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The Quintessential Naturalist

Honoring the Life and Legacy of Oliver P. Pearson

Edited by Douglas A. Kelt, Enrique P. Lessa, Jorge Salazar-Bravo, and James L. Patton

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THE QUINTESSENTIAL NATURALIST: HONORING THE LIFE AND LEGACY OF OLIVER P. PEARSON

To Paynie and Anita,
for their friendship, scholarship, and continuing inspiration

THE QUINTESSENTIAL NATURALIST: HONORING THE LIFE AND LEGACY OF OLIVER P. PEARSON

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A NEW SPECIES OF *PHYLLOTIS* (RODENTIA, CRICETIDAE, SIGMODONTINAE) FROM THE UPPER MONTANE FOREST OF THE YUNGAS OF NORTHWESTERN ARGENTINA

UNA NUEVA ESPECIE DE *PHYLLOTIS* (RODENTIA, CRICETIDAE, SIGMODONTINAE) DEL BOSQUE MONTANO SUPERIOR DE LAS YUNGAS DEL NOROESTE ARGENTINO

J. Pablo Jayat, Guillermo D'Elía[1], Ulyses F. J. Pardiñas, and Juan G. Namen

"When I returned from my first trip to the Andes in 1940, I found it impossible to identify many specimens of Phyllotis *in accordance with the existing taxonomy… A revision of the genus therefore seemed desirable"*
Oliver P. Pearson (1958:394)

ABSTRACT

We describe a new sigmodontine species of the genus *Phyllotis*. It was collected near Hualinchay, Tucumán, Argentina. The new species, which is a sister taxon to *P. osilae*, can be distinguished from other members of the genus by the following combination of traits: large size (slightly smaller than *P. osilae* and *P. xanthopygus*); dorsal color dark gray; light ochraceous belly; ears covered internally and externally by obscure brown hairs; manus with digits and distal dorsum covered with white hair, proximal dorsum of the manus and pes darker; tail slightly bicolored and slightly haired, not penicillate; incisors with white to yellowish-white enamel; noticeably hypsodont molars; and several molecular synapomorphies. The new species is an endemic from the alder forests of the upper Yungas. The low number of specimens captured, despite intensive trapping efforts, suggests that it is rare and restricted to this type of forest. Considering the rapid anthropogenic habitat loss in the Yungas, we argue that further intensive biodiversity studies and conservation plans are critical for this region

Keywords: Argentina, leaf-eared mouse, Muroidea, new species, Phyllotini, Sigmodontinae, taxonomy, Tucumán, Yungas

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RESUMEN

Se describe una nueva especie de sigmodontino del género *Phyllotis*. Esta fue colectada en las cercanías de Hualinchay, provincia de Tucumán, Argentina. La nueva especie, hermana de *P. osilae*, puede distinguirse del resto de los miembros del género por la siguiente combinación de caracteres: tamaño grande (apenas menor que el de *P. osilae* o *P. xanthopygus*); pelaje dorsal de coloración gris oscura; vientre de color ocre claro; orejas cubiertas externa e internamente por pelos de color marrón oscuro; dígitos y porción distal de las manos con pelos blancos; porción dorso proximal de las manos y pies oscura; cola apenas bicoloreada y escasamente peluda, sin pincel terminal; esmalte de los incisivos color blanco a blanco-amarillento; molares con notable hipsodoncia; numerosas sinapomorfías moleculares. La nueva especie es una forma endémica de los bosques de alisos del piso superior de las Yungas. El bajo número de ejemplares capturados, pese a los elevados esfuerzos de muestreo, sugiere que la nueva especie es poco común y restringida a este tipo de hábitat. Considerando el fuerte impacto antrópico que las Yungas argentinas están sufriendo, enfatizamos que la intensificaión de los estudios de biodiversidad y la aplicación de planes de conservación son críticos para esta ecoregión.

Palabras claves: Argentina, especie nueva, Muroidea, pericote, Phyllotini, Sigmodontinae, taxonomía, Tucumán, Yungas

INTRODUCTION

Northwestern Argentina is geographically and environmentally heterogeneous, and as such it is inhabited by around 40 species of sigmodontine rodents. In recent years intense work has resulted in a better knowledge of the regional sigmodontine community, including the description of new living (Mares and Braun, 1996; Díaz et al., 1999; Diaz and Barquez, this volume) and fossil taxa (Ortiz et al., 2000b) and contributions on the distribution, systematics, paleontology, and ecology of the different species (Mares et al., 1981; Ojeda and Mares, 1989; Bustos, 1995; Capllonch et al., 1997; Mares et al., 1997; Díaz, 1999; Díaz and Barquez, 1999, this volume; Ortíz et al., 2000a; Teta and Ortíz, 2002).

Phyllotis is one of the most diverse genera of the subfamily. This genus ranges along the Andes and nearby desert and semi-desert environments from the southern continental tip (Argentina and Chile) to Ecuador (Steppan, 1998; Kramer et al., 1999). The alpha taxonomy and phylogenetics of *Phyllotis* have been addressed with morphological (e.g., Pearson, 1958; Hershkovitz, 1962; Braun, 1993; Steppan, 1993, 1995, 1998), karyotypic (e.g., Pearson, 1972; Pearson and Patton, 1976; Spotorno, 1976; Walker et al., 1984), and molecular (Steppan, 1998; Steppan et al. this volume) evidence. Musser and Carleton (2005) recognize 13 species in the genus; these are *P. amicus, P. andium, P. bonaeriensis, P. caprinus, P. darwini, P. definitus, P. haggardi, P. limatus, P. magister, P. osgoodi, P. osilae, P. wolffsohni*, and *P. xanthopygus*. At the same time, Musser and Carleton (2005) place *P. gerbillus* in *Paralomys* (following, in part, the results of Braun, 1993); meanwhile Steppan and Ramirez (pers. comm.) retain this species in *Phyllotis* and transfer *wolffsohni* to the recently described *Tapecomys* (see also Steppan et al., this volume).

To date, 4 *Phyllotis* species have been reported for northwestern Argentina (Pearson, 1958; Hershkovitz, 1962; Díaz and Barquez, this volume). *P. xanthopygus* is represented by 3 subspecies: *P. x. rupestris*, in the east side of the Andes of the Province of Jujuy; *P. x. ricardulus* along the central and eastern Andes, from the northern provinces of Salta and Jujuy to Catamarca Province; and *P. x. vaccarum* in the latter province. Similarly, *P. osilae* presents 3 subspecies in the region: *P. o. osilae* and *P. o. nogalaris* in Jujuy Province, and *P. o. tucumanus* in the eastern side of the Andes in Catamarca and Tucumán provinces. *P. caprinus* inhabits the Province of Jujuy and has no described subspecies. Finally, *P. wolffsohni* was recently cited for the Province of Jujuy by Díaz and Barquez (this volume).

In the present paper we describe a new species of *Phyllotis* from the montane cloud forest of northwestern Argentina, based on both morphological and molecular evidence.

MATERIALS AND METHODS

The specimens of the new species were trapped with Museum Special and Sherman traps baited with oats. Voucher specimens (skin and skull plus complete skeleton) are deposited in the Colección Mamíferos Lillo (CML), Universidad Nacional de Tucumán, Tucumán, Argentina, and at the Colección de Mamíferos del Centro Nacional Patagónico (CNP), Puerto Madryn, Chubut, Argentina. Tissue samples (heart, liver, and kidney preserved in 70% ethanol) are deposited at the Colección de Tejidos del Laboratorio de Evolución, Facultad de Ciencias, Universidad de la República, Uruguay. Comparisons were made against the descriptions of each of the species and subspecies of *Phyllotis* presented by Pearson (1958). In addition, based in geographic distribution, and results of the phylogenetic analysis (see below), we studied series' of *Phyllotis caprinus*, *P. osilae osilae*, *P. o. nogalaris*, *P. o. tucumanus*, *P. xanthopygus rupestris, P. x. ricardulus*, and *P. x. vaccarum*. All specimens studied in this paper are listed in Appendix 1.

Morphologic Data Analyses.---Standard external measurements (HB: length of head and body; T: tail length; HF: length of hind foot with claw; E: ear length) and weight (W) were recorded in the field following Pearson (1958). Dental and cranial descriptions follow Reig (1977) and Steppan (1995), and Wahlert (1985), Voss (1988), and Abdala and Díaz (2000), respectively. In order to facilitate comparisons with other species of the genus we measured craniodental measurements following Myers et al. (1990). These included (measured with digital calipers to the nearest 0.01 mm): GLS (greatest length of skull), CIL (condyloincisive length), ZB (zygomatic breath), WBC (braincase breadth), IB (interorbital breadth), UTR (upper tooth row length), NL (nasal length), RW2 (mid-rostral width), DL (upper diastema length), IFL (incisive foramen length), OCW (occipital condyle width), BOL (basioccipital length), MFW (mesopterygoid fossa width), and ZP (zygomatic plate depth). In addition, we also recorded the greatest length of the mandible (excluding the incisor, ML), the alveolar length of the lower tooth row (LTR). Finally, we measured the depth (distance between greater and lesser curvatures) and width (measured across the enameled tip) of one upper incisor of the holotype (CML 6379).

Molecular Data Analyses.--- We sequenced 2 specimens (the holotype CML 6379 and

the paratype CNP 736) of the new species for the first 801 base pairs of the gene that codes for cytochrome *b* (cyt *b*) following the protocol in D'Elía et al. (2003). Sequences were visualized, reconciled, and translated to proteins to proof for stop codons using Sequence Navigator (Applied Biosystems, 1994).

Cyt *b* sequences were analyzed by Steppan et al. (this volume) as part of their broad phylogenetic analysis of *Phyllotis*, where the new species appears as *Phyllotis* n. sp. 2. Details of phylogenetic analyses are provided therein.

Molecular synapomorphies were documented by examining outputs from PAUP* 4.0b10 (Swofford, 2000) and visualized using MacClade 3.05 (Maddison and Maddison 1992). Molecular transformations were optimized on the trees resulting from the maximum parsimony analysis of the cyt *b* matrix of Steppan et al. (this volume). Only those changes unambiguously optimized irrespective of the kind of character transformation used (i.e., accelerated, ACCTRAN, or delayed, DELTRAN) were taken into account.

RESULTS

Results of the phylogenetic analysis (see Steppan et al., this volume) indicate that the new species (there labeled as *Phyllotis* n. sp. 2) is a sister taxon to *P. osilae*. Therefore, we focused our morphological comparisons with *P. osilae*. We also compared the new species with other *Phyllotis* inhabiting the northwestern Argentina.

Phyllotis anitae, new species

Holotype.---CML 6379, adult female, collected by J. P. Jayat on 30 April 2003 (original field number JPJ 977), skin, skull, full skeleton, tissues in alcohol.

Type Locality.---ARGENTINA: Province of Tucumán, Department of Trancas, 10 km by road south of Hualinchay on the trail to Lara (26° 19′ 20.2″ S, 65° 36′ 45.5″ W, 2316 m) (Fig. 1).

Diagnosis.---A member of the genus *Phyllotis* (Sigmodontinae) distinguishable from all other species of the genus by the following combination of characters: size large; dorsal color dark gray; belly light ochraceous; ears covered internally and externally by dark brown hairs; manus with digits and distal dorsum covered with white hair, proximal dorsum of the manus and pes dark; tail slightly bicolored and haired, not penicillate; skull robust with short rostrum; zygomatic notches and nasolacrimal capsules inconspicuous; interorbital region narrow, hourglass-shaped and without overhanging borders; posteropalatal pits to the level of anterior border of mesopterygoid fossa; incisors white to yellowish-white; molars noticeably hypsodont; third upper molar simple, not "S" or "Z" shaped; the molecular synapomorphies listed in Table 1 (note that no sequences of *P. caprinus, P. definitus, P. gerbillus*, and *P. haggardi* were analyzed).

Paratypes.---Paratypes include 5 live-trapped specimens prepared as skins, skulls plus full skeletons, and tissues in alcohol: CNP 736, young male, collected by J. G. Namen on May 1 2002 (original field number JPJ 761); CNP 737, young female, collected by J. G.

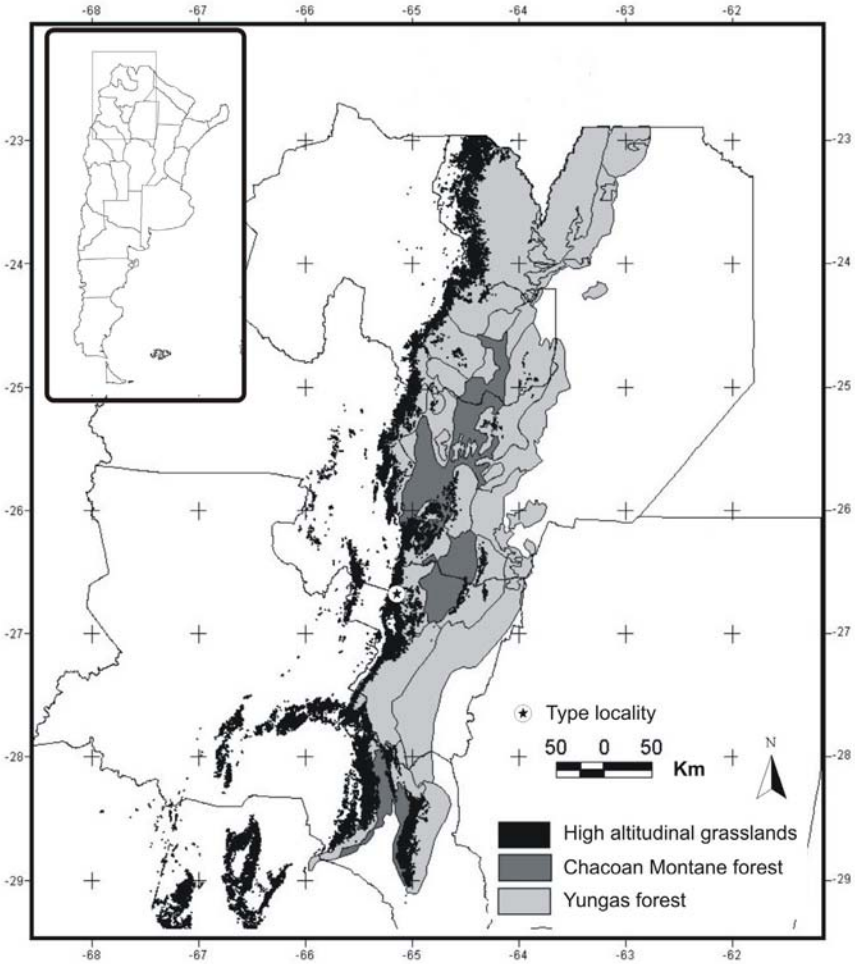

Figure 1.--- Map of northwestern Argentina and principal vegetation units occurring there; white areas to the east are the Chaco and those to the west are Prepuna, Puna, and High Andean biomes.

Namen on May 20 2001 (original field number JPJ 482); CNP 809, adult male, collected by J. P. Jayat on May 5 2004 (original field number JPJ 1124; CML 6380, young male, collected by J. P. Jayat on May 1 2003 (original field number JPJ 979); and CML 6381, young male, collected by J. P. Jayat on May 2 2003 (original field number JPJ 994).

Measurements of the Holotype.--- External measurements (in mm; see Table 3 for comparison with other species in *Phyllotis*): HB, 119; T, 124; HF, 29; E, 21; W, 37.5 g. Cranial measurements (in mm): GLS, 30.72; CIL, 27.80; ZB, 16.06; WBC, 14.10; IB, 4.02; UTR, 5.78; NL, 12.48; RW2, 5.00; DL, 7.80; IFL, 7.24; OCW, 7.04; BOL, 3.78; MFW, 1.68; breadth of zygomatic plate, 2.82; ML, 15.40; LTR, 5.70; upper incisor depth, 1.60; upper incisor width, 1.20. See Table 2 for paratypes measurements.

Etymology.---Dedicated to Anita Kelley Pearson and through her to Oliver P. Pearson,

Table 1.--- Molecular synapomorphies of *Phyllotis anitae* as revealed by maximum parsimony analysis of cyt b gene sequences (801 base pairs). Molecular transformations were optimized on a strict consensus tree of the 1764 most parsimonious trees (3310 steps; CI = 0.269) resulted from the analysis of the cyt b matrix of Steppan et al. (this volume). Twenty five fixed derived character states were found in *P. anitae*. Of these, 8 derived character states (indicated by asterisks) have not evolved independently in any species of *Phyllotis*. Some of these characters have a consistency index <1 because the character state present in 1 *P. anitae* also has evolved independently in at least 1 of the non-*Phyllotis* taxa included in the analysis. The remaining 17 derived character states of *P. anitae* have also secondarily appeared in at least 1 species of *Phyllotis*.

	Nucleotide position/ Codon position	Character State in *Phyllotis anitae*	Character Consistency Index
1	21/3	C	0.182
2	51/3*	T	1
3	96/3	T	0.333
4	123/3*	C	0.333
5	186/3*	G	1
6	189/3	T	0.167
7	222/3	C	0.067
8	240/3	T	0.222
9	255/3	T	0.100
10	282/3	G	0.125
11	294/3*	T	0.214
12	300/3	G	0.250
13	360/3*	T	0.167
14	427/1*	C	0.176
15	469/1	C	0.071
16	514/1	T	0.083
17	523/1	C	0.222
18	554/2	T	0.111
19	590/2*	T	1
20	593/2	T	0.111
21	625/1	G	0.600
22	655/1	T	0.111
23	691/1	G	0.333
24	769/1	C	0.200
25	791/2*	G	1

Table 2.-- Measurements of 5 paratypes (in mm) of *Phyllotis anitae* new species. Abbreviations as provided in text.

	CML 6381	CML 6380	CNP 736	CNP 737	CNP 809
HB	100	82	89	99	123
T	-	94	99	-	112
HF	30	27	30	30	31
E	21	18	19	20	21
W	28.5	20.5	21.0	25.0	50
GLS	28.66	26.56	27.38	28.20	31.26
CIL	25.54	23.30	24.42	25.46	28.26
ZB	14.64	14.08	14.02	14.36	16.26
WBC	13.80	13.26	13.50	13.42	13.96
IB	3.90	4.14	4.06	3.90	3.94
UTR	5.90	5.70	5.88	5.80	5.58
NL	10.76	9.44	9.92	10.72	12.58
RW2	4.62	4.36	4.26	4.62	5.26
DL	6.66	6.10	6.24	6.94	8.36
IFL	6.44	5.94	5.90	6.50	7.52
OCW	7.00	6.78	6.94	7.06	7.14
BOL	3.64	3.26	3.74	3.35	3.76
MFW	1.52	1.46	1.51	1.55	1.60
ZP	2.48	2.14	2.20	2.60	3.12
ML	14.48	13.90	14.30	14.84	16.26
LTR	6.22	5.68	6.00	5.82	6.00

who upon receiving his Doctorate Honoris Causa from the Universidad Nacional de La Plata, La Plata, Argentina (November 2000), expressed "yo solo soy un simple atrapador de ratones y nada hubiera sido posible sin Anita." It also is worth mentioning that in 1958 Oliver P. Pearson was the first author to review the genus *Phyllotis*.

Distribution.---Known only from the type locality.

Description.---The dorsal coloration is dark gray, spattered with ochraceous hairs. The holotype and the adult paratype (CNP 809) are slightly lighter than the remaining paratypes, which are all young individuals. Most of the dorsal hairs (hair length = 9 mm) are totally dark gray to black, with ochraceous tips. Some totally black hairs (length = 19 mm) also are present. Coloration of the sides and belly gradually blends to an ochraceous gray, without a sharp contrast between dorsal and ventral regions. The ventral hairs are basally gray and distally ochraceous. The throat and cheeks are

lighter than the belly, including some hairs entirely white, but lacking a definite spot. The ears are moderate in size, internally and externally covered by dark brownish to almost black hairs.

Facial vibrissae are disposed in mystacial, submental, genal, and superciliary fields. The mystacials are abundant (although less so than in *P. xanthopygus*), some white and short, others black and long, extending beyond the posterior margins of the pinnae. The submental vibrissae are short and completely white. The genal and superciliary vibrissae are sparse (generally three and one, respectively), short, basally black and distally white.

Manus and pes are dark in general, covered by dense and short hairs. These hairs are drab with white tips. The dorsal coloration pattern of the manus is noticeable: the digits and distal dorsum show only white hair, contrasting with the darker coloration of the proximal carpus. The dorsal pes coloration is uniformly drab. The manus claws (length = 1.8 mm) are shorter than those of the pes (length = 3.7 mm), and in both fore and hind feet the ungual tufts surpass the end of the claws. These ungual tufts are white in the manus and are more abundant, larger, and more drab in the pes. In the manus, digits III and IV are the largest and are approximately subequal; digit II (with claw) surpasses the middle point of digits III and IV, and digit V is the shortest. Plantar pads include 3 small interdigitals and 2 metacarpals. Pes digits II, III, and IV are the largest; digit I is less than the 50% as long as digit II. There are 6 plantar pads, including 4 small interdigitals, 1 very small hypothenar, and 1 large thenar. The soles of both manus and pes are naked.

The tail is slightly bicolored and moderately hairless, with the ventral surface paler and more haired than the dorsal surface. The scales are readily visible to the naked eye.

Eight mammae are present in the holotype (the only known adult female), arrayed in 4 pairs: 1 pectoral, 1 postaxial, and 2 inguinal.

The skull of *P. anitae* is similar in general morphology to those of the *P. osilae* and *P. xanthopygus* (Figs. 2, 3). In lateral view, the dorsal profile is flat. The rostrum is moderately gracile and enlarged. The anterior one third of the nasal bones are expanded and surpass the anterior face of the upper incisors; posteriorly, the nasals terminate at the level of the lacrimal bones. The lacrimals are well developed. The zygomatic notches and the nasolacrimal capsules are inconspicuous in dorsal view. The premaxillo-maxillary suture is oriented nearly vertically with respect to the basal plane of the skull. The zygomatic plate is narrow and high, with a straight anterior border and a short, free upper border. The interorbital region is narrow, hourglass-shaped, and the frontal edges are smooth. The fronto-parietal suture is straight and the interparietal is large and wide. The braincase is rounded in dorsal view, without evident temporal and lambdoidal crests. In ventral view, the posterior ends of the incisive foramina surpass the anterior face of M1. The mesopterygoid fossa is wide and its hamular processes diverge posteriorly, similar to those of *P. osilae*, and it is wider than those of *P. xanthopygus*. The anterior border of the mesopterygoid fossa typically is U-shape, with a small median spinous process on the palatine. A pair of posterolateral palatal pits are present adjacent to the anterior margin of the mesopterygoid fossa. These pits are smaller than those of *P. xanthopygus*. The mesopterygoid roof is deeply excised. The parapterygoid fossae are well-developed and moderately excavated. The carotid circulation system includes stapedial and sphenofrontal foraminae, and a squamosal-alisphenoid groove. This is the common pattern for the genus (Steppan,

Figure 2. *Phyllotis anitae*, new species (holotype, CML 6379): skull in dorsal (upper, left) and ventral (upper, right) views, and skull and mandible in lateral view (bottom). Scale = 10 mm.

1995). The hamular process is delicate and distally attached to the mastoidal capsule, determining a large subsquamosal and a small postglenoid foramina. The tympanic tegmen contacts the squamosal. A strut of the alisphenoid is absent. The auditory bullae are moderately small with a short and tubular eustachian tube.

In the mandible (Fig. 2) the condyloid and coronoid processes are subequal in height. The former is moderately short, as is the angular process. The capsular projection is inconspicuous. The upper and lower masseteric crests are well developed, joining anteriorly at the level of the mental foramen. In the lingual side of the mandible, a well-developed mandibular foramen is present. The medioventral process of the mandibular ramus is weak.

The upper incisors are moderately narrow, opisthodont, and possess a long and straight dentine fissure. The anterior enamel is totally white in young individuals and yellowish-white in the holotype.

The upper tooth rows are parallel. Hypsodonty is noticeable (with respect to other species of *Phyllotis*) in both upper and lower molars, conferring a prismatic form particularly to the M1 (Figs. 2, 4). The primary cusps are slightly alternate. M1 has a well developed procingulum, which is anterior-posteriorly compressed, and with an

Figure 3.--- Dorsal (top), ventral (middle), and lateral (bottom) views of skulls in (from left to right) *Phyllotis anitae*, new species (holotype, CML 6379), *P. osilae* (JPJ 748), and *P. xanthopygus* (PEO 13). Scale = 10 mm.

anteromedian flexus reduced to a shallow notch. M2 shows a moderate 8-shape, with a deep and oblique mesoflexus. M3 is small and has a hypoflexus pinched off to form a lake; this condition is widespread in *Phyllotis* (see Steppan, 1995). In young individuals

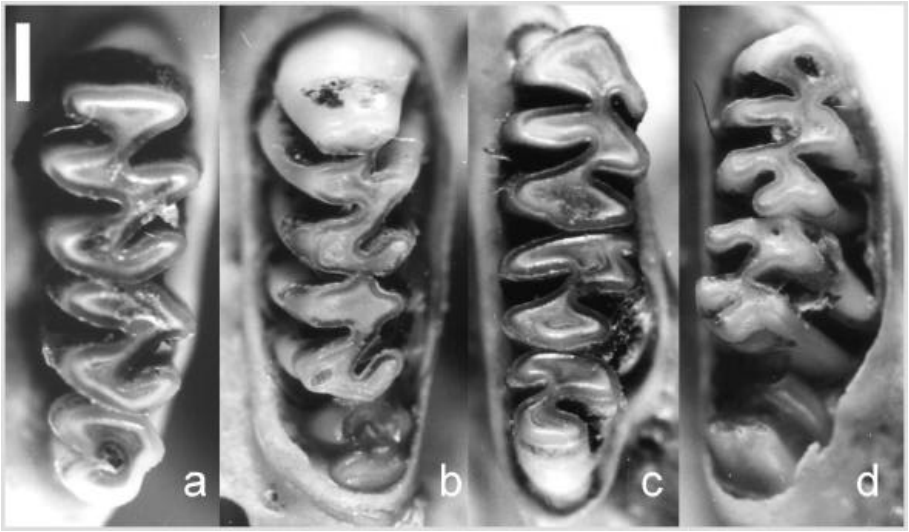

Figure 4. *Phyllotis anitae*, new species: Left upper and right lower molar rows in adult (a and c; holotype, CML 6379) and young specimens (b and d; paratype, CML 6380). Scale = 1 mm.

M2 displays a shallow anteroflexus and a persistent fossetus on the hypocone (Fig. 4).

The lower incisors are more delicate and paler than the upper ones. m1 has a trilophodont pattern in the holotype, but in young individuals this molar is tetralophodont, with both anteromedian flexid and anteromedian fossetid well developed. The anterolabial cingulum also is well developed and does not coalesce to the protoconid. The metalophid is oriented transversally, and the entolophid is fused with the posterolophid. m2 displays a bilophodont pattern in adults, with a wide hypoflexid. A persistent short anterolabial cingulum is also present. m3 is moderately large relative to m2.

Phyllotis anitae has 13 thoracic ribs and 7 cervical, 12-13 thoracic, 6 lumbar, and 28-36 caudal vertebrae (*N* = 3 specimens examined).

There are no chromosomal data on this species.

Two specimens of *P. anitae* were studied genetically, and carry the same cyt *b* haplotype.

Comparisons.---Several traditionally recognized species of *Phyllotis* are easily distinguishable from *P. anitae* by their small size. This is the case of *P. haggardi*, *P. amicus*, *P. gerbillus*, and *P. andium* (see Gyldenstolpe, 1932; Hershkovitz, 1962). Moreover, results of the phylogenetic analysis (Steppan et al., this volume) shows that *P. anitae* is not closely related to *P. amicus*, *P. andium*, or *P. gerbillus*. This analysis did not include *P. haggardi. P. wolffsohni* (transferred to *Tapecomys* by Steppan et al., this volume) displays trenchant skull and dental characters (e.g., frontals with divergent and sharp edges, M3 S- or Z-shaped) that easily differentiate it from *P. anitae*.

The only species of *Phyllotis* known to be sympatric to *P. anitae* is *P. osilae*. Despite the high morphologic variability of the latter species in northwestern Argentina (see Pearson, 1958; Hershkovitz, 1962), numerous features are useful to distinguish it from *P. anitae*. Although *P. osilae* specimens from humid regions are in general darker than

those that inhabit dry ones (Pearson, 1958), *P. anitae* is always darker than *P. osilae*. Ventrally, *P. osilae* frequently present an ochraceous streak, absent in *P. anitae*. The manus and pes of *P. osilae* are covered by white hairs, contrasting with the generally dark hairs of *P. anitae*. In addition, the tail of *P. osilae* is clearly bicolored, and the ears are covered by whitish hairs. Differences between the 2 species also are present in skull and dental morphology (Fig. 3). The posterior extent of the nasals in *P. osilae* is longer than in *P. anitae*, surpassing the lacrimals. The nasolacrimal capsules of *P. osilae* are well inflated. The incisors have orange enamel, contrasting with the white or yellowish-white condition found in *P. anitae*. Finally, the molars in *P. osilae* are less hypsodont than those of *P. anitae*. *Phyllotis o. nogalaris* occupies similar habitat to *P. anitae*. Pearson (1958) characterized this form as a *P. osilae* with coarse pelage, dorsally brown and darker than *P. o. tucumanus*. Nine individuals trapped in the cloud grasslands of Sierra del Centinela (Jujuy Province; Appendix I) are in accordance with this description. These specimens present a lighter and richer coloration than *P. anitae*. They have a lateral ochraceous strip and a buffy belly with a pectoral ochraceous streak; their manus and pes are white and the tail bicolored and more haired than in *P. anitae*, and the hairs that covered the ears have an ochraceous tip. Additionally, *P. o. nogalaris* is, in almost all dimensions, larger than *P. anitae* (see Pearson, 1958; Table 3). Although somewhat variable, *P. o. osilae* is the subspecies with paler dorsal coloration in northwestern Argentina, and therefore, it is clearly separable from *P. anitae*. Díaz (1999) described this subspecies, based on specimens from Jujuy Province, as a form with an ochraceous strip crossing the venter, tail bicolored, and whitish manus and pes. A series from Bárcena (Jujuy Province; Appendix I), referred to *P. o. osilae*, has a yellowish dorsum with sparse black hairs, the manus and pes are white, and the tail is strongly bicolored. *Phyllotis o. tucumanus*, like *nogalaris*, is another dark subspecies. We examined several individuals of this form from Catamarca Province (Appendix I). These specimens are intermediate in dorsal coloration between *P. o. osilae* and *P. o. nogalaris*, and are, in general, lighter colored than *P. anitae*.

The widespread *P. xanthopygus* is morphologically similar to *P. anitae*. *P. xanthopygus* has a denser, softer, and noticeably lighter pelage than *P. anitae*. The dorsum of *P. xanthopugus* has fewer black hairs, and the venter is whiter, than *P. anitae*. Contrasting with *P. anitae*, the facial vibrissae in *P. xanthopygus* are long and distinctly colored, the ears are larger and less haired, both manus and pes are white, and the tail is strongly bicolored. Cranially, *P. xanthopygus* has larger posterolateral palatal pits that in specimens from northwestern Argentina are anterior to the mesopterygoid fossa (Fig. 3; see also Pearson, 1958). The incisor enamel is orange and molar hypsodonty is less developed than in *P. anitae*. *P. xanthopygus* inhabit desert and semi-desert environments, in general associated with stones or rock outcrops and scattered xerophytic vegetation (brush, tola, cacti). According to Pearson (1958), *P. x. rupestris* is a paler form with noticeably large ears, and it is therefore easily distinguishable from *P. anitae*. In northwestern Argentina, *P. x. rupestris* occupies Puna, Prepuna, and High-Andean regions, but not Yungas environments. Several specimens from Jujuy Province (Appendix I) have a light gray dorsal coloration, a whitish belly, ears covered by yellowish tipped hairs, pure white manus and pes, and a strongly bicolored tail. The molars of this form are much more delicate, smaller, and less hypsodont than those of *P. anitae*. *Phyllotis x. ricardulus* is another subspecies present in northwestern Argentina and has been characterized as a rich-colored form, with buff lateral and pectoral strips (Pearson, 1958). These traits are present in 5 specimens from Abra Pampa (Jujuy Province; Appendix I). In addition,

Figure 5. *Alnus* cloud forest habitat of *Phyllotis anitae* at Hualinchay (Tucumán province, Argentina).

the tail in this subspecies is more haired than in *P. anitae*, and the molar toothrow is, on average, longer (Table 3). *Phyllotis x. vaccarum* is a subspecies with light coloration, larger than *P. anitae* (Pearson, 1958). The same is true for *P. x. bonariensis*, an endemic form from central-eastern Argentina (Crespo, 1964).

Phyllotis caprinus has a distribution restricted to localities in the Puna and Prepuna of northwestern Argentina and Bolivia (Pearson, 1958). It can be distinguished from *P. anitae* by its larger size, general coloration (similar to that of *P. xanthopygus*), ears covered by yellowish hairs, interorbital region with divergent and sharp frontal edges, a V-shaped fronto-parietal suture, and orange incisors (Pearson, 1958).

Habitat and Natural History.---Hualinchay, the type locality of *P. anitae*, is in the ecotone between montane forest and high-altitude grasslands, in the upper altitudinal limit of the Yungas. This vegetation level is characterized by alder forests (*Alnus acuminata*) and grassland communities dominated by *Festuca hieronymi*, *Deyeuxia polygama*, and

Table 3.-- Measurements of various taxa of *Phyllotis*. For each measurement, we provide mean ± standard deviation, range (in parentheses), and sample size.

	P. anitae n. sp. Holotype	*P. o. osilae*	*P. o. nogalaris*	*P. o. tucumanus*	*P. x. rupestris*	*P. x. ricardulus*	*P. x. vaccarum*
HB	119	118±4.92 (108-124); 9	126±5.67 (116-137); 17	119±5.12 (111-123); 6	105±6.24 (100-112); 3	118±4.93 (115-124); 3	127±2.83 (125-129); 2
T	124	118±6.10 (111-130); 9	137±8.65 (118-148); 17	130±5.48 (122-136); 6	124±11.53 (112-135); 3	103±7.64 (95-110); 3	134±20.51 (119-148); 2
HF	29	30±0.71 (29-31); 9	30±1.69 (27-32); 18	30±1.27 (28-31); 7	25±1.00 (24-26); 3	20±1.53 (19-22); 3	26±0.71 (26-27); 2
E	21	22±1.01 (21-24); 9	22±1.20 (20-24); 18	23±2.14 (22-28); 7	25±0.58 (24-25); 3	20±4.00 (16-24); 3	28±5.66 (24-32); 2
W	37.5	41.5±5.85 (32.5-49); 9	56.8±11.36 (41-82); 18	52.4±11.99 (40-74); 7	41.5±4.09 (38-46); 3	---	58; 1
GLS	30.72	29.90±0.67 (28.94-30.68); 9	31.52±1.11 (29.60-33.46); 18	30.69±0.87 (29.42-31.80); 7	28.22±0.41 (27.78-28.58); 3	29.60±1.73 (28.38-30.82); 2	31.82±0.23 (31.66-31.98); 2
CIL	27.80	27.97±0.56 (26.88-28.54); 9	29.37±1.13 (27.46-31.34); 18	28.65±0.78 (27.80-30.12); 7	26.08±0.47 (25.56-26.48); 3	27.12±1.98 (25.72-28.52); 2	29.69±0.04 (29.66-29.72); 2
ZB	16.06	16.02±0.34 (15.60-16.60); 9	16.85±0.62 (15.86-18.80); 18	16.25±0.42 (15.62-16.82); 7	14.75±0.59 (14.12-15.30); 3	15.82; 1	16.10±0.14 (16.00-16.20); 2
WBC	14.10	13.55±0.28 (13.22-13.98); 9	13.99±0.43 (13.20-14.74); 18	13.72±0.29 (13.38-14.12); 7	13.42±0.36 (13.08-13.80); 3	12.93±0.02 (12.90-12.94); 3	13.52±0.17 (13.40-13.64); 2
IB	4.02	4.19±0.16 (3.90-4.38); 9	4.23±0.17 (3.90-4.50); 18	4.15±0.11 (3.98-4.26); 7	4.19±0.22 (4.04-4.44); 3	3.96±0.25 (3.70-4.20); 3	4.26±0.31 (4.04-4.48); 2

Table 3 (continued).

UTR	5.78	5.58±0.19 (5.38-5.82); 9	5.69±0.17 (5.38-6.00); 18	5.42±0.12 (5.24-5.56); 7	4.87±0.25 (4.60-5.10); 3	5.18±0.22 (4.96-5.40); 3	5.63±0.38 (5.36-5.90); 2
NL	12.48	12.44±0.69 (11.20-13.16); 9	13.26±0.71 (12.24-14.36); 18	13.23±0.46 (12.42-13.80); 7	11.87±0.56 (11.32-12.44); 3	13.29±1.20 (12.46-14.66); 3	13.37±0.04 (13.34-13.40); 2
RW2	5.00	5.23±0.20 (4.90-5.56); 9	5.57±0.26 (5.12-5.92); 18	5.30±0.09 (5.18-5.44); 7	4.96±0.27 (4.70-5.24); 3	5.14±0.20 (5.00-5.28); 2	5.18±0.31 (4.96-5.40); 2
DL	7.80	7.58±0.32 (6.94-8.06); 9	8.04±0.58 (7.20-9.18); 18	7.80±0.34 (7.38-8.42); 7	7.29±0.24 (7.10-7.56); 3	7.65±0.74 (6.84-8.30); 3	8.18±0.45 (7.86-8.50); 2
IFL	7.24	7.02±0.42 (6.36-7.58); 9	7.34±0.41 (6.70-8.34); 18	7.15±0.33 (6.74-7.72); 7	6.57±0.19 (6.36-6.74); 3	6.95±0.46 (6.58-7.46); 3	7.65±0.30 (7.44-7.86); 2
OCW	7.04	6.94±0.15 (6.66-7.10); 9	7.50±0.34 (6.08-7.50); 18	6.90±0.20 (6.60-7.24); 7	6.57±0.09 (6.46-6.64); 3	6.86; 1	7.06±0.20 (6.92-7.20); 2
BOL	3.78	4.05±0.11 (3.92-4.20); 9	4.42±0.27 (4.04-5.00); 18	4.34±0.26 (4.06-4.76); 7	4.31±0.08 (4.26-4.40); 3	4.15±0.35 (3.90-4.40); 2	4.49±0.13 (4.40-4.58); 2
MFW	1.68	1.60±0.20 (1.26-1.86); 9	1.64±0.17 (1.38-2.06); 17	1.52±0.13 (1.40-1.80); 7	1.17±0.06 (1.10-1.22); 3	---	1.52±0.11 (1.44-1.60); 2
ZP	2.82	3.18±0.14 (2.90-3.40); 9	3.32±0.24 (3.04-3.76); 18	3.14±0.07 (3.00-3.20); 7	2.83±0.06 (2.76-2.88); 3	3.15±0.60 (2.64-3.82); 3	3.27±0.04 (3.24-3.30); 2
ML	15.40	16.32±0.41 (15.86-16.98); 9	17.02±0.53 (16.14-17.82); 18	16.47±0.47 (15.94-17.26); 7	14.93±0.31 (14.74-15.28); 3	15.92±1.24 (14.50-16.80); 3	16.74±0.17 (16.62-16.86); 2
LTR	5.70	5.48±0.22 (5.18-5.80); 9	5.54±0.19 (5.14-5.80); 18	5.14±0.15 (5.00-5.40); 7	4.93±0.25 (4.74-5.22); 3	4.65±0.53 (4.04-4.96); 3	5.45±0.58 (5.04-5.86); 2

Stipa eriostachia (Grau and Veblen, 2000; Fig. 5). Specimens of *P. anitae* were trapped near isolated and large rocks. The soil, with a well-developed organic horizon, was covered by abundant leaf detritus. The climate in this region shows a bimodal pattern with precipitations concentrated during summer and early autumn. In the wet season (January to May) mean rainfall reaches 1500 mm, contrasting with <60 mm during the dry season. These dramatic changes in precipitation result in abrupt vegetation modifications, from dense development of grasses and ferns during the wet season to an almost naked soil during the dry season. An additional humidity input, in cloud form, characterizes this region year-through (Brown et al., 2001). Temperatures also vary seasonally, with an annual mean value of 11.9°C. Snow falls occasionally in winter.

Phyllotis anitae seems to be a rare and specialist taxon of the high-altitude *Alnus* forest. Of 350 small mammals trapped at the type locality surroundings (including 8 trapping sites between 1700 and 2800 m in grassland and montane forest environments) only 5 specimens belong to this species. All *P. anitae* individuals except 1 were captured at night. The holotype was a lactating female. Both the holotype female as well as the female paratype had closed vaginas, and the male paratypes had abdominal testicles.

Other small mammals trapped at Hualinchay were the sigmodontines *Abrothrix illuteus*, *Akodon lutescens caenosus, Akodon simulator, Akodon spegazzini tucumanensis, Andinomys edax*, *Phyllotis osilae*, and undetermined species of the genera *Akodon*, *Oligoryzomys*, *Oxymycterus*, and the didelphine *Thylamys*.

DISCUSSION

In contrast with other highly polytypical genus of sigmodontine rodents (such as *Akodon*, *Calomys*, *Oligoryzomys*, and *Oryzomys*), the alpha diversity of *Phyllotis* has not been augmented in recent decades. The last valid species erected was *P. caprinus*, with type locality in Tilcara, Jujuy Province (Pearson, 1958). Several years later Crespo (1964) described the subspecies *P. xanthopygus bonaerensis* (formerly, *P. darwini*) from the isolated system of Ventana in the eastern Pampean region of Buenos Aires Province, Argentina. Although this form has been considered as a valid species by several authors (Reig, 1978; Galliari et al., 1996; Musser and Carleton, 2005) its status at the species level has not been correctly assessed. The description of *P. anitae* indicates that the static scenario of *Phyllotis* alpha diversity can be attributed more fundamentally to the lack of collections in vast geographic areas of the Andean region, than to a stabilized and well-resolved alpha taxonomy.

As noted above, *Phyllotis anitae* is sister taxon to *P. osilae*. Both species are easily distinguishable at both morphological and molecular (cyt *b* gene) levels. For instance, *P. anitae* is more hypsodont, with white or yellowish-white incisors, a delicate rostrum, and a distinct coloration (see above for details). Similarly, cyt *b* haplotypes of *P. anitae* and *P. osilae* are very divergent; the lowest value of observed divergence between haplotypes of both species is 9.36%. Remarkably, this high value of observed divergence is the lowest observed between haplotypes recovered from *P. anitae* specimens and individuals of any other *Phyllotis* species. This fact, together with the morphological comparisons detailed in the previous section, clarifies that *P. anitae* is distinct to all other known species of *Phyllotis*.

Phyllotis generally inhabit open areas, mainly grasslands and xerophytic

environments (Pearson, 1958). The exceptions to this pattern are *P. anitae* and *P. o. nogalaris*, which are the only known *Phyllotis* forms that inhabit the Yungas. The Yungas have a rich sigmodontine fauna, which has been poorly studied. In spite of the lengthy time period between the descriptions of the first species known from the region (e.g., Allen, 1901, Thomas, 1916, 1918, 1921a, 1921b, 1925) and recent contributions covering different aspects of the sigmodontine fauna (e.g., Barquez, 1976; Olrog, 1979; Barquez et al., 1980; Mares et al., 1981; Kajon et al., 1984; Ojeda and Mares, 1989; Mares et al., 1997; Díaz, 1999; Díaz and Barquez, 1999; Díaz et al., 1999; Ortíz et al., 2000a, 2000b; Ortíz and Pardiñas, 2001), knowledge of several species remains sparse. The Argentine part of the Yungas has, at least, 27 sigmodontine species, which are included in 12 genera.

In northwestern Argentina the Yungas reach their southern limit and become fragmented. The Yungas here are characterized by a strong altitudinal gradient, where climatic conditions vary strongly over short distances. This variation determines altitudinally structured vegetation zones (Brown et al., 2001). The upper montane forest, which is inhabited by *P. anitae*, constitutes a band from 1500 to 3000 meters above see level, distributed in patches, mainly on the eastern slopes of northwestern Argentina mountain chains. This band is highly heterogeneous, especially at the transition zone with the cloud grasslands (Brown et al., 2001).

Traditionally, mammalogists have concentrated their efforts at lower vegetation levels; meanwhile, the upper montane forest have received less attention. Of the 27 sigmodontines recorded for the Yungas, 18 have been observed in upper montane forests. The finding of *P. anitae* as well as other new taxa currently under study (e.g., a new *Oxymycterus*) indicates that this number is an underestimate of the local diversity.

Unfortunately, the Yungas are suffering substantial human impacts. Cattle raising, fire, and wood exploitation are among the main factors underlying the deterioration of the Yungas. As is the case for several unique South American biomes (e.g., Chaco), conservation strategies based on sound biological knowledge are lacking, and the effects of these stressors on the sigmodontine fauna, as well as in other small mammals, have not been assessed.

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APPENDIX 1: SPECIMENS EXAMINED

Specimens of *Phyllotis* used in this study are listed below. All specimens were used in morphological analysis; specimens used in molecular and quantitative analyses are indicated by [m] and [q], respectively. Museum and Collection acronyms and personal field numbers are as follows: CML, Colección Mamíferos Lillo, Tucumán, Argentina; CNP, Colección de Mamíferos del Centro Nacional Patagónico, Puerto Madryn, Chubut, Argentina; MMP-Ma, Museo de Ciencias Naturales y Tradicional de Mar del Plata "Lorenzo Scaglia," Mar del Plata, Argentina; JPJ, field number of Jorge P. Jayat (to be deposited at CML); MMD, field number of M. Mónica Díaz (to be deposited at CML); and PEO, field number of Pablo E. Ortiz (to be deposited at CML).

Phyllotis anitae (5).---TUCUMÁN: 10 km by road south of Hualinchay on the trail to Lara (CML 6379[mq] [holotype], CML 6380[q], CML 6381[q], CNP 736[mq], CNP 737[q], CNP 809[m]).

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

Phyllotis osilae nogalaris (9).---JUJUY: La Antena, Sierra del Centinela, al S de El Fuerte, 2350 m (JPJ 933[q], JPJ 936[q], JPJ 940[q], JPJ 955[q], JPJ 956, JPJ 958[q], JPJ 962[q], JPJ 969[q], JPJ 970).

Phyllotis osilae osilae (8).---JUJUY: Bárcena, aprox. 3 km al S, sobre Ruta Nacional N° 9, 1808 m (JPJ 632, JPJ 636, JPJ 637, JPJ 638, JPJ 639, JPJ 646, JPJ 655, JPJ 668).

Phyllotis osilae tucumanus (7).--- CATAMARCA: unión entre las rutas provinciales N° 9 y 18, 3,4 km al S, sobre Ruta Provincial N° 18, 1529 m (JPJ 19, JPJ 24, JPJ 31, JPJ 41, JPJ 1129, JPJ 1137, JPJ 1149).

Phyllotis osilae ssp. (103).---CATAMARCA: Aprox. 2 km al SE de Huaico Hondo, sobre Ruta Provincial N° 42, al E del Portezuelo, 1992 m (JPJ 412, JPJ 781, JPJ 790); El Rodeo, 1.5 km NE of Hwy 4, el. 4500 ft (CML 3448); km 33 de la Ruta Provincial N° 47, al S de Capillitas, 2500 m (JPJ 674, JPJ 676, JPJ 677, JPJ 680, JPJ 681, JPJ 685[q], JPJ 686, JPJ 688, JPJ 693, JPJ 695[q], JPJ 702[q], JPJ 703[q], JPJ 704[q], JPJ 705[q], JPJ 706[q], JPJ 707, JPJ 713[q], JPJ 715[q]); Las Chacritas, aprox. 28 km al NNW de Singuil, sobre Ruta Provincial N° 1, 1888 m (JPJ 567, JPJ 568). JUJUY: Termas de Reyes, aprox. 15 km al N, sobre Ruta Provincial N° 4 (JPJ 291, JPJ 315); Termas de Reyes, mirador, sobre Ruta Provincial N° 4 (JPJ 122[q], JPJ 296, JPJ 324, JPJ 333, JPJ 334). SALTA: Abra de Ciénaga Negra, aprox. 3 km al SE, 3090 m (JPJ 722, JPJ 723, JPJ 727[q], JPJ 738[q]); Aprox. 15 km al W de Escoipe, sobre Ruta Provincial N° 33, 2680 m (JPJ 51, JPJ 57, JPJ 60, JPJ 65, JPJ 68, JPJ 71, JPJ 74, JPJ 86, JPJ 1034, JPJ 1048, JPJ 1056, JPJ 1059); Campo Quijano aprox. 5 Km al NO, Km 30 de la ruta Nacional 51 (Quebrada del Toro), alt. aprox. 1600 msnm (JPJ 91, JPJ 92[q], JPJ 97[q], JPJ 98, JPJ 101, JPJ 102, JPJ 103, JPJ 104[q], JPJ 135, JPJ 136[q], JPJ 137, JPJ 140, JPJ 141, JPJ 142[q]). TUCUMÁN: Aprox. 10 km al S de Hualinchay, sobre el camino a Lara, 2300 m (JPJ 435, JPJ 444[q], JPJ 451[q], JPJ 453[q], JPJ 456, JPJ 460, JPJ 461, JPJ 467, JPJ 469, JPJ 474, JPJ 476, JPJ 483, JPJ 487, JPJ 488,

JPJ 771); Aprox. 16 km de Hualinchay, sobre el camino a Lara, 2750 m (JPJ 746, JPJ 748[q], JPJ 749, JPJ 751, JPJ 765, JPJ 767, JPJ 769[q], JPJ 776, JPJ 777[q]); aprox. 7 km al NO de la finca de la familia Usandivara, Altos de Medina, 1717 m (JPJ 810, JPJ 831[q], JPJ 837, JPJ 839[q]); Carapunco, km 81 de la Ruta Provincial N° 307, 2960 m (JPJ 1063, JPJ 1071); Hualinchay, sobre el camino a Cafayate, 1861 m (JPJ 173, JPJ 175, JPJ 176, JPJ 178, JPJ 183, JPJ 187, JPJ 189, 218, JPJ 220, JPJ 223, JPJ 227, JPJ 228).

Phyllotis xanthopygus ricardulus (5).---JUJUY: Abra Pampa (CML 1276[q], CML 1277, CML 1278[q], CML 1283); La Ciénaga, Abra Pampa (CML 1280[q]).

Phyllotis xanthopygus rupestris (4).---JUJUY: 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[q], MMD 436[q], MMD 438).

Phyllotis xanthopygus vaccarum (3).---CATAMARCA: Chumbicha, 1 km NW by rd. from balneario, el. 2600 ft (CML 3451[q]). SAN JUAN: Estancia Leoncito, 2 km E observatorio Astronómico (CML 3624); San Guillermo (CML 1080[q]).

Phyllotis xanthopygus ssp. (7).---JUJUY: 4 km al O de Rinconada (PEO 11, 13); Avedrez (PEO 8); Curques, 24 km al N de Susques, sobre ruta 74 (MMD 291[q]). TUCUMÁN: Cerro Bayo (CML 5563); Cerro Muños (CML 382); km 99 Ruta 307 (Tafí-Amaicha) (CML 5564).

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