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4 authors:

Horacio Zeballos
Pontifical Catholic University of Peru

R. EDUARDO Palma
Pontifical Catholic University of Chile

Pablo A Marquet
Pontifical Catholic University of Chile

Gerardo Ceballos
Universidad Nacional Autónoma de México

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PHYLOGENETIC RELATIONSHIPS OF *Calomys sorellus* COMPLEX (RODENTIA: CRICETIDAE), WITH THE DESCRIPTION OF TWO NEW SPECIES

Horacio Zeballos[1], R. Eduardo Palma[2], Pablo A. Marquet[2,3], and Gerardo Ceballos[4]

[1] Instituto de Ciencias de la Naturaleza, Territorio y Energías Renovables, Pontificia Universidad Católica del Perú, Av. Universitaria 1801, San Miguel, Lima 32, Perú
[2] Departamento de Ecología, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Alameda 340, Santiago 6513677, Chile
[3] Instituto de Ecologia & Biodiversidad (IEB), Casilla 653, Santiago, Chile
[4] Instituto de Ecología, Universidad Nacional Autónoma de México, Apartado Postal 70-275, Mexico D.F. 04510, México

Autor de correspondencia: Horacio Zeballos; correo electrónico: horaciozeballos@gmail.com

ABSTRACT

We reviewed the phylogenetic relationships of forms assigned to *Calomys sorellus* based on the Cytochrome *b* gene sequences and morphological comparisons. We present the first description of the evolutionary relationships within the *C. sorellus* species complex. The results show a clade with species from lowlands of Eastern of Andes and other clade with Andean species which contains: *C. musculinus*, *C. sorellus* and *C. lepidus* which would be species complex. One of the new species occurs in the Atiquipa Lomas in the coastal desert of southern Peru, and other on the occidental slope of southern Peru in Arequipa and Moquegua. These new species are based upon considering their phenotypic characteristics (size, coloration, pelage), geographic distribution, and molecular phylogeny.

Key words: New species, rodent, Sigmodontinae, biodiversity, Peru.

RESUMEN

Revisamos las relaciones filogenéticas de las formas asignadas a *Calomys sorellus* **basados en secuencias nucleotídicas del gen mitocondrial Citocromo** *b* **así como de caracteres morfológicos. Los resultados muestran un clado que agrupa a las formas de las tierras bajas al este de los Andes y a un clado andino, compuesto por:** *Calomys musculinus*, *Calomys sorellus* **y** *Calomys lepidus* **que serían complejos de especies.** *C. sorellus* **estaría compuesto por al menos cinco especies, tres de ellas previamente fueron definidas como subespecies, a las que agregamos dos especies nuevas. Una de ellas habita en las lomas de Atiquipa en la costa desértica del sur del Perú, y la otra en las vertientes occidentales de los Andes del sur del Perú en Arequipa y Moquegua. Estas nuevas especies están definidas por sus diferencias morfológicas y moleculares y por su tamaño corporal, pelaje y distribución geográfica.**

Palabras clave: Especie nueva, roedor, Sigmodontinae, biodiversidad, Perú.

Introduction

Sigmodontine rodents are one of the most diverse groups of mammals in the world inhabiting almost all terrestrial environments of South America (Catzeflis *et al.*, 1992; Wilson and Reeder, 2005). The tribe Phyllotini, one of the most diverse groups in this subfamily, includes two very diverse genera, *Phyllotis* and *Calomys*. The genus *Calomys* inhabits a large region between Venezuela and Argentina in the Andean highlands and the eastern lowlands and is related to the oldest forms of the Sigmodontine radiation (Baskin, 1978). Most of these species inhabit the eastern lowlands of the Andes. Cabrera (1961) and Ellerman (1941) recognized 10 to 15 species in this genus, but the number was reduced to four by Hershkovitz (1962). However, two of these species *Calomys laucha* and *Calomys callosus*, have been considered a species' complex (Massoia *et al.*, 1968; Pearson and Patton, 1976; Williams and Mares, 1978; Reig, 1986; Corti *et al.*, 1987; Olds, 1988; Bonvicino and Almeida, 2000) and a recent revisions of the genus have recognized at least 13 species within it (Salazar-Bravo *et al.*, 2001; Bonvicino *et al.*, 2010; Musser and Carleton, 2005; Almeida *et al.*, 2007; González-Ittig *et al.*, 2007; Haag *et al.*, 2007).

In the Peruvian Andes two species of *Calomys* have been recognized. *Calomys lepidus* occurs in the highlands of the Andes above 3,000 m, from central Peru to northwestern Argentina (Pearson, 1951; Cabrera, 1961; Heshkovitz, 1962; Steppan, 1995). The second species, *Calomys sorellus*, is endemic to Peru, where it is widely distributed along the Andes from the northern most part of the country to the Peruvian Andes around Titicaca Lake (Pacheco, 2002). In the northern part of its range, *C. sorellus* lives above 2,000 m whereas in the Andean regions of southern Peru it occurs over 3,300 m (Cabrera, 1961; Heshkovitz, 1962; Pearson, 1951; Steppan, 1995), and its occurrence in western Bolivia is also very likely (Anderson, 1997). Three subspecies of *C. sorellus* have been recognized: *C. s. sorellus*, *C. s. frida*, and *C. s. miurus*.

Oliver Pearson (pers. comm.) captured one individual of the *Calomys* genus in the coastal region of Arequipa, without assigning it to any species. We collected additional specimens in the same locality. At first glance, those specimens did not appear to be similar to any species of the *Calomys* species already described. Therefore, to define the identity of those specimens we carried out analyses of phylogenetic relationships. So, in this paper we analyze molecular and morphological traits of the genus *Calomys* in Peru to evaluate its phylogenetic relationships and species composition.

MATERIALS AND METHODS

Study area

The *Calomys* specimens we used in this study included all its geographic range in Peru (Figure 1). The distribution range of *Calomys* in Peru extends along the Puna from the northern Andes to the southern international border with Bolivia and Chile. The genus is also known form a small area on the southern coast of the Arequipa department where the seasonal fog input supports the development of rich vegetation along hills know as "Loma formations" (Figure 1).

Morphological characteristics

We reviewed 240 *Calomys* specimens which are stored in the following collections: the Bolivian Collection of Fauna (CBF) in La Paz, Bolivia; the Museum of Natural History at the Universidad Nacional Mayor de San Marcos (MUSM) in Lima, Peru; and the Scientific Collection of Museum of Natural History of the Universidad Nacional de San Agustin (MUSA) in Arequipa, Peru (Appendix 1). We followed the terminology for cranial and dental morphology described by Hershkovitz (1962), Carleton and Musser (1989), Voss 1988, and Steppan (1995). External and cranial measurements (Tables 1, 2) were recorded in millimeters (mm) and weight in grams (g). Body measurements were obtained from the skin label; tail length was subtracted from total length to obtain the head-and-body length (HB). Other measurements included: To-

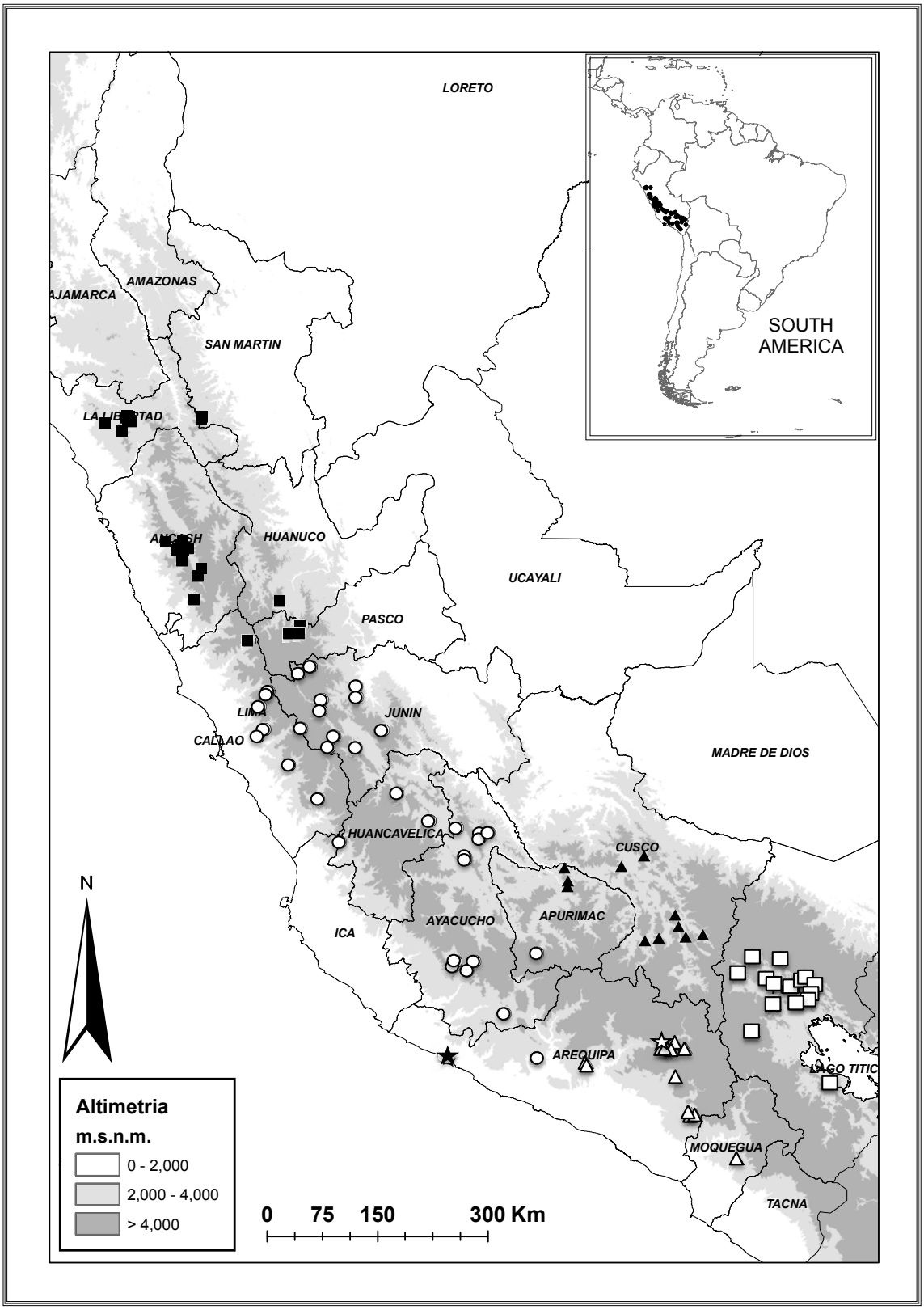

Figure 1. Map of species distribution of *Calomys* from Peru: *C. sorellus* (black squares); *C. miurus* (white circles); *C. frida* of Cusco (black triangles); *C. frida* of Puno (White squares); *C. achaku* (white triangles, type white star); and *C. chinchilico* (black star).

tal length (T); tail length (TL); hind foot length (HF); EL, ear length (EL); and weight (W). Cranial measurements corresponded to: Condyle-Incisive Length; (CIL); LN, Nasallength (NL); Breadth of Braincase (BB); Breadth of Rostrum (BR); Zygomatic Breadth (ZB); Least Interorbital Breadth (LIB); LD, Length of Diastema (LD); Length of the Maxillary Molars (LM);Breadth of Bony Palate Across First Upper Molars (BP); Breadth of MI (BM1); Breadth of the Incisor Tips (BIT); Height of Incisor (HI); Bullar length (BL);Bullar breadth (BW); Interbullar breadth (IBB); Interglenoid fossa breath (GB); and Mandible length (ML). We also assessed the cranial anatomy of specimens used during the study. We develop a comparative revision trait by trait between all species, choosing differential traits between them in order to obtain the diagnostic characters in every form. We followed Ridgway (1912) for color nomenclature.

Molecular analyses

We used the modified phenol-chloroform method (Longmire *et al.,* 1988 and Laird *et al.,* 1991) to extract DNA from tissues (liver or muscle) previously fixed with 96% ethanol. We amplified the Cytochrome *b* gene of the mitochondrial genome (mtDNA) through the polymerase chain reaction (PCR; Saiki *et al.*, 1988). Primers used were H-15767 (Edwards *et al.*, 1991) and L-14724 (Kocher *et al.,* 1989). The thermal profile was 95 °C for 1.5 minutes for denaturation, 56 °C for 15 seconds for the annealing, and 72 °C for 1.5 minutes for extension; this process was repeated for 30 cycles. We included a sample of distilled water without DNA as a negative control in each reaction. We then used agarose gels coated with ethidium bromide to visualize the PCR products, and the successful reactions were purified using the QIAquick method (Qiagen, Valencia, California, USA). Sequencing reactions were performed using the same PCR primers labeled with the Big Dye Terminator Cycle Sequencing Ready Reaction kit (from Applied Biosystems, Foster City, California, USA.). DNA sequences were analyzed with the automatic sequencer ABI Prism 310 (Applied Biosystems) at the laboratory of Molecular Diversity, Pontificia Universidad Católica de Chile. Sequences were aligned using the Clustal X 1.83 program (Thompson *et al.*, 1997), checked visually, and edited with the programs BioEdit 7.0 (Hall 1999) and DnaSP 4.1 (Rozas *et al.*, 2003).

Phylogenetic analyses

We chose the evolution model that best fit the data using the Akaike Information Criterion (AIC; Akaike, 1974) implemented in the program ModelTest (Posada and Crandall, 1998). The best model of evolution was GTR + I + G (-lnL = 8538.9287, AIC = 17097.8574) with a proportion of invariable sites of 0.3052 and a 0.9353 gamma distribution. Base frequencies were: A = 0.29980, C = 0.28740, G = 0.12070 and T = 0.29210; and the substitution rates AC = 1.3623, AG = 4.6718, AT = 1.5242, CG = 0.4259, CT = 7.8241 and GT = 1.0000. We estimated the index of substitution saturation (Iss) with the program DAMBE 4.2.13 (Xia *et al.*, 2003), and our calculated value of Iss = 0.3494 was significantly less than the Iss (0.4782), suggesting little saturation and that the data matrix can be used in phylogenetic reconstructions. The phylogenetic reconstruction was performed using the Maximum Likelihood approach (ML) implemented in PAUP 4.0 (Swofford, 2002). We also conducted a Bayesian analysis implemented in MrBayes 3.1 (Huelsenbeck and Ronquist, 2001, Ronquist and Huelsenbeck, 2005). To measure the confidence of the trees generated with ML, a bootstrap was used (ML) (Felsenstein, 1981; 1985). To build consensus trees and to estimate the probability values of its nodes (By), the Bayesian analyses estimated three million generations; this number did not include the first generations, which represented 25% of the total. In addition, to infer the phylogeny we performed Maximum Parsimony and distance analyses (Minimum Evolution) implemented in PAUP 4.0 (Swofford, 2002). To root the trees we use the out group criterion, including four species of phyllotines: *Eligmodontia puerulus*, *Andalgalomys pearsonomys*, *Auliscomys sublimis* and *Loxodontomys micropus*. The

rate of nucleotide evolution was estimated using the Kimura 2 parameter model, (K2P Kimura, 1980) implemented in the program MEGA5 (Tamura *et al.*, 2011). The phylogenetic analyses involved 26 nucleotide sequences of the genus *Calomys*. Since that all analyzed lowland species are recognized as full species (except "innominate") (Salazar-Bravo *et al.*, 2001; Bonvicino *et al.*, 2003, 2010; Musser and Carleton, 2005; Almeida *et al.*, 2007; González-Ittig *et al.*, 2007; Haag *et al.*, 2007) we use our values of genetic distance and long branch to define the specific separation in the Andean species.

Results

Phylogenetic relationships of Andean *Calomys*

Species in the *C. sorellus* complex showed a high degree of morphological similarity. However, external and cranial measurements showed some significant differences when compared with t-student test (Tables 1, 2). The genus *Calomys* consists of two sister clades; the "Lowlands clade", that includes the species in the eastern Andean lowlands and a Venezuelan species, and the "Andean clade" that includes forms of the Andes from Peru and Bolivia to northern Chile and northwestern Argentina (Figure 2).

Our analyses revealed that the Andean clade included *C. sorellus* and *C. lepidus* which are monophyletic complexes of species. *C. sorellus* consists of five full species: *C. sorellus*, *C. frida*, and *C. miurus* and two undescribed species of Arequipa and Moquegua. The other group contains forms currently assigned to *Calomys sorellus*, which our results also indicate that constitutes a species complex (Figure 1). In fact, the molecular and morphological analyses suggest that the *sorellus* group consists of at least five distinct species between the two strongly supported clades (By: 1.00, ML: 98). One consists of *C. sorellus* from northern Peru and an undescribed species of Atiquipa (New species 1), located in the "Lomas" formations in the coastal desert of southern Peru (ML: 69, B: 0.99). Both species are separated by about 600 km (Figure 1). The other subclade includes *C. miurus* of west central Peru and *C. frida*

Table 1. Number of specimens, average, standard deviation, and range of external measurements of *Calomys* species from Central Andes, with special reference to Peruvian forms. These measurements include Total length (T); Tail length (TL); Head and body (HB); Hind foot (HF); Ear length (EL); Weight (W). Single asterick (*) indicates Cusco and Abancay forms and a double asterisk (**) indicates Arequipa and southwestern Puno forms.

	T	TL	HB	HF	EL	W
sorellus						
(24)	140.00 ± 14.06 116 – 156 (18)	55.70 ± 8.67 43 – 67 (18)	84.30 ± 6.63 70 – 89 (17)	19.50 ± 2.16 18 – 23 (17)	16.90 ± 2.16 16 – 19 (17)	17.30 ± 1.51 14.5 – 19 (14)
frida Cusco						
(12)	168.33 ± 7. 34 155 – 174 (10)	80.86 ± 6.47 69 – 90 (11)	85.14 ± 5.93 76 – 92 (11)	22.19 ± 3.04 20.5 – 29 (10)	18.43 ± 0.53 18 – 19 (11)	18.75 ± 5.44 13 – 26 (7)
frida Puno						
(6)	152.50 ± 25.63 103 – 174 (6)	73.40 ± 3.78 71 – 80 (5)	91.33 ± 10.01 80 – 103 (6)	17.93 ± 1.43 15.29 – 19.1 (6)	17.57 ± 1.42 14.9 – 18.8	22 ± 6.08 15 – 26 (3)
achaku						
(24)	151.35 ± 13.62 129 – 178 (20)	70.76 ± 5.88 59 – 80 (20)	80.40 ± 10.03 65 – 99 (22)	18.09 ± 1.42 14.6 – 20 (22)	16.45 ± 1.79 14.14– 21.02 (22)	17.92 ± 6.53 7 – 28 (12)
miurus						
(80)	149.48 ± 9.75 118 – 171 (71)	65.81 ± 7.59 42 – 80 (71)	83.66 ± 6.72 69 – 98 (71)	18.78 ± 1.48 11 – 22 (73)	17.43 ± 1.62 13 – 21.3 (74)	16.56 ± 3.59 11.1 – 28 (62)
chinchilico						
(22)	144.53 ± 10.45 128 – 161 (21)	66.82 ± 4.76 60 – 75 (21)	77.89 ± 8.31 61.9 – 89 (21)	18.33 ± 0.93 16.5 – 19.6 (21)	16.76 ± 1.22 14 – 19.6 (21)	14.61 ± 2.81 11 – 19 (9)

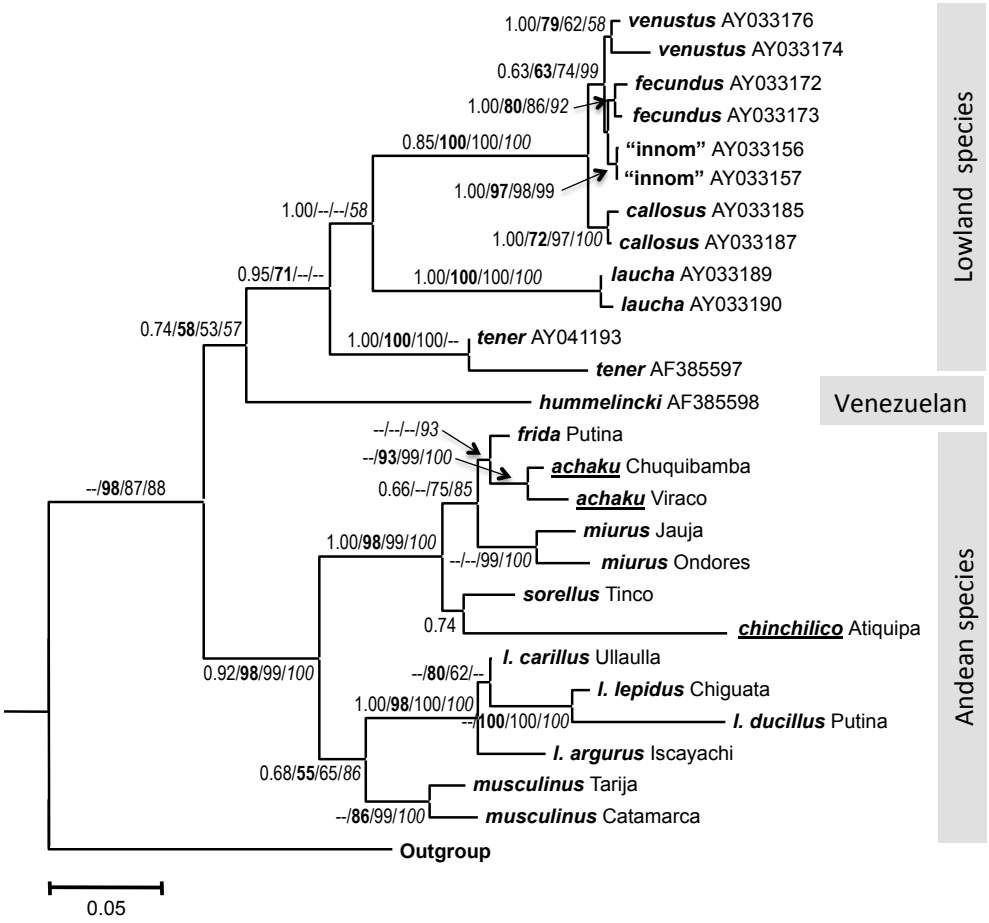

Figure 2. Tree of phylogenetic relationships of the genus *Calomys* genus in the Central Andes obtained through Bayesian Inference, Maximum-Likelihood, Maximum Parsimony and Minimum Evolution analyses based on cytochrome *b* mitochondrial gene sequences. First numbers indicate posterior probability, and bootstrap values for Maximum Likelihood (bold), Maximum Parsimony (third) and Minimum Evolution (italic). Only bootstrap values above 50% are shown. New species underlined.

group (By: 0.66) in Puno, Cusco and Arequipa departments (Figures 1, 2); the Arequipa and Moquegua form (southwestern of Peru) is an undescribed species (New species 2, Figures 1, 2).

The *Calomys lepidus* is formed by two sister groups strongly sustained (By: 0.92, ML: 98), namely *Calomys lepidus* and *Calomys musculinus*. The *Calomys lepidus* group is a species complex. Our results showed that *C. l. argurus* from southern Bolivia and northern Argentina is separated from forms of *C. lepidus* from Peru and Bolivia (By: 1.00, ML: 98). Additionally, our analyses indicated that *C. l. lepidus* and *C. l. ducilla* are also strongly differentiated (ML: 100) with a remarkably long branch.

Interestingly, the branch length of the closely related species of the Andes is larger than those of the lowlands. We also found that K2P distance values between Cytochrome *b* sequences within the same species were below 0.99% with the exception of *C. tener* and *C. venustus* (Table 5). The same distance values between species were greater than 1.85%; the Andean specific forms exhibited higher values than lowland species (Table 5).

Morphological comparisons

Species in the *C. sorellus* complex showed a high degree of morphological similarity. However, external and cranial measurements (Tables 1, 2) showed some significant differences when compared with t-student test. The undescribed form from Lomas of Atiquipa is the sister species of the nominal form, *C. sorellus* (Figure 2), both differ from each in body size, skull size,

Table 2. Number of specimens and average and standard deviation (in parenthesis) of cranial measurements of *Calomys* species from the Central Andes, with special reference to Peruvian forms. Single asterisk (*) indicates Cusco and Abancay forms and a double asterisk (**) Puno.

	chinchilico	*frida**	*frida **	*achaku*	*miurus*	*sorellus*
	(22)	(12)	(7)	(19)	(80)	(24)
CIL	20.50	21.39	21.66	20.75	21.17	21.76
	(0.78)	(0.82)	(1.36)	(0.35)	(0.73)	(1.12)
LN	9.03	9.52	8.87	9.20	9.45	9.56
	(0.49)	(0.69)	(0.93)	(0.80)	(0.48)	(0.63)
BB	10.60	11.13	10.99	9.20	10.92	11.06
	(0.44)	(0.33)	(0.58)	(0.80)	(0.29)	(0.39)
BR	4.07	4.29	4.02	4.07	4.28	4.365
	(0.18)	(0.32)	(0.46)	(0.37)	(0.24)	(0.24)
ZB	11.80	12.50	12.22	12.29	12.22	12.63
	(0.47)	(0.66)	(0.93)	(0.66)	(0.44)	(0.56)
LIB	3.67	3.99	3.84	3.65	3.91	3.92
	(0.11)	(0.13)	(0.22)	(0.16)	(0.16)	(0.28)
LD	5.50	5.82	5.46	5.49	5.68	5.89
	(0.26)	(0.43)	(0.7)	(0.49)	(0.27)	(0.41)
LM	3.49	3.74	3.68	3.45	3.62	3.68
	(0.09)	(0.09)	(0.26)	(0.12)	(0.13)	(0.26)
BP	4.84	4.96	4.93	4.85	4.96	5.14
	(0.17)	(0.19)	(0.35)	(0.27)	(0.19)	(0.19)
BM1	1.16	1.22	1.2	1.16	1.18	1.17
	(0.06)	(0.08)	(0.07)	(0.10)	(0.06)	(0.09)
BIT	1.25	1.37	1.25	1.31	1.32	1.29
	(0.09)	(0.07)	(0.11)	(0.16)	(0.08)	(0.12)
HI	3.33	3.58	3.62	3.55	3.573	3.69
	(0.28)	(0.33)	(0.27)	(0.31)	(0.27)	(0.26)
BL	3.71	3.86	3.75	3.84	3.60	3.73
	(0.17)	(0.24)	(0.45)	(0.17)	(0.26)	(0.39)
BW	3.05	3.03	3.15	2.99	3.06	3.19
	(0.14)	(0.25)	(0.24)	(0.23)	(0.19)	(0.26)
IBB	2.43	2.56	2.61	2.42	2.55	2.44
	(0.27)	(0.32)	(0.18)	(0.26)	(0.23)	(0.26)
GB	9.89	10.30	10.37	10.05	10.20	10.41
	(0.38)	(0.48)	(0.51)	(0.37)	(0.34)	(0.37)
ML	14.01	14.79	14.16	13.87	14.42	14.88
	(0.66)	(0.72)	(1.06)	(1.02)	(0.54)	(0.72)

hind feet, and morphologic cranial structures and coloration (Figure 3; Tables 3, 4). They showed subtle differences with *C. miurus*, differing in color, size of hind feet, skull size, and cranial structures (Table 4). The other undescribed form of the southwestern Andes of Peru (Figures 1, 2), differed from all other species by its pale coloration and morphology (Table 1, 2, 3 and 4). Finally, the phylogenetic analysis showed that this form is closely related to *C. frida* and *C. miurus* (Figure 2). The undescribed form from Lomas of Atiquipa also differs markedly from nominal *C. frida* from Cusco and Apurimac in all measurements, but with similar weight and cranial structures, coloration, and external morphology (Tables 3, 4).

The morphological differences in external and cranial features, molecular phylogeny, and differential measurements across the *C. sorellus* complex support our proposition of species level differentiation for five taxa (*Calomys sorellus*, *Calomys frida*, *Calomys miurus* and two new species). The description of these differences is also presented in the description of the new species.

Forms of the Calomys sorellus complex

Calomys frida, Thomas 1917

Hesperomys frida Thomas 1917
Hesperomys frida frida Gylden stolpe 1932
Calomys frida Frida Cabrera 1961
Calomys sorellus Pacheco *et al.* 2009

Type locality— Chospyoc, Cusco, Peru.

Distribution— *Calomys frida* is distributed in the Andean valleys of Cusco and Apurimac Departments above 2800 m and in the Department of Puno above 3500 masl (Figure 1).

Diagnosis— We retain in *C. frida* the forms of *C. sorellus* complex from Puno because we lack molecular sequences for differentiation; however both exhibit differential morphology that may suggest a specific separation (Figure 3). *Calomys frida* have two morphological forms, one inhabiting the Cusco and Apurimac Department sand the other inhabiting Puno. The nominal form (Cusco) has a long tail in relation to HB (92.27% versus 83.19%); the foramen ovale shows a transverse process that presents a double foramen condition; petrotympanic reduced; parapterigoid-fossa square and in some cases slightly rounded; postero palatal fenestra reduced to two small holes or may disappear altogether in one side; the hamular process is attached or nearly attached along the temporal bone; interparietal bone is elongated and of approximately uniform thickness throughout its length; third molar is smaller than half the second molar; style anteromedial is absent in

Table 3. Comparison of external measurements and length of the skull (CIL) of *Calomys chinchilico* with other forms of *Calomys sorellus* group. With the t test.The values that differ significantly in bold.

A	T	TL	HB	HF	EL	W	CIL
chinchilico-frida Cusco	0,0001	0,0237	0,2438	0,0001	0,0001	0,0843	0,0081
chinchilico-frida Puno	0,2167	0,0078	0,0025	0,4037	0,0621	0,0136	0,0213
chinchilico-achaku	0,0519	0,0262	0,2131	0,4890	0,8940	0,1731	0,5488
chinchilico-miurus	0,5430	0,5162	0,1358	0,0492	0,3808	0,1507	0,0011
chinchilico-sorellus	0,4783	0,7289	0,0170	0,0134	0,0719	0,0144	0,0004
achaku-frida Cusco	0,0353	0,0128	0,0256	0,0002	0,0026	0,9766	0,2328
achaku-frida Puno	0,8846	0,3367	0,0256	0,8136	0,1391	0,3457	0,2525
achaku-miurus	0,3343	0,1607	0,5851	0,0185	0,2858	0,5664	0,3099
achaku-sorellus	0,2856	0,0021	0,2207	0,0000	0,1221	0,7975	0,0341

Table 4. Morphological Comparisons within *Calomys sorellus* complex.

frida Cusco	*frida* Puno	*achaku*	*miurus*	*sorellus*	*chinchilico*
Size (HB: 83.88mm, s=5.4)	Size (HB: 91.33 mm, s= 10.01)	Size (HB: 80.40 mm, s= 10.03)	Size (HB: 80.02 mms=8.87)	Size (HB: 84.35 mms=9.57)	Size (HB: 76.66 mm, s=9.29)
Tail long (92.27% of HB).	Tail medium (83.19% of HB).	Tail medium (83.43% of HB)	Tail medium (83.43% of HB).	Tail short (75.82% of HB)	Tail medium (88.32% of HB)
Dorsal pelage Chamois to Isabelle-color, with black hairs	Dorsal pelage Chamois to Isabelle-color, with black hairs	Dorsal pelage Paler, Cartridge buff to Cream buff, with black hairs	Dorsal pelage Richly colored, Chamois, whit out black hairs or very few	Dorsal pelage Chamois to Isabelle-color, with black hairs	Dorsal pelage Deep Olive buff to Dark Olive buff, with variable number of black hairs
Foramen ovale Large aproximately equal to M3. Generally with a transverse process complete or incomplete that gives a double foramen condition.	Foramen ovale Large sometimes equal to M3 whit out transverse process.	Foramen ovale Does not present a transverse process and is medium to large. Abouth al for more of M3	Foramen ovale Reduced. Less than half of M3	Foramen ovale Reduced. Less than one third of M3	Foramen ovale Reduced. Less than one third of M3
Petro tympanic fissure Reduced or large	Petro tympanic fissure Comparatively large. Is significantly larger than *f. frida* and *miurus*	Petro tympanic fissure Comparatively large. Is significantly larger than *f. frida* and *miurus*	Petro tympanic fissure Developed and broad.	Petro tympanic fossa Developed and bilobed	Petro tympanic fissure developed and broad. Is comparatively wider than *C. frida*. The postero palatal fenestrais conspicuous unlike *C. miurus*.*C. frida* and *C. sorellus* in which are small.
Mesopterigoid fossa Square. In some cases slightly rounded.	Mesopterigoid fossa Acute with parapterygoids divergent or paralels	Mesopterigoid fossa quadrangular to acute with parapterygoids paralels	Mesopterigoid fossa Acute with parapterygoids divergents and lyre shaped	Mesopterigoid fossa Lyre shaped. In Pasco lyre shaped or with parapterygoids divergents	Mesopterigoid fossa Rounded

Table 4. Continuation...

Postero palatalpits Reduced to two small holes or may disappear al together in one side. Currently asymmetrics or just one present	Postero palatalpits Reduced to two conspicuous small holes, always present	Postero palatalpits Reduced to two conspicuous small holes. Frecuently obliterated. But always symmetrics	Postero palatalpits Presenton both sides. Almost symmetrics	Postero palatalpits Reduced. Asymmetrics	Postero palatalpits Small always present
Hamular process of squamosal Frecuently is attached to temporal bone. As a ring. In Puno separated from the frontal bone	Hamular process of squamosal Separated from the temporal bone.	Hamular process of squamosal Separated from the temporal bone.	Hamular process of squamosal Is free and separate of the temporal.	Hamular process of squamosal Free and separated fromthe temporal.	Hamular process of squamosal Free and widely separated from the temporal.
Interparietal Elongated and of approximately uniform thickness throughout its length;	Interparietal Wider and rhomboidal	Interparietal Wider and rhomboidal	Interparietal Wider at its central portion.	Interparietal Is wider at its central portion.	Interparietal Is wider in its central portion.
Antero median style Absent. in a few specimens very light	Antero median style Absent.	Antero median style Absent sometimes present (in 2 of 22)	Antero median style Absent (Huancayo and Lima) to present (Ayacucho)	Antero median style Present	Antero median style Absent
Antero median flexus Present (Cusco) orabent (Puno	Antero median flexus Absent	Antero median flexus Absent in 18 of 22, if present light	Antero median flexus Presente in 28 of 29	Antero median flexus Present	Antero median flexus Absent all specimens

Table 5. Matrix with estimates of Evolutionary Divergence between sequences of genus *Calomys*, using Kimura two parameters model and including all positions for cytochrome b sequences. 1, *chinchilico*; 2, *frida achaku*; 3, *frida frida*; 4, *miurus*-Jauja; 5, *miurus*-Ondores; 6, *sorellus*; 7, *lepidus lepidus*; 8, *lepidus ducillus*; 9, *lepidus carilla*; 10, *argurus*; 11, *frida achaku*; 12, *musculinus* Bolivia; 13, *musculinus*_Argentina; 14, *callosus*_AY033185; 15, *callosus*_AY033187; 16, *fecundus*_AY033172; 17, *fecundus*_AY033173;18, *hummelincki*;19, *laucha*_AY033189; 20, *laucha*_AY033190; 21, innomi_AY033156; 22, innom_AY033157; 23, *tener*_AF385597; 24, *tener*_AY041193; 25, *venustus*_AY033176; 26, *venustus*_AY033174.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
1		0,168	0,182	0,232	0,215	0,178	0,337	0,398	0,288	0,312	0,211	0,291	0,292	0,518	0,515	0,516	0,513	0,451	0,501	0,504	0,512	0,511	0,536	0,486	0,515
2	0,077		0,033	0,073	0,041	0,077	0,247	0,308	0,259	0,235	0,033	0,208	0,209	0,428	0,425	0,458	0,455	0,361	0,411	0,414	0,422	0,421	0,446	0,396	0,425
3	0,072	0,024		0,059	0,065	0,063	0,233	0,294	0,184	0,160	0,053	0,194	0,195	0,414	0,411	0,444	0,441	0,347	0,397	0,400	0,408	0,407	0,432	0,382	0,411
4	0,083	0,056	0,045		0,042	0,092	0,263	0,324	0,214	0,190	0,097	0,224	0,225	0,444	0,441	0,474	0,471	0,377	0,427	0,430	0,438	0,437	0,462	0,412	0,441
5	0,072	0,042	0,036	0,019		0,098	0,269	0,330	0,220	0,196	0,202	0,230	0,231	0,450	0,447	0,480	0,477	0,383	0,433	0,436	0,444	0,443	0,468	0,418	0,447
6	0,062	0,048	0,042	0,069	0,056		0,208	0,269	0,159	0,135	0,088	0,162	0,163	0,389	0,386	0,419	0,416	0,322	0,372	0,375	0,383	0,382	0,407	0,357	0,386
7	0,143	0,134	0,135	0,143	0,138	0,119		0,083	0,053	0,091	0,116	0,172	0,173	0,399	0,396	0,429	0,426	0,332	0,382	0,385	0,393	0,392	0,417	0,367	0,396
8	0,143	0,134	0,135	0,143	0,138	0,119	0,000		0,114	0,152	0,238	0,233	0,234	0,460	0,457	0,490	0,487	0,393	0,443	0,446	0,454	0,453	0,478	0,428	0,457
9	0,134	0,131	0,128	0,136	0,128	0,109	0,017	0,017		0,042	0,121	0,123	0,124	0,350	0,347	0,380	0,377	0,283	0,333	0,336	0,344	0,343	0,368	0,318	0,347
10	0,152	0,154	0,149	0,156	0,147	0,140	0,059	0,059	0,044		0,145	0,147	0,148	0,374	0,371	0,404	0,401	0,307	0,357	0,360	0,368	0,367	0,392	0,342	0,371
11	0,080	0,014	0,026	0,057	0,050	0,050	0,136	0,136	0,129	0,156		0,223	0,224	0,443	0,440	0,473	0,470	0,376	0,426	0,429	0,437	0,436	0,461	0,411	0,440
12	0,123	0,117	0,108	0,121	0,109	0,113	0,098	0,098	0,088	0,127	0,116		0,041	0,309	0,306	0,339	0,336	0,242	0,292	0,295	0,303	0,302	0,327	0,277	0,306
13	0,126	0,121	0,114	0,121	0,112	0,116	0,104	0,104	0,094	0,121	0,122	0,039		0,310	0,307	0,340	0,337	0,243	0,293	0,296	0,304	0,303	0,328	0,278	0,307
14	0,194	0,178	0,176	0,190	0,178	0,187	0,187	0,187	0,174	0,187	0,179	0,163	0,169		0,009	0,045	0,042	0,313	0,231	0,228	0,042	0,041	0,266	0,216	0,037
15	0,191	0,178	0,180	0,194	0,182	0,184	0,183	0,183	0,171	0,189	0,179	0,164	0,169	0,010		0,042	0,036	0,310	0,228	0,225	0,045	0,044	0,263	0,213	0,034
16	0,197	0,180	0,180	0,199	0,186	0,182	0,189	0,189	0,176	0,192	0,185	0,177	0,178	0,020	0,016		0,011	0,310	0,228	0,225	0,021	0,020	0,299	0,249	0,022
17	0,189	0,172	0,174	0,192	0,180	0,174	0,189	0,189	0,176	0,191	0,178	0,181	0,182	0,022	0,017	0,007		0,307	0,225	0,222	0,018	0,017	0,296	0,246	0,019
18	0,160	0,166	0,152	0,162	0,149	0,148	0,184	0,184	0,166	0,181	0,169	0,157	0,150	0,159	0,156	0,156	0,154		0,296	0,299	0,319	0,318	0,285	0,235	0,342
19	0,193	0,175	0,170	0,183	0,172	0,180	0,195	0,195	0,192	0,195	0,181	0,155	0,167	0,160	0,157	0,166	0,168	0,171		0,007	0,225	0,224	0,249	0,199	0,224
20	0,191	0,174	0,169	0,181	0,170	0,178	0,197	0,197	0,194	0,197	0,179	0,153	0,165	0,158	0,155	0,164	0,166	0,169	0,001		0,228	0,227	0,252	0,202	0,227
21	0,201	0,180	0,182	0,204	0,191	0,186	0,193	0,193	0,180	0,195	0,185	0,177	0,182	0,024	0,020	0,010	0,009	0,162	0,172	0,170		0,003	0,304	0,254	0,019
22	0,199	0,178	0,180	0,202	0,189	0,184	0,191	0,191	0,178	0,193	0,183	0,175	0,180	0,023	0,019	0,009	0,007	0,160	0,170	0,168	0,001		0,303	0,253	0,018
23	0,196	0,189	0,187	0,190	0,177	0,191	0,192	0,192	0,181	0,198	0,200	0,174	0,174	0,180	0,180	0,177	0,182	0,195	0,176	0,174	0,182	0,180		0,060	0,303
24	0,160	0,137	0,138	0,146	0,137	0,150	0,163	0,163	0,151	0,162	0,146	0,138	0,138	0,149	0,149	0,149	0,151	0,171	0,145	0,143	0,151	0,149	0,048		0,253
25	0,191	0,174	0,176	0,194	0,181	0,176	0,189	0,189	0,176	0,191	0,179	0,177	0,178	0,023	0,019	0,011	0,010	0,158	0,168	0,166	0,013	0,011	0,178	0,147	
26	0,202	0,187	0,189	0,201	0,188	0,191	0,190	0,190	0,177	0,192	0,192	0,180	0,181	0,030	0,029	0,024	0,023	0,161	0,171	0,169	0,026	0,024	0,183	0,150	0,019

Table 5. Continuation...

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
1																									
2	0.077																								
3	0.072	0.024																							
4	0.083	0.056	0.045																						
5	0.072	0.042	0.036	0.019																					
6	0.062	0.048	0.042	0.069	0.056																				
7	0.143	0.134	0.135	0.143	0.138	0.119																			
8	0.143	0.134	0.135	0.143	0.138	0.119	0																		
9	0.134	0.131	0.128	0.136	0.128	0.109	0.017	0.017																	
10	0.152	0.154	0.149	0.156	0.147	0.14	0.059	0.059	0.044																
11	0.08	0.014	0.026	0.057	0.05	0.05	0.136	0.136	0.129	0.156															
12	0.123	0.117	0.108	0.121	0.109	0.113	0.098	0.098	0.088	0.127	0.116														
13	0.126	0.121	0.114	0.121	0.112	0.116	0.104	0.104	0.094	0.121	0.122	0.039													
14	0.194	0.178	0.176	0.19	0.178	0.187	0.187	0.187	0.174	0.187	0.179	0.163	0.169												
15	0.191	0.178	0.18	0.194	0.182	0.184	0.183	0.183	0.171	0.189	0.179	0.164	0.169	0.01											
16	0.197	0.18	0.18	0.199	0.186	0.182	0.189	0.189	0.176	0.192	0.185	0.177	0.178	0.02	0.016										
17	0.189	0.172	0.174	0.192	0.18	0.174	0.189	0.189	0.176	0.191	0.178	0.181	0.182	0.022	0.017	0.007									
18	0.16	0.166	0.152	0.162	0.149	0.148	0.184	0.184	0.166	0.181	0.169	0.157	0.15	0.159	0.156	0.156	0.154								
19	0.193	0.175	0.17	0.183	0.172	0.18	0.195	0.195	0.192	0.195	0.181	0.155	0.167	0.16	0.157	0.166	0.168	0.171							
20	0.191	0.174	0.169	0.181	0.17	0.178	0.197	0.197	0.194	0.197	0.179	0.153	0.165	0.158	0.155	0.164	0.166	0.169	0.001						
21	0.201	0.18	0.182	0.204	0.191	0.186	0.193	0.193	0.18	0.195	0.185	0.177	0.182	0.024	0.02	0.01	0.009	0.162	0.172	0.17					
22	0.199	0.178	0.18	0.202	0.189	0.184	0.191	0.191	0.178	0.193	0.183	0.175	0.18	0.023	0.019	0.009	0.007	0.16	0.17	0.168	0.001				
23	0.196	0.189	0.187	0.19	0.177	0.191	0.192	0.192	0.181	0.198	0.2	0.174	0.174	0.18	0.18	0.177	0.182	0.195	0.176	0.174	0.182	0.18			
24	0.16	0.137	0.138	0.146	0.137	0.15	0.163	0.163	0.151	0.162	0.146	0.138	0.138	0.149	0.149	0.149	0.151	0.171	0.145	0.143	0.151	0.149	0.048		
25	0.191	0.174	0.176	0.194	0.181	0.176	0.189	0.189	0.176	0.191	0.179	0.177	0.178	0.023	0.019	0.011	0.01	0.158	0.168	0.166	0.013	0.011	0.178	0.147	
26	0.202	0.187	0.189	0.201	0.188	0.191	0.19	0.19	0.177	0.192	0.192	0.18	0.181	0.03	0.029	0.024	0.023	0.161	0.171	0.169	0.026	0.024	0.183	0.15	0.019

most specimens. In Cusco forms dorsal color Chamois to Isabelle-color with abundant black hair, with reduced lateral band without black hairs; pale olive-grey belly; ears cinnamon buff to citrine; tail bicolor drab above and olive buff below; Hind foots olive buff.

Calomys miurus, Thomas 1926

Hesperomys frida miurus, Thomas 1926
Calomys frida miurus, Cabrera 1961
Calomys sorellus, Arana-Cardo y Ascorra 1994
Calomys sorellus, Pacheco *et al.* 2009

Type locality.— Yanamayo, Tarma River, Junín Department, Peru.

Distribution.— *Calomys miurus* is distributed in the Andes of central Peru from Lima and Junín above 2,550 masl, to the Maran-Ocoña River in the north of the Arequipa Department above 3,300 masl (Figure 1).

Diagnosis.— The tail is medium-sized (83.43%,s = 13.94 of HB); the foramen ovale is reduced; the petrotympanic fissure is developed and broad; the parapterigoid pit is characteristically square; the posteropalatal fenestra is present on both sides; the hamular process is free and separated of the temporal; the interparietal bone wider at its central portion; the third molar is approximately half the size of the second; and the anteromedial style is always present (Figure 3). It is the most colorful of all species of Peruvian *Calomys*, dorsally Chamois to Isabella-color with very few dark hairs, absent in most specimens; whitish belly; ears honey-yellow to chamois; hind foots olive buff; tail bicolor citrine-drab dorsally and olive-buff ventrally.

Calomys sorellus, Thomas 1900

Eligmodontia sorella, Thomas 1900,
Hesperomys sorella, Trouessart 1905
Hesperomys sorella, Thomas 1916

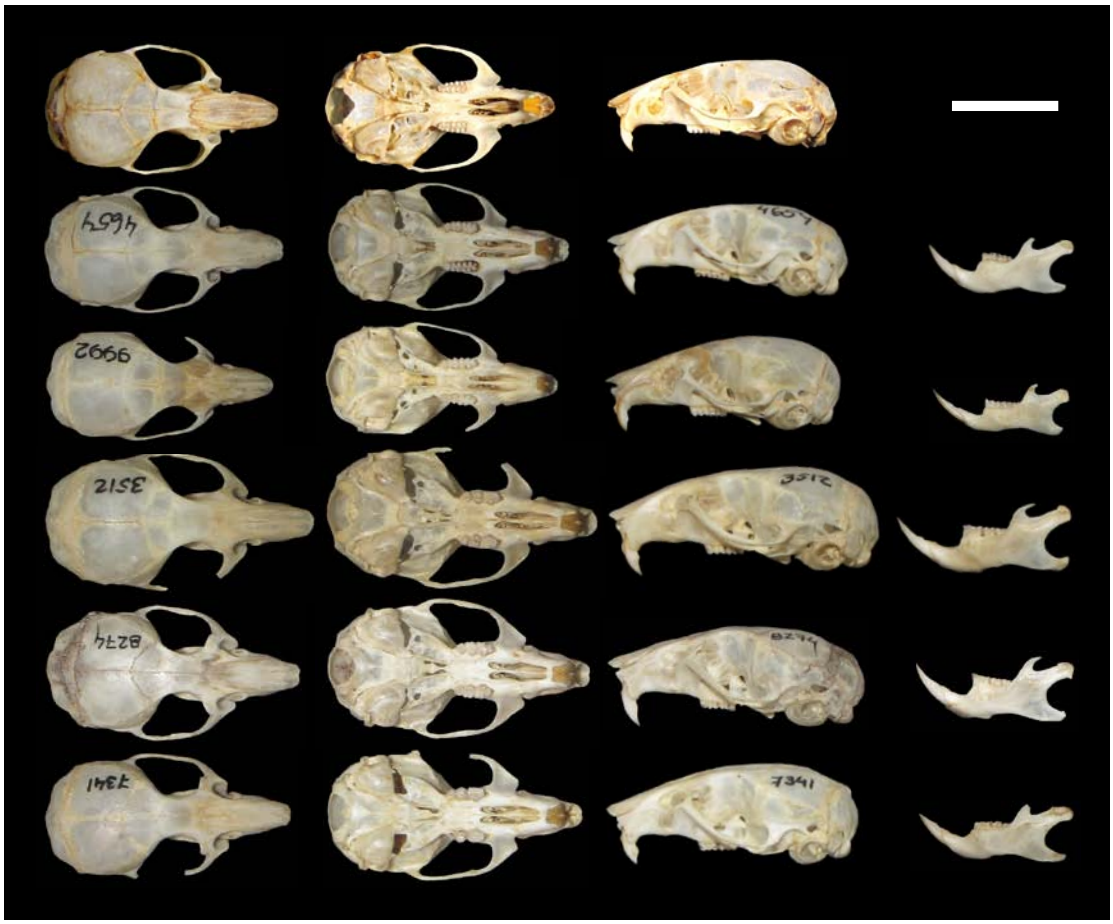

Figure 3. Comparison of Peruvian forms of *Calomys sorellus* complex, from top to bottom: *C. sorellus, C. miurus, C. frida from Cusco, C. frida* from Puno, *C. achaku*, and *C. chinchilico.*

Calomys lepidus ducillus, Cabrera 1961
Calomys lepidus sorellus, Cabrera 1961
Calomys sorellus, Pacheco *et al.* 2009

Type locality.— 8 miles south of Huamachuco, La Libertad Department, Peru.

Distribution.— *Calomys sorellus* is distributed in the Andean region northern Lima, Ancash, La Libertad Departments, above 2000 m, and Andean regions of Pasco Department.

Diagnosis.— The tail is comparatively short (about 75.82%, s = 14.94 of HB); the foramen ovale is reduced; the petrotympanic fossa is well developed and broad; the parapterigoid fossa is lyre shaped; the posteropalatal fenestra is reduced; the hamular process is free and separated from the temporal; the interparietal bone is wider at its central portion; the third molar is reduced and covers approximately one third of the second molar; and the anteromedial style is absent (Figure 3). Dorsal color Chamois to Isabelle-color with abundant black hair, with reduced lateral band without black hairs; pale olive-grey belly; ears Isabelle-color; tail bicolor Saccardo´s Umber above and whitish below; hind foots whitish.

Calomys achaku, new species

Holotype.— Adult male, skin (adult pelage), skull and partial skeleton, under collection number MUSA 8274 (Figure 4) obtained on May 2, 2010, by Horacio Zeballos under field catalogue number HZP 5233 from Linde, between Lari and Ichupampa, Colca Valley, Caylloma Province, Department of Arequipa, southern Peru (15° 38' 32.70" S and 71° 44' 01.43" W at 3,292 masl).

Paratypes.— MUSA 2729, La Laguna, Valle de los Volcanes, Castilla Province; 7194 El Rayo, Yanque, Caylloma Province; 8262, 8293 Linde between Lari and Ichupampa, Colca Valley, Caylloma Province; 10665 Chuquibamba, Condesuyos Province.

Figure 4. Dorsal, ventral and lateral views of the skull of the holotype of *Calomys achacu*.

Distribution.— Currently known only from the highlands of the Andes of Arequipa Departmentand from the southwestern area of Puno Department in southern Peru (Figure 1).

Diagnosis.— Small size (body length: 80.40 mm, s = 10.03 mm), short tail (83.43%, s = 7.28 of head and body length); pelage of dorsum varying from pale gray to brown grayish with orange hairs in some specimens and white in the belly; foramen ovale large; petrotympanic fissure comparatively large; postero palatal fenestra small but always present; hamular

process separated from the temporal; third molar about half the size of the second. This species is supported with a molecular phylogeny based on the Cytochrome *b* gene, with K2P genetic distance of 2.4% and branch length (Table 5). With respect to Puno forms assigned to *C. frida*, the nodal support is high (Figure 2); with respect to nominal *C. frida* it differs by being of smaller size (external and cranial measurements) and shorter tail.

Description and comparison.— *C. achaku*, the sister taxon of *C. frida* (Figure 2), is distinguished by a medium tail (83.43% of the length of HB as compared with *C. frida* which has the tail length equal to 92.27% of the head and body length, but is not different from the Puno forms); it also differs in size (Table 1, 2, and 3A) and by being of a pale coloration. Indeed, *C. achaku* is the paler form of all Peruvian *Calomys*; the dorsal color is cartridge buff to creamy buff with black hairs; lateral band pure Cartridge buff; whitish belly; hairs of ear Chamois; tail bicolor with Light Brownish Olive above and Cartridge buff below. The foramen ovale which does not present a transverse process is very large; the petrotympanic fissure is significantly larger than in the nominal form; the parapterygoid fossa is quadrangular to acute; the postero palatal fenestra generally is reduced to two conspicuous small holes; the hamular process is well-separated from the temporal bone; the interparietal bone is wide and rhomboidal; the third molar is approximately half the size of the second; and the anteromedial style is absent in most specimens. Other small sympatric rodents in their distribution range are: *Oligoryzomys* cf. *andinus*, *Abrothrix andinus*, *Akodon* spp., *Calomys lepidus* and *Mus musculus*, all of them with similar body sizes; *Oligoryzomys andinus* differs in its naked and larger tail (greater than 88 mm and 133% of head and body length), and comparatively large legs (greater than 22.5 mm); *Abrothrix andinus* and *Akodon* have small ears and shorter tail and grayish or dark olivaceus coloration; *C. lepidus* is smaller and shorter tail; *Mus musculus* has a naked appearing tail and ears, not usual whitish ventral coloration, and its tail is similar in size to the length of head and body. The rest of rodents in the area are larger, including: *Phyllotis limatus*, *Phyllotis magister*, *Auliscomys* spp, *Neotomys ebriosus*, *Abrothrix jelskii* and *Rattus rattus*.

Measurements.— External measurements for the holotype are: total length, 156 mm; length of tail, 69 mm; head and body length, 87 mm; length of hind foot, 18.9 mm; ear from notch, 16.4 mm; body weight 26.5 g. The average and standard deviation of the external measurements of this type and five paratypes: total length, 151.80 ± 17.88 mm; length of tail, 71.40 ± 6.07 mm; head and body length, 80.40 ± 13.85 mm; length of hind foot, 19.08 ± 0.81 mm; ear from notch, 16.56 ± 2.90 mm; body weight 17.70 ± 9.13 g. The external measurements of 32 specimens are presented in Table 1.

Etymology.— The name *Calomys*, which literally translates as "*beautiful mouse*", is derived from the Greek "*kalos*" meaning beautiful and "*mys*" meaning mouse. The word "*achaku*" means mouse in the Aymara language, one of the three languages spoken in the southern Andes of Peru.

Hábitat.— This species occurs in highlands of the western slopes of southern Peru Andes in Arequipa department, in grassland communities, "tolares" and xeric vegetation assemblages composed mainly of grasses (*Stipa ichu*, *Festuca orthophyla*, *Calamagorstis* spp.), scrubs, called tolar (*Lepidophyllum lepidophylla*, *Lepidophyllum quadrangulare*, *Bacchahris tricuneata*), farmlands in Andean valleys and *Polylepis* forest (Figure 1, 5).

Calomys chinchilico, new species

Holotype.— MUSA 7341. Adult male, skin, skull, partial skeleton, tissues. Obtained on 1999, July 27 by Kateryn Pino under field catalogue number KPB13 (Figures 5, 6) from Cerro Lloque, Atiquipa District, Caraveli Province, Department of Arequipa, southern Peru (15° 46´ 56,65" S and 74° 21´13,14" W at 900 m, Figure 1).

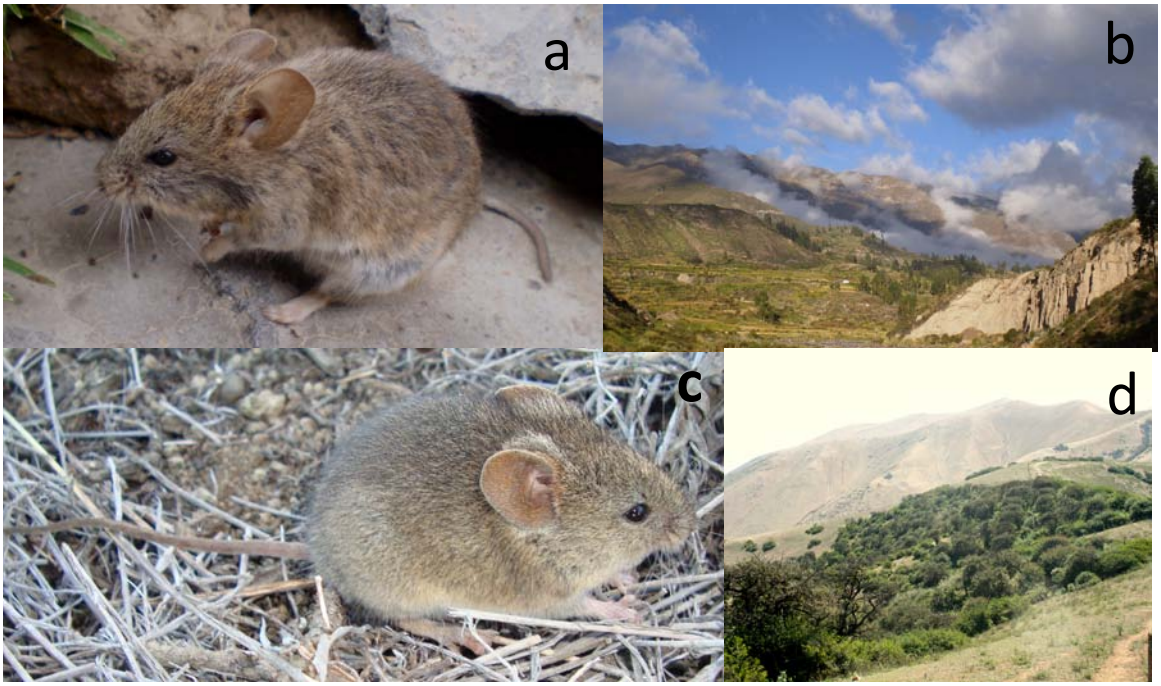

Figure 5. Photos of species and habitats: a) male adult of the new species *Calomys achaku* (Type) taken by Horacio Zeballos; b) Type locality of *C. achaku*, Linde, Colca Valley; c) New species *Calomys chinchilico*, (type) taken by Alexander Pari; and d) type locality of *C. chinchilico*, lomas of Atiquipa, Atiquipa District, Province of Caraveli, Department of Arequipa, Southwestern Peru.

Paratypes.— musa: 1568, 1569, 1570, Quebrada de la Vaca, Lomas de Taymara, Caraveli Province, Arequipa Department, Peru; 5641, Lomas de Atiquipa, Caraveli Province, Arequipa Department, Peru; 7341, 7342, Cerro Lloque, Lomas de Atiquipa, Caraveli Province, Arequipa Department, Peru.

Distribution.— Known only from the Lomas of Atiquipa and Taymara in the coastal desert of southwestern Peru (Figure 1), between 280 and 980 m.

Etymology.— The name *Calomys*, which literally translates as beautiful mouse, is derived from the Greek "*kalos*" meaning beautiful and "*mys*" meaning mouse. The name "*chinchilico*" is a Quechua word that describes a mythological little elf-like human that lives in the galleries of gold mines. The proposed name for this species, which lives in an area known for gold deposits, makes reference to both its Andean cultural identity and its small size.

Description.— The *Calomys chinchilico* is a small mouse (Figure 5) and the external measurements for the holotype are: total length, 159 mm; length of tail, 75 mm; length of hind foot, 18.6 mm; length of the ear, 17.3 mm; body weight, 17g. The rhinarum is more developed and more inflated than in other Peruvian *Calomys*. The ears are ovoid with the most distal border sharp and whiskers are long and extend beyond the ears; the tragus is long and extends one-third of the length of the ear; the ears are hairy with orange hairs on the inner side, dark brown on the outside, and a patch of white hairs at the base. Guard hairs that protrude from the coat, especially in the back, less than 8 mm on the back.The dorsal fur varies from Deep Olive buff to Dark Olive buff and some specimens have a higher concentration of black hairs on the back, but they are not concentrated as distinct bands; the coat has a diffuse longitudinal band Chamois to Deep Olive buff; the sides of the head and body and the belly are whitish to Pallid Smoke grey with a base of the dark gray hairs which contrasts with the color of the sides and the back; ears tawny olive; hind foot and ventral part of the tail is pallid olive buff. The soles have six tubercles; the tarsal tubercle is very small, it is covered with small and rounded

Figure 6. Dorsal, ventral and lateral views of the skull of the holotype of *Calomys chinchilico*.

granulations in all surfaces, and it is hairy from heel to center sole. The tail is short (86% of the length of head and body) and bicolored, yellowish-brown above and whitish below. Legs have white hairs. The first finger is a vestigial paw and has no claw and the toes of the hind legs are thin. Cranial characteristics (Figure 6) are: skull is delicate and slightly inflated in the frontal and parietal bones and has a long, thin and non-rhomboid interparietal; the foramen ovale is reduced; the petrotympanic fissure is developed and broad; the parapterygoid fenestra is rounded; the posteropalatal fenestra is small but always present; the hamular process is free and widely separated from the temporal; the interparietal is wider in its central portion; the anteromedial style is absent; the upper incisors are opisthodont without grooves; the molars are crested, more in M2 and M3 and M1 has a small antero lingual conule that is not noticeable in old specimens; the M2 molar has a small island of enamel.

Comparisons.— *Calomys chinchilico* differs from other coastal rodents of similar size by the following combination of characteristics: comparatively small size; short tail (less than 75 mm or 86% of head and body length); absence of hair tufts of at the tip; hairy ears are less than 16.76 ± 1.22 mm; typically have a post auricular patch of white hairs at the base of ears. Three small sympatric rodents, the *Oligoryzomys arenalis*, *Phyllotis amicus*, and the *Mus musculus* have similar body size. The *Oligoryzomys arenalis* differs in its naked and larger tail (greater than 88 mm and 133% of head and body length); and comparatively large legs (greater than 22.5 mm). The *Phyllotis amicus* has a tail longer than head and body length (greater than 80 mm and 111.6% of the head and body length) and a tuft of hair on the end of the tail; and comparatively longer ears (larger than 19 mm). *Mus musculus* has a naked appearing tail and ears, not usual whitish ventral coloration, and its tail is similar in size to the length of head and body. The rest of rodents in the area are larger, which include *Aegialomys xantheolus*, *Phyllotis limatus*, *Phyllotis* sp., and *Rattus rattus*.

This species differs from other Peruvian *Calomys* based on several characteristics including: fur length which is shorter (less than 8 mm for the dorsal hairs); its coat is yellowish brown to grayish brown, has fewer black hairs on the back, and it lacks gray shades; its ears have slightly pointed edges; the hind feet have comparatively small and delicate tubercles; the rhinarium is more developed and inflated; it has a small antero lingual conule on the first upper molar and an enamel island in the second molar (which may not be noticeable in very old

individuals). They also have a different distribution range in lowlands of the Peruvian coast and separated of *C. sorellus* its closest relative by 615 km.

The *C. chinchilico* is similar in body size and weight to *C. lepidus* (Table 1), but its tail length (more than 60 mm) is longer than the tail of the *C. lepidus* (less than 56 mm), slightly larger than that of *C. sorellus*, similar size to that of *C. miurus*, and shorter than that in *C. frida*. While the coat of *C. chinchilico* has a diffuse orange band on the sides of head and body, the fur is generally ofthe *C. l. lepidus* and *C. l. ducillus* is grayish and most specimens have abundant black hairs on the back that may look like a dark diffuse band. The ears of *C. chinchilico* are ovoid with elongated and acute edges and elongated tragus, and hairy with orange colored hairs in the inside. Postdigital tubercles in *C. lepidus* are developed with short and thick fingers, whereas in the *C. chinchilico* the sole is hairy at the center of the heel and has abundant garnulations throughout the plant of the foot, and in *C. sorellus*, *C. achaku*, *C. frida* and *C. miurus* granulations are not present in the middle part of the plant and the soles are less hairy. *C. chinchilico* differs from *C. sorellus*, *C. achaku*, *C. frida* and *C. miurus* by a more inflated rhinarium. The vibrissae of *C. chinchilico* extends beyond the ears, while in other species it only reaches the ears. The interparietal is long and narrow in the *C. chinchilico* and less rhomboidal in the other species, and the medial width of the frontal bone is approximately equal to or usually less than the maximum width of the rostrum. The foramen ovale differs from that in the *C. sorellus* and is simple and less developed than in the *C. frida* and *C. achaku*. The petrotympanic fissure is comparatively wider in the *C. chinchilico* when compared to that in the *C. achaku* and *C. frida*, and the posteropalatal fenestra is conspicuous, unlike that in *C. miurus*, *C. achaku*, *C. frida* and *C. sorellus* in which they are small. The wide separation of the hamular process from the temporal bone and the greater width of the middle of the interparietal in the *C. chinchilico* distinguish it from *C. frida*.

Habitat.— This species inhabits only the Taymara and Atiquipa lomas, an area where tree and shrub formations obtain moisture from mist condensation (Figure 5). *C. chinchilico* is more abundant in shrub associations of *Grindelia glutinosa*, *Mimosa albida*, *Croton nodiflora* and *Lippia alnifolius* and in isolated patches of *Nicotiana paniculata*. It is rarely found in areas with dense vegetation of shrubs of *Duranta armata*, *Citarexilum flexuosum*, arboreal vegetation of *Caesalpinia spinosa*, or the Atiquipa endemic tree *Myrciantes ferreyrae*. Its greater abundance in small bushes, especially *G. glutinosa*, suggests that this new species has a preference for open land dotted with tall and low shrubs, such as is found in the high Andes.

Discussion

Molecular evidence suggests a close phylogenetic relationship between *C. sorellus*, *C. musculinus* and *C. lepidus* (Salazar-Bravo *et al.*, 2001; Almeida *et al.*, 2007; Haag *et al.*, 2007; Bonvicino *et al.*, 2010). Collectively, they constitute a sister clade relative to other species (*C. hummelincki*) in the eastern lowlands of the Andes and the northern Andes of South America. We suggest that the Andean *Calomys* species exhibit remarkable morphological, molecular and karyotypic differences underlying the recognition of full species status to various forms previously included in *C. sorellus* and *C. lepidus* (Espinoza *et al.*, 1997; Salazar-Bravo *et al.*, 2001; Mattevi *et al.*, 2005; Bonvicino *et al.*, 2010). In addition, their remarkably allopatric distributions may have fostered the evolution of these distinct species.

At the molecular level we found that species of the eastern lowlands are well defined and supported (Salazar-Bravo *et al.*, 2001; Almeida *et al.*, 2007; Haag *et al.*, 2007, Bonvicino *et al.* 2010). In those works the genetic distance (K2P) varied from 1.3%to 4.1% in closely related species, such as *C. callosus*-*C. fecundus* (called *C. boliviae* by Bonvicino *et al.* 2010 and Haag *et al.* 2007). Our results (Table 5) described lower values to genetic distance in closed forms of lowlands from 1.0% between

C. fecundus and *C. venustus*; 1.6% between *C. callosus* and *C. fecundus*; 1.9% in "innominate" with *C. fecundus* or *C. callosus*; or *C. venustus-C. fecundus*. In contrast, the genetic distance in the Andean forms range from 2.4 % and 4.5% in closely species such as *C. frida*, with *C. achaku* or *C. miurus* respectively; to values exceeding 6.0% for more distantly related species such as *C. chinchilico* and *C. sorellus*. Comparatively all Andean species of *Calomys* are highly supported by both bootstrap and posterior probability estimates (Figure 2), revealing a wide diversity comparable to that in the lowlands of the eastern of Andes. However, more samples and studies at a higher resolution are needed to more precisely describe the status of *C. lepidus* and *C. frida*. In particular, the *C. frida* forms from Puno are assigned to this species only tentatively (due to lack of molecular data) as they doshow remarkable morphological differences that suggests a specific level differentiation.

C. sorellus is a complex of at least five species (Figure 2), all of which are endemic from Peru: *C. sorellus* from northern Lima, Ancash Trujillo, northern most Junin and Andean Pasco Departments; *C. miurus* from Lima, Huancayo, Junin, Ayacucho and Huancavelica and northern most Arequipa Departments; *C. frida* with two forms: the nominal form from Abancay and Cusco Departments, and Puno´s forms; two new species described in this paper, *C. chinchilico*, which inhabits the coastal lomas of Taymara and Atiquipa in the southwestern region of Arequipa Department, and *C. achaku* from the western slopes of southern Andes of Arequipa and Moquegua Departments. The latter new species is the only non-Andean form of this radiation and its presence on the coast is explained by the recurrent phenomena associated with climate dynamics of this part of America (Betancourt *et al.*, 2000; Latorre *et al.*, 2007).

Our preliminary results from *C. lepidus* samples and the data clearly show that *C. lepidus* is a species complex which needs to be further explored by incorporating samples from Bolivia and Argentina. All Andean species and *C. musculinus* are monophyletic, and the basal position of *C. musculinus* is consistent with its geographical distribution. Molecular studies show that the genus *Calomys* is one of the most diverse genera of the open lands of South America, and recently this observation has been documented also for the lowlands (Almeida *et al.*, 2007; Bonvicino *et al.*, 2010). Our research has recognized that *Calomys* in the high Andes is more diverse than previously thought and that evolutionary processes leading to speciation have been highly significant in the Andes.

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Annex 1. Analyzed specimens (Museo de Historia Natural de la Universidad San Agustín, MA; Colección Científica asociada al Museo de Historia Natural de la Universidad Nacional de San Agustín de Arequipa, MUSA; Colección Boliviana de Fauna, CBF; Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, MUSM)

Calomys frida. Perú.- Apurímac: Pachachaca, Abancay (MUSA 11267); Carboncallana, Abancay (MUSM 15138, 15139). Ayacucho: Camino a Acocro, Huamanga (MUSA 10730, 10739, 10740); Ichupampa, Huamanga (MUSA 10744, 10745, 10752); Pausa, Paúcar del Sara Sara (MUSA 10753); Alrededores de Putaja, Cochas (MUSA 10746, 10748). Cusco: Acjanaco, Paucartambo (MUSA 4006, 4011, 4072); 5 km N. Huancarani (MUSM 1821); Qda. Quellouno, Calca (MUSA 5642, 5643, 5644, 5645); Matarococha, Yanaoca (MUSA 8734); Yayapara, Yanaoca (MUSA 9991); Lag. Pomacanchi, Acomayo (MUSA 9992, 9993). Puno: Pasincha, Azángaro (MUSA 1343); Hda Checayani, Azángaro (MUSM 2317); Lag. Ticani Moho (MUSA 3500, 3505); Cerro Saiguane, Río Ucumarini (MUSA 3512, 3515); 4.5 km NE. San Anton (MUSM 2312, 2313). ***Calomys achaku.*** Perú.-Arequipa: Achoma (MUSM 2314, 2315, 2316); Tuctumpaya (MUSA 11073, 11248, 11256, 11261, 11264, 11266, 11268, 11271, 11328); La Laguna, Valle de los Volcanes (MUSA 2729); Huanacaure, Andahua (MUSA 2757, 2758, 2759, 2760); Hda. Jjocca, Pillone (MUSA 75); Chaco, Río Colca (MUSA 272); Chivay, Río Colca (MUSA 280); El Rayo, Yanque (MUSA 7194); Linde, Ichupampa, Río Colca (MUSA 8245, 8259, 8262, 8264, 8274, 8293); Chuquibamba (MUSA 10428, 10665). Moquegua: Mariscal Nieto, Torata, Mina Cuajone, Rio Torata (MUSM 14999, 15018, 15026).Tacna: Anexo Tacjata, Comunidad de Vilacota, Susapaya, Tarata (MUSA 12309). ***Calomys miurus.*** Perú.-Arequipa: Ayacucho: Cochas (MUSA 7688); Patibamba (MUSA 7680, 5943, 5944, 5946); Qda. Campana (MUSA 5942, 7697, 7698). Huancavelica: San Pedro de Coris (MUSA 12013); sin localidad (MUSM 2639, 5948, 5949, 5951, 5954, 5959, 5960, 5961, 5962, 5964, 5965, 5966, 5967, 5968, 5969, 5973). Huancavelica: Acobamba (MUSM 16136, 16138). Huánuco: Acococha, Quio-Caina (MUSA 10675). Junín: entre Jauja y Acolla (MUSA 4633, 4634, 4635, 4636, 4637, 4638, 4639, 4640, 4641, 4643, 4647, 4648, 4649, 4650, 4651, 4652, 4653, 4654, 4658, 4659, 4660, 4662, 4663, 4664,4665, 4666, 4667, 4668, 4669, 4670, 4671, 4672, 4673, 4674, 4675, 4676); SAIS Tupac Amaru, Jauja (MUSM 8439, 8441, 8443, 8444, 8446, 8449); Canchayllo (MUSA 5295, 5323, 5339, 5340, 5341, 8697, 8701); Ondores, Lago Junín (MUSA 4920, 4945). Lima: Bosque Karka, Vilca (MUSA 5355, 5357); Vitis, Yauyos (MUSA 8666, 8667); Atavillos Alto; Huaral (MUSA 11943, 11944); Pacomanta, Huarochiri (MUSM 573, 574); 1 km N. San Pedro de Casta, Huarochirí (MUSM 575); Alto Río Sta. Eulalia (MUSM 576, 577); ***Calomys sorellus.*** Perú.- Ancash: Tinco, 14,5 km E de Huaraz (MUSA 4799). Huánuco: Acococha, Ambo (MUSA 10675). Lima: Oyon (MUSM 10751, 10753, 10754, 10755). Pasco: Yacupianan, Huariaca (MUSA 12137); Ancatana, Pampa Hermosa, Huariaca (MUSA 13128); Tingo/Hatun Putahua, Ticlacayan (MUSA 12147, 12152, 12153, 12154, 12158, 12159). ***Calomys chinchilico.*** Perú.- Arequipa: Cerro Lloque, Lomas de Atiquipa (MUSA 7340, 7341, 7342, 7358, 7359, 7360, 7365, 7366, 7367); Lomas de Atiquipa (MUSA 4093, 4094, 5641, 10958, 11071, 11072); Lomas de Taymara (MUSA 1449, 1568, 1569, 1570). ***Calomys lepidus.*** Bolivia.-La Paz: Reserva Nacional de Fauna Ulla Ulla, a 11 km de la Cabaña IBTA (CBF 6412, 6435, 6436). Oruro: 1,5-2 km SO Sajama (CBF 2201, 2205, 2207), Parque Nacional Sajama (CBF 2208); E del Lago Poopo, 4 km by rd N Huancane (CBF 6038); Abaroa, desvío km 181 S Oruro (CBF 6041). Cochabamba: 13Km N de Colomi, Chaparé (CBF 3616, 3675). Peru.- Ancash: Huaraz, Cordillera Negra (MUSM 11621, 11622, 11624, 11626, 11627, 11627). Arequipa: San Juan de Tarucani MUSA 7126, 7137); Lag. Orcococha, Cármen de Chaclaya (MUSA 8314, 8330), Pampa Cañahuas (MUSA 7127, 7129, 7130); Quenco, Callalli (MUSA 79); Imata (MUSA 74), Mauca Arequipa, Imata (MUSA 1150); Tapay, río Colca (MUSA 12015, 12016); Chajhui, Hda. Quilcapata (MUSA 83, 84); Chalhuanca, Yanque (MUSA 6980, 8622); Ayacucho: Camino a Acocro, Huamanga (MUSA 10741, 10742, 10743); Ichupampa, Huamanga (MUSA 10749, 10751); Cusco: Pallpata, Espinar (MUSA 8116). Huancavelica: Chacapampa San Pedro de Coris (MUSA 12013). Huánuco: Yanapacho, Ambo (MUSA 10729). Junín: Canchayllo, Jauja (MUSA 5311). Pasco: Huayllay (MUSA 9994, 10427); Ticlayán, Tingo/Hatun Putahua (MUSA 12142). Puno: Caccachara (MUSA 4386); Cieneguilla, Cabana (MUSA 8720); 4.5 km NE. (by rd) San Anton (MUSM 2309, 2310); Ilave, ca Puno (MUSM 2311). Tacna: Laguna Blanca, Palca (MUSA 12454). ***Calomys musculinus.*** Bolivia.-Chuquisaca: 2 km N Tarabuco, Yamparaes, (CBF 1083); Tarija: 1 km E Tucumillas, Méndez (CBF 2089, 2093); Tucumillas, San Lorenzo (CBF 2246), Tapecuá, Entre Ríos (CBF 2306).

Annex 2. List of species, cytochrome b gene sequences used for phylogenetic reconstruction and, localities records. We used sequences obtained from GeneBank and samples obtained by our field collection.

Calomys venustus: AY033176 (Santiago del Estero, Argentina); AY033174 (Córdova, Argentina); ***Calomys fecundus:*** AY033172 (Porvenir, Tarija, Bolivia): AY033173 (Tucumán, Argentina); ***Calomys* "innominado":** AY033156 (Chumano, Beni, Bolivia); AY033157 (La República, Beni, Bolivia); ***Calomys callosus:*** AY033185 (Cerro Cora, Paraguay); AY033187 (Monte Palma, Paraguay); ***Calomys laucha:*** AY033189 (Estancia Bolívar, Tarija, Bolivia); AY033190 (Boquerón Filadelfia, Paraguay); ***Calomys tener:*** AY041193 (Brasil); AF385597 (Brasil); ***Calomys hummelincki:*** AF385598 (Isiro, Falcón, Venezuela); ***Calomys frida:*** U03543 (Putina, Puno, Perú); ***Calomys argurus:*** AF159294 (Iscayachi, Bolivia) ***Calomys lepidus ducillus:*** AF159294 (Ulla Ulla, La Paz, Bolivia); U03544 (Putina, Puno, Perú); ***Calomys musculinus:*** NK23706 (Tarija, Bolivia); AF385603 (Catamarca, Argentina); ***Eligmodontia hirtipes:*** AF 159289 (La Paz, Bolivia); ***Andalgalomys pearsoni:*** AF 159285 (Santa Cruz, Bolivia); ***Loxodontomys micropus:*** AF 108690 (Rio Negro, Argentina). Additional sequences of: ***Calomys achaku:*** (Viraco, Arequipa, Perú); (Chuquibamba, Arequipa, Perú); ***Calomus miurus:*** (Jauja, Perú); (Ondores, Junín, Perú); ***Calomys sorellus:*** (Tinco, Ancash, Perú); ***Calomys chinchilico:*** (Atiquipa, Perú); ***Calomys lepidus lepidus:*** Chiguata, Arequipa, Perú; ***Auliscomys sublimis*** (Tocra, Arequipa, Perú).