance–covariance matrix (above) and for canonical variates (CV) 1 and 2, extracted from 3-group discriminant function analysis (below).

fall on the negative side of principal component I, whereas northern Chiloé-mainland samples typically have positive values. Variables with higher loadings on principal component I include several affecting the length of the skull (GLS, NL, IL, IW, PL) but also some breadth measurements (e.g., FSW, RW, ZB, ZW). The discriminant function analysis showed complete separation between the 3 forms, *A. lanosa*, *A. sanborni*, and the northern Chiloé-mainland one, with 100% of the specimens correctly classified (Wilks' Lambda: 0.0212634; *F* = 15.37; *P* < 0.000001).

#### **DISCUSSION**

A broad phylogenetic analysis of the genus *Abrothrix* permitted identification of an unnamed lineage that is restricted to the Valdivian forest (Fig. 2); this lineage was marginally supported in the Bayesian analysis conducted in MrBayes, whereas it was strongly supported in those performed in BEAST. Importantly, morphological comparisons of members of this lineage with those of the remaining species of *Abrothrix* (Figs. 3 and 4) support its distinction, allowing us to hypothesize that the newly uncovered Valdivian lineage represents a biological species, which is described as follows.

> Sigmodontinae Wagner, 1843 Abrotrichini D'Elía et al., 2007 *Abrothrix* Waterhouse, 1837 *Abrothrix manni*, new species Mann's soft-haired mouse (Figs. 4–6; Supporting Information S3)

Akodon (Abrothrix) sanborni: Osgood, 1943:194, part. Akodon longipilis sanborni: Mann, 1978:157, part. Abrothrix sanborni: Tamayo et al., 1987:5, part. A[kodon]. longipilis x sanborni hybrids?: Patterson et al., 1989.

Abrothrix sanborni: Pearson, 1995:108, part. Abrothrix sanborni: Palma et al., 2010:1105. Abrothrix sanborni: Cañón et al., 2014:445, part. Abrothrix sanborni: Patterson et al., 2015, part. Abrothrix sp.: Teta, 2013:13.

*Holotype.*—UACH 7283, collected by Guillermo D'Elía on 8 April 2008 (original number GD 1190), preserved as skull, body in fluid, and tissue sample in alcohol.

*Type locality.*—Chile, Región de Los Lagos, Lago Tagua Tagua, Rampa Los Canelos (41°38.858′S, 72°10.333′W).

Diagnosis.—A member of the genus Abrothrix characterized by a unique combination of characters including: dorsal coloration uniformly blackish brown to olive brown with a chestnut tinge on the midline in some individuals; venter dark grayish brown to grayish; skull delicate, with the interorbital constriction hourglass-shaped and the braincase well rounded; rostrum narrow and long; nasals and premaxillae well projected anterior to the incisors; naso-frontal suture strongly acuminate, surpassing posteriorly the plane defined by the posterior point of lacrimals; zygomatic plate slender with the anterior margin straight and vertical to slightly inclined backward; palate ending slightly posterior to the plane defined by the posterior margins of the M3; roof of the mesopterygoid fossa with "slit"-like palatine vacuities; molars mesodont; M1 without anteromedian flexus in adult individuals; parastyle and mesoloph present, the latter usually fused to the paracone; stomach unilocular-hemiglandular; terminal crater of the phallus ventrally directed; cartilaginous apical elements absent.

*Description.*—The new species is characterized by its nearly uniform dark coloration and a moderately short tail (~70% of head and body length). The dorsal pelage is soft, woolly, and dense; it is composed of almost entirely dark gray hairs with cinnamon to buffy tips, the cinnamon tint more obvious at the midline and giving a general dark brownish to blackish appearance. Dorsal hairs are 13–17 mm long and longest in the midrump region; guard hairs are slightly longer, projecting 2–4 mm beyond the fur on the rump. The rhinarium and the lips



Fig. 4.—Dorsal, lateral, and ventral view of the skulls and labial view of the mandibles of *A. manni* n. sp. (UACH 7283, holotype, above), *A. sanborni* (UACH 7277, middle), and *Abrothrix lanosa* (CNP 1395, below). Scale = 5 mm.

are covered by short, thin ochraceous hairs. Mystacial vibrissae are abundant, dark, and moderately long, reaching the base of the ear when pressed alongside the head. Interamal and submental vibrissae are short and white. Ears are short, rounded, and dark brown in coloration, with the margin of the inner surface covered with short fine blackish hairs. Flanks are similar to the dorsum but slightly grayer. Ventrally the color is ashy gray, each individual hair being dark gray at the base and paler at the tip. Fore- and hindfoot are dorsally covered by short ochraceous hairs. Ungual tufts are pale brown, shorter than claws in the forefeet and larger than claws on the hindfeet. There are 6 plantar pads, including a nearly oval and large thenar pad, a rounded hypothenar pad, and 4 rounded to nearly ovoid interdigital pads. The tail is uniformly blackish.

The skull (Figs. 4–6) is delicate, with a long rostrum, inflated frontal sinuses, and a rounded braincase. The nasals and premaxillae are moderately extended beyond the anterior plane of the incisors, forming a conspicuous rostral tube or "trumpet." The nasals are posteriorly divergent and broad, in dorsal view almost covering the rostrum over a third of their length. The naso-frontal suture is markedly acute, "V"-shaped, and extends posteriorly behind the plane of the lacrimals. The interorbital region is smoothly rounded, with well-developed frontal sinuses. The coronal suture is wide and semicircular.



**Fig. 5.**—Selected cranial details of *Abrothrix manni* n. sp. (based on the holotype, UACH 7283): A) nasals (n), with their posterior margin forming a sharp angle; zygomatic notches (zn) slightly excavated; B) infraorbital foramen (iof), with its lumen narrow and compressed at its base, nearly piriform in shape; C, E) nasals and premaxillae (px) projecting well in front of the upper incisors (i) as a tube; scar for the origin of the superficial masseteric muscle (mt) indicated as a osseous prominence, rounded and elevated; D) tympanic bulla (tb) not inflated, Eustachian tube (et) distinct; E) incisive foramina long, parenthesis shaped, with a constriction between the middle and the posterior third; maxillary septum short, subequal to half of the length of incisive foramina (if); F) palate, mesopterygoid (fm), and parapterygoid fossae (pp); G) orbital region, with an indication of the relative position of the ethmoid foramen (ef); H) posterior portion of the skull in lateral view; I) interorbital region, hour-glass shaped, with the frontal sinus (fs) well inflated; J) interparietal (ip) reduced. f = frontal; lf = lacerate foramen; lp = lateral projection of the parietal; pf = postglenoid foramen; p = parietal; pt = petrosal; se = subsquamosal fenestra; zp = zygomatic plate. Figures not to scale.



**Fig. 6.**—Development of the sphenopalatine vacuities (sv) in *Abrothrix manni* n. sp. (UACH 7283 [holotype], and UACH 7282): present, but reduced to narrow slits mostly along the presphenoid (ps) and in *A. sanborni* (UACH 7277): present as large apertures along the presphenoid, reaching basisphenoid (bs). fm = mesopterygoid fossa; pp = paraptergoid fossa.

The interparietal is small. The occipital region is well inflated and without ridges. The zygomatic plate is narrow and medium in height, with its anterior border nearly vertical to slightly inclined backwards; a visible masseteric scar is present at its base. The zygomatic notches are moderate in size. The infraorbital foramen has a narrow lumen, compressed at its base,

and nearly piriform in shape. The subsquamosal fenestra and the postglenoid foramen are subequal in size and crossed by a broad hamular process of the squamosal. The cranial foramina associated with the cephalic arterial pattern and other osteological traits of the squamosal-alisphenoid region include a large foramen ovale, a 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. The alisphenoid strut is absent. All these traits plus a large stapedial foramen indicate that the cephalic blood supply in A. manni is similar to the presumably primitive muroid pattern (cf. Carleton 1980). The incisive foramina are long, reaching the anterolingual conules of the 1st upper molars. The palate is broad, ending slightly posterior to the plane defined by the posterior margins of the M3. The mesopterygoid fossa is broader than the parapterygoid fossae and its roof is open to usually reduced, "slit"-like, sphenopalatine vacuities. The auditory bullae are medium sized and not inflated; the mastoid has a relatively large, rounded fenestra in its posterodorsal corner.

The mandible is proportionally long, low, and slender, with a moderately deep diastema; the upper and lower masseteric crests are slightly marked, the latter extending forward to the middle of m1; the incisor capsule, which lies at the level of the coronoid process, is smooth and indistinct; the coronoid process is relatively short, and the condyloid process is low and elongate, slightly projected backward.

The upper incisors are opisthodont, with front enamel orange; molars (Supporting Information S3) are moderately hypsodont, with terraced occlusal surfaces; the procingulum of M1/m1 has a "fan"-shaped contour in occlusal view; the anteromedian flexus/id is moderately developed; the anteroloph and parastyle are well developed in both M1 and M2; the paracone and metacone of M1 and M2 are oriented forward; the mesoflexus is usually absorbed by the fusion of para- and mesoloph and sometimes persisting as an enamel island; the M3 is subcircular, with a central enamel ring and a much reduced hypoflexus; the m1 has a conspicuous protostylid; the metaconid and entoconid of m1 and m2 are oriented backward; a mesolophid on m1 and m2 is well expressed; both m1 and m2 have well-defined ectostylids and ectolophids; the m3 has a sigmoid aspect (Supporting Information S3).

*Comparisons.—Abrothrix sanborni* resembles *A. manni* in external and cranial appearance; minor differences between the species include (in *A. sanborni*) darker coloration, with dark gray hairs with blackish to brownish tips; less contrasting gray tones in the individual hairs of the venter; rhinarium and lips covered by short, thin blackish hairs; and fore- and hindfoot dorsally covered by short brown hairs. *A. sanborni* is also slightly smaller in most cranial dimensions than the new species and usually has much larger and more irregular palatine vacuities (Table 1; Figs. 4 and 6). Remarkably, in the original description of *A. sanborni*, Osgood (1943:195) noted that mainland specimens, which are here assigned to *A. manni*, were larger than the typical form and would probably deserve "separation" if larger series were available.

Abrothrix lanosa has reduced eyes and ears that are barely visible through its dense and woolly pelage, a reduced countershading between the dorsum and venter, and the dorsal surface of manus and pes covered by short, thin white-to-cream hairs; its skull has smaller lacrimals, a less acutely shaped nasofrontal suture, nasals less expanded anteriorly, gnathic process less developed, larger palatine vacuities, and orthodont, pale-yellow upper incisors. The mandible of *A. lanosa* is morphologically distinctive from the mandibles of *A. manni* and *A. sanborni*, being characterized by its slender constitution, a marked constriction of the horizontal ramus below m3, and a deeply excavated angular notch (Fig. 4; see also Feijoo et al. 2010). *Cytb* haplotypes of *A. manni* and *A. lanosa* by 5.7%.

Sympatric *A. hirta* is larger in most external and cranial dimensions and has distinct countershading, with a sharp contrast between the darker dorsum (usually reddish on the midline) and paler venter; the dorsal surface of the manus and the pes is covered by short, thin white-to-cream hairs. Cranially, the new species most resembles *A. hirta*, although the latter has larger lacrimals, larger interparietal, broader zygomatic plate, less developed masseteric scars, and large sphenopalatine vacuities. *A. manni* and *A. hirta* differ on average by 10.9% in *Cytb* sequences.

Sympatric *A. olivacea* is externally smaller, with a dark brown to olive brown dorsal coloration and grayish venter, and have a blunter, more rounded muzzle (Osgood 1943). Its skull is small (condylo-incisive length < 27 mm) and delicate, with a much shorter rostrum, more bowed dorsal profile, and moderately extended nasals and premaxillae that are not trumpet shaped; its baculum is small and rod like, with three distinct but reduced apical digits. The *Cytb* haplotypes of the new species and *A. olivacea* differ on average by 12%.

*Measurements of the holotype.*—External measurements (in mm): TL, 190; T, 83; HF (with claw), 25; E, 14; W, 28 g. Cranial measurements (in mm): SL, 27.6; CIL, 26.2; BL, 22.5; ZB, 12.9; BB, 11.9; PL, 10.9; IL, 6.3; IW, 2.0; DL, 6.9; TL, 4.3; ZW, 1.8; NW, 3.7; RW, 4.7; FSW, 6.8; IB, 5.0; ML, 13.7; CL, 6.2; CH, 6.0; RD, 2.5.

*Paratypes.*—Two specimens collected at Chile, Los Lagos, Pichiquillaipe, Parque Katalapi (41°31.179′S, 72°45.131′W; 41°31.278′S, 72°45.231′W): UACH 7260 (GD 1138), an adult female; UACH 7282 (GD 1144), an adult female.

*Distribution.*—Known from a small geographic area  $(39^{\circ} \text{ to } 43^{\circ}\text{S})$  in the south-central regions of Los Lagos, both on the mainland and the northern part of Chiloé Island, and Los Ríos (both in Chile), as well as from a single locality in nearby Neuquén, Argentina (Fig. 1).

*Etymology.*—Dedicated to the memory of the prominent Chilean zoologist Guillermo Mann (1919–1967), considered by his peers as one of the most important zoologists of Chile in his day (Donoso-Barros 1974; Jaksic et al. 2012; see also Etcheverry 1990). Mann authored numerous key contributions on the Chilean fauna; in particular, his book "Los Pequeños Mamíferos de Chile," posthumously published in 1978,

Abrothrix lanosa Abrothrix manni n. sp. Abrothrix sanborni  $\overline{X}$ SD  $\overline{X}$  $\overline{X}$ п Min Max. n SD Min. Max. п SD Min Max. 5 26.17 0.54 25.22 25.22 27.48 29.02 Skull length 26.47 61 28.12 0.87 30.16 24 0.79 26.1 Condylo-basal length 5 24.82 23.47 25.48 26.66 0.95 23.47 28.67 24 25.76 0.81 24.3 27.29 0.8 61 Basal length 5 22.02 0.73 20.7722.62 61 23.44 0.81 20.77 25.66 24 22.06 0.68 20.57 23.63 5 12.02 12.31 12.95 0.47 13.94 24 12.48 0.44 11.2 12.99 Zygomatic breadth 0.26 11.68 61 11.68 5 11 47 11.28 12 19 0.36 11.28 12.82 24 12.07 0.23 12 41 Braincase breadth 0.14 11.66 61 11.64 Palatal length 5 10.4 0.31 9.85 10.6 11.05 0.36 9.85 11.79 24 10.63 0.39 9.78 11.38 61 Incisive foramina length 5 5.9 0.23 5.5 6.1 61 6.43 0.27 5.5 6.99 24 6.36 0.29 5.82 7.18 5 2.13 0.12 1.97 2.28 1.92 0.18 1.64 2.5 24 2.03 0.21 2.38 Incisive foramina width 61 1.68 Diastema length 5 6.72 0.33 6.16 6.94 61 7.13 0.29 6.16 7.62 24 6.86 0.31 6.2 7.5 3.48 Maxillary toothrow length 5 3.54 0.06 3.65 61 4.17 0.24 3.48 4.67 24 4.020.14 3.78 4.29 5 2.2 24 Zygomatic plate width 1.55 0 14 1 31 1 65 61 1 79 0.16 1 31 1 74 0.13 1.5 1 98 Nasal width 5 2.93 0.13 2.77 3.08 61 3.52 0.28 2.77 3.95 24 3.44 0.25 2.93 3.84 5 24 Rostrum width 4.73 0.16 4.5 4.92 61 4.73 0.25 4.3 5.56 4.45 0.26 3.96 5.06 Rostral sinus width 5 6.05 0.15 5.82 6.23 61 6.51 0.28 5.82 7.14 24 6.3 0.27 5.94 6.99 Interorbital width 5 4.64 0.08 4.5 4.72 61 5.1 0.23 4.5 5.92 24 4.99 0.12 4.8 5.27 5 24 14.76 Mandibular length 13.18 0.32 12.62 13.39 61 14.20.6412.62 16.79 13.65 0.73 12 Condylar length 6.73 5 6 27 5 23 045 23 7 35 24 6.35 0.38 54 0.6 61 6 6 4 6.83 Condylar height 5 4.58 0.27 4.15 4.8 61 6.03 0.51 4.15 6.95 24 5.55 0.28 4.9 6.05 5 2.48 2.74 2.32 Ramus depth 0.11 2.31 2.57 61 0.17 2.31 3.1 24 2.57 0.12 2.84

Table 1.—Summary statistics (mean, SD, range) of cranial measurements (in mm) of adult samples (n) of Abrothrix lanosa, A. manni n. sp., and A. sanborni.

remains fundamental reading for those interested in Chilean small mammals.

Nomenclatural statement.—A life science identifier (LSID) number was obtained for the new species Abrothrix manni: urn:lsid:zoobank.org:act:B88DB8C9-AA69-4ECA-BB4F -9EC7B21D552E

*Natural history.*—Much of the available data about the life history of Mann's soft-haired mouse has been reported in the literature under *A. sanborni* or of purported hybrids between that species and *A. hirta* (referred as *A. longipilis*). *A. manni* is active both day and night (Meserve et al. 1982). Its diet includes high proportions of fungi, moderate amounts of mature arthropods and larvae, plant foliage, seeds, and fruits (Meserve et al. 1988). *A. manni* breeds through the spring and summer (Meserve et al. 1982). Most of the captures of this species occurs at sites with dense canopy cover, tall trees, sparse shrubbery cover, deep litter, high ground cover of bryophytes and bamboo, and gentle slopes (Patterson et al. 1990). These attributes characterize rainforests at lower elevations (< 820 m) where this mouse is taken most frequently (Patterson et al. 1989).

*Genetic variation.*—The *Cytb* sample of *A. manni* consists of 19 sequences that present 24 variable sites defining 8 haplotypes; on average the *Cytb* whole sample diverge by 0.5%. None of the 8 haplotypes is found at more than 1 recording locality.

*Conservation.*—The discovery of *A. manni* further underscores the distinctiveness of the biota of the Valdivian ecoregion and its biodiversity importance. The Valdivian ecoregion—a biogeographic island separated from climatically similar areas by deserts and extensive ocean barriers—has been largely degraded by humans through intensive logging to raise livestock, extract wood for fuel and construction, and convert native forests to timber plantations (Armesto et al. 1998, 2010; Smith-Ramirez 2004). Insofar as known, Mann's soft-haired mouse is protected

at Parque Nacional Vicente Peres Rosales and in 3 privately owned areas: Senda Darwin (locality 52 in Fig. 1) on northern Chiloé Island, the small (18 ha) Parque Katalapi (locality 48) on the nearby mainland, and Fundo San Martin (locality 42) at the northern limit of its distribution. In addition, A. manni probably inhabits other private and public protected areas found across its rather small distribution. According to the IUCN, A. sanborni (sensu lato, including A. manni) is Near Threatened (Patterson and D'Elía 2008). As such, given that A. manni occupies a fraction of the range originally considered for A. sanborni by Patterson and D'Elía (2008) and extensive habitat fragmentation within that range, this species may qualify as threatened under criterion B1 (B1ab[ii,iii]). In addition, we consider that A. sanborni as now delimited should be regarded as Vulnerable (VU B2ab[ii,iii]), given that is known from fewer than 10 localities, and it occupies a small area that is under intense human impact (even if some of it is nominally protected in the privately owned Parque Tantauco Park).

*Biogeography.*—The mean estimates for stem and crown ages for the species of *Abrothrix* are older to those obtained in previous studies (Cañon et al. 2014; see also Parada et al. 2013). However, our confidence intervals overlap (e.g., *Abrothrix*: 3.1–7.5 Ma in this study versus 1.03–4.69 Ma in Cañon et al. 2014) and, as such, differences are not significant. Notwithstanding, it is of interest to understand the cause of the differences (e.g., taxonomic coverage, genealogical diversity) and should be taken into account at the moment to evaluate scenarios of abrotrichine historical biogeography. In this regard, it is of interest that our estimates for species splits and species differentiation (Fig. 2; Table 2) are, in agreement with the estimates of Lessa et al. (2010), much older than the Last Glacial Maximum (LGM), questioning the relevance of the last glaciation for the diversification of austral small mammals.

Regarding the known distribution of *A. manni* and *A. san*borni, they appear to be allopatric, including on Chiloé Island.

**Table 2.**—Divergence age estimates for the main clades of the genus *Abrothrix* based on a matrix of *Cytb* gene sequences. Ages (Ma) are mean node heights from highest posterior density (HPD) and intervals at 95% (upper–lower).

Clade	Mean (Ma)	95% HPD (Ma)
A. manni n. sp.	0.55	0.18-1.04
A. lanosa	0.16	0.04-0.34
A. sanborni	0.87	0.38-1.58
A. lanosa–A. sanborni	1.28	0.7-2.07
A. manni n. sp.–A. lanosa–A. sanborni	1.89	0.92-3.08
A. olivacea	1.38	0.71-2.26
A. olivacea–A. andina	1.61	0.83-2.55
A. illutea–A. jelskii	2.74	2.51-3.20
A. olivacea species group	3.93	2.53-5.50
A. manni n. sp.–A. lanosa–A. sanborni–	4.24	2.53-5.98
A. olivacea species group		
A. hirta	1.63	0.85-2.66
A. longipilis	0.29	0.07-056
A. hirta–A. longipilis	3.62	2.00-5.77
Abrothrix	5.12	3.11-7.55

A. sanborni is distributed on the southern half of the island, which was covered by an icesheet during the LGM (Heusser 2003). In this regard, the record of A. sanborni on the mainland at Puerto Ibañez, Aysen, Chilean Patagonia (specimen FMNH 130197; locality 75) is important biogeographically; interestingly this specimen shares its Cytb haplotype with specimens FMNH 127565 and UACH 7273 from Chiloé (localities 71, 72). Future studies should clarify how A. sanborni, whose observed genealogical variation has an age of 0.8 Ma (0.4-1.6), reached Chiloé if, as it appears, it did not survive the LGM there. Even its current range in Aysen was also covered by ice (Heusser 2003), so the species range during the LGM remains unknown. Mann's soft-haired mouse occupies the northern part of Chiloé Island, which was free of ice during the LGM and connected to the mainland given that the shallow Chacao Chanel was free of water during the LGM. The observed genealogical variation is much older, as estimated by means of molecular clock (Table 2), than the LGM. Additional sampling of both A. manni and A. sanborni is needed to better document current distributional ranges of both species and to assess the presumably contrasting effect of the ice ages, in particular the LGM, on the range and recent demography of these species.

Systematic considerations.—The genus Abrothrix is the most diverse of the tribe Abrotrichini. Recently, in a broad phylogenetic study of the tribe, Cañón et al. (2014) found that in the concatenated analysis of 6 loci, including the 2 analyzed here, species of Abrothrix fall into 2 well-supported clades that match overall morphological variation and geographic distribution. The olivacea group, composed by A. andina, A. illutea, A. jelskii, and A. olivacea, was recovered with moderate to high support by the solo analysis of 5 loci (all but the Cytb locus; and not the Bayesian analysis of the Fgb-I7 locus). The longipilis group contains the species A. lanosa, A. longipilis, and A. sanborni and was recovered by the analysis of only 3 loci (the Cytb locus did not recover it; the Fgb-I7 locus did recover it but with significant support only in the Bayesian analyses). Therefore, topologies where the longipilis group is not recovered as monophyletic, but its species fall into 2 groups (*A. lanosa*, *A. sanborni*, and *A. manni* on one hand and *A. hirta* and *A. longipilis* on the other; Fig. 2) that are not sister to each other, are not unexpected (see also Teta 2013 who in a morphological-based phylogenetic analysis did not recover a monophyletic *olivacea* group). This result should be considered if *Abrothrix* as currently delimited is split into 2 or more genera (see the corresponding discussion in Cañon et al. 2014:449 and also in Teta et al. 2011 and Patterson et al. 2015).

*Final remarks.*—The description of a new mammal species from Chile is not unexpected given the recent description of *Eligmodontia dunaris* by Spotorno et al. (2013) and the fact that other groups (e.g., *Aconaemys, Octodon*) await integrative revisions. Even in countries with supposedly well-characterized mammalian assemblages, additional basic collection-based research and fieldwork are needed. Given its fundamental importance, this message should be made clear to ecologists and physiologists interested in Chilean vertebrates, as well as to governmental authorities that finance Chilean science and evaluate applications for collection permits.

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## SUPPORTING INFORMATION

The Supporting Information documents are linked to this manuscript and are available at Journal of Mammalogy online (jmammal.oxfordjournals.org). The materials consist of data provided by the author that are published to benefit the reader. The posted materials are not copyedited. The contents of all supporting data are the sole responsibility of the authors. Questions or messages regarding errors should be addressed to the author.

**Supporting Information S1.**—Topologies of the Bayesian analyses of *Cytb* and *Fgb*-I7 gene sequences of the genus *Abrothrix*. **Supporting Information S2.**—Observed genetic distance of the *Cytb* gene within and between pairs of species of *Abrothrix*. **Supporting Information S3.**—Molars of *Abrothrix manni* n. sp.

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### **Appendix I**

List of studied specimens and their collection localities. Specimens only assessed morphologically are denoted with an "m"; specimens only included in the genetic-based analyses are indicated with a "g." An asterisk (\*) is used to denote specimens whose DNA sequences were obtained from dried tissues. GenBank accession numbers are given following specimen numbers, 1st those corresponding to the *Cytb* gene and 2nd those of the Fgb-I7 gene. When only one accession number is given, it corresponds to *Cytb* sequences; in cases where only the Fgb-I7 was analyzed for a given specimen, the accession number is provided following a "-,". Numbers following accession numbers correspond to haplotype numbers as labeled in Fig. 2 and Supporting Information S1). Locality numbers are used in Fig. 2 and those of A. manni n. sp. and A. sanborni are also used in Fig. 2. Acronyms correspond to the following collections: Colección de Mamíferos del Centro Nacional Patagónico, Puerto Madryn, Argentina (CNP); Field Museum of Natural History, Chicago, Illinois (FMNH); Museo de Historia Natural de la Universidad Nacional de San Agustín de Arequipa, Arequipa, Peru (MUSA; sequence downloaded from GenBank); Museum of Vertebrate Zoology, University of California, Berkeley, California (MVZ); Museo de Zoología de la Universidad de Concepción, Concepción, Chile (MZUC-UCCC); Museum of Southwestern Biology, University of New Mexico, Albuquerque, New Mexico (NK; sequences downloaded from GenBank); Colección de Flora y Fauna Profesor Patricio Sánchez Reyes, Pontificia Universidad

Católica de Chile, Santiago, Chile (SSUCMA; sequence downloaded from GenBank); Colección de Mamíferos de la Universidad Austral, Valdivia, Chile (UACH); Burke Museum of Natural History and Culture, University of Washington, Seattle, Washington (UWBM). ER corresponds to the field catalog of Enrique Rodríguez (see Palma et al. 2010:1103; these sequences were downloaded from GenBank); JPJ corresponds to the field catalog of Pablo Jayat.

Abrothrix and ina (n = 2): CHILE: 1) Metropolitana, Farellones, 7.4 km E on road to Valle Nevado (UWBM 49048<sup>s</sup>: -, KJ614592, 23). PERU: 2) Arequipa, 2 km W Sumbay (MVZ 174066<sup>s</sup>: AF108671; 26).

Abrothrix hirta (n = 80): ARGENTINA: Neuquén, 3) Laguna Varvarco (CNP 2831: KJ614628, 41, KJ614601, 11). Río Negro, 4) Subida del Naciente (CNP 514: EU683434; 52). Chubut, 5) 1 km E Lago Blanco (CNP 1286<sup>m</sup>, 1365<sup>m</sup>), 6) Laguna Larga (CNP 1124: HM167785; 34), 7) Sierra de Tepuel, Cañadón de La Madera (CNP 2690<sup>m</sup>, 2802<sup>m</sup>, 2835<sup>m</sup>, 2860<sup>m</sup>, 2862<sup>m</sup>), 8) Extremo W-SW Lago Blanco (CNP 374<sup>m</sup>, 378<sup>m</sup>, 502<sup>m</sup>, 1208<sup>m</sup>, 1257<sup>m</sup>). Santa Cruz, 9) Estancia Cerro Ventana (CNP 2789<sup>m</sup>), 10) Estancia La Ensenada (CNP 1769<sup>m</sup>, 2698<sup>m</sup>, 2712<sup>m</sup>, 2720<sup>m</sup>, 2728<sup>m</sup>, 2736<sup>m</sup>, 2822<sup>m</sup>, 2823<sup>m</sup>, 2825<sup>m</sup>), 11) extremo E Lago Burmeister (CNP 2762<sup>m</sup>), 12) Río Ecker, 500 m aguas abajo casco Estancia Casa de Piedra (CNP 2691<sup>m</sup>). CHILE: Maule, 13) Lircay (UACH 7259: KP666019, 38, KJ614600, 14; UACH7309<sup>g</sup>: KP666021, 37). BioBio, 14) Shangrila (UACH7308g: KP666020, 42), 15) Tomé (NK 120084<sup>g</sup>: GU564031, 43, GU564095, 16), 16) Quilleco (NK 120140g: GU564022, 40; NK 120141g: GU564023, 40; NK 120147<sup>g</sup>: GU564026, 36; NK 120149<sup>g</sup>: GU564027, 36). Araucania, 17) Malalcahuello (UACH 7258: -, KJ614599, 15), 18) Gorbea (NK 120125<sup>g</sup>: GU564033, 50, GU564096, 16; NK 120129<sup>g</sup>: GU564035, 51, GU564097, 16). Los Ríos, 19) Fundo San Martín (UACH7310<sup>g</sup>: KP666022, 49; UACH7311<sup>g</sup>: KP666023, 46; UACH7312<sup>g</sup>: KP666024, 46; UACH7313<sup>g</sup>: KP666025, 46), 20) La Chabelita (UACH7314<sup>g</sup>: KP666026, 44; UACH7315<sup>g</sup>: KP666027, 48; UACH7316<sup>g</sup>: KP666028, 48; UACH7317<sup>g</sup>: KP666029, 45; UACH7318<sup>g</sup>: KP666030, 47). Los Lagos, 21) Osorno, Puyehue, Pampa Frutilla (UACH 3731<sup>m</sup>, 3732<sup>m</sup>, 3734<sup>m</sup>), 22) Valle La Picada (UACH 1858<sup>m</sup>, 1876<sup>m</sup>, 1877<sup>m</sup>, 1878<sup>m</sup>, 1879<sup>m</sup>, 1880<sup>m</sup>, 1881<sup>m</sup>, 1882<sup>m</sup>, 4078<sup>m</sup>, 4079<sup>m</sup>, 4081<sup>m</sup>, 4082<sup>m</sup>, 4084<sup>m</sup>, 4085<sup>m</sup>, 4086<sup>m</sup>, 4089<sup>m</sup>, 4092<sup>m</sup>, 4093<sup>m</sup>, ER 82<sup>g</sup>: GU564042, 39, GU564098, 17; ER 84<sup>g</sup>: GU564044, 39, GU564099, 17; ER 85<sup>g</sup>: GU564045, 39, GU564100, 17). Aysen, 23) Cerro Castillo (NK 160644<sup>g</sup>: GU564070, 32, GU564101, 12; NK 160648<sup>g</sup>: GU564073, 33, GU564102, 12; NK 160649g: GU564074, 33, GU564103, 12), 24) Puerto Bertrand (UACH7257<sup>g</sup>: HM167789, 29; KJ614598, 10). Magallanes, 25) Torres del Paine (NK 105738g: GU564077, 31, GU564098, 12; NK 105760g: -, GU564107, 13), 26) Fuerte Bulnes (NK 142556g: GU564063, 30, GU564098, 13; NK 142557<sup>g</sup>: GU564064, 30, GU564105, 13), 27) Tierra del Fuego, Porvenir (NK 160181<sup>g</sup>: GU564079, 35, GU564098, 13).

*Abrothrix illutea* (n = 3): ARGENTINA: Tucumán, 28) approx. 10 km S of Hualinchay (CNP 1489: HQ189528,

27), 29) Trancas (JPJ 1411<sup>g</sup>: -, KJ614593, 24), 30) Monteros (JPJ 1479<sup>g</sup>: -, KJ614594, 24).

Abrothrix jelskii (n = 3): PERU: Puno, 31) Carabaya, Hacienda Aricoma (MUSA 2727<sup>g</sup>: -, GU564113, 25), 32) 6.5 km SW Ollachea (MVZ 173073<sup>g</sup>: M35714, 28; MVZ 173076<sup>g</sup>: -, KJ614595, 26).

*Abrothrix lanosa* (n = 13): ARGENTINA: Tierra del Fuego, 33) Bahía Zaratiegui (CNP 1374<sup>m</sup>, CNP 1384<sup>m</sup>); 34) Bahía Ensenada (CNP 1376: KP666018, 18; CNP 1385<sup>m</sup>); 35) Laguna Verde (CNP 1377: KP666017, 17; CNP 1380<sup>m</sup>, CNP 1383<sup>m</sup>); 36) Ushuaia, CADIC (CNP 1394<sup>m</sup>, CNP 1396: -, KJ614596, 19; CNP 1398<sup>m</sup>, CNP 1399: KP666016, 20, KJ614597, 19). CHILE: Magallanes, 37) Madre de Dios Island, Egg Chanel (MZUC-UCCC 32943: KP666015, 19), 38) Porvenir (NK 160196<sup>g</sup>: HM004435, 20).

*Abrothrix longipilis* (n = 34): CHILE: Coquimbo, 39) La Serena (NK 106120<sup>g</sup>: -, GU564087, 18; NK 106122<sup>g</sup>: GU564006, 54, GU564085, 18; NK 106134<sup>g</sup>: GU564007, 54, GU564086, 18), 40) Comuna de Elqui, Fundo El Salitre (UACH 2667<sup>m</sup>, 2669<sup>m</sup>), 41) Parque Nacional Fray Jorge (UACH 1159<sup>m</sup>, 1161<sup>m</sup>, 1163<sup>m</sup>, 1166<sup>m</sup>, 1168<sup>m</sup>, 1170<sup>m</sup>, 1172<sup>m</sup>, 1174<sup>m</sup>, 1176<sup>m</sup>, 2474<sup>m</sup>, 2676<sup>m</sup>, 2678<sup>m</sup>, 2680<sup>m</sup>, 1163<sup>m</sup>, 1168<sup>m</sup>, 1171<sup>m</sup>, 1172<sup>m</sup>, 1175<sup>m</sup>, 1176<sup>m</sup>, NK105517<sup>g</sup>: GU564008, 53, GU564088, 18), 42) Quebrada de Las Vacas (UACH 2671<sup>m</sup>, 2670<sup>m</sup>, 2672<sup>m</sup>). Valparaíso, 43) Parque Nacional La Campana (UACH 5618<sup>m</sup>, 5619<sup>m</sup>, 5620<sup>m</sup>), 44) Santo Domingo (NK 106009<sup>g</sup>: GU564017, 55, GU564090, 18; NK 106013<sup>g</sup>: GU564018, 56, GU564089, 18; NK 106015<sup>g</sup>: GU564019, 56). Metropolitana, 45) San Carlos de Apoquindo (NK 106006<sup>g</sup>: GU564015, 56).

Abrothrix manni n. sp. (n = 69): ARGENTINA: 46) Neuquén, NW shore Lago Quillén (MVZ 163374<sup>m</sup>). CHILE: Los Ríos, 19) Fundo San Martín (UACH 3109<sup>m</sup>, 3110<sup>m</sup>). Los Lagos, 47) Puyehue (UACH 5607<sup>m</sup>), 22) Parque Nacional Pérez Rosales, La Picada (UACH 253<sup>m</sup>, 263<sup>m</sup>, 265<sup>m</sup>, 267<sup>m</sup>, 268<sup>m</sup>, 274<sup>m</sup>, 275<sup>m</sup>, 277<sup>m</sup>, 278<sup>m</sup>, 279<sup>m</sup>, 283<sup>m</sup>, 284<sup>m</sup>, 285<sup>m</sup>, 286<sup>m</sup>, 290<sup>m</sup>, 291<sup>m</sup>, 1432<sup>m</sup>, 1435<sup>m</sup>, 2081<sup>m</sup>, 2082<sup>m</sup>, 2083<sup>m</sup>, 2084<sup>m</sup>, 2086<sup>m</sup>, 2087<sup>m</sup>, 2089<sup>m</sup>, 2091<sup>m</sup>, 2094<sup>m</sup>, 2096<sup>m</sup>, 2098<sup>m</sup>, 2100<sup>m</sup>, 2102<sup>m</sup>, 2103<sup>m</sup>, 4147<sup>m</sup>, 4155<sup>m</sup>, 4160<sup>m</sup>, 4161<sup>m</sup>, 4162<sup>m</sup>, 4167<sup>m</sup>, 4425<sup>m</sup>, FMNH 127597<sup>m</sup>, ER 48<sup>g</sup>: GU564049, 2, GU564110, 2; ER 49<sup>g</sup>: GU564050, 2, GU564111, 2; ER 52<sup>g</sup>: GU564051, 3; ER 53<sup>g</sup>: GU564052, 2, GU564112, 2; ER 55<sup>g</sup>: GU564053, 2; ER 61<sup>g</sup>: GU564054, 2; ER 62<sup>g</sup>: GU564055, 2; ER 63<sup>g</sup>: GU564056, 2; ER 67<sup>g</sup>: GU564057, 2; ER 68<sup>g</sup>: GU564058, 2; ER 74<sup>g</sup>: GU564046, 6; ER 75<sup>g</sup>: GU564047, 6; ER 76<sup>g</sup>: GU564048, 5), 48) Peulla, Lago de Todos Los Santos (FMNH 50321<sup>m</sup>, 50322<sup>m</sup>, 50324<sup>m</sup>), 49) Puerto Montt (FMNH 22732<sup>m</sup>), 50) 23 km SE Puerto Montt, 7 km E Lenca (FMNH 132448<sup>m</sup>), 51) Pichiquillaipe, Parque Katalapi (UACH 7280: KP665998, 7, KP665988, 4; UACH 7260: KP665999, 7, KJ614602, 4; UACH 7281: KP666001, 7; UACH 7282: KP666000, 4, KP665989, 1), 52) Lago Tagua Tagua, Rampa los Canelos (UACH 7283: KP666003, 8, KP665990, 3), 53) 19.7 km N Rio Negro & 26.7 km S Contao (FMNH 130713), 54) Senda Darwin (UWBM 79697<sup>g</sup>: KP666002, 1).

Abrothrix olivacea (n = 24): ARGENTINA: Mendoza, 56) Valle Hermoso (RAO 111<sup>s</sup>: KP665997, 24), 57) La

Valenciana (CNP 1750<sup>§</sup>: -, KJ614603, 21) Río Negro, 58) Cerro Corona (CNP 2582: HM167800, 21). Chubut, 59) Estancia Talagapa (CNP 994<sup>§</sup>: -, KJ614606, 21; CNP 1017<sup>m</sup>, 1216<sup>m</sup>), 60) Pico Salamanca (CNP 2154<sup>m</sup>, 2156<sup>m</sup>, 2157<sup>m</sup>, 2163<sup>m</sup>). Santa Cruz, 61) 4 km W Punta Quilla, along the RP 288 (CNP 2556<sup>m</sup>, 2557<sup>m</sup>), 62) Estancia Cerro del Paso (CNP 2543<sup>m</sup>, 2553<sup>m</sup>), 9) Estancia Cerro Ventana (CNP 2541<sup>m</sup>, 2552<sup>m</sup>), 63) Estancia Don Braulio (CNP 256<sup>m</sup>), 64) Río Gallegos (CNP 3458<sup>m</sup>). Tierra del Fuego, 65) Estancia San Martín (CNP 2550: HM167792, 25), 66) Puesto Beta (CNP 1424<sup>§</sup>: -, KJ614607, 21). CHILE: Arica y Parinacota, 67) Camarones (SSUCMA 00212<sup>§</sup>: AY341034, 23). Valparaiso, 68) Valparaiso (FMNH 132348<sup>§</sup>: AF027306, 22). BioBio, 14) Shangrila (UACH 7256<sup>§</sup>: -, KJ614605, 22). Aysen, 69) Puerto Vagabundo (UACH 7255<sup>§</sup>: -, KJ614604, 20). *Abrothrix sanborni* (*n* = 28): CHILE: Los Lagos, Chiloé Island 70) Parque Nacional Chiloé, 1 km N Cucao (FMNH 132269\*: KP666014; FMNH 132276<sup>m</sup>), 71) Parque Tantauco, sector Lago Chaiguata (UACH7319<sup>m</sup>; UACH 7272: KP665991, 11, KP666004, 7; UACH 7273: KP666005, 12, KP665992, 9; UACH 7274: KP665993, 13, KP666006, 7; UACH 7275: KP666007, 14, KP665994, 6; UACH 7276: KP666008, 9, KP665995, 8; UACH 7277: KP666009, 15, KP665996, 9; UACH 7278: KP666010, 15), 72) Cocauque, Yaldad (FMNH 127565\*: KP666012, 12; UACH 2106<sup>m</sup>, 2107<sup>m</sup>, 2108<sup>m</sup>, 2109<sup>m</sup>, 2111<sup>m</sup>), 73) Quellón (FMNH 22706<sup>m</sup>, 22710<sup>m</sup>, 22711<sup>m</sup>, 22713<sup>m</sup>, 22714<sup>m</sup>), 74) Río Inio (FMNH 22721<sup>m</sup>, FMNH 22724: KP666011, 10; FMNH 22726<sup>m</sup>, 22728<sup>m</sup>, 22730<sup>m</sup>, 22826<sup>m</sup>). Aysen, 75) 4 km NW Puerto Ibáñez (FMNH 130197: KP666013, 12).