Research Article

Taxonomical notes on the long-clawed mole mice of the genus *Geoxus* (Cricetidae), with the description of a new species from an oceanic island of southern Chile

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Abstract

The rodent genus *Geoxus* was largely considered as monotypic; however, a growing body of evidence suggests that this figure is incorrect. In this work, based on qualitative and quantitative morphological evidence and DNA sequence data, we reviewed the alpha taxonomy of this genus. Based on the examination of 134 specimens, four species are recognized within *Geoxus*: *G. annectens* (until recently referred to the genus *Pearsonomys*), *G. michaelseni*, *G. valdivianus*, and one species described herein as new. The four species have unique combinations of qualitative and quantitative morphological characters and were recovered as monophyletic using mitochondrial DNA sequences. The new species diagnosed and named here is endemic of Guafo Island, a small island of 299 square kilometers on southern Pacific Chile. Phylogenetic analysis placed the new species as sister of *G. michaelseni*, a form widely distributed in southern Argentinean and Chilean Patagonia.

Introduction

The tribe Abrotrichini, with five genera and 14 living species, represents a small clade within the speciose rodent subfamily Sigmodontinae (Cricetidae). Even when its diversity is moderate, this tribe constitutes one of the most extant successful radiations of mammals at the southern cone of South America (Rodríguez-Serrano et al., 2008; Cañón et al., 2014; D'Elía et al., 2015a). Abrotrichines are mostly Andean, reaching their greatest diversity in southern Argentina and Chile (Cañón et al., 2014; Teta et al., 2016). As currently understood (Teta et al., 2016), Abrotrichini includes two main clades, one composed by the cursorial genus *Abrothrix* Waterhouse, 1837 and another encompassing the fossorial genera *Chelemys* Thomas, 1903, *Geoxus* Thomas, 1919 (including *Pearsonomys* Patterson, 1992; see below), *Notiomys* Thomas, 1890, and *Paynomys* Teta, Cañón, Patterson and Pardiñas, 2016 (see Teta et al., 2016).

During most of the last 60 years, the genus *Geoxus* was considered as monospecific, with *G. valdivianus* (Philippi, 1858) as its single species (e.g., Cabrera, 1961; Mann, 1978; Pearson, 1984; Teta et al., 2015). However, a growing body of evidence suggests that this figure is incorrect (Lessa et al., 2010; Teta, 2013; Cañón et al., 2014). In fact, *G. valdivianus*, as demonstrated by phylogenetic analysis of genetic and morphological data (Lessa et al., 2010; Cañón et al., 2014; Teta et al., 2016), includes two lineages of species level, which would correspond to *G. valdivianus* s.s. and *G. michaelseni* (Matschie, 1898). Moreover, these two species are not sister to each other, but form a paraphyletic

group respect to *Pearsonomys annectens* Patterson, 1992. These results suggested that *Pearsonomys* is a synonym of *Geoxus* (see Teta et al., 2016), bringing to three the number of valid species of *Geoxus*. We note, however, that there are not comprehensive studies about the qualitative and quantitative morphological variation within *Geoxus* neither emended morphological diagnosis for the species referred above.

In this work, based on qualitative and quantitative morphology and cytochrome- b sequence data, we provide a preliminary review of the genus *Geoxus*. As part of it, based on two specimens collected at Isla Guafo, southern Pacific Chile, we describe a new species of this genus.

Methods

Studied samples

We studied a total of 134 specimens of the genus *Geoxus*, housed at various natural history collections (see Appendix for a complete list of examined individuals), including skins, skull, and fluids, as well as tissue samples.

Morphological analysis

Descriptions of anatomical traits are based on the nomenclature proposed by Reig (1977) for dental features, and Carleton (1980); Carleton and Musser (1989) and Patterson (1992) for external and skull morphology.

Standard external measurements (in mm) were recorded from specimen tags or field catalogs: total length (TL), head and body length (HBL), tail length (TL), hindfoot length (HFL), ear length (EL), and weight (W, in g). We considered 20 craniodental variables, which were selected as descriptors of key skull dimensions. All measurements
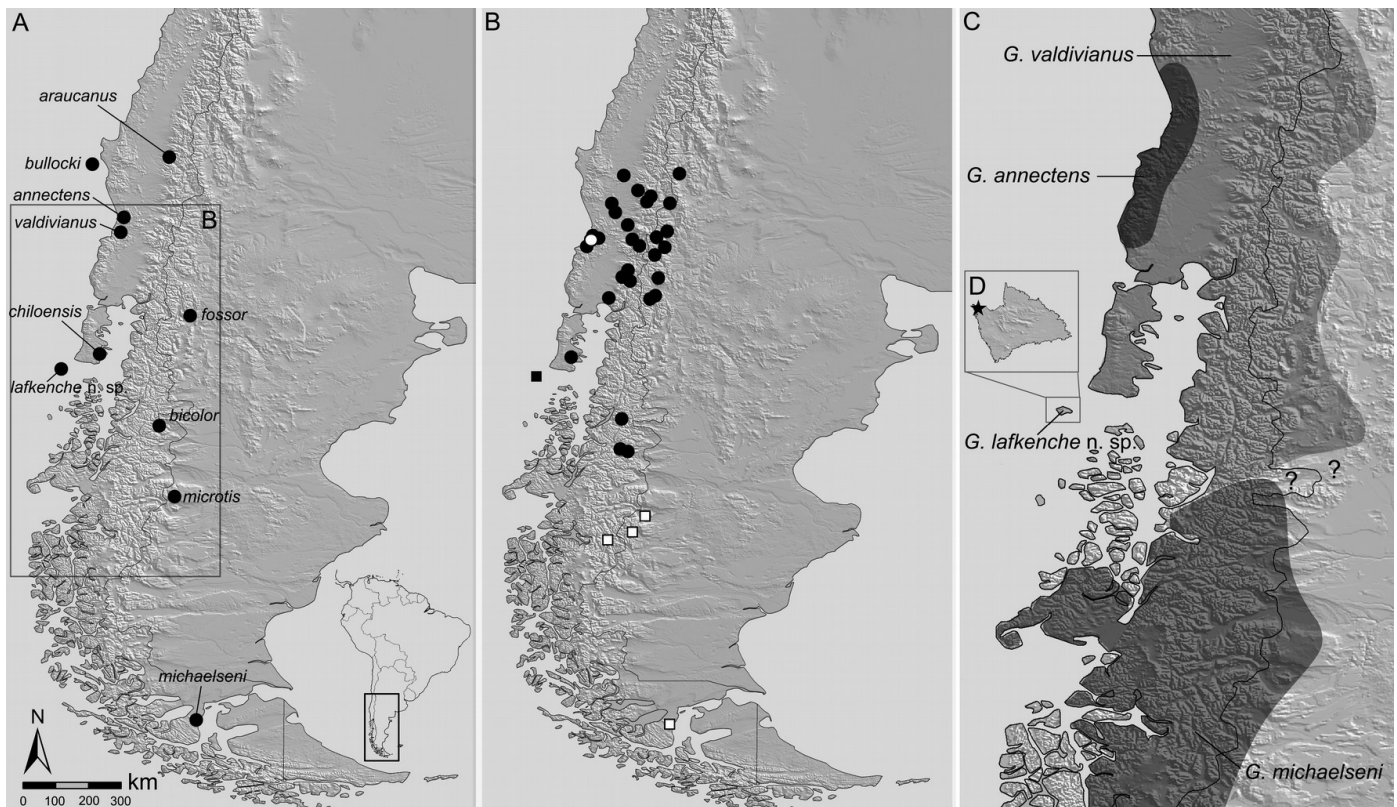
Figure 1 – A: map of southern South America indicating the names associated with *Geoxus* and placement of their type localities. **B**: Placement of the collection localities of the specimens studied in this work: white circle = *G. annectens*; black circles = *G. valdivianus*; white square = *G. michaelseni*; black square = *G. lafkenche* n. sp. **C**: Map of part of southern Chile and southwestern Argentina showing, as shadowed areas, the approximate distribution of the four species of *Geoxus* recognized in this work. **D**: Close up of Guafo Island; the star depicts the type locality of *G. lafkenche* n. sp.

were obtained with digital calipers and recorded to the nearest 0.01 mm following the definitions provided by Patterson (1992): skull length (SL), condylo-incisive length (CIL), zygomatic breadth (ZB), braincase breadth (BB), palatilar length (PalL), incisive foramina length (IL), incisive foramina width (IW), diastema length (DL), maxillary toothrow length (TRL), palatal width at M1 (PWM1), palatal width at M3 (PWM3), zygomatic plate width (ZW), nasal length (NL), nasal width (NW), rostrum width (RW), frontal sinus width (FSW), interorbital breadth (IB), frontal length (FL), parietal length (ParL), mesopterygoid fossa breadth (MB).

Morphometric analyses were performed on a set of 48 adult specimens of both sexes (age classes 3–5; following the tooth-wear criteria defined by Patterson (1992) including representatives of all three recognized species of *Geoxus* (*G. annectens* [AN], *G. michaelseni* [MI], *G. valdivianus* [VA]; Fig. 1) and the new species described here [HU]. In order to explore the geographic variation within *Geoxus valdivianus*, specimens were grouped using the criteria of Vanzolini and Williams (1970; see also Musser, 1968 and Chiquito et al., 2014), which includes close geographical proximity, absence of major geographical barriers among localities, and lack of obvious discrepancy in size and shape among contiguous samples. The following groups were constituted: Argentina: NN = northern Neuquén, SN = southern Neuquén; Chile: CA = Quetropillán, CH = Chiloé, MA = Malleco, OS = Osorno, VL = Valdivia. The studied sample included specimens of all recognized subspecies of *G. valdivianus* (*sensu* Osgood, 1943), except *G. v. bullocki*. To summarize morphometric variation, we performed a principal component analysis (PCA) based on a variance-covariance matrix of the log-transformed data set of craniodental measurements. To account for the effect of size, a second PCA analysis was performed using variables corrected by the geometric mean (each species measurement divided by the nth root of the product of values of a species vector of n variables; see Meachen-Samuels and Van Valkenburgh, 2009). Finally, we used discriminant functions (DFA) to determine which craniodental variables discriminate between the occurring groups. To perform the DFA and due the absence of discrete morphological differences, we

pooled together samples referred to *G. valdivianus*. All analyses were run using InfoStat (di Rienzo et al., 2008).

Genetic and phylogenetic analyses

Genetic comparisons and phylogenetic analyses were based on the first 801 base pairs of the mitochondrial cytochrome-b gene (hereafter *cyt-b*). Analyses included 13 sequences gathered from specimens of all recognized species of *Geoxus* (Appendix). Of the *cyt-b* sequences analyzed, 2 belong to a new species described below and were gathered from specimens collected at Isla Guafo. Sequences from representatives of *Chelemys megalonyx* (DQ309559) and *Notiomys edwardsii* (accession number U03537) were used to form the outgroup. DNA sequences were generated by us or downloaded from GenBank. Those gathered here were obtained using primers MVZ 05 and MVZ 16 as outlined in Cañón et al. (2010).

Sequences were aligned with Clustal as implemented in MEGA 6 (Tamura et al., 2013) using the default parameter values. Observed genetic *p*-distances were calculated in MEGA 6. Genealogical relationships were inferred via Bayesian analyses (BA) using Mr.Bayes 3.1 (Ronquist and Huelsenbeck, 2003) by means of two independent runs, each with 5 heated and 1 cold Markov chains. The substitution model HKY+G was selected using jModelTest (Darriba et al., 2012). All model parameters were estimate in MrBayes. Uniform-interval priors were assumed for all parameters except bas composition and substitution model parameters, which assumed a Dirichlet prior. Runs were allowed to proceed for 20 million generations; parameters and trees were sampled every 1000 generations. Plotting log-likelihood values against generation time checked convergence on a stable log-likelihood value. The first 25% of the trees were discarded as burn-in; remaining trees were used t compute a 50% majority rule consensus tree and to obtain posterior probabilit (PP) estimates for each clade.
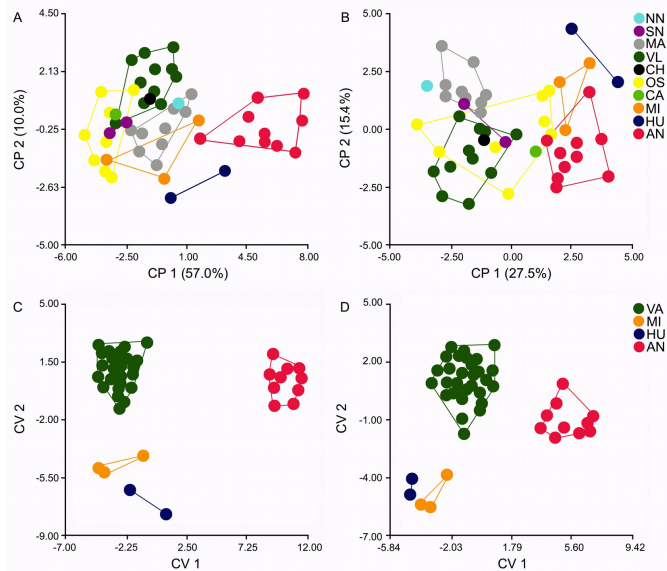
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Figure 2 – Specimen scores of adult individuals (ages 3–5) of *Geoxus* (N = 48) for principal components 1 and 2 (A, B [those on B correspond to variables corrected by the geometric mean]) and for canonical variates 1 and 2, extracted from four-group discriminant function analysis (C, D [those on D correspond to variables corrected by the geometric mean]). See Material and Methods for an explanation of the abbreviations.

Divergence Time Estimation

Dating of cladogenetic events was done using the *cyt-b* dataset and BEAST v2.3.2 (Bouckhaert et al., 2014). A Yule model using an initial random tree was set as a prior. The employed substitution model, selected using jModeltest, was HKY+G with empirical base frequencies, and four G rate categories. Runs were performed under a strict clock model. Three independent runs of 4×10^7 generations, sampled every 9×10^3 generations were performed. Convergence to stable values was checked with Tracer v.1.6 (Rambaut et al., 2014) obtaining an effective sample size (ESS) greater than 200 for all parameters. Tree and log files (14703 trees after a 2% burn-in) were combined using LogCombiner (Bouckhaert et al., 2014). Resulting trees were then compiled into a maximum clade credibility (MCC) tree with TreeAnnotator (Bouckhaert et al., 2014) displaying mean ages and highest posterior density (HPD) intervals (95% upper and lower) for each node. As the fossil record of *Geoxus* is restricted to the Holocene (Teta, 2013), to calibrate the clock we used a secondary calibration point (i.e., an age estimate with its corresponding associated error) obtained from Cañón et al. (2014; who calibrated their phylogeny with a fossil of the genus *Abrothrix* related to *A. jelskii* and of an age of 3.02 Ma). It corresponds to the age estimated for the most recent common ancestor (tmrca) of *Geoxus* (2.36 Ma; range 1.73 Ma–3.91 Ma). As such, the calibration was done with a lognormal prior distribution with mean 0.09, sigma 0.56 and offset 1.38 establishing a 95% highest probability interval of 1.73 Ma–3.91 Ma with median equal to 2.36 Ma.

Results

Morphological analyses

Qualitative morphological differences among species of *Geoxus* are discussed below in the species accounts and summarized on Tab. 1.

Principal components I and II accounted for 57.0% and 10.0% of the total variance, respectively (Fig. 2A; Tab. 2).

Bivariate plots (Fig. 2) show that the two specimens from Guafo Island do not overlap with the cloud of any of the species of *Geoxus*. Similarly, *G. annectens* segregates in the multivariate space. *G. michaelseni* partially overlaps with *G. valdivianus*. Within the sample of this latter species, two main groups could be recognized, one including those individuals from MA and NN and another encompassing specimens from CA, CH, OS, SN, and VL. The discriminant function analysis showed complete separation between the four species, with 100% of the specimens correctly classified (Wilks' Lambda: 0.021365;

F=60.75; *p*<0.000001; Fig. 2C; Tab. 3). Similar results were obtained on the PCA and discriminant functions performed using the variable values adjusted by the geometric means (Fig. 2B, D; Tabs. 2 and 3). On this second PCA, where the principal components I and II accounted for 27.5% and 15.4% of the total variance (Fig. 2B; Tab. 2), the multivariate space of *G. michaelseni* does not overlap with that of *G. valdivianus*, suggesting that differences between these two species are mostly in shape. Both the results of the PCA and discriminant functions shown that the two specimens from Guafo Island differentiate both in size and shape from those of *G. annectens*, *G. michaelseni* and *G. valdivianus*.

Phylogeny and divergence times

The genetic evidence is in line with the morphologic data. The resulting tree from MrBayes (Supplemental Figure S1) resembles that generated using BEAST (Fig. 3).

The genus *Geoxus* was recovered monophyletic, although it lacks significantly support (here and afterwards posterior probability values are those gathered with MrBayes and BEAST, respectively; PP=0.83; not applicable because the tmrca of *Geoxus* was constrained as monophyletic in the dating analysis). Haplotypes of *Geoxus* fall into four main and highly supported clades (Fig. 3). These clades correspond to the three recognized species of the genus and to the lineage formed by haplotypes of specimens from Guafo Island. *Geoxus michaelseni* (PP=1; PP=1) is sister (PP=1; PP=1) to the clade formed by the haplotypes from Guafo (PP=1; PP=1); meanwhile, *G. annectens* (PP=1; PP=1) and *G. valdivianus* (PP=1; PP=1) are sister to each other (PP=0.98; PP=1). Within the clade of *G. valdivianus* there is geographic structure; haplotypes of *G. valdivianus* form two allopatric clades that latitudinally replace each other. One clade (PP=0.99; PP=1) is form by haplotypes gathered from Río Negro, Argentina and Los Ríos, Chile; while the other clade (PP=1; PP=1) is constituted by haplotypes from northern Neuquén, Argentina and Malleco, Chile.

Average divergence values within and among species of *Geoxus* are given in Tab. 4. Estimates of divergence times among forms of *Geoxus* are provided in Fig. 3; all fall within the Pleistocene.

Taxonomy

Results of quantitative and qualitative morphological analyses as well as those of molecular based analyses support the existence of four species within the genus *Geoxus*; these are *G. annectens*, *G. michaelseni*, *G. valdivianus*, and a fourth, for which no name is available, and as such is described and named at the end of this section.
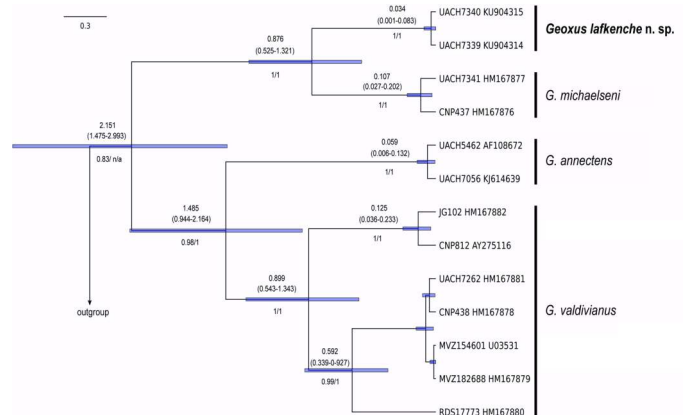
Figure 3 – Chronogram illustrating the diversification of the genus *Geoxus* obtained from the Bayesian analysis of a matrix of *cyt-b* gene sequences. Numbers above branches correspond to ages of the nodes at right; ages are represented as mean node height for a maximum clade credibility tree compiled from post-burning trees topologies obtained in BEAST; 95% highest posterior density credibility intervals are given between parentheses and illustrated with bars. Numbers below branches are a posteriori probability values found in Bayesian analyses conducted in MrBayes and BEAST, respectively. Terminal labels are as follow: specimen number and Genbank accession number.

Table 1 – Selected traits for a morphological comparison among species of *Geoxus*.

Character	G. annectens	G. michaelseni	G. valdivianus	G. lafkenche n. sp.
Head and body length	~120 mm	~110 mm	~95 mm	~110 mm
Relative tail length	~64% of HBL	~40.5% of HBL	~42% of HBL	~63% of HBL
Dorsal coloration	Blackish or brownish	Brownish	Blackish	Brownish
Body pelage pattern	Countershaded or not	Countershaded	Not countershaded	Not countershaded
Ear length	~19 mm	~11 mm	~11 mm	~12 mm
Anterior margin of the zygomatic plate	Convex	Nearly straight	Convex	Convex
Zygomatic arches	Not flaring	Flaring	Not flaring	Not flaring
Upper zygomatic root	Slightly larger than one third of the anteroposterior length of the zygomatic plate	Larger than a half of the anteroposterior length of the zygomatic plate	Larger than a half of the anteroposterior length of the zygomatic plate	Nearly equal to one half of the anteroposterior length of the zygomatic plate
Palate length	Long, exceeding maxillary toothrow by almost the length of M2	Long, exceeding maxillary toothrow by more than one half of the length of M2	Long, exceeding maxillary toothrow by less than a half of the length of M2	Long, exceeding maxillary toothrow by approximate a length of one third of the M2

Family **Cricetidae** Fischer, 1817
Subfamily **Sigmodontinae** Wagner, 1843
Tribe **Abrotrichini** D'Elía, Pardiñas, Teta and Patton, 2007
Genus *Geoxus* Thomas, 1919

Synonyms
Oxymycterus: Philippi, 1858:303; part.
[*Acodon*]: Thomas, 1894b:362; part.
Hesperomys (**Acodon**): Matschie, 1898:5; part.
Mus (**Oxymycterus**): Philippi, 1900:21; part.
Acodon (**Chelemys**): J. A. Allen, 1905:80.
Geoxus Thomas, 1919:208; type species *Geoxus fossor* Thomas, by original designation.
Notoxus Thomas, 1919:209; *lapsus calami* for *Geoxus* Thomas.
Notiomys: Osgood, 1925:115; part.
bfemPearsonomys Patterson, 1992:137.

Distribution — Type localities of all nominal forms currently included within *Geoxus* are depicted on Fig. 1A.

Taxonomic remarks — A emended diagnosis for the genus, including *Pearsonomys* in its synonymy, was provided by Teta (2013) and Teta et al. (2016). Rodents belonging to the genus *Geoxus* are characterized by the following combination of characters (taken from Teta et al., 2016): size small to medium (head and body length >120 mm; tail length <80 mm; weight ~25 g–42 g); pelage long and thick, somewhat hispid in some species (*annectens*) to dense and short in others (*michaelseni*, *valdivianus*); general coloration blackish to dark brown, becoming paler on the venter; pinnae small to relatively large, externally visible and semicircular; manual claws well developed, with a ventral keel that runs nearly half of their length; skull delicate, with a rounded braincase and flaring to scarcely expanded zygomatic arches; rostrum proportionally long and narrow, with nasals and premaxillae well projected as a tube surpassing the upper incisors; frontal sinuses inflated; interorbital region anteriorly divergent, narrowest in its posterior half; ethmoid foramen dorsal or posterior to M3; anterior border of alisphenoid well projected anteriorly as a free osseous flake; zygomatic plate narrow and low and somewhat to conspicuously slanted backward from the base; infraorbital foramen with its lumen wide and

Table 2 – Results of principal components analyses (first and second columns) and principal components analyses using the variables corrected by the geometric mean (third and fourth columns) comparing adult specimens (ages 3–5) of *Geoxus* (N=48). See Materials and Methods for details of the analyses and explanation of the abbreviations.

	PCA		PCA corrected	
	PC1	PC2	PC1	PC2
SL	0.27	−0.15	0.36	0.16
CIL	0.28	−0.11	0.35	0.12
ZB	0.25	0.14	−0.23	0.17
BB	0.27	−0.05	−0.16	0.31
PalL	0.28	−0.13	0.33	0.11
IL	0.26	−0.02	0.26	−0.22
IW	0.20	0.07	0.03	−0.20
DL	0.27	−0.03	0.33	−0.09
TRL	0.20	−0.28	−0.10	0.44
PWM1	0.24	−0.05	−0.21	0.29
PWM3	0.23	−0.12	−0.05	0.20
ZW	0.10	0.31	−0.18	−0.08
NL	0.19	−0.26	0.11	0.31
NW	0.16	0.40	−0.24	−0.14
RW	0.10	0.50	−0.25	−0.13
FSW	0.25	0.26	−0.31	−0.10
IB	0.24	0.13	−0.18	−0.17
FL	0.21	0.04	0.16	−0.14
ParL	0.17	−0.36	0.06	0.27
MB	0.19	0.19	0.03	−0.37
Eigenvalue	11.41	1.99	5.51	3.09
% Variance	0.57	0.10	0.28	0.15

Table 3 – Results of four-group discriminant function analysis (first and second columns) and discriminant function analysis using the variables corrected by the geometric mean (third and fourth columns) of adult specimens (ages 3–5) of *Geoxus* (N = 48). See Materials and Methods for details of the analyses and explanation of the abbreviations .

	DFA		DFA corrected	
	CV1	CV2	CV1	CV2
SL	0.18	−1.28	−0.50	−0.71
CIL	1.43	1.78	1.17	0.95
ZB	−0.65	−0.21	0.13	−0.44
BB	0.18	−0.75	−0.37	−0.41
PalL	−0.52	−1.21	−0.33	−0.89
IL	0.90	0.99	1.02	0.46
IW	0.63	−0.18	0.25	−0.11
DL	−0.88	−0.76	−0.39	−0.35
TRL	0.07	−0.29	−0.26	0.12
PWM1	−0.24	0.27	−0.34	0.39
PWM3	0.55	0.91	0.83	0.71
ZW	−0.30	0.04	−0.42	0.26
NL	−0.31	−0.40	−0.69	0.05
NW	−0.27	−0.09	−0.54	0.27
RW	−0.29	−0.19	−0.30	−0.04
FSW	0.12	1.75	0.59	0.87
IB	0.42	−0.50	−0.33	−0.25
FL	0.38	−0.47	−0.06	−0.25
ParL	0.39	−0.04	0.24	−0.13
MB	0.70	0.44	0.62	0.31
Eigenvalue	30.57	4.43	8.77	3.59
% Variance	83.23	12.06	62.58	25.64

Table 4 – Observed genetic *p*-distance of the cytochrome b gene within and among four species of *Geoxus*. Numbers in parentheses refer to the number of sequences studied for each species.

	intraspecific	interspecific		
G. annectens (2)	0.003	—	—	—
G. lafkenche n. sp. (2)	0.001	0.108	—	—
G. michaelseni (2)	0.006	0.105	0.057	—
G. valdivianus (7)	0.034	0.080	0.101	0.112

nearly ovate in shape; incisive foramina parenthesis-shaped, with a constriction between the middle and the posterior third; mesopterygoid fossa parallel sided and "U"-shaped; parapterygoid fossa at the same level of the palate; sphenopalatine vacuities large; anterodorsal portion of the ectotympanic rounded to subquadrate and well separated from the mastoid; orbicular apophysis of the malleus with its peduncle proportionally narrow and long and ending in a bulbous button; mandible proportionally long and low with a small capsular projection; diastema slightly excavated, smoothly concave throughout; coronoid process short; incisors orthodont; molars simple and small, brachyodont and crested; procingulum of M1 small; mesoloph on M1 present but small in young individuals to coalesced with paracone in adults; M3 small and rounded in outline; mesoloph on m1-2 absent; procingulum on m1 "fan"-shaped and without anteromedian flexid; metaconid and protoconid broader than entoconid and hypoconid; stomach unilocular-hemiglandular with the glandular epithelium covering both the antrum and proximal portion of corpus near esophageal opening; phallus with a dorsal hood usually present; baculum with 3 well-developed cartilaginous digits; ampullary and bulbourethral glands present and larger than is typical for Abrotrichini.

Geoxus annectens

Synonyms

Pearsonomys annectens Patterson, 1992:137.

Type locality — "Near Mehuín, 42 km N and slightly E of Valdivia, in the Provincia de Valdivia, Región de Los Lagos [now Región de Los Ríos], Chile (39°26′ S, 73°10′ W; Paynter, 1995), at 100 m elevation."

Emended morphological diagnosis (modified from Patterson, 1992) — A large-sized species of the genus *Geoxus* (length of head and body ∼120 mm, skull length ∼30.5 mm), characterized by its large ears (∼19 mm), relatively long tail (∼77 mm), long hindfoot (∼26.5 mm) and small molar teeth; pelage hispid and coarse, blackish or dark brown and slightly to well counter shaded; the venter is blackish to gray washed with buff; tail uniformly brown; skull elongate and delicate, with scarcely flaring zygomata; nasals and premaxillae trumpeted; zygomatic plate strongly inclined; upper zygomatic root narrow, slightly larger than to $1/3$ of the anteroposterior length of the zygomatic plate; frontal sinus inflated; interorbital region smoothly rounded; palate long, exceeding maxillary toothrow by almost the length of M2; parapterygoid fossa large; middle lacerate foramen broad, bridged or not by a sharp, well developed, stapedial process; tympanic bullae proportionally large and globose; length of M3 nearly equal to the half of the length of M2.

Distribution — Known from only five localities in a small fraction of the Coastal Cordillera of southern Chile between 39° S and 40°54′ S in Los Ríos and Los Lagos regions (D'Elía et al., 2006). This species is sympatric with *G. valdivianus* in some localities near Valdivia, Chile (D'Elía et al., 2006).

Taxonomic remarks — Described as the single species of the genus *Pearsonomys* (Patterson, 1992), molecular and morphological evidence support its inclusion within *Geoxus* (Lessa et al., 2010; Teta, 2013; Cañón et al., 2014; Teta et al., 2016).

Geoxus michaelseni

Synonyms

Hesperomys (Acodon) michaelseni Matschie, 1898:5.

Oxymycterus microtis J.A. Allen, 1903:189.

Oxymycterus delfini Cabrera, 1905:15.

Notiomys valdivianus bicolor Osgood, 1943:155.

Type locality — "Süd- Patagonien, Punta Arenas", Región de Magallanes y Antártica Chilena, Chile.

Emended morphological diagnosis — A medium-sized species of the genus *Geoxus* (length of head and body ∼110 mm, skull length ∼28 mm), characterized by small ears (∼11 mm), short tail (∼44.5 mm), and small molar teeth; pelage thick, short, fine and uniformly brown to olive brown, sharply contrasted with the gray or whitish gray of the venter; tail sharply bicolor or uniformly brown; skull elongate and fragile, with largely flaring zygomata; nasals and premaxillae trumpeted; zygomatic plate slightly inclined backwards and with its anterior border nearly straight; upper zygomatic root broad, larger than the half of the anteroposterior length of the zygomatic plate; frontal sinus inflated; interorbital region smoothly rounded; parapterygoid fossa large; palate long, exceeding maxillary toothrow by more than the half of the length of M2; length of M3 nearly equal to the half of the length of M2.

Distribution — As here delimited, *G. michaelseni* occurs in forested and ecotonal areas of Argentina and Chile along the Andes and piedmont from the 44.5° S towards the South to the vicinities of Punta Arenas. The northern limit of the species distribution needs clarification, especially in those areas where appears as sympatric, although not syntopic, with *G. valdivianus* (see Kelt, 1994).

Distribution — *Oxymycterus microtis* was described by Allen (1903) with type locality on "Pacific slope of the Cordilleras, near the head of the Rio Chico de Santa Cruz", Argentina (restricted by Pardiñas, 2013 to 1 km N Ea. Tucu Tucu, 48.46° S, 71.97° W, departamento Río Chico, Santa Cruz, Argentina). Osgood (1925, 1943) noted the external and cranial similarities between *microtis* and *michaelseni*, including the former into the synonymy of the second. As in *michaelseni*, the holotype of *Oxymycterus microtis* (Allen, 1905: Plate IX, figs 4–4b) has largely flaring zygomata, long palate, and minute M3. Later, Osgood (1943) described *Notiomys valdivianus bicolor*, from "Casa Richards, Rio Nirehuao [= Río Ñirehuao], [Aysén], Chile. Lat. 45°3′ S [45.260° S, 71.705° W]". Subsequent authorities linked *bicolor* to *valdivianus* (e.g. Pearson, 1984); however, phylogenetic analysis of molecular data placed the mitochondrial haplotype of one individual from near the type locality of *bicolor* as sister to that of a topotype of *microtis*. In addition, as *microtis*, *bicolor* shares with *michaelseni* a relatively large size and a general brownish coloration, sharply contrasted with the gray or whitish gray of the venter. Following Teta (2013), *Oxymycterus delfini* Cabrera, 1905 (type locality "Punta Arenas"; the holotype is lost), a form sometimes allied with *Paynomys macronyx*, is here considered as a synonym of *michaelseni*. Despite the brief description provided by Cabrera (1905), the external measurements (HBL=106 mm; TL=63; EL=11; HFL [without claw]=22) and coloration pattern (dark brownish above, paler below), as well some skull characters (e.g., minute m3) are in agreement with those of *michaelseni*. In synthesis, we considered that *delfini*, *bicolor*, *michaelseni*, and *microtis* are part of a cohesive, morphologically diagnosable group within *Geoxus*, for which we use the oldest available name, *G. michaelseni* (see Teta, 2013; Teta et al., 2016). To test this hypothesis, further studies are needed; these should be based on the morphological analysis of a larger series of individuals, including the direct inspection of available holotypes as well as analysis of more genes. Additional data on measurements for a large series of individuals was provided by Patterson (1992).

Geoxus valdivianus

Synonyms

Oxymycterus valdivianus Philippi, 1858:303.

Geoxus fossor Thomas, 1919:208.

Notiomys valdivianus araucanus Osgood, 1925: 117.

Notiomys valdivianus chiloensis Osgood, 1925: 117.

Notiomys valdivianus bullocki Osgood, 1943:154.

Type locality — "Valdivia", Región de Los Ríos, Chile.

Emended morphological diagnosis — A small species of *Geoxus* (length of head and body ∼95 mm, skull length ∼26.5 mm), character-

ized by its small ears (∼11 mm), short tail (∼40 mm), and proportionally large molar teeth; pelage soft and dense, usually blackish to dark brown and slightly counter shaded; tail uniformly blackish or brown to slightly bicolor; skull elongate and fragile, with scarcely flaring zygomata; nasals and premaxillae trumpeted; zygomatic plate inclined with a nearly convex anterior border; upper zygomatic root nearly equal to a half of the anteroposterior length of the zygomatic plate; frontal sinus inflated; interorbital region smoothly rounded; palate long, although only exceeding maxillary toothrow by less than a half of the length of the M2; length of M3 nearly equal to three quarters of the length of M2.

Distribution — *G. valdivianus* is found in forested areas of southwestern Argentina and south-central Chile. In Argentina it had been recorded from central Neuquén province (∼38.5° S) to southern Chubut (∼45° S). In Chile it is found from about 36° S, including Mocha and Chiloé islands, to around 44.50° S (Osgood, 1943; Mann, 1978).

Taxonomic remarks — *Geoxus fossor* was described by Thomas (1919), with type locality at "Maiten [= El Maitén, Cushamen], W. Chubut. 700 m,´´ Argentina. Osgood (1925) maintained its rank at the species level, but later considered it as a subspecies of *valdivianus*. *Notiomys valdivianus araucanus* was erected by (Osgood, 1925, p. 117) with type locality on "Tolhuaca, Province of Malleco, [Región de la Araucanía], Chile´´, but later, based on the examination of a large series of individuals, (Osgood, 1943, p. 152) concluded that *araucanus* was "insufficiently characterized for recognition". Molecular and morphological data (this work), including the assessment of some topotypical specimens, suggest that *araucanus*, *fossor*, and *valdivianus* are representatives of the same biological species, characterized by a small size and an uniformly blackish to dark brownish coloration, delicate skulls and proportionally shorter palates (Teta, 2013). The subspecies *chiloensis*, endemic to Chiloé Island, was described by Osgood (1925; type locality at "Quellon [= Quellón], Chiloe Island [Isla Grande de Chiloé, Los Lagos], Chile´´) as darker and smaller than typical *valdivianus* (Osgood, 1925). However, our qualitative and quantitative morphological analyses suggest that these differences dilute when large series of individuals are revised (see Fig. 2 A, B). Although we have not studied any specimen from Isla Mocha, from where *Notiomys valdivianus bullocki* was described (Osgood, 1943; type locality: "Mocha Island, coast of southern Chile, Province of Arauco [Región del Biobío]"), the description provided by Osgood (1943) clearly links this form with our concept of *valdivianus* (i.e., size small, dark coloration), an hypothesis that also has sense on biogeographical grounds, given that Isla Mocha lies close to the coast at the northern part of the continental distribution of this species (Fig. 1).

The genetic data and results of the quantitative morphological analysis indicate that two forms, which are geographically segregated, can be differentiated within *valdivianus* (Figs. 2, 3). One form distributes in the northern range of the species (northern Neuquén, Argentina and Malleco in the Chilean Región de la Araucania), while the other occurs in the southern part of the range (southern Neuquén, Argentina, and the Chilean provinces of Cautín, Valdivia, Osorno and Chiloe). These forms differ on average by 5.5% at the cyt b gene. This value is relatively high and only slightly below that observed between *G. michaelseni* and the species described below. The calibrated molecular clock indicates that genes now private of both clades coalesce at 0.889 Ma (0.543–1.343 Ma). Despite these differences, we prefer to not taxonomically innovate until this scenario eventually consolidates after the analysis of more evidence, including the analysis of additional genes and the inclusion of all involved nominal forms (e.g., *bullocki*). Similarly, the assessment of additional samples, which also enlarge the geographic coverage, is also needed to better delimit the distributional ranges of both clades.

Geoxus lafkenche n. sp.

Synonyms
None

Holotype — Specimen UACH 7339 (original number GD 1512), an adult female preserved as skull, body in fluid, and tissue sample in alcohol (Fig. 4). A partial (792 bp) DNA sequence of the cytochrome-b gene gathered from this specimen was deposited in Genbank with

Figure 4 – Holotype of *Geoxus lafkenche* n. sp., from Isla Guafo, Chile (UACH 7339): skull in right lateral (above), dorsal (below, left) and ventral (below, right) views, and left dentary (reversed) in labial view. Scale = 5 mm.

accession number KU904314; which is considered as hologenetype (sensu Chakrabarty, 2008).

Type locality — Punta Weather, Guafo Island, Región de Los Lagos, Chile (43°34.000′ S, 74°49.500′ W; Fig. 1B).

Morphological diagnosis — A large species of the genus *Geoxus* (length of head and body ∼106 mm, skull length ∼29.5 mm), characterized by its small ears (∼12 mm), relatively long tail (∼66.5 mm), and small molar teeth; pelage somewhat coarse and uniformly dark brown, slightly paler at the venter; skull elongate and fragile, with scarcely flaring zygomata; nasals and premaxillae trumpeted; zygomatic plate inclined with a nearly convex anterior border; upper zygomatic root broad, larger than to a half of the anteroposterior length of the zygomatic plate; frontal sinus inflated; interorbital region smoothly rounded; toothrow short; palate long, although only exceeding maxillary toothrow by the approximate length of one third of M2; parapterygoid fossa large; middle lacerate foramen broad, bridged by a sharp, well developed stapedial process; length of M3 nearly equal to three quarters of the length of M2.

Etymology — The specific epithet correspond to the group of the indigenous Mapuche people that live along the Pacific coast of south-central Chile. The word itself is a composite of two words in mapudungun, the language spoken by Mapuches: *lafken* (sea) and *che* (people). We selected this name to remark the oceanic insular distribution of this mouse, but also as a way to homage the Lafkenche people.
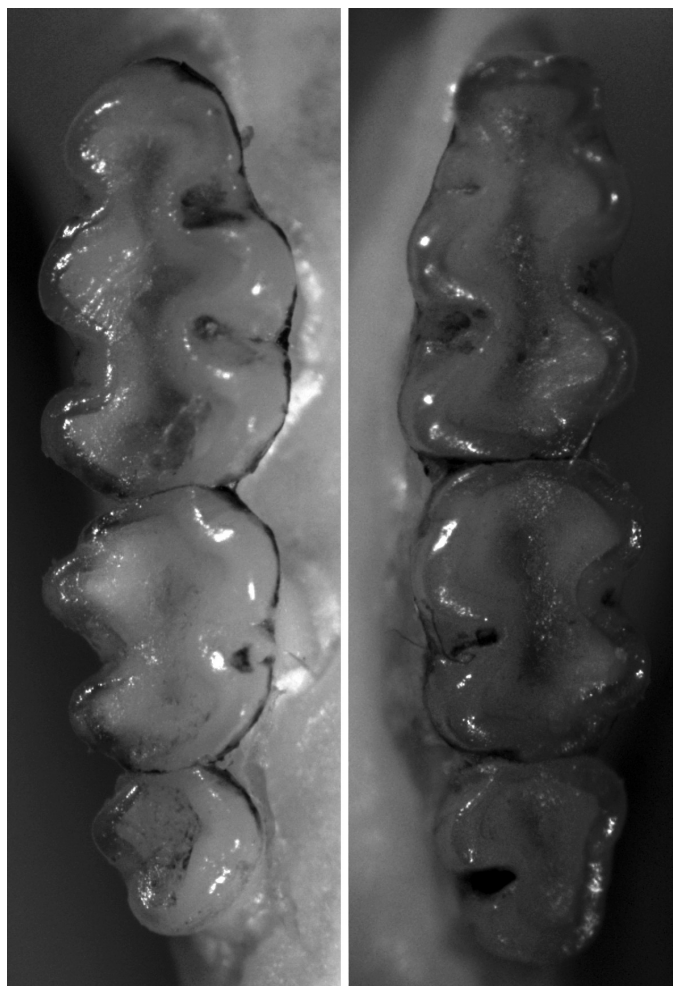
Figure 5 – Right upper (left; 3.73 mm) and lower left (right; 3.76 mm) molar rows of the holotype of *Geoxus lafkenche* n. sp., from Isla Guafo, Chile (UACH 7339).

Measurements of the holotype — External measurements (in mm): TL, 173; T, 67; HF (with claw), 15; HF (without claw), 12; E, 12.5. Cranial measurements (in mm): SL, 31.38; CIL, 28,22; ZB, 13.09; BB, 12.90; PalL, 11.90; IL, 5.51; IW, 1.69; DL, 8.16; TRL, 3.73; PWM1, 5.12; PWM3, 4.29; ZW, 1.79; NL, 11.89; NW, 3.49; RW, 4.29; FSW, 6.68; IB, 5.33; FL, 8.90; ParL, 6.75; MB, 1.45.

Paratype — UACH 7340, an adult female, collected at the same locality of the holotype; external measurements = TL, -; T, 66; HF (with claw), 14; HF (without claw), 11; E, 12.0. Cranial measurements (in mm): SL, 28.65; CIL, 26.01; ZB, 12.51; BB, 12.75; PalL, 11.47; IL, 5.16; IW, 1.37; DL, 7.27; TRL, 3.80; PWM1, 5.12; PWM3, 4.68; ZW, 1.45; NL, 11.40; NW, 3.16; RW, 4.24; FSW, 6.34; IB, 5.35; FL, 9.07; ParL, 5.73; MB, 1.35. A partial (793 bp) DNA sequence of the cytochrome-b gene gathered from this specimen was deposited in Genbank with accession number KU904315; which is considered as paragenetype (sensu Chakrabarty, 2008).

Morphological description — Size large in the context of the genus (head and body length ∼106 mm; tail length ∼66.5 mm); pelage long, thick, and somewhat coarse; dorsal hairs are dark gray at their base and dark brown at their tips; ventral hairs are similar to those of the dorsum, although paler; pinnae are small, semicircular and externally visible; tail is well clothed with hairs and almost entirely dark brown; manus and pes are dorsally covered by short brown hairs; ungueal hairs are short and sparse; manual claws are well developed (∼5 mm) and has a ventral keel that runs nearly half of their length; mystacial vibrissae are short, not reaching the base of the ears.

The skull is slender and fragile; the rostrum is proportionally narrow and long; premaxillary bones are extended slightly in front to the anterior face of the upper incisors; nasals are long and slightly larger than premaxillae; frontal sinus are inflated; interorbital region has smooth and rounded borders; braincase is rounded; the interparietal is broad and relatively large; the zygomatic plates are reduced, narrow, and slanted posteriorly from bottom to top; the upper free border on the zygomatic plate is almost absent; the zygomatic notches are moderate in size; the alisphenoid is anteriorly expressed and in lateral view hides the sphenofrontal foramen; the subsquamosal fenestra and the postglenoid foramen are subequal in size and crossed by a thick 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 relatively large foramen ovale, a reduced anterior opening of the alisphenoid canal, a broad trough for the masticatory-buccinator nerve, and a squamosal-alisphenoid groove that connects anteriorly to a sphenofrontal foramen; the alisphenoid strut is absent; the incisive foramina are extended to the anterior face of the M1s; the palate is broad and long, well extended behind the level of third molars, and lacks posterior palatal pits; the pterygoid region is long; the mesopterygoid fossa has nearly parallel sides and a rounded anterior border; the stapedial process of the bulla is fused to parapterygoid (Fig. 4).

The mandible is low and slender, with a smooth diastema, short coronoid process and a small capsular projection; the condyloid process is not inclined inward (Fig. 4).

The upper incisors are slender, orthodont, and anteriorly covered by an orangish enamel; molars are small, and narrow, simple and brachydont. Upper molars have transversely oriented para- and metaflexi; the para- and mesoloph are coalesced, and both mesostyle and anterostyle are missing; the M1 has a reduced procingulum, shallow anteroflexus, and no anteromedian flexus; the M3 is reduced to nearly the half of the length of M2, without a metacone; lower molars have transverse lophids and flexids with little infolding; the procingulum of the m1 is narrow and lacks an anteromedian flexid; a protostylid is present; the m3 is also reduced, less than three-fourths the length of M2, and with a simplified enamel pattern (Fig. 5).

Morphological comparisons — *Geoxus lafkenche* n. sp. is a relatively large and long tailed form within *Geoxus*. Its size is intermediate between *G. annectens* and *G. michaelseni*. It differs from *G. annectens* by its much smaller ears, shorter palate and less globose tympanic bullae. *G. lafkenche* n. sp. can be differentiated from *G. michaelseni* in having a proportionally larger tail, less flared zygomatic arches, and by the convex anterior border of the zygomatic plate. Compared with *G. valdivianus*, the new species is more brownish in its overall appearance and larger in most external and cranial dimensions, with a comparatively longer rostrum and proportionally shorter toothrow. Other cranial differences among species are summarized on Tab. 1 (see also Figs. 6 and 7).

Genetic comparisons — *Geoxus lafkenche* n. sp. is genetically more similar to *G. michaelseni*; at the cyt b gene both species diverge (*p*-distance) by 5.7%. The new species differs at the same gene by 10.1% and 10.8% from *G. valdivianus* and *G. annectens*, respectively.

Distribution — Only known from Guafo Island, southern Chile. Guafo (−43.5°, −74.7°) is located about 120 km west of the mainland and 39 km southwest of Chiloé Island, outlying the entrance of the gulf of Corcovado.

Natural history — Unknown. The only two known specimens were collected on the ground in a dense coastal forest. As in other parts of the island, the vegetation was mostly composed by the southern beech *Nothofagus dombeyi*, accompanied by the trees *Laureliopsis philippiana*, *Podocarpus nubigenus*, and *Weinmannia trichosperma*. Annual mean precipitation on Guafo is ∼1670 mm.

Conservation — *G. lakquenche* n. sp. is restricted to a small island of ca. 299 square kilometers and about 72 km of perimeter. Most of the island is covered by native Valdivian forest with suitable habitats for *Geoxus*. However, considering the small surface of this island, the negative effects produced by the invasion of commensal rodents of the genus *Rattus* (Moreno-Gómez et al., 2010), undergoing considerations to start charcoal extraction, and other human activities (e.g., tourism, temporal camps made by algae collectors), this species could be seri-

Figure 6 – Dorsal (A-D), ventral (E-H) and lateral (I-L) views of the skull and left dentaries in labial views of four species of *Geoxus*: *G. annectens* (A, E, I; UACH 1064), *G. michaelseni* (B, F, J; CNP 437), *G. valdivianus* (C, G, K; UACH 2170) and *G. lafkenche* n. sp. (D, H, L; UACH 7339). Photographs are not in scale to facilitate trait comparisons..
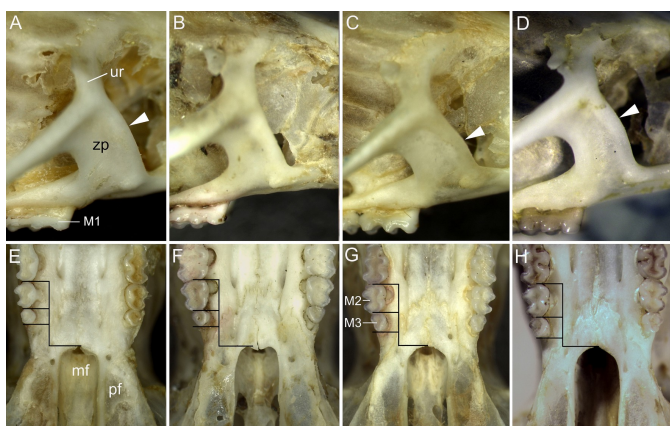

Figure 7 – Selected anatomical traits in four species of *Geoxus*: *G. annectens* (A, E; UACH 1064), *G. michaelseni* (B, F; CNP 437), *G. valdivianus* (C, G; UACH 2170) and *G. lafkenche* n. sp. (D, H; UACH 7339). A-D depict the contour of the anterior border of the zygomatic plate, whose convexity is indicated by a white arrow and the relative size of the upper zygomatic root (ur). E-H illustrate the relative size of the M3 to M2 and the position of the posterior border of the palate relative to the posterior plane of M3. Abbreviations: mf = mesopterygoid fossa; pf = parapterygoid fossa; zp = zygomatic plate. Photographs are not in scale to facilitate comparisons among proportions.

ously endangered in the near future. Therefore, an assessment of the population status of *G. lafkenche* n. sp. is worth of conducting.

Discussion

Systematics

Most of the here associated with *Geoxus* were based on a limited number of specimens; moreover, taxa such as *annectens*, *bicolor*, or *michaelseni* were based on a single individual each. Similarly, revisionary works were based on reduced series of animals; in his first revision, Osgood (1925) studied 19 individuals, while in the second one (Osgood, 1943) this number was augmented to 40. This situation imposed some limitations, especially in order to grasp the variation within and among taxa. Osgood (1925) revised *Geoxus*, considered by him a synonym of *Notiomys*, recognizing three species: *valdivianus* (with *araucanus* and *chiloensis* as subspecies), *fossor*, and *michaelseni*. Eighteen years later, Osgood (1943) subsumed all these forms under *Notiomys valdivianus*, for which he considered six subspecies (i.e., *bicolor*, *chiloensis*, *bullocki*, *fossor*, *michaelseni*, and *valdivianus*). This view of a monospecific *Geoxus* with a wide array of subspecies replacing each other latitudinally prevailed, even when new specimens progressively become available (e.g., Mann, 1978; Patterson, 1992), until now (e.g., Teta et al., 2015). Similar scenarios were constructed by Osgood (1943) for other rodent species, such as *Abrothrix hirta*, *A. olivacea* and *Paynomys macronyx*, which also contrasted with modern views based on gene trees and morphological analyses of large series of specimens (e.g., Pearson and Smith, 1999; Smith et al., 2001; Alarcón et al., 2011; Lessa et al., 2010; Palma et al., 2010; Teta et al., 2014; Teta and Pardiñas, 2014).

Recent analyses of molecular data (Lessa et al., 2010) called attention to the need of revising the alpha taxonomy of *Geoxus* when haplotypic variants retrieved from populations referred to *valdivianus* (at this time, including *michaelseni*) become paraphyletic to those of *Pearsonomys annectens* and formed two highly divergent groups. Additional studies, based on an extensive survey of qualitative morphological characters (Teta, 2013; Teta et al., 2016) and quantitative data (this work) clarified the panorama within this genus, allowing placing *Pearsonomys* in the synonymy of *Geoxus* as well as recognizing four distinct species. Nonetheless, we note that some forms, such as *bullocki* and the one described here, are still poorly known, especially regarding the individual variation of some traits (e.g., external coloration). In addition, the intraspecific taxonomic scenario is in need of further assessments, based on larger sample sizes and complementary lines of evidence. Similarly, distributional boundaries among species, especially between *G. michaelseni* and *G. valdivianus* also need refinement. Finally, the fact that in the present analysis *Geoxus* lacks significant support deserves further attention; although we note that in the multilocus phylogenetic analysis of Cañón et al. (2014) the monophyly of *Geoxus* was statistically supported.

The case of *Geoxus*, together with those seen in other genera (e.g., *Abrothrix*,[Teta and Pardiñas, 2014; D'Elía et al., 2015b]; *Paynomys* [Alarcón et al., 2011; Teta et al., 2014]; *Dromiciops* [D'Elía et al., 2016a]) suggest that the specific diversity of some mammals associated with southern beech forests departs from the traditional view of low specific diversity. In this sense, our understanding of the Quaternary dynamics of the biota from southern South American surely will benefit with further taxonomic studies.

Biogeography

Geoxus lafkenche n. sp. is endemic to Guafo Island, a Pacific island situated about 39 km southwest of the much larger Chiloe Island. With the evidence at hand, *G. lafkenche* n. sp. is recovered as sister to *G. michaelseni* from southern Patagonia and not to *G. valdivianus*, whose distribution includes the nearby Chiloe Island. Stem *G. lafkenche* diverged from the lineage leading to *G. michaelseni* 0.876 Ma (0.525–1.321 Ma). Of course, this is not necessarily the age at which *G. lafkenche* reaches Guafo Island, but only the age when genes, apparently, now private of *G. lafkenche* coalesced with genes now private in

G. michaelseni. As such, the lineage leading to *G. lafkenche* may have reached Guafo Island more recently than 0.876 Ma (0.525–1.321 Ma). Having said that, little is known about the geologic history of Guafo Island; but data indicate that Guafo was not covered by ice during the Last Glacial Maximum (Basualto, 2009; McCulloch et al., 2000; Sugden et al., 2002). Congruently, given that under neutrality, divergence is a function of time, a phylogeographic study of the frog *Eupsophus calcaratus* shows that haplotypic variants from Guafo are markedly differentiated from those of other populations, constituting one of the five main clades that form the genealogy of the species (Nuñez et al., 2011). This result indicates that the population of *E. calcaratus* from Guafo, as we shown here for that of *Geoxus*, has remained isolated from those from the mainland and Chiloé for a long time. Similarly, mitochondrial haplotypes from Guafo Island of the freshwater crab *Aegla alacalufi* form one of the six main clades of the species genealogy (Xu et al., 2009). On the contrary, a similar study of the lizard *Liolaemus pictus* indicates that variants from Gaufo Island are nested in a large clade of variants form Chiloe Island, suggesting that *L. pictus* recently colonized Guafo from Chiloe Island (Vidal et al., 2012; see also Vera-Escalona et al., 2012). This last result just shows that the non-marine fauna of Guafo Island encompasses, as expected, distinct histories.

Our limited molecular sampling, both in terms of geographic coverage and characters (i.e., one locus), precludes advancing a detailed scenario accounting for the biogeographic history of *Geoxus*. As such, the clarification of this interesting biogeographic issue should be the focus of future studies.

Final considerations

The discovery of a new Chilean mammal species reinforces the notion that, even when Chile is not remarkably diverse regarding its non-marine mammal fauna (see the species list in Iriarte, 2008; see also Teta and D'Elía, 2009 and the new species for Chile presented in Spotorno et al., 2013; D'Elía et al., 2015b, 2016a,b), knowledge about fundamental issues such as its specific diversity is still incomplete (D'Elía et al., 2015b). *Geoxus lafkenche* n. sp. is based on two recently collected specimens; this fact highlights the importance of continued collection of specimens in the field and goes against the view held in some biologists circles (e.g. Minteer et al., 2014) that consider that animal collection is no longer needed or justified. ✐

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Appendix

List of specimens used in the morphological analyses and diagnoses, including skins, skeletons and fluid-preserved materials. Those specimens included in the genetic analyses are followed with Genbank accession numbers; an asterisk (*) indicates that a given specimen was no morphologically assessed. Acronyms correspond to the following collections: Argentina: Buenos Aires, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN), La Plata, Museo de La Plata (MLP); Chubut, Puerto Madryn, Colección de Mamíferos del Centro Nacional Patagónico (CNP); Chile: Valdivia, Colección de Mamíferos de la Universidad Austral (UACH); USA: California, Berkeley, Museum of Vertebrate Zoology (MVZ).

Geoxus annectens (n=12): CHILE: Los Ríos, San José, Fundo San Martín (UACH 686, 1063, 1064, 1744, 1745, 3851, 4478, 4479, 5443, 5462* [AF108672], 5464, 5465, 5737, 7056* [KJ614639]).

Geoxus lafkenche n. sp. (n=2): CHILE: Los Lagos, Isla Guafo, Punta Weather (UACH 7399 [KU904314], 7340 [KU904315]).

Geoxus michaelseni (n=4): ARGENTINA: Santa Cruz, Estancia La Ensenada (CNP 437 [HM167876]; topotype of *microtis*), Parque Nacional Perito Moreno (MACN 24675); CHILE: Aysén, Capitán Prat, El Manzano (UACH 7341 [HM167877]); Magallanes, Punta Arenas, Río Las Minas (UACH 2168; topotype of *michaelseni*).

Geoxus valdivianus (n=116): ARGENTINA: Neuquén, Caviahue (CNP 812 [AY275116]), Hua Hum (MLP 8-X-96-2), km 2, sendero península Quetrihué (CNP 438 [HM167878]), Lago Lolog (MLP 8-X-96-6), Lago Quillén (RDS17773* [HM167880]), Parque Nacional Lanín, Pampa Hui Hui (UACH 4480); Río Negro, 43 km SSW Bariloche (MVZ154601* [U03531]), Río Castaño Overo (MVZ182688* [HM167879]). CHILE: Aysén, Lago Atravesado (UACH 6166, 6167), Coyhaique, Reserva Forestal Coihaique (UACH 7141), Almirante Simpson, Lago Verde, Villa Amengual (UACH 6165); Araucanía, Malleco, Collipulli, Parque Nacional Tolhuaca (UACH 703, 704, 2574–2577); Curacautín, Malalcahuello (UACH 2436—2447, JG102* [HM167882]), Lonquimay, Bosque de Nirre (UACH 7147), Cordillera Las Raíces (UACH 5459), Paso de Pino Hachado (UACH 3859–3864), Río Colorado (UACH 2426–2435, 3865, 3866); Cautín, Villarica, Parque Nacional Villarica-Quetrupillán (UACH 2448–2450, 3867–3869, 4326, 4483, 4484); Los Lagos, Chiloé, Yaldad (UACH 2904, 2905, 2174), Palomar Fundo El Venado (UACH 1746), Puerto Carmen (1747); Osorno, Valle La Picada (UACH 705, 706, 2170–2173, 3487–3494, 4171, 4172, 4482, 5735), Parque Nacional Puyehue (UACH 5428, 5429), Llanquihue, Peulla (MVZ 163801); Los Ríos, Valdivia (topotypes of *valdivianus*), 6 km S Puerto Fui (MVZ 173699), Choshuenco (UACH 2425, 3852–3857), Costa Rio Cainahue (UACH 7262* [HM167881]), Fundo La Dehesa (UACH 1060, 2578), Fundo Los Pinos (UACH 5733), San José, Fundo San Martín (UACH 698-702, 1061, 1062, 1748–1754, 3133–3136, 3486, 4481, 5734), La Unión (UACH 4778), Mehuín (UACH 1756), Rupanco, Piedras Negras (UACH 6164).

Supplemental information

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

Figure S1 Genealogical relationship of 13 haplotypes of the cyt b gene of the genus *Geoxus* recovered in the Bayesian analysis conducted with MrBayes.