Mammalian Biology
Zeitschrift für Säugetierkunde
www.elsevier.de/mambio

ORIGINAL INVESTIGATION

A new species of *Phyllotis* (Rodentia, Cricetidae, Sigmodontinae) from Tucumán province, Argentina

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Received 12 May 2009; accepted 20 September 2009

Abstract

A new species of rodent of the genus *Phyllotis* is described based in cranial and external morphology, as well as morphometric data. Additionally, sequences of the mitochondrial gene cytochrome-b were used to asses the phylogenetic relationships. We have compared our specimens with all the extant species of the genus *Phyllotis* and also with some species of related genera, particularly with the most similar and with those that occur in the province of Tucumán and northwestern Argentina. The new species is large compared to the average size of the genus, and can be easily distinguished from all other species essentially by coloration and by cranial morphology. It is closely related to the recently described *P. anitae*, and these two species are, in turn, sister to *P. osilae.* The only two localities where the new species has been found are in the Upper Montane Forests of the southern portion of the Yungas Ecoregion, in the province of Tucumán, Argentina.

Keywords: Rodents; Yungas Forests; Aconquija range; Campo de los Alisos National Park; Taxonomy

Introduction

During the last several decades intense sampling efforts were made to collect small mammals in the Yungas forests of northwestern Argentina, but mainly in the lowland regions below 2000 m of elevation, and neglecting the highest altitudes that could still be considered as poorly sampled areas. During the past few years we have focused our sampling effort in different elevational belts of the Yungas forests and particularly in the highlands. As a result of these studies we have been able to find several specimens of a leaf-eared mice genus *Phyllotis*, which was not then possible to identify at the species level.

Phyllotis is a genus of sigmodontine rodent, including 13 species, whose range extends from Ecuador to southern Argentina (Musser and Carleton 2005). The systematic history of the genus is complex and includes authors recognizing the species as they were originally described (see Pearson 1958), as well as the lumping of several species into one, as done later by Hershkovitz (1962). More recent reviews included a phylogenetic approach of the tribe Phyllotini (Braun 1993; Steppan 1993, 1995). Steppan et al. (2007) presented a re-evaluation of the species of the genus and related groups

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doi:10.1016/j.mambio.2009.09.005

based on molecular analyses, concluding that *Phyllotis* is monophyletic, as opposed to the arrangement proposed by Braun (1993). Recently, the species from Argentina were listed (Díaz et al. 2006) in the context of a comprehensive analysis of the mammals of the country (Barquez et al. 2006). They considered the tribe Phyllotini to include nine genera in Argentina: *Andalgalomys*, *Auliscomys*, *Calomys*, *Eligmodontia*, *Graomys*, *Loxodontomys*, *Phyllotis*, *Salinomys* and *Tapecomys*, (*Andinomys*, *Euneomys*, *Irenomys* and *Reithrodon* being excluded from the tribe following D′Elía, 2003). Díaz et al. (2006) recognized five species of *Phyllotis* inhabiting Argentina (*P. caprinus*, *P. osilae*, *P. wolffsohni*, *P. xanthopygus*, and *P. anitae* then mentioned as *Phyllotis* sp., also from the province of Tucumán).

In this paper we describe a new species of *Phyllotis* from the montane forests of southern Tucumán province in northwestern Argentina. We offer detailed comparison with the other species from the province, mainly with *Phyllotis anitae* to which it is most closely related.

Material and methods

The area where all specimens of the new species have been collected is part of the Nevados del Aconquija mountain range, which represents the northernmost extension of the Sierras Pampeanas geological formation, and constitutes the first great steppe of the Andes after the Pampas and the Chaco plain (Aceñolaza and Toselli, 1981; Ferro and Barquez, in press). Phytogeographically it is one of the altitudinal districts proposed by Cabrera (1976), the Upper Montane Forests, located from 1200 up to 2500 m and typified by grasslands, Andean Alder forests (*Alnus acuminata*) and ‘‘queñoa’’ forests (*Polylepis australis*).

The specimens were captured with snap traps (Victor mousetraps) and Sherman live traps baited with a mixture of oat and fat. They were measured following the protocols established in Díaz et al. (1998) and prepared either as skin and skeleton, or fixed in 10 percent formalin solution and preserved in ethanol 70 percent and deposited in the Colección Mamíferos Lillo (CML), University of Tucumán, Argentina. Tissues samples were taken from liver and muscle and preserved in 96 percent ethanol.

We compared the new species with several species deposited at the CML and Colección de Mamíferos del Museo Argentino de Ciencias Naturales Bernardino Rivadavia (MACN), Buenos Aires, Argentina (see specimens examined), as well as comparing with descriptions in the literature (Pearson 1958; Hershkovitz 1962; Steppan 1995; type descriptions, and others). Specimens that have not yet been cataloged in the CML are identified with the acronym LIF, belonging to the field catalog of the collector, Luis Ignacio Ferro.

For terminology of cranial and dental structures we followed Reig (1977), Wahlert (1985), Voss (1988), Steppan (1995), and Abdala and Díaz (2000). External measurements (in mm) taken from specimens in the field, and from labels in museum specimens were: total length (TL), length of tail (T), length of hind foot (F), length of ear (E), and weight (W) (in grams). Twenty cranial measurements were taken with digital calipers, recorded to the nearest 0.05 mm, following the definitions of Myers et al. (1990): Condyloincisive length (CIL), zygomatic breadth (ZB), braincase breadth (BB), interorbital constriction (IOC), rostral length (RL), nasal length (NL), rostral width (RW), mid-rostral width (RW2), orbital length (OL), diastema length (DL), maxillary tooth row length (MTRL), incisive foramen length (IFL), alveolar width (AW), occipital condyle width (OCW), mastoid breadth (MB), basioccipital length (BOL), mesopterygoid fossa length (MFL), mesopterygoid fossa width (MFW), and cranial depth (CD); width of the zygomatic plate (WZP) was measured as the widest length of the plate in lateral view.

All cranial measurements were used to perform a Principal Component Analysis (PCA) on a variance-covariance matrix in order to evaluate the degree of morphological similarity between species of *Phyllotis* from northwestern Argentina, particularly from the province of Tucumán.

Specimens examined.—We examined 352 specimens of seven species of *Phyllotis* from the following localities and collections:

P. amicus (1).–PERU: Lima, Lomas de Asia, 1 (CML 1672).

P. anitae (3).–ARGENTINA: Tucumán: App. 10 Km al sur de Hualinchay sobre camino a Lara, 2316 m, 3 (CML 6379, 6380, 6381).

P. caprinus (16).–ARGENTINA: Jujuy: Maimará, 2 (CML 282, MACN 31.34); Maimará, 2230 m, 3 (MACN 27112, 27113, 27115); Maimará, 2300 m, 2 (MACN 27120, 31.35); Maimará, 2500 m, 2 (CML 282, MACN 31.36); Maimará, 2700 m, 1 (MACN 31.32); Sierra de Zenta, 4500 m, 4 (MACN 32.52, 32.54, 31120, 31125); La Lagunita, 4500 m, 1 (MACN 32.53); La Lagunita, Sierra de Zenta, 1 (MACN 32.56).

P. haggardi (2).–ECUADOR: Pichinchas, Monjas (MACN 31150, 31151).

P. osilae (116).–ARGENTINA: Catamarca: 3,4 km al S de la unión entre las rutas provinciales 18 y 9, sobre ruta provincial nº 18, 1 (CML 7229); 6 km SW of Hwy 9 on Hwy 18, alt. 5000 ft., 1 (CML 3446); Chumbicha, 600 m, 1 (MACN 20264); El Rodeo, 1.5 Km NE of Hwy 4, 4500 ft., 2 (CML 3448, 3449); Estancia Narváez, 5.5 km al N de Las Chacritas, sobre ruta provincial nº 1, 2 (CML 7228, 7230); Las Cuevas, 8 (MACN 42128, 42134, 42137, 42147, 42148, 42152, 42163, 42165); Río Vallecito, 2900 m, 1 (MACN 50441). Jujuy: Cerro Monte Hermoso, 5 (MACN 19524, 19526, 19527, 19536, 19537); Chilcayoc, 1 (CML 7231); Cerro San Francisco, 1 (CML 379); Calilegua, San Francisco, 1 (CML 478); El Duraznillo, Cerro Calilegua, 2600 m, 2 (CML 1724, 1725). Tucumán: Aconquija, 3000 m, 10 (MACN 29259, 29260, 29261, 29262, 29263, 29264, 29266, 29267, 29268, 29270); Cerro San Javier, 2000 m, 1 (MACN 26145); Ciénaga Grande, San José de Chasquivil, 17 (LIF 200, 208, 209, 210, 222, 223, 227, 234, 235, 238, 239, 242, 243, 251, 253, 255, 256); El Kenqueo, Parque Nacional Campo de los Alisos, 3165 m, 20 (LIF 632, 633, 634, 635, 636, 637, 638, 639, 640, 645, 646, 650, 651, 652, 653, 654, 655, 664, 665, 666); El Papal, 2175 m Parque Nacional Campo de los Alisos, 1 (LIF 771); La Ciénaga, frente a la escuela, 2 (LIF 62, 63); Los Nacimientos (La Cascada), Parque Nacional Campo de los Alisos, 11 (LIF, 680, 681, 682, 683, 687, 689, 690, 691, 692, 705, 706); Pie de la cuesta a Chasquivil, 5 km río arriba de la Hoyada, sobre río hoyada, 1700 m, 5 (LIF 128, 135, 164, 165, 169); Piedra Blanca, 3 (LIF 73, 74, 75); San José de Chasquivil, La Sala, 2 (LIF 351, 370); San José de Chasquivil, Río Liquimayo, 13 (LIF 13, 20, 21, 22, 25, 36, 37, 38, 39, 41, 42, 43, 44); Tafí del Valle, 2000 m, 2 (CML 745, 746). BOLIVIA: Cochabamba, Colomi Chapare, 1 (MACN 50352); Taquiña a 2700 m, 1 (MACN 50398); Tiraque 3295 m, 1 (MACN 50407).

P. wolffsohni (5).–ARGENTINA: Salta: Santa Victoria Oeste, 2100 m, 5 (MACN 17719, 17720, 17721, 17722, 17723).

P. xanthopygus (209).–ARGENTINA: Catamarca: Laguna Blanca, 3200 m, 5 (MACN 29255, 29256, 29257, 29265, 29749); Laguna Blanca, 4500 m, 1 (CML 366); Belén, 1 (CML 99); Agua Tapada, Hualfín, 1 (CML 884); Pasto Ventura, 1 (CML 7196, 7197). Chubut: Lago Lunco, entre El Maitén y Paso del Sapo, 1 (CML 1961); Estancia Bernarda, 60 km al S de Paso del Indio, 3 (CML 1972, 1977, 1983). Jujuy: Abra Pampa, 3480 m, 1 (CML 1285); Abra Pampa, 6 (CML 1276, 1277, 1278, 1279, 1282, 1283); Abra Pampa, La Ciénaga, 3700 m, 1 (CML 1274); La Ciénaga, 3700 m, 1 (CML 1259); La Ciénaga, 5 (CML 621, 1249, 1250, 1251, 1264); La Ciénaga, Abra Pampa, 3700 m, 2 (CML 1280, 1281); La Lagunita, 4500 m, Sierra de Zenta, 3 (MACN 27118, 27119, 27121); Maimará, 2500 m, 2 (CML 317, 338); Maimará, 3 (CML 317, 328, 338); Sierra de Zenta, 2 (CML 320, 285); Sierra de Zenta, 4500 m, 6 (CML 378, MACN 32.50, 32.51, 32.55, 31119, 31121); Sierra de Zenta, E de Maimará, 4500 m, 1 (MACN 27117); Yavi, 3600 m, 1 (CML 2871); Yavi, 1 (CML 2870). La Rioja: Cerro Famatina, 3200 m, 7 (CML 762, 766, 767, 770, 773, 775, 776); Famatina, 3300 m, 1 (MACN 20263); Laguna Brava, 2 (MACN 18846, 18847); San Antonio, 2700 m, 1 (MACN 34276); San Antonio, Sierra de Velasco, 1 (MACN 34274); Velasco al oeste de puesto viejo, 2500 m, 1 (MACN 34275). Mendoza: 2 km N Valle Grande Dike along Hwy 173, 2700 ft., 2 (CML 3633, 3634); 2 km S Puesto Punta del Agua, 2700 ft., 1 (CML 3632); 2 millas al E Gendarmería Cruz de Piedra, 1 (CML 4382); 3 km W Refugio Militar General Alvarado, 7 (CML 3625, 3626, 3627, 3628, 3629, 3630, 3631); 4 km al S de Uspallata, 1 (CML 4433); 7 km S Uspallata, 6 (CML 4477, 4478, 4480, 4481, 4482, 4483); Arroyo de los Tambillos, 11 (CML 4420, 4421, 4422, 4423, 4424, 4425, 4427, 4428, 4429, 4430, 4431). Neuquén: 18 km S, 3 km E (by rd) Lonco Luan, 1 (CML 3636); 2 km S Lonco Luan along Hwy 23, 3860 ft., 1 (CML 3635); Collón Cura, 1 (CML 237); Lago Lacar, San Martín de los Andes, 1 (CML 287); Lit-Las Coloradas, 1 (MACN 14568); Lit-Las Coloradas, Campo Grande a 1000 m, 2 (MACN 13482, 13627); San Martín de Los Andes, 1 (CML 287). Salta: 17 Km NW Cachi, 10350 ft., 6 (CML 7115, 7116, 7117, 7118, 7119, 7120); 26 km WSW Santa Rosa de los Pastos Grandes, 1 (CML 7234); Chorrillos, 4500 m, 2 (CML 303, 387); Chorrillos, 5000 m, 1 (CML 387); San Antonio de los Cobres, 1 (MACN 47.33); San Antonio de los Cobres, 3700 m, 13 (MACN 30.42, 30.43, 30.44, 30.46, 30.47, 30.57, 30.58, 30.59, 30.60, 30.64, 30104, 30110, 30111). San Juan: 2 Km al E de Complejo Astronómico el Leoncito, 1 (CML 3624); 3 Km al E de Complejo Astronómico el Leoncito, 1 (CML 3623); Agua de la Peña, Ischigualasto, 1 (CML 1294); Quebrada de las flores, 4 Km E and 5 Km N Guayamas, 3 (CML 3620, 3621, 3622); Reserva San Guillermo, 19 (MACN 18830, 18831, 18832, 18833, 18834, 18835, 18836, 18837, 18838, 18839, 18840, 18841, 18842, 18843, 18844, 18845, 18848, 18849, 18850); San Guillermo, 1 (CML1132, 1132); San Guillermo, 3700 m, 1 (CML 1080); Valle Fértil, Ischigualasto, 2 (MACN 13767, 13786). Santa Cruz: 18 Km al S de Caleta Olivia, 1 (MACN 16380); Estancia El Tranquilo, 60 km al SO de Bosques Petrificados, 1 (CML 1951); Estancia Los Manantiales, bosque petrificado, 2 (CML 1967, 1978); Estancia Roca Blanca, 250 km al S de Colonia Las Heras, 1 (CML 1429). San Luis: 1 Km N Paso del Rey, along Arroyo de la Cañada Honda, 4400 ft., 4 (CML 3605, 3606, 3607, 3608); 15 Km N Paso el Rey, 4700 ft., 1 (CML 3617); 6 km W Hualtaran Parque Provincial Sierras de las Quijadas, 2800 ft., 1 (CML 3613); 9 Km N Paso del Rey, 4800 ft., 1 (CML 3618); La Calera, 12 km NW of Los Araditos, 2800 ft., 3 (CML 3614, 3615, 3616); Quebrada de López, San Francisco del Monte de Oro, 896 m, 4 (CML 3609, 3610, 3611, 3612); Río Gómez, 7 km E of downtown San Francisco del Monte de Oro, 2800 ft., 3 (CML 3602, 3603, 3604). Tucumán: Amaicha del Valle, km 98, Ruta 307, 3 (CML 2223, 2225, 2226); Cerro Bayo, Cumbres Calchaquíes, 4 (CML 2233, 5561, 5562, 5563); Cerro Muñoz, 4100 m, 3 (CML 376, 382, 385); Ciénaga Grande, San José de

Chasquivil, 5 (LIF 211, 216, 217, 224, 252); La Junta, 4300 m Parque Nacional Campo de los Alisos, 2 (LIF 716, 719); Lagunas de Huaca Huasi, 18 (LIF 257, 258, 262, 263, 264, 265, 266, 272, 276, 279, 282, 283, 377, 378, 381, 385, 391, 392).

Molecular data analyses.–We extracted DNA employing the standard phenol-chloroform method (Maniatis et al. 1982) from tissues preserved in ethanol belonging to type and paratype specimens (CML 7542 and CML 7543 respectively) of the new species. We amplified the complete mitochondrial gene cytochrome b with the primers Mus14095 (5' GAC ATG AAA AAT CAT CGT TGT AAT TC 3') and Mus15398 (5' GAA TAT CAG CTT TGG GTG TTG RTG 3') (Anderson and Yates 2000). PCR reactions were performed in a final volume of 50 μl: 1 × buffer [75 mM Tris-HCl pH 8.8, 20 mM $(NH_4)SO_4$, 0.01% Tween-20], 24 nM each dNTP (dATP, dCTP, dGTP, dTTP), 0.2 pmol/μl Mus14095, 0.2 pmol/μl Mus15398, 2.0 mM $MgCl_2$, 1.5 U *Taq* polimerase (Fermentas, Brazil) and 5-15 ng of template DNA. The cycling program consisted in the following conditions: initial denaturation for three minutes at 94 °C, 35 cycles at 94 °C for one minute, annealing temperature for one minute at 50 °C, extension at 72 °C for one minute and a final extension at 72 °C for five minutes. PCR products were sequenced at Macrogen USA (www.macrogenusa.com) in an ABI PRISM 3730xl DNA automatic analyzer using the same primers as those mentioned above. The sequences were submitted to Genbank with the following accession numbers: GQ119625 and GQ119626.

Multiple-sequence alignments were done with Muscle (Edgard 2004) using the default parameters. To examine the phylogenetic position of the new species among the other species of *Phyllotis* we employed both maximum parsimony analysis (MP) using TNT (Goloboff et al. 2003, 2008), and Bayesian inference (BI) using MrBayes 3.1 (Huelsenbeck and Ronquist 2001). Parsimony reconstructions were done with all sites weighted equally and gaps treated as missing characters. The heuristic searches for MP phylogenetic reconstructions were made with 250 random addition sequences, saving five trees per replicate and TBR branch swapping algorithm. We summarized the trees of maximum parsimony in a strict consensus tree. The nodes support was evaluated by 1000 Bootstrap replication and with 1000 Jackknife (JK) replication with a removal probability of 0.36, following Farris et al. (1996). For BI we used GTR model with a gamma parameter and a proportion of invariable sites. The model that fitted better with our data set was selected using Modeltest 3.7 (Posada and Crandall 1998). A Bayesian analysis was initiated with two random starting trees with four chains each one (one cold and three heated chains) and run for one million generations. We used the standard deviation of split frequencies as convergence diagnostic, the run was stopped after this was sufficiently low (< 0.002). The Markov chains were sampled every 100 generations, of the resulting 10001 trees, 250 were discarded as burn-in, and the remaining 9751 trees were summarized in 50% majority rule consensus tree. In order to determine the numbers of trees discarded as burn-in we plotted the log likelihood values of cold chains over the generations sampled. All the values of PSRF (potential scale reduction factor) in the evolution model were closed to 1.00. Published *Phyllotis cyt b* sequences included (with Genbank accession numbers): *Phyllotis amicus* (AY956708), *Phyllotis andium* (AY956706, U86818), *Phyllotis anitae* (AY627299, AY627298), *Phyllotis bonariensis* (AY956731, AY956732), *Phyllotis darwini* (AY956723, AY956722, U86819), *Phyllotis gerbillus* (AY956712, AY956713), *Phyllotis limatus* (AY956740), *Phyllotis magister* (AF484213, AF484214), *Phyllotis osilae osilae* (U86828, U86827), *Phyllotis osilae phaeus* (AY956700, AY956701), *Phyllotis sp.* (VPT 2318, 2324 , an undescribed species reported in Steppan et al. (2007), catalogue numbers belonging to Victor Pacheco-Torres) (AY956714, AY956715), *Phyllotis xanthopygus chilensis* (U86830, U86831), *Phyllotis xanthopygus posticalis* (AY956730), *Phyllotis xanthopygus rupestris* (AF484211, AY956738), *Phyllotis xanthopygus vaccarum* (AF484209, AY956735) and *Phyllotis xanthopygus xanthopygus* (AY956737, U86833). All trees were rooted with *Calomys* species: *Calomys lepidus* (AF385606), *Calomys sorellus* (AF385608), *Calomys venustus* (AY033175) and *Calomys callosus* (DQ447282).

The genetic distance between species was estimated using Kimura 2 parameters (K2P) distance for saving multiple hits as implemented in MEGA 3.1 (Kumar et al. 2004).

Results

Phyllotis alisosiensis, new species

Holotype.–Adult male, preserved as skin, skull and skeleton, and tissues in alcohol, CML 7542, collected 15 October 2007 by Luis Ignacio Ferro and Ana María López, original field number LIF 772.

Paratype.–Subadult male, preserved as skin, skull and skeleton, and tissues in alcohol, CML 7543, collected 13 October 2007 by Luis Ignacio Ferro and Ana María López, original field number LIF 769.

Type locality. – El Papal, 2175 m (27°11'S 65°57'W), Parque Nacional Campo de Los Alisos, Departmento Chicligasta, Tucumán, Argentina (Fig. 1).

Etymology.–The new species is named in allusion to "Campo de los Alisos National Park" (Parque Nacional Campo de los Alisos), the origin of the type series, and all additional specimens, except for one obtained in

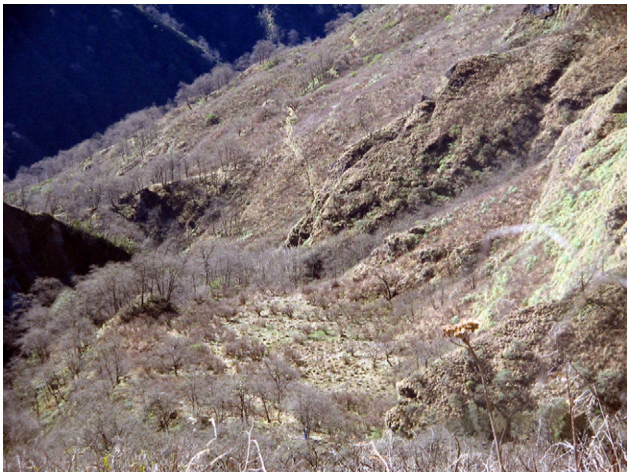

Fig. 1. Habitat of *Phyllotis alisosiensis* at the type locality. Photo taken on July 20, 2006, by L. Ignacio Ferro.

another locality. The name of the park is in reference to the dominant tree, an alder (*Alnus acuminata*). This is the first national park in Tucumán, and represents a model for conservation of nature in the province.

Additional Specimens (8).–Argentina, Tucumán Province: El Papal, 2175 m (27°11'S, 65°57'W), Parque Nacional Campo de Los Alisos, Departmento Chicligasta, 7 (4 females CML 7544, 7546, 7548, 7549; 1 male CML 7545; 2 sex unknown CML 7547, 7550); Reserva Provincial Los Sosa, Ruta 307, km 35, campamento de Vialidad Provincial (27°01'S 65°39'W), 1234 m, 1 (CML 4106).

Distribution.–*P. alisosiensis* is known only from two localities in the province of Tucuman, Argentina. The two localities (Fig. 2) are inside protected areas of the eastern slopes of the Aconquija's mountain range; the type locality is within a national park and the other is in a provincial reserve. The elevation range of this species extends from 1234 to 2175 m.

Habitat.–*P. alisosiensis* inhabits the southernmost portion of the Yungas Phytogeographic Province (Cabrera, 1976) of northwestern Argentina, in the province of Tucumán. Specimens from the type locality were collected at the Upper Montane Forest (Bosques Montanos). There, the landscape is dominated by deciduous forest of Andean alder, *Alnus acuminata* (Betulaceae) with scattered *Polylepis australis* thicket and native grasses of "cortadera" (*Cortaderia* sp.) in the steepest rocky slopes. The other locality, where one specimen was collected, is evergreen forest dominated by species of *Myrcianthes,* with epiphytes, lianas and also grasses of "cortadera". This Myrtaceous cloud forest is the upper district of the Lower Montane Forests (Hueck 1978). The two collecting sites indicate the current altitudinal range of this species, which extends from the upper part of the myrtaceous forests up to the alder forests of *Alnus acuminata*.

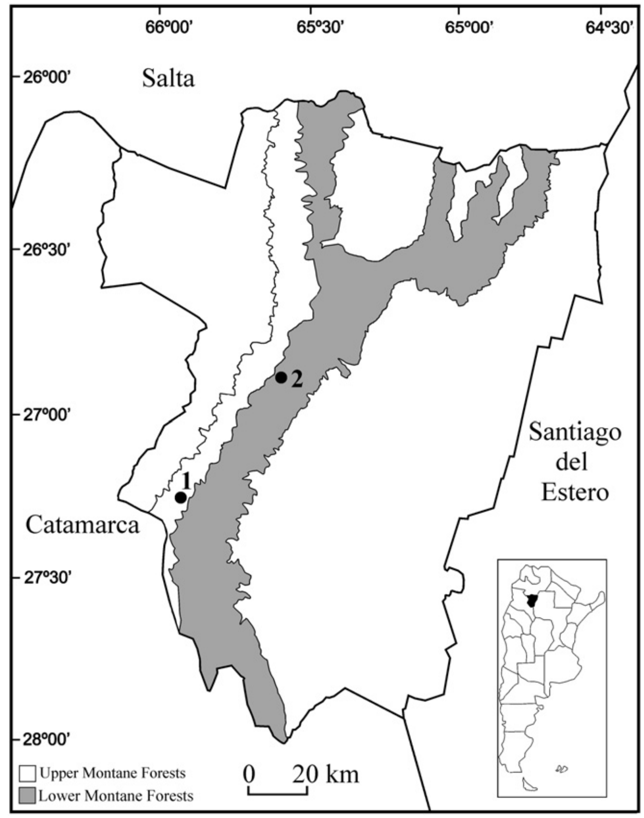

Fig. 2. Map of Tucumán province, Argentina, showing the distribution of *Phyllotis alisosiensis*: 1) Type locality, 2) Reserva Provincial Los Sosa, Ruta 307, km 35, campamento de Vialidad Provincial.

Diagnosis (Figs. 3, 4).–A member of the genus *Phyllotis* (Cricetidae, Sigmodontinae) that can be easily recognized by its strong cinnamon ventral coloration. The skull is robust with a very narrow interorbital constriction, less than 3.6 mm. The anterior end of the zygomatic arch is high, and from lateral view the antorbital bridge is flat and hardly visible. In fully developed adults the width of the zygomatic plate is never less than the length of the interorbital constriction.

Description.–The majority of the species of *Phyllotis* resemble one another, many of them with grayish to yellowish tones dorsally, some with intermixed dark and pale hairs, even some white hairs that confer a characteristic external appearance. Unlike most congeners, the new species is large, with long and fluffy fur, and a cinnamon-brown dorsal coloration with scattered black hairs; the ventral coloration is a strong shade of cinnamon. Dorsal hairs average 16 to17 mm on the rump, are banded, include a short white basal band of about 1 mm long, followed by a broad plumbeous band of about 12 to 13 mm long, and tipped by a shorter brownish/somewhat cinnamon terminal band of 3 mm. Entirely black guard-hairs are present on the dorsum, projecting 4 to 5 mm beyond the level of the fur, and with tips becoming white on the rump.

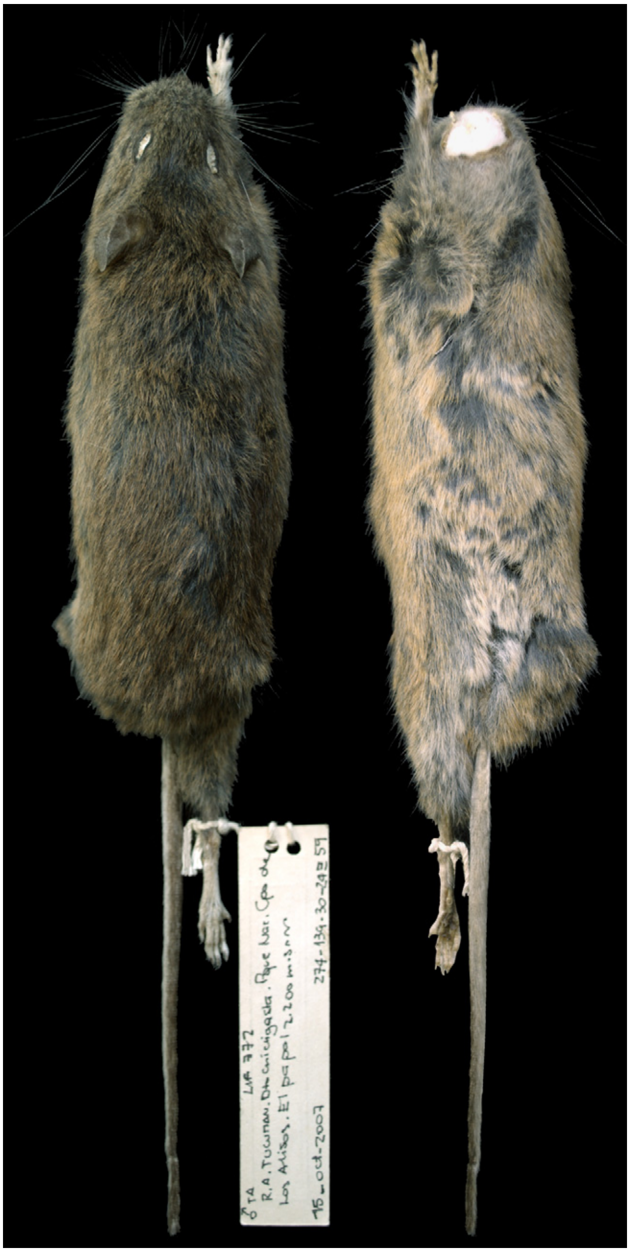

Fig. 3. Dorsal and ventral views of the type specimen of *Phyllotis alisosiensis.*

Along the sides the hairs are about 13 mm long, with a 1 mm white band at the base, an 8 mm middle plumbeous band, and a 4 mm cinnamon tip which gives the sides of the body a clear coloration so the flanks are gradually paler, bright cinnamon; guard hairs are still present with an increasing white band distally that reaches almost 50% of each hair near the belly. Transition between dorsal and ventral coloration is gradual and not sharply contrasting. Ventral hairs average 14 mm long, with basal white bands of 1 mm followed by 7.5 to 8 mm plumbeous bands and 3 to 4 mm cinnamon tips. Some hairs on the venter are long and have a wide white band on the third distal part of each hair. The tips of the hairs of the inguinal region are paler; the chin and the throat are slightly darker, almost grayish.

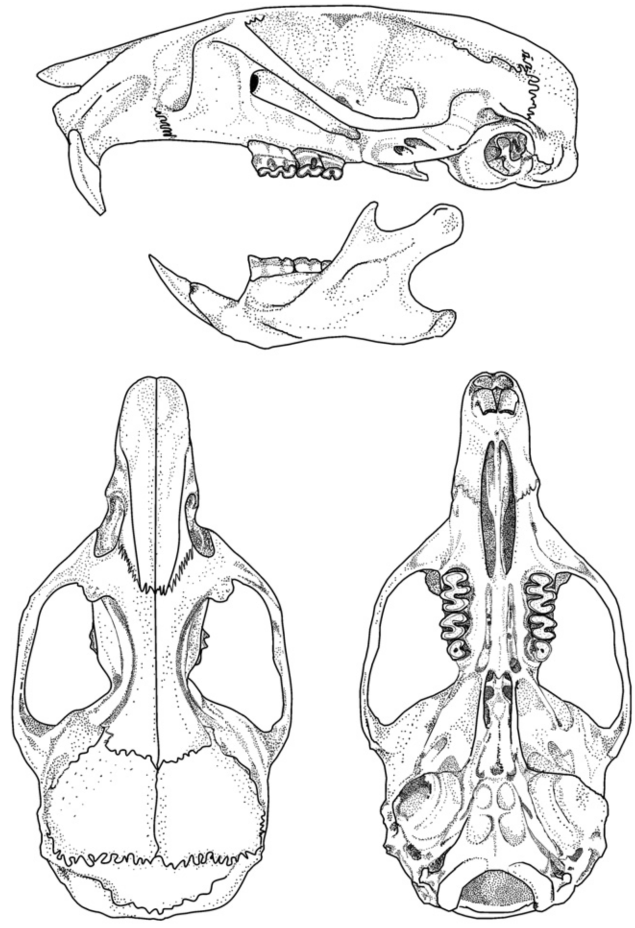

Fig. 4. Lateral, dorsal, and ventral views of the skull of the Type of *Phyllotis alisosiensis* (CML 7542); Scale = 10 mm. Drawing by R. M. Barquez, made with camera lucida.

Ears are dark, averaging 22.44 mm, scarcely haired externally except for a small but conspicuous patch on the anterior edge. Internally the ears are covered with dark brown hairs at the mid-ventral part and at the dorsal edge. An inconspicuous grayish post-auricular patch is present in all specimens examined. The tail is strongly bicolored, dark gray dorsally and whitish ventrally; about the same size as head and body and without a terminal brush. Manus and pes are entirely covered by short but dense white hairs on their dorsal surface up to the wrist and ankle respectively, with a tuft of hairs covering each claw. The most ventral mystacial vibrissae are short and white, while the dorsals are longer, black basally and white distally.

The skull (Fig. 4) is robust and wide, with a large rostrum. The nasals are large and surpass the anterior border of the incisors; posteriorly they are rounded and terminate slightly behind the fronto-maxillary suture.

Interorbital constriction is narrow (never more that 3.6 mm), with smooth but well marked edges. Fronto-parietal suture is nearly straight, not crescent or angular shaped as in the other species; parietal bones are slightly projected anteriorly, as acute wedges, in the posterior border of the frontals. Interparietal bone well developed.

The incisive foramina are long and narrow, surpassing posteriorly the anterior plane of the first molars, but never reach the anteroflexus; the palate is long and extended behind the M3; the posterior median border of palate triangular shaped, with a well developed median spinous process. Mesopterygoid fossae long and wide, with their margins running almost parallel. Posteropalatal pits large, well developed and located near the anterior border of the parapterygoid fossae, and at the sides of the antero-lateral margins of the mesopterygoid fossae. Tympanic bullae quite rounded, moderately inflated; their anteroposterior length without tubes, approximately equal to the alveolar length of molar row. Eustachian tubes are short. Zygomatic plate is wide in lateral view, equal to or wider than the interorbital constriction. Its anterior border is slightly concave, almost vertical, with the upper corner rounded. Upper incisors opisthodont with the anterior enamel yellow in all specimens examined, except in one old specimen in which it is whitish (CML 7550).

Upper and lower molars are hypsodont, wide and have a simplified pattern. The M1 has a trilophodont pattern, with the major cusps alternate; the lingual cusps slightly anterior to the labial cusps. The labial flexus is oblique and the lingual flexus are transverse to the medial plane of the molar. The procingulum is well developed, wide and without anteromedian flexus. The M2 is "S" or "Z" shaped with the hypoflexus anteriorly oriented and the metaflexus transverse. The M3 has a deep hypoflexus that surpasses the medial plane of the molar. The lower incisors are yellowish but paler than the upper ones. One old individual (CML 7550) has whitish lower incisors. The m1 is trilophodont; only one young individual (CML 4106) has anteromedian fossetid and a small posteroflexid. The m2 has a bilophodont pattern in the adult specimens. The young specimen (CML 4106) has a small protoflexid, reduced to a notch, and a posteroflexid also small but somewhat larger than the protoflexid. The m3 is bilophodont with the hypoflexid more developed than the metaflexid.

Measurements—see Table 1

Phenetic analysis.–The PCA revealed a strong effect of size in the ordination diagram (Fig. 5). The first

Table 1. External and cranial measurements (in mm; weight in grams) of the type, paratype, and three additional adult specimens of *Phyllotis alisosiensis* (see text).

CHARACTER	CML 7542 Holotype	CML 7543 Paratype	CML 7544	CML 7547	CML 7550
Total length	274	250	259	-	276
Tail	139	126	130	-	132
Hind foot	30	29	31	-	30
Ear	24	21	23	-	24
Weight	59	49	60	-	70
Condyloincisive length	30.5	29.3	29.4	31.1	32.5
Zygomatic breadth	16.9	16.6	16.5	17.3	18.8
Braincase breadth	14.0	14.2	14.5	14.1	15.0
Interorbital constriction	3.2	3.4	3.6	3.3	3.2
Rostral length	13.0	12.5	12.1	13.4	13.2
Nasal length	13.6	13.2	13.2	14.5	14.5
Rostral width	5.5	5.3	5.5	5.7	6.0
Mid-rostral width	4.6	4.4	4.6	4.6	5.0
Orbital length	11.2	11.9	11.1	11.9	12.4
Diastema length	9.0	8.3	8.3	9.4	9.8
Maxillary toothrow length	5.9	5.9	6.1	5.8	6.1
Incisive foramen length	7.6	7.1	6.7	7.4	8.2
Alveolar width	6.8	6.7	6.8	6.7	7.0
Occipital condyle width	7.1	7.3	7.2	–	7.3
Mastoid breadth	13.7	13.8	13.6	–	14.4
Basioccipital length	4.9	4.6	4.6	–	5.7
Mesopterygoid fossa length	5.0	5.0	4.7	5.5	–
Mesopterygoid fossa width	1.7	1.6	1.6	1.7	2.0
Width of zygomatic plate	3.7	3.4	3.6	3.5	4.1
Cranial depth	11.8	11.5	11.6	11.9	12.3

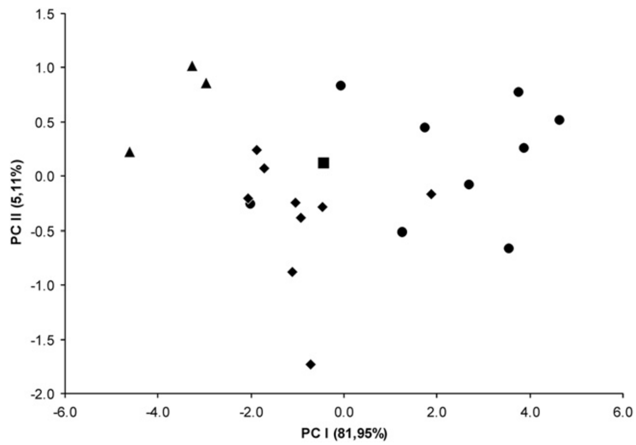

Fig. 5. Specimens scores for principal components I and II extracted from a variance covariance matrix of the 20 cranial measurements. Triangles: *Phyllotis alisosiensis*; diamonds: *Phyllotis osilae*; solid circles: *Phyllotis xanthopygus*, and square: *Phyllotis anitae* (holotype).

component account for 81.95% for total variance and the second component just for 5.11% of total variance. All individuals of *Phyllotis alisoensis* are located on the negative side of the first axis, and on the positive side of the second axis, well separated from all others species of the genus. All variables are correlated with the first principal component (Table 2).

Phylogenetic analysis.–Our phylogenetic reconstructions resembles to that presented by Steppan et al. (2007). In MP analysis we obtained two MP trees (length 1544, CI 0.431, RI 0.725). The results of MP and BI are presented in Fig. 6. The new species is a member of a well supported clade (76 JK and 1.00 PP) (the "*osilae* group" *sensu* Steppan et al. 2007), that includes ((*P. anitae* + *P. alisosiensis)* *P. osilae*) (Fig. 6). The mean genetic K2P distance between *Phyllotis alisoensis* and *P. anitae* is relatively low, 1.47%, whereas with *P. osilae* the distance takes values near to 12%. With the other members of the genus the genetic distances exceed the 15% of divergence. However, both the MP and the BI, analysis showed high node supports for the new species (97 JK and 0.94 PP). *P. alisoensis* is closely related to *P. anitae* and these two species are in turn sister to *P. osilae.*

Comparisons (Figs. 7, 8; Table 3).–Some species of *Phyllotis* have buff or ochraceous ventral tones, sometimes with a pectoral streak or spots. Hershkovitz (1962) mentioned two specimens from Sierra de Zenta (See Díaz and Barquez 2007, for the actual location of this area) of what he called *Phyllotis darwini caprinus*, with an old pelage "cinnamon phase" *rupestris*". However, the specimens indicated by Hershkovitz have a whitish venter with only small spots of ochre, which is far from being cinnamon (a photo of the FMNH 85849 was kindly sent by Dr. Bruce Patterson). No other mention of the cinnamon color as a strong character for a species of *Phyllotis* was made by any author. In *Phyllotis alisosiensis* the most remarkable character that externally allows differentiating it from all other species in the genus is the strong cinnamon ventral coloration. Also a combination of characters such as the large body size, long hairs and fluffy fur distinguish it from all other species of the genus. *Phyllotis anitae* is externally the most similar, so the comparisons with this species are more detailed. Also, comparisons indicate the differences with sympatric species or with those cited from nearby places in the province of Tucumán, and in other provinces of Argentina. Jayat et al. (2007) already presented the differences between *P. anitae* and the species known at that time. Now with the finding of a new species that is genetically and morphologically very close to, and that also lives in areas geographically proximate to *P. anitae*, it is necessary to establish first which characters diagnose and separate *P. alisosiensis*. The new species has larger and denser fur than *P. anitae*, with the average length of the dorsal hairs 16-17 mm as opposed to 9 mm in *anitae*; these are clearly banded with a short pure white basal band, followed by a broad plumbeous medial band and terminating in shorter and clear bands, brownish or sometimes cinnamon, while in *P. anitae* the dorsal hairs are totally dark gray to black, with ochraceous tips.

Table 2. Factor-variable correlations, based on covariances of cranial measurements among four species of *Phyllotis*. See method for the variables abbreviation.

Variables	*Eigenvector*		
	PC I	PC II	PC III
CIL	-0,641709	-0,067395	-0,279081
ZB	-0,341844	0,098522	0,191810
BB	-0,117886	0,386814	-0,113334
IOC	0,100063	0,003889	0,053129
RL	-0,326399	0,030905	-0,234586
NL	-0,282290	-0,269954	0,275267
RW	-0,148067	-0,046496	0,009393
RW2	-0,122399	-0,091208	0,041980
OL	-0,247739	0,301228	0,560526
DL	-0,258633	-0,302215	-0,240007
MTRL	-0,075770	0,272750	0,128789
IFL	-0,143479	-0,186903	-0,184516
AW	-0,109486	0,151054	0,149725
OCW	-0,042527	0,250825	-0,176433
MB	-0,056812	0,549239	-0,266492
BOL	-0,034812	0,223539	-0,089205
MFL	-0,159078	-0,020824	0,388883
MFW	-0,035160	0,040401	-0,094315
ZP	-0,086359	0,095804	-0,041085
CD	-0,132233	-0,108600	0,142276
Eigenvalue	6,53	0,41	0,22
Variance (%)	81,95	5,11	2,76

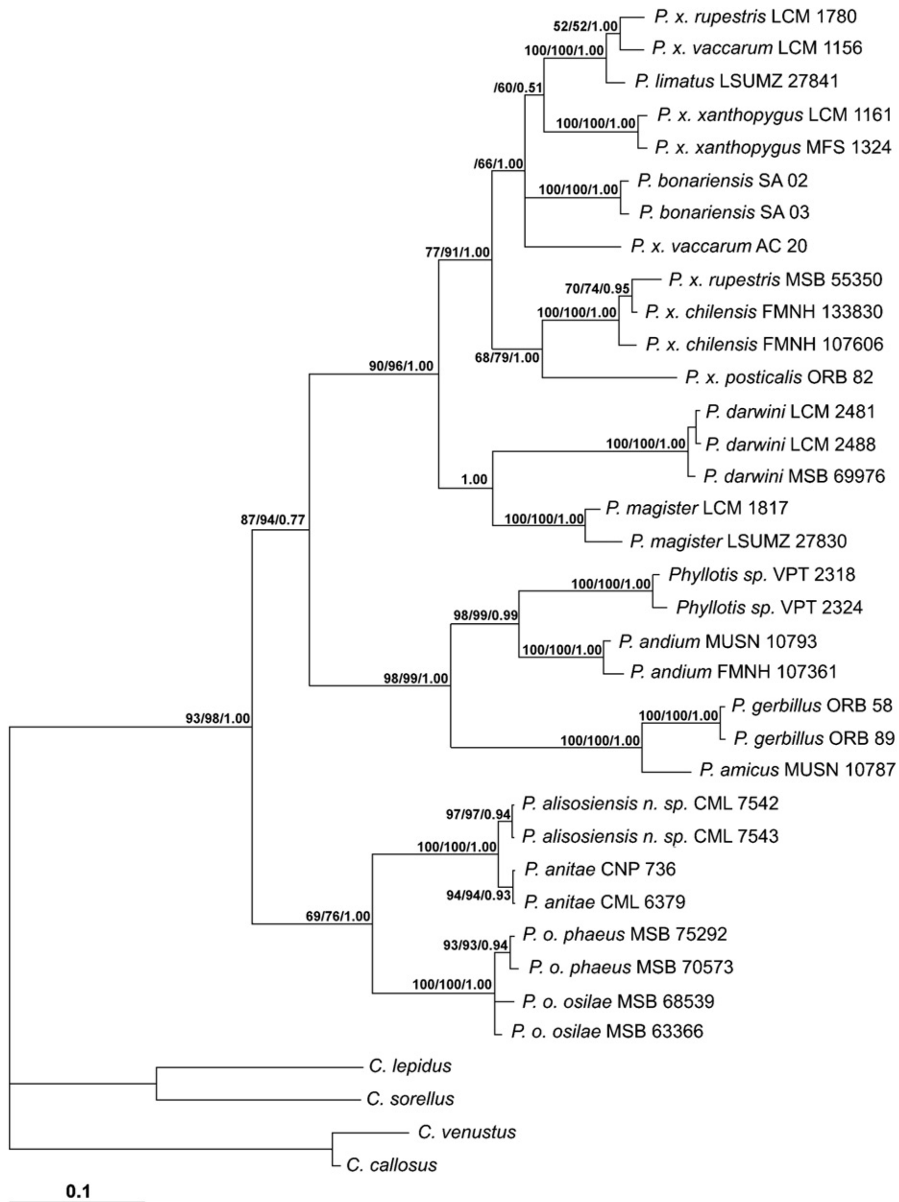

Fig. 6. Bayesian 50% majority rule consensus tree. Numbers in nodes are Bootstrap and Jackknife supports (1000 replicates) for MP analysis and Bayesian posterior probability. In each terminal specimen identification is given: CML, Colección Mamíferos Lillo, Universidad Nacional de Tucumán; CNP, Colección de Mamíferos del Centro Nacional Patagónico, CONICET; FMNH, Field Museum of Natural History; LCM, Laboratorio de Citogenética de Mamíferos, Universidad de Chile; LSUMZ, Louisiana State University, Museum of Zoology; MFS, collection of Margaret F. Smith; MSB, Museum of Southwestern Biology, University of New Mexico; MUSN, Museo de Historia Natural, Universidad Nacional Mayor de San Marcos; ORB, collection of Oswaldo Ramirez-Baca; SA, AC, collections of U. F. J. Pardiñas and VPT, collection of Victor Pacheco-Torres.

The ventral coloration is strong cinnamon sometimes brushed with reddish tones in *alisosiensis*, while it is pale ochraceous in *anitae*. Both species are dark dorsally but while *P. alisosiensis* is cinnamon brown with a tinge of olive, *P. anitae* is darker and gray. The manus are dorsally covered with white hairs reaching the wrists in *P. alisosiensis*, while the proximal dorsum of the manus is dark in *P. anitae,* with only the digits white. Both manus and pes are covered by entirely white hairs in *P. alisosiensis*; but in *P. anitae* are covered with bicolored hairs with dark bases and clear tips.

In *P. alisosiensis* the tail is sharply bicolored, and hairy to a level that the scales cannot be seen with the naked eye; in *P. anitae* the tail is slightly bicolored and moderately hairless so the scales are readily visible to the naked eye. Hairs of the ventral side of the tail are pure white in *P. alisosiensis* while they are bicolor (dark bases and clear tips) in *anitae. P. alisosiensis* is larger than

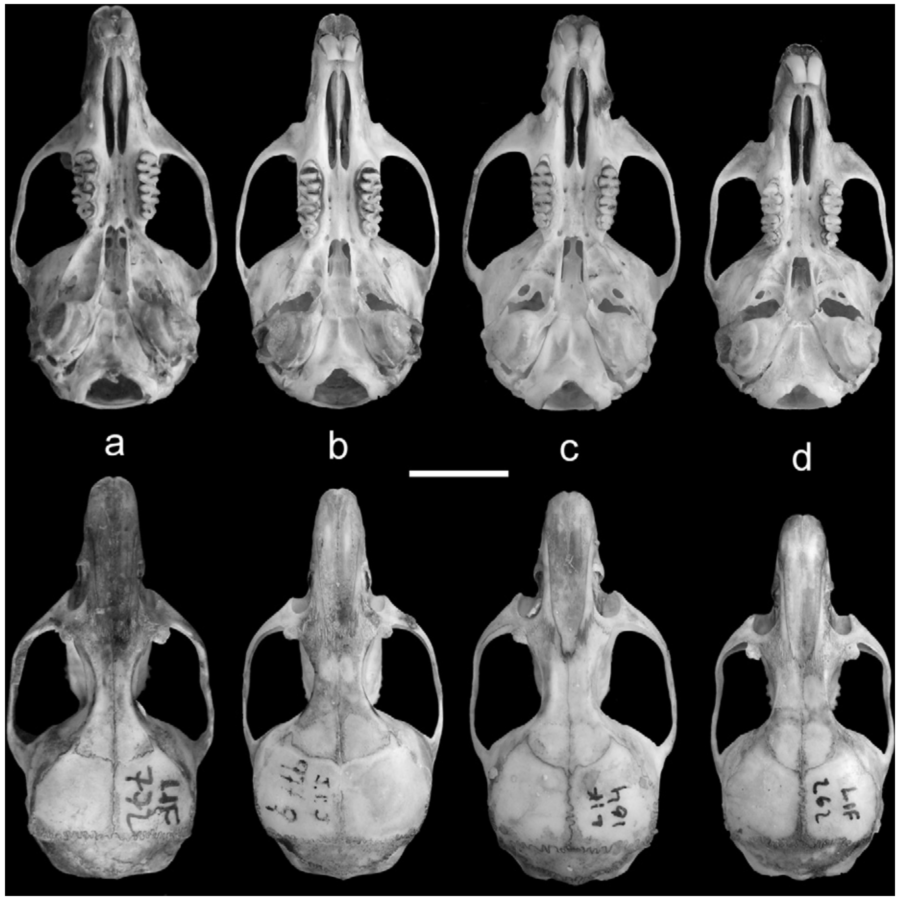

Fig. 7. Ventral and dorsal skull views of: a) *Phyllotis alisosiensis* (CML 7542), b) *Phyllotis anitae* (CML 6379), c) *Phyllotis osilae* (LIF 164) and d) *Phyllotis xanthopygus* (LIF 262). Scale = 10 mm.

P. anitae in almost all body and skull measurements (Table 3).

The skull of *P. alisosiensis* is more robust and heavier than that of *P. anitae* when individuals of the same age are compared. The interorbital constriction is clearly narrower, the palate and zygomatic plates are wider, and the basioccipital is longer in *alisosiensis*. The anterior border of the mesopterygoid fossa is U-shaped in *anitae*, with a small median spinous process on the palatine, while in *alisosiensis* it is lyre-shaped and the spinous process is well developed. The dental morphology also shows some distinctive features, mainly in color of the upper incisors. The anterior enamel of upper incisors of *P. alisosiensis* is notably yellow while in *P. anitae* is whitish in young individuals and whitish yellow in the holotype. The M2 of *P. anitae* has a small procingulum and an anteroflexus reduced with tooth wear that was not seen in specimens of *P. alisosiensis* of the same age.

Compared with the other two species of *Phyllotis* that are close geographically, *P. alisosiensis* is clearly distinguishable by its color pattern: *P. osilae* and *P. xanthopygus*, as well as most of the known *Phyllotis,* have paler bellies, whitish or grayish, sometimes with ochraceous streaks in the chest. *P. alisosiensis* has no traces of white on the venter, which is uniformly cinnamon. The skull of *P. alisosiensis* is easily distinguishable from that of both *P. osilae* and *P. xanthopygus* because of its extremely narrow interorbital constriction and by the presence of a spinous process at the anterior margin of the mesopterygoid fossa, among several other characters.

Discussion

The discovery of new species of mammals in northern Argentina has occurred frequently during the last several years (Braun and Mares 1995, 2002; Mares and Braun 1996, 2000; Díaz et al. 1999; Braun et al. 2000; Mares et al. 2000, 2008; Jayat et al. 2007, 2008). This phenomenon is contrary to what might be expected because the mammals of the area have been intensively surveyed for over 40 years, particularly in lowland forests and vegetation below 2000 meters of altitude. These surveys were almost always related to road infrastructure that made the sampling sites relatively

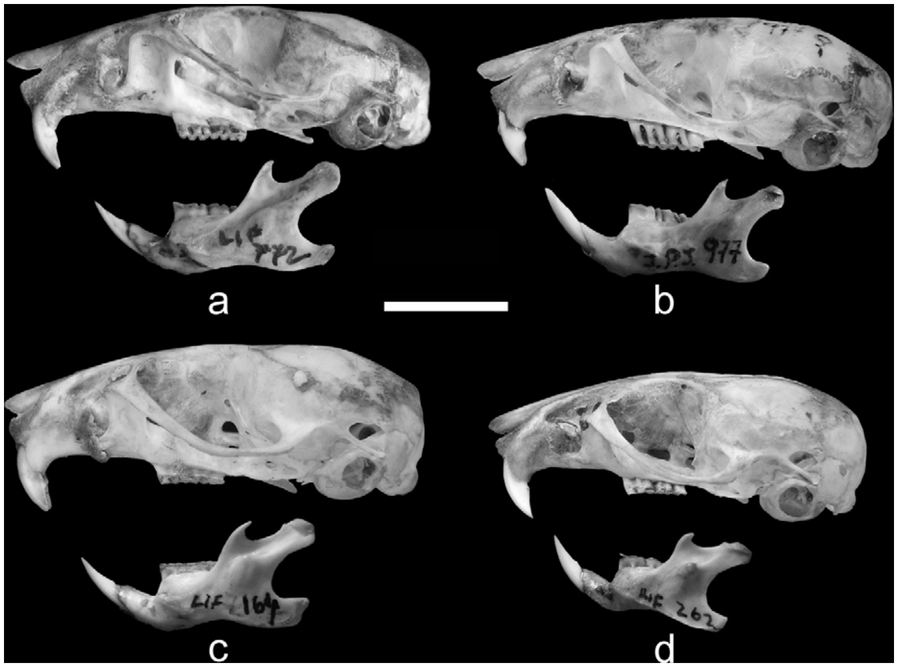

Fig. 8. Lateral views of the skulls and mandibles of the specimens shown in Fig. 3: a) *Phyllotis alisosiensis*, b) *Phyllotis anitae*, c) *Phyllotis osilae*, and d) *Phyllotis xanthopygus*. Scale = 10 mm.

accessible but also with more anthropic impact. However, the majority of the discovered species were found in relatively isolated sites far from towns. For example, the description in 1978 of a new genus and species of rodent (*Andalgalomys olrogi*) from an isolated area of the Monte Desert of Catamarca province (Williams and Mares 1978), a place close to the salt flats, where 22 years later another new genus and species of rodent was found (Mares et al. 2000). Also noteworthy is the collection of *Akodon aliquantulus* (Díaz et al. 1999) from isolated grasslands in Tucumán province, and the recent description of a new *Phyllotis* from the same province (Jayat et al. 2007), but from the alder forests. Beyond the description of new species to science the addition of species to Argentina has also been notable: these are the cases of *Tapecomys primus*, a new genus and species described from Bolivia and recently added to Argentina (Barquez et al., 2006), or the discovery of a new marsupial, *Cryptonanus ignitus*, through a specimen deposited in a museum 40 years before its description (Díaz et al. 2002).

During the last 50 years the description of new species of *Phyllotis* has not been as frequent as in other genera of rodents (e.g. *Akodon*, *Thomasomys*). However this tendency is being reversed with the recent increase in exploration of previously inaccessible areas in the high Andean and Patagonian regions, where the species of this genus mainly inhabit.

The new species is closely related to the recently described *P. anitae*. Both are sister species, inhabit the Upper Montane Forests of adjacent mountains of the southern Yungas in northwestern Argentina, and have a low genetic divergence at sequences of the gene coding for cytochrome *b*. This low level for cyt *b* gene divergence could be interpreted as a signal of co-specificity, but it does not necessarily imply that speciation process is incomplete (see Bradley and Baker 2001). In fact the two species are clearly distinguishable by fixed differences despite geographic, sex or ontogenetic variations. Based on these constant morphological characters as well as in the reciprocal monophyly of the two species, we decided to apply a new name to our specimens.

The two localities where the specimens of *P. alisosiensis* were captured are part of the Upper Montane Forest and range from 1200 up to 2200 m altitude. At the type locality the vegetation includes alder trees (*Alnus acuminata*) intermixed with ‘‘mountain bamboo’’, or ‘‘colihue’’ (Genus C*husquea*), ferns (*Blechnum occidentalis*), small forests of queñoa (*Polylepis australis*) and grasslands of ‘‘cortadera’’ (*Cortaderia* spp.) and ‘‘sauco’’ (*Sambucus peruviana*). At the type locality, *P. alisosiensis* co-exists with seven other species of sigmodontine rodents: *Abrothrix illuteus*, *Akodon spegazzinii*, *Andinomys edax*, *Oligoryzomys destructor*, *O. flavescens*, *Oxymycterus* sp. and *Phyllotis osilae.*

The two known localities for the actual distribution of *P. alisosiensis* are in protected areas. The type locality, as mentioned above, is within a National Park of Argentina, while the other locality is at ‘‘Reserva Provincial Los Sosa’’ (Chebez 2005), where the vegetation is mainly Myrtaceous forests, which is part of the

Table 3. Measurements of the four species of *Phyllotis* cited for Tucumán province (*P. alisosiensis*, *P. anitae*, *P. osilae* and *P. xanthopygus*). Mean ± Standard deviation, range and sample size (in parenthesis) are given for each measurement.

	P. alisosiensis	*P. anitae*	*P. osilae*	*P. xanthopygus*
Total length	271.75 ± 30.62 243-342 (8)	202.33 ± 35.73 176-243 (3)	235.77 ± 27.31 45-303 (103)	217.29 ± 31.68 103-274 (187)
Tail	130.88 ± 5.57 121-139 (8)	102.33 ± 18.93 89-124 (3)	120.64 ± 17.75 70-210 (103)	110.81 ± 16.34 73-190 (183)
Hind foot	29.89 ± 1.05 29-32 (9)	29.20 ± 1.30 27-30 (5)	26.23 ± 2.30 20-30 (97)	25.19 ± 2.75 17-31 (190)
Ear	22.44 ± 1.33 20-24 (9)	19.80 ± 1.3 18-21 (5)	21.60 ± 2.20 15-27 (107)	23.89 ± 2.76 18-32.5 (177)
Weight	56.17 ± 11.62 35-70 (9)	26. 50 ± 6.96 20.5-37.5 (5)	46.98 ± 12.56 21-86 (74)	42.94 ± 15.23 18-86 (97)
Condyloincisive length	29.98 ± 1.84 27.1-32.5 (6)	25.26 ± 1.59 23.3-27.6 (5)	28.06 ± 1.92 23.6-30.7 (16)	26.19 ± 1.54 24.3-29.0 (9)
Zygomatic breadth	16.82 ± 1.3 14.8-18.8 (6)	14.58 ± 0.72 14.0-15.8 (5)	16.10 ± 0.88 14.1-17.4 (16)	14.84 ± 0.79 13.9-16.2 (9)
Braincase breadth	14.23 ± 0.48 13.6-15.0 (6)	13.60 ± 0.29 13.3-14.0 (5)	13.54 ± 0.33 13.0-14.1 (16)	13.36 ± 0.38 13.0-14.2 (9)
Interorbital constriction	3.38 ± 0.18 3.2-3.6 (6)	3.98 ± 0.08 3.9-4.1 (5)	3.91 ± 0.17 3.8-4.2 (16)	4.23 ± 0.19 4.0-4.6 (9)
Rostral length	12.84 ± 0.53 12.1-13.4 (5)	11.80 - (1)	11.25 ± 0.95 8.9-12.6 (15)	10.56 ± 0.72 9.4-11.8 (9)
Nasal length	13.80 ± 0.66 13.2-14.5 (5)	10.66 ± 1.18 9.4-12.5 (5)	12.83 ± 1.12 10.3-14.4 (15)	11.71 ± 0.55 11.2-13.0 (9)
Rostral width	5.60 ± 0.26 5.3-6.0 (5)	5.00 - (1)	5.29 ± 0.42 4.5-5.9 (16)	4.64 ± 0.40 4.2-5.3 (9)
Mid-rostral width	5.57 ± 0.27 4.2-5.0 (6)	4.44 ± 0.15 4.3-4.6 (5)	4.38 ± 0.28 3.8-4.8 (16)	3.93 ± 0.44 3.0-4.5 (9)
Orbital length	11.65 ± 0.50 11.1-12.4 (6)	10.30 - (1)	10.38 ± 0.78 9.1-11.8 (16)	9.77 ± 0.50 9.0-10.5 (9)
Diastema length	8.70 ± 0.87 7.4-9.8 (6)	6.72 ± 0.68 6.1-7.8 (5)	7.83 ± 0.68 6.4-8.6 (16)	7.09 ± 0.68 6.0-8.4 (9)
Maxillary toothrow length	5.92 ± 0.16 5.7-6.1 (6)	5.80 ± 0.10 5.7-5.9 (5)	5.41 ± 0.27 5.0-5.9 (16)	5.36 ± 0.23 4.9-5.6 (9)
Incisive foramen length	7.25 ± 0.62 6.5-8.2 (6)	6.36 ± 0.50 5.9-7.1 (5)	6.93 ± 0.60 5.6-7.7 (16)	6.47 ± 0.35 6.0-7.0 (9)
Alveolar width	6.73 ± 0.20 6.4-7.0 (6)	6.40 - (1)	6.15 ± 0.24 5.7-6.5 (16)	5.91 ± 0.28 5.5-6.4 (9)
Occipital condyle width	7.18 ± 0.13 7.0-7.3	6.94 ± 0.15 6.7-7.1	6.83 ± 0.25 6.2-7.2	6.76 ± 0.21 6.5-7.0

Table 3. (*continued*)

	P. alisosiensis	*P. anitae*	*P. osilae*	*P. xanthopygus*
	(5)	(5)	(16)	(9)
Mastoid breadth	13.88 ± 0.36	13.0	12.81 ± 0.39	13.07 ± 0.41
	13.6-14.4	-	11.9-13.4	12.5-13.6
	(4)	(1)	(16)	(9)
Basioccipital length	4.84 ± 0.51	3.58 ± 0.24	4.31 ± 0.52	4.32 ± 0.14
	4.4-5.7	3.3-3.9	3.3-5.2	4.1-4.6
	(5)	(5)	(16)	(9)
Mesopterygoid fossa length	5.05 ± 0.33	4.5	4.64 ± 0.42	3.86 ± 0.33
	4.7-5.5	-	3.8-5.4	3.6-4.7
	(4)	(1)	(16)	(9)
Mesopterygoid fossa width	1.73 ± 0.15	1.52 ± 0.08	1.53 ± 0.18	1.47 ± 0.17
	1.6-2.0	1.4-1.6	1.2-1.8	1.3-1.8
	(6)	(5)	(16)	(9)
Width of zygomatic plate	3.58 ± 0.31	2.44 ± 0.29	3.34 ± 0.46	2.98 ± 0.20
	3.2-4.1	2.1-2.8	2.6-4.6	2.6-3.3
	(6)	(5)	(16)	(9)
Cranial depth	11.82 ± 0.31	10.90	11.58 ± 0.42	10.94 ± 0.42
	11.5-12.3	-	10.6-12.4	10.4-11.7
	(5)	(1)	(16)	(9)

altitudinal divisions of the yungas. Dominant trees there are "Laurel de Cerro" (*Phoebe porfiria*), "Horco Molle" (*Blefarocalix gigantea*), "Mato" (*Eugenia mato*) and the "Arrayan" (*Eugenia uniflota*). There, the alders are restricted to the borders of the rivers that cross all along the reserve. At Los Sosa, *P. alisosiensis* co-exists with six sigmodontine rodents: *Abrothrix illuteus, Akodon spegazzinii, A. lutescens, Andinomys edax, Oligoryzomys destructor* and *O. flavescens.* Only one species of *Phyllotis* (*P. osilae*) is sympatric with the new species throughout its distributional range. The facts that *Phyllotis anitae* and *P. alisosiensis* are allopatric sister species, closely related in morphological and genetic characters, and that their distributional ranges are associated with montane environments in two adjacent mountain chains, suggest the possibility that a process of geographic speciation has happened relatively recently, probably as a consequence of a vicariance event in mountain habitats during the last glacial period. Both species are, in turn, a sister group of *P. osilae* and represent a group of species with common evolutionary origins within the frame of the phylogenetic relationships of the genus (see Steppan 1998).

Acknowledgements

We greatly appreciate the help of the personnel of Parque Nacional Los Alisos, especially to Daniel Vega, who facilitate basic and logistic support for the field expeditions. Also thanks to Felipe Nieva and Juan Santillán. The research was conducted with permission from National Parks Administration of Argentina. Thanks to Noemí Gardenal for infraestructural support. Funds were facilitated by the CONICET (Consejo Nacional de Investigaciones de Argentina) and by the Agencia Nacional de Promoción Científica y Tecnológica de Argentina. We appreciate the kindness of Bruce Patterson for sending us a photograph of a specimen from the collections of the Field Museum. Mónica Díaz, Marcos Mirande and Norberto Giannini helped in the discussion of several topics of this investigation. David Flores, Valentina Segura, Maria Sandoval, and Ana López, has helped in some of the field trips. We thank William W. Lamar who helped us extensively by reading early versions of the manuscript and improving the English.

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