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Taxonomy of the *Phyllotis osilae* species group in Argentina; the status of the "Rata de los nogales" (*Phyllotis nogalaris* Thomas, 1921; Rodentia: Cricetidae)

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Abstract

The taxonomic status of populations of the genus *Phyllotis* from northwestern Argentina (NWA) has undergone recent changes, with the addition of two species (*P. alisosiensis* and *P. anitae*) to the traditionally recognized forms (*P. caprinus*, *P. xanthopygus*, and *P. osilae*). Three of these species (*P. anitae*, *P. osilae*, and *P. alisosiensis*) were included within the *Phyllotis osilae* species group. Most authors recognized three subspecies of *P. osilae* for NWA: *P. osilae osilae*, *P. o. nogalaris*, and *P. o. tucumanus*. Morphological, morphometric, and molecular studies based on recently collected specimens suggest that current classification does not reflect the diversity of this group in NWA, revealing the need of some taxonomic reallocations and new distributional delimitations. Here we propose that *P. nogalaris* must be recognized as a valid species and the restriction of *P. osilae* to southern Peru and central Bolivia. Following our results, we expect an outstanding improvement in the taxonomic knowledge of the *Phyllotis osilae* species group in the coming years.

Key words: highland grasslands, Phyllotini, Sigmodontinae, species boundary, Yungas

Introduction

The understanding of the taxonomy and distribution of sigmodontine rodents from northwestern Argentina (NWA) has drastically changed in the last fifteen years. Comparing the species list advanced by Galliari *et al*. (1996) with that of the last review of Argentinean mammals (Barquez *et al*. 2006a), no less than 15 changes can be identified. Furthermore, at least ten new species were added to the list of sigmodontines present in the region since Barquez et al. contribution (Jayat *et al*. 2011a; Patton *et al*. 2015). Most of these changes correspond to the provision of records for NWA of species previously known from other areas (e.g., Barquez *et al*. 2006b; Jayat *et al*. 2006). However, new species based on material collected in NWA were also described (e.g., Jayat *et al*. 2007, 2008a; Mares *et al*. 2008). Finally, disagreements on the distinction of different populations have prompted changes in the taxonomic status of some nominal forms (e.g., Ferro & Martínez 2009; Jayat *et al*. 2010).

During the last few years, several forms of *Phyllotis* Waterhouse from NWA have undergone some of the changes listed above. Currently, five species of *Phyllotis* are recognized for this region: *P. caprinus* Pearson and *P. xanthopygus* Waterhouse inhabiting arid and semi- arid open environments; *P. alisosiensis* Ferro, Martínez and Barquez and *P. anitae* Jayat, D'Elía, Pardiñas and Namen, mentioned for humid and moderately forested areas; and *P. osilae* J A Allen, mainly an inhabitant of high altitudinal grasslands above the Yungas forests belt (Pearson 1958; Hershkovitz 1962; Kramer *et al*. 1999; Jayat & Pacheco 2006; Jayat *et al*. 2007, 2008b; Ferro *et al*. 2010). Two of these species (*P. anitae* and *P. osilae*) were included within the so called *Phyllotis osilae* species group by Steppan *et al*. (2007), a scheme later expanded to include *P. alisosiensis* (Ferro *et al*. 2010). Of these three species, only *P. osilae* was known at the time of the revisionary works of Pearson (1958) and Hershkovitz (1962). These authors listed three subspecies of *P. osilae* for NWA: *P. osilae osilae* J A Allen, widely distributed from southern Peru to northernmost Argentina, in Jujuy province; *P. o. nogalaris* Thomas, restricted to Jujuy province; and *P. o.*

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tucumanus Thomas, in Tucumán and Catamarca provinces. With the exception of a few new locality records (e.g., Díaz & Barquez 2007; Jayat *et al.* 2007), there have been no additional publications on these subspecies in this region; for example, Steppan *et al.* (2007) did not evaluate the status of NWA populations in their extensive revisionary study of *Phyllotis*. Current knowledge on *P. osilae tucumanus* and *P. o. nogalaris* comes from the sketchy descriptions provided by Thomas (1912, 1921; as *P. darwini tucumanus* and *P. nogalaris,* respectively) on the base of small series of specimens collected at their type localities. Pearson (1958) and Hershkovitz (1962) studied these nominal forms, but without adding relevant new information respect to the original descriptions. Recent mentions of these subspecies were limited to providing a handful of new locality records (e.g., Díaz & Barquez 2007; Jayat *et al.* 2007).

Recent surveys of mammals in NWA resulted in the collection of several specimens of the *P. osilae* species group. Morphological and molecular analyses of this sample and previously collected specimens revealed the existence of marked population differentiation suggesting that current classificatory scheme does not reflect the species diversity of this group in NWA. In this contribution we suggest that *P. nogalaris* Thomas represents a distinct species and that *P. osilae* must be removed from Argentina. Similarly, we show the need of more detailed studies of the nominal forms *P. alisosiensis* and *P. osilae tucumanus*.

Material and methods

Specimens of *Phyllotis* studied here were newly collected by us using Sherman traps or already housed at natural history collections (Appendix). Newly captured specimens were deposited at the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" collection (MACN) or provisionally housed in the collection of one of the authors (JPJ; these specimens will be properly housed at MACN). Some of the new specimens were caught near the type localities of *P. osilae tucumanus* (*P. darwini tucumanus* Thomas) and *P. osilae nogalaris* (*P. nogalaris* Thomas).

Genetic comparisons and phylogenetic analyses were based on a fragment of 801 base pairs of the cytochrome-b gene (*cyt b*). A total of 64 sequences, of which 56 belong to specimens of *Phyllotis*, were analyzed. Sequences were retrieved from Genbank (accession numbers in the Appendix) or gathered by us as detailed below. Taxonomic coverage is broad; it includes representatives of 14 species of *Phyllotis* (sensu Steppan & Ramirez 2015, see also Pacheco *et al*. 2014 and Rengifo and Pacheco 2015; Appendix). The outgroup was conformed with sequences of the other genera of the phyllotine clade to which *Phyllotis* belongs to (Salazar-Bravo *et al.* 2013): *Auliscomys pictus* (APU03545), *Andalgalomys pearsoni* (AF159285), *Eligmodontia typus* (HM167862), *Galenomys garleppi* (JQ434423), *Graomys griseoflavus* (AY275117), *Loxodontomys micropus* (AY275122), *Salinomys delicatus* (AF159292), and *Tapecomys primus* (AF159287). Thirty-three DNA sequences were acquired using primers MVZ 05 and MVZ 16 (da Silva & Patton 1993) following the protocol outlined in Cañon *et al.* (2010). Amplicons were purified and sequenced by Macrogen Inc., Korea. New sequences were deposited in GenBank (KF442273-KF442282, KT024789- KT024811).

Sequence alignment was accomplished with Clustal X (Thompson *et al.* 1997) using the default values for all alignment parameters. No adjustment by eye was needed as alignment was unambiguous. Aligned sequences were subject to Bayesian analysis (BI; Rannala & Yang 1996) and maximum likelihood (ML; Felsenstein 1981). BI analysis was performed in MrBayes 3.1 (Ronquist & Huelsenbeck 2003), by means of two independent runs with 5 heated and 1 cold Markov chains each. The HKY+I+G model, selected with jModelTest (Darriba *et al*., 2012), was specified; all model parameters were estimated in MrBayes. Uniform interval priors were assumed for all parameters except base composition and HKY parameters, which assumed a Dirichlet process prior. Runs were allowed to proceed for 20 million generations, with trees being sampled every 1 thousand generations. Log-likelihood values against generation time were plotted to check that the runs converged on a stable log-likelihood value. The first 25% of the sampled trees were discarded as burn-in; the remaining trees were used to compute a 50% majority rule consensus tree and obtain posterior probability (PP) estimates for each clade. ML analysis was conducted in Treefinder (Jobb *et al*. 2004). The best-fitting model of nucleotide substitutions was selected in Treefinder using the "propose model" routine; the J2+G model (J2 is a special case of the GTR model that includes 2 transversion parameters, one for transversions TA and CA and the other for transversions TG and CG) was selected. Except for this constraint, base frequencies, substitution rates, and gamma shape parameter were freely estimated from the data (Jobb 2011). We used the tree search algorithm 2 as implemented in Treefinder; nodal support was estimated with 1,000 bootstrap pseudoreplicates (BS). Pairwise comparisons between haplotypes, localities or species were calculated with MEGA 6 (Tamura *et al.* 2013) in the form of *p*-distances.

Standard external measures were recorded from specimen tags or field catalogs: TL: total length; T: tail length, HF: hind foot length (including claw), E: ear length, and W: weight. The following skull measurements were recorded with a Vernier caliper to the nearest of 0.01 mm following Myers *et al.* (1990): MSL: maximum skull length; CIL: condyle-incisive length; BL: basal length; PL: palatal length; PB: palatal bridge; NL: nasal length; RL: rostral length; OL: orbital length; RW2: mid rostral width; ZP: zygomatic plate depth; IOC: interorbital constriction; ZL: zygomatic length; ZB: zygomatic breadth; BB: braincase breadth; DL: diastema length; MTRL: maxillary toothrow length; IFL: incisive foramina length; BPL: basal- posterior length; ILL: interlacrimal length; ML: mandible length; mTRL: mandibular toothrow length. Nomenclature used to describe the skull and its structures follows Voss (1988) and Wahlert (1985) and that of the molars corresponds to Reig (1977). Age classes were defined according the tooth wear classes of Figure 1.

A Principal Components Analysis (PCA) for individuals of age class 2–3, the larger subset of available specimens, was carried out with the aim of reducing the dimensionality of morphometric data and exploring morphometric variation (James & McCulloch 1990). The principal components were extracted from the variance-covariance matrix and computed by using the variables after transformations to Log 10. Statistical significance of the PC's was evaluated following the Brocken Stick test (Peres-Neto *et al.* 2005). Additionally, we conduct a discriminant analysis (DA) to test the hypothesis of differentiation between groups formed a priori (following the results of the phylogenetic analysis; see below). For this analysis we used the same variables and specimens as in the PCA. Statistical analyses were conducted in PAST (Hammer *et al.* 2001).

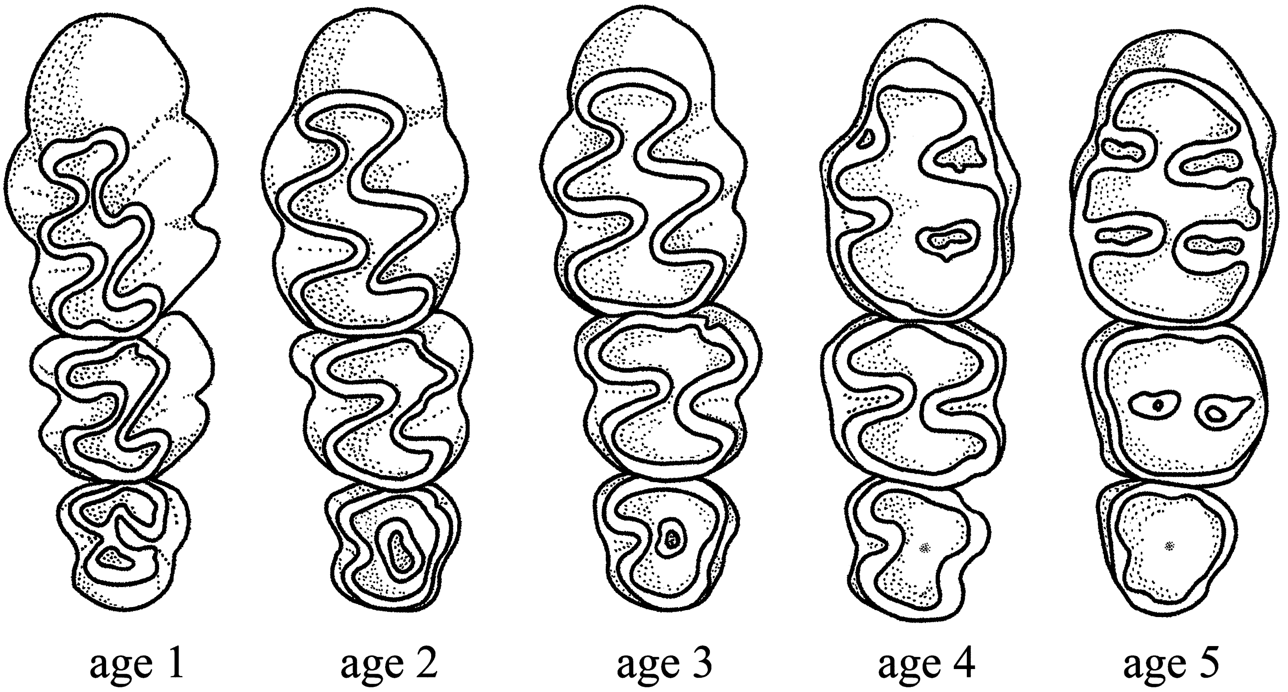

FIGURE 1. Toothwear age classes in *Phyllotis osilae* species complex. Age class 1: M3 is incompletely erupted or unworn. Age class 2: M3 is fully erupted and exhibits moderate wear, M1-2 unworn. Age class 3: M3 is well worn, the occlusal surface is flat or concave; M1–2 exhibit moderate wear. Age class 4: M3 heavily worn, being generally concave; M1–2 have cusps worn and flat. Age class 5: M1–3 are all worn and concave; most details of the occlusal topography are obliterated.

Results

Phylogenetic analysis. BI and ML (ln = -7812.622) analyses recover congruent topologies regarding relationships within and among species of *Phyllotis*; discrepancies pertain to relationships among outgroup taxa. As such, only the topology derived from the Bayesian analysis is presented along with ML Bootstrap proportions (Fig. 2).

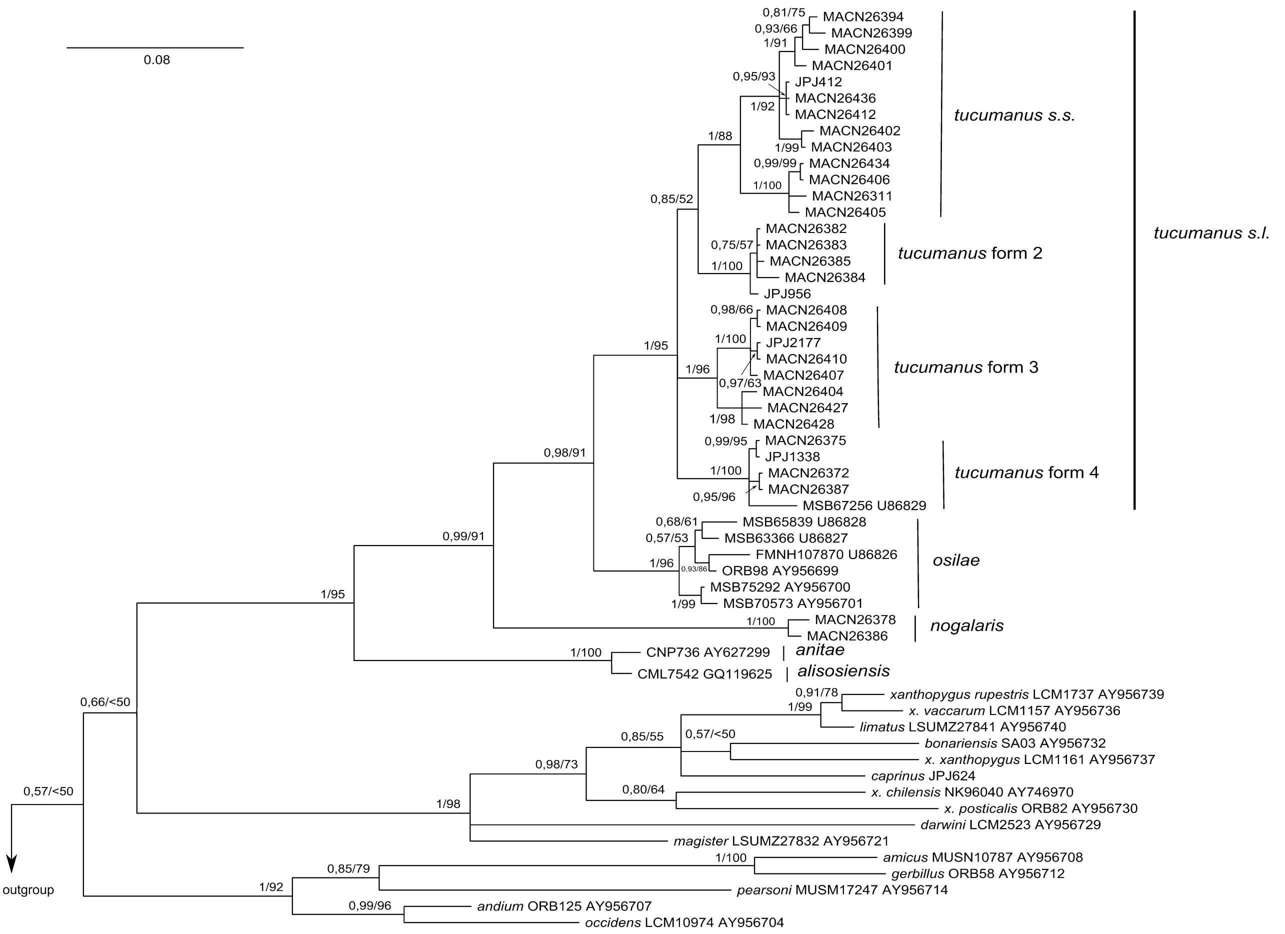

FIGURE 2 Genealogical relationship of 56 haplotypes recovered from specimens of *Phyllotis* and eight haplotypes of representatives of the other eight phyllotine genera obtained in a Bayesian analysis (see text for details). Numbers at branches indicate Bayesian posterior probability values (left to the diagonal) and Maximum Likelihood Bootstrap proportions (right to the diagonal). A less-than sign (<) indicates that the given clade receives less than 50 % of Bootstrap support in the Maximum Likelihood analysis. A dash (-) indicates that in the Maximum Likelihood analysis that clade was not recovered. For haplotypes retrieved from Genbank, catalogue and accession numbers are shown in haplotype labels. For haplotypes generated by us catalogue numbers are shown in haplotype labels and accession numbers in the Appendix.

Phyllotis was recovered monophyletic, although weakly supported (PP = 0.57; BS > 50). Species of *Phyllotis* fall into three main and well-supported clades that correspond to the *P. andium*/*amicus*, *P. darwini*, and *P. osilae* species groups (Steppan *et al.* 2007). The *P. andium*/*amicus* group (PP = 1; BS = 92) is formed by *P. amicus*, *P. andium*, *P. gerbillus*, *P. pearsoni*, and *P. occidens* (Steppan *et al.* 2007; Pacheco *et al.* 2014; Rengifo & Pacheco 2015). The *P. darwini* species group (PP = 1; BS = 98) is composed by *P. darwini*, *P. magister*, and *P. xanthopygus*, which appears paraphyletic with respect to *P. bonariensis, P. caprinus* and *P. limatus*. The *P. osilae* species group (PP = 1; BS = 95) includes the southern Yungas species *P. anitae* and *P. alisosiensis* (but see below) and a broadly distributed clade (PP = 1; BS = 91) formed by haplotypes recovered from specimens currently assigned to *P. osilae* (including the forms *phaeus*, *nogalaris*, *osilae*, and *tucumanus*).

The large clade of haplotypes from specimens currently assigned to *P. osilae* is highly structured (Fig. 2). Haplotypes recovered from two specimens (MACN 26386, 26378) from the proximities of the type locality of *P. nogalaris* are sister to a clade (PP = 0.99; BS = 91) formed by all other haplotypes, including five gathered from specimens secured at the same locality where specimens MACN 26386 and 26378 were collected. Haplotypes gathered from specimens assignable to *P. osilae* from southern Peru and northern Bolivia (see Steppan *et al.* 2007), form a distinct clade (PP = 1; BS = 96) of that formed by haplotypes of individuals from southern Bolivia and NWA (PP = 1; BS 95). Within this latter clade, here referred as *P. tucumanus s.l.*, there is strong genealogical structure; haplotypes are arranged in four strongly supported clades, which are here labelled as *P. tucumanus s.s.*

(PP = 1; BS = 88), *P. tucumanus* form 2 (PP = 1; BS = 100), *P. tucumanus* form 3 (PP = 1; BS = 96), and *P. tucumanus* form 4 (PP = 1; BS = 100). Relationships among these four clades are not resolved. The only recovered relationship is the clade formed by *P. tucumanus s.s.* and *P. tucumanus* form 2, although it lacks significant support (Fig. 2).

Morphologic analysis. At a first glance, NWA specimens traditionally assigned to *Phyllotis osilae* are homogeneous and present the character states observed by Pearson (1958), including the broad rostrum, with a conspicuous swelling in the mid- lateral portion; a pinched and hour-glass shaped interorbital constriction lacking overhanging borders; and small posteropalatal pits located approximately at the same line of the anterior border of the relatively broad mesopterygoid fossa. Notwithstanding, among these specimens, we observed several morphological differences that delimit groups that are mostly congruent with the topology of *cyt b* gene tree, and which can be summarized in three main points:

1. *P. nogalaris*, as represented by specimens coming from the vicinities of the type locality, are noticeably different in morphologic and morphometric characters from the type specimens of *P. osilae* (and from other *P. osilae* specimens coming from southern Perú and northern Bolivia, Table 1 and Fig. 3) and all others studied specimens from NWA (Table 2). *P. nogalaris* is comparatively large for the genus, having the fur fluffy and richly colored, and the skull heavily built, with the rostrum broad, the zygomatic notches broad and deep, and the zygomatic arches well expanded (see the emended diagnosis in following paragraphs for a complete enumeration of the state character that differentiate this species).

2. All major clades obtained for NWA (*P. tucumanus s.s.*, *P. tucumanus* form 2, *P. tucumanus* form 3, and *P. tucumanus* form 4) can be morphologically differentiated. In *Phyllotis tucumanus* form 2 the fur is ochraceous, with hairs comparatively short and the skull without a developed median spine in the mesopterygoid fossa. Furthermore, the zygomatic plate of *P. tucumanus* form 2 shows a tiny spiny process on the free upper border generally not seen in other species of the *P. osilae* group. Representatives of *P. tucumanus* form 3 have the fur with a somewhat decolored pattern, with not well contrasting eye-ring, less orange flanks, and less ochraceous venter. Furthermore, *P. tucumanus* form 3 has a proportionally broad zygomatic plate and long incisive foramina. Specimens of *P. tucumanus* form 4 have the clearest skins compared with the other forms in NWA; showing a less developed eye ring, a less conspicuous lateral and pectoral orange fringes, and a clearest tail. The skull of *P. tucumanus* form 4 is also noticeably delicate, but with a comparatively broader interorbital constriction, a relatively broader zygomatic plate, and a more robust tympanic hook (for a more detailed comparison of all these forms with *P. nogalaris* see the comparisons sections in following paragraphs).

3. The southern clade, here assigned to *P. tucumanus s.s.*, has a remarkable morphologic variation and their different populations can overlap in skin coloration patterns and skull characters with some of the other forms presents in NWA. Notwithstanding, *P. tucumanus s.s.* can be characterized as a form intermediate in size, with the skull not well robust (but with a proportionally broader interorbital constriction) and the molars not laminated and not well hypsodont. In *P. tucumanus s.s.* the zygomatic plate lacks of the tiny spiny process on its free upper border.

Morphometric analysis. Descriptive statistics segregate NWA specimens of *Phyllotis nogalaris* from that of *P. osilae osilae* from Cuzco and Puno, in Peru, and from north-central Bolivia on the base of some measurements which show practically no overlapping ranges (e.g. HF, MTRL, ZB, BB). Additionally, *P. nogalaris* is, on average, larger for all the compared measurements (Table 1).

In the PCA (Fig. 4) NWA specimens of the *Phyllotis osilae* species group (*P. anitae* and *P. alisosiensis* not included) form four main groups. The first three principal components summarize 75.76% of the total variation but only the first (PCI, 62.13% of the explained variance) was statistically significant according to the Brocken Stick test (Table 3). This was mostly a size component, as the variables representing cranial longitude had the same sign and the most weight on this axis (e.g., CIL, BL, MSL, PL, OL, ML, and RL). Although non-significant, the second and third components (summarizing 8.15% and 5.48% of the total variation, respectively) separated individuals mainly on account of the following variables: mTRL, MTRL, PB, RW2, and IOC.

The DA (Table 4) was used to test the hypothesis of differentiation between groups previously outlined by the molecular and morphologic analyses; in general the DA showed a good separation among groups, with a low value for Wilk's lambda (0.024 [21, 4, 69 df]; approx. F ratio= 3,67 [84, 191 df]; p= 0.000) and high percentages of correct classifications in most cases (100% for *P. nogalaris* and *P. tucumanus* form 4, 98% for *P. tucumanus s.s.*, 88% for *P. tucumanus* form 2, but only 50% for *P. tucumanus* form 3).

TABLE 1. External and craniodental measurements for adult specimens of *Phyllotis nogalaris* in northwestern Argentina and *P. osilae* from Peru and Bolivia (taken from Pearson, 1958; Appendix I). X: mean; SD: standard deviation; r: range; n: sample size.

	P. nogalaris			*P. osilae osilae* Cuzco region			*P. osilae osilae* Titicaca drainage, Peru			*P. osilae osilae* North - central Bolivia		
	n	X ± SD	r	n	X ± SD	r	n	X ± SD	r	n	X ± SD	r
TBL	6	268 ± 11.28	248–279	-	-	-	-	-	-	-	-	-
HB	**6**	**128 ± 6.84**	**118–137**	**6**	**114.5**	**103–125**	**51**	**119.6 ± 7.5**	**105–133**	**20**	**107.0 ± 7.8**	**95–120**
TL	**6**	**140 ± 6.28**	**130–149**	**5**	**129.2**	**123–140**	**51**	**123.4 ± 10.2**	**96–147**	**20**	**124.0 ± 9.0**	**108–145**
HF	**6**	**32 ± 0.75**	**31–33**	**6**	**25.5**	**25–27**	**51**	**26.2**	**23–29**	**16**	**25.7**	**25–28**
E	**6**	**23 ± 0.55**	**22–23**	**6**	**21.5**	**20–23**	**41**	**22.9 ± 1.6**	**20–28**	**16**	**22.5**	**20–25**
W	6	56.8 ± 13.14	43.0–82.0	-	-	-	-	-	-	-	-	-
TSL	**6**	**31.42 ± 0.98**	**29.90–32.68**	**5**	**29.78**	**28.5–31.5**	**42**	**30.05 ± 1.19**	**27.8–32.2**	**18**	**28.77 ± 1.31**	**26.7–31.9**
CIL	6	29.46 ± 1.10	27.84–31.14	-	-	-	-	-	-	-	-	-
BL	6	26. 86 ± 1.02	25.32–28.24	-	-	-	-	-	-	-	-	-
PL	6	16.21 ± 0.32	15.78–16.58	-	-	-	-	-	-	-	-	-
DL	6	8.43 ± 0.33	8.00–8.84	-	-	-	-	-	-	-	-	-
PB	6	5.57 ± 0.19	5.36–5.86	-	-	-	-	-	-	-	-	-
MTRL	**6**	**5.75 ± 0.19**	**5.54–6.02**	**6**	**5.28**	**5.0–5.4**	**42**	**5.18 ± 0.03**	**4.9–5.6**	**21**	**5.06 ± 0.19**	**4.7–5.3**
IFL	6	7.14 ± 0.17	6.92–7.40	-	-	-	-	-	-	-	-	-
ZL	6	16.09 ± 0.50	15.44–16.78	-	-	-	-	-	-	-	-	-
ZP	6	3.31 ± 0.25	2.96–3.58	-	-	-	-	-	-	-	-	-
ZB	**6**	**17.13 ± 0.87**	**16.42–18.80**	**5**	**15.1**	**14.5–15.9**	**39**	**15.38**	**14.3– 16.5**	-	-	-
BB	**6**	**14.59 ± 0.28**	**14.26 - 14.92**	-	-	-	**40**	**13.44**	**12.9–14.2**	-	-	-
IOC	**6**	**4.35 ± 0.07**	**4.28–4.46**	-	-	-	**38**	**4.06 ± 0.15**	**3.8–4.4**	-	-	-
RW2	6	5.54 ± 0.27	5.20–5.90	-	-	-	-	-	-	-	-	-
NL	6	12.91 ± 0.55	12.16–13.50	-	-	-	-	-	-	-	-	-
RL	6	11.97 ± 0.40	11.26–12.30	-	-	-	-	-	-	-	-	-
OL	6	10.93 ± 0.52	10.18–11.60	-	-	-	-	-	-	-	-	-
BPL	6	10.66 ± 0.64	9.66–11.56	-	-	-	-	-	-	-	-	-
ILL	6	8.83 ± 0.24	8.62–9.24	-	-	-	-	-	-	-	-	-
ML	6	16.86 ± 0.45	16.22–17.62	-	-	-	-	-	-	-	-	-
mTRL	6	5.76 ± 0.20	5.58–6.08	-	-	-	-	-	-	-	-	-

TABLE 2. Comparative measurements of young specimens (age classes 2) of 5 species of *Phyllotis* in northwestern Argentina. X: mean; SD: standard deviation; r: range; n: sample size.

	Phyllotis nogalaris			*P. tucumanus s.s.*			*P. tucumanus* 2			*P. tucumanus* 3			*P. tucumanus* 4		
	n	X ± SD	r	n	X ± SD	r	n	X	r	n	X ± SD	r	n	X ± SD	r
TBL	2	243.5 ± 13.4	234–253	2	233.5 ± 21.9	218–249	1	240	-	4	238 ± 4.6	233–244	13	212 ± 9.0	195–232
TL	2	131 ± 8.5	125–137	2	114 ± 8.5	108–120	1	125	-	4	126 ± 7.0	116–132	13	111 ± 5.2	100–120
HF	2	32 ± 0.7	32–33	3	31 ± 1.2	30–32	1	30	-	4	30 ± 1.3	29–32	13	28 ± 0.8	27–30
E	2	23 ± 0.7	23–24	3	22 ± 0.6	22–23	1	22	-	4	22 ± 0.8	21–23	13	22 ± 0.7	21–23
W	2	39 ± 7.1	34.0–44.0	3	46.5 ± 4.9	42.5–52	1	42.0	-	4	37.5 ± 2.4	35.5–41.0	13	28.5 ± 4.4	23.0–38.0
MLS	2	30.03 ± 1.17	29.20–30.86	3	30.90 ± 0.98	29.80–31.68	1	29.86	-	4	29.52 ± 0.21	29.22–29.70	13	28.05 ± 0.63	27.28–29.22
CIL	2	27.48 ± 1.33	26.54–28.42	3	28.56 ± 0.83	27.60–29.08	1	27.92	-	4	27.45 ± 0.18	27.20–27.62	13	25.67 ± 0.58	24.60–26.50
BL	2	25.14 ± 1.16	24.32–25.96	3	26.19 ± 0.65	25.46–26.70	1	25.16	-	4	25.09 ± 0.19	24.80–25.24	13	23.27 ± 0.50	22.38–23.96
PL	2	15.28 ± 0.93	14.62–15.94	3	15.77 ± 0.31	15.42–16.00	1	15.06	-	4	15.12 ± 0.22	14.96–15.44	13	14.31 ± 0.41	13.58–15.02
DL	2	7.84 ± 0.23	7.68–8.00	3	7.93 ± 0.14	7.76–8.02	1	7.26	-	4	7.76 ± 0.22	7.50–8.00	13	7.19 ± 0.21	6.96–7.64
PB	2	5.56 ± 0.79	5.00–6.12	3	5.33 ± 0.07	5.26–5.40	1	5.24	-	4	5.49 ± 0.16	5.28–5.64	13	4.96 ± 0.31	4.40–5.52
MTRL	2	5.94 ± 0.17	5.82–6.06	3	5.65 ± 0.12	5.56–5.78	1	5.60	-	4	5.28 ± 0.10	5.16–5.40	13	5.12 ± 0.15	4.88–5.40
IFL	2	6.64 ± 0.23	6.48–6.80	3	7.27 ± 0.31	7.00–7.60	1	6.76	-	4	6.69 ± 0.30	6.36–7.08	13	6.43 ± 0.33	6.00–6.96
ZL	2	14.95 ± 0.21	14.80–15.10	3	15.41 ± 0.38	14.84–15.68	1	14.86	-	4	15.09 ± 0.11	15.00–15.22	13	14.06 ± 0.32	13.54–14.68
ZP	2	3.00 ± 0.14	2.90–3.10	3	3.44 ± 0.16	3.28–3.60	1	2.92	-	4	3.18 ± 0.18	3.00–3.40	13	2.90 ± 0.12	2.68–3.12
ZB	2	15.86 ± 0.71	15.36–16.36	3	16.34 ± 0.48	15.84–16.80	1	15.92	-	4	15.45 ± 0.39	15.00–15.88	13	14.86 ± 0.36	14.26–15.32
BB	2	14.13 ± 0.52	13.76–14.50	3	13.91 ± 0.48	13.38–14.32	1	14.20	-	4	13.67 ± 0.16	13.52–13.80	13	13.39 ± 0.24	13.06–13.78
IOC	2	4.08 ± 0.11	4.00–4.16	3	4.12 ± 0.07	4.06–4.20	1	4.36	-	4	4.07 ± 0.12	3.92–4.18	13	4.18 ± 0.18	3.92–4.48
RW2	2	5.26 ± 0.48	4.92–5.60	3	5.29 ± 0.11	5.20–5.42	1	5.10	-	4	5.06 ± 0.12	4.90–5.20	13	4.84 ± 0.12	4.66–5.04
NL	2	12.17 ± 0.47	11.84–12.50	3	12.99 ± 0.59	12.32–13.42	1	12.90	-	4	11.91 ± 0.18	11.64–12.00	13	11.84 ± 0.40	11.36–12.70
RL	2	11.42 ± 0.34	11.18–11.66	3	11.53 ± 0.51	10.94–11.84	1	11.24	-	4	10.84 ± 0.13	10.66–10.96	13	10.44 ± 0.34	10.00–11.02
OL	2	10.41 ± 0.38	10.14–10.68	3	10.63 ± 0.05	10.60–10.68	1	10.38	-	4	10.26 ± 0.06	10.20–10.34	13	9.85 ± 0.30	9.36–10.26
LBP	2	9.65 ± 0.27	9.46–9.84	3	10.33 ± 0.39	9.92–10.70	1	9.90	-	4	9.93 ± 0.23	9.68–10.22	13	9.09 ± 0.22	8.76–9.58
ILL	2	8.49 ± 0.47	8.16–8.82	3	8.50 ± 0.35	8.10-8.70	1	8.06	-	4	7.83 ± 0.16	7.68–8.04	13	7.65 ± 0.27	7.26–8.12
ML	2	15.90 ± 0.76	15.36–16.44	3	16.55 ± 0.49	16.00-16.96	1	16.10	-	4	15.93 ± 0.15	15.74–16.10	13	15.09 ± 0.42	14.34–15.66
mTRL	2	5.97 ± 0.07	5.92–6.02	3	5.55 ± 0.20	5.34-5.74	1	5.28	-	4	5.12 ± 0.11	4.96–5.22	13	5.03 ± 0.17	4.76–5.26

TABLE 3. Results of principal components analysis of craniodental measurements of young specimens (age classes 2 and 3, n = 74) of 5 populations of *Phyllotis osilae* group from northwestern Argentina: *P. nogalaris* (n = 6), *P. tucumanus s.s.* (n=49), *P. tucumanus* form 2 (n = 8), *P. tucumanus* form 3 (n = 6), and *P. tucumanus* form 4 (n = 5). Asterisk indicates significant principal components after the Broken-stick test.

Variable	Pearson correlation		
	PC1	PC2	PC3
MSL	0.267	-0.061	0.016
CIL	0.270	-0.092	-0.027
BL	0.269	-0.108	-0.033
PL	0.252	0.074	-0.071
DL	0.227	-0.185	0.118
PB	0.134	0.331	-0.132
MTRL	0.169	0.366	-0.343
IFL	0.128	-0.289	0.074
BPL	0.190	-0.264	0.187
ZL	0.254	-0.017	-0.140
ZP	0.171	-0.135	-0.318
ZB	0.249	0.002	0.106
BB	0.185	0.273	0.320
IOC	0.084	0.327	0.697
RW2	0.240	-0.005	0.042
NL	0.228	-0.197	0.018
RL	0.260	-0.059	0.005
OL	0.252	-0.031	-0.043
ILL	0.221	0.126	0.140
ML	0.255	-0.029	-0.103
mTRL	0.136	0.529	-0.221
Eigenvalue	13.048	1.711	1.151
% of variance	62.134	8.149	5.485
Broken-stick eigenvalue	3.645*	2.645	2.145

Discussion

Species boundaries within the genus *Phyllotis* and relationships among its species have been studied by several authors (e.g., Pearson 1958; Hershkovitz 1962; Pearson & Patton 1976; Spotorno & Walker 1983; Steppan 1998; Steppan *et al.* 2007). Notwithstanding, and in contrast with what happened with other sigmodontine genera, the taxonomic composition of *Phyllotis* did not substantially change during the last half of the XX century. That static scenario was attributed to the lack of taxonomic studies and not to a well-resolved alpha taxonomy (Jayat *et al.* 2007). In recent years, however, new nominal forms were proposed, as well as the exclusion of one species now placed in the genus *Tapecomys* (Jayat *et al.* 2007; Steppan *et al.* 2007; Ferro *et al.* 2010; Pacheco *et al.* 2014; Rengifo & Pacheco 2015)

The results here obtained support this idea, revealing a higher species diversity in the *P. osilae* species group than previously envisioned, even when focusing at a relatively small area of high altitudinal grasslands in NWA. This topographically and environmentally complex area, largely ignored by mammalogists, has been in the last decade the source for many additions to the Argentinean sigmodontine fauna (Jayat *et al.* 2006, 2008b, 2011a), including the discovery of new species (e.g., Jayat *et al.* 2007, 2008a).

TABLE 4. Results of Discriminant Analysis of young specimens (age classes 2 and 3, n = 74) of 5 populations of *Phyllotis osilae* group from northwestern Argentina. Standardized coefficients for canonical variables. Specimens included: *P. nogalaris* (n = 6), *P. tucumanus s.s.* (n=49), *P. tucumanus* form 2 (n = 8), *P. tucumanus* form 3 (n = 6), and *P. tucumanus* form 4 (n = 5).

	Canonical Discriminant Functions			
	1	2	3	4
MSL	1.69	1.356	0.201	0.902
CIL	0.015	1.184	0.793	0.985
BL	-0.307	0.673	-0.683	0.477
PL	-0.311	-0.204	-0.119	-0.137
DL	0.05	-1.8	1.215	-0.168
PB	0.442	0.133	0.497	0.352
MTRL	0.501	-0.51	-0.396	0.393
IFL	0.237	0.31	0.268	-0.489
BPL	0.36	0.043	0.429	-0.054
ZL	-0.043	0.197	0.677	0.262
ZP	-0.229	0.401	0.286	-0.61
ZB	0.436	0.54	-0.127	-0.453
BB	0.698	-0.229	-0.248	0.306
IOC	-0.452	-0.081	-0.562	-0.127
RW2	-0.093	-0.161	-0.799	0.213
NL	-0.672	0.023	-0.628	-0.098
RL	-0.837	-1.569	-0.92	-0.418
OL	-0.98	-1.154	0.409	-0.462
ILL	0.151	-0.198	0.206	-0.498
ML	0.595	0.707	-0.638	-0.541
mTRL	0.223	-0.177	0.434	-0.875
Eigenvalues	3.694	1.803	1.324	0.35
Canonical correlations	0.887	0.802	0.755	0.509
Cumulative % of variance	0.515	0.767	0.951	1

Currently, three species of the *P. osilae* species group, *P. alisosiensis*, *P. anitae*, and *P. osilae*, are recognized in NWA. However, the present results indicate that probably six distinct species of the group inhabit the uppermost Yungas forests and high altitude grasslands of this area. Three of these forms range on the eastern slopes of the Santa Victoria and Zenta ranges, along the border of Jujuy and Salta provinces; the fourth is associated to the Centinela range, an isolated mountain system in southeastern Jujuy; and the last two extend on the humid eastern slopes of mountain ranges in southernmost NWA (Fig. 5). However, we here took a conservative position by proposing only two nomenclatorial acts consisting in removing from the synonymy of *P. osilae* two nominal forms, *nogalaris* and *tucumanus*, and considering them as taxa deserving species status within *Phyllotis*. As a consequence of these changes, we suggest that *P. osilae* does not occur in Argentina.

The status of the forms identified within what we consider *P. tucumanus s.l.* (i.e., *P. tucumanus s.s.*, *P. tucumanus* form 2, *P. tucumanus* form 3, and *P. tucumanus* form 4) must be evaluated at the light of additional evidence and more detailed analyses; currently that study is undergoing (Jayat *et al.* in prep.).

***Phyllotis nogalaris* as a distinct species of *Phyllotis*.** Specimens of two morphs of the *Phyllotis osilae* species group were trapped in sympatry near the type locality of *P. nogalaris* Thomas, only one of which agrees with the morphological description given by Thomas (1921) for this taxon. Currently, the form *nogalaris* is considered a subspecies of *P. osilae* (Musser & Carleton, 2005; Steppan & Ramirez, 2015). However, we consider *P. nogalaris* as a distinct species of *Phyllotis* because: a) two haplotypes recovered from specimens morphologically assignable to *nogalaris* form a clade sister to that formed by all other haplotypes of *P. osilae s.l.* (Fig. 2); b) genetic divergence between members of these two clades is considerable (10.2%; Table 5); and c) the morphologic/morphometric evidence clearly separate members of these two clades. Below we provide an emended diagnosis and a re-description of this species, and compare it with the holotype of *P. osilae osilae*, specimens assigned to *P. osilae phaeus*, and specimens of *P. anitae* and *P. alisosiensis*.

TABLE 5. Observed genetic distance of cytochrome b gene sequences within and among species of the *Phyllotis osilae* species group. Numbers between parentheses indicate the number of sequences studied for each species.

	intraspecific	interspecific						
		P. anitae	*P. alisosiensis*	*P. nogalaris*	*P. osilae*	*P. tucumanus s.s*	*P.tucumanus* 2	*P. tucumanus* 3
P. anitae (1)	--							
P. alisosiensis (1)	--	0.013						
P. nogalaris (2)	0.009	0.110	0.112					
P. osilae (6)	0.017	0.101	0.103	0.100				
P. tucumanus s.s. (13)	0.019	0.108	0.103	0.106	0.070			
P. tucumanus 2 (5)	0.003	0.113	0.114	0.095	0.056	0.042		
P. tucumanus 3 (8)	0.012	0.107	0.103	0.102	0.057	0.045	0.042	
P. tucumanus 4 (5)	0.007	0.105	0.099	0.099	0.064	0.045	0.041	0.041

Phyllotis nogalaris Thomas, 1921

(Figs. 3, 6 and 7)

Phyllotis nogalaris Thomas, 1921. Ann. & Mag. Nat. Hist., 9 (8): 611.
Phyllotis osilae nogalaris Pearson, 1958. Univ. Cal. Publ., Zool., 56 (4): 427.

Holotype. Adult male. B.M. 21.11.1.22. Original number 1472 (col. E. Budin).

Type locality. "Higuerilla, 2000 m", Jujuy, Argentina (Thomas 1921); restricted by Pardiñas *et al.* (2007) to Pampichuela, Valle Grande, Jujuy (23°32' S, 65°02' W, 1735 m) (Fig. 5).

Emended diagnosis. A member of the tribe Phyllotini distinguishable from all other species of *Phyllotis* by the following combination of state characters: size large for the genus (mean values in mm for adult specimens [age classes 3–5]: length of head and body, 128; tail length, 140; condyle-incisive length, 29.46; maxillary tooth row length, 5.75; Table 1); fur dense and soft, richly colored; dorsal coloration uniform, obscure buffy brown but with notorious blackish eye rings; flanks with a striking yellowish-orange fringe extended from cheeks to the rump; venter buffy white with a ochraceous pectoral streak; tail relatively dark and bicolored along most of its length with the exception of the entirely blackish distal end; skull heavily built, with the rostrum relatively long and broad; nasals extending beyond the level of the lacrimal bones; large lacrimals; zygomatic notches broad and deep; interorbital region narrow and pinched, hour-glass shaped, without sharply squared posterior margins; zygomatic plate relatively broad; zygomatic arches well expanded; mesopterygoid fossa relatively broad and with a median spine; incisors whitish-yellow; molars hypsodont and robust, relatively long and broad.

Description. Dorsal coloration dark buffy brown and heavily streaked with black hairs. Head of the same general color than dorsum but with conspicuous blackish eye rings. Sides of the body yellowish-orange (this coloration pattern constitute a fringe extending from cheeks to rump). Venter buffy white, with a mid-ventral yellowish-orange pectoral streak. Chin and throat lighter than belly, including some hairs entirely white in the chin. Ears of the same color than dorsum. Manus and pes covered by dense and short white hairs. In both fore and hind feet the ungual white tufts surpass the end of the claws. Tail relatively dark, with the ventral surface strongly paler than dorsum, but with the distal tip entirely blackish, and with a small tuft of hairs.

The skull of *P. nogalaris* looks more strongly built than those of the other species of the *P. osilae* group (Fig. 3). Rostrum broad and elongated, with nasals extending beyond the level of the lacrimal bones. Lacrimals comparatively well developed. Zygomatic notches deep and broad. Zygomatic plate relatively broad and high (see

Tables 1 and 2), with a straight anterior border. Interorbital region narrow, hour-glass shaped, and pinched. Braincase broad, without evident temporal and lambdoidal crests. Posterior ends of the incisive foramina surpass the anterior face of M1. Mesopterygoid fossa wide in the context of the *P. osilae* species group, bearing a well-developed median spine on the palatine. Two posterolateral palatal pits are adjacent to the anterior margin of the mesopterygoid fossa. Parapterygoid fossae well developed and moderately excavated. Hamular process delicate and distally attached to the mastoidal capsule. Auditory bullae with a short and broad bony eustachian tube. Mandibular condyle slightly lower than coronoid process, extending posteriorly just behind the angular process. Capsular projection moderately developed. Upper and lower ridges of the masseteric crests joining anteriorly at the level of the protoflexid of m1 and extending approximately to the mental foramen.

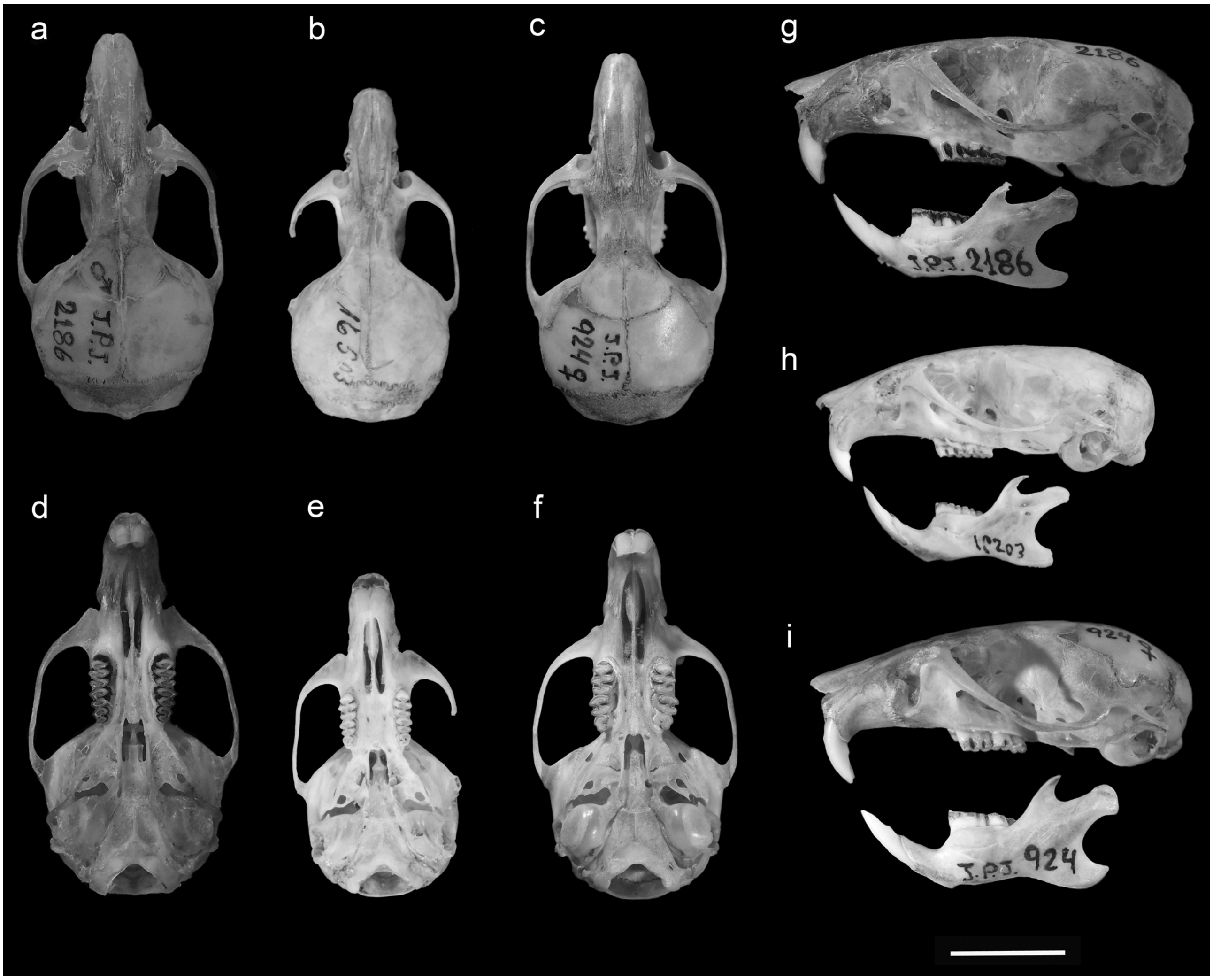

FIGURE 3. Dorsal, ventral, and lateral views of skulls in three species of the *Phyllotis osilae* species group: *P. nogalaris* (JPJ 2186; a, d and g), *P. o. osilae* (AMNH M-16503, holotype; b, e and h), and *P. anitae* (JPJ 924; c, f and i). Scale bar = 10 mm.

Upper incisors orthodont, with the anterior enamel whitish-yellow. Molars relatively hypsodont, with tendency to lamination, and the primary cusps slightly alternate (Fig. 6). M1 with a procingulum antero-posteriorly compressed, without anteromedian flexus. Lingual flexi transverse and labial flexi oblique respect to the longitudinal axis of the molar. M2 is "S" or "Z"-shaped, with a deep and oblique mesoflexus, and without anteroflexus. M3 with a deeply excavated hypoflexus, sometimes forming a lake. Lower incisors more delicate and yellowish than the upper ones. Young specimens with vestigial anteromedian flexid, and well developed anteroflexid and posteroflexid in m1. Anterolabial cingulum well developed, coalescing with the protoconid in adult specimens, and isolating the protoflexus. Protoflexid and posteroflexid of m2 reduced in young specimens. The m3 is large, slightly smaller than m2.

Phyllotis nogalaris has 13 thoracic ribs and 7 cervical, 13 thoracic, 8–9 lumbar, and 27–34 caudal vertebrae (N = 5 specimens).

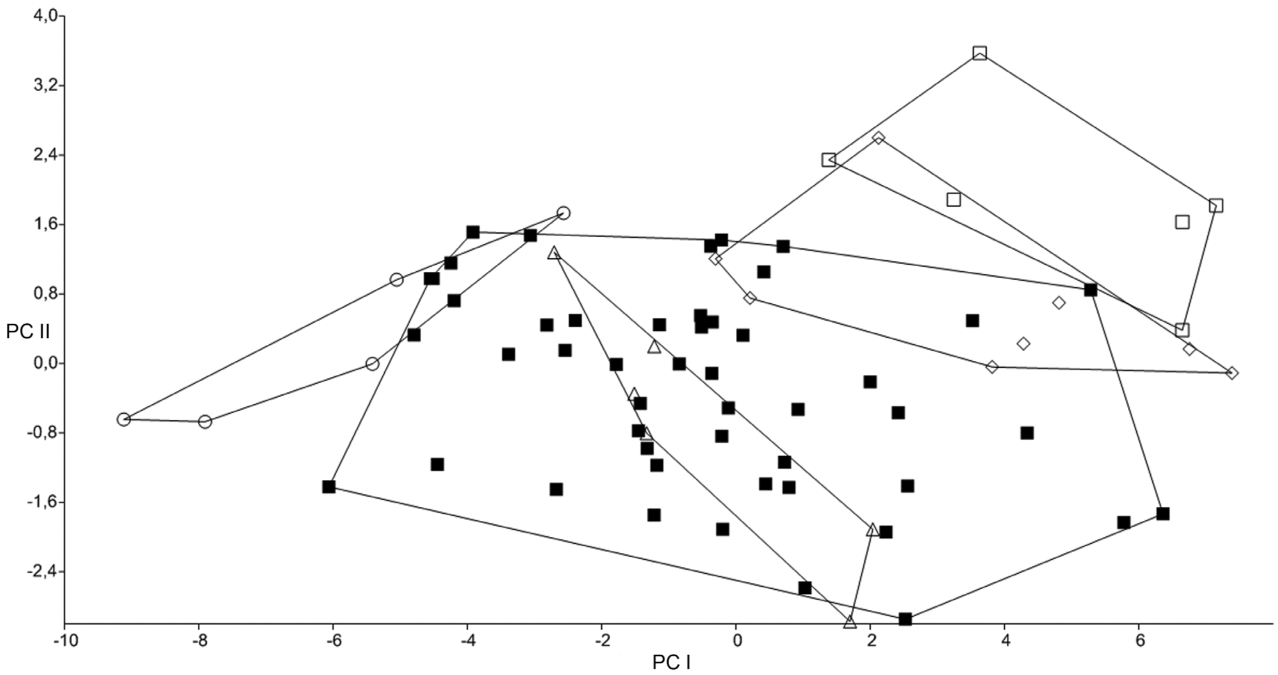

FIGURE 4. Individual specimen scores based on log-transformed values of 20 cranial measurements, projected onto the first and second principal components extracted from analysis of young specimens (age classes 2 and 3, n = 74) of *Phyllotis nogalaris* and 4 forms of *P. tucumanus* in Northwestern Argentina: *P. nogalaris* (white squares), *P. tucumanus s.s.* (black squares), *P. tucumanus* form 2 (white diamonds), *P. tucumanus* form 3 (white triangles), and *P. tucumanus* form 4 (white circles). Character loadings and percentage of variance explained by each of three PCs in Table 3.

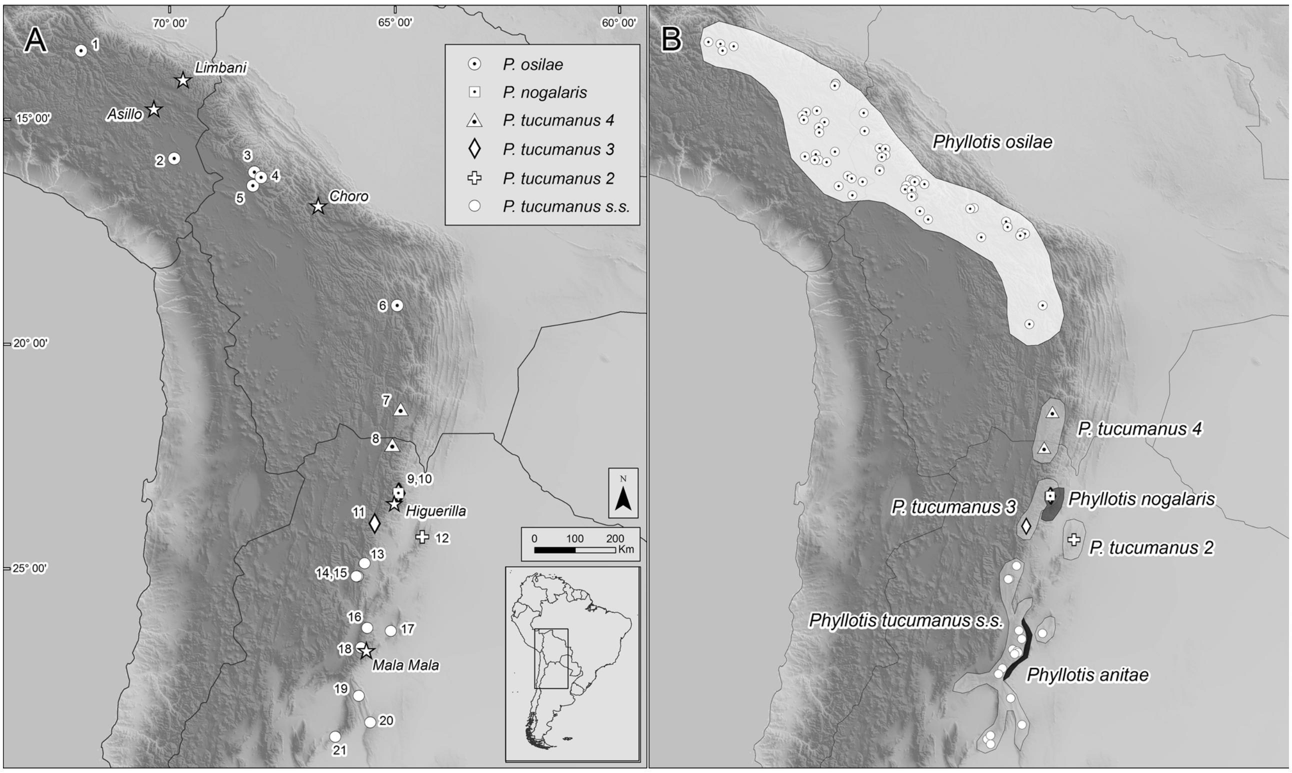

FIGURE 5. Map of central Andes in South America. A. Collection localities of the sequenced specimens of the *Phyllotis osilae* species group used in this study. Stars indicate type localities of the nominal forms of this species group. B. Collection localities and approximate distribution of the species in the *Phyllotis osilae* species group as recognized in this study.

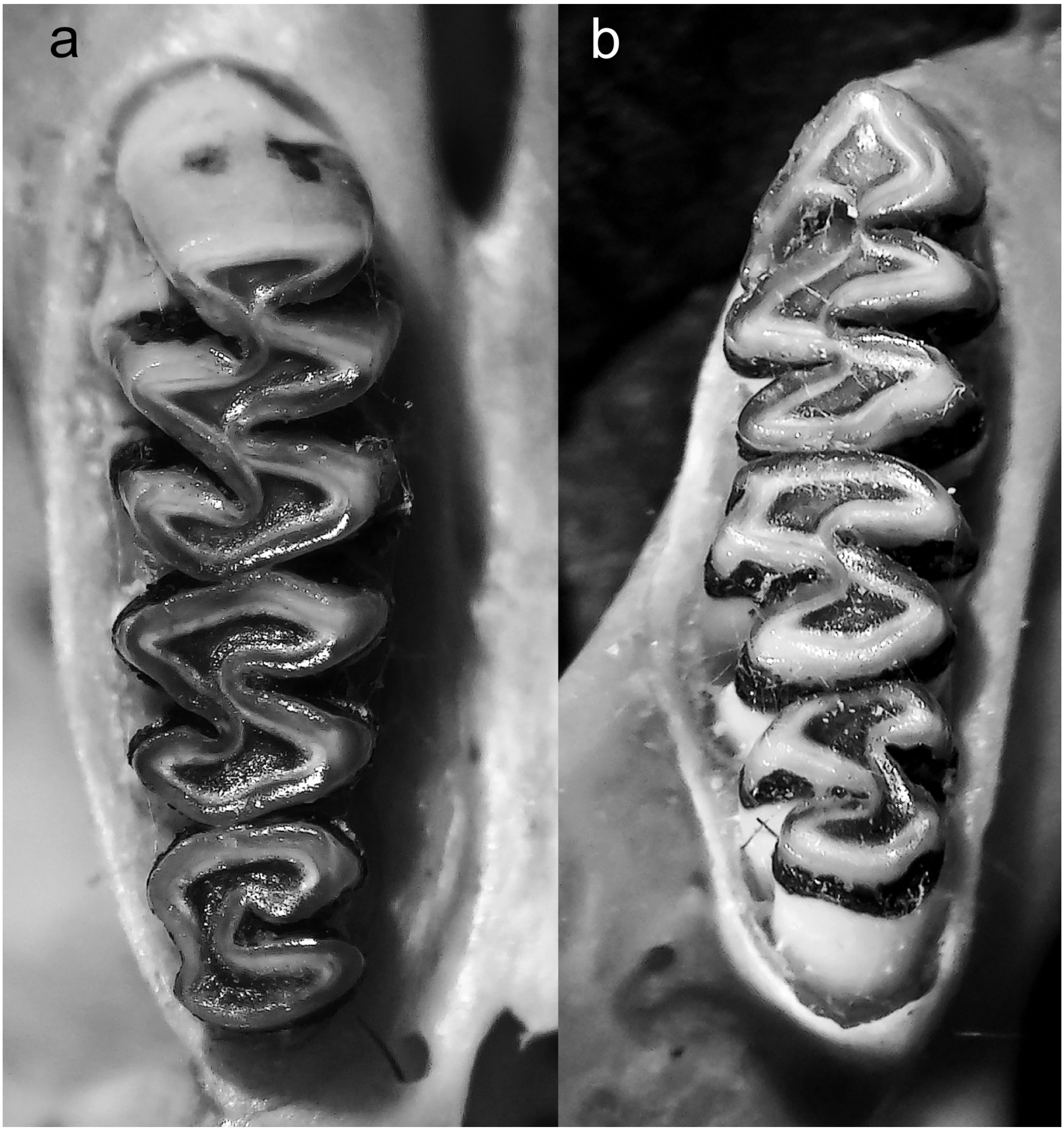

FIGURE 6. Left upper (a) and left lower (b) molar rows in a young specimen (age class 2) of *Phyllotis nogalaris*.

Morphologic variability. Studied specimens of *Phyllotis nogalaris* are uniform in external and skull characters, although minor variation exists. The development of the lateral yellowish-orange sides and the mid-ventral yellowish-orange pectoral streak varies among specimens. In the skull we observe variation in the width of the zygomatic plate and the development of the median spine on the palatine. Similarly, some specimens show a slightly more developed mandibular capsular projection.

Comparisons. *Phyllotis nogalaris* can be distinguished from *P. osilae* (as represented by specimens from southern Peru and central Bolivia, from where the nominal subspecies *P. osilae osilae* and *P. osilae phaeus* come) by its notably larger size in almost all external and skull measurements (see Pearson 1958; Hershkovitz 1962) (Table 1), more obscure and colored skin, presence of a well-defined yellowish-orange lateral fringe (Fig. 7), lacrimals more developed, broader braincase, deeper and broader zygomatic notches, noticeably more developed median spine on the palatine, broader bony eustachian tubes, molars more robust and hypsodont (Fig. 3), and noteworthy genetic divergence (Table 5).

FIGURE 7. Dorsal, lateral, and ventral views of skins in three species of the *Phyllotis osilae* species group: *P. o. osilae* (MACN 50.352; a, b and c), *P. anitae* (JPJ 924; d, e and f), and *P. nogalaris* (MACN 26378; g, h and i).

Several external and cranial features differentiate *Phyllotis nogalaris* from *P. anitae* and *P. alisosiensis*. *P. nogalaris* is clearer in general coloration, less dark-grayish in the dorsum and less ochraceous or cinnamon in the venter (Fig. 7). Young specimens of *P. anitae* have the digits and the distal dorsum of manus and pes white but the proximal dorsum dark, and the tail is only slightly bicolored. The nasolacrimal capsules and the zygomatic notches are less developed in *P. anitae* and *P. alisosiensis*. *P. anitae* and *P. alisosiensis* also have molars with stronger degree of hypsodonty, which differentiate these species from *P. nogalaris* (Fig. 3; see also Fig. 4 in Ferro *et al.*, 2010). Genetic divergence between *P. nogalaris* and *P. anitae* is 11.0 % and between *P. nogalaris* and *P. alisosiensis* is 11.2 %.

P. tucumanus s.s. is broadly distributed in southernmost NWA, occupying many different habitats. Across its distribution, this form is morphologically highly variable (Fig. 4). Specimens coming from high altitudinal grasslands are easily differentiated from *P. nogalaris* in the skin coloration pattern, being notably clearer and with weaker tinges; but in populations from the humid eastern slopes, in the ecotone area between the high altitude grasslands and Yungas forest, skins are similar to those of *P. nogalaris*. Notwithstanding, *P. nogalaris* has broader rostrum and braincase, and a proportionally narrower interorbital constriction. Additionally, molars of *P. nogalaris* are notably more robust, laminated and hypsodont.

Skins of *P. nogalaris* and representatives of *Phyllotis* coming from the Centinela range (*Phyllotis tucumanus* form 2) are practically indistinguishable at first glance, sharing the intense and dark general hue. However, in *P. nogalaris* the fur is dense and softer, with longer hairs and with a greater prevalence of black guard hairs, making the fur comparatively more grayish. Instead, in *P. tucumanus* form 2 the general coloration is more ochraceous, and the hairs are shorter and less dense. Morphometric values for the skull of these two forms are also similar (Table 2 and Fig. 4), but some characters allow differentiating them. *Phyllotis nogalaris* has narrower and shallower zygomatic notches, lacrimals somewhat larger, and a well-developed median spine in the mesopterygoid fossa always present. Furthermore, the zygomatic plate of *P. tucumanus* form 2 shows a tiny spiny process on the free upper border, feature not seen in the examined series of *P. nogalaris*. All the specimens referred to *P. tucumanus* form 2 come from small patches of high altitude grassland intermingled with forests of *Alnus acuminata* on an isolated eastern range, separated for more than 100 km of Yungas and Chaco lowland forested areas from the Zenta range, where *P. nogalaris* distributes (see Fig. 5).

Compared to the sympatric *P. tucumanus* form 3, *P. nogalaris* has a more dense fur, with longer and darker hairs, more contrasting eye-ring, more orange flanks, and more ochraceous venter. Furthermore, *P. nogalaris* is in average larger in most of the analyzed morphometric variables, with the molar series and the interlacrimal distance conspicuously longer. Notwithstanding, *P. nogalaris* has a proportionally narrow zygomatic plate and short incisive foramina. Although both forms were registered at the same locality, they occupy different microhabitats, with *P. nogalaris* being trapped exclusively on humid and forested patches and *P. tucumanus* form 3 only caught in open environments dominated by dense grasslands interspersed with rocky outcrops.

Specimens referred to *P. tucumanus* form 4 (coming from Rodeo Pampa, northernmost Salta province) have the clearest skin among the species here studied. Compared with *P. tucumanus* form 4, the fur of *P. nogalaris* is denser, having longer hairs, more colored by a higher prevalence of black guard hairs, showing a more developed eye ring, and more conspicuous lateral and pectoral orange fringes. The tail is darker in *P. nogalaris*, having a blackish ventral distal end, feature not seen in *P. tucumanus* form 4. The skull of *P. nogalaris* is clearly more robust, with a broader rostrum, more flared zygomatic arches and more inflated braincase. In *P. nogalaris* the zygomatic notch is in general broader and deeper, lacrimals are more robust, and nasals extend further back than in *P. tucumanus* form 4. Many other anatomical structures are more developed in *P. nogalaris*, including a larger tympanic bulla, a broader mesopterygoid fossa, and larger, more robust and hypsodont molars. However, *P. tucumanus* form 4 shows a comparatively broader interorbital constriction, a relatively broader zygomatic plate, and a more robust tympanic hook. Populations of these species also occupy different environments, with *Phyllotis tucumanus* form 4 occurring in open areas of highland grasslands and *P. nogalaris* found only in forested patches.

Other species of *Phyllotis* that do not belong to the *P. osilae* species group and are present in NWA, as *P. xanthopygus* and *P. caprinus*, are clearly distinguishable from *P. nogalaris* in external, cranial, dental and genetic characters, and they will not be compared here (see Pearson, 1958 for morphologic comparison).

Distribution. *Phyllotis nogalaris* was only known from a few localities in Jujuy province at the southern end of the Zenta range, on the Cordillera Oriental orographic system (e.g., Pearson, 1958; Díaz & Barquez, 2007). Here we record the species for Salta province, in central areas of the same mountain range. Some authors mentioned *nogalaris* (as a subspecies of *P. osilae*) for additional areas. Jayat & Pacheco (2006) and Jayat *et al.* (2007) assigned specimens from Centinela range to *nogalaris* but these belong to a putative undescribed form (see below). Díaz & Barquez (2007) assigned specimens from dry Puna environments, above 3700 m, to *nogalaris*; several of these specimens were later re-identified by Jayat *et al.* (2007) as *P. xanthopygus*. Díaz & Barquez (2007) also referred two specimens from El Duraznillo, Jujuy province, to *nogalaris*. We have not examined those specimens but the environmental characteristics of El Duraznillo are similar to that of areas where *P. nogalaris* was in fact collected. Heinonen & Bosso (1994) suggested the possibility that specimens of *Phyllotis* from Selva Montana environments of the Calilegua National Park belong to *nogalaris*.

Natural history. *Phyllotis nogalaris* preferentially inhabits the upper-forested belts of the Yungas, from the Selva Montana at 1200 m to the Bosque Montano-Pastizales de Neblina transition at almost 3100 m. Thomas (1921) nominated *P. nogalaris* because the type specimens were caught in areas with "nogales" (*Juglans australis*). However, other records come from alder forests (*Alnus acuminata*) and *Polylepis* woodlands intermingled with high altitudinal grasslands (e.g., *Festuca*, *Pennisetum*, *Stipa*). Specimens from Quebrada Alumbriojo were obtained from *Polylepis* woodlands on a humid ravine near a mountain stream; understory was characterized by rocky outcrops and grasslands mixed with several species of ferns. Specimens from Abra de Ciénaga Negra were also obtained on forested areas, but situated on more humid easternmost slopes of Zenta range, where *Alnus acuminata* was the dominant tree species.

None of the seven specimens (three males and four females) caught in Quebrada Alumbriojo in June showed signs of reproductive activity, and only one was molting. Two males captured at Abra de Ciénaga Negra in November were molting and showed semi-scrotal testes.

Comments. Even after removing *Phyllotis nogalari*s, data at hand suggest that specimens currently assigned to *P. osilae* in NWA may encompass more than one biological species. Our sampling includes haplotypes from several localities of Argentina, Bolivia, and Peru (Fig. 5). Results show deep genealogical diversity that is mostly geographically structured and that is congruent with the observed pattern of morphological variation. Haplotypes recovered from specimens from southern Peru and northern Bolivia, which can be assignable to *P. osilae*, form a well-supported clade (Fig. 2) sister to a clade formed by haplotypes of individuals from southern Bolivia and all NWA (*P. tucumanus s.l.*, Fig. 2); haplotypes of both clades diverge on average by 6.4 %. Given this result and the geographic segregation of both clades, even when noting that in our sampling there is a gap between both clades, it seems reasonable to limit *P. osilae* to the northern clade. This suggestion implies that *P. osilae* does not occur in Argentina.

The name *tucumanus*, coined by Thomas (1912) as *Phyllotis darwini tucumanus* on the base of specimens collected at Cumbres de Mala Mala, Tucumán province, is available for the southern clade (Fig. 2). The name *P. lutescens* Thomas, also included in the synonymy of *P. osilae* (Musser & Carleton 2005; Steppan & Ramirez, 2015), has priority over *tucumanus*; but this name is based on specimens from Cochabamba, Bolivia, a locality distant from the known distribution of the southern clade. In this context, the southern clade could be referred as *P. tucumanus s.l.* We refer as to *P. tucumanus s.s.* one of the four morphologically distinct subclades (Figs. 2 and 4) that composes the large *P. tucumanus s.l.* clade. The three other forms, here referred as *P. tucumanus* form 2, *P. tucumanus* form 3, and *P. tucumanus* form 4 (see appendix and Fig. 2) show deep genetic divergences (Table 5) and clear differences in morphologic and morphometric characters among them and respect to *P. osilae* and *P. nogalaris*. Notwithstanding the noteworthy pattern of morphologic and genetic variation, we consider that a geographically larger sample as well as other genes (i.e. nuclear markers) must be analyzed before these unnamed forms are formally recognized.

The taxonomic status of *Phyllotis alisosiensis*, recently described on base of a small sample from the upper montane forest of the Yungas on the Aconquija range, Tucumán (Ferro *et al.* 2010), needs re-evaluation. This nominal form is genetically and morphologically very similar to *P. anitae*, which ranges in the same area and inhabits the same Yungas environment. Sequenced specimens from these nominal forms diverge in less than 1.3%, a value well below the average observed genetic divergence for other pairs of species of *Phyllotis* and in line to intraspecific values (Table 5). The few morphological characteristics that differentiate both forms must be taken with caution given the limited number of specimens in which both nominal forms were based and because the type material of each form belong to different age classes. A more detailed examination about the likely synonymy of these nominal forms is also under development (Jayat *et al.*, in prep.).

Biogeography. The complex picture showed by our research for populations from NWA of the *Phyllotis osilae* species group may seem surprising. The diversity here uncovered may be the result of the tight association of the *P. osilae* species group with the high altitude grasslands and their ecotones (Fig. 5). These grasslands form isolated patches at the top of the mountain ranges, in which populations of *Phyllotis* would have differentiated prompted by the cyclical grassland expansions and retractions related to climatic events that these systems undergone during the late Cenozoic (Ortiz *et al.* 2011 and references therein). A similar scenario has been suggested for other species at the light of paleontological (e.g., Ortiz *et al.* 2000; Ortiz & Pardiñas, 2001), phylogenetic and phylogeographic analyses (D'Elía *et al.* 2008).

More in general, the complex physiographic and environmental features of NWA coupled with its unique biogeographic history surely have constituted a major driving force for the striking sigmodontine diversity of the region. A recent account mentioned at least 50 species for this relatively small area (Jayat *et al.* 2011a), many of which are environmentally restricted and thus, confined to narrow distributional ranges (e.g., Jayat *et al.* 2007, 2008a; Mares *et al.* 2008; Teta *et al.* 2011). However, as shown in the present study, considerable uncertainties still remain regarding such basic subjects as species boundaries, identity and distribution, while most of the area and environments still are to be appropriately surveyed (Jayat *et al.* 2011a, b). We expect that during the next coming years a significant improvement in the knowledge of NWA small mammal assemblage will be accomplished, with the recognition of new entities and the synonymy of others (e.g., as preliminary indicated here for *P. xanthophygus* and its associated form *caprinus*; Fig. 2).

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APPENDIX

Specimens examined and/or used in phylogenetic analysis. Acronyms for institutions and personal catalogs are as follows. USA: American Museum of Natural History (AMNH), New York. Argentina: Colección Mamíferos Lillo (CML), Tucumán; Colección de Mamíferos del Centro Nacional Patagónico (CNP), Puerto Madryn; Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN), Buenos Aires; Museo Municipal de Mar del Plata "Lorenzo Scaglia" (MMPMa), Buenos Aires. JPJ: field number of J. Pablo Jayat and PEO: field number of Pablo E. Ortiz, to be deposited at MACN. Localities are listed in alphabetic order. Genbank accession numbers for cyt b DNA sequences are provided between [ ] next to collection numbers of the specimens from where haplotypes were gathered. Asterisks (*) indicates specimens used in the Principal Component Analysis and the Discriminant Analysis. The numbers (Nº) before localities indicate collecting sites of the specimens used in phylogenetic analysis (see map on fig. 5A).

Phyllotis anitae (9). ARGENTINA: Tucumán Province: 10 km by road south of Hualinchay on the trail to Lara (CML 6379 [holotype], CML 6380, CML 6381, CNP 736 [AY627299], CNP 737, CNP 809; JPJ 924, 1225); El Papal, 2175m (27° 11'S 65° 57' W), Parque Nacional Campo de Los Alisos (CML 7542, holotype *P. alisosiensis* [GQ119625]).

Phyllotis caprinus (9). ARGENTINA: Jujuy Province: Bárcena, 3 km S Ruta 9, 1808 m (JPJ 132, JPJ 624 [KF442273], JPJ 626, JPJ 640, JPJ 671); Chilcayoc, Puente Bailey, 2239 m (JPJ 130); Maimará, 2500 m (CML 98, CML 282); Tilcara (MMPMa 3073).

Phyllotis nogalaris (8). ARGENTINA: Jujuy Province: (9) Quebrada Alumbriojo, aprox. 8 km al NE de Santa Ana, 2900 m (JPJ 2186*, 2198*, MACN 26378 [KT024789]*, 26379*, 26380, 26386 [KF442274]*). Salta Province: Abra de Ciénaga Negra, app. 3 km al SE, 3090 m (JPJ 738, MACN 26377*).

Phyllotis osilae osilae (6). PERU: Cuzco Department: (1) Quenko (ORB 98 [AY956699]); Puno Department: 5 miles north of Puno (AMNH M-213622, skull photograph); (2) Chucuito, 35 km S, 5 km W Llave (FMNH 107870 [U86826]); Osila (AMNH M-16503, holotype skull photograph). BOLIVIA: Chuquisaca Department: (6) 2 km N, 3 km E Tarabuco (MSB 63366 [U86827]). La Paz Department: (4) Mina Lourdes (MSB 65839 [U86828]).

Phyllotis osilae phaeus (3). BOLIVIA: La Paz Department: (5) La Paz (MSB 70573 [AY956701]); Pongo (AMNH M-72916, skull photograph); (3) Zongo, Laguna Viscachani, 3690 m (MSB 75292 [AY956700]).

Phyllotis tucumanus s.s. (60): ARGENTINA: Catamarca Province: Agua del Gauchi, aproximadamente 1 km al E del Mogote Los Cocos, 2024 m (JPJ 1252* 1258*, MACN 26423*); (20) aproximadamente 2 km al SE de Huaico Hondo, sobre Ruta Provincial Nº 42, al E del Portezuelo, 1992 m (JPJ 781*, MACN 23485 [KT024803]); aproximadamente 10 km al W de Los Varela, sobre Ruta Provincial Nº 4, Sierra de Humaya, 2006 m (JPJ 1312*); km 33 de la Ruta Provincial Nº 47, al S de Capillitas, 2500 m (JPJ 685*, 686*, 688*, 695*, 702*, 713*, 715*; MACN 26315*, 26429*, 26430*, 26431*, 26432*, 24845*); Las Chacritas, aproximadamente 28 km al NNW de Singuil, sobre Ruta Provincial Nº 1, 1888 m (JPJ 567*, 568*); Loma Atravesada, aproximadamente 3 km al NO del puesto de Leandro Vega, NO de Chumbicha (JPJ 1157*, 1162*, 1167*, 1168*, 1169*); (21) Mogote Las Trampas, aproximadamente 15 km al NW de Chumbicha, 2300 m (JPJ 1439*, 1459*; MACN 26411*, 26412 [KT024811]*, 26413*, 26414*, 26415*, 26416*); (19) unión entre las rutas provinciales Nº 9 y 18, 3,4 km al S, sobre Ruta Provincial Nº 18, 1529 m (JPJ 24*; MACN 26434 [KT024808], 26436 [KT024809]). Salta Province: (14) Aproximadamente 15 km al W de Escoipe, sobre Ruta Provincial Nº 33, 2680 m (JPJ 1057*; MACN 23498*, 26405 [KT024807]); (13) Campo Quijano aproximadamente 5 Km al NO, Km 30 de la ruta Nacional 51 (Quebrada del Toro), alt. App. 1600 m.s.n.m. (JPJ 101*, 102*, 103*, 104*; MACN 23502*, 26310*, 26311 [KT024802]*, 26369*, 26370*); (15) Cuesta del Obispo, aproximadamente 5 km al NE de Piedra del Molino, sobre Ruta Provincial Nº 33, 3174 m (MACN 26406 [KT024810]*). Tucumán Province: (17) Aproximadamente 7 km al NO de la finca de la familia Usandivara, Altos de Medina, 1717 m (JPJ 839*, MACN 26402 [KT024805], 26403 [KT024806]); (16) aproximadamente 10 km al S de Hualinchay, sobre el camino a Lara, 2300 m (JPJ 451*; MACN 26394 [KT024804]); (18) Carapunco, km 81 de la Ruta Provincial N° 307, 2960 m (JPJ 1071, 1104; MACN 26397, 26398, 26399 [KF442282], 26400 [KF442281], 26401 [KF442280],); Hualinchay, sobre el camino a Cafayate, 1861 (JPJ 228*); El Infiernillo, ruta 307, km 74, 2562 m (MACN 19069, 19070); Tafí del Valle, 2000 m (CML 745, 746).

Phyllotis tucumanus form 2 (9). ARGENTINA: Jujuy Province: (12) La Antena, Sierra del Centinela, al S de El Fuerte, 2350 m (JPJ 933*, 956 [KT024796]*, 962*, 969*; MACN 26381*, 26382 [KT024795]*, 26383 [KF442278]*, 26384 [KT024798], 26385 [KT024797]*).

Phyllotis tucumanus form 3 (14). ARGENTINA: Jujuy Province: (11) Bárcena, aproximadamente 3 km al S, sobre Ruta Nacional Nº 9, 1808 m (MACN 26404 [KT024790]); (10) Quebrada Alumbriojo, aprox. 8 km al NE de Santa Ana, 2900 m (JPJ 2177 [KF442276], 2188, 2217*; MACN 26366*, 26367, 26368, 26407 [KF442277]*, 26408 [KT024791], 26409 [KT024792], 26410 [KT024793]). Salta Province: (9) Abra de Ciénaga Negra, aprox. 3 km al SE, 3090 m (JPJ 726*; MACN 26427 [KT024794]*, 26428 [KF442275]*).

Phyllotis tucumanus form 4 (17). ARGENTINA: Salta Province: (8) 1 km ENE de Rodeo Pampa, km 59 de Ruta Provincial Nº 7, 3080 m (JPJ 1314, 1316, 1319, 1323, 1324, 1326, 1329*, 1332, 1336, 1338 [KF442279]*; MACN 23509, 26372 [KT024800], 26373, 26374, 26375 [KT024799]*, 26376*, 26387 [KT024801]*). BOLIVIA: Tarija Department: (7) Serranía Sama (MSB 67256 [U86829]).

Phyllotis xanthopygus (72). ARGENTINA: Catamarca Province: Agua del Gauchi, aproximadamente 1 km al E del Mogote Los Cocos, 2024 m (JPJ 1286); Chumbicha (MACN 20264); Chumbicha, 1 km NW by rd. from balneario, el. 2600 ft (CML 3451); El Bolsón, 2309 m (JPJ 2073); Laguna Blanca, 3200 m (MACN 29256); Laguna Blanca, 3243 m (JPJ 1870, 1871, 1872, 1873, 1874); Las Cuevas (MACN 42137); Mogote Las Trampas, aproximadamente 15 km al NW de Chumbicha, 2300 m (JPJ 1421, 1423, 1431, 1432, 1441, 1442, 1444, 1453, 1454, 1468, 1471, 1472, 1474, 1475). Jujuy Province: 4 km al O de Rinconada (PEO 11, 13); 17 km al W de La Quiaca, sobre ruta provincial N° 5 y 3 km al S de la misma ruta (MMD 433, MMD 434, MMD 436, MMD 438); Abra Pampa (CML 1276, CML 1277, CML 1278, CML 1283); Ajedrez (PEO 8); Curques, 24 km al N de Susques, sobre ruta 74 (MMD 291); La Ciénaga, Abra Pampa (CML 1280). La Rioja Province: Cueva de Perez, 3800 m (JPJ 2221, 2222, 2224; MACN 24038); km 14 de la Ruta Provincial N° 73, aprox. 1 km de Pampa de La Viuda, 2100 m (JPJ 2365, 2370, 2398, 2399, 2402, 2403, 2425, 2426); km 19 de la Ruta Provincial N° 73, Pampa de La Viuda, 2150 m (JPJ 2379, 2380, 2385, 2386, 2406, 2408, 2413); Laguna Brava (MACN 18846); San Antonio, Sierra de Velazco E, a 2700 m (MACN 34274). Salta Province: 1 km ENE de Rodeo Pampa, km 59 de Ruta Provincial Nº 7, 3080 m (JPJ 1331); Chorrillos, 4500 m (MACN 30104); Cuesta del Obispo, aproximadamente 5 km al NE de Piedra del Molino, sobre Ruta Provincial Nº 33, 3174 m (JPJ 1213); San Antonio de Los Cobres, 3700 m (MACN 30110). San Juan Province: Estancia Leoncito, 2 km E observatorio Astronómico (CML 3624); Reserva San Guillermo, Agua del Godo (MACN 18842); San Guillermo (CML 1080). Santiago del Estero Province: Pozo Grande (JPJ 381, 382, 384, 385). Tucumán Province: Cerro Bayo (CML 5563); Cerro Muñoz (CML 382); km 99 Ruta 307 (Tafí-Amaicha) (CML 5564).