Original Study

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Uncovering cryptic diversity does not end: a new species of leaf-eared mouse, genus *Phyllotis* (Rodentia, Cricetidae), from Central Sierras of Argentina

Abstract: Based on previously published molecular (mitochondrial) and herein provided morphological (qualitative and quantitative data) evidence, we describe a new species of leaf-eared mouse of the genus *Phyllotis*. The new species is morphometrically distinct when compared with other phylogenetically or geographically close species of *Phyllotis*, showing several quantitative differences in their external and craniodental characters (e.g., proportionally broader nasals and interorbital region, and proportionally smaller tympanic bullae). The new species is endemic to central Argentina, occurring on rocky grasslands at elevations of 650–2,800 m a.s.l. This is the only species of *Phyllotis* inhabiting the Central Sierras, a mountain system of medium elevation, isolated from the Andes by low elevation arid and semiarid environments.

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1 Introduction

The genus *Phyllotis* Waterhouse, 1837 includes 26 species of small to medium sized cricetid rodents widely distributed, from highland areas in Ecuador throughout the Andes and Andean foothills to southern Argentina and Chile (Jayat et al. 2016, 2021; Ojeda et al. 2021; Pacheco et al. 2014; Rengifo and Pacheco 2015; Steppan and Ramírez 2015). The number of recognized species within this genus is increasing rapidly, both by elevating to species level of several nominal forms previously considered as subspecies of some widely distributed taxa, as well as by describing new species. For example, Jayat et al. (2016) reviewed the southern populations of the grassland leaf-eared mouse *Phyllotis osilae* J.A. Allen, 1901, recognizing at least three different taxa within it and three candidate species. Similarly, Rengifo and Pacheco (2015) split *Phyllotis andium* Thomas, 1912 into three species, one of them being at the time new to science. However, the case of the yellow-rumped leaf-eared mouse *Phyllotis xanthopygus* (Waterhouse, 1837) is more extreme. Several successive contributions during the last two decades depict that this species is paraphyletic with respect to *Phyllotis bonariensis* Crespo 1964 (Steppan et al. 2007), *P. caprinus* Pearson 1958 (Jayat et al. 2016), and *P. limatus* Thomas, 1912 (Kuch et al. 2002; Steppan et al. 2007), indicating also high levels of genetic variation among their widely distributed populations. Based on these results, and using the largest analyzed dataset of DNA sequences to date for this complex, Ojeda et al. (2021) suggested that *P. xanthopygus* encompasses at least eight species (and perhaps 10), including two for which no names were available (Figure 1).

Recently, Jayat et al. (2021) used qualitative and quantitative morphological traits and DNA sequences to review the
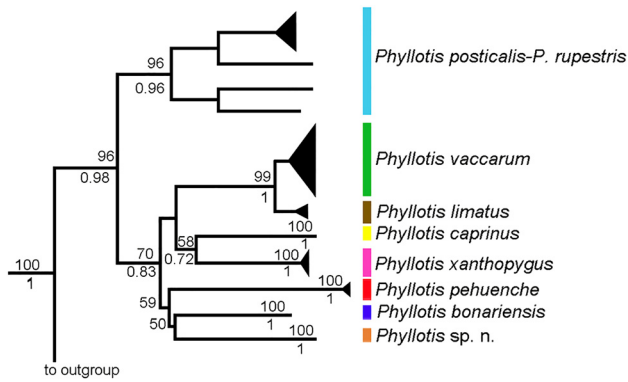
Figure 1: Phylogenetic consensus tree (ML) of 114 cytochrome-*b* gene sequences of *Phyllotis*. Color bars indicate the eight different clades recovered in the maximum likelihood (ML) analyses (simplified from Ojeda et al. 2021). Numbers above nodes indicate ML bootstrap support values and numbers below nodes indicate posterior probability values of the adjacent nodes.

is one of the two candidate species identified by Ojeda et al. (2021). The second unnamed form is exclusive to the Central Sierras of Córdoba and San Luis provinces, in central Argentina, and was recovered as sister to *P. bonariensis* in mitochondrial DNA-based phylogenies (Ojeda et al. 2021; Steppan et al. 2007). This lineage was previously referred in the literature as *P. x. vaccarum* (e.g., Steppan 1998), *P. x. ricardulus* (Pardiñas et al. 2017), or *Phyllotis* sp. 1 (Ojeda et al. 2021). However, all these names correspond to, or are considered as synonyms of, other clades identified by Ojeda et al. (2021). Because no name is available for this morphologically distinctive lineage (e.g., Teta et al. 2018), we name and describe it here as a new species. In addition, we provide additional detailed morphological comparisons with other species of the genus *Phyllotis*, and some biogeographical considerations.

populations of *Phyllotis* in western Argentina. As part of that contribution, these authors rediagnosed *Phyllotis vaccarum* Thomas, 1912, elevating it to the species level, and described a new species, *Phyllotis pehuenche*, from southern Mendoza and Neuquén provinces, Argentina. This latter nominal form

2 Materials and methods

The 335 specimens studied in this report are housed in the following biological collections: AMNH, American Museum of Natural History, New York, USA; CMI, Colección de Mamíferos del Instituto Argentino
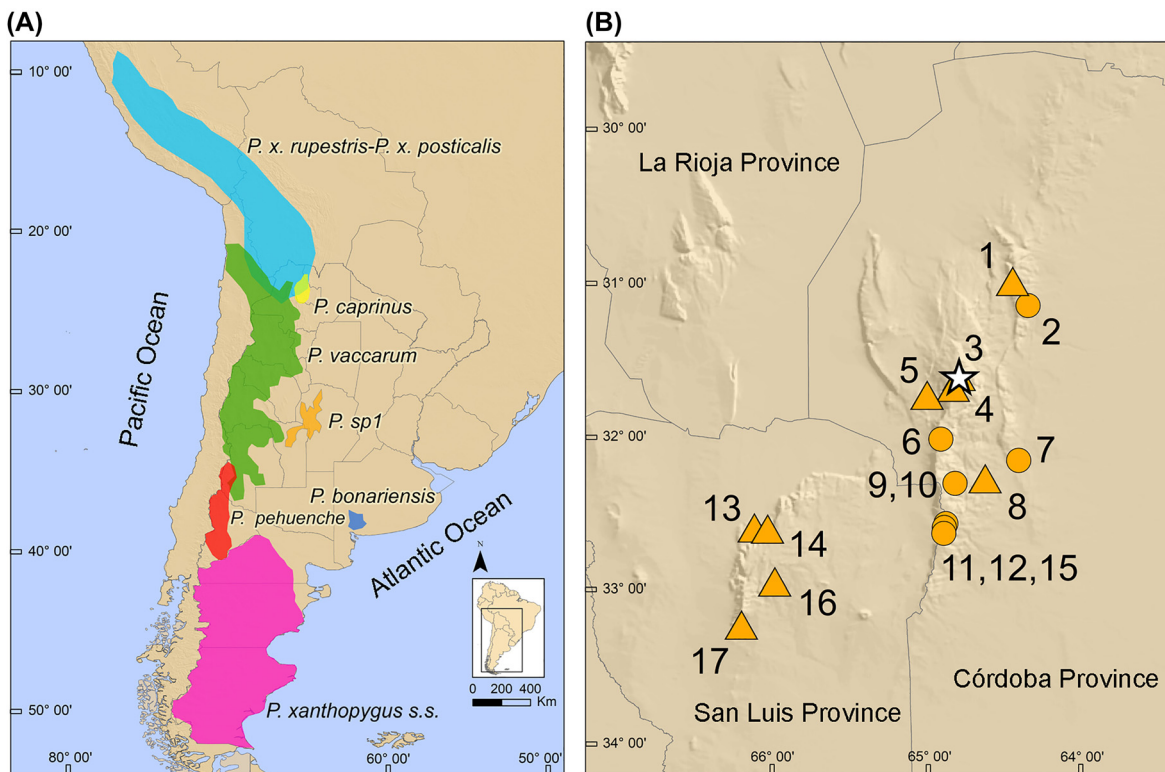
Figure 2: (A) Map of Southern South America showing, as shadowed areas, the approximate distribution of the seven species of the *Phyllotis xanthopygus* complex documented for Argentina. (B) Map of central Argentina depicting the highlands areas and locality records for *P. camiari* sp. n.: the star corresponds to the type locality, triangles refer to reviewed specimens, and circles to those individuals mentioned in the literature (for reference numbers, see Supplementary Material 3).

Table 1: Descriptive statistics (*N* [sample size], mean, SD [standard deviation], range) for 19 craniodental variables of *Phyllotis*.

	Phyllotis bonariensis					*Phyllotis camiari* sp. n.					*Phyllotis pehuenche*					*Phyllotis vaccarum*				
	N	Mean	SD	Min.	Max.	*N*	Mean	SD	Min.	Max.	*N*	Mean	SD	Min.	Max.	*N*	Mean	SD	Min.	Max.
TLS	20	31.95	1.25	29.77	34.88	14	29.72	1.20	26.70	32.09	35	31.2	1.62	27.72	34.61	41	30.67	0.96	28.74	32.77
CIL	20	29.49	1.42	27.04	33.19	14	27.11	1.35	23.82	29.32	35	28.73	1.77	24.85	32.70	41	28.31	1.02	26.54	30.89
NL	20	14.22	0.88	12.73	16.10	14	12.81	0.64	11.25	14.10	35	13.52	1.15	10.73	15.40	41	13.59	0.59	12.24	14.89
NW	20	4.78	0.26	4.34	5.45	14	4.24	0.26	3.75	4.69	35	4.16	0.24	3.70	4.740	41	4.06	0.27	3.34	4.57
RW	20	5.76	0.30	5.14	6.41	14	5.17	0.32	4.58	5.69	35	5.04	0.37	4.28	5.71	41	4.89	0.27	4.27	5.41
IOC	20	4.46	0.18	4.07	4.85	14	4.46	0.17	4.18	4.74	35	4.15	0.18	3.64	4.56	41	4.22	0.18	3.79	4.57
ZB	20	16.47	0.67	15.51	18.33	14	15.38	0.73	13.88	16.49	35	15.82	0.90	14.02	17.61	41	15.69	0.51	14.5	16.79
BB	20	14.05	0.28	13.56	14.71	14	13.35	0.4	12.69	13.81	35	13.77	0.39	12.84	14.50	41	13.69	0.34	12.89	14.52
FL	20	8.80	0.60	7.79	10.07	14	8.15	0.53	6.90	8.93	35	8.60	0.63	7.57	10.05	41	8.40	0.64	6.78	9.53
PL	20	5.83	0.35	5.09	6.34	14	5.95	0.40	5.23	6.81	35	6.12	0.44	5.28	7.20	41	5.72	0.41	4.67	6.79
ZPB	20	3.34	0.19	2.85	3.65	14	3.07	0.16	2.72	3.41	35	3.31	0.37	2.63	4.10	41	3.22	0.23	2.74	3.64
IFL	20	7.63	0.44	6.94	8.68	14	6.93	0.47	6.18	7.79	35	7.65	0.50	6.58	8.87	41	7.33	0.42	6.48	8.24
IFW	20	2.34	0.22	2.02	2.76	14	2.12	0.15	1.90	2.40	35	1.96	0.22	1.14	2.43	41	1.95	0.23	1.11	2.42
PB	20	6.27	0.24	5.72	6.68	14	5.58	0.28	5.01	5.99	35	5.81	0.31	5.11	6.68	41	5.59	0.37	4.77	6.64
DL	20	8.49	0.55	7.61	9.72	14	7.61	0.52	6.73	8.48	35	8.11	1.23	1.92	9.60	41	8.04	0.45	7.08	8.97
TRL	20	5.79	0.24	5.35	6.20	14	5.28	0.20	4.89	5.60	35	5.62	0.25	5.09	6.12	41	5.29	0.24	4.79	5.79
BPM1	20	6.19	0.20	5.84	6.55	14	5.74	0.19	5.32	6.12	35	5.91	0.25	5.51	6.62	41	5.81	0.22	5.38	6.24
BOL	6	4.83	0.35	4.28	5.20	16	4.17	0.48	3.38	4.90	24	4.82	0.45	3.75	5.80	191	4.37	0.35	3.35	5.42
BL	6	5.18	0.14	4.93	5.29	16	4.71	0.18	4.32	5.01	24	5.68	0.25	5.04	6.32	191	5.31	0.25	4.72	6.07

See materials and methods section for explanation of variable abbreviations.

de Investigaciones de Zonas Áridas, Mendoza, Argentina; CMNH, Carnegie Museum of Natural History, Pittsburgh, USA; CNP, Colección de Mamíferos del Centro Nacional Patagónico, Chubut, Argentina; FMNH, Field Museum of Natural History, Chicago, USA; LCM, Laboratorio de Citogenética de Mamíferos, Santiago, Chile; MACN-Ma, Colección Nacional de Mastozoología, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Ciudad Autónoma de Buenos Aires, Argentina; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, USA; MVZ, Museum of Vertebrate Zoology, University of California, Berkeley, USA; SNOMNH, Sam Noble Oklahoma Museum of Natural History, Norman, USA; UACH, Colección de Mamíferos de la Universidad Austral de Chile, Valdivia, Chile; UMMZ, University of Michigan Museum of Zoology, Ann Arbor, USA; USNM, National Museum of Natural History, Smithsonian Institution, D.C., USA; UWBM, University of Washington, Burke Museum of Natural History, Seattle, USA (see Figure 2 and Supplementary Materials 1 and 2 for details). Studied specimens included the holotype and paratypes of *P. bonariensis*, *P. pehuenche*, and some topotypes of *P. vaccarum*.

Terminology used to describe external and qualitative skull traits follows Voss (1988), Olds and Anderson (1989), and Steppan (1995). Quantitative and qualitative morphological comparisons among taxa were guided by the results of phylogenetic analyses of DNA sequences (Ojeda et al. 2021; Figure 1). For 111 of the specimens (see Supplementary Material 1 for details), and whenever possible, we recorded five external and 17 craniodental measurements (in mm). External measurements include total length (TL), length of tail (T), hindfoot length (with claw, H), length of ear (E) and weight (W), that were transcribed from skin labels and field catalogues. Cranial and dental measurements were taken with digital calipers to the nearest 0.01 mm and include: total length of the skull (TLS), condylo-incisive length (CIL), nasal length (NL), nasal width (NW), rostrum width (RW), interorbital constriction (IOC), greatest zygomatic breadth (ZB), breadth of braincase (BB), frontal length (FL), parietal length (PL), zygomatic plate breadth (ZPB), incisive foramina length (IFL), incisive foramina breadth (IFW), palatal bridge (PB), upper diastema length (DL), upper toothrow length (TRL), and breadth of palate at the level of the first upper molars (BPM1). Basioccipital length (BOL) and bullar length (BL) were measured for a separate set of 231 skulls as part of the dataset described in Steppan (1997) as well from six *P. bonariensis* included in the set of 111 individuals measured for the other skull characters (see Supplementary Material 2 for details). For descriptions and illustrations of the analytical endpoints of these measurements see Steppan (1997) and Rengifo and Pacheco (2015).

Qualitative and quantitative morphologic comparisons were structured based on the phylogenetic hypothesis proposed by Ojeda et al. (2021) and following the taxonomy proposed by Jayat et al. (2021). Patterns of variation among recognized species were assessed through descriptive statistics (i.e., mean, minimum and maximum values, standard deviation) and multivariate statistical analyses. Principal components analysis (PCA) and canonical variates (CV) were conducted on the variance-covariance matrix of the 17 log10-transformed craniodental variables. We restrict the quantitative morphological comparisons to the clades of *P. bonariensis*, *P. pehuenche*, and *P. vaccarum*, because those species appear close to *Phyllotis* sp. 1 in the phylogenetic analysis of DNA sequences (e.g., Ojeda et al. 2021) or were linked to it based on geographical and morphological grounds (e.g., Jayat et al. 2021; Steppan 1998). Multivariate analyses were

conducted only on adult specimens (i.e., those of the ages 3–5, sensu Steppan 1997), using the software PAST v. 2.17 (Hammer et al. 2001).

To identify and delimit species lineages we use an integrative approach, analyzing qualitative and quantitative morphological traits (this work) and mitochondrial DNA sequences (using previously published sequences; see Ojeda et al. 2021 and Figure 1). We interpreted the results under the so-called General Lineage Concept of species (de Queiroz 2007), which is one of the most frequently used in current works centered on rodent systematics (D'Elía et al. 2019). This published work and the nomenclatural act it contains have been registered in ZooBank. The LSID for this publication is: urn:lsid:zoobank.org:pub:D2FA0EB7-9936-49AD-A625-4268D547DD42.
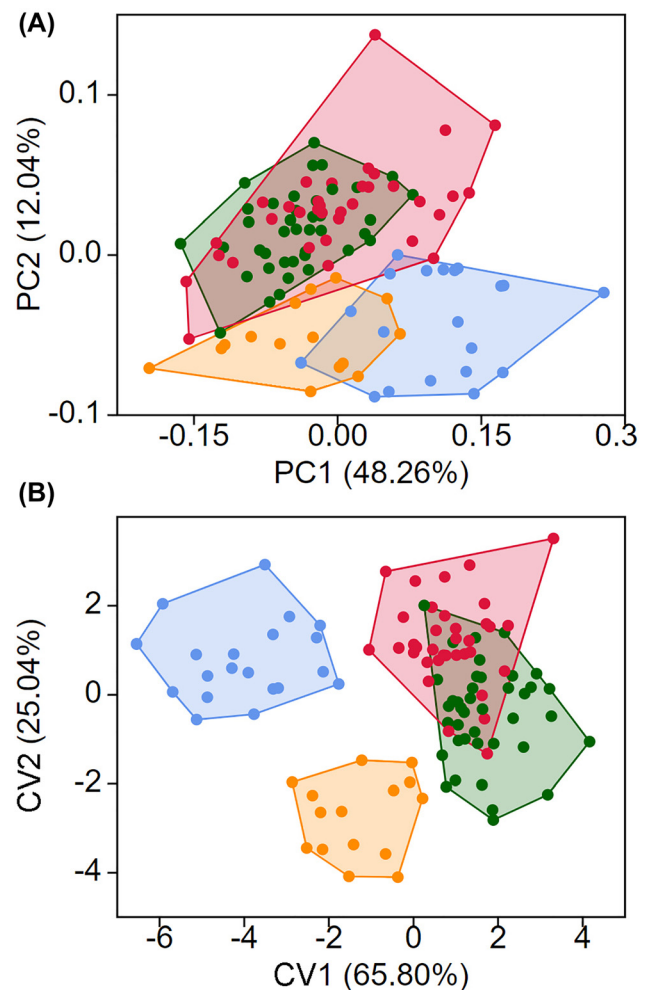
Figure 3: Individual specimen scores based on log-transformed values of 17 cranial measurements, projected onto the first and second principal components (A), and the first and second canonical variates (B), extracted from analysis of adult specimens of *Phyllotis bonariensis* (blue dots, N = 20), *P. camiari* sp. n. (orange dots, N = 15), *P. pehuenche* (red dots, N = 35), and *P. vaccarum* (green dots, N = 41). Character loadings and the variance explained by each of the first two principal components and canonical variates appear in Table 2.

3 Results

Qualitative morphological traits that characterized each species here recognized are summarized in the Discussion section. Quantitative morphological variation is presented in the next paragraph of this section.

Descriptive statistics (i.e., mean, minimum and maximum values, standard deviation) for selected craniodental variables are summarized on Table 1. PCA shows that all variables were positively correlated with the 1st principal component (PC1 48.26% of the total variance), that is in accordance with its interpretation as a size vector (Figure 3A, Table 2). Highest loadings along PC1 correspond to rostral breadth variables, including IFW, NW, and RW. In the 2nd principal component (PC2, 12.04% of the total variance), the most important variables were ZPB with positive loadings and IFW with negative ones. Overall, there are three main clusters along the first and second PCs, with a minimal overlap between them: one composed of individuals referred to *P. bonariensis*, another including *Phyllotis* sp. 1, and a third represented by *P. pehuenche* and *P. vaccarum*.

CV analysis revealed the existence of four major clusters along the two first axes (Figure 3B; Table 2), each corresponding to each of the four taxa included in this study (i.e., *P. bonariensis*, *Phyllotis* sp. 1, *P. pehuenche*, and *P. vaccarum*). Multivariate envelopes of *P. bonariensis* and

Phyllotis sp. 1 did not overlap, neither with each other, nor with other species (Figure 3B); in turn, *P. pehuenche* and *P. vaccarum* are moderately overlapped along the first and second axes (Figure 3B), that accounted for 65.80 and 25.04% of the total variance, respectively (Table 2). CV1 separated specimens referred to *P. bonariensis* from the other taxa due to larger values for IFW, NW, and RW (Table 2). CV2 segregated samples identified as *Phyllotis* sp. 1 from *P. pehuenche* and *P. vaccarum* by having larger DL, IFL, and TRL.

In addition to distinguishing *Phyllotis* sp. 1 by multivariate ordination, this candidate species was distinctive for the small size of its auditory bullae, overlapping in relative size only with the smallest individuals of *P. vaccarum* (Figure 4).

4 Discussion

Recent integrative studies showed that several nominal species of *Phyllotis*, such as *P. andium*, *P. osilae* or *P. xanthopygus* represented complexes of closely related and cryptic taxa (e.g., Jayat et al. 2016, 2021; Ojeda et al. 2021; Rengifo and Pacheco 2015). In each case, phylogenetic analysis of molecular markers provided a novel framework to evaluate the geographic variation in qualitative and quantitative morphological characters, allowing the detection of previously overlooked discontinuities in anatomical

Table 2: Results of principal components analysis (PCs; first and second columns) and canonical variates (CVs; third and fourth columns) performed on adult specimens of *Phyllotis* (*N* = 111).

	PC1	PC2	CV1	CV2
TLS	0.2102	0.1335	−0.0021	0.0057
CIL	0.2438	0.1684	−0.0020	0.0067
NL	0.2597	0.1278	−0.0024	0.0060
NW	**0.3626**	−0.1963	**−0.0123**	0.0035
RW	**0.3722**	−0.2592	**−0.0123**	0.0033
IOC	0.0304	−0.3493	−0.0053	−0.0055
ZB	0.2134	0.0864	−0.0030	0.0040
BB	0.0779	0.0507	−0.0012	0.0037
FL	0.1632	0.1842	−0.0026	0.0065
PL	0.0588	0.1253	−0.0003	0.0039
ZPB	0.2944	**0.3956**	−0.0014	0.0088
IFL	0.2476	0.2669	−0.0010	**0.0108**
IFW	**0.3671**	**−0.6045**	**−0.0138**	0.0001
PB	0.2360	−0.0600	−0.0075	0.0079
DL	0.3012	0.2310	−0.0024	**0.0101**
TRL	0.1640	−0.0010	−0.0048	**0.0096**
BPM1	0.1420	0.0017	−0.0039	0.0052
Eigen value	0.0073	0.0018	4.5250	1.7221
% Variance	48.26	12.04	65.80	25.04

See materials and methods section for explanation of variable abbreviations. Numbers in bold correspond to highest loadings.
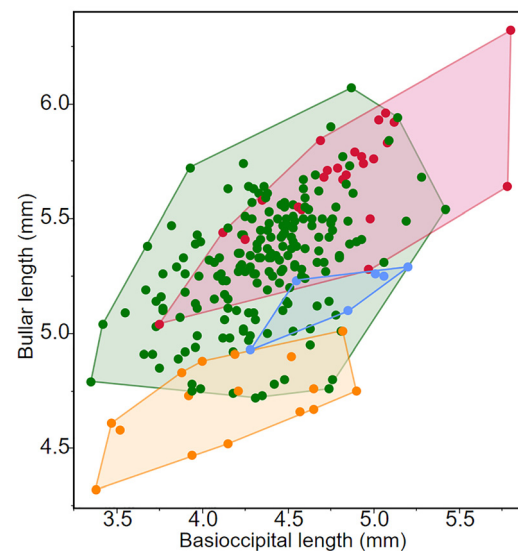
Figure 4: Bivariate scatterplots of basioccipital length (mm) on bullar length (in mm) in four species of *Phyllotis* (*N* = 237): *Phyllotis bonariensis* (blue dots, *N* = 6), *P. camiari* sp. n. (orange dots, *N* = 16), *P. pehuenche* (red dots, *N* = 24), and *P. vaccarum* (green dots, *N* = 191).

traits. The case of *P. xanthopygus* is noteworthy, since this species was the object of several successive revisionary works, all of which retained it as a morphologically diverse and widely distributed taxon (e.g., Riverón 2011; Steppan 1998; Teta et al. 2018). And, as a logical corollary of such diversity, most previous authors recognized several subspecies within *P. xanthopygus*, most of these apparently diagnosable by a combination of external and craniodental characters (cf. Hershkovitz 1962; Pearson 1958).

As was demonstrated by previous authors, most lineages within the *P. xanthopygus* species complex can be discriminated by a combination of qualitative and quantitative morphological and karyological traits (Jayat et al. 2021; Ojeda et al. 2021; Teta et al. 2018). Some of the clades included within *P. xanthopygus* sensu lato can be equated to previously recognized subspecies (e.g., *P. vaccarum*, *P. xanthopygus*), while others are novel. For example, the lineage referred as *Phyllotis* sp. 1, which was first recognized by phylogenetic analysis of DNA sequences (see Riverón 2011; Steppan et al. 2007), represents a morphologically cohesive form that is distinguishable from all others in the genus (Teta et al. 2018; this work). Most closely related to *P. bonariensis* for mitochondrial DNA (Ojeda et al. 2021), these animals are endemic to the Central Sierras of Argentina (Córdoba and San Luis provinces) and represent an ancient eastward expansion of the genus. Because the available evidence supports *Phyllotis* sp. 1 as a new species to science, and because no name is available for it, we describe it here as follow:

Phyllotis camiari sp. n. (Figures 5–7) LSIDurn:lsid:zoobank.org:act:95000D25-AF82-4056-BD9A-E8B3048C455E.

Phyllotis darwini: Polop 1989: 55.

[*P. xanthopygus*] *vaccarum*: Steppan 1998: 574.

P.[*hyllotis*] *x.*[*anthopygus*] *vaccarum*: Steppan 2007: 822.

Figure 6: Cranium in lateral, dorsal and ventral views, and mandible in labial view of *Phyllotis camiari* sp. n. (MACN-Ma 29429, holotype). Scale = 5 mm.

*P.*[*hyllotis*] *x.*[*anthopygus*] *ricardulus*: Pardiñas et al. 2017: 525.

Phyllotis sp. 1: Ojeda et al. 2021: 3.

Holotype: MACN-Ma 29429 (JPJ 2155), adult male (age class 4); skin, skull and skeleton, and tissues, collected on 18 August 2008 by J. P. Jayat and P. E. Ortiz (Figures 5–7). DNA sequence of the cytochrome *b* gene gathered from this

Figure 5: Two different views of the same individual of *Phyllotis camiari* sp. n. (MACN-Ma 29429, holotype), an adult male from approx. "6 km (por ruta 34) al E de la antena repetidora La Posta, 2.300 m s.n.m.," San Alberto Department, Córdoba Province, Argentina.
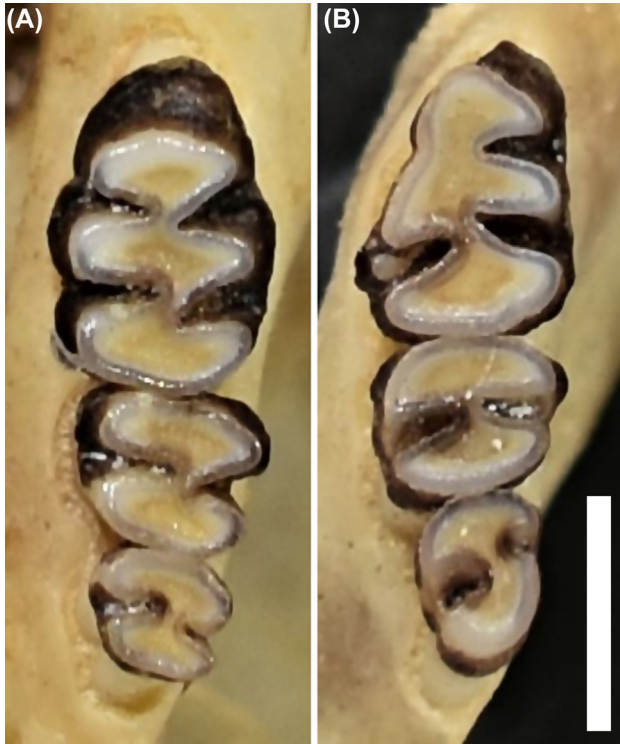
Figure 7: Upper left (A) and lower right (B) toothrows in occlusal views of *Phyllotis camiari* sp. n. (MACN-Ma 29429, holotype). Scale = 2 mm.

specimen, which is considered as the hologenetype, was deposited in Genbank with accession number MT776477.

Type locality: Argentina, Provincia de Córdoba, Departamento San Alberto, Pampa de Achala, aprox. "6 km (por ruta 34) al E de la antena repetidora La Posta, 2.300 m s.n.m." (ca. −31,61200, −64,79900; see Figure 8).

Paratypes: MACN-Ma 29430 (JPJ 2156), adult male (age class 4); preserved as skin, skull and skeleton and tissue sample (a DNA sequence of the cytochrome *b* gene gathered from this specimen was deposited in Genbank with accession number MT776476), collected on 18 August 2008 by J.P. Jayat and P.E. Ortiz, and MACN-Ma 29585 (JPJ 2157), adult male (age class 4); preserved as skull, collected on 18 August 2008 by J.P. Jayat and P.E. Ortiz.

Measurements of the holotype (in mm): Total length, 269; length of tail, 145; hindfoot length, 30; length of ear, 22; weight, 50 (g). Total length of the skull, 30.61; condylo-incisive length, 28.04; nasal length, 13.04; nasal width, 4.24; rostrum width, 5.69; interorbital constriction, 4.54; greatest zygomatic breadth, 16.49; breadth of braincase, 13.71; frontal length, 8.87; parietal length, 5.95; zygomatic plate breadth, 3.21; incisive foramina length, 6.95; incisive foramina breadth, 2.40; palatal bridge, 5.61; upper diastema length, 7.60; upper toothrow length, 5.28;

Figure 8: Four views of the environment (rocky grasslands) around the type locality of *Phyllotis camiari* sp. n., approx. "6 km (por ruta 34) al E de la antena repetidora La Posta, 2.300 m s.n.m.," San Alberto Department, Córdoba Province, Argentina.

breadth of palate at the level of the first upper molars, 5.78; length of tympanic bullae, 4.57; basioccipital length, 4.63.

Diagnosis: A medium-sized species of the *P. xanthopygus* species complex, with a range of total length of 212–259 mm, diagnosable by the following combination of morphological traits: dorsal fur from the head to rump sepia to brownish olive, finely streaked with black hairs; flanks, cheeks and the area around the eyes and nose lighter, forming a slightly developed yellowish fringe that separate the flanks from the venter in some specimens; venter predominantly whitish, with a buffy pectoral streak; tail bicolored, brownish above and creamy to grayish-white below; dorsal surface of manus and pes covered by short whitish hairs; skull moderately robust, with a rounded braincase and a "U shaped" fronto-parietal suture; interorbital borders nearly parallel without overhanging borders; rostrum and nasals proportionally broad (nasals not as widened as in *P. bonariensis*); zygomatic arches comparatively well expanded; zygomatic notches proportionally broad and deeply excavated; zygomatic plates broad, with a slightly concave to nearly straight anterior border; posterolateral palatal pits large and placed ahead of the anterior border of the mesopterigoyd fossa; tympanic bullae especially small and globose; upper incisors robust and orthodont, frontally covered by an orangish enamel; molar series comparatively robust; upper molar series with a simplified enamel pattern.

Morphological description: *P. camiari* sp. n. is medium sized for the genus. External measurements for adults (age classes 4, *N* = 9) are: total length 212–259 mm; tail 111–144 mm; hindfoot 24–28 mm; ears 20–23 mm; body weight 36–46 g.

Dorsal fur from the head to rump sepia to brownish olive, finely streaked with black hairs. Individual hairs on dorsum (9–10 mm) plumbeous at base and yellowish to brownish at tip; guard hairs entirely blackish, surpassing the rump by 4–5 mm. Flanks, cheeks and the area around the eyes and nose lighter, forming a slightly developed yellowish fringe that separates the flanks from the venter in some specimens. Ventral fur predominantly whitish, with hairs gray based and tipped by white; an small and narrow buffy pectoral streak of 10–15 mm is present in all the reviewed specimens. Vibrissae moderately abundant, surpassing the ears when extended backward. A small area of hairs completely white is present on the chin. Eyes surrounded by a thin blackish ring. Ears medium-sized and moderately covered by yellowish hairs. Tail conspicuously bicolored, being brownish above and creamy to grayish-white below, and ending in a small pencil (ca. 5 mm) of brown hairs; scales are evident without magnification.

Dorsal surface of manus and pes covered by short whitish hairs (Figure 5).

Skull moderately robust, with a rounded braincase, a "U shaped" fronto-parietal suture and the rostrum and nasals proportionally broad; nasals anteriorly extended ahead of the plane of the anterior face of upper incisors and surpassing in its posteriormost point the level of the lacrimals; interorbital borders nearly parallel and not sharp-edged; zygomatic arches comparatively well expanded; zygomatic notches proportionally broad and deeply excavated; lacrimals moderately developed; temporal and lamboidal crests weak to moderately developed; interparietal large and broad; zygomatic plates broad, with a slightly concave to nearly straight anterior border; incisive foramina proportionally short, extending to the procingulum of M1; postero lateral palatal pits large and placed ahead of the anterior border of the mesopterigoyd fossa; mesopterygoid fossa relatively narrow, with a square anterior margin and without median spine; anterior border of the mesopterygoid fossa placed behind the posterior margin of the alveolus of M3; parapterygoid fossae moderately excavated, with straight, and somewhat divergent backwards, lateral margins; tympanic bullae especially small and globose, with moderately large Eustachian tubes (Figure 6). Some clinal variation in bullar size is evident, with all the individuals with the relatively smallest bullae (outside the range of any other species of *Phyllotis* here studied) being from Córdoba, whereas bullae from those individuals from San Luis overlap with the smallest bullae among *P. vaccarum* (Figure 4).

Mandible moderately robust, with the usual shape observed in *Phyllotis*, characterized by a short and broad coronoid process that reaches the same or just surpassing the level of the condyle; angular process narrow and only slightly shorter than the condyle; upper and lower masseteric ridges moderately developed, anteriorly extended to the anterior face of m1 and ending at level or just above of mental foramen; capsular projection conspicuous, located below the coronoid process or the anterior margin of the sigmoid notch and slightly slanted backward; sigmoid notch comparatively shallow; lunar notch well excavated (Figure 6).

Upper incisors robust and orthodont, frontally covered by an orangish enamel; molar series comparatively robust, with the general pattern observed in *Phyllotis*; upper and lower molars with their main cusps almost completely transversely oriented; M1 with a fan-shaped procingulum; anterolingual and anterolabial conules are almost equal in size; anteromedian flexus not distinguishable; protocone

Figure 9: Dorsal (A–D) and ventral views (E–H) of the skulls of *Phyllotis bonariensis* (A, E; MACN-Ma 14919, holotype), *P. camiari* sp. n. (B, F; MACN-Ma 29429, holotype), *P. pehuenche* (C, G; CMI 6791, holotype), and *P. vaccarum* (D, H; CML 4480). Scale = 5 mm.

and paracone and hypocone and metacone are nearly equal in size and with rounded outer margins; hypoflexus transverse and metaflexus somewhat oblique and oriented backward; M2 similar to the same portion on M1, but with a deeply excavated hypoflexus; M3 comparatively small and somewhat circular in outline, retaining a distinct hypoflexus and mesoflexus even in adult individuals. Lower molars as for the genus in their general pattern, with a S-shaped m3 (Figure 7).

Morphological comparisons: *P. camiari* sp. n. is smaller than *P. bonariensis*, being characterized by proportionally narrower nasals, rostra and zygomatic arches and smaller tympanic bullae and posterolateral palatal pits (Crespo 1964). Overall, the dorsal view of the anteriormost portion of the rostrum of *P. bonariensis* is more quadrate in outline that in any other species in this complex (Figure 9). In addition, *P. camiari* sp. n. has a brighter dorsal coloration, especially when compared to *P. bonariensis*, that is overall paler. Pairwise genetic distances between *P. camiari* sp. n. and *P. bonariensis* range from 8.1 to 9.2% (Ojeda et al. 2021). *P. camiari* sp. n. is geographically isolated from *P. bonariensis* by no less than 700 km.

P. camiari sp. n. differs from *P. pehuenche* by its more brightly colored skins, darker ears, and more contrasting bicolored tails. In addition, *P. pehuenche* usually lacks the buffy pectoral streack that characterizes *P. camiari* sp. n. Cranially, *P. camiari* sp. n. has a heavier skull, with relatively broader rostra and nasals, a broader interorbital constriction and more robust molars (Figure 9), but much smaller bullae (Figure 4). Pairwise genetic distances between *P. camiari* sp. n. and *P. pehuenche* range from 10.1 to 11.0% (Ojeda et al. 2021). *P. camiari* sp. n. is geographically restricted to central Argentina, being geographically isolated from *P. pehuenche* by more than 550 km.

P. camiari sp. n. differs from *P. vaccarum* by having a proportionally smaller bulla and broader interorbital

constriction (Figure 9). Additionally, *P. vaccarum* has a more complex molar pattern, characterized by a generally deep paraflexus on M2 and by the presence of a small mesoloph complex on M1 and M2. Externally, *P. camiari* sp. n. has a buffy pectoral band that is only occasionally present in *P. vaccarum*. Pairwise genetic distances between the *P. camiari* sp. n. and *P. vaccarum* range from 7.9 to 10.1% (Ojeda et al. 2021). These two taxa were not recovered as sister clades in any of the available phylogenetic analyses (e.g., Ojeda et al. 2021; Riverón 2011; Storz et al. 2020), despite being geographically the nearest one to *P. camiari* sp. n. (Figure 2).

Regarding those taxa of the *P. xanthopygus* complex not included in our multivariate statistical comparisons, *P. camiari* sp. n. is larger and longer tailed than the Argentinean representatives of the Altiplano clade referred to as *P. x. posticalis*-*P. x. rupestris* (Ojeda et al. 2021). Pairwise genetic distances between *P. camiari* sp. n. and the *P. x. posticalis*-*P. x. rupestris* clade range from 9.2 to 11.3% (Ojeda et al. 2021). In turn, *P. camiari* sp. n. is slightly larger than *P. xanthopygus*, from which it also differs by its smaller bullae and broader nasals, rostra and interorbital constriction. Externally, *P. xanthopygus* has a relatively darker dorsal coloration and a conspicuous buffy venter, without pectoral band (Pearson 1958). Pairwise genetic distances between *P. camiari* sp. n. and *P. xanthopygus* range from 8.7 to 10.4% (Ojeda et al. 2021). In addition, both clades are separated by not less than 800 km.

Karyotype: Polop (1989) documented the karyotypes for three females and three males from Pampa de Achala (specimens not examined), reporting a $2N = 38$, with 18 pairs of bi-armed autosomes, and the X and Y also bi-armed.

Etymology: from the word "camiari," that in the language spoken by the Comechingones ethnic group, which inhabited the area before the arrival of the European conquerors, means "serrano" (Montes 1957), i.e., that pertains to the "sierras" (= hills). The name alludes to its distribution in the Central Sierras of Córdoba and San Luis provinces, Argentina.

Distribution: the new species is known from several localities in Córdoba and San Luis provinces (650–2,800 m a.s.l.), Argentina (Figure 2; Supplementary Material 3). Given the habitat continuity, one record for the Sierra de Ambargasta, Santiago del Estero (Jayat et al. 2006), preserved only as skin, could also correspond to this species, although no tissues or skeletons are available to test this hypothesis.

Biogeographical considerations: the Central Sierras (= Sierras Centrales or Sierras Pampeanas) are a low-altitude mountain range (650–2,800 m a.s.l.) that encompass a complex of peaks, valleys, steep slopes, and high plains located in central Argentina. The new species of *Phyllotis* appears to be endemic from to these "sierras" which, as are other non-Andean highland regions, were recognized as a distinctive biogeographic area by high levels of endemism in several unrelated taxa (see Arana et al. 2021; Bukowski et al. 2017). Among mammals, there are at least another species (*Akodon polopi*; Cricetidae) and one subspecies (*Lycalopex culpaeus smithersi*; Canidae) endemic to this same general area (Jayat et al. 2010; Polop 1989), and that have their populations mostly restricted to upper grasslands environments. This situation is relevant to conservation because these hilly grassy ranges are currently affected by climatic change and human disturbances, including high livestock densities, intentional fires, and soil erosion (Cingolani et al. 2015; Giorgis et al. 2020; Renison et al. 2010).

Natural history: *P. camiari* sp. n. is found in grassy rocky outcrops and cliffs, with some scattered patches of low and open woodlands of "tabaquillo" (*Polylepis australis*), and thickets dominated by "romerillos" (*Heterothalamus alienus*) (Polop 1989; Polop et al. 1985; Priotto et al. 1996). It is the most frequently captured rodent species (trapping success = 3.59%) in the "rocky gullies" of Pampa de Achala, which are pockets of elevated humidity in the shelter of rock outcrops where there are large stands of the grasses *Paspalum quadrifolium* and *Poa stutckertii* and other herbs (Polop 1989). In this same general area, the probability of capturing this species in other habitats was: bedrocks, 1.05%; cliffs, 3.36%; and woodlands, 0.78% (Polop 1989). Pregnancies raised up to 25% at the end of the spring (November and December) (Polop 1989); average number of fetuses per female was 3.2 (range = 3–4) (Polop 1989). This new species was caught in the same traplines that *A. polopi*, *Oligoryzomys flavescens*, *Oxymycterus rufus*, and *Reithrodon auritus* (Jayat et al. 2010; Polop 1989, this work).

Conservation: *P. camiari* sp. n. is known from almost 20 localities in the provinces of Córdoba and San Luis, from a general area of more than 25,000 km^2 (Figure 2). Trapping data indicate that this mouse is a relatively common species in some microhabitats (Polop 1989), suggesting a Least Concern status. Part of the range of *P. camiari* sp. n. is included whitin the Quebrada del Condorito National Park and the Pampa de Achala Provincial Reserve, two protected areas in the Córdoba province which together extend about 140,000 ha (Chébez 2006). Nonetheless, most of the upper grassland habitats of the Central Sierras are currently affected by climatic change and other anthropogenic disturbances (e.g., high livestock densities, intentional fires; see Medina et al. 2020 and references therein), indicating the need to monitor their populations in the long term.

5 Final considerations

With the description of *P. camiari* n. sp., the number of endemic mammal species from Argentina increased to 85, of which 5 correspond to the genus *Phyllotis* (i.e., *P. anitae* [including *P. alisosiensis*; see Ojeda et al. 2021], *P. bonariensis*, *Phyllotis nogalaris*, *P. pehuenche*, plus the new species; Teta et al. 2021, with modifications). If we take into account the last four decades, which coincide with the generalization of new methodologies and conceptual developments, one new mammal species (on average) was described per year in Argentina (this number is 25 for the entire world, cf. Burgin et al. 2018). In almost all cases these new species are rodents of small to medium size, morphologically cryptic, but corresponding to genetically divergent lineages, coinciding with the global tendency to recognize new taxa within this order (13.8 new species per year since 2000; cf. D'Elía et al. 2019).

The inclusion of other molecular markers, especially nuclear ones, will surely improve our taxonomic understanding of *Phyllotis*, which is based mainly on mitochondrial genes and morphological traits. Likewise, detailed karyological studies, such as those presented by Labaroni et al. (2014), are also necessary, since for some species our knowledge on this topic is incomplete or non-existent (e.g., for *P. bonariensis*).

Additional fieldwork is also needed to correctly address the distributional limits of *P. camiari* sp. n. For example, it is possible that, given the continuity of hilly environments to the north, those populations reported for southern Santiago del Estero province (cf. Jayat et al. 2006) also correspond to this species. The same would be true regarding those individuals from northwestern San Luis province (no specimens examined), which are known to occur in the hilly system of Sierra de las Quijadas (cf. Ochoa et al. 2021), and that could correspond to this new species or even to *P. vaccarum*. There is a large gap between the Sierras Centrales and the Andean foothills where, despite the existence of isolated rocky outcrops, we have no records of *Phyllotis*. Filling that gap is another step to better understand the history of colonization, settlement, and the biogeography of this genus in southern South America.

References

Arana, M.D., Natale, E., Ferretti, N., Romano, G., Oggero, A., Martínez, G., Posadas, P., and Morrone, J.J. (2021). *Esquema biogeográfico de la República Argentina*. *Opera Lilloana*, Vol. 56. Fundación Miguel Lillo, Tucumán, Argentina, pp. 1–238.

Bukowski, B., Lavinia, P.D., Trujillo Arias, N., Kopuchian, C., Tubaro, P., and Lijtmaer, D. (2017). First genetic assessment of the level of endemism in the avifauna of the Central Sierras in Southern South America. J. Avian Biol. 48: 726–737.

Burgin, C.J., Colella, J.P., Kahn, P.L., and Upham, N.S. (2018). How many species of mammals are there? J. Mammal. 99: 1–14.

Chébez, J.C. (2006). *Guía de las reservas naturales de Argentina: Zona Centro*. Editorial Albatros, Buenos Aires, Argentina.

Cingolani, A., Poca, M., Giorgis, M.A., Vaieretti, M.V., Gurvich, D.E., Whitworth Hulse, J.I., and Renison, D. (2015). Water provisioning services in a seasonally dry subtropical mountain: identifying priority landscapes for conservation. J. Hydrol. 525: 178–187.

Crespo, J.A. (1964). Descripción de una nueva subespecie de roedor filotino. Neotrópica 10: 99–101.

D'Elía, G., Fabre, P.H., and Lessa, E.P. (2019). Rodent systematics in an age of discovery: recent advances and prospects. J. Mammal. 100: 852–871.

de Queiroz, K. (2007). Species concepts and species delimitation. Syst. Biol. 56: 879–886.

Giorgis, M., Cingolani, A., Teich, I., and Poca, M. (2020). Can livestock coexist with *Polylepis australis* forest in mountain central Argentina? Setting thresholds for a land sharing landscape. For. Ecol. Manag. 457: 117728.

Hammer, Ø., Harper, D.A.T., and Ryan, P.D. (2001). PAST: paleontological statistics software package for education and data analysis. Palaeontol. Electron. 4: 1–9.

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

Jayat, J.P., Ortiz, P.E., González, R., and D'Elía, G. (2016). Taxonomy of the *Phyllotis osilae* species group in Argentina; the status of the "Rata de los nogales" (*Phyllotis nogalaris* Thomas, 1921; Rodentia: Cricetidae). Zootaxa 4083: 397–417.

Jayat, J.P., Ortiz, P.E., Pardiñas, U.F.J., D' Elía, G., and Salazar-Bravo, J. (2010). The *boliviensis* group of *Akodon* (Rodentia: Cricetidae) in Northwestern Argentina: species limits, distribution and the description of a new species. Zootaxa 2409: 1–61.

Jayat, J.P., Ortiz, P.E., Teta, P., Pardiñas, U.F.J., and D'Elía, G. (2006). Nuevas localidades argentinas para algunos roedores sigmodontinos (Rodentia: Cricetidae). Mastozool. Neotrop. 13: 51–67.

Jayat, J.P., Teta, P., Ojeda, A.A., Steppan, S.J., Osland, J.M., Ortiz, P.E., Novillo, A., Lanzone, C., and Ojeda, R.A. (2021). The *Phyllotis xanthopygus* complex (Rodentia, Cricetidae) in Central Andes, systematics and description of a new species. Zool. Scripta 50: 689–706.

Kuch, M., Rohland, N., Betancourt, J.L., Latorre, C., Steppan, S.J., and Poinar, H.N. (2002). Molecular analysis of a 11 700–year–old rodent midden from the Atacama Desert, Chile. Mol. Ecol. 11: 913–924.

Labaroni, C.A., Malleret, M.M., Novillo, A., Ojeda, A., Rodriguez, D., Cuello, P., Ojeda, R., Martí, D., and Lanzone, C. (2014). Karyotypic variation in the Andean rodent *Phyllotis xanthopygus* (Waterhouse, 1837) (Rodentia, Cricetidae, Sigmodontinae). Comp. Cytogenet. 8: 369–381.

Medina, M., De Santi, N.H., Rivero, D., Verzi, D.H., and Tonni, E.P. (2020). Fossorial rodents and applied zooarchaeology to ecosystem conservation in Sierras of Córdoba, Argentina. Austral Ecol. 46: 139–147.

Montes, A. (1957). *Nomenclador cordobense de toponimia autóctona: primera parte*. Universidad Nacional de Cuyo, Mendoza.

Ochoa, A.C., Gatica, A., Carrizo, M.C., Martínez Retta, L., Puegher, D.M., Kajin, M., and Mangione, A.M. (2021). Nuevos registros de mamíferos pequeños para el Parque Nacional Sierra de las Quijadas, San Luis, República Argentina. Notas Mam. Sud. 3: 2–12.

Ojeda, A.A., Teta, P., Jayat, J.P., Lanzone, C., Cornejo, P., Novillo, A., and Ojeda, R.A. (2021). Phylogenetic relationships among cryptic species of the *Phyllotis xanthopygus* complex (Rodentia, Cricetidae). Zool. Scripta 50: 269–281.

Olds, N. and Anderson, S. (1989). A diagnosis of the tribe Phyllotini (Rodentia, Muridae). In: Redford, K.H. and Eisenberg, J.F. (Eds.), *Advances in neotropical mammalogy*. Sandhill Crane Press, Gainesville, Florida, USA, pp. 55–74.

Pacheco, V., Rengifo, E.M., and Vivas, D. (2014). Una nueva especie de ratón orejón del género *Phyllotis* Waterhouse, 1837 (Rodentia: Cricetidae) del norte del Perú. Therya 5: 481–508.

Pardiñas, U.F.J., Myers, P., León-Paniagua, L., Ordóñez Garza, N., Cook, J., Kryštufek, B., Haslauer, R., Bradley, R., Shenbrot, G., and Patton, J.L. (2017). Family Cricetidae. In: Wilson, D.E., Mittermeier, R.A., and Lacher, T.E. (Eds.), *Handbook of the mammals of the world. Volume 7, Rodents II*. Lynx Edicions, Barcelona, España.

Pearson, O.P. (1958). A taxonomic revision of the rodent genus Phyllotis, Vol. 56. University of California, Publications in Zoology, California, USA, pp. 391–496.

Polop, J.J. (1989). Distribution and ecological observationsecological observations of wild rodents in Pampa de Achala, Córdoba, Argentina. Stud. Neotrop. Fauna Environ. 24: 53–59.

Polop, J.J., Martínez, R.L., and Torres, M.P. (1985). Distribución y abundancia de poblaciones de pequeños roedores en la zona del embalse de Río Tercero. Córdoba. Hist. Nat. 5: 33–44.

Priotto, J.W., Morando, M., and Avila, L.J. (1996). Nuevas citas de roedores de los pastizales de altura de la Sierra de Comechingones, Córdoba, Argentina. Facena 12: 135–137.

Rengifo, E.M. and Pacheco, V. (2015). Taxonomic revision of the Andean leaf–eared mouse, *Phyllotis andium* Thomas 1912 (Rodentia: Cricetidae), with the description of a new species. Zootaxa 4018: 349–380.

Renison, D., Hensen, I., Suárez, R., Cingolani, A., Marcora, P., and Giorgis, M. (2010). Soil conservation in *Polylepis* mountain forests of Central Argentina: is livestock reducing our natural capital? Austral Ecol. 35: 435–443.

Riverón, S. (2011). *Estructura poblacional e historia demográfica del "pericote patagónico" Phyllotis xanthopygus (Rodentia: Sigmodontinae) en Patagonia Argentina*, Ph.D. dissertation. Uruguay, Universidad de la República.

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

Steppan, S.J. (1997). Phylogenetic analysis of phenotypic covariance structure. I. Contrasting results from matrix correlation and common principal component analysis. Evolution 51: 571–586.

Steppan, S.J. (1998). Phylogenetic relationships and species limits within *Phyllotis* (Rodentia: Sigmodontinae): concordance between mtDNA sequence and morphology. J. Mammal. 7: 573–593.

Steppan, S.J. and Ramírez, O. (2015). Genus *Phyllotis* Waterhouse, 1837. In: Patton, J.L., Pardiñas, U.F.J., and D'Elía, G. (Eds.), *Mammals of South America. Volume 2: Rodents*. The University of Chicago Press, Chicago and London, pp. 535–555.

Steppan, S.J., Ramirez, O., Banbury, J., Huchon, D., Pacheco, V., Walker, L.I., and Spotorno, A.E. (2007). A molecular reappraisal of the systematics of the leaf–eared mice *Phyllotis* and their relatives. In: Kelt, D.A., Lessa, E.P., Salazar-Bravo, J., and Patton, J.L. (Eds.), *The quintessential naturalist: honoring the life and legacy of Oliver P. Pearson*. University of California, Publications of Zoology, California, USA, pp. 799–826.

Storz, J.F., Quiroga-Carmona, M., Opazo, J.C., Bowen, T., Farson, M., Steppan, S.J., and D'líaD'Elía, G. (2020). Discovery of the world's

highest-dwelling mammal. Proc. Natl. Acad. Sci. U. S. A. 117: 18169–18171.

Teta, P., Argoitia, A., Barbero, S., Campo, D.H., d'Hiriart, S., Troyelli, A., Lucero, S., and Cassini, G. (2021). Mamíferos de Argentina: patrones, tendencias y perspectivas en la acumulación de conocimientos sistemáticos. Mastozool. Neotrop. 8: e0514.

Teta, P., Jayat, J.P., Lanzone, C., Novillo, A., Ojeda, A., and Ojeda, R.A. (2018). Geographic variation in quantitative skull traits and systematics of southern populations of the leaf-eared mice of the *Phyllotis xanthopygus* complex (Cricetidae, Phyllotini) in southern South America. Zootaxa 4446: 68–80.

Voss, R.S. (1988). Systematics and ecology of ichthyomyine rodents (Muroidea): patterns of morphological evolution in a small adaptative radiation. Bull. Am. Mus. Nat. Hist. 2: 259–493.