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Phylogenetic relationships among cryptic species of the *Phyllotis xanthopygus* complex (Rodentia, Cricetidae)

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Abstract

The leaf-eared mouse, *Phyllotis xanthopygus* (Waterhouse 1837) is a widely distributed sigmodontine rodent in South America, with populations ranging from central Peru to southern Argentina and Chile. Previous morphological and molecular contributions have suggested that *P. xanthopygus* represents a species complex. In order to characterize and disclose this cryptic species complex, we perform a molecular genetic/phylogenetic analysis of representative samples across its geographical distribution. Phylogenetic analyses were based on sequences of *cytochrome-b gene* (801 base pairs; $n = 114$ specimens) and analysed by maximum likelihood and Bayesian approaches. We also employed a Bayesian implementation of the Poisson tree processes (bPTP) as a unilocus species delimitation method. Results from our phylogenetic analyses retrieve eight well-supported clades. Five of these clades belong to populations known as *P. xanthopygus* s.l., which were paraphyletic to the closely related species *P. bonariensis*, *P. caprinus*, and *P. limatus*, displaying strong genetic divergences (>8%). The (bPTP) analyses recovered ten species within *P. xanthopygus* s.l. plus related forms (i.e. *P. bonariensis*, *P. caprinus*, and *P. limatus*). Our results, coupled with chromosomal and morphological evidences, support the recognition of these clades at the species level and provide a new framework to characterize the leaf-eared mice complex. Our study highlights the importance of integrative approaches in disentangling the biodiversity of Neotropical rodents.

1 | INTRODUCTION

The genus *Phyllotis* Waterhouse 1837 includes at least 20 species of small to medium-sized saxicolous rodents (cf. Steppan & Ramírez, 2015; Jayat et al., 2016; Rengifo & Pacheco, 2015, 2017;). Species of *Phyllotis* are mostly distributed from the highlands of Ecuador throughout the Andes, and adjacent arid to semiarid habitats, to the southern tip of continental South America (Steppan & Ramírez, 2015). This genus is one of the most studied taxa of Neotropical cricetid rodents and form the core focus of two monographic contributions between the 50's and 60's (Pearson, 1958; Hershkovitz, 1962;). A plethora of cytogenetic, morphological and ecological studies are available for this taxon, contributing to our knowledge of this genus in a greater degree than perhaps any other sigmodontine (e.g. Hershkovitz, 1962; Pearson & Patton, 1976; Pizzimenti & de Salle, 1980; Walker et al., 1984; Kelt, 1994; Kramer et al., 1999; Steppan et al., 2007; Labaroni et al., 2014; Sassi

et al., 2017). Despite these contributions, our understanding of the species-level taxonomy of *Phyllotis* is far from being completely understood. Systematic studies based both on morphological and molecular data contributed to solving some of the relationships among species (Steppan, 1995, 1998; Steppan et al., 2007; Jayat et al., 2016; Rengifo & Pacheco, 2017), laid the foundations to describing new ones (Jayat et al., 2007; Ferro et al., 2010; Pacheco et al., 2014; Rengifo & Pacheco, 2015), or provided evidence to raise others from the list of synonymies (Rengifo & Pacheco, 2015; Jayat et al., 2016).

Phylogenetic analysis of morphological traits and molecular markers conducted by Steppan (1993, 1995) and Steppan et al., (2007) provides the basis for the recognition of three species groups within *Phyllotis*. Of these, the *darwini* group, including *P. darwini* (Waterhouse, 1837), *P. bonariensis* Crespo, 1964, *P. caprinus* Pearson, 1958, *P. limatus* Thomas 1912, *P. magister* Thomas 1912, *P. osgoodi* Mann 1945, and *P. xanthopygus* (Waterhouse 1837), is the most speciose. Among these taxa, the leaf-eared mouse, *P. xanthopygus* is the most widely distributed and one of the most common and dominant species in some habitats, with populations from central Peru to southern Argentina and Chile (Steppan & Ramírez, 2015), from sea level to 6,739 m.a.s.l. (Storz et al., 2020). The leaf-eared mouse occurs in arid and semiarid Andean ecosystems and is mostly associated with rocky outcrops and cliffs in shrubby to herbaceous steppes. In addition, some geographically isolated populations occur in the Andean foothills of central and eastern Argentina, within temperate grassland environments (Steppan & Ramírez, 2015; Teta et al., 2018).

Pearson (1958) and Hershkovitz (1962) considered *P. darwini* as a widely distributed, polytypic species, including several nominal forms as subspecies, such as *xanthopygus*, *chilensis* Mann 1945, *posticalis* Thomas 1912, *ricardulus* Thomas 1919, *rupestris* P. Gervais 1841, and *vaccarum* Thomas 1912 (to which Crespo [1964] added *bonariensis*). Based on karyotypic and crossbreeding evidence, this view began to change when Walker et al. (1984) proved that true *P. darwini* is geographically restricted to central Chile, leaving all the other nominal taxa under *P. xanthopygus*. Since then, the status of *P. xanthopygus* underwent additional removal of the nominal forms *bonariensis* and *limatus*, which were both considered as valid species (Reig, 1978; Steppan, 1998; Steppan & Ramírez, 2015). More recently, phylogenetic analyses of molecular markers challenged the traditional classification of *P. xanthopygus* into six subspecies, showing that this taxon is paraphyletic with respect to *P. bonariensis*, *P. caprinus* and *P. limatus* (Albright, 2004; Jayat et al., 2016; Riverón, 2011). Different approaches, with some differences in their geographical sampling, suggest that as currently understood, *P. xanthopygus* is a complex of two or more cryptic species (Albright, 2004; Steppan et al., 2007; Riverón, 2011) (see the Table S1 for a synthesis of the taxonomic history of this species complex).

We report here the results of genetic/phylogenetic analyses and species delimitation methods conducted on the *P. xanthopygus* complex and other recognized and related species within *Phyllotis*. The main purpose of our research is to examine the phylogenetic relationships across populations of *P. xanthopygus* under the hypothesis that this taxon constitutes a complex set of cryptic species. Furthermore, we discuss some issues about other species limits within the genus, their biogeographic distribution, and made some comments on their diversification.

2 | MATERIALS AND METHODS

2.1 | Sampling, amplification, and sequencing

We analysed 114 specimens of *Phyllotis* from 66 localities along most of the distributional range of this genus (Figure 1 and Appendix S1). The total sample includes some specimens coming from the type localities (or nearby areas) and all the recognized species of *Phyllotis*. Forty-two specimens are included as new data and are integrated into a dataset containing GenBank sequences from *P. xanthopygus* species complex and the other recognized species of the genus *Phyllotis* (Appendix S1). The specimens collected by us were live-trapped using Sherman-like traps and were collected in accordance with collection permits (N° 461–1–04–03873. RES 405) from the Dirección de Recursos Renovables, Mendoza, Argentina. Animals were prepared following standard procedures, and tissues were preserved in 96% ethanol or frozen. Voucher specimens and tissue samples are housed in the following biological collections of Argentina: Mammal Collection of the Instituto Argentino de Investigaciones de las Zonas Áridas (CMI)-(IADIZA), CCT Mendoza-CONICET, Mendoza; Colección Nacional de Mastozoología, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN-Ma), Ciudad Autónoma de Buenos Aires; and Colección de Mamíferos del Centro Regional de Investigaciones Científicas y Transferencia Tecnológica de La Rioja (CRILAR), La Rioja. All parts of the study involving live animals followed the guidelines of the American Society of Mammalogists (Sikes et al., 2016).

2.2 | Genetic and phylogenetic analyses

Genetic and phylogenetic analyses were based on an 801 base-pair fragment of *cytochrome-b* gene (*Cyt-b*). GenBank accession numbers of the 114 specimens of *Phyllotis* here analysed are provided in Appendix S1. The 42 sequences

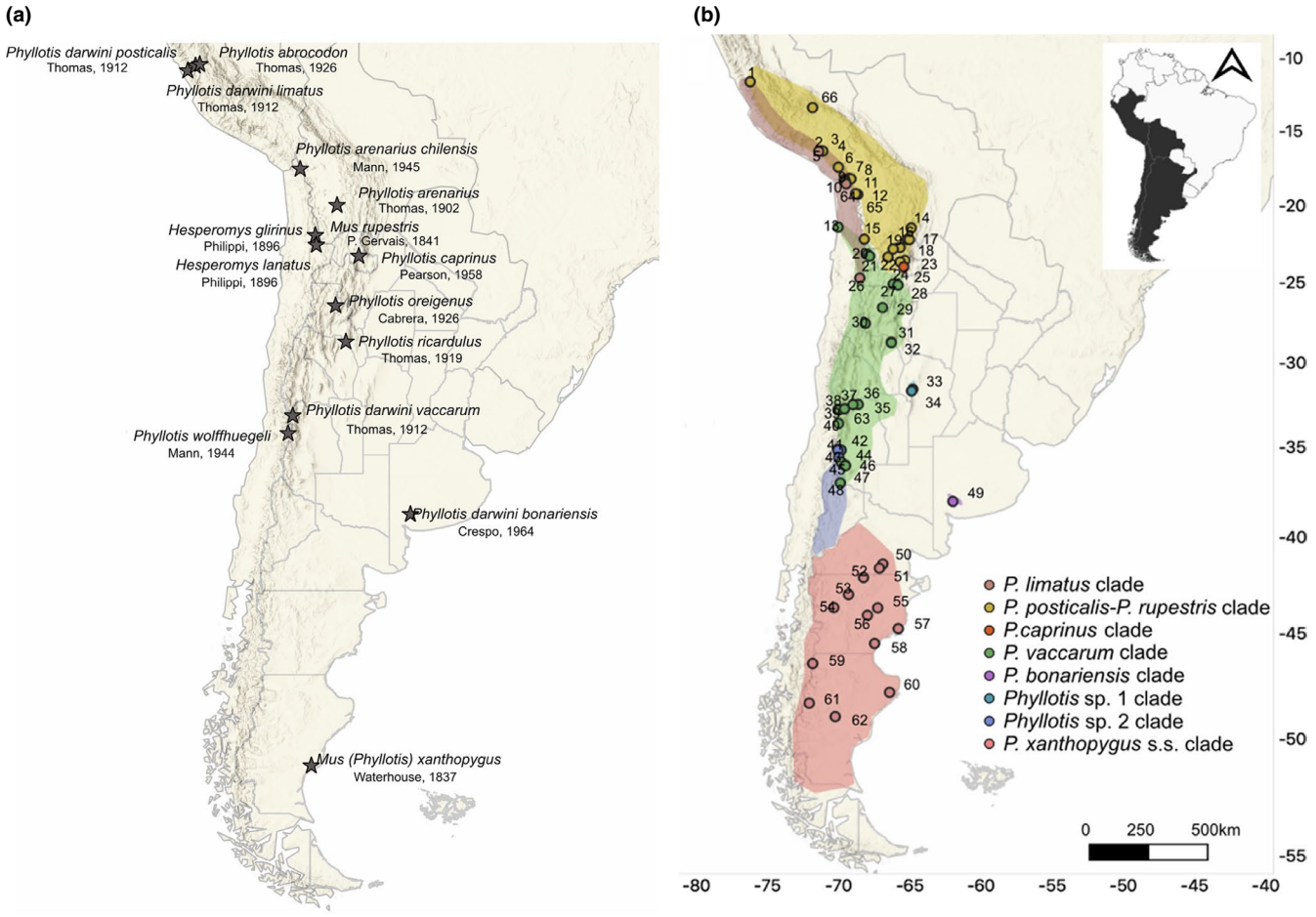
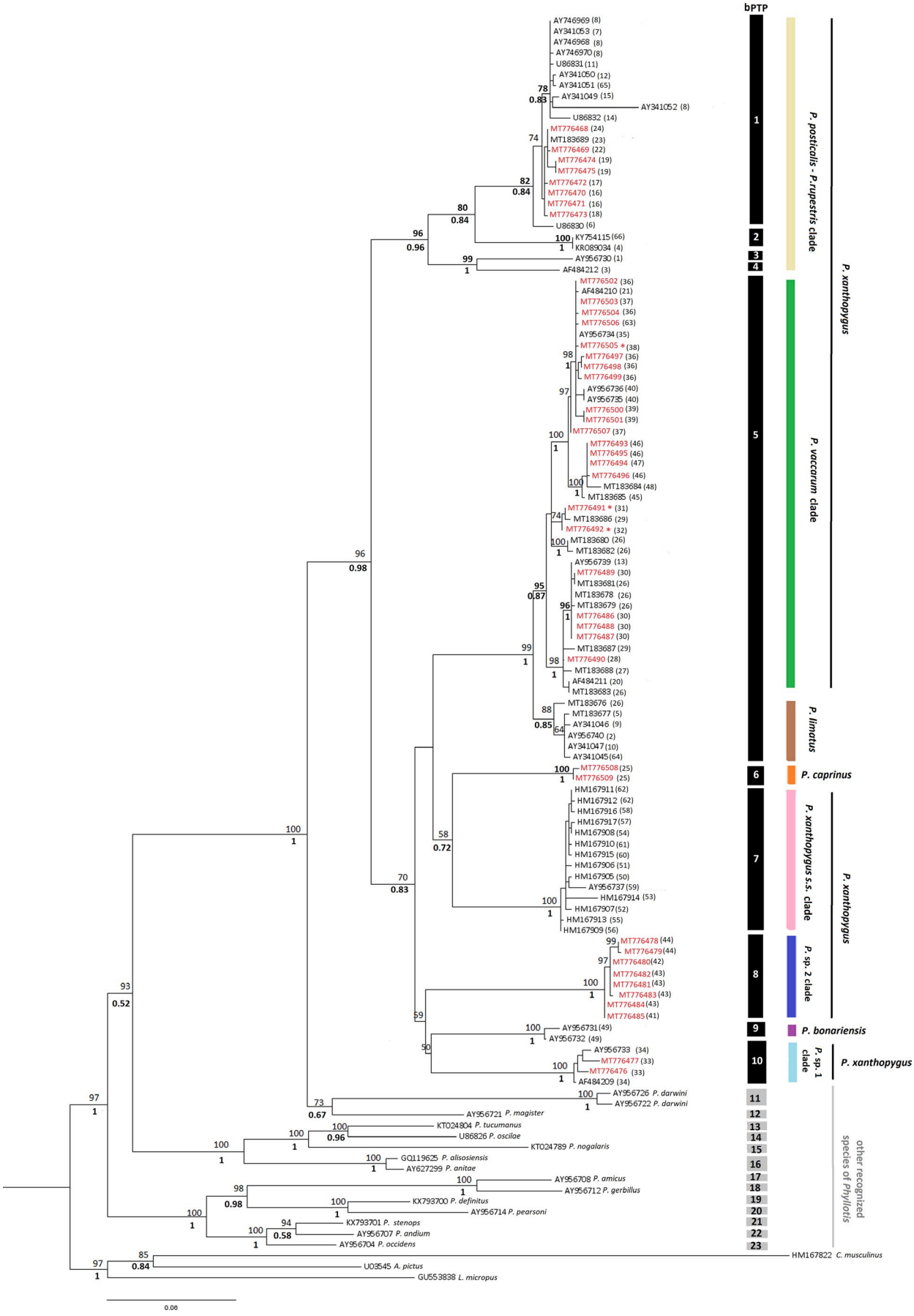


FIGURE 1 (a) Map showing the type localities of the nominal forms related with the *Phyllotis xanthopygus* complex. (b) Localities (numbers and circles with the mid-central point) and distributional ranges (shaded areas) of the sequences used in this work. Colour indicates the different clades recovered in the phylogenic tree

gathered here were generated using primers MVZ 05 and MVZ 16 (da Silva & Patton, 1993) following the protocol outlined in Cañón et al. (2010). Polymerase chain reaction (PCR) products were purified and sequenced at the Unidad de Genómica del INTA Castelar (Buenos Aires), Argentina. Newly generated sequences were deposited in GenBank (MT776468-MT776509). As outgroup taxa, we used *Cyt-b* sequences from other phyllotine: *Calomys musculinus*, *Loxodontomys micropus* and *Auliscomys pictus* (accession numbers in Appendix S1).

Sequence alignment was performed using the default parameters of CLUSTAL X (Thompson et al., 1997) followed by visual inspection to check for stop codons and reading frame shifts. Pairwise genetic distances were calculated to assess within- and among species difference using the p-distance method in MEGA7 (Kumar et al., 2016). Phylogenetic reconstructions were carried out using Maximum Likelihood (ML) and Bayesian inferences. The best-fit model of nucleotide substitution (HKY + I+G) was determined based on the Bayesian Information Criterion (BIC) using jModeltest2 (Darriba et al., 2012). We run ML analyses using IQTREE (Nguyen et al., 2015), as implemented in the IQ-TREE web server (Trifinopoulos et al., 2016), specifying the selected model of molecular evolution, with perturbation strength set to 0.5, and the number of unsuccessful iterations set to 100. Branch support was estimated through 1,000 replicates of ultrafast bootstrap (BL). Bayesian analysis was conducted in MrBayes 3.1.2 (Ronquist & Huelsenbeck, 2003) with three heated and one cold Markov chains each, which proceeded for 10 million generations and trees were sampled every 1,000 generations. The first 25% of the trees were discarded as burn-in and the remaining trees were used to compute a 50% majority-rule consensus tree with posterior probability (PP) estimates for each clade.

For species identification, we used the unilocus species delimitation method termed the Bayesian implementation of the Poisson tree processes (bPTP), which is an update version of the PTP (Zhang et al., 2013) based on the mtDNA tree alone. This method is intended to delimit species based on single locus molecular data (Zhang et al., 2013). An advantage of bPTP is that it does not need an ultrametric calibration like other coalescent approaches,


bPTP
AY746969 (8)
AY341053 (7)
AY746968 (8)
AY746970 (8)
U86831 (11)
AY341050 (12)
AY341051 (65)
AY341049 (15)
AY341052 (8)
U86832 (14)
MT776468 (24)
MT183689 (23)
MT776469 (22)
MT776474 (19)
MT776475 (19)
MT776472 (17)
MT776470 (16)
MT776471 (16)
MT776473 (18)
U86830 (6)
KY754115 (66)
KR089034 (4)
AY956730 (1)
AF484212 (3)
MT776502 (36)
AF484210 (21)
MT776503 (37)
MT776504 (36)
MT776506 (63)
AY956734 (35)
MT776505 * (38)
MT776497 (36)
MT776498 (36)
MT776499 (36)
AY956736 (40)
AY956735 (40)
MT776500 (39)
MT776501 (39)
MT776507 (37)
MT776493 (46)
MT776495 (46)
MT776494 (47)
MT776496 (46)
MT183684 (48)
MT183685 (45)
MT776491 * (31)
MT183686 (29)
MT776492 * (32)
MT183680 (26)
MT183682 (26)
AY956739 (13)
MT776489 (30)
MT183681 (26)
MT183678 (26)
MT183679 (26)
MT776486 (30)
MT776488 (30)
MT776487 (30)
MT183687 (29)
MT776490 (28)
MT183688 (27)
AF484211 (20)
MT183683 (26)
MT183676 (26)
MT183677 (5)
AY341046 (9)
AY956740 (2)
AY341047 (10)
AY341045 (64)
MT776508 (25)
MT776509 (25)
HM167911 (62)
HM167912 (62)
HM167916 (58)
HM167917 (57)
HM167908 (54)
HM167910 (61)
HM167915 (60)
HM167906 (51)
HM167905 (50)
AY956737 (59)
HM167914 (53)
HM167907 (52)
HM167913 (55)
HM167909 (56)
MT776478 (44)
MT776479 (44)
MT776480 (42)
MT776482 (43)
MT776481 (43)
MT776483 (43)
MT776484 (43)
MT776485 (41)
AY956731 (49)
AY956732 (49)
AY956733 (34)
MT776477 (33)
MT776476 (33)
AF484209 (34)
AY956726 P. darwini
AY956722 P. darwini
AY956721 P. magister
KT024804 P. tucumanus
U86826 P. oscilae
KT024789 P. nogalaris
GQ119625 P. alisosiensis
AY627299 P. anitae
AY956708 P. amicus
AY956712 P. gerbillus
KX793700 P. definitus
AY956714 P. pearsoni
KX793701 P. stenops
AY956707 P. andium
AY956704 P. occidens
HM167822 C. musculinus
U03545 A. pictus
GU553838 L. micropus
0.06
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P. posticalis - P. rupestris clade
P. xanthopygus
P. vaccarum clade
P. limatus
P. caprinus
P. xanthopygus s.s. clade
P. xanthopygus
P. sp. 2 clade
P. bonariensis
P. sp. 1 clade
P. xanthopygus
other recognized species of Phyllotis

FIGURE 2 Phylogenetic consensus tree obtained in the Maximum likelihood analysis of 114 *cytochrome-b* gene sequences of *Phyllotis xanthopygus* complex and other recognized species of *Phyllotis*. Numbers above nodes indicate Maximum likelihood bootstrap support values (BL) and numbers below nodes indicate posterior probability values of the adjacent nodes (PP). Labels in red corresponds to new sequences gathered in this study. Asterisk indicates specimens topotype. Numbers in parenthesis refers to the localities in the map. Colour bars indicate the eight different clades recovered in the ML analyses, black bars indicate the ten species of the *P. xanthopygus* complex delimited through bPTP and grey bars indicates other recognized species of *Phyllotis* delimited by bPTP

avoiding errors and computer intensive processes (Zhang et al., 2013). The method relies on the number of substitutions between haplotypes and assumes that more molecular variability is expected between species than within a species (Zhang et al., 2013). The analyses were conducted on the web server (available at http://species.h-its.org/ptp/). The parameters for the run were 500,000 MCMC generations, a thinning interval of 100% and 25% of burn-in.

In order to tie the recognized clades in our phylogenetic approach with available names, we use several criteria: (a) first at all, we search for morphological diagnostic features referred in the original descriptions of the involved nominal forms and subsequent revisionary contributions (e.g. Hershkovitz, 1962; Pearson, 1958), in order to test its congruence with our direct inspection of large samples of individuals, including topotypes or nearly topotypes, from different geographical areas; (b) inclusion of sequenced specimens coming from the type localities (or surroundings) of the different nominal forms currently considered into the synonymy of *P. xanthopygus* s.l. (e.g. *rupestris*, *vaccarum*, *xanthopygus*), considering its availability and priority (see the discussion below, on each clade account); (iii) inclusion in our analyses of sequenced specimens coming from the type localities (or surroundings) of the nominal forms recognized by previous authors as valid species (*P. bonariensis*, *P. caprinus*, and *P. limatus*). For those clades for which no names are available, we use a sequential numeration (i.e. *P*. sp. 1 and *P*. sp. 2). Informal names were also used for those clades in which larger samples of sequenced individuals and additional morphological approaches are further needed.

3 | RESULTS

3.1 | Genetic, phylogenetic and delimitation species analyses

Phylogenetic analyses of our data set using maximum likelihood (lnL = −7396.3385), and Bayesian inference produced trees topologies mostly congruent, with slight differences in the statistical supports of the nodes and in its internal relationships. The analyses recovered eight monophyletic groups with well support of the nodes (between 88%–100% BL and 0.87–1.0 PP) (Figure 2; Figure S1). Phylogenetics trees display two major groupings. One includes *P. xanthopygus* s.s., *P. bonariensis*, *P. caprinus*, *P. limatus, P. vaccarum,* and two additional clades named here *P*. sp. 1, and *P*. sp. 2. The other major grouping is named here the *P. posticalis-P. rupestris* clade, which is a diverse clade including specimens from different populations and localities from northern Argentina, northern Chile, Bolivia, and southern Peru.

Phylogenetic relationships between the *P. xanthopygus* s.s. clade and *P. caprinus* (BL = 58; PP = 0.72), as well as between the *P. vaccarum* clade and *P. limatus* (BL = 99; PP = 1.0) are consistent and recovered in the different phylogenetic analyses. However, other expected relationships, such as the case of the *P*. sp. 2 and *P. vaccarum* clade, which have contiguous and sympatric distributions in the region of Mendoza and Neuquén Provinces, are not substantiated in any analyses (Figures 1 and 2; Figure S1).

On the other hand, the bPTP species delimitation analyses indicate 10 lineages (species) within the *P. xanthopygus* complex and related forms (*P. bonariensis*, *P. caprinus* and *P. limatus*) (Figure 2; Figure S2). Among them, *P. limatus*, a previously recognized species based on morphological and molecular characters, was clustered with *P. vaccarum* as one species. The other five lineages correspond to: *P. caprinus*, *P. xanthopygus s.s*., *P*. sp. 1, *P*. sp. 2, and *P. bonariensis*. Within the *P. posticalis - P. rupestris* clade four species were delimited (Figure 2; Figure S2).

Mean genetic p-distances within the eight main clades analysed in our study ranged from 0.2% within *P. caprinus*, to 3.1% within the *P. posticalis-P. rupestris* clade. The mean genetic distances between clades ranged from 3.0% between the *P. vaccarum* and *P. limatus*, to 10.6% between *P*. sp. 1 and *P*. sp. 2 and between *P. posticalis-P. rupestris* and *P*. sp. 2 (Table 1). The genetic distances between the ingroup taxa and the outgroup (*C. musculinus, L. micropus* and *Auliscomys pictus*) average approximately 16.1%. Remarkably, the mean intraspecific distance observed within the *P. posticalis-P. rupestris* clade is relatively high and similar to those found between well-established species (e.g. *P. vaccarum* clade and *P. limatus*) (Table 1). Also, some clades, which are sympatric in part of their distributions, display large genetic divergences. Such is the case of *P. caprinus* and the *P. vaccarum* clade, or *P. caprinus* and the *P. posticalis-P. rupestris* clade, with sympatric distribution in north-western Argentina (Jujuy Province) showing mean genetic distances between 7.9% and 9.6% respectively. Similarly, *P. limatus* and *P. posticalis-P. rupestris* clade which are sympatric in Antofagasta, Chile, display a genetic distance of 9.3%. Finally, the *P. vaccarum* and *P*. sp. 2 clades possess a mean genetic distance

TABLE 1 Mean genetic p-distance between the sequences of *Phyllotis xanthopygus* complex studied here

	***P.* sp. 1**	***P.* sp. 2**	***P. bonariensis***	***P. limatus***	***P. vaccarum***	***P. caprinus***	***P. xanthopygus***	***P. posticalis-rupestris***	**outgoup**
P. sp. 1	**1.1** (0.8–1.5)								
P. sp. 2	10.6 (10.1–11.0)	**0.3** (0–0.7)							
P. bonariensis	8.6 (8.1–9.2)	9.6 (9.4–9.9)	**0.8** -						
P. limatus	9.2 (8.5–10.5)	8.8 (8.4–9.6)	8.7 (8.5–9.0)	**0.5** (0–1.3)					
P. vaccarum	9.2 (7.9–10.1)	9.0 (8.4–9.6)	8.5 (7.8–9.0)	3.0 (2.4–4.6)	**1.7** (0–3.4)				
P. caprinus	9.3 (9.0–9.5)	10.2 (10.0–10.5)	8.6 (8.5–8.7)	7.7 (7.2–8.1)	7.9 (7.4–8.4)	**0.2** -			
P. xanthopygus	9.4 (8.7–10.4)	9.6 (8.9–10.4)	8.1 (7.8–8.7)	9.0 (8.2–11.2)	8.6 (7.9–9.8)	8.3 (8.0–8.6)	**0.7** (0.1–1.8)		
P. posticalis -P. rupestris	9.8 (9.2–11.3)	10.6 (9.9–11.9)	9.5 (9.1–10.6)	9.3 (5.3–12.6)	9.7 (6.6–12.5)	9.6 (9.0–11.8)	10.3 (9.4–11.1)	**3.1** (0–10.8)	
outgoup	16.1 (14.9–18.2)	17.1 (16.1–17.7)	15.4 (14.4–17)	15.5 (13.9–17.9)	16.2 (13.7–17.7)	15.6 (14.5–16.7)	16.8 (15.3–18.3)	16.3 (14.6–18.6)	**15.3** (13.2–17.1)

Note: The ranges are shown in parentheses.

The mean intraspecific distances are in bold.

of 9.0% between sympatric populations of central-western Argentina (Mendoza Province; Figure 1, Table 1).

4 | DISCUSSION

4.1 | Speciation and species limits within the complex of *Phyllotis xanthopygus*

According to our phylogenetic results, eight main clades can be distinguished within the *Phyllotis xanthopygus* complex using a combination of mitochondrial characters (i.e. base pairs of the Cyt-b gene). Five of these clades are included within the concept of *P. xanthopygus* s.l. (i.e. those referred as *P. posticalis* - *P. rupestris*, *P. vaccarum*, *P. xanthopygus* s.s., *P.* sp. 1, and *P.* sp. 2), while the other three correspond to the monophyletic and morphologically diagnosable species *P. bonariensis*, *P. caprinus* and *P. limatus* (Steppan, 1998; Steppan and Ramírez, 2015). Based on these results, we can safely assume that there are at least eight distinguishable lineages of species level within the *P. xanthopygus* species complex. Some of these clades exhibit a molecular divergence comparable to the amount found between other well-established species of the genus *Phyllotis* as a whole (see also Riverón, 2011). However, we predict further changes in this species complex since sampling populations, particularly those from northern regions (i.e. Peru and Bolivia), are still far from being complete. In fact, our analyses identified the *P. posticalis-P. rupestris* clade as a remarkably diverse group, with certain geographical structure and high intra-clade genetic distances like those found between other species within the complex (see Table 1). Consistent with our results, previous authors have found evidence of geographic structuring within the clade here referred to as *P. posticalis-P. rupestris* (e.g. Albright, 2004). Furthermore, our results of the bPTP method delimited four species within *P. posticalis-P. rupestris* (Figure 2; Figure S2). These results lead us to suggest that there might be more than one species within the so-called *P. posticalis-P. rupestris* clade.

Following to De Queiroz (2007), in the context of a unified species concept, any property that provides evidence of lineage separation is relevant to inferring the boundaries and numbers of species. However, species delimited by multiple pieces of evidence and different species delimitation methods produce stronger hypotheses (De Queiroz, 2007). As the molecular data itself could be insufficient to sustain the specific separation between the eight clades here defined under the *P. xanthopygus* species complex, here we discuss additional insights from morphology and cytogenetics. In most cases, each clade can be diagnosed based on a combination of qualitative and quantitative morphological traits (e.g. Pearson, 1958; Teta et al., 2018) and some differences in their karyotypes (e.g. the fundamental autosomal arm numbers and the amount of constitutive heterochromatin; cf. Walker et al., 1984; Walker et al., 1991; Labaroni et al., 2014). All these lines of evidences, combined with the geographic distributional patterns of the clades, reinforce the recognition of each one as representatives of a taxa at the species level. In the next section, we discuss different issues regarding the clades recovered in this paper, including information about morphology, karyotypes, and distribution (for a synthesis, see Table 2).

4.2 | The *Phyllotis bonariensis* clade

This clade corresponds to a geographically isolated population endemic from central-eastern Argentina (south-western Buenos Aires Province). This nominal form is exclusively found in the Ventania Hill system, a small hilly belt of ~190 km in length and low elevation (>250 m.a.s.l.). *Phyllotis bonariensis* was either considered as a valid species (e.g. Reig, 1978; Galliari et al., 1996; Steppan & Ramírez, 2015; Rengifo and Pacheco, 2017), or as a synonym of *P. xanthopygus* (e.g. Díaz et al., 2006; Teta et al., 2018). Steppan and Ramírez (2015) provided a morphological diagnosis of this mouse, highlighting its large-sized body (head and body length = 127–151 mm), relatively small ears (23–25 mm) and hindfeet (25–28 mm), well-developed vibrissae, large posterolateral palatal pits, nasals anteriorly widened, and orthodont upper incisors. Teta et al., (2018) observed that population´s of this nominal form were the most divergent among southernmost populations of *P. xanthopygus* in morphometric studies. The mean pairwise genetic distances between *P. bonariensis* and the other clades within the complex of *P. xanthopygus* range from 8.1% to 9.6% (Table 1). These values are similar, or well above from those observed for other recognized species of the genus (see Rengifo and Pacheco, 2017). The phylogenetic position of the *P. bonariensis* it was always more or less related to the *Phyllotis* sp. 1 clade (specimens from Córdoba, central Argentina, usually referred as *P. xanthopygus vaccarum*). This situation was also reported in previous molecular studies (Albright, 2004; Riverón, 2011). Likewise, Teta et al. (2018) linked *P. bonariensis* with populations from central Argentina (*P. xanthopygus vaccarum*) based on quantitative morphological data.

4.3 | The *Phyllotis caprinus* clade

The Capricorn leaf-eared mouse, *P. caprinus* was described by Pearson (1958), who found it sympatric with the clade here referred as *P. posticalis-P. rupestris* (see below). The geographic distribution of *P. caprinus* is relatively small, occurring in shrubby habitats on the eastern Andean slopes of north-western Argentina and southern Bolivia, between 2,100 and 4,500 m.a.s.l. (Steppan and Ramírez, 2015). Shortly after its description, Hershkovitz (1962) considered

TABLE 2 Main conclusions extracted from our results, including the recognized clades, their possible synonyms, approximate distributions, and references to previous studies in morphology and karyotypes

Clade	Synonyms	Distribution	Morphology	Karyotypes
Phyllotis bonariensis		EC Argentina (Buenos Aires province)	Crespo (1964); Steppan and Ramírez (2015)	
P. caprinus		NW Argentina (Jujuy province), SW Bolivia	Pearson (1958)	Pearson and Patton (1976)
P. limatus		N Chile, E Peru	Steppan (1998)	Pearson (1972)
P. posticalis–P. rupestris	*capito* Philippi, 1,860; *glirinus* Philippi, 1896; *lanatus* Philippi, 1896; *arenarius* Thomas, 1902; *abrocodon* Thomas, 1926; *chilensis* Mann, 1944	NW Argentina (Jujuy and northern Salta provinces), W Bolivia, N Chile, and S and C Peru	Pearson (1958), Hershkovitz (1962)	Pearson and Patton (1976), Labaroni et al. (2014)
P. vaccarum	*ricardulus* Thomas, 1919; *oroigenus* Cabrera, 1926; *wolffhuegeli* Mann, 1944	W Argentina and adjoining areas of Chile	Pearson (1958)	Walker et al. (1984), Labaroni et al. (2014)
P. xanthopygus s.s.		S Argentina and Chile	Pearson (1958), Hershkovitz (1962)	Walker et al. (1991)
P. sp. 1		C Argentina (Córdoba and San Luis provinces)	Pearson (1958, in part)	Labaroni et al. (2014)
P. sp. 2		WC Argentina (Mendoza and Neuquén provinces)		

this nominal form as a subspecies of *P. darwini* (= *P. xanthopygus*), but subsequent authors retained it as a different species (e.g. Cabrera, 1961; Steppan, 1998). The Capricorn leaf-eared mouse has a head and body length of 102–140 mm (larger than specimens of the *P. posticalis-P. rupestris* clade from north-western Argentina); additionally, its skull is characterized by a flat, sharp-edged, long-waisted interorbital region, long frontal bones, V-shaped frontoparietal suture, and heavy rostrum (Pearson, 1958; Steppan & Ramírez, 2015). The karyotype is identical to that found in other populations of the *P. xanthopygus* species complex, having a 2n = 38, FN = 72, with 36 size-graded biarmed autosomes, a large meta-submetacentric X, and a small metacentric Y chromosome (Pearson & Patton, 1976).

Our molecular phylogenetic analyses were consistent in recovering *P. caprinus* as the sister group of the *P. xanthopygus* s.s. clade. This relationship is remarkable, given a separation of more than 1,600 km between the distribution records of these two species (Figure 1). The molecular divergences found between *P. caprinus* and *P. xanthopygus* s.s. is high (8.3%), suggesting that these populations have been diverging in relative isolation for a considerable amount of time. The mean pairwise genetic distances between *P. caprinus* and other clades within the *xanthopygus* complex range from 7.7% to 10.2% (Table 1). This notable genetic divergence stands even when comparing *P. caprinus* with populations of the *P. posticalis-P. rupestris* (9.6%) and the *P. vaccarum* (7.9%) clades, which are sympatric and geographically close, respectively. This geographic discontinuity in mtDNA lineages is concordant with some morphologic and morphometric differences among these three taxa, which reinforces the hypothesis of its specific status.

4.4 | The *Phyllotis limatus* clade

The Lima leaf-eared mouse is narrowly distributed along the arid coast and Pacific Andes slopes from central Peru south to northern Chile, from the sea level to 2,500 m.a.s.l. in the north and sea level to 5,070 m.a.s.l. in the south (Steppan, 1998; Steppan & Ramírez, 2015; Storz et al., 2020). Both, Pearson (1958) and Hershkovitz (1962) considered it as a subspecies of *P. darwini*. Steppan (1998), based both on morphological and molecular grounds, distinguished this nominal form from others in the *P. darwini* species group, from which differ by its deep and narrow upper incisors, short to moderate maxillary toothrows (4.2–5.8 mm), and light coloration. Likewise, Steppan (1998) proposed that *P. limatus* recently derived from a western lineage of the form here recognized as *P. vaccarum*, perhaps during the most recent ice age. This idea was later corroborated by Kuch et al. (2002). Specimens from central Peru have karyotypes with 2*n* = 38, FN = 72, with the same chromosome morphology of other species within the complex of *P. xanthopygus* (Pearson, 1972). But there are no studies with banding techniques that allow to contrast, for example, the distribution of heterochromatin, a frequently variable characteristic among *Phyllotis* species

(Walker et al., 1991; Labaroni et al., 2014). We maintain the name *limatus* for this group following the opinion of Steppan & Ramirez (2015, but see Steppan, 1998).

Our phylogenic analyses identified *P. limatus* as a monophyletic group closely related to the *P. vaccarum* clade, with strong statistical support in the analyses (Figure 2, Figure S1). This relationship displays the lowest mean genetic distances (3.0%), when compared with the distances reported among other members of the complex (Table 1). Also, the bPTP analyses identified *P. limatus* and *P. vaccarum* as a single species, suggesting that these two clades belong to one identified unit. Previous studies report similar molecular distances between those clades (Kuch et al., 2002; Palma et al., 2005; Riverón, 2011). The mean pairwise genetic distances between *P. limatus* and other clades within the complex of *Phyllotis xanthopygus* (excluding the *vaccarum* clade) range from 7.7% to 9.3% (Table 1).

4.5 | The *Phyllotis posticalis–P. rupestris* clade

This is a widely distributed Altiplanic clade, ranging from central Peru to northern Argentina and Chile. Populations within this clade were previously referred in the literature as *P. x. chilensis*, *P. x. posticalis*, and *P. x. rupestris* (Pearson, 1958; Hershkovitz, 1962; Steppan & Ramírez, 2015). Albright (2004) recognized a main division of this group in two subclades, suggesting that this clade might include more than one taxon at a species level. However, additional specimens, including topotypical samples, are much needed to correctly tie the available names to putative taxa within this clade. In this work, we informally refer this group as *P. posticalis–P.rupestris*. Externally, these animals ranged from being large-bodied and long tailed to small-bodied and short tailed, and dark grey to pale brown dorsally (cf. Pearson, 1958). Southern representatives of this clade (i.e. from Jujuy and Salta Provinces, Argentina) are among the smallest-sized individuals of the *P. xanthopygus* complex in Argentina and show qualitative state characters that differ from representatives of other clades (more notably, from the sympatric *P. caprinus* and *P. vaccarum* clades; Jayat et al., in prep.).

Specimens from north-western Argentina (e.g. Jujuy Province) have karyotypes with $2n = 38$, FN = 70–71–72, with chromosomal variants not found in other populations (Pearson & Patton, 1976; Labaroni et al., 2014). In addition, they also differ from other samples from western Argentina (e.g. Catamarca Province) in the amount and localization of constitutive heterochromatin (Labaroni et al., 2014), a feature that also differentiates other species in the genus (Walker et al., 1984). As we mentioned previously, this group displays high intra-clade genetic distances, similar to those found between species within the complex (e.g. *P. vaccarum–P. limatus*, see Table 1), and we also observe some geographic structure within this clade (Figures 1 and 2). This, combined with bPTP results, which delimited four species within this group, suggest that the Altiplano populations here referred to *P. posticalis-P. rupestris* could include more than one species. Mean pairwise genetic distances between the *P. posticalis-P. rupestris* clade and other clades of the complex range from 9.3% to 10.6% (Table 1). Based on the direct inspection of large samples from norther Chile, western Bolivia and central and southern Peru, including some topotypical specimens, we provisionally included under this nominal form the taxa *abrocodon* Thomas 1926, *arenarius* Thomas 1902, *chilensis* Mann 1945, *glirinus* Phillipi 1896, and *lanatus* Phillipi 1896 (Table S1).

4.6 | The *Phyllotis xanthopygus s.s.* clade

This is a widely distributed clade that occupies rocky outcrops, cliffs, and stone walls in shrubby to herbaceous steppes of southern Argentina and Chile, from ca. 40° S to the Straits of Magellan. Despite its wide distributional range, samples from southern Argentina and Chile were morphologically homogeneous (Teta et al., 2018). This is consistent with the hypothesis of a relatively recent expansion of the Patagonian populations from at least one refuge south of 41° south latitude (Lessa et al., 2010; Riverón, 2011). The leaf-eared mouse, *Phyllotis xanthopygus,* is a relatively large animal (head and body length = 107–142 mm) with a proportionately short tail (106–145 mm), and relatively dark dorsal coloration with a conspicuous buffy venter. Populations here referred to *P. xanthopygus* can be distinguished from closely distributed clades (i.e. *P. vaccarum*, and *P.* sp. 2) based on quantitative morphological traits (Teta et al., 2018). Specimens from southern Chile have karyotypes with $2n = 38$, FN = 72, although they differ from other samples from central and northern Chile in the amount of constitutive heterochromatin (Walker et al., 1991). Pairwise genetic distances between *P. xanthopygus* and other clades within the complex of *Phyllotis xanthopygus* range from 8.1% to 10.3% (Table 1). This species is sister to the geographically distant *P. caprinus*.

4.7 | The *Phyllotis vaccarum* clade

As is here defined, this taxon includes populations from northern Chile and north-western Argentina (this work) south to north-eastern Neuquén Province, Argentina (cf. Riverón, 2011). Some samples within this group

were previously referred to *P. x. ricardulus* (north-central Argentina) and to *P. x. rupestris* (north-western Argentina and northern Chile) (e.g. Pearson, 1958; Hershkovitz, 1962). Broadly viewed, the northern distribution of this clade could encompass the type locality of *rupestris* Gervais 1841; so, we cannot discard the priority of this name over *vaccarum* Thomas 1912 to refer to this clade. However, due to the imprecise definition of the type locality of *rupestris* Gervais 1841 (see Steppan, 1998), we choose to use the name *vaccarum* for this clade. As advantage, this name had been widely used for these same populations by previous authors (e.g. Pearson, 1958; Steppan, 1997, 1998). Furthermore, we note that Pearson (1958) used the name *rupestris* for a short tailed, small sized, and pale form, distributed from southern Peru to north-western Argentina (in Jujuy Province), while the individuals in this clade are large-bodied and long tailed (skin colour pattern are highly variable geographically but in general are not pale), and are distributed from northern Chile and southern Jujuy, Argentina, south to Central Chile and west-central Argentina (cf. Pearson, 1958).

As is here defined, the morphological distinction of this form compared to the closely distributed *P*. sp. 2 is subtle in quantitative terms (Teta et al., 2018), although both taxa have some constant qualitative integumental and dental differences (Jayat et al., in prep.). Furthermore, we do not recover them as sister clades in any of our phylogenetic analysis. Similarly, specimens referred to this clade from western Argentina and central Chile have differences in the amount of constitutive heterochromatin of their karyotypes when compared with individuals of other clades (cf. Walker et al., 1991; Labaroni et al., 2014). As we mention above, our analyses show a close phylogenetic relationship between *P. vaccarum* and *P. limatus*, and a lowest genetic distance of all comparison (3.0%). Also, the bPTP analyses recovered them as one lineage. Taking all this evidence together could suggest a recent divergence between them. The region where both clades converge has a complex Andean topography characterized by the presence of several volcanoes which have had an intense tectonic activity for more than ten million years ago (Allmendinger et al., 1997), which could have act as a geographic barrier favouring that divergence. In this region, it has been recorded that other pairs of sigmodontinae sister species also diverge, such is the case of *Eligmodontia puerulus* and *E. hirtipes* (Armella Sierra et al., 2017). This coincidence of geographic barriers and genetic discontinuities in different lineages are consistent with a model of allopatric speciation. Pairwise genetic distances between the *P. vaccarum* and other clades within the complex of *Phyllotis xanthopygus* (excluding *P. limatus*) range from 7.9% to 9.7% (Table 1) and differing in average 9.0% and 9.7% with the sympatric *P*. sp. 2 and *P. posticalis-rupestris* clades, respectively. In addition to *ricardulus*, we also include under this nominal form the taxa *oreigenus* Cabrera 1926 and *wolffhuegeli* Mann 194 (Table S1).

4.8 | The *Phyllotis sp*. 1 clade

This clade, for which no name is available, is geographically restricted to central Argentina, occupying isolated rocky habitats in high altitude grasslands (above 2,000 m.a.s.l. in Córdoba and San Luis Provinces). Pairwise genetic distances between *P*. sp. 1 and other clades within the complex of *P. xanthopygus* range from 8.6% to 10.6% (Table 1). Samples of these mice are quantitatively different in some cranial features from other populations of *Phyllotis* (Teta et al., 2018). This isolated area in which this mouse is distributed also promoted the divergence, probably through allopatric speciation, of sigmodontinae rodents such as *Akodon polopi* (Jayat et al., 2010).

4.9 | The *Phyllotis sp*. 2 clade

This is the second clade for which no name is available. We obtained specimens of this clade from central-western Argentina (south-western Mendoza Province). In addition, Riverón (2011) refers individuals of this clade for Neuquén Province, Argentina. These populations were previously referred as *P. xanthopygus vaccarum* or *P. x. xanthopygus* (Pearson, 1958; Hershkovitz, 1962; Steppan, 1998). This clade was firstly evidenced by phylogenetic analysis of molecular data (e.g. Albright, 2004; Riverón, 2011). Pairwise genetic distances between *P*. sp. 2 and other clades within the complex of *Phyllotis xanthopygus* range from 8.8% to 10.6% (Table 1). The relationship of this and other clades of the *P. xanthopygus* complex varies in the phylogenetic reconstructions (Figure 2, Figure S1), being the sister clade of *P*. sp. 1 + *P. bonariensis* (ML analysis), or forming a polytomy with other clades, except the *P. posticalis-P. rupestris* clade (Bayesian analysis). However, it never appears related to the sympatric *P. vaccarum* clade. Its morphological distinction regarding the closely distributed *P. vaccarum* is subtle in quantitative terms (Teta et al., 2018); although both taxa have some constant qualitative integumental and dental differences (Jayat et al. in prep.). In spite of having the same diploid number reported for other populations of *Phyllotis*, specimens of this clade (i.e. $2n = 38$, FNa = 71–72) have some important differences in the amount and distribution of the constitutive heterochromatin when compared with all other clades (Labaroni et al., 2014), as is common in *Phyllotis* (Walker et al., 1984, 1991). The chromosome differentiation detected lead to suggest that these populations suffered a marked reduction and isolation that promoted the maintenance of a rare chromosome variant (Labaroni

et al., 2014). This isolation also could be promoted its differentiation at the species level. This new species is currently in the process of being formally described (Jayat et al., in prep.).

4.10 | Sympatry

Most of the clades recovered in our analysis are allopatric, with few examples of sympatric to nearly sympatric distributional ranges. The case of *P. caprinus* is one of the best known. Since its description (Pearson, 1958), it is recognized as being mostly sympatric with the clade here defined as *P. posticalis-P. rupestris*. In contact areas, species of both clades occupy different microhabitats, with *caprinus* mostly captured along brushy hedgerows and stone walls and *posticalis-rupestris* in mountain slopes with tumbled rocks, cacti, and bromeliads (Pearson, 1958). Another example is that of *P. limatus* and *P. posticalis–P. rupestris*, which occupies different types of vegetational belts along the Peruvian Andes (Pearson, 1958). In addition, our results suggest the potential sympatry of the widely distributed clade of *P. vaccarum* with *P. posticalis-P. rupestris* to the north and with *P.* sp. 2 to the south. In fact, both the northern and southern boundaries of the geographical range of *P. vaccarum* are unclear. For example, we found an individual morphologically referable to *P. vaccarum* placed well within the distributional range of the *P. posticalis-P. rupestris* clade in north-western Argentina (southern Jujuy Province, Jayat et al., in prep.), while Riverón (2011) referred specimens of both the *P. vaccarum* and *P.* sp. 2 clades for the same locality (Bardas Blancas) in southern Mendoza Province, west-central Argentina. This is not a minor issue, since several nominal forms, such as *glirinus*, *lanatus*, and *rupestris*, all with type locality in northern Chile, came from areas of putative sympatry between the clades here defined as *limatus*, *posticalis-rupestris*, and *vaccarum*. Within this context, ecological mechanisms (i.e. trophic and habitat use, and others) that allow for the coexistence of different clades are mostly unknown and represent potential lines of inquiry in community ecology of aridland rodent assemblages.

4.11 | Suggestions for future research

Morphological studies are much needed, in order to test more accurately the morphological diagnosability of the clades here proposed. Ongoing research on morphological characters will provide new source of evidence to complement the delimitation of the proposed clades (Jayat et al., in prep.). Judging by the literature, qualitative (i.e. discrete) morphological traits vary little between populations of *Phyllotis*. A possible explanation is that the association of these mice on rocky microenvironments could promote stabilizing selection processes, which favour niche conservatism, and explains some of the observed morphological stasis. Quantitative morphological studies are much required, since some available contributions (i.e. Teta et al., 2018) depict moderate to high metric differences between some of the clades recognized here. At this point, it is important to highlight that some of the previous morphometric approaches (e.g. Pearson, 1958) were conducted under a different taxonomic scenario, where populations were arranged in subspecies based on external coloration and overall size-differences. For example, the concept of *P. x. vaccarum* constructed by Pearson (1958) was mostly based on specimens here referred to the *P. vaccarum* clade and some of the *P.* sp. 2 clade. Therefore, the absence of congruence between the classical arrangement in subspecies for *P. xanthopygus* and the molecular data could be only an artefact of the manner in which previous authors defined their groups.

Despite *Phyllotis* being one of the most studied genera of South American rodents, with a few exceptions (e.g. Steppan, 1998; Teta et al., 2018), integrative approaches are still lacking for the complex of *P. xanthopygus*. In other species complexes within *Phyllotis*, (e.g. *P. andium*, *P. osilae*) the integrative approach proves to be very useful to disentangle intricate taxonomic issues (e.g. Pacheco et al., 2014; Rengifo & Pacheco, 2015; Jayat et al., 2016). On the other hand, genomics has revolutionized many aspects of biological sciences; during the last ten years, rodent systematics is undergoing a transition into the "genomic era" (Lessa et al., 2014; D'Elía et al., 2019; Nery et al., 2020). The implementation of genomic data and methods will allow to obtain a more precise inference of the relationships between the different branches and to investigate in greater detail the intraspecific genetic diversity in the *P. xanthopygus* complex. Also, the use of ancient DNA taken directly from the holotypes (or type series) would surely be useful to test the adequacy of the names provisionally used in this contribution for each recognized clade.

We also note the need for a more detailed study of some nominal forms within *Phyllotis*, as is the case of *P. alisosiensis* and *P. anitae*. A low genetic distance was already observed between type samples of these species (Ferro et al., 2010; Jayat et al., 2016). Among our results we corroborate this low genetic distance (1.3%) and the bPTP analyses clustered them together as one single species (Figure 2; Figure S2). The synonymy between these two nominal forms was previously suggested by Jayat et al. (2016) on the base of the similar external and skull morphology (with the scarce observed differences assigned to the different age classes of the type series of both forms).

As *Phyllotis* is widely distributed, occurring on both sides of the Andes and some adjoining lowlands areas, it represents an excellent model to assess the role of the Andean orogeny and the development of arid and semiarid lowland habitats in South American mammalian diversification.

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REFERENCES

Albright, J. C. (2004). *Phylogeography of the sigmodontine rodent, Phyllotis xanthopygus, and a test of the sensitivity of nested clade analysis to elevation–based alternative distances*, pp. 46. Ph. D. Dissertation. The Florida State University.

Allmendinger, R. W., Jordan, T. E., Kay, S. M., & Isacks, B. L. (1997). The evolution of the altiplano-puna plateau of the central andes. *Annual Review of Earth and Planetary Sciences*, *25*, 139–174. https://doi.org/10.1146/annurev.earth.25.1.139

Armella Sierra, A. B., Castillo, E. R., Labaroni, C., Barrandeguy, M. E., Martí, D. A., Ojeda, R., & Lanzone, C. (2017). Genetic studies in the recently divergent *Eligmodontia puerulus* and *E. moreni* (Rodentia, Cricetidae, Sigmodontinae) from Puna and Monte deserts of South America. *Mammalian Biology*, *87*, 93–100. https://doi.org/10.1016/j.mambio.2017.06.001

Cabrera, A. (1961). Catálogo de los mamíferos de América del Sur. *Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia". Ciencias Zoológicas*, *4*, 309–732.

Cañón, C., D'Elia, G., Pardinas, U. F. J., & Lessa, E. P. (2010). Phylogeography of *Loxodontomys micropus* with comments on the alpha taxonomy of *Loxodontomys* (Cricetidae: Sigmodontinae). *Journal of Mammalogy*, *91*, 1449–1458. https://doi.org/10.1644/10-MAMM-A-027.1

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

D'Elía, G., Fabre, P.-H., & Lessa, E. P. (2019). Rodent systematics in an age of discovery: Recent advances and prospects. *Journal of Mammalogy*, *100*, 852–871. https://doi.org/10.1093/jmammal/gyy179

Da Silva, M. M., & Patton, J. L. (1993). Amazonian phylogeography: mtDNA sequence variation in arboreal echimyid rodents (Caviomorpha). *Molecular Phylogenetics and Evolution*, *2*, 243–255. https://doi.org/10.1006/mpev.1993.1023

Darriba, D., Taboada, G. L., Doallo, R., & Posada, D. (2012). jModelTest 2: More models, new heuristics and parallel computing. *Nature Methods*, *9*, 772. https://doi.org/10.1038/nmeth.2109

De Queiroz, K. (2007). Species concepts and species delimitation. *Systematic Biology*, *56*, 879–886. https://doi.org/10.1080/10635150701701083

Díaz, M. M., Teta, P., Pardiñas, U. F. J., & Barquez, R. M. (2006). Tribu Phyllotini. In R. M. Barquez, M. M. Díaz, & R. A. Ojeda (Eds.), *Mamíferos de Argentina: Sistemática y distribución* (pp. 175–189). Tucumán: Sociedad Argentina para el Estudio de los Mamíferos.

Ferro, L. I., Martínez, J. J., & Barquez, R. M. (2010). A new species of *Phyllotis* (Rodentia, Cricetidae, Sigmodontinae) from Tucumán Province, Argentina. *Mammalian Biology*, *75*, 523–537. https://doi.org/10.1016/j.mambio.2009.09.005

Galliari, C. A., Pardiñas, U. F. J., & Goin, F. J. (1996). Lista comentada de los Mamíferos de Argentina. *Mastozoología Neotropical*, *3*, 39–67.

Hershkovitz, P. (1962). Evolution of Neotropical cricetine rodents (Muridae) with special reference to the phyllotine group. *Fieldiana Zoology*, *46*, 1–524. https://doi.org/10.5962/bhl.title.2781

Jayat, J. P., D'Elia, G., Pardiñas, U. F. J., & Namen, J. G. (2007). A new species of *Phyllotis* (Rodentia, Cricetidae, Sigmodontine) from the upper montane forest of the Yungas of north-western Argentina. InD. A. Kelt, E. P. Lessa, J. Salazar-Bravo, & J. L. Patton (eds.). *The quintessential naturalist: honoring the life and legacy of Oliver P. Pearson*, (pp. 775–798). University of California. Publications in Zoology, 134. https://doi.org/10.1525/california/9780520098596.003.0022

Jayat, J. P., Ortiz, P. E., González, F. R., & 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. https://doi.org/10.11646/zootaxa.4083.3.5

Jayat, J. P., Ortiz, P. E., Salazar-Bravo, J., Pardiñas, U. F. J., & D'Elía, G. (2010). The *Akodon boliviensis* species group (Rodentia: Cricetidae: Sigmodontinae) in Argentina: Species limits and distribution, with the description of a new entity. *Zootaxa*, *2409*, 1–61. https://doi.org/10.11646/zootaxa.2409.1.1

Kelt, D. A. (1994). The natural history of small mammals from Aisén Region, southern Chile. *Revista Chilena De Historia Natural*, *67*, 183–207.

Kramer, K. M., Monjeau, J. A., Birney, E. C., & Sikes, R. S. (1999). *Phyllotis xanthopygus*. *Mammalian Species*, *617*, 1–7. https://doi.org/10.2307/3504375

Kuch, M., Rohland, N., Betancourt, J. L., Latorre, C., Steppan, S., & Poinar, H. N. (2002). Molecular analysis of a 11 700–year–old rodent midden from the Atacama Desert, Chile. *Molecular Ecology*, *11*, 913–924. https://doi.org/10.1046/j.1365-294X.2002.01492.x

Kumar, S., Stecher, G., & Tamura, K. (2016). MEGA7: Molecular evolutionary genetics analysis version 7.0 for bigger datasets. *Molecular Biology and Evolution*, *33*, 1870–1874. https://doi.org/10.1093/molbev/msw054. Epub 2016 Mar 22

Labaroni, C. A., Malleret, M. M., Novillo, A., Ojeda, A., Rodriguez, D., Cuello, P., Ojeda, R., Marti, D., & Lanzone, C. (2014). Karyotypic variation in the Andean rodent *Phyllotis xanthopygus* (Waterhouse, 1837) (Rodentia, Cricetidae, Sigmodontinae). *Comparative Cytogenetics*, *8*, 369–381. https://doi.org/10.3897/CompCytogen.v8i4.8115

Lessa, E. P., Cook, J. A., D'Elía, G., & Opazo, J. C. (2014). Rodent diversity in South America: Transitioning into the genomics era. *Frontiers in Ecology and Evolution*, *2*, 1–7. https://doi.org/10.3389/fevo.2014.00039

Lessa, E. P., D'Elia, G., & Pardiñas, U. F. J. (2010). Genetic footprints of late Quaternary climate change in the diversity of Patagonian-Fueguian rodents. *Molecular Ecology*, *19*, 3031–3037. https://doi.org/10.1111/j.1365-294X.2010.04734.x

Nery, M., Ramos, E., Souza, E., & Ribeiro, P. (2020). Present and prospects of research on neotropical mammals using genomic approaches. *Mastozoología Neotropical*, *27*, 101–119. https://doi.org/10.31687/saremMN_SI.20.27.1.09

Nguyen, L. T., Schmidt, H. A., von Haeseler, A., & Minh, B. Q. (2015). IQTREE: A fast and effective stochastic algorithm for estimating maximum likelihood phylogenies. *Molecular Biology and Evolution*, *32*, 268–274. https://doi.org/10.1093/molbev/msu300

Pacheco, V., Rengifo, E. M., & Vivas, D. (2014). Una nueva especie de ratón orejón del género *Phyllotis* Waterhouse, 1837 (Rodentia: Cricetidae) del norte del Perú. *Therya*, *5*, 81–508. https://doi.org/10.12933/therya-14-185

Palma, R. E., Marquet, P. A., & Boric-Bargetto, D. (2005). Inter and intraspecific phylogeography of small mammals in the Atacama Desert and adjacent areas of northern Chile. *Journal of Biogeography*, *32*, 1931–1941. https://doi.org/10.1111/j.1365-2699.2005.01349.x

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

Pearson, O. P. (1972). New Information on ranges and relationships within the rodent genus *Phyllotis* in Peru and Ecuador. *Journal of Mammalogy*, *53*, 677–686. https://doi.org/10.2307/1379206

Pearson, O. P., & Patton, J. L. (1976). Relationships among South American phyllotine rodents based on chromosome analysis. *Journal of Mammalogy*, *57*, 339–350. https://doi.org/10.2307/1379693

Reig, O. A. (1978). Roedores cricétidos del Plioceno superior de la provincia de Buenos Aires (Argentina). *Publicaciones Del Museo Municipal De Ciencias Naturales De Mar Del Plata Lorenzo Scaglia*, *2*, 164–190.

Rengifo, E. M., & 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. https://doi.org/10.11646/zootaxa.4018.3.2

Rengifo, E. M., & Pacheco, V. (2017). Phylogenetic position of the Ancash leaf-eared mouse *Phyllotis definitus* Osgood 1915 (Rodentia: Cricetidae). *Mammalia*, *82*, 153–166. https://doi.org/10.1515/mammalia-2016-0138

Riverón, S. (2011). *Estructura poblacional e historia demográfica del "pericote patagónico" Phyllotis xanthopygus (Rodentia: Sigmodontinae) en Patagonia Argentina*. Ph. D. Dissertation, Universidad de la República, Uruguay, pp. 100.

Ronquist, F., & Huelsenbeck, J. P. (2003). MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics*, *19*, 1572–1574. https://doi.org/10.1093/bioinformatics/btg180

Sassi, P. L., Cuevas, M. F., Menéndez, J., & Dacar, M. A. (2017). Feeding strategies of a small mammal (*Phyllotis xanthopygus*, Rodentia Cricetidae) at diverse altitudes in the Central Andes, Argentina. *Ethology Ecology & Evolution*, *29*, 351–366. https://doi.org/10.1080/03949370.2016.1188158

Sikes, R. S.,Gannon, W. L. & The Animal Care and Use Committee of the American Society of Mammalogists. (2016). Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. *Journal of Mammalogy*, *97*, 663–688. https://doi.org/10.1644/10-MAMM-F-355.1

Steppan, S. J. (1993). Phylogenetic relationships among the Phyllotini (Rodentia: Sigmodontinae) using morphological characters. *Journal of Mammalian Evolution*, *1*, 187–213. https://doi.org/10.1007/BF01024707

Steppan, S. J. (1995). Revision of the tribe Phyllotini (Rodentia: Sigmodontinae), with a phylogenetic hypothesis for the Sigmodontinae. *Fieldiana Zoology, New Series*, *80*, 1–112. https://doi.org/10.5962/bhl.title.3336

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. https://doi.org/10.1111/j.1558-5646.1997.tb02444.x

Steppan, S. J. (1998). Phylogenetic relationships and species limits within *Phyllotis* (Rodentia: Sigmodontinae): Concordance between mtDNA sequence and morphology. *Journal of Mammalogy*, *7*, 573–593. https://doi.org/10.2307/1382988

Steppan, S. J., & Ramírez, O. (2015). Genus *Phyllotis* Waterhouse, 1837. InJ. L. Patton, U. F. J. Pardiñas, & G. D'Elía (Eds.), *Mammals of South America, Volume 2, Rodents* (pp 535–555). The University of Chicago Press. Chicago and London. https://doi.org/10.7208/chicago/9780226169606.001.0001

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

Storz, J. F., Quiroga-Carmona, M., Opazo, J. C., Bowen, T., Farson, M., Steppan, S. J., & D'Elía, G. (2020). Discovery of the world's highest-dwelling mammal. *Proceedings of the National Academy of Sciences of the United States of America*, *117*, 18169–18171. https://doi.org/10.1073/pnas.2005265117

Teta, P., Jayat, J. P., Lanzone, C., Novillo, A., Ojeda, A., & 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. https://doi.org/10.11646/zootaxa.4446.1.5

Thompson, J. D., Gibson, T. J., Plewniak, F., Jeanmougin, F., & Higgins, D. G. (1997). The CLUSTAL_X windows interface: Flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acids Research*, *25*, 4876–4882. https://doi.org/10.1093/nar/25.24.4876

Trifinopoulos, J., Nguyen, L. T., Von Haeseler, A., & Minh, B. Q. (2016). W-IQ-TREE: A fast online phylogenetic tool for maximum likelihood analysis. *Nucleic Acids Research*, *44*, 232–235. https://doi.org/10.1093/nar/gkw256

Walker, L. I., Spotorno, A. E., & Arrau, J. (1984). Cytogenetic and reproductive studies of two nominal subspecies of *Phyllotis darwini* and their experimental hybrids. *Journal of Mammalogy*, *65*, 220–230. https://doi.org/10.2307/1381161

Walker, L. I., Spotorno, A. E., & Sans, J. (1991). Genome size variation and its phenotypic consequences in *Phyllotis* rodents. *Hereditas*, *115*, 99–107. https://doi.org/10.1111/j.1601-5223.1991.tb03542.x

Zhang, J., Kapli, P., Pavlidis, P., & Stamatakis, A. (2013). A general species delimitation method with applications to phylogenetic placements. *Bioinformatics*, *29*, 2869–2876. https://doi.org/10.1093/bioinformatics/btt499

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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