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The *Akodon boliviensis* species group (Rodentia: Cricetidae: Sigmodontinae) in Argentina: species limits and distribution, with the description of a new entity

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ABSTRACT

Akodon, with about 42 living species, is the most diverse genus of the subfamily Sigmodontinae. The *Akodon boliviensis* species group includes small-bodied, morphologically similar forms inhabiting Altiplano grasslands and grassland/forest ecotones of the eastern slope of the Andes, from central Peru to central Argentina. Northwestern Argentina contains the largest diversity of species of the group; the taxonomic treatment of these species has been based largely on unsupported and some weakly based opinions as underscored by recurrent changes. Based on morphologic and molecular data we assessed species limits among Argentinean populations of the *Akodon boliviensis* species group. We conclude that four species of the *A. boliviensis* species group inhabit northwestern Argentina. These are: *A. boliviensis*; *A. caenosus* (under which we synonymyze *A. aliquantulus*); *A. spegazzinii* (of which the nominal forms *alterus*, *leucolimnaeus*, and *tucumanensis* are junior synonyms); and *A. sylvanus*. Additionally, we described here a new species of the *A. boliviensis* species group, *Akodon polopi*, which inhabits central Argentina. This is the only species of the *A. boliviensis* species group inhabiting the Sierras Grandes range (ca. 2000 m), mountain system of medium height, isolated (ca., 600 km) from the main Andean chain by low elevation arid and semiarid environments. Additionally, our phylogenetic analyses suggests that the *Akodon varius* species group is polyphyletic.

Key words: *Akodon boliviensis*, *Akodon caenosus*, *Akodon polopi* n. sp., *Akodon spegazzinii*, *Akodon sylvanus*, *Akodon varius*, Akodontini, new species, Argentina, Pampa de Achala, taxonomy

INTRODUCTION

As currently understood, *Akodon* Meyen is the most diverse sigmodontine genus with ca. 42 living forms recognized at the species level. The taxonomic and nomenclatorial complexity of *Akodon* is now widely recognized (Myers 1989; Myers *et al.* 1990; Pardiñas *et al.* 2005, 2006; Patton & Smith 1992; Reig 1987; Smith & Patton 2007). Although recent contributions (e.g., Braun *et al.* 2000; 2008; Christoff *et al.* 2000; Geise *et al.* 1998, 2001; Hershkovitz 1998; Jayat *et al.* 2007a; Myers 1989; Myers & Patton 1989a; Myers *et al.* 1990;

Pardiñas *et al.* 2003, 2005; Smith & Patton 2007) have greatly improved our understanding of *Akodon* diversity, several issues remain unresolved. The dubious biological status of several nominal forms, the poorly known geographic distribution of most species, and an almost complete lack of information about their biology (with few exceptions, e.g., *A. azarae* Fischer [Bilenca & Krávetz 1998; Priotto & Steinmann 1999; Busch *et al.* 2001; Andreo *et al.* 2009], *A. dolores* Thomas [Martinez *et al.* 1990; Piantanida & Barrantes 1998; Castellarini *et al.* 2003]) constitute the main areas where research is needed. Thus, the description of several new species in the last two decades (Braun *et al.* 2000; Christoff *et al.* 2000; Díaz *et al.* 1999; Gonzalez *et al.* 1998; Hershkovitz 1990, 1998; Myers & Patton 1989a,b; Myers *et al.* 1990; Pardiñas *et al.* 2005) and the regular extensions of the known range for many others (e.g. Anderson 1997; Emmons 1997; Jayat *et al.* 2006, 2007a; Salazar-Bravo *et al.* 2002) illustrate the fragmentary status of our knowledge about this genus.

Based on phenetic and phylogenetic analyses, most species of *Akodon* have been grouped into species groups (e.g., Smith & Patton 2007 and references therein). The one including the type species of the genus is the *A. boliviensis* species group, originally characterized on morphologic grounds by Myers *et al.* (1990). This group includes small-bodied, closely related, morphologically similar forms inhabiting Altiplano grasslands and grassland/forest ecotones of the eastern slope of the Andes, from central Peru to northwestern Argentina (i.e., according to Myers *et al.* [1990] *A. boliviensis*, *A. juninensis*, *A. puer* [including *caenosus* and *lutescens* as subspecies], *Akodon subfuscus* [including *arequipae* as subspecies]). This definition of the *Akodon boliviensis* group—which we embrace—is qualitatively different from that coined by Hershkovitz (1990) who disregarded phylogenetic relationships and grouped taxa according to body size (see Smith & Patton 2007).

Northwestern Argentina, a physiographically complex region, contains the largest diversity of species of the *A. boliviensis* group, currently including *A. aliquantulus* Díaz, Barquez, Braun & Mares, *A. boliviensis* Meyen, *A. lutescens* J. A. Allen, *A. leucolimnaeus* Cabrera, *A. spegazzinii* Thomas, and *A. sylvanus* Thomas (Pardiñas *et al.* 2006; Jayat *et al.* 2006). The taxonomic treatment of these species in the region has been based on some unsupported opinions and recurrent changes, facts that are reflected in a complex taxonomic history and a provisional treatment of some nominal forms. Adding to the importance of the region towards the understanding of the *Akodon boliviensis* group is that a number of nominal forms associated with it have their type localities in northwestern Argentina (*Akodon aliquantulus*, *A. alterus* Thomas, *A. puer caenosus* Thomas, *A. leucolimnaeus*, *A. spegazzinii*, *A. sylvanus* and *A. tucumanensis* J. A. Allen [Galliari *et al.* 1996, Jayat *et al.* 2007a, Myers *et al.* 1990, Smith & Patton 2007, Pardiñas *et al.* 2007]).

The objectives of this work are two-fold. First, we conduct a phylogenetic analysis of cytochrome *b* gene sequences to further test the monophyly of the *A. boliviensis* species group with the most comprehensive taxonomic and geographic sampling available to date. Second, we examine detailed patterns of morphological and morphometric variation in the lineages identified in the phylogenetic analyses. Our emphasis is on populations inhabiting northwestern Argentina in the understanding that a previous contribution by Myers *et al.* (1990) complements this work by including populations from Peru and Bolivia. These analyses allowed us to characterize a new species from central Argentina, which we describe below.

MATERIALS AND METHODS

Studied specimens were collected by us, borrowed from museum collections, or recovered from owl pellets (Appendix I). Trapped individuals were measured, weighted, sexed, and prepared as skin plus complete skeleton; tissue samples were preserved in alcohol (70%). Collected specimens were recorded in the personal catalogue of the authors (JPJ, PEO). Voucher specimens will be or are already deposited at Colección de Mamíferos Lillo (CML), Universidad Nacional de Tucumán, Tucumán, Argentina; Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (MACN), Buenos Aires, Argentina; Colección de la Universidad Nacional de Río Cuarto (CUNRC), Córdoba, Argentina; and Colección de Mamíferos del Centro Nacional Patagónico (CNP), Puerto Madryn, Chubut, Argentina (Appendix I). Owl pellet samples were deposited in the pellets personal collection of Pablo E. Ortiz (PEO-e). The geographic position of all the localities mentioned in the text is given in Appendix II.

Standard external measurements recorded include: TBL: total body length; TL: tail length, HF: hind foot length (including the claw), EL: ear length, and W: weight. The following skull measurements were recorded following Myers *et al.* (1990): CIL: condyloincisive length, DL: diastema length, RW2: mid rostral width, MTRL: maxillary toothrow length, IFL: incisive foramina length, ZB: zygomatic breadth, BB: braincase breadth, IOC: interorbital constriction, NL: nasal length, RL: rostral length, OCW: occipital condyle width, ZP: zygomatic plate breadth. Additionally, we recorded maximum skull length (MSL), mandibular length (ML) and mandibular toothrow length (MdTRL). Nomenclature used to describe the skull and its structures follows Voss (1988) and Wahlert (1985) and that of the molars corresponds to Reig (1977).

Genetic and phylogenetic analyses

Genetic comparisons and phylogenetic analyses were based on partial (i.e., the first 801 base pairs) cytochrome-b gene (hereafter cyt b) sequences. Our analyses were based on thirty-six sequences from representatives of seven species of the *Akodon boliviensis* group, 33 of which were acquired by us as detailed below. The ingroup was completed with representatives of each *Akodon* species not belonging to the *Akodon boliviensis* group available in Genbank. Representatives of the remaining genera of the *Akodon* division (see D'Elía 2003) were used as an outgroup. As such, the matrix analyzed included 71 sequences of *Akodon* and 4 sequences used as outgroup. Details of the specimens included in the phylogenetic analyses are presented in Appendix I and Figure 1. This sampling includes topotypes or near topotypes of *Akodon alterus*, *A. tucumanensis*, *A. spegazzinii*, *A. leucolimnaeus*, *A. sylvanus*, and *A. puer caenosus*.

Cyt b sequences acquired in this study were gathered using primers MVZ 05 and MVZ 16 as in D'Elía & Pardiñas (2004). We edited DNA sequences using SeqMan (DNASTAR 2003); new sequences were accessioned in GeneBank (GU189317-GU189349).

Sequences were aligned using the default parameter values in Clustal X (Thompson *et al.* 1997). Observed genetic distances (p) were calculated in MEGA 4 (Tamura *et al.* 2007). Phylogenetic relationships among haplotypes were inferred using maximum parsimony (MP; Farris 1982) and Bayesian analysis (BA; Ronquist & Huelsenbeck 2003). MP analyses were carried out in PAUP* (Swofford 2000) with characters treated as unordered and equally weighted, 200 replicates of heuristic searches with random addition of sequences and tree bisection reconnection (TBR) branch swapping. Relative support of the recovered clades was calculated by performing 1000 jackknifed replications (JK) with the deletion of 33 % of the characters, one random sequence addition per replicate, and MAXTREE set to 5000. Bayesian analysis was conducted using Mr.Bayes 3.1 (Ronquist & Huelsenbeck 2003), with two independent runs, each with 3 heated and 1 cold Markov chains. The model used included six categories of base substitution, a gamma-distributed rate parameter, and a proportion of invariant sites; all model parameters were estimated in MrBayes. Uniform-interval priors were assumed for all parameters except base composition and GTR parameters, which assumed a Dirichlet prior process. Runs were allowed to proceed for 3 million generations with trees sampled every 100 generations per chain. To check for convergence on a stable log-likelihood value, we plotted the log-likelihood values against generation time for each. The first 25% of the trees were discarded as burn-in and the remaining trees were used to compute a 50% majority rule consensus tree and obtain posterior probability (PP) estimates for each clade.

Molecular synapomorphies were documented by examining outputs from PAUP* and visualized using MacClade 3.05 (Maddison & Maddison 1992). Molecular transformations were optimized on the MP consensus tree. Only those changes unambiguously optimized irrespective of the kind of character transformation used (i.e., accelerated, ACCTRAN, or delayed, DELTRAN) were taken into account.

Morphological and morphometric analyses

The morphological and morphometric studies were guided by the results of the phylogenetic analyses, the genetic comparisons, and geographic distribution.

Specimens were aged based on tooth wear following the general model established by Myers (1989) for the genus *Akodon*. We conducted a one-way ANOVA (type VI) and a post hoc unequal N HSD test (Tukey honest significant difference for unequal N) to compare the statistical significance of the morphometric differences between different pairs of samples, including populations of the same species and different species. All probabilities were evaluated at $\alpha = 0.05$ for hypothesis testing. Principal components analyses (PCA) for adult (ages 3-5) and young (ages 2) individuals were carried out with exploratory aims. In order to gather more representative samples, the PCA analyses included different subset of dimensions for each age group. The principal components were extracted from the variance-covariance matrix and computed by using the variables after transformations to Log_{10} using the program PC-ORD (McCune & Mefford 1997). Additionally, we conduct discriminant analysis (DA) to test the hypothesis of differentiation between groups formed a priori. For this analysis we used the same variables and specimens as in the PCA. The specimens used for these comparisons are listed in Appendix I.

Species accounts

With the exception of the new species identified below and *Akodon spegazzinii*, the species accounts that follow include scientific name, author, synonymy, holotype, type locality, description, karyotype, variation, comparisons, distribution, habitat, natural history, and comments. Specimens identified as belonging to the new species were compared with the original descriptions of all nominal forms currently included in the *boliviensis* group, compared to the holotypes and/or topotypes of Argentinean species, and other species inhabiting central and northern Argentina. We re-describe *Akodon spegazzinii*, a species known only for the sketchy original description by Thomas (1897) and a few morphological characters mentioned in subsequent revisionary works (Myers *et al.* 1990). Karyotype information was extracted from the literature for those taxa for which we were able to verify identification of voucher specimens or we had reasons to believe the vouchers were properly identified. Patterns of geographic and non-geographic (sexual and ontogenetic) variation were included for those species with large enough sample sizes and localities. We compared the species of the *boliviensis* group against each other as well as with other species that occur in northwestern Argentina. In the Distribution section of each species account, we describe the latitudinal and altitudinal range extension for each species, emphasizing their range in northwestern Argentina; under the heading of Habitat we enumerate the environmental affinities of the species following the phytogeographic scheme of Burkart *et al.* (1999). Data about reproduction, molting pattern, and coexistence with other sigmodontine species are summarized in the Natural History section. In Comments we emphasize taxonomic issues, specimen reallocations, and highlight the relevant new data obtained for each species.

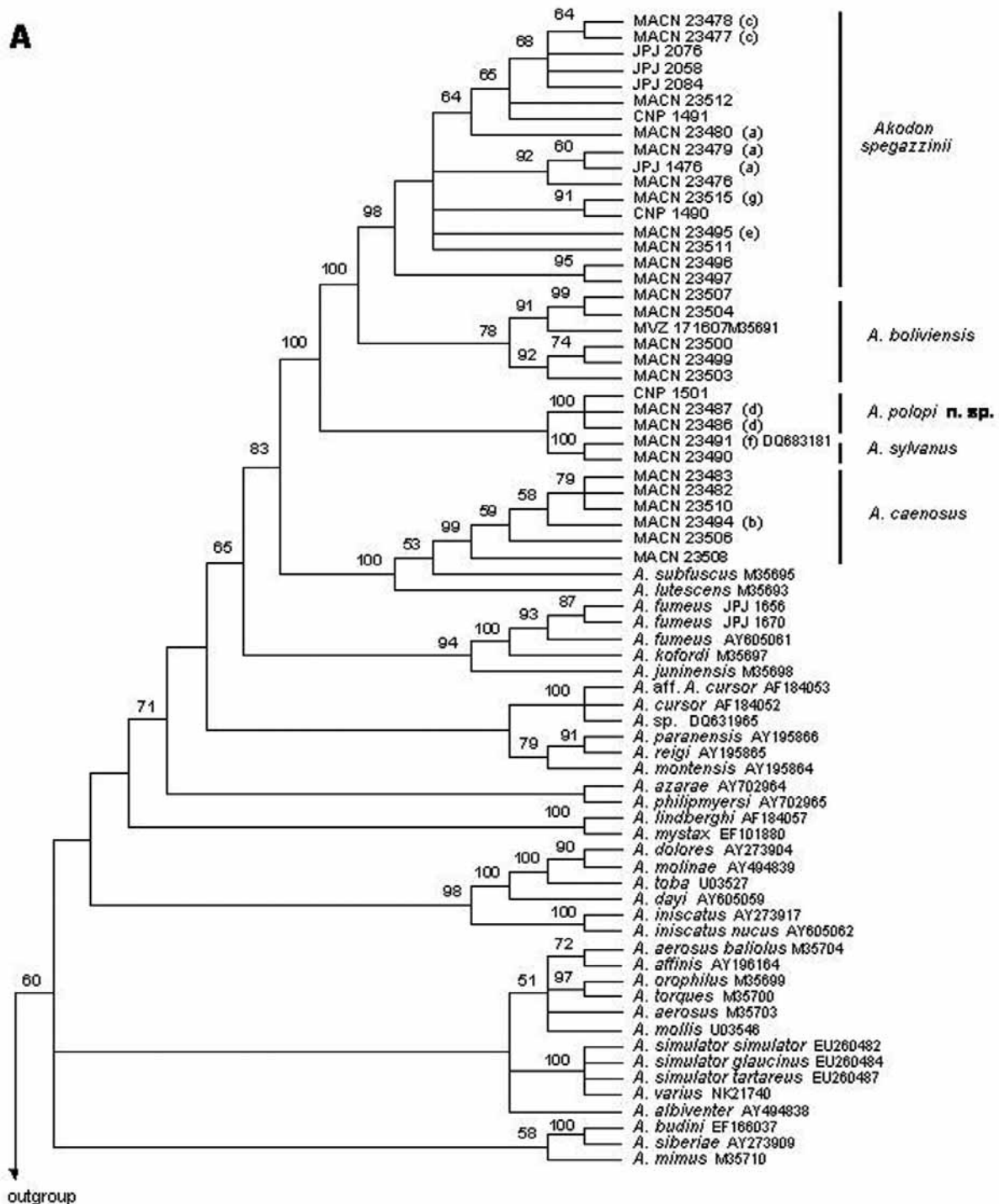
RESULTS

Phylogenetic results

MP analysis recovered 220 shortest trees, each 1563 steps long (CI=0.287; RI=0.675). The strict consensus of these trees (Fig. 1a) is well resolved; there are 9 polytomies of which 5 involve intraespecific relationships. Results of the Bayesian analysis (Fig. 1b) are congruent with those of MP; differences relate to those areas of the trees weakly supported in one or both analyses. Relationships among species of the *A. boliviensis* group are discussed in the species accounts.

As the focus of this study is the *A. boliviensis* group we neither detail nor discuss all aspect of the inferred phylogenetic trees. In general, our results are similar to those of Smith & Patton (2007) and we refer the reader to that study if interested in the relationships outside the *A. boliviensis* group. However, two issues deserve to be highlighted; first, like Smith & Patton (2007) we recovered an *Akodon* clade with low support (JK=60) in the MP analysis, or even paraphyletic with respect to *Deltamys* (or depending on where the root is

placed paraphyletic to the clade formed by *Necomys*, *Thalpomys*, and *Thaptomys*) in the BA. In some of their analysis Smith & Patton (2007) also found *Akodon* to be paraphyletic to *Deltamys*. However, in a study with much broader phylogenetic coverage of sigmodontine genera D'Elia *et al.* (2003) and in one based on both nuclear and mitochondrial DNA sequences D'Elia (2003) found *Deltamys* as sister to *Akodon*. Therefore, the nature of the discrepancy between the MP and Bayesian topologies of the present study is not clear.



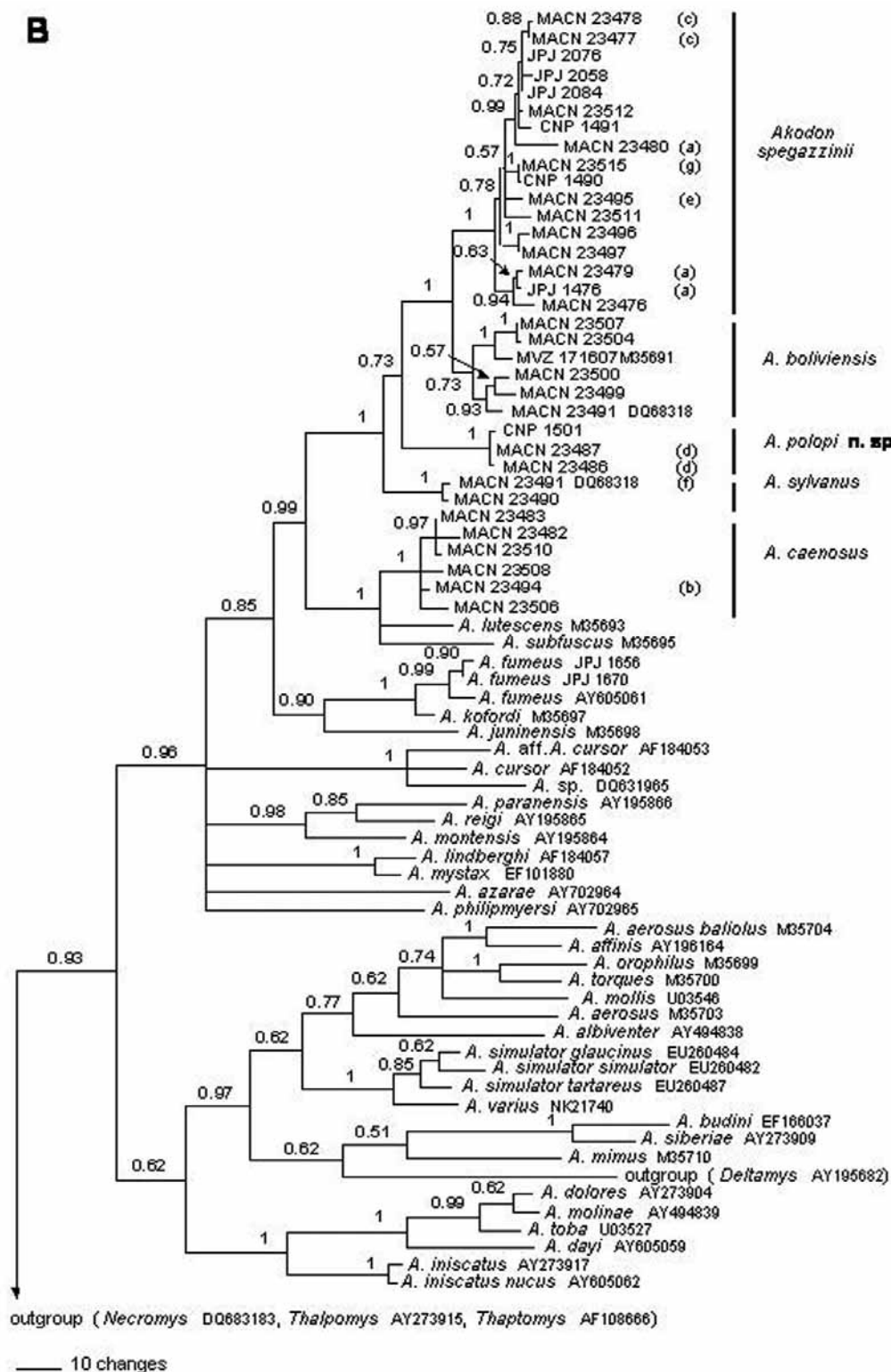


FIGURE 1. Results of the phylogenetic analyses based on the first 801 bases of the cyt b gene of 71 sequences of *Akodon*. Topotype specimens included in the analyses are marked as follows: (a) *A. alterus*; (b) *A. puer caenosus*; (c) *A. leuocolimnaeus*; (d) *A. polopi* new species (including the holotype); (e) *A. spegazzinii*; (f) *A. sylvanus*; and (g) *A. tucumanensis*. For those sequences retrieved from Genbank, accession numbers are provided next to species labels. For those sequences gathered by us, specimen collection numbers are provided next to species label; see Appendix I for locality data and Genbank accession numbers. A) Strict consensus tree of the 220 most parsimonious trees (length 1563, CI = 0.287, RI = 0.675). Numbers indicate parsimony jackknife values of the nodes at their right. Only jackknife values above 50 % are shown. B) Majority-rule consensus resulting from the Bayesian analysis. Numbers indicate posterior probability values of the nodes at their right.

A second issue in this phylogeny is that the *A. varius* species group (sensu Myers 1989; see also Braun *et al.* 2008) was never recovered monophyletic in either the MP analysis nor in the BA. The mainly Yungas inhabitants *A. simulator* Thomas and *A. varius* Thomas form a clade (JK=100; PP=1) distantly related to the one (JK=98; PP=1) formed by the mostly lowland species *A. dayi*, *A. dolores*, *A. iniscatus* (including *nucus*), *A. molinae*, and *A. toba*. Seven extra steps are needed to recover a monophyletic *A. varius* species group. The Yungas clade forms part of a large central Andean clade also composed by the *A. aerosus* species group plus *A. albiventer*. This large clade received some support in the BA (PP=0.89) but less than 50% in the MP analysis. The position of the lowland clade varies depending on the analysis (Fig. 1).

The *A. boliviensis* species group received good support in both analyses (JK=83; PP=0.99; Fig. 1); its basal dichotomy leaves to two strongly supported clades whose components do not vary between analyses. One of these two main clades (JK=100; PP=1) is composed of *A. caenosus*, *A. subfuscus*, and *A. lutescens*; in the MP analysis the former two species are sister to each other (JK=53), while in the BA relationships among the three species are unresolved. The second main clade (JK=100; PP=1) of the *A. boliviensis* species group is formed by four species whose relationships are fully resolved, although with some variation between analyses. *A. boliviensis* and *A. spegazzinii* are sister to each other in both analyses (JK=100; PP=1). In the MP analysis *A. sylvanus* forms a weakly supported clade (< 50%) with an unnamed form of *Akodon* from Córdoba, Argentina. Then, this later clade is sister to the *A. boliviensis*-*A. spegazzinii* clade. Although, in the BA the unnamed form of *Akodon* from Córdoba forms a weakly supported clade (PP=0.73) with the *A. boliviensis*-*A. spegazzinii* clade. Finally, *A. sylvanus* is sister to the ((*A. boliviensis*, *A. spegazzinii*) unnamed *Akodon* from Córdoba) clade. The different position of the form from Córdoba reinforces the notion that it represents a lineage, which is undescribed, at the species level.

Patterns of morphometric variation

Members of the *A. boliviensis* group in northwestern Argentina overlap considerably in virtually all analyzed measurements. *Akodon caenosus* and *A. boliviensis* were the smallest species, *A. sylvanus* and the unnamed form the largest ones, and *Akodon spegazzinii* was intermediate (Table 1). Notwithstanding, the means of many of the measurements were significantly different among the species (Table 2). The PCA analysis (Fig. 2) showed this size order, with the first three principal component summarizing 87.07 % of the total variation but only the first (PCI, 77.39% of the explained variance) was statistically significant (Table 3). This was clearly a size component, since all character eigenvectors have the same sign and are similar in their values. The variables with the heaviest load on PCI were CIL, RL, NL, IFL, and ZB. The second component separated individuals mainly by the breadth of zygomatic plate (ZP).

Notwithstanding the pattern of overlapping size, the DA showed a clear separation between groups, with Wilk's lambda (λ) near zero (0.041) (F [44, 705]= 20.76; 44 df; $p < 0.00$) and high percentages of correct classifications (80% for *A. boliviensis*, 100% for *A. caenosus*, 87.5% for the unnamed species of *Akodon*, 91.11% for *A. spegazzinii*, and 97.95 for *A. sylvanus*) (Table 4). The most influential variables for the first analyzed axis (with eigenvalues of 5.54) were RL and MTRL. All the axes were statistically significant according to Chi-square test (p level < 0.05).

The univariate morphometric analysis, which includes topotype specimens of the nominal taxa *A. spegazzinii*, *A. tucumanensis*, *A. alterus* and *A. leucolimnaeus* indicated little differentiation among these individuals (Table 5). Morphometrically, the taxa pairs *A. spegazzinii*/*A. alterus* and *A. tucumanensis*/*A. leucolimnaeus* are indistinguishable, although the last two forms were significantly larger than *A. spegazzinii* and *A. alterus* in a handful of measurements (Table 6). All these taxa showed complete overlap on a PCA analysis (Fig. 3), with the first principal component, the only one statistically significant, summarizing only 52.39 % of the total variation (Table 7). Likewise, the DA (Table 8) also failed to found a clear separation between groups, with a high value of Wilk's lambda (λ) (0.47) (F [33, 451]= 3.94; 33 df; $p < 0.00$) and low percentages of correct classifications (27.78% for *A. alterus*, 75% for *A. leucolimnaeus*, 47.50% for *A. spegazzinii*, and 88.11 for *A. tucumanensis*). In this case, only two axes were statistically significant according to a Chi-square test ($p < 0.05$) with eigenvalues of 0.45 and 0.33.

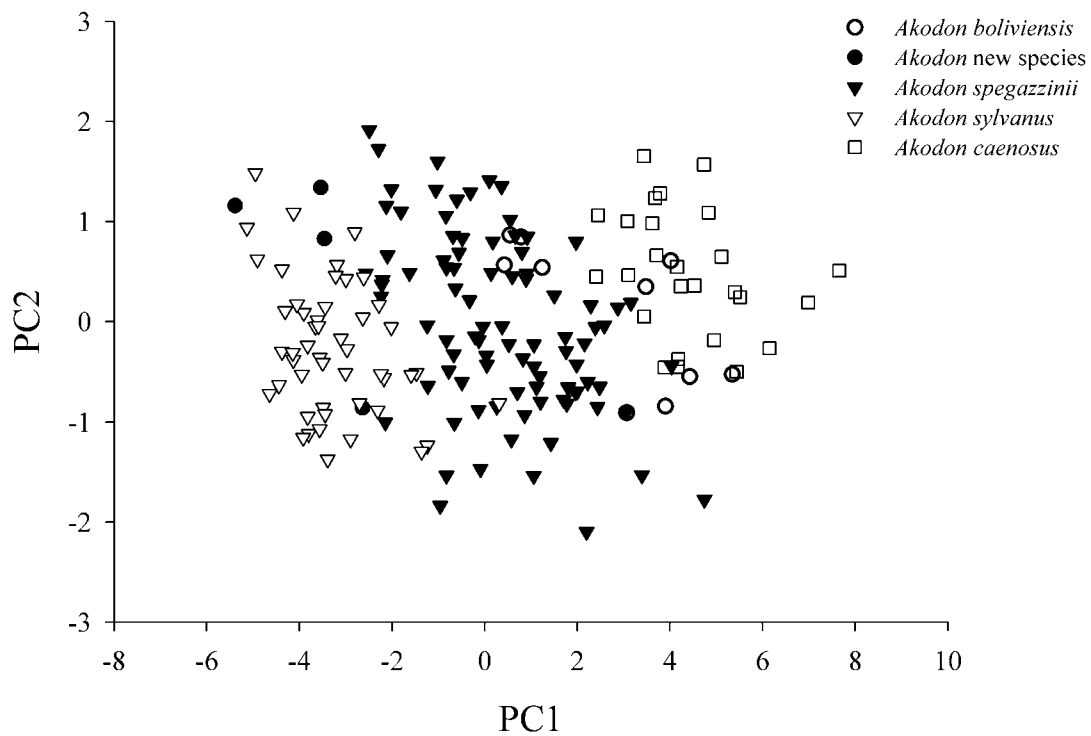


FIGURE 2. Individual specimen scores based on log-transformed values of 11 cranial measurements, projected onto the first and second principal components extracted from analysis of adult specimens (age class 3 and 4, $n = 199$) of 5 species of the genus *Akodon*: *A. boliviensis*, *A. caenosus*, *Akodon* n. sp., *A. spegazzinii* and *A. sylvanus*. Results of principal components analysis in table 3.

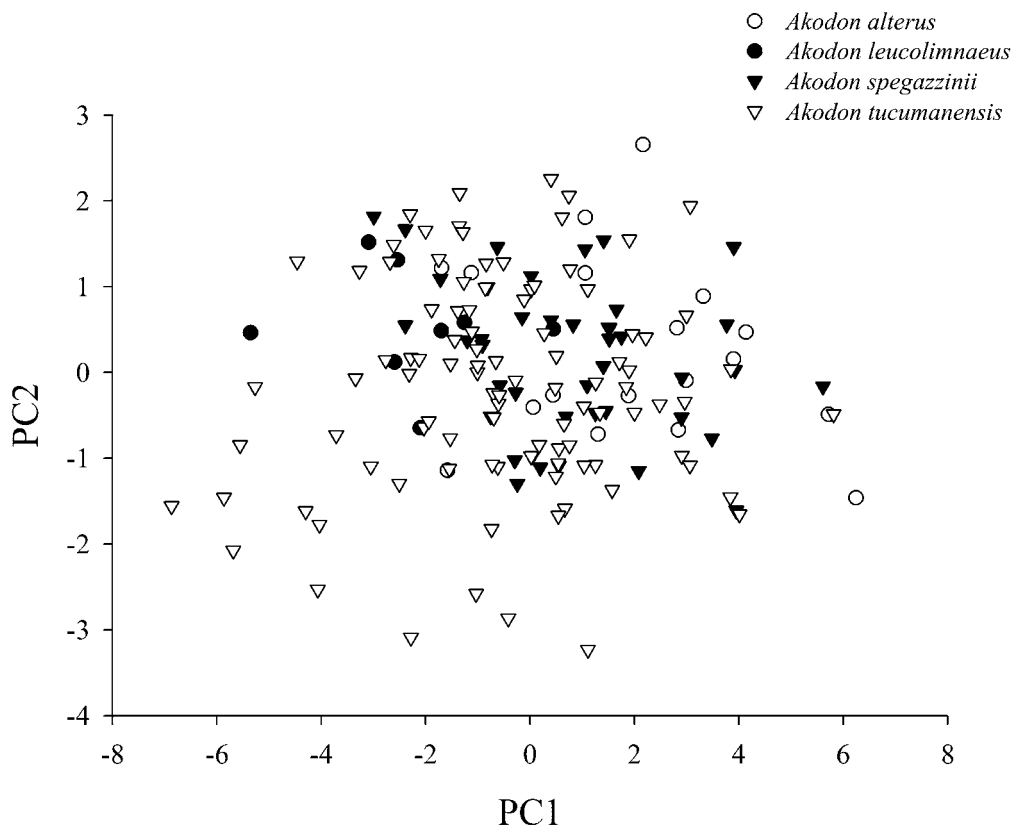


FIGURE 3. Individual specimen scores based on log-transformed values of 11 cranial measurements, projected onto the first and second principal components extracted from analysis of young specimens (age class 2, $n = 167$) of *A. spegazzinii* as here understood. Some of the specimens labelled as *Akodon spegazzinii* and *Akodon tucumanensis* were collected at the type locality of each form. Meanwhile, those labelled as *Akodon alterus* and *Akodon leucolimnaeus* were all collected at the type locality of each form. Results of principal components analysis in table 7.

TABLE 1. Comparative measurements of adult specimens (age classes 3 and 4) of 5 species of the *Akodon boliviensis* group in Argentina: *A. caenosus*, *A. boliviensis*, *A. spegazzinii*, *A. sylvanus*, and *Akodon* new species. X: mean; SD: standard deviation; r: range; n: sample size.

	<i>Akodon caenosus</i>			<i>Akodon boliviensis</i>			<i>Akodon spegazzinii</i>			<i>Akodon sylvanus</i>			<i>Akodon</i> n. sp.		
	n	X ± SD	r	n	X ± SD	r	n	X ± SD	r	n	X ± SD	r	n	X ± SD	r
TBL	12	151 ± 14.47	124-169	10	155 ± 8.48	143-167	120	158 ± 13.05	93-196	46	176 ± 10.64	151-203	19	170 ± 9.41	150-188
TL	12	62 ± 8.87	46-75	10	65 ± 4.56	57-73	120	66 ± 5.71	46-83	46	77 ± 5.69	68-89	19	70 ± 4.56	60-76
HF	12	21 ± 1.79	20-26	10	22 ± 0.84	20-23	117	23 ± 1.15	18-25	45	25 ± 1.40	22-27	20	24 ± 1.19	21-25
EL	12	13 ± 0.79	12-15	10	14 ± 0.74	13-15	122	14 ± 1.14	12-21	46	17 ± 1.21	14-21	20	15 ± 0.66	14-16
W	12	19.3 ± 5.19	10.5-27.5	10	21.8 ± 3.58	16-27.5	109	21.6 ± 4.64	13.0-38.0	44	26.4 ± 4.07	17.0-35.5	20	25.6 ± 7.03	15.5-39.0
MSL	11	23.09 ± 1.05	21.32-24.22	10	23.74 ± 0.87	22.52-25.28	112	24.71 ± 0.91	22.24-27.00	43	26.90 ± 0.61	25.30-28.30	24	25.95 ± 1.02	24.00-28.80
CIL	11	21.24 ± 1.06	19.24-22.52	10	21.80 ± 0.93	20.47-23.18	115	22.79 ± 0.96	20.50-25.30	44	24.76 ± 0.76	22.68-26.28	24	24.53 ± 0.97	22.78-27.04
RL	12	8.35 ± 0.41	7.50-8.76	10	8.52 ± 0.40	8.02-9.22	117	9.09 ± 0.43	7.96-10.12	45	10.26 ± 0.33	9.56-11.08	24	9.58 ± 0.44	8.74-10.74
ZB	11	11.57 ± 0.44	10.82-12.26	10	11.98 ± 0.28	11.52-12.32	105	12.46 ± 0.41	11.34-13.44	45	13.29 ± 0.30	12.60-13.96	24	13.22 ± 0.43	12.56-14.34
BB	11	10.70 ± 0.28	10.30-11.20	10	11.05 ± 0.25	10.64-11.34	116	11.46 ± 0.29	10.66-12.74	45	12.10 ± 0.29	11.50-12.86	24	11.60 ± 0.23	11.12-11.96
IOC	12	4.24 ± 0.13	4.00-4.46	10	4.36 ± 0.10	4.22-4.50	119	4.50 ± 0.17	4.10-4.88	46	4.74 ± 0.12	4.50-5.04	24	4.57 ± 0.12	4.30-4.82
MTRL	12	3.69 ± 0.09	3.52-3.80	10	3.94 ± 0.15	3.74-4.16	122	4.16 ± 0.15	3.80-4.60	46	4.37 ± 0.15	4.04-4.70	24	4.40 ± 0.14	4.14-4.64
NL	12	8.34 ± 0.53	7.54-9.22	10	8.45 ± 0.57	7.58-9.50	117	8.94 ± 0.49	7.64-10.10	45	9.97 ± 0.29	9.44-10.60	24	9.40 ± 0.52	8.30-10.90
RW2	12	4.29 ± 0.22	3.88-4.50	10	4.57 ± 0.23	4.26-4.88	119	4.51 ± 0.37	3.80-7.30	46	4.86 ± 0.16	4.50-5.26	24	4.93 ± 0.23	4.50-5.32
DL	12	5.65 ± 0.37	4.90-6.00	10	5.88 ± 0.40	5.34-6.44	120	6.13 ± 0.36	5.34-7.02	46	6.84 ± 0.34	5.96-7.58	24	6.95 ± 0.28	6.48-7.40
IFL	12	5.21 ± 0.33	4.54-5.74	10	5.53 ± 0.30	5.12-6.06	120	5.74 ± 0.35	4.76-6.68	44	6.31 ± 0.33	5.20-7.02	24	6.27 ± 0.26	5.70-6.78
OCW	12	5.83 ± 0.17	5.56-6.12	10	5.84 ± 0.20	5.50-6.14	116	6.15 ± 0.17	5.70-6.56	45	6.57 ± 0.19	6.10-6.92	24	6.47 ± 0.19	6.04-6.76
ZP	12	2.08 ± 0.13	1.86-2.32	10	2.01 ± 0.24	1.70-2.36	120	2.18 ± 0.20	1.70-2.78	46	2.40 ± 0.18	2.06-2.90	24	2.43 ± 0.11	2.22-2.60
ML	12	11.58 ± 0.52	10.76-12.20	10	11.93 ± 0.57	11.16-12.66	117	12.76 ± 0.48	11.60-13.94	46	13.53 ± 0.36	12.58-14.20	24	13.75 ± 0.41	13.10-14.36
MdTRL	12	3.77 ± 0.11	3.60-3.98	10	4.03 ± 0.10	3.88-4.18	119	4.24 ± 0.15	3.90-4.80	46	4.47 ± 0.16	4.12-4.76	24	4.47 ± 0.14	4.24-4.80

TABLE 2. Significant average values among adult specimens (age classes 3 and 4) of 5 species of the *Akodon boliviensis* group in Argentina according the N HDS test. Abbreviations as provided in text.

	<i>A. caenosus</i>	<i>A. boliviensis</i>	<i>A. spegazzinii</i>	<i>A. sylvanus</i>
<i>A. caenosus</i>				
<i>A. boliviensis</i>	BB, MTRL, RW2, MdTRL			
<i>A. spegazzinii</i>	HF, EL, MSL, CIL, RL, ZB, BB, IOC, MTRL, NL, DL, IFL, OCW, ML, MdTRL	RL, ZB, BB, MTRL, OCW, ML, MdTRL		
<i>A. sylvanus</i>	TBL, TL, HF, EL, W, MSL, CIL, RL, ZB, BB, IOC, MTRL, NL, RW2, DL, IFL, OCW, ZP, ML, MdTRL	TBL, TL, HF, EL, MSL, CIL, RL, ZB, BB, IOC, MTRL, NL, RW2, DL, IFL, OCW, ZP, ML, MdTRL	TBL, TL, HF, EL, W, MSL, CIL, RL, ZB, BB, IOC, MTRL, NL, RW2, DL, IFL, OCW, ZP, ML, MdTRL	
<i>Akodon</i> n. sp.	TBL, TL, HF, EL, W, MSL, CIL, RL, ZB, BB, IOC, MTRL, NL, RW2, DL, IFL, OCW, ZP, ML, MdTRL	TBL, HF, MSL, CIL, RL, ZB, BB, IOC, MTRL, NL, RW2, DL, IFL, OCW, ZP, ML, MdTRL	TBL, MSL, CIL, RL, ZB, MTRL, NL, RW2, DL, IFL, OCW, ZP, ML, MdTRL	TL, HF, EL, MSL, RL, BB, IOC, NL, OCW

TABLE 3. Results of principal components analysis of craniodental measurements of adult specimens (age classes 3 and 4, n = 199) of 5 species of the *Akodon boliviensis* group in Argentina: *A. boliviensis* (n = 10), *A. caenosus* (n = 26), *Akodon* new species (n = 24), *A. spegazzinii* (n = 90) and *A. sylvanus* (n = 49). Asterisk indicates significant principal components after the Broken-stick test.

Variable	Pearson correlation		
	PC1	PC2	PC3
CIL	-0.3316	-0.1778	0.0940
MTRL	-0.2841	0.1702	-0.6707
IFL	-0.3064	-0.0835	-0.0710
ZP	-0.2588	-0.6159	-0.2128
ZB	-0.3273	-0.0206	-0.0247
BB	-0.2855	0.4564	-0.1053
IOC	-0.2754	0.4496	0.4706
RW2	-0.2994	-0.2647	0.2451
NL	-0.3116	-0.1158	0.2984
RL	-0.3293	-0.0253	0.1827
OCW	-0.2980	0.2410	-0.2745
Eigenvalue	8.51	0.67	0.38
% of variance	77.39	6.17	3.51
Broken-stick eigenvalue	3.02*	2.02	1.52

TABLE 4. Results of Discriminant Analysis for adult specimens (age classes 3 and 4) of 5 species of the *boliviensis* group in Argentina. Standardized coefficients for canonical variables. Specimens included: *A. boliviensis* (n = 10), *A. caenosus* (n = 26), *Akodon* new species (n = 24), *A. spegazzinii* (n = 90), *A. sylvanus* (n = 49).

Variable	Canonical Variables			
	First	Second	Third	Fourth
CIL	7.6966	-60.8210	-38.8226	26.2479
MTRL	-34.3220	-39.8127	27.5720	30.1827
IFL	-2.8900	-15.4708	11.2706	-15.4029
ZP	7.4359	2.5600	-14.3057	6.9303
ZB	-24.1477	-20.5742	-22.1570	20.2459
BB	-17.9623	37.1134	44.9321	-1.8894
IOC	-0.6991	8.1670	-3.8833	-14.9684
RW2	15.7092	-22.8368	24.1459	-58.9437
NL	10.5584	20.2548	-18.5198	-8.7862
RL	-41.4222	79.5604	41.9533	10.5147
OCW	-20.2220	1.9085	-66.8603	-8.0833
Canonical correlation	0.92	0.76	0.47	0.39
Eigenvalue	5.54	1.40	0.28	0.18
% of variance	0.74	0.18	0.03	0.02

In addition, there were no significant morphometric differences between representatives of *A. caenosus* and the type specimens of *A. aliquantulus* in the univariate analysis. The measurements registered for the only two known specimens of *A. aliquantulus* were inside the ranges observed for topotypes of *Akodon caenosus* (app. 3 km N León, Jujuy) and those from additional localities of northwestern Argentina (Table 9). Only one (RW2) of the twenty morphometric variables used showed a statistical difference. The PCA (Table 10 and figure 4) shows no overlap between *A. aliquantulus* and *A. caenosus* specimens of age class 5, but age class 4 specimens were clearly overlapping. The first principal component in this case summarizes 68.79% of the total variation and it was the only one significant according to the Broken-stick test. The more informative variables in this analysis were CIL, RL, AZ, and NL. The DA failed to discriminate among individuals assigned to *A. aliquantulus* and *A. caenosus* (Wilks' λ = 0.34; $F(10, 3) = 0.56$; 10 df; $p < 0.78$), with one of the two *A. aliquantulus* specimens misclassified as *A. caenosus* (percentage of correct classifications: 69.23% for *A. caenosus* age class 4, 84.21% for *A. caenosus* age class 5, and 50% for *A. aliquantulus*). Only one axis was statistically significant ($\chi^2 = 7.43$, $p < 0.68$) in the DA analysis with an eigenvalue of 1.64 (Table 11).

Morphological results

We observed a clear pattern of morphological uniformity for all the studied specimens belonging to the *A. boliviensis* species group in northwestern Argentina. For example, specimens from populations collected in forested and more humid environments were darker than populations collected in open and drier areas. Likewise, as most sigmodontine species, young specimens were usually darker than older ones. Interestingly, lactating females had more reddish pelages than non-lactating individuals regardless of the time of the year they were trapped.

TABLE 5. Comparative measurements of young specimens (age class 2) of *A. spegazzinii* Thomas and all its associated nominal forms: *A. alterus* Thomas, *A. leucolimnaeus* Cabrera, and *A. tucumanensis* J. A. Allen. X: mean; SD: standard deviation; r: range; n: sample size.

	<i>Akodon spegazzinii</i>			<i>Akodon tucumanensis</i>			<i>Akodon alterus</i>			<i>Akodon leucolimnaeus</i>		
	n	X ± SD	r	n	X ± SD	r	n	X ± SD	r	n	X ± SD	r
TBL	40	145 ± 8.01	127–162	95	153 ± 10.45	129–186	19	144 ± 7.61	130–158	7	157 ± 6.63	145–164
TL	40	59 ± 4.16	50–69	98	66 ± 5.48	53–80	19	60 ± 3.71	54–66	7	67 ± 4.31	59–72
HF	43	22 ± 1.07	20–24	99	22 ± 1.09	20–25	19	22 ± 0.92	20–24	8	24 ± 0.52	23–24
EL	43	14 ± 0.73	12.0–16.0	99	14 ± 0.67	12.0–15.0	19	14 ± 0.46	13.0–15.0	8	14 ± 0.64	13.0–15.0
W	41	20.2 ± 3.18	14.0–27.5	96	19.8 ± 4.19	13–32	19	16.5 ± 2.76	11.0–23.0	8	21.5 ± 1.83	19.0–25.0
MSL	41	23.92 ± 0.60	22.28–25.14	102	24.43 ± 0.79	22.22–26.50	18	23.77 ± 0.66	22.66–24.70	8	24.61 ± 0.53	23.74–25.50
CIL	43	21.86 ± 0.65	20.30–23.10	101	22.37 ± 0.84	20.52–25.20	18	21.53 ± 0.65	20.48–22.64	8	22.65 ± 0.54	21.72–23.42
RL	42	8.61 ± 0.34	7.80–9.12	102	8.88 ± 0.37	7.86–9.96	19	8.57 ± 0.31	8.04–9.22	8	8.98 ± 0.30	8.68–9.64
ZB	42	12.26 ± 0.34	11.70–13.34	102	12.33 ± 0.35	11.20–13.32	19	12.00 ± 0.40	11.16–12.70	8	12.79 ± 0.23	12.54–13.12
BB	43	11.40 ± 0.16	11.06–11.72	102	11.50 ± 0.26	10.82–12.04	18	11.46 ± 0.32	10.66–12.02	8	11.67 ± 0.27	11.20–12.10
IOC	43	4.40 ± 0.15	4.08–4.70	102	4.43 ± 0.16	4.08–4.82	19	4.37 ± 0.16	4.12–4.64	8	4.39 ± 0.11	4.18–4.50
MTRL	43	4.14 ± 0.15	3.84–4.50	102	4.15 ± 0.13	3.86–4.46	19	4.09 ± 0.11	3.94–4.28	8	4.21 ± 0.13	4.02–4.42
NL	42	8.51 ± 0.29	7.80–9.00	102	8.67 ± 0.42	7.70–9.80	19	8.42 ± 0.34	7.90–9.12	8	8.60 ± 0.32	8.28–9.12
RW2	43	4.36 ± 0.16	4.06–4.68	102	4.43 ± 0.21	3.88–5.00	19	4.22 ± 0.21	3.88–4.50	8	4.69 ± 0.20	4.34–5.06
DL	43	5.81 ± 0.22	5.20–6.12	102	5.99 ± 0.29	5.24–6.76	19	5.73 ± 0.23	5.24–6.12	8	6.18 ± 0.19	5.86–6.42
IFL	43	5.36 ± 0.24	4.98–6.04	102	5.64 ± 0.27	5.10–6.42	19	5.37 ± 0.31	5.04–5.96	8	5.63 ± 0.21	5.28–5.90
OCW	42	6.10 ± 0.16	5.76–6.38	101	6.14 ± 0.19	5.70–6.76	18	6.07 ± 0.13	5.80–6.30	8	6.37 ± 0.13	6.24–6.54
ZP	43	2.11 ± 0.12	1.94–2.40	102	2.16 ± 0.18	1.80–2.68	19	1.99 ± 0.12	1.70–2.24	8	2.33 ± 0.08	2.24–2.46
ML	43	12.35 ± 0.36	11.36–12.84	102	12.47 ± 0.43	11.44–13.74	19	12.13 ± 0.38	11.46–12.74	8	13.03 ± 0.24	12.74–13.52
MdTRL	43	4.16 ± 0.19	3.32–4.52	102	4.21 ± 0.14	3.94–4.52	19	4.21 ± 0.12	4.04–4.48	8	4.31 ± 0.13	4.18–4.56

TABLE 6. Significant average values among young specimens (age class 2) of *A. spegazzinii* Thomas and all its associated nominal forms: *A. alterus* Thomas, *A. leucolimnaeus* Cabrera, and *A. tucumanensis* J. A. Allen; according the N HDS test. Abbreviations as provided in text.

	<i>A. alterus</i>	<i>A. spegazzinii</i>	<i>A. leucolimnaeus</i>
<i>A. alterus</i>			
<i>A. spegazzinii</i>	W		
<i>A. leucolimnaeus</i>	TBL, TL, HF, W, CIL, ZB, RW2, DL, OCW, ZP, ML	TL, HF, ZB, RW2, DL, OCW, ZP, ML	
<i>A. tucumanensis</i>	TBL, TL, W, MSL, CIL, RL, ZB, RW2, DL, IFL, ZP, ML	TBL, TL, MSL, CIL, RL, DL, IFL	ZB, RW2, OCW, ML

TABLE 7. Results of principal components analysis of craniodental measurements of young specimens (age class 2, n = 199) of *A. spegazzinii* Thomas (n = 40) and all its associated nominal forms: *A. alterus* Thomas (n = 18), *A. leucolimnaeus* Cabrera (n = 8), and *A. tucumanensis* J. A. Allen (n = 101). Asterisk indicates significant principal components after the Broken-stick test.

Variable	Pearson correlation		
	PC1	PC2	PC3
CIL	-0.3809	-0.2104	-0.0249
MTRL	-0.2422	0.2667	0.5364
IFL	-0.2872	-0.3432	-0.1274
ZP	-0.2917	-0.1172	0.1527
ZB	-0.3392	0.1883	-0.0628
BB	-0.2360	0.5418	-0.1576
IOC	-0.1697	0.4672	-0.5352
RW2	-0.3347	0.0203	-0.1835
NL	-0.3312	-0.3193	-0.0969
RL	-0.3706	-0.2269	-0.0865
OCW	-0.2647	0.2281	0.5535
Eigenvalue	5.76	1.26	0.89
% of variance	52.39	11.42	8.11
Broken-stick eigenvalue	3.02*	2.02	1.52

TABLE 8. Results of Discriminant Analysis for young specimens (age class 2) of *A. spegazzinii* Thomas and all its associated nominal forms. Standardized coefficients for canonical variables. Topotype specimens included: *A. spegazzinii* (n = 40), *A. leucolimnaeus* (n = 8), *A. alterus* (n = 18), *A. tucumanensis* (n = 101).

Variable	Canonical Variables	
	First	Second
CIL	-0.333977	-0.277009
MTRL	-0.105986	0.041825
IFL	0.343646	-0.728667
ZP	0.493848	0.102126
ZB	0.587580	0.704908
BB	-0.297757	-0.470796
IOC	-0.152458	-0.123009
RW2	0.534473	0.323655
NL	-0.785807	0.306341
RL	0.235033	-0.748255
OCW	0.321117	0.294627
Canonical correlation	0.56	0.49
Eigenvalue	0.45	0.33
% of variance	0.52	0.37

TABLE 9. Comparative measurements of adult specimens (age classes 3 and 4) of *A. caenosus* and holotype and para-type of *A. aliquantulus* (age class 4). The values for specimens of around the type locality of *A. lutescens caenosus* from Jujuy province are distinguished from those of remaining localities of Northwestern Argentina. Measurements for *A. aliquantulus* were extracted from Díaz et al. (1999), except for those indicated with an asterisk; these were taken by us. X: mean; SD: standard deviation; r: range; n: sample size.

	<i>Akodon caenosus</i>						CML 6121	CML 6122
	Jujuy			NOA				
	n	X ± SD	r	n	X ± SD	r		
TBL	4	150 ± 10.25	136–160	8	151 ± 16.82	124–169	139	139
TL	4	59 ± 9.83	46–68	8	64 ± 8.58	51–75	60	62
HF	4	20 ± 0.00		8	22 ± 2.00	20–26	17	19
EL	4	13 ± 0.57	13.0–14.0	8	13 ± 0.92	12.0–15.0	13	13
W*	4	21.1 ± 4.17	17.0–25.0	8	18.4 ± 5.66	10.5–27.5	13.0	14.0
MSL*	4	23.07 ± 0.58	22.22–23.48	7	23.11 ± 1.29	21.32–24.22	21.7	21.8
CIL	4	21.39 ± 0.52	20.62–21.72	7	21.26 ± 1.31	19.24–22.52	20.00	19.95
RL	4	8.37 ± 0.30	7.94–8.66	8	8.34 ± 0.49	7.50–8.76	7.80	7.72
ZB	4	11.60 ± 0.40	11.02–11.92	7	11.55 ± 0.49	10.82–12.26	11.10	11.20
BB	4	10.90 ± 0.29	10.54–11.20	7	10.59 ± 0.22	10.30–10.96	10.38	10.32
IOC	4	4.28 ± 0.06	4.20–4.34	8	4.22 ± 0.16	4.00–4.46	4.18	4.13
MTRL	4	3.69 ± 0.12	3.52–3.80	8	3.69 ± 0.09	3.56–3.78	3.57	3.58
NL	4	8.28 ± 0.44	7.62–8.56	8	8.37 ± 0.60	7.54–9.22	7.79	7.82
RW2	4	4.26 ± 0.20	4.00–4.46	8	4.30 ± 0.23	3.88–4.50	3.94	3.34
DL	4	5.70 ± 0.24	5.34–5.86	8	5.62 ± 0.43	4.90–6.00	5.25	5.36
IFL*	4	5.10 ± 0.17	4.94–5.30	8	5.27 ± 0.38	4.54–5.74	5.0	5.0
OCW*	4	5.85 ± 0.11	5.70–5.96	8	5.81 ± 0.20	5.56–6.12		5.5
ZP*	4	2.10 ± 0.19	1.86–2.32	8	2.08 ± 0.10	1.92–2.20	1.9	2.0
ML*	4	11.45 ± 0.38	10.88–11.68	8	11.65 ± 0.59	10.76–12.20		11.4
MdTRL*	4	3.86 ± 0.15	3.68–3.98	8	3.73 ± 0.07	3.60–3.82	3.7	3.6

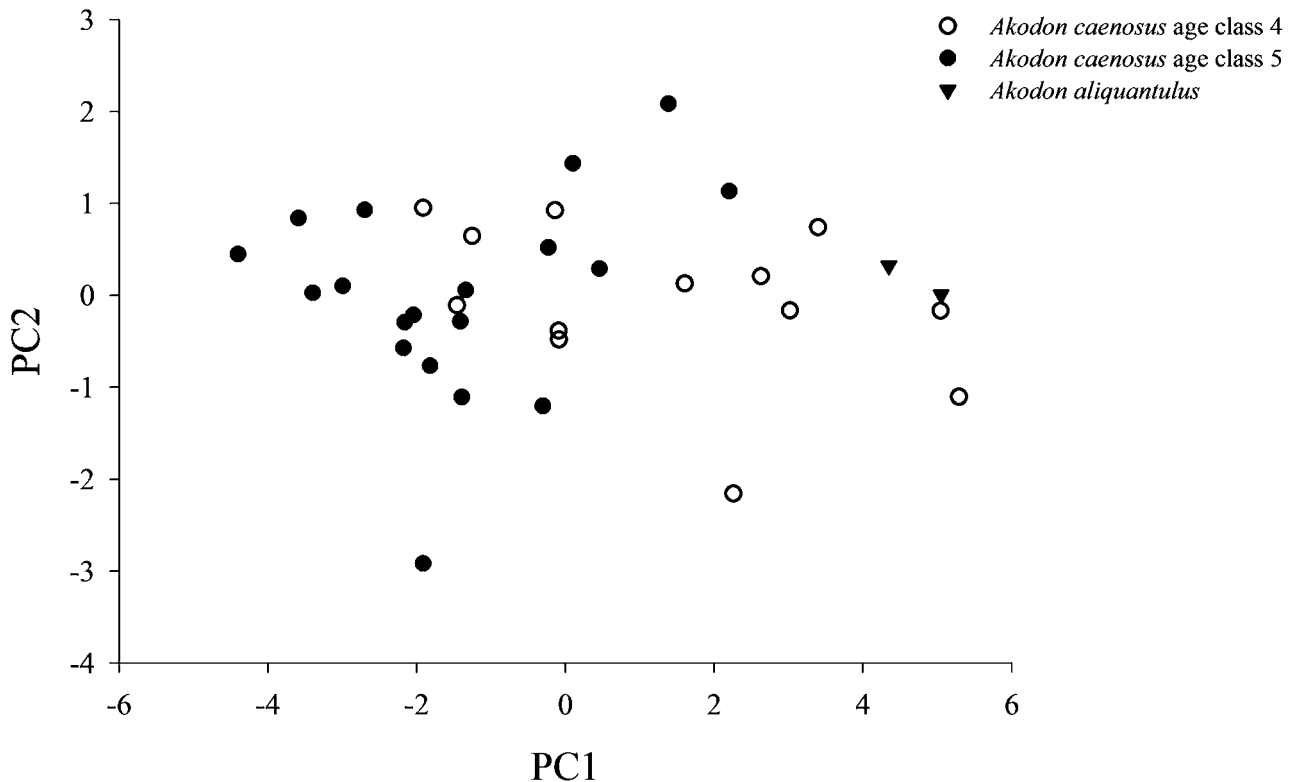


FIGURE 4. Individual specimen scores based on log-transformed values of 10 cranial measurements, projected onto the first and second principal components extracted from analysis of adult specimens (age class 4 and 5, n = 34) of two species of the genus *Akodon*: *A. aliquantulus* and *A. caenosus*. Results of principal components analysis in table 10.

TABLE 10. Results of principal components analysis of craniodental measurements of adult specimens (age classes 4 and 5, n = 34) of *A. caenosus* and holotype and paratype of *A. aliquantulus* (age class 4). Asterisk indicates significant principal components after the Broken-stick test.

Variable	Pearson correlation		
	PC1	PC2	PC3
CIL	-0.3677	-0.1303	0.0706
MTRL	-0.2712	0.1283	-0.7781
IFL	-0.3254	0.0216	0.2086
ZP	-0.2791	-0.4586	-0.1090
ZB	-0.3413	0.0491	-0.0904
BB	-0.3026	0.4077	-0.2681
IOC	-0.2288	0.7022	0.3692
RW2	-0.3254	-0.1478	0.2943
NL	-0.3354	-0.2513	0.1625
RL	-0.3588	-0.0957	0.0690
Eigenvalue	6.88	0.92	0.64
% of variance	68.79	9.20	6.44
Broken-stick eigenvalue	2.92*	1.92	1.42

TABLE 11. Results of Discriminant Analysis for adult specimens (age 4 and 5) of *A. aliquantulus* and *A. caenosus*. Standardized coefficients for canonical variables. Specimens included: *A. aliquantulus* (n = 2), *A. caenosus* (n = 32).

Variable	Canonical Variables	
	First	Second
CIL	-1.07395	-0.32889
MTRL	-0.22002	0.27627
IFL	0.64921	-0.53786
ZP	0.23264	0.06596
ZB	0.61860	-0.27531
BB	-0.52478	-0.06526
IOC	0.03422	0.23399
RW2	-0.44767	1.49658
NL	-0.27740	0.65392
RL	0.08479	-1.47008
Canonical correlation	0.78	0.58
Eigenvalue	1.64	0.52
% of variance	0.75	0.25

As shown before, most differences among species in the *boliviensis* group are morphometric in nature (Fig. 5). Externally, the distinction among species is equally complicated. In fact, in some cases we observe more striking differences among populations of the same species than between selected population of different species. In general, all the forms here studied share many external characteristics (e.g., uniform agouti pelage with brownish olivaceous fur, weakly developed yellowish eyerings, and inconspicuous small patches of white fur on the chin). Similarly, all species share a delicate skull, with unflared zygomatic arches, weakly expressed lambdoid and temporal crests, and narrow braincases. However, there is enough variation, so that a combination of characters (external, cranial and dental), considered in a geographic context, may be used to distinguish among species.

Species account

Available evidence supports the occurrence of 4 species of the *Akodon boliviensis* group in northwestern Argentina, including *A. boliviensis*, *A. caenosus*, *A. spegazzinii*, and *A. sylvanus*. Additionally, our analyses indicate the presence -in central Argentina- of an undescribed species belonging to this group which is described at the end of this section.

Order Rodentia Bowdich, 1821

Family Cricetidae Fischer, 1817

Subfamily Sigmodontinae Wagner, 1843

Tribe Akodontini Vorontsov, 1959

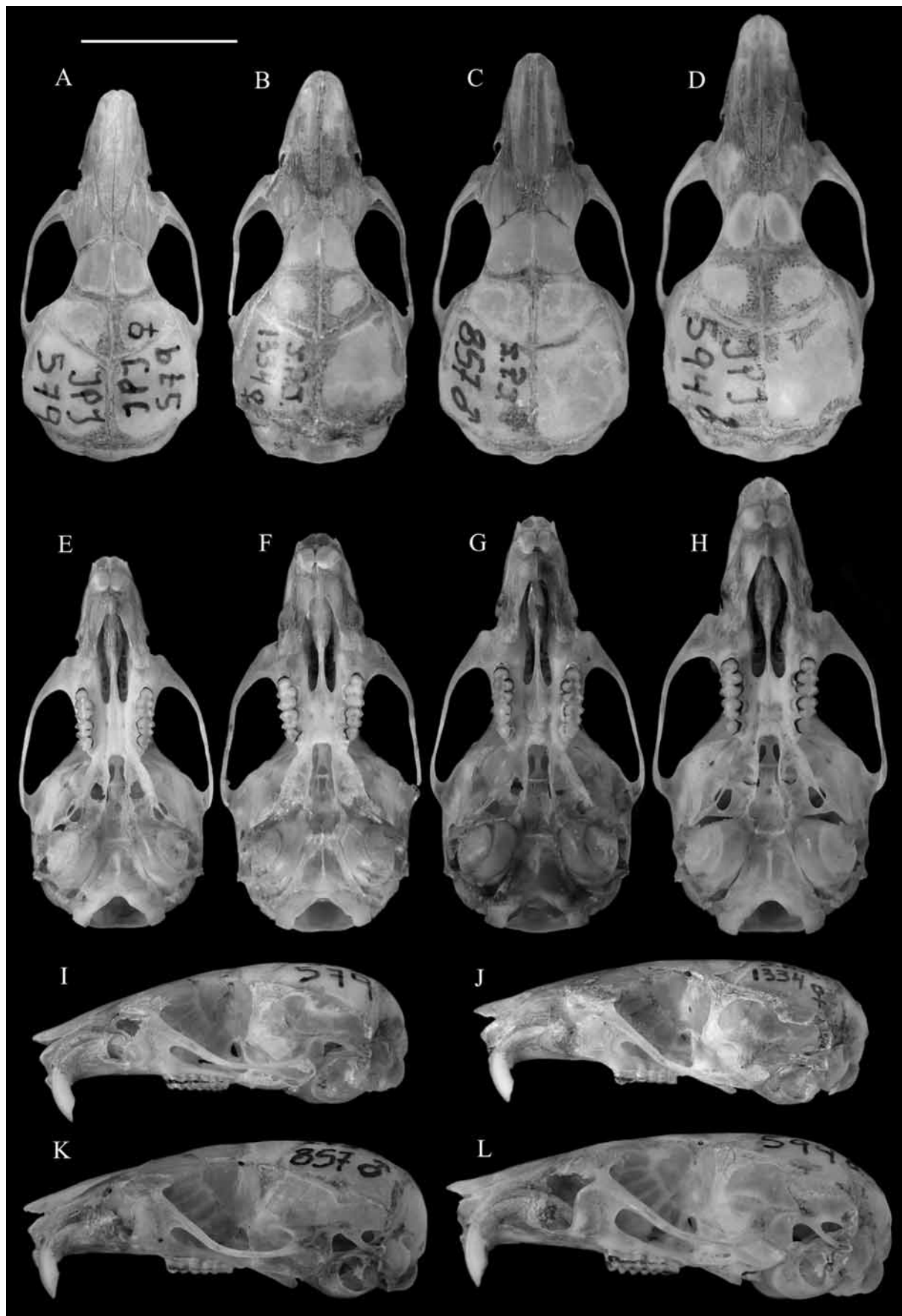


FIGURE 5. Dorsal, ventral, and lateral views of skulls in *A. caenosus* (JPI 579; A, E and I), *Akodon boliviensis* (JPI 1334; B, F and J), *A. spegazzinii* (JPI 857; C, G and K) and *A. sylvanus* (JPI 594; D, H and L). All specimens of age class 4. Scale bar = 10 mm.

***Akodon boliviensis* Meyen, 1833**

Akodon boliviense Meyen, 1833. Verhandlungen der Kaiserlichen Leopoldinisch-Carolinischen Akademie der Naturforscher, 16(2):600, pl. 43, fig. 1.

Holotype: no holotype was designated by Meyen.

Type locality: “Auf der Hochebene von Hochperu, in dem Indianer-dorfe Pichu-pichun, auf einer Höhe von 14,000 fuss gefangen.” Pichu-Pichún, 14,000 ft., Chucuito Province, Puno Department, Peru (as clarified by Myers *et al.* 1990).

Description: Detailed morphological description in Myers *et al.* (1990). The specimens of northwestern Argentina follow, in general, this description and can be distinguished from the remaining species present in this region by the following combination of characters. Dorsal fur soft and somewhat dense, with dorsal coloration uniform pale brown with an olivaceous tinge and lightly streaked with black hairs. Yellow eyerings well defined. Ears of the same color as dorsum and densely covered with hairs. Coloration of sides similar to or somewhat lighter than dorsum. Venter buffy, clearly contrasting with dorsum. Chin with a small patch of completely white hairs. Inguinal region almost rufous in some individuals. Fore and hind feet of the same general coloration than the venter, with bicolored hairs, brown on base and whitish or pale buff on tip. Tail heavily covered with hairs and bicolored, dark brown dorsally and whitish or pale buffy ventrally.

Skull with rostrum short and relatively broad. Zygomatic notches proportionally broad and deep. Frontal sinuses slightly swollen. Interorbital region slightly divergent with margins in posterior half something squared in adult specimens. Zygomatic arches relatively well developed. Braincase inflated with temporal and lambdoidal crests relatively well developed. Zygomatic plate with anterior margin flat or slightly concave, oriented vertically or slopes gently backward from bottom to top. Most of examined specimens shows a posterior ascending process of alisphenoid projected at least to the squamoso-alisphenoid groove. Incisive foramina extending to the level of the hypoflexus of M1 or surpassed it. Mesopterygoid fossa narrow with straight borders and sides either parallel or gradually diverging posteriorly, and anterior margin rounded or squared. Parapterygoid fossae broader than mesopterygoid fossa, diverging backward and with straight to slightly convex lateral margins. Mandibular ramus delicate with masseteric crest extending slightly behind of the anterior border of m1, although in some individuals it only reaches the level of protoflexid. Capsular projection well developed and generally situated below the sigmoid notch.

Upper incisors generally orthodont. The M1 with procingulum and anteromedian flexus well developed. The anteroloph and mesoloph are always present, the enteroloph is tiny and present only in some specimens. The M2 shows a well developed mesoloph and the M3 is large and complex, with well developed metaflexus and hypoflexus making it distinctively “8”-shaped in most specimens. The m1 presents a well developed procingulum and a penetrating anteromedian flexid. Protostylid and ectostylid are always presents but the second is poorly defined in some individuals. A small mesolophid-mesostylid is present in a few specimens. In m2 most of the examined specimens have an ectostylid, and a mesolophid-mesostylid is present only in a few individuals but always vestigial (the only young specimen and two adults individuals). The m3 is proportionally large (nearly a half of m2), showing a poorly developed anterior cingulid in most specimens.

Karyotype: 2n = 40, FN = 40-42, from Puno and Tacna Departments, Peru (Gardner & Patton, 1976; Myers *et al.*, 1990).

Variation: In the few known specimens from northwestern Argentina most variation is age-dependent. Pelage color of young specimens is slightly darker than that of adults. Young individuals also present a shorter and more delicate rostrum, narrower zygomatic notch, less swollen frontal sinuses, broader interorbital region and more inflated braincase. Moreover, the incisive foramina and the mesopterygoid fossa are narrower and the parapterygoid fossae not as deeply excavated. Some variable characters unrelated with age include the general coloration, with some individuals more richly colored; eye ring, development of the hamular process of the squamosal (i.e., tympanic hook in Myers *et al.*, 1990) and the shape of anterior margin of the mesopterygoid fossa. Representatives of this species in northwestern Argentina are morphometricly indistinguishable from those of Peru and Bolivia although they are slightly smaller in some measurements (e.g. CIL, RL) and slightly larger in others (e.g. IOC, IFL, RW2). Nine specimens coming from Abra de Cienaga Negra and one

from Azul Cuesta show subtle morphologic and morphometric differences respect to the specimens from Rodeo Pampa and Pampa Verde (whose haplotypes were more closely related to that of a Peruvian specimen MVZ 171607). These specimens are more richly colored, have a broader interorbital constriction (IOC) and rostral width (RW2), and a thinner zygomatic plate (ZP).

Comparisons: *Akodon boliviensis* is a medium sized species within the *boliviensis* group and is, on average, larger than *A. caenosus* for most of the analyzed measurements (Table 1). Nevertheless, only braincase breadth (BB), mid rostral width (RW2) and molars series (MTRL and MdTRL) were statistically different according to the N HSD test (Table 2). The PCA analysis indicates some overlap between these species (Fig 2) but the DA misclassified only one of the specimens of *A. boliviensis* as *A. caenosus*. In general, the coloration of *A. boliviensis* is somewhat paler than *A. caenosus* and the ears are more densely furred. Cranial traits such as a more developed zygomatic notches and a proportionally narrower interorbital region distinguish *A. boliviensis*. Contrary to that observed in *A. boliviensis*, only in few studied specimens of *A. caenosus* in northwestern Argentina the posterior ascending process of the alisphenoid extend to the squamoso-alisphenoid groove. As Myers *et al.* (1990) recognized, the shape of M3 and the thickness of the hamular process of squamosal also differentiate both species. However, *A. caenosus* shows a great variability in these traits. Additionally, these species show a relatively high average percentage (7.0%) of genetic divergence (Table 12). The examined skins of *Akodon boliviensis* are very similar to those of specimens of *Akodon spegazzinii* from high altitude localities, sharing similar hue and color patterns. However, *A. boliviensis* is on average smaller than *A. spegazzinii* for most morphometric measurements (Table 1) with the N HSD test indicating significant differences in seven of these measurements (Table 2). In this sense, *A. boliviensis* presents a more delicate skull, with shorter rostrum and molar series, narrower braincase, narrower and more shallow zygomatic notches and less flared zygomatic arches. The PCA analysis indicates some overlap (Fig 2) but the DA was efficient in separating these species, with only two misclassified specimens. The genetic distance between these taxa is relatively small (2.8%).

The striking morphometric and coloration pattern differences between *A. boliviensis* and *A. sylvanus* preclude confusing these species. *Akodon boliviensis* is conspicuously paler, with a drabby brown color, whereas *A. sylvanus* is dark brown with a strong olivaceous tinge. The contrast between dorsum and venter is more conspicuous in *A. boliviensis*. In addition, this species shows a more developed eyering and white spot on the chin. The skull of *A. boliviensis* is clearly more slender, with a shorter and more delicate rostrum, and narrower braincase, interorbital region and mesopterygoid fossa. The molars in *A. boliviensis* are smaller and clearly less hypsodont. The morphometric differences between these species are notorious with practically no overlap in PCA and none misclassified specimens in DA (Tables 1, 2 and figure 2). The average percentage of genetic divergence between these species is 4.9 %.

The comparison between *A. boliviensis* and the new species will be addressed under the treatment of the latter.

Distribution: In northwestern Argentina *A. boliviensis* is restricted to northernmost Salta Province, mainly above 2500 m (Jayat *et al.* 2006). All known records come from the Zenta and Santa Victoria ranges. Thus, it is likely that the species probably reaches adjacent Jujuy province due to the continuity of habitats along these mountain ranges (Fig. 6).

Habitat: We captured most specimens in highland grasslands, both in upper forest/humid grassland ecotones as well as in drier grasslands more typical of Andean environments. Most of the collecting localities are characterized by grasslands interspersed with rocky outcrops, although in Pampa Verde (locality 6 on figure 6) the humid grasslands are adjacent to alder (*Alnus acuminata*) forest along humid ravines.

Natural history: Four individuals captured in winter (July and August) were molting with only one of them with reproductive activity signs. All specimens caught in spring (nine specimens collected in November) showed reproductive activity and were molting. Other sigmodontine species registered in northwestern Argentina alongside *A. boliviensis* include *Akodon caenosus*, *Akodon budini* Thomas, *Necromys lactens* Thomas, *N. amoenus* Thomas, *Oligoryzomys* cf. *O. flavescens* (Waterhouse), *Oxymycterus paramensis* Thomas, *Phyllotis osilae* J. A. Allen and *P. xanthopygus* (Waterhouse).

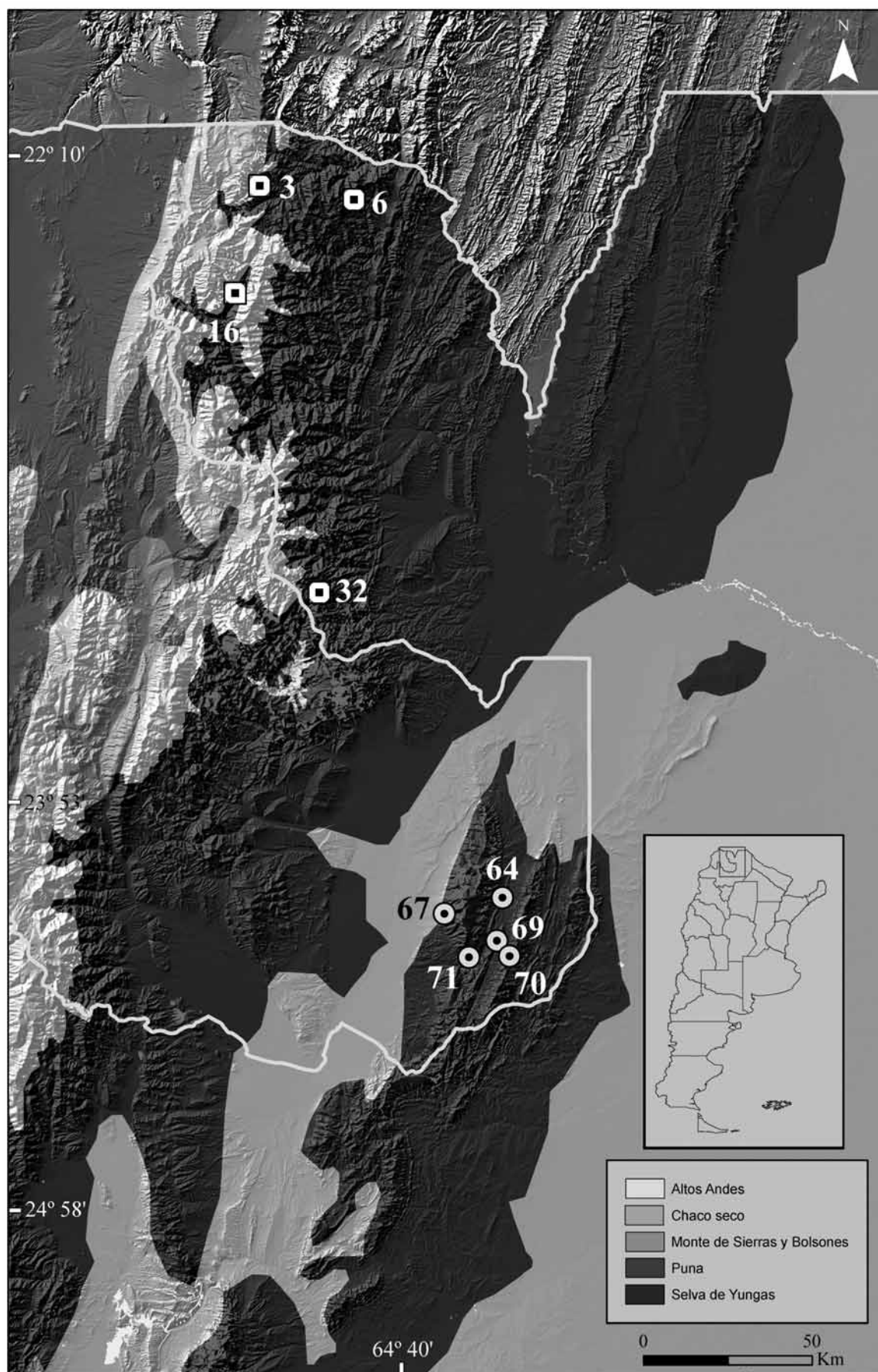


FIGURE 6. Recorded localities of *A. boliviensis* (square) and *A. sylvanus* (circles) in Northwestern Argentina. Localities and geographic position in Appendix II.

TABLE 12. Average percentage of observed sequence divergence within and between seven species of the *Akodon boliviensis* species group. Standard error estimates are shown between parentheses and were obtained by a bootstrap procedure (500 replicates) in MEGA 4. Positions containing missing data were excluded only in pairwise sequence comparisons. Intraspecific values for *A. lutescens* and *A. subfuscus* were not calculated because a single sequence was available for each species.

Species	intra-specific	interspecific					
		<i>A. boliviensis</i>	<i>A. lutescens</i>	<i>A. caenosus</i>	<i>A. polopi</i> n. sp.	<i>A. spegazzinii</i>	<i>A. subfuscus</i>
<i>A. boliviensis</i>	1.7 (0.3)						
<i>A. lutescens</i>	-- --	7.0 (0.8)					
<i>A. caenosus</i>	1.0 (0.2)	7.0 (0.8)	3.5 (0.6)				
<i>A. polopi</i> n. sp.	0.2 (0.1)	5.0 (0.7)	7.0 (0.8)	6.2 (0.7)			
<i>A. spegazzinii</i>	1.2 (0.2)	2.8 (0.5)	7.6 (0.9)	7.7 (0.8)	5.5 (0.7)		
<i>A. subfuscus</i>	-- --	8.3 (0.9)	5.1 (0.8)	4.7 (0.7)	8.0 (0.9)	8.5 (0.9)	
<i>A. sylvanus</i>	0.3 (0.2)	4.9 (0.7)	7.0 (0.9)	6.7 (0.8)	4.7 (0.7)	4.9 (0.7)	8.1 (1.0)

Comments: Cabrera (1961) considered *A. spegazzinii* and *A. tucumanensis* as subspecies of *A. boliviensis*, and *A. alterus* as a synonym of *A. boliviensis tucumanensis*, a position followed by many authors through the 1980s (e.g. Apfelbaum & Reig 1989; Barquez *et al.* 1980; Mares *et al.* 1981; Ojeda & Mares 1989). In the first revision of these small Andean forms, Myers *et al.* (1990) defined the *Akodon boliviensis* group, characterized the morphological and distributional boundaries of *A. boliviensis*, and considered *A. spegazzinii* as a valid species (with two subspecies *A. s. spegazzinii* and *A. s. tucumanensis*).

Jayat *et al.* (2006) erroneously cited *A. boliviensis* for Escoipe, in central Salta province. This record was based on one specimen (JPJ 69) whose morphometric characteristics were similar to those of *A. boliviensis*; however, our molecular studies indicate that this and other small specimens caught in the same locality are referable to *A. spegazzinii*.

Díaz (1999) and Díaz & Barquez (2007) referred one specimen (MMD 395) from Miyuyoc, at 3700 m, Jujuy province to *Akodon alterus*. We did not examine this specimen, but based on the latitudinal position and characteristics of the reported locality where the specimen was trapped, we note that it may represent another record of *A. boliviensis*.

***Akodon caenosus* Thomas, 1918**

Akodon diminutus Barquez, Díaz and Goytia, 1994. Nomen nudum (see Galliari *et al.*, 1996).

Akodon aliquantulus Díaz, Barquez, Braun and Mares, 1999. Journal of Mammalogy, 80:788.

Holotype: BMNH 18.1.1.38, adult male.

Type locality: León, Jujuy, 1500 m (Thomas, 1918).

Description: Detailed morphological description in Myers *et al.* (1990) (as *A. puer caenosus*). Additional morphological and morphometric data for some populations of northwestern Argentina can be found in Thomas (1918; original description of *A. puer caenosus*), Barquez *et al.* (1980) and Díaz (1999). Here we summarize the characteristics of populations along the latitudinal and altitudinal gradients of northwestern Argentina.

Akodon caenosus is the smallest species of the *boliviensis* group in northwestern Argentina. Dorsal coloration uniform and highly variable, ochraceous brown with yellowish, rufous, or olivaceous casts. Ears of the same color than the dorsum and with a tuft of hairs in front. Laterals clearer than dorsum and more richly colored in some specimens. Venter paler, whitish gray, buffy gray, yellowish or even ruddy, clearly contrasting with dorsum. Chin with few white hairs that do not form a conspicuous patch. Inguinal region with a more intense tinge than the rest of the venter in some specimens. Fore and hind feet covered with whitish or buffy

hairs. Tail strongly bicolored, dorsally blackish-brown and ventrally whitish or buffy, densely or sparsely covered depending on the analyzed populations and individuals.

The skull is the smallest among the *Akodon* species of northwestern Argentina. Rostrum short, with very narrow and shallow zygomatic notches and frontal sinuses not well developed. Interorbital region comparatively broad, with hourglass shaped and with margins rounded or slightly squared. Zygomatic arches not flared, braincase small and inflated, with temporal and lambdoid crests not well developed. Zygomatic plate narrow with anterior border straight or slightly concave and generally slopes gently backward from bottom to top. In most of the studied specimens the posterior ascending process of alisphenoid does not reach the squamoso-alisphenoid groove or only touch their lower margin. Hamular process of squamosal delicate, but in a few individuals it is strongly built. Incisive foramina generally extended to the protocone of M1, but in some individuals its reach the hypoflexus or even further back. Mesopterygoid fossa very narrow, its anterior margin rounded or slightly squared and with lateral margins straight and slightly divergent backward. Parapterygoid fossa generally broader than mesopterygoid, with convex border and slightly divergent backward. Mandibular ramus very delicate. Masseteric crest extends slightly behind the anterior margin of m1. Capsular projection generally poorly developed and situated at the same level or behind the coronoid process. Angular process is less extended backward than the condyle.

Upper incisors orthodont or slightly opistodont. The procingulum and anteromedian flexus of M1 are well developed. Anteroloph and mesoloph are always present and in some individuals an enteroloph can be observed. The M2 has a conspicuous mesoloph and the M3 shows great variability. In old individuals it is completely oval shaped but in young ones anteroflexus, metaflexus and hipoflexus are present. The m1 has the procingulum and anteromedian flexid well developed and presents protostylid and ectostylid. In some individuals a remnant of metastylid and mesostylid can be observed. The m2 retains only the labial stylid although some specimens have a very small ectostylid. The m3 presents deep labial and lingual flexids. Some individuals show a small protostylid.

Karyotype: $2n = 34$, $FN = 40$, based on six specimens from León, Jujuy, and two from El Cadillal, Tucumán (Barquez *et al.*, 1980; Vitullo *et al.*, 1986 as *A. puer*).

Variation: We have observed substantial morphological variation for this species. Within the same population, we find pale and dark individuals, some of them with striking rufous tones, particularly lactating females. Among the cranial characters, the development of zygomatic notches, zygomatic plate, and the thickness of hamular process show some variability. We also observed morphometric variations for individuals of the same age and population, with remarkable differences among some of the studied localities. In addition, consistent variation in the coloration pattern with elevation and some geographic variation for some morphometric variables are also apparent. The specimens from high altitude populations are conspicuously paler than those from lower localities, showing more buffy tinges in the coloration of the fur and more developed eyerings. These populations come from open environments characterized as the ecotone between humid grasslands and semiarid areas (e.g., the Prepuna or impoverished grasslands of high-Andean region). Specimens from central Salta and central Tucumán provinces are on average smaller than individuals from Bárcena and Reyes, southern Jujuy, near the type locality.

Comparisons: Externally this species can be confused with *A. boliviensis* and young individuals of *A. spegazzinii*. The differences between *A. caenosus* and *A. boliviensis* were described in detail by Myers *et al* (1990) and are summarized above.

In areas of sympatry *A. caenosus* and *A. spegazzinii* follow similar variation patterns in coloration through altitudinal gradients. However, many morphometric values and several cranial characters are useful in specimen determination. In 15 of the 20 analyzed morphometric variables, *A. caenosus* is significantly smaller than *A. spegazzinii* (Tables 1 and 2). This is also verified by the minimum overlap in the PCA analysis (Fig 2) and the lack of missclasifications in the DA. In addition, *Akodon caenosus* shows narrower and shallower zygomatic notches, comparatively broader interorbital constriction, temporal and mastoid ridges less developed, narrower mesopterygoid fossa and less hypsodont molars. The average percentage of genetic divergence between these species is the greatest (7.7%) observed for the *boliviensis* group in northwestern Argentina (Table 12).

Akodon caenosus and *A. sylvanus* represent two extremes in the morphometric variation observed within the *boliviensis* group in northwestern Argentina (Tables 1 and 2; figure 2). *Akodon caenosus* is, furthermore, paler than *A. sylvanus*, showing a more evident contrast between dorsum and venter, and has more developed eyerings. The skull of *A. caenosus* has a shorter and narrower rostrum, less swollen frontal sinuses, narrower braincase and interorbital region and a narrower mesopterygoid and parapterygoid fossa. The upper incisors in *A. caenosus* are less orthodont and the molars less hypsodont than *A. sylvanus*. Additionally, these species show a high average percentage of genetic divergence (6.7%).

The differences between *A. caenosus* and the new species are listed under the treatment of the latter.

Distribution: *Akodon caenosus* is the more broadly distributed species of the *boliviensis* group in northwestern Argentina, with records from northernmost Salta to southern Catamarca, from 400 m to 3100 m elevation (Fig. 7).

Habitat: Most of the records come from Yungas environments, from the lower altitudinal belt to high altitude grasslands. Notwithstanding, we have recorded the species in Chacoan environments near the ecotone with Yungas and in the lower altitudinal limit of the High Andean grasslands.

Natural history: Although we have recorded specimens in reproductive condition throughout the year, most of the individuals were active between November and January. We observed the highest proportion of molting animals in fall and winter. In their broad distributional range *A. caenosus* can be found coexisting with many different species depending on the altitudinal or latitudinal sector in northwestern Argentina. Thus, in the north *A. caenosus* was captured alongside *Akodon sylvanus*, *A. simulator*, *Oxymycterus paramensis*, *Oligoryzomys* cf. *O. flavescens* and *Oligoryzomys* sp. in high altitudinal grasslands at 1400 m. At the same latitude in upper belts above 2000 m, *A. caenosus* is sympatric with *A. boliviensis*, *Necromys lactens*, *N. amoenus*, *Calomys musculus* (Thomas), *Phyllotis caprinus* Pearson, *P. osilae* and *P. xanthopygus*. In the south, in Yungas areas of Tucumán province, the species was caught together with *Akodon spegazzinii*, *A. simulator*, *Necromys lactens*, *N. lasiurus* (Lund), *Oxymycterus paramensis*, *Oxymycterus wayku* Jayat *et al.*, *Oligoryzomys* cf. *O. flavescens*, *Oligoryzomys* sp., *Phyllotis anitae*, *P. osilae*, *Andinomys edax* and *Abrothrix illutea*. At this same latitude in Chacoan environments in transition with Yungas *A. caenosus* is sympatric with *Akodon spegazzinii*, *A. simulator*, *Necromys* sp., *Oligoryzomys* cf. *O. flavescens*, *Oligoryzomys* sp., *Calomys* sp. and *Graomys centralis*.

Comments: Although originally described as a subspecies of *Akodon puer* (Thomas 1918), the form *caenosus* was soon considered as a valid species by Thomas (1920); this latter suggestion was followed by Cabrera (1961), Barquez *et al.* (1980), and Mares *et al.* (1981). Vitullo *et al.* (1986) and Apfelbaum & Reig (1989) considered specimens from León, Jujuy Province (type locality of *caenosus*) as *A. puer* and Myers *et al.* (1990) followed this position (but see Hershkovitz 1990), considering *caenosus* as the subspecies of *A. puer* inhabiting northwestern Argentina (see also Barros *et al.* 1990). Anderson (1997) also recognized three subspecies for *A. puer* but noted the priority of the name *lutescens* over *puer*. Since then, the nomenclature used for this species has been constantly changing. Capllonch *et al.* (1997) and Mares *et al.* (1997) listed *caenosus* as valid species whereas Díaz *et al.* (1999, 2000) recognized *caenosus* as subspecies of *puer* for the populations of the northwestern Argentina. Notwithstanding, Díaz (1999) and Díaz & Barquez (2007) considered again the nominal form *caenosus* as representing a valid biological species including *A. lutescens puer* as an additional sigmodontine species in northwestern Argentina. Musser & Carleton (2005) and Pardiñas *et al.* (2006) followed the conclusions of Myers *et al.* (1990).

Díaz *et al.* (1999) described *Akodon aliquantulus*, from the ecotone between upper Yungas forest and highland grassland in Tucumán province (Las Agüitas, Cumbres del Taficillo, 1700 m, 26° 42' S, 65° 22' W), and related it to the *A. boliviensis* group on the basis of its morphology. The unimpressive morphological distinction from *A. lutescens*, based only on multivariate ordinations and univariate overlap, induced some authors to recommend a revision of the status of this form (Musser & Carleton 2005; Jayat *et al.*, 2008a). This species was diagnosed and differentiated from *A. caenosus* (as *A. puer caenosus*) and *A. spegazzinii* on the account of being smaller in a number of measurements and the “weakly developed eye ring” of two individuals originally preserved in fluid and then prepared as skin plus skull. We could not distinguish the type specimens of *A. aliquantulus* from *A. caenosus* following the diagnosis provided by Díaz *et al.* (1999). Most of the

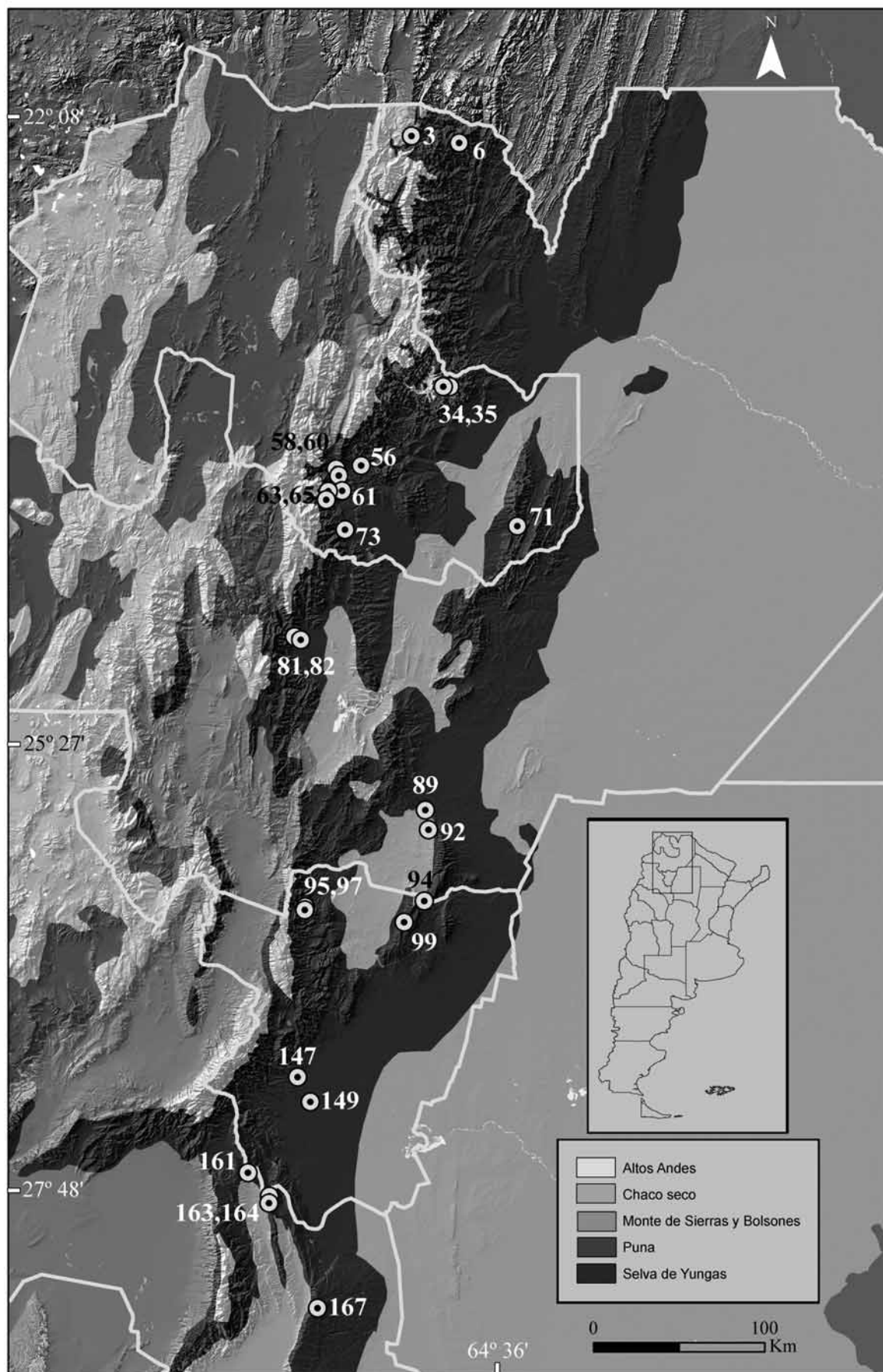


FIGURE 7. Recorded localities of *A. caenosus* in Northwestern Argentina. Localities and geographic position in Appendix II.

characters used for the diagnosis of *A. aliquantulus* (centered, as said, on a few external and cranial dimensions) are subtle, highly variable in many sigmodontine species, and what is most important are age-dependent. Although Díaz *et al.* (1999) considered the two specimens as old individuals (age-class 5) our observations indicate that they must be assigned to the age class 4 of Myers (1989) (Figure 8). The morpho-

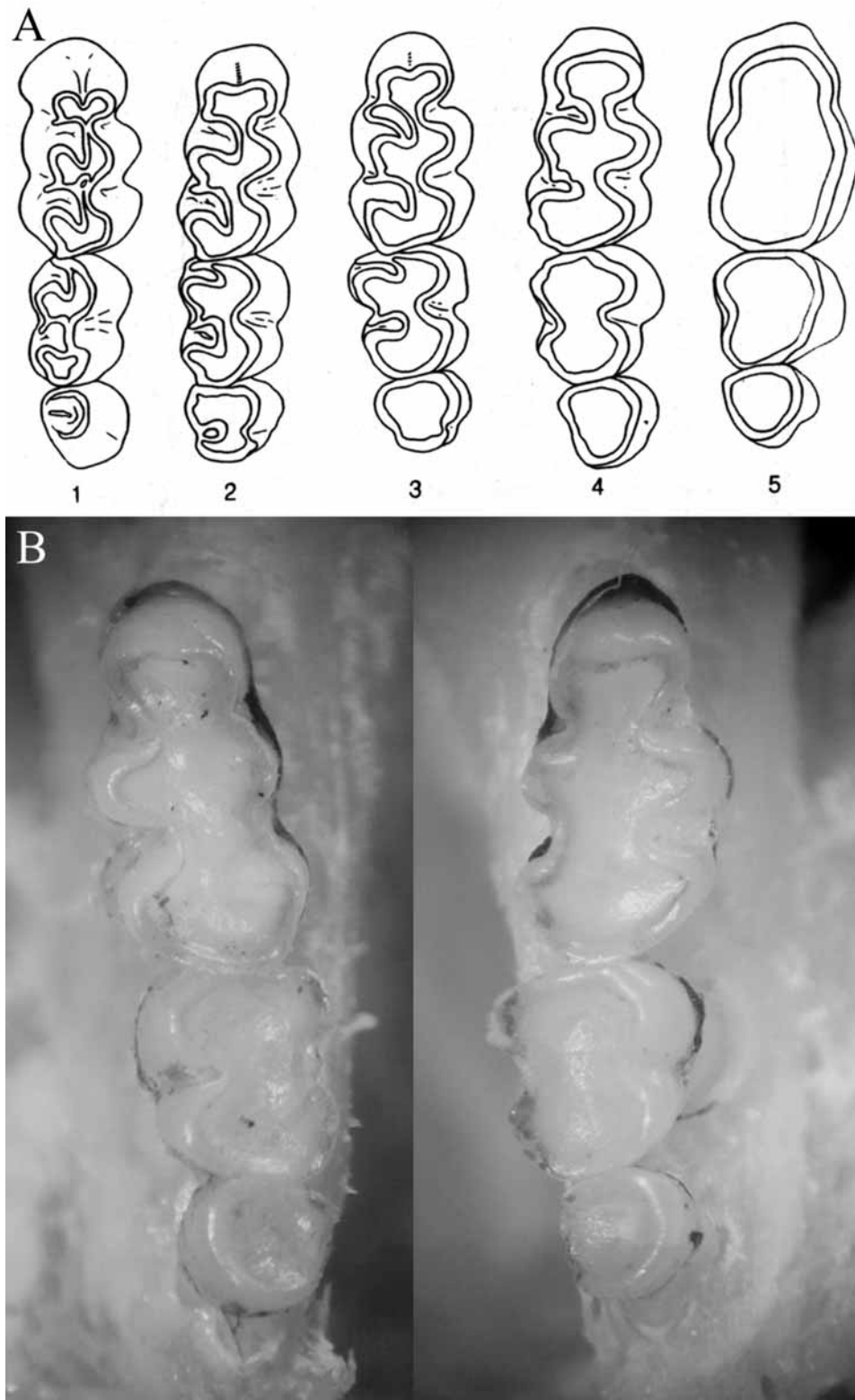


FIGURE 8. Comparison between the toothwear classes of Myers (1989) (A) and *Akodon aliquantulus* left upper molar rows (left; Holotype, CML 6122 and right; paratype, CML 6121) (B). Scale bar= 1 mm.

metric distinction between *A. aliquantulus* and *A. caenosus* was based on a PCA analysis with a relatively low explained variance (63.3%, 7.9% and 5.1% for components 1, 2 and 3 respectively) and the statistic significance of the observed differences was not provided by the authors. We think that the erroneous assignment of age for the two specimens by Díaz *et al.* (1999) misinform their conclusions. The analysis of table 1 of Díaz *et al.* (1999) clearly indicates the overlap between *A. aliquantulus* specimens and *A. caenosus* exemplars of age-class 4 (see also Table 9 of this work). Remarkably, even some of the diagnostic skull measurements (e.g. braincase breadth, maxillary toothrow length) are included in the observed range for age-class 5 individuals of *A. caenosus*. Moreover, all the characters mentioned in the description of *A. aliquantulus* are within the levels of morphological variation observed in *A. caenosus* of Northwestern Argentina. Therefore, we find no defensible argument to consider *A. aliquantulus* as a distinct species and consider it a junior synonym of *A. caenosus*.

***Akodon spegazzinii* Thomas, 1897**

Akodon spegazzinii Thomas, 1897. Annals and Magazine of Natural History, 6(20): 216.

Akodon tucumanensis J. A. Allen, 1901. Bulletin of the American Museum of Natural History, 14: 410.

Akodon alterus Thomas, 1919. Annals and Magazine of Natural History, 9(3): 496.

Akodon leucolimnaeus Cabrera, 1926. Revista Chilena de Historia Natural, 30:320.

Holotype: B.M. 97.5.5.14.

Type locality: Lower Cachi (Thomas 1897). Probably Thomas referred to the lower course of the Río Cachi which passes through the town of Cachi, close to the junction with the Río Calchaquí. The town is situated in the Department of Cachi, in central Salta Province (25° 07' 11.93"S, 66° 09' 47.00"W, 2341 m).

Description: Because of the terse description of the species (Thomas 1897) and the paucity of specimens available to later workers (Myers *et al.* 1990; Díaz 1999), here we offer a more detailed description of *A. spegazzinii* based on topotypic specimens but including also material coming from the known range of the species.

General coloration remarkably variable, with individuals ochraceous brown, ruddy brown, fulvous brown, and buffy brown, and darker or paler depending on individuals and populations. Dorsal coloration uniform from head to rump and with more or less spattered black or dark brown hairs. The yellow eye ring are always present but its development is variable. Ears of same color as dorsum. Flanks with the same coloration as dorsum but some clearer. The venter is buffy, ruddy gray or ochraceous gray and contrast lightly with the dorsum. The chin is covered by a few isolated white hairs that do not form a conspicuous patch. Inguinal region of some individuals with a more intensive hue. Both fore and hind feet covered with bicolored hairs and whitish, buffy or greyish in appearance. Claws covered with tufts of hairs greyish brown at the base and tipped white. Tail conspicuously bicolored, dorsally brown or blackish brown and ventrally whitish or buffy, more or less furred depending on population.

Skull of intermediate size for the *boliviensis* group and characterized by a well-developed rostrum, relatively narrow zygomatic notches, and lightly swollen frontal sinuses. Interorbital region hourglass shaped, with rounded or slightly squared margins and without overhanging borders. Zygomatic arches not specially flared. The braincase is relatively inflated, but some variation exists among individuals. Temporal and lambdoid crests relatively well developed, mainly in old individuals. Dorsal profile of the cranium relatively arched, especially in young specimens. Zygomatic plate breadth generally intermediate in size but highly variable among individuals. The anterior margin is straight or slightly concave with its dorsal root gently sloping backward. Hamular process generally slender and expanded in its distal end. Posterior ascending process of alisphenoid reaches or surpasses the squamoso-alisphenoid groove. Postglenoid foramen and subsquamosal fenestra are developed, and the ratio between them is highly variable. Incisive foramina relatively long, extended in some specimens to the anterior border of hypocone of M1. Mesopterygoid fossa of intermediate breadth for the group, with the anterior margin slightly rounded or squared and with the lateral borders straight and slightly divergent backward. The medial process of posterior palate can be present but never is

well developed. Posteropalatal pits generally tiny and situated at the same level or slightly backward with respect to the anterior margin of mesopterygoid fossa. Parapterygoid fossae of the same breadth or slightly broader than mesopterygoid fossa, relatively shallow, with lateral margins straight or slightly convex, diverging backwards. Tympanic bullae not especially developed with Eustachian tubes generally broad and short. Mandibular ramus delicate. Anterior end of masseteric crest situated just behind the level of the anterior border of M1. The development and position of the capsular projection is variable: in general, it is conspicuous and situated slightly behind the posterior border of the coronoid process. This process is delicate and extends just above the condyloid process. The condyle extends behind the posterior margin of angular process.

Upper incisors orthodont, with yellowish orange enamel. Molars with crested crown. M1 with well developed procingulum and anteromedian flexus. The anteroloph is conspicuous, the mesoloph is short and the enteroloph is very small (sometimes missing). A small parastyle can be observed in some specimens. The posteroflexus is poorly developed. M2 with a remnant of anteroloph, which determines a relatively well-developed paraflexus. A weak mesoloph and a very shallow protoflexus and posteroflexus also characterize this molar. M3 with paraflexus and metaflexus clearly visible in most of the examined individuals (excepting very old individuals), sometimes as enamel islands. This molar is not “8” shape because the hypoflexus is vestigial and disappears at a very young age. The m1 shows a conspicuous procingulum, well-developed anteromedian flexid and anterolabial cingulum, a tiny ectostylid, and a vestigial mesolophid. The m2 shows a very shallow protoflexid; a tiny ectolophid and a vestigial mesolophid are observable in a few specimens. The m3 presents a remnant of protoflexid, a mesoflexid and a transverse and conspicuous hypoflexid, making it “S” shaped. This molar has no trace of posteroflexid.

Akodon spegazzinii has 13-14 thoracic ribs; the vertebral column includes 13-14 thoracic, 7-8 lumbar, and 23-26 caudal vertebrae (n = 19).

Karyotype: 2n = 40, FN = 40, based on four specimens from Catamarca and one from Tucumán (Barquez *et al.* 1980; Myers *et al.* 1990).

Variation: There is considerable variation in external characters among the different populations of *A. spegazzinii*. Most of these differences probably reflect the different environments from where they were trapped. Populations from humid and low altitude areas are darker, with predominance of black guard hairs. This condition is extreme in populations living in Yungas forest. On the other hand, those populations from open and semiarid environments, such as the Monte desert (e.g. Cachi, type locality of *A. spegazzinii*) and Puna, are remarkably paler. Moreover, specimens from high altitude localities have fur, ears and tails more densely covered and with longer hairs. Variation within populations includes different color patterns, with ruddy, drabby and dark brown animals. These variations were observable even in mice trapped in the same traplines, in some cases related to reproductive condition or the age of individuals. For example, lactating females were particularly reddish in hue and young individuals darker. Morphometric differences are also conspicuous, even in individuals of the same age class. Some qualitative characters also show some variability. The zygomatic plate is highly variable, with both straight or concave anterior borders more or less sloping backwards. The zygomatic notches can be more or less narrow and shallow. The mesopterygoid fossa can be more or less broad and its anterior border rounded or squared. Our genetic sample includes 17 specimens of *A. spegazzinii* collected at 10 localities from Catamarca, Salta, and Tucumán provinces. This sample has high haplotypic diversity with 16 haplotypes recovered. However, all are similar as average pairwise comparison among them is 1.2%, and geographic structure is nonexistent.

Comparisons: For comparisons between *A. spegazzinii* and *A. boliviensis* or *A. caenosus* please see those accounts. Below we compare it with the remaining species of *Akodon* present in Yungas of Northwestern Argentina.

Jayat *et al.* (2007a) made detailed comparisons between *A. spegazzinii* and *A. sylvanus*. The most relevant differences included general size, with *A. sylvanus* slightly larger for all the morphometric characters analyzed (Tables 1 and 2). The PCA (Fig. 2) shows some overlap for this species but the DA was very efficient, with only four of 139 individuals not reciprocally well classified. *Akodon sylvanus* presents also relatively less developed zygomatic notches, more inflated frontal sinuses, broader mesopterygoid fossa, broader and deeper parapterygoid fossa, more developed foramen oval, and conspicuously larger foramen magnum. The general

coloration of *A. sylvanus* is included in the observed variation for the different populations of *A. spegazzinii*. Notwithstanding, the latter has a more conspicuous eye ring and white spot on the chin. The average percentage of genetic divergence between these species is 4.9% (Table 12).

Akodon budini is substantially larger and shows very distinguishable craniodental characteristics. It has a very broad braincase and mesopterygoid fossa, elongated rostrum and relatively narrow and shallow zygomatic notches. The mandible is also distinguishable by the short masseteric crest and lightly developed capsular projection. Moreover, the conspicuous hypsodont molars of *A. budini* uniquely characterize this species.

Akodon simulator and *A. spegazzinii* are sympatric in parts of their ranges; however, these species are easily differentiable by the larger size of *A. simulator* and, more importantly, several characteristics of the skin. For example, *A. simulator* has a more greyish general coloration, more contrast between dorsum and venter, and presents a conspicuous white spot on chin and throat. The skull of *A. simulator* is more robust, with more divergent and squared interorbital region and broader mesopterygoid fossa. Furthermore, this species has more proodont incisors.

The differences between *A. spegazzinii* and the new species are considered in detail below.

Distribution: *A. spegazzinii* occurs in southern and central areas of northwestern Argentina, from 24° 27' S in central Salta to 28° 47' S in southern Catamarca, from 400 to about 3500 m. A single specimen (CNP 1897) is known from southern Mendoza province (Laguna Llanquanelo, 1335 m, Malargüe Department, 35° 45' S, 69° 08' W); this locality, the first reported for Mendoza province, extends the known distribution of *A. spegazzinii* 850 km to the south. Records from La Rioja province (Thomas 1920b as *A. alterus*), corresponding to specimens not examined by us, need confirmation (Fig. 9).

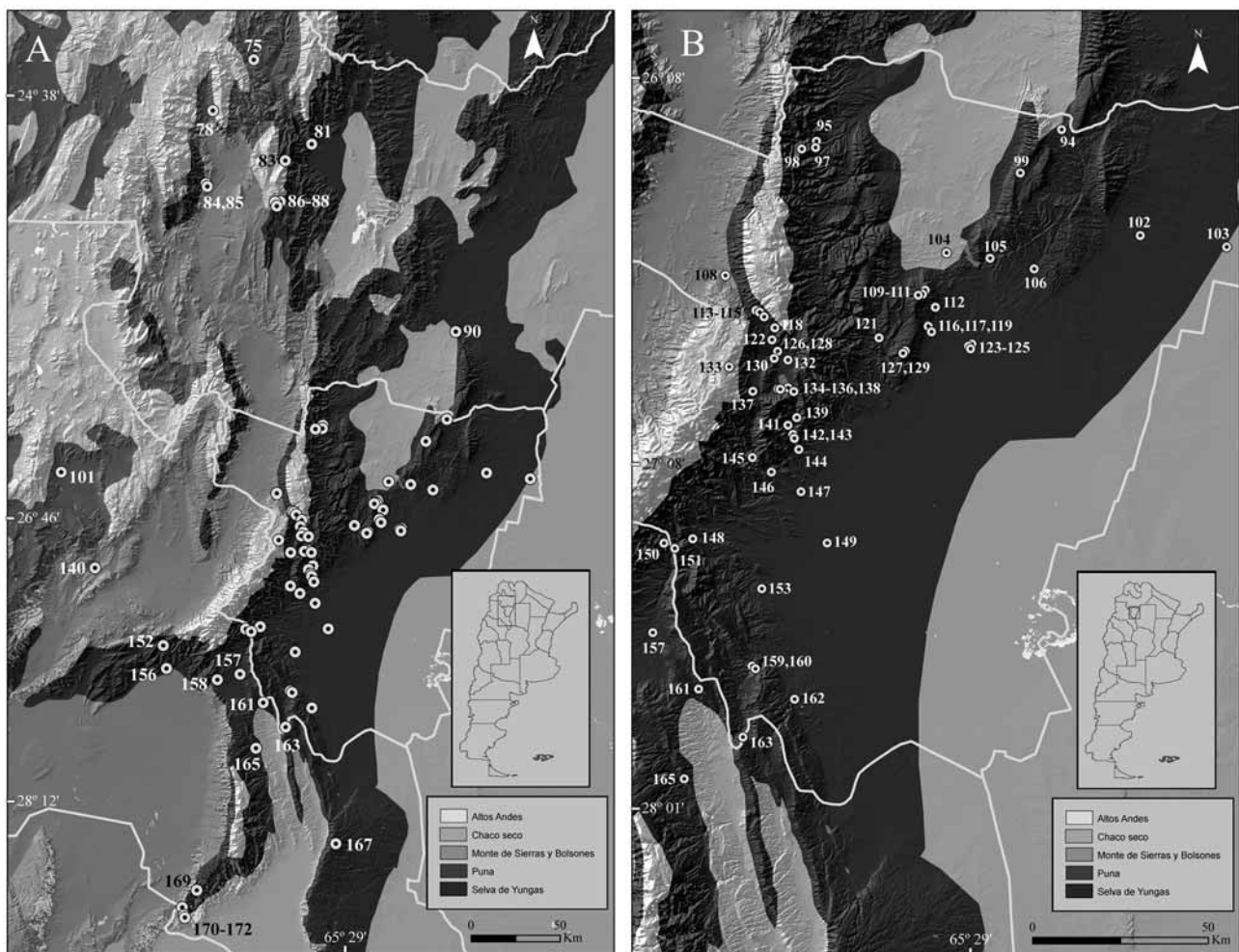


FIGURE 9. Recorded localities of *A. spegazzinii* in northwestern Argentina. Localities and geographic position in Appendix II.

Habitat: *A. spegazzinii* occurs in all altitudinal belts of the Yungas forest (even ecotonal areas with low-land thorn woodlands of Chaco), Monte de Sierras y Bolsones, Puna and Altos Andes. Thus, the species inhabits forests, woodlands and grasslands. In dry areas, such as the Monte desert and Puna, it is only found in grassy zones along streams and rivers. *Akodon spegazzinii* is especially abundant in cloud grasslands in the upper altitudinal belts of Yungas, where it constitutes the dominant sigmodontine species (Fig. 10).

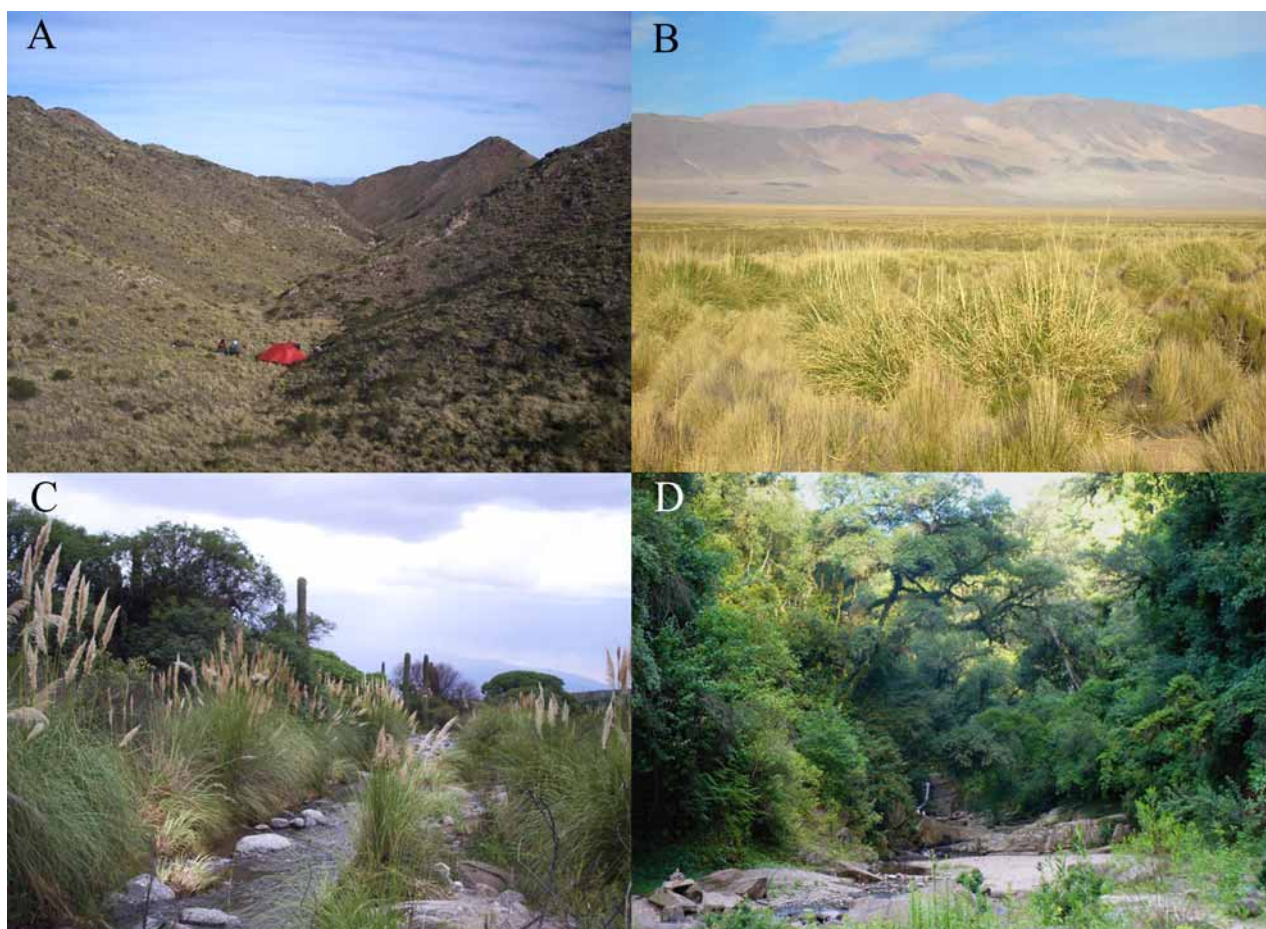


FIGURE 10. Habitats of the type localities of the four nominal forms associated with *A. spegazzinii*: A) High altitudinal grasslands at 2400 m, near Otro Cerro, type locality of *A. alterus* Thomas. B) Puna environments in Laguna Blanca, 3200 m, type locality of *A. leucolimnaeus* Cabrera. C) Monte environments near Cachi, 2500 m, type locality of *A. spegazzinii* Thomas. D) Rain forest at Horco Molle, about 700 m, near the type locality of *A. tucumanensis* J. A. Allen.

Natural History: Reproduction appears to occur yearlong, with a clear peak between November and April. Most of the individuals were molting in fall and winter (April to August). As it can be expected from the general ubiquity of the species, *Akodon spegazzinii* coexists with a number of sigmodontine species in the region of interest. In high altitudinal localities, above 3000 m, it has been registered alongside *Calomys lepidus* (Thomas), *Eligmodontia* sp., *Phyllotis xanthopygus*, *Reithrodon auritus* (G. Fischer) and *Neotomys ebriosus* Thomas. In cloud grasslands it was caught with *Necomys lactens*, *N. lasiurus* and *Phyllotis osilae*. In forested areas of Yungas *A. spegazzinii* coexists with *Abrothrix illutea*, *Oligoryzomys* sp., *Oxymycterus paramensis*, *O. wayku* and *Phyllotis anitae*. In ecotonal environments of Yungas and Chaco, *A. spegazzinii* was caught with *Calomys fecundus* Thomas, *Graomys centralis* and *Necomys* sp. Other species broadly distributed in the region, such as *Akodon caenosus*, *Akodon simulator*, *Oligoryzomys* cf. *O. flavescens*, *Calomys musculus* and *Andinomys edax*, have also been registered in sympatry with *A. spegazzinii*.

Comments: Myers *et al.* (1990) viewed *spegazzinii* as a valid species and considered *tucumanensis* (type locality Tucumán, 450 m) as a subspecies. Moreover, *Akodon alterus* (from Otro Cerro, 3000 m) was consid-

ered “properly allied” to these forms. Blaustein *et al.* (1992) studied the status of *A. alterus* and *A. tucumanensis* and found weak morphologic and morphometric differences and identical cytogenetic characteristics in the studied populations. Notwithstanding, Mares *et al.* (1997) listed *alterus* and *tucumanensis* as valid species mainly based on their different ecological associations (see also Capllonch *et al.* 1997; Díaz *et al.* 1997; Díaz 1999). In the last ten years the treatment of *alterus* continued to be confused, alternatively considered as a valid species (Díaz 1999; Díaz & Barquez 2007), as a subspecies of *A. spegazzinii* (Díaz *et al.* 2000) or simply as a synonym of this last form (Musser & Carleton 2005; Pardiñas *et al.* 2006). On the other hand, *A. tucumanensis* has been recently considered as a synonym of *A. spegazzinii* (Musser & Carleton 2005), as a subspecies of this last form (Pardiñas *et al.* 2006) or as a valid species (Díaz & Barquez 2007). Cabrera (1926) described *A. leucolimnaeus* based on two specimens of Laguna Blanca and one from Salar de Antofalla, Catamarca Province. Gyldenstolpe (1932) suggested that this form be included in the genus *Necomys* Ameghino. For many years this nominal form was considered as a synonym of *Necomys lactens* Thomas (Cabrera 1961; Reig 1987; Musser & Carleton 1993; Mares *et al.* 1997) but Galliari *et al.* (1996) regarded it a valid species, allied to the *A. boliviensis* group. This view was maintained by Musser & Carleton (2005) and Pardiñas *et al.* (2006) but its status was considered provisional.

Here we offer the first detailed description for *A. spegazzinii* (see above). We formally tested the taxonomic status of *A. alterus* and *A. leucolimnaeus* and established their conspecificity with respect to *A. spegazzinii*. Moreover, we corroborated the conspecificity of *tucumanensis* and *A. spegazzinii*, as suggested by Myers *et al.* (1990). No clear or constant morphologic differences in skull characters among the specimens coming from Cachi, Laguna Blanca, vicinities of Otro Cerro, and Yungas forest in Tucumán were found (Fig. 11). Moreover, haplotypes recovered from specimens collected near the type locality of *alterus*, and assignable to this form, and at the type localities of *leucolimnaeus* and *tucumanensis* form part of the *spegazzinii* clade (Fig. 1). Therefore, the combination of genealogical, genetic (Table 12), morphologic, and morphometric (Tables 5- 8) evidence prompt us to suggest that *A. alterus*, *A. leucolimnaeus*, and *A. tucumanensis* are conspecific with *A. spegazzinii*. We submit that the lack of large samples, coupled with the geographic and ecotypic variation in pelage described above, misinformed the original authorities of these nominal forms. Specimens from Tucumán (type locality of *tucumanensis*) have very dark tones, almost black in some exemplars, which is typical of humid cloud forest dwellers. On the contrary, specimens from Laguna Blanca, in puna environments, have very clear tones, with buffy brown coloration. Individuals coming from Cachi and Otro Cerro are intermediate in coloration although they also differ among them. Cachi presents the typical environmental features of Monte de Sierras y Bolsones, with arid to semi-arid conditions, while Otro Cerro is dominated by relatively humid grasslands communities that are characteristic of the upper belt of Yungas in transition with high Andean environments (Fig. 10).

***Akodon sylvanus* Thomas, 1921**

Akodon sylvanus Thomas, 1921. Annals and Magazine of Natural History, 9 (7):184.

Holotype: B.M. 21.1.1.27, an old male.

Type locality: “Sierra de Santa Barbara, S.E. Jujuy. Type from Sunchal, 1200 m” (Thomas 1921:185). Sunchal is located in Santa Bárbara Department, Jujuy Province (24° 15' S, 64° 26' W, 1454 m).

Description: We summarize here the most relevant characters for comparison and refer the reader to Jayat *et al.* (2007a) who redescribe this species in detail. The dorsal coloration is uniform, olivaceous brown finely spattered with black hairs, not well contrasting with ventral region. Ears with the same color as the dorsum. Eye rings absent or poorly developed. White spot on the chin barely developed. Tail slightly bicolored, ventrally clearer. Skull relatively narrow and elongated, with prominent rostrum. Zygomatic notches not particularly broad nor deep. Zygomatic arches comparatively slightly expanded and braincase poorly inflated. Interorbital region with rounded margins. Mesopterygoid fossa relatively narrow, with anterior border rounded or squared, without medial process. Upper incisors orthodont. The molars are the most hypsodont among the

species of the *boliviensis* group. M1 with well developed anteroloph-parastyle. In some specimens the mesoloph extends to the lateral margin of the teeth. Mesoloph and paraflexus of M2 less developed than M1. M3 with poorly developed paraflexus and conspicuous hypoflexus. Protostylid of m1 well developed but the metastylid, mesolophid and mesostylid are tiny. In m2 there is no evidence of either an ectolophid (ectostylid) or mesolophid. The m3 shows hipoflexid and mesoflexid well developed.

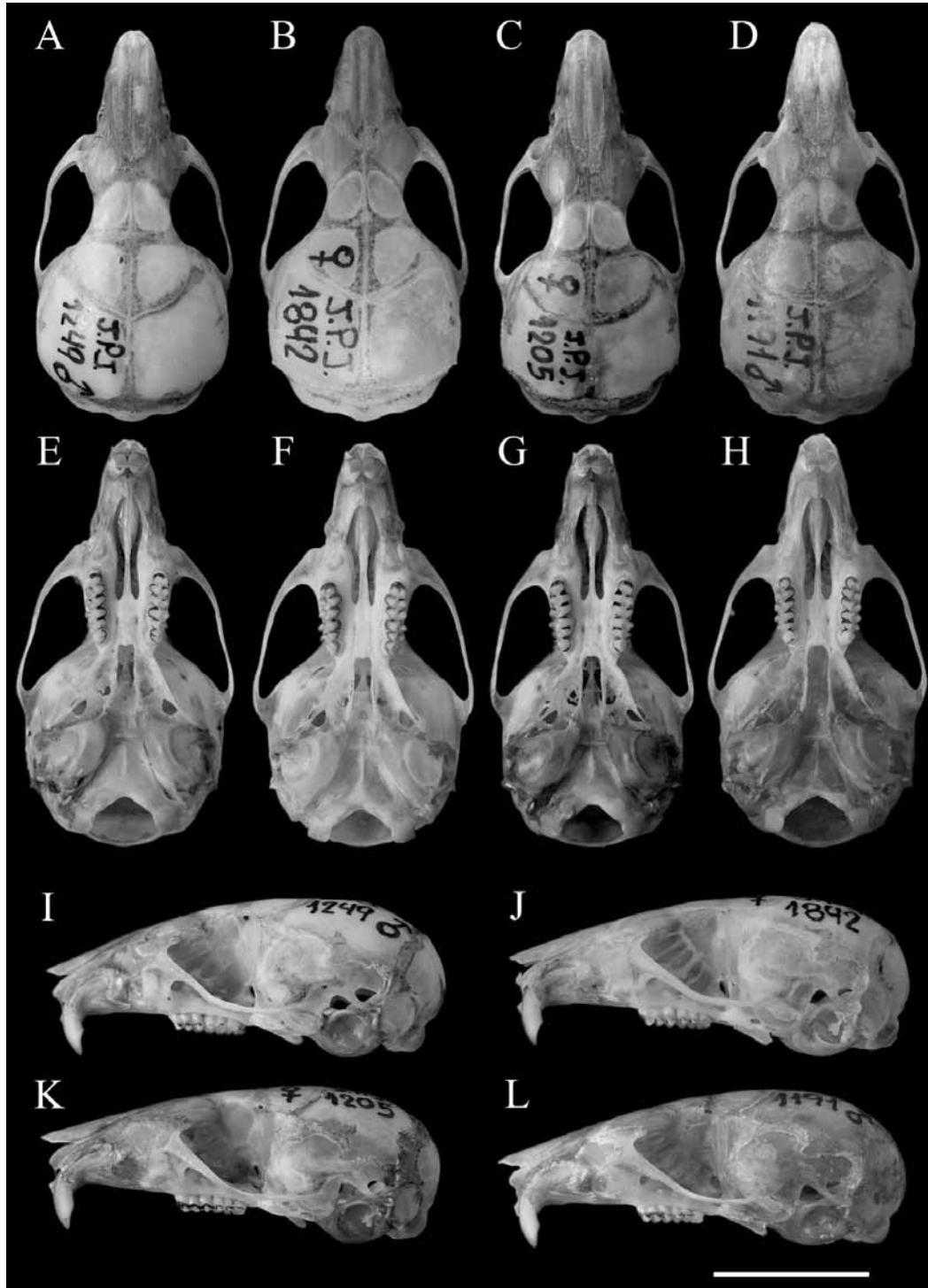


FIGURE 11. Dorsal, ventral, and lateral views of skulls in *Akodon alterus*, Thomas (JPJ 1249; A, E and I), *A. leucolimnaeus*, Cabrera (JPJ 1842; B, F and J), *A. spegazzinii*, Thomas (JPJ 1205; C, G and K) and *A. tucumanensis*, J. A. Allen (JPJ 1191; D, H and L). All specimens of age class 2. Scale bar = 10 mm.

Karyotype: Unknown.

Variation: Individuals near the type locality are uniform in color with some specimens with a more intense hue. Most variation in cranial morphology is age-dependent: young specimens present proportionally broad braincases and frontal sinuses but less developed zygomatic notches. Notwithstanding, the breadth of the zygomatic plate is highly variable among individuals of the same age class. The hamular process of the squamosal also is variable, from extremely thin to relatively broad and the capsular projection in mandible can be a slight elevation or a distinctive capsule.

Comparisons: Comparisons of *Akodon sylvanus* with *A. boliviensis*, *A. caenosus*, and *A. spegazzinii* are given in the treatment of these species. In addition, Jayat *et al.* (2007a) distinguished *A. sylvanus* from *A. azarae* and other species of *Akodon* present in northwestern Argentina. Detailed comparisons between *A. sylvanus* and the new species are described below.

Distribution: *Akodon sylvanus* is restricted to Sierra de Santa Barbara and neighboring areas in Jujuy province (Fig. 6).

Habitat: the species has been recorded at all altitudinal belts of the Yungas forest, from 700 m, in transitional pedemontane forest, to 2300 m in cloud highland grasslands. Additional specimens were collected in grasslands associated with Chacoan environments at 1400 m (Jayat *et al.* 2006, 2007a, 2008a)

Natural History: most of the individuals caught in winter (June) were reproductively inactive; sexual activity appears to start in late August. *Akodon sylvanus* was caught with other 10 sigmodontine species. In La Herradura, a few kilometers from the type locality, *A. sylvanus* was registered in sympatry with *Akodon caenosus*, *A. simulator*, *Oligoryzomys* cf. *O. flavescens*, *Oligoryzomys* sp. and *Oxymycterus paramensis*. In El Piquete, pedemontane forest in Sierra de Santa Bárbara, *A. sylvanus* is sympatric with *A. simulator*, *Oligoryzomys chacoensis*, *Oligoryzomys* cf. *O. flavescens*, *Oligoryzomys* sp., *Euryoryzomys legatus*, *Rhipidomys austrinus* and *Calomys* cf. *C. fecundus*. In cloud highlands grasslands in Sierra del Centinela, *A. sylvanus* coexists with *Necromys lactens*, *Oligoryzomys* cf. *O. flavescens*, *O. paramensis* and *Phyllotis osilae nogalaris*. In their distributional range *A. sylvanus* is frequently caught, with 40 to 60% of all sigmodontine individuals in La Herradura (n = 50) and Sierra del Centinela (n = 46).

Comments: Thomas (1921) described *Akodon sylvanus* from southeastern Jujuy province and later erected *A. sylvanus pervalens*, from Tarija Department, Bolivia (Thomas, 1925). The taxonomic status of both taxa has fluctuated since then. Yepes (1933) indicated the presence of *pervalens* in Argentina, from Aguaray (northern Salta Province), listing both subspecies in Argentina (Yepes 1935). Cabrera (1961) included *sylvanus* in the synonymy of *A. azarae* (Fischer) whereas *pervalens* was synonymized with *A. varius* Thomas. Myers (1989) tentatively treated *azarae* and *sylvanus* as different species and considered *pervalens* different from *varius*. Musser & Carleton (1993) considered *sylvanus* as a valid species (with *pervalens* as a subspecies). Díaz (1999), Musser & Carleton (2005) and Pardiñas *et al.* (2006) considered *sylvanus* as a valid species and different from *pervalens*. Recently, Jayat *et al.* (2007a), based on both genetic and morphologic analyses, validated *A. sylvanus* and incorporated it in the *boliviensis* group.

Recently, we erroneously assigned individuals from the area of Parque Nacional Baritú and Las Capillas to *Akodon sylvanus* (Jayat *et al.* 2007a). Morphological and molecular studies of more complete series of specimens of these areas indicate that they belong to *A. fumeus*. Consequently, some of the morphological, morphometric and distributional observations of Jayat *et al.* (2007a) are corrected here. Some characters previously considered as variations of *A. sylvanus*, such as a reddish hue and a broad mesopterygoid fossa, correspond to character states of *A. fumeus* specimens. Moreover, the smaller general size of these specimens lowered the average size of some of the measurements given by Jayat *et al.* (2007a) (compare Tables 1 and 2 of Jayat *et al.* [2007a] with Table 1 herein). In view of these amendments, the known distribution of *A. sylvanus* is restricted to southeastern Jujuy, in the vicinity of Sierra de Santa Barbara.

***Akodon polopi*, new species**

Akodon sp. sensu Polop, 1989:53. Studies on Neotropical Fauna and Environments 24:53–59.

Akodon boliviensis sensu Polop, 1991:115. Revista de la Universidad Nacional de Río Cuarto 11:115–121.

Akodon sp. sensu Pinna-Senn *et al.*, 1992 Mendeliana 10: 59–70.
Akodon alterus sensu Priotto *et al.*, 1996:135. Facena 12: 135–138.
Akodon boliviensis sensu Morando & Polop, 1997:132. Mastozoología Neotropical 4 (2): 129–136.
Akodon spegazzinii sensu D'Elía, 2003: 310. Cladistics 19:307–323.
Akodon spegazzinii sensu D'Elía *et al.*, 2003:354. Mammalian Biology 68:351–364.
Akodon spegazzinii sensu Kufner *et al.*, 2004:120. Ecología Aplicada 3 (1,2):118–121.
Akodon spegazzinii sensu Pardiñas *et al.*, 2005: 473. Journal of Mammalogy 86 (3):462–474.
Akodon spegazzinii sensu Rodrigues Gonçalves *et al.*, 2007: 23. Miscellaneous Publications of the Museum of Zoology, University of Michigan 197: 1–24.
Akodon spegazzinii sensu Smith & Patton, 2007: 831. University of California Publications in Zoology 134:1–981.
Akodon sp. sensu Jayat *et al.*, 2007a: 203. Mastozoología Neotropical 14 (2):201–225.

Holotype: MACN 23486, Adult male (age class 4), collected by J. Pablo Jayat, Pablo E. Ortiz, Daniel García Lopez, and Rodrigo Gonzalez on August 17, 2008 (original field number JPJ 2125), skin, skull, skeleton and tissues in alcohol (Figs. 12 and 13).



FIGURE 12. *Akodon polopi*, new species (holotype MACN 23486): dorsal (upper left), ventral (upper right) and lateral (middle) views of skull and labial view (bottom) of mandible. Scale bar = 10 mm.



FIGURE 13. *Akodon polopi*, new species (holotype MACN 23486): live trapped specimen.

Type locality: Pampa de Achala, 6 km E (by highway 34) from antenna repetidora La Posta, 2200 m (31° 36' 44.5" S, 64° 48' 48.7" W), San Alberto Department, Córdoba Province, Argentina (Fig. 14).

Diagnosis: A member of the Subfamily Sigmodontinae distinguishable from all other species of *Akodon* by the following combination of characters: size intermediate for the genus (mean values in mm for individuals of age class 4; length of head and body, 100; tail length, 70; condyloincisive length, 24.53; maxillary tooththrow length, 4.40); fur dense and soft; general coloration uniform, buffy brown; chin with a small but distinguishable white patch; claws on fore and hind feet somewhat long (mean values in mm for 10 individuals of age class 4 in the medial finger: 2.81 and 3.26 respectively); skull with the rostrum relatively short and broad; interorbital region hour-glass shaped but with sharply squared posterior margins; temporal and lambdoid ridges well developed; zygomatic plate relatively broad; mesopterygoid fossa narrow. Upper incisors slightly proodont; first lower molar with a conspicuous metastylid and mesostylid. Molecular apomorphies are listed in Table 13 (note that sequences of some *Akodon* species were not analyzed, and that only three haplotype of *Akodon polopi*, new species were available; therefore, these character states should be taken with caution).

Measurements of the holotype: External measurements (in mm): length of head and body, 103; tail length, 76; length of hind foot (with claw), 25; ear length, 15; weight (in g): 35. Cranial measurements (in mm): greatest length of skull, 26.80; condyloincisive length, 25.50; zygomatic breadth, 13.84; braincase breadth, 11.84; interorbital constriction, 4.58; maxillary tooththrow length, 4.60; nasal length, 10.10; mid rostral width, 5.00; diastema length, 7.12; length of incisive foramen, 6.54; width across occipital condyles, 6.70; breadth of zygomatic plate, 2.50. See Table 14 for measurements of paratypes.

Paratypes: Seven specimens collected at the type locality (CNP 1927, 1928; CML 7672, 7673; and MACN 23487, 23488, 23489) (Table 14).

Other referred specimens: Twenty one specimens from the type locality (JPJ 2118, 2120, 2121, 2123, 2126 to 2129, 2131, 2133 to 2135, 2139, 2141, 2144, 2146, 2147, 2149, 2150, 2158, 2159); four specimens from Pampa de Achala (CUNRC 2805, 10145, 10178, 50151); three specimens from Pampa de Achala, 2163 m (CUNRC 44748, 44749, 44750); three specimens from Pampa de Achala, 2247 m (CUNRC 44744, 44745, 44747), and nine specimens from Repetidora La Posta, Pampa de Achala, 2171 m (CNP 1500 to 1508).

Distribution: The new species is only known from few localities in Córdoba Province, Argentina: Pampa de Achala, a highland plateau situated in the Sierras Grandes (Polop 1989, 1991), three localities in Río Cuarto Department (Cerro de Oro, Puesto Gonzalez and La Ventana, all above 1500 m elevation; Priotto *et al.* 1996), and two additional sites in Pampa de San Luis, Cruz del Eje Department (SW of Pampa de San Luis, 1900 m, and near Cuchilla Nevada, 1700-1800 m; Kufner *et al.* 2004) (Fig. 14).

TABLE 13. Molecular synapomorphies of *Akodon polopi* new species 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 220 most parsimonious trees (1563 steps; CI = 0.287) resulted from the analysis of a cyt b matrix of 71 sequences of *Akodon*. Seventeen fixed derived character states were found in *A. polopi* new species. Of these, one derived character state, which is indicated by an asterisk, has not evolved independently in any other species of *Akodon*; this character has a consistency index < 1 because other character states (not the one present in *Akodon polopi* new species) has evolved independently in more than one clade of *Akodon*. The remaining 16 derived character states of *A. polopi* new species have also secondarily appeared in at least 1 species of *Akodon*.

	Nucleotide position / Codon position	Character State in <i>Akodon polopi</i> new species	Character consistency index
1	18/3	G	0.333
2	48/3	T	0.200
3	54/3	T	0.091
4	63/3	T	0.429
5	75/3*	G	0.286
6	222/3	T	0.167
7	384/3	C	0.167
8	387/3	G	0.400
9	444/3	C	0.056
10	513/3	T	0.125
11	516/3	G	0.200
12	579/3	T	0.200
13	580/1	T	0.143
14	615/3	T	0.167
15	618/3	T	0.143
16	717/3	T	0.333
17	786/3	T	0.500

TABLE 14. Measurements of seven paratypes of *Akodon polopi*, new species (age class 4). Abbreviations as provided in text.

Variable	Paratypes						
	CNP 1927	CNP 1928	CML 7672	CML 7673	MACN 23487	MACN 23488	MACN 23489
TBL	172	150	173	(181)	180	179	164
TL	76	60	72	(72)	74	71	68
HF	25	22	23	25	24	23	23
EL	16	15	14	15	15	15	14
W	27.5	16.0	25.0	27.0	36.5	26.0	20.5
MSL	26.30	24.00	25.86	27.02	26.90	26.00	25.14
CIL	25.16	22.78	24.64	25.44	25.36	24.70	23.64
RL	9.62	8.74	9.34	9.94	10.18	9.66	9.30
ZB	13.50	12.64	13.38	13.24	13.40	13.52	12.86
BB	11.46	11.54	11.78	11.48	11.58	11.46	11.14
IOC	4.64	4.42	4.56	4.38	4.66	4.66	4.30
MTRL	4.30	4.14	4.62	4.26	4.44	4.40	4.54
NL	9.28	8.30	8.98	9.94	9.92	9.14	9.28
RW2	5.00	4.50	4.88	5.00	5.20	5.00	4.68
DL	7.30	6.52	6.98	7.18	7.18	7.06	6.50
IFL	6.44	5.70	6.20	6.22	6.48	6.50	6.00
OCW	6.72	6.48	6.56	6.74	6.54	6.40	6.04
ZP	2.46	2.24	2.46	2.60	2.60	2.46	2.32
ML	14.36	13.22	13.90	14.28	14.00	13.94	13.40
MdTRL	4.28	4.30	4.56	4.44	4.44	4.42	4.52

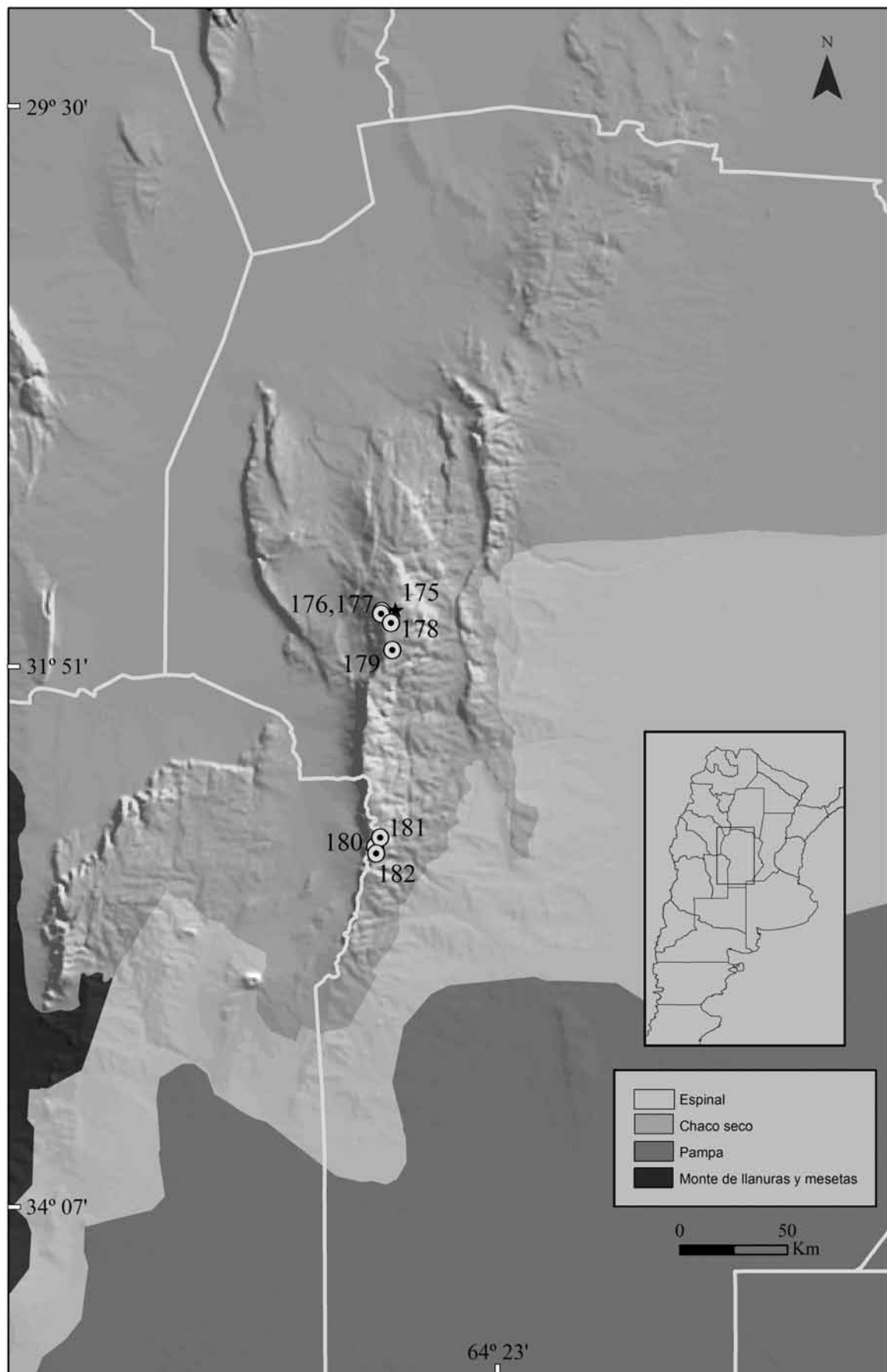


FIGURE 14. Type locality and additional localities of *Akodon polopi*, new species (Province of Córdoba, Argentina).

Etymology: Dedicated to our friend and colleague Jaime José Polop (Universidad Nacional de Río Cuarto, Córdoba, Argentina) for his invaluable contributions to the understanding of the ecology of sigmodontine rodents from central Argentina. In addition, Jaime collected many of the specimens used in the characterization of the new species and even pointed-out the distinctiveness of this form (Polop 1989: 58).

Morphological description: Fur dense and soft. Dorsal coloration uniform, buffy brown lightly spattered with black hairs. Guard hairs generally black excepting those from the rump, which are distally whitish. In this region, the guard hairs extend beyond the level of the fur hairs by approximately 5 mm. Flanks coloration clearer and more richly colored. Ventral side clearly contrasting with dorsum and flanks, with buffy or tawny tinges. Chin with a small but distinguishable white patch. Ears densely covered by hairs of the same general color as the dorsum. Fore and hind feet whitish or buffy and densely furred. Tail clearly bicolored, blacky brown dorsally and whitish ventrally. Claws on fore and hind feet somewhat longer than in the other species of the *boliviensis* group and densely covered by a whitish tuft.

Skull heavily constructed in the context of the *boliviensis* group, with the rostrum relatively short and broad. Nasals short, not acuminate, and extended almost to the anterior face of incisors; frontal sinuses clearly inflated and zygomatic notches broad and deep. Interorbital region hour-glass shaped, with rounded or lightly squared borders and with posterior margins having a greater tendency to be sharply squared than is usually the case for the *boliviensis* group. Temporal and lambdoid ridges well developed for this group. Zygomatic plate relatively broad, with its anterior margin straight and vertical in most of the individuals. Hamular process relatively robust but showing a variable development, with distal end expanded. Incisive foramina long, with posterior ends reaching the hypoflexus of M1. Mesopterygoid fossa narrow, with its anterior margin rounded and lateral borders slightly divergent backward. Posterior palatal pits small and variable in position. Parapterygoid fossae slightly excavated and broader than mesopterygoid fossa, with lateral margins generally straight and divergent posteriorly. Auditory bullae of intermediate size for the genus, with short and wide Eustachian tubes. Mandible similar to the remaining species of the *boliviensis* group but somewhat more robust, with the horizontal ramus higher and the coronoid process broader. The capsular projection clearly posterior to the coronoid process. Anterior point of diastema located below the alveolar plane. The angular process ends just ahead the condyloid process. Masseteric crest reaches the level of the anterior margin of m1 or slightly behind.

Teeth of typical *Akodon* pattern (Fig. 15). Upper incisors approximately orthodont, but many individuals somewhat proodont. M1 with procingulum and anteromedian flexus well developed. A small anteroloph and mesoloph are present on the labial side and on the lingual side a tiny enteroloph is visible in some young specimens. M2 with a reduced procingulum and a vestigial mesoloph present. The posteroflexus not well developed. M3 shows the paraflexus and metaflexus always present in young specimens. The hypoflexus is present in only a few individuals. Lower molars crested and transversally compressed. The m1 has a well developed procingulum with a deep anteromedian flexid and a clearly defined anterolabial cingulum. All the young individuals bear a well-developed ectostylid. On the lingual side, young individuals (age classes 1 and 2) show a well-developed metastylid and a relatively robust mesolophid. The m2 preserves an anterolabial cingulum and a small ectostylid but the mesolophid is vestigial. The m3 is large and “S” shaped.

Akodon polopi has 13-14 thoracic ribs; the vertebral column includes 13-14 thoracic, 8 lumbar, and 26-27 caudal vertebrae (n = 6).

Karyotype: 2n = 40. The autosomal pairs 1 to 18 are telocentric and the pair 19 is metacentric. The X chromosomes are subacrocentric and the Y is small metacentric (Polop 1989; Pinna-Senn *et al.* 1992).

Variation: In spite of marked uniformity in fur coloration, we observed slightly darker and more richly colored specimens. Some individuals have a more slender zygomatic plate, with a slightly concave anterior margin, which determine shallower zygomatic notches. The hamular process also shows a variable development, more delicate in some specimens. The posterior palatal pits also vary in position with regard to the anterior border of the mesopterygoid fossa.

Comparisons: *Akodon polopi* is one of the largest and more robust species of the *A. boliviensis* group. The species is distinguishable from the remaining species by their denser and softer fur, a large skull, with broad rostrum, deep and broad zygomatic notches, and well-expanded zygomatic arches. However, the new species

has a comparatively short rostrum, narrow interorbital constriction and a not inflated braincase. A comparatively well developed metastylid in m1 of young individuals is another distinctive feature of *A. polopi*.

In addition to the previously mentioned characteristics, the new species can be differentiated from *Akodon boliviensis* by the interorbital region with its posterior margins sharply squared, temporal and lambdoid ridges well developed, and the M3 that does not show an “8” shape. The numerous morphometric differences between these species include 17 of the 20 measurements analyzed (Table 2). Cyt b haplotypes of *A. polopi* and *A. boliviensis* differ by an average of 5.0% (Table 12). *Akodon boliviensis* was registered in Argentina only in its northernmost end, always above 2400 m, whereas *A. polopi* lives below 2300 m on isolated mountain ranges from central Argentina, almost 900 km toward the south.

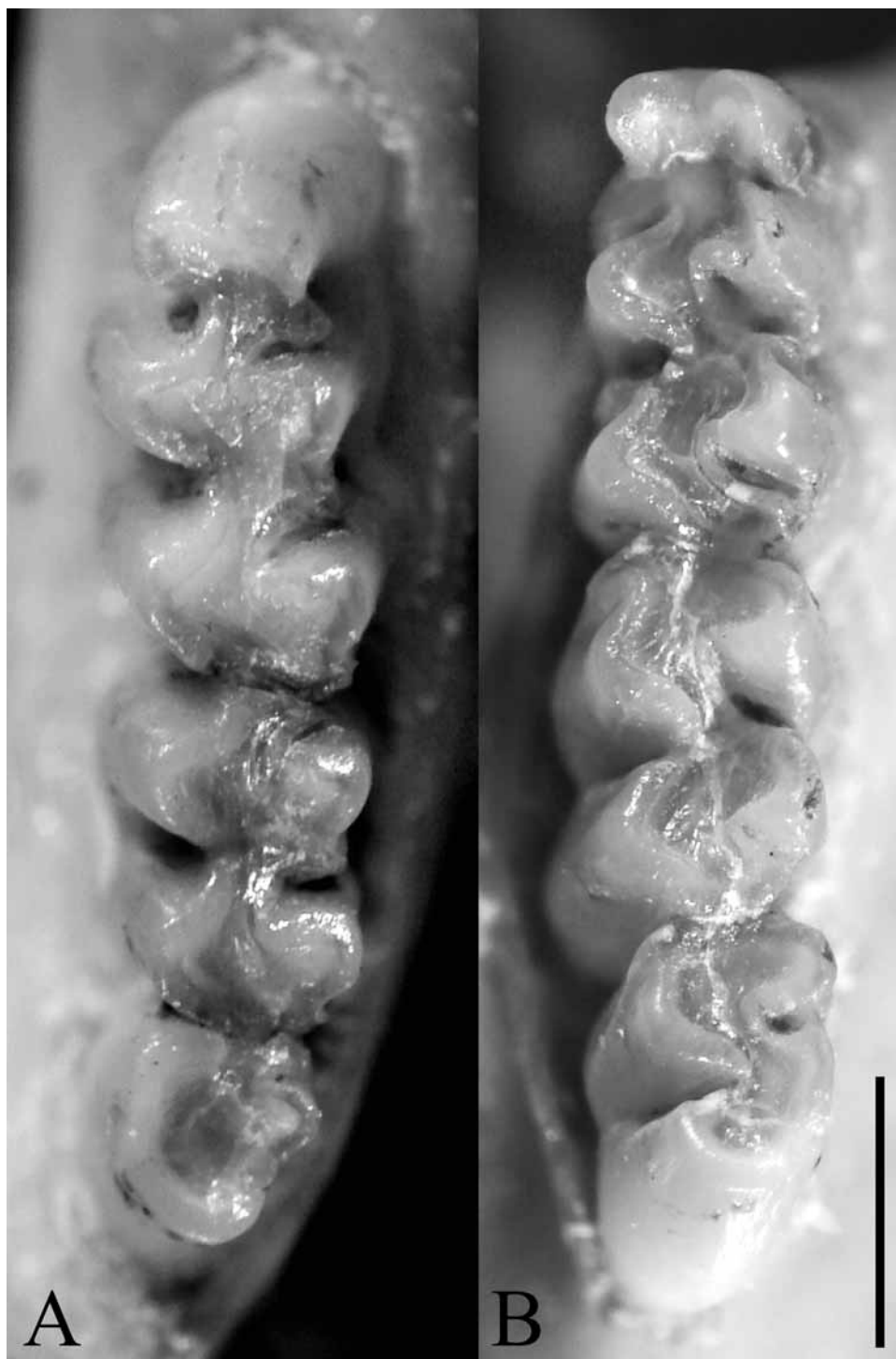


FIGURE 15. *A. polopi*, new species: Left upper (A) and left lower (B) molar rows in a young specimens (age class 2, CNP 1503). Scale = 1 mm.

Like *A. boliviensis*, *Akodon caenosus* does not have a sharply squared interorbital posterior region or well developed temporal and lambdoid ridges. *A. caenosus* is unmistakable because it is situated at the opposite end in the morphometric range values, with no overlap in most of the analyzed measurements (Table 1) being all of them statistically different (Table 2). Likewise, cyt b haplotypes of *A. polopi* and *A. caenosus* are very divergent (6.2%).



FIGURE 16. Two different views, and habitat types, at the type locality of *Akodon polopi*, new species A) Steppe grasslands of *Stipa* sp. and *Festuca hieronymii*; B) Large stands of grasses of *Paspalum quadrifarium* and *Poa stutckertii* in rocky outcrops.

A. polopi can be differentiated from *Akodon spegazzinii* by many characteristics. The former has an inter-orbital region with posterior margins more sharply squared, temporal and lambdoid ridges more developed and a proportionally shorter molar series. The morphometric differences between these species include 14 of the 20 analyzed measurements (Table 2). Cyt b haplotypes of *A. spegazzinii* and *A. polopi* differ by on average 5.5%.

Akodon sylvanus is very similar to *A. polopi* in many of the variables we measured, with less than 50% (9 of 20) significantly different. However, the DA efficiently separated both species and no reciprocally misclassified specimens occurred. The anterior region of the skull of *A. polopi* is shorter and more robust, the zygomatic notches are deeper and broader, and the braincase is less inflated. In ventral view, the mesopterygoid fossa in *A. polopi* is narrower, and the upper incisors tend to be more proodont. The cyt b haplotypes of *A. sylvanus* and *A. polopi* differ on average by 4.7 %. Like *A. boliviensis*, *A. sylvanus* appears to show a disjunct distribution with regards to *A. polopi*; thus far, *A. sylvanus* is known from only the neighborhood of its type locality in the Sierra de Santa Bárbara in Yungas forest habitats almost 800 km to the north of the type locality of *A. polopi*.

Natural history: The habitat in Pampa de Achala is characterized by extensive highland grasslands dominated by *Festuca* and *Stipa*, between 1800 and 2300 m elevation (Fig 16). Intermingled with the grasslands there are scattered small patches of woodlands of *Polylepis australis*, *Heterothalamus alienus*, *Eupatorium buniifolium*, *Berberis ruscifolia*, *Baccharis myrtilloides* and *Cassia hockeriana*, and rocky outcrops (Polop 1989, 1991). None of the specimens that we captured during the end of winter 2008 (August) showed signs of reproductive activity. These data suggest that the species is reproductively active in the late spring and summer seasons and agree with previous studies where the largest number of pregnancy were in Novembre and December (Polop 1989). This author registered an average number of embryos per female of 4.7 (range 3 to 7). Few of the specimens captured in winter show signs of pelage molting. Other sigmodontine species registered at the type locality and surroundings, in the same habitat, include *Oxymycterus rufus* (as *O. paramensis* in Polop 1989), *Oligoryzomys flavescens*, *Phyllotis xanthopygus*, and *Reithrodon auritus*. *Akodon polopi*, new species is the dominant cricetid in the places where it was registered. In previous studies (Kufner *et al.* 2004) and our surveys, it constituted more than 70% of the captured animals but Polop (1989, 1991) indicated a minor percentage (53% and 34% respectively).

Comments: Although early considered as an undescribed species (Polop 1989), *Akodon polopi* was alternatively treated as *A. boliviensis* (Polop 1991; Morando & Polop 1997), *A. alterus* (Priotto *et al.* 1996) or *A. spegazzinii* (D'Elía 2003; D'Elía *et al.* 2003; Kufner *et al.* 2004; Pardiñas *et al.* 2005; Rodrigues Gonçalves *et al.* 2007 and Smith & Patton 2007).

DISCUSSION

Relationships among species of *Akodon* have been the focus of several recent studies. We refer the reader to the most recent one, that of Smith & Patton (2007; and citations therein), for a treatment of these issues and a good historical perspective.

The polyphyly of the *Akodon varius* species group

The focus of this contribution is the *Akodon boliviensis* species group; however, before centering on it we discuss a novel and relevant finding gleaned from our phylogenetic analyses that concerns the *Akodon varius* species group sensu Myers (1989). Neither the MP nor the BA recovered a monophyletic *Akodon varius* species group. The predominantly Yungas species *A. simulator* and *A. varius* form a clade (JK=100; PP=1) that is not sister to the one (JK=98; PP=1) formed by the lowland species *A. dayi*, *A. dolores*, *A. iniscatus* (including *nucus*), *A. molinae*, and *A. toba*. The lowland group was also recovered in combined analysis of nuclear and mitochondrial DNA sequences (D'Elía, 2003; there a specimen of *A. toba* is wrongly identified as belonging to *A. varius*). The Yungas clade (i.e., *A. varius* group s.s.) is part of a large central Andean clade also inte-

grated by the *A. aerosus* species group and *A. albiventer*. This large clade is well supported in the BA (PP=0.89) but although recovered in the MP analysis it has less than 50% of support. The position of the lowland clade, for which we suggest the name of the *A. dolores* species group, varies depending on the analysis. Recently, a study focused on the systematics of the *A. varius* group (Braun *et al.*, 2008) provided a molecular based phylogeny in which the two clades (i.e., *A. varius* group s.s. and *A. dolores* group) were recovered; however, the polyphyly of the *A. varius* species group s.l. was not found due to the design of the study. In addition to representatives of the *A. varius* group, Braun *et al.* (2008) only included sequences of *Necomys*, which were used as the outgroup (i.e., in addition to the fact that *Necomys* is not sister to *Akodon* [D'Elía, 2003], much of the radiation of *Akodon* was not represented). Therefore, the monophyly of the *A. varius* group was not rigorously tested (we note, however, that in the goals of the study to test the monophyly of the group was not stated). The present study which includes the broadest taxonomic coverage for *Akodon* s.s. to date, clearly -and for the first time- suggests the polyphyly of the *A. varius* group sensu Myers (1989).

***Akodon boliviensis* species group**

The great morphological similarity among species of the *A. boliviensis* group, as well as high levels of intraspecific variability, has precluded a clear and stable taxonomy for the group and in particular for those forms present in northwestern Argentina. This situation, together with the lack of studies of representative series of specimens, including the holotypes and additional specimens collected at the type localities, resulted in the suggestion, along the years, of different taxonomic scenarios, sometimes quite distinct among themselves.

As in previous instances (e.g., Patton *et al.*, 2000), the integration of morphologic and molecular data interpreted in a geographic context has proven useful to assess species boundaries of a taxonomically confusing group. In this regard, the evidence presented herein indicates the existence of four species of the *A. boliviensis* group in northwestern Argentina with a new species belonging to this group from central Argentina.

The taxonomic status of *A. spegazzinii* (including *alterus*, *leucolimnaeus*, and *tucumanensis*) with respect to *A. boliviensis* is the most debatable of the taxonomic decisions we make. Based on a small series of specimens, Myers *et al.* (1990) had earlier proposed the valid status of this form. In line, much of the available evidence here considered suggests that *A. spegazzinii* represents a distinct species from *A. boliviensis*. For example, they form reciprocally monophyletic groups (Fig. 1) that are allopatrically distributed; in addition, they are clearly identifiable in morphometric multivariate space and morphological grounds (see comparison above). Moreover, these species have different karyotypes, including the presence of heteromorphism in the largest autosomal pair and the X chromosome in *A. spegazzinii* (Gardner & Patton, 1976; Barquez *et al.*, 1980; Myers *et al.*, 1990), and different ecological preferences. Our records indicate disjunct distribution for these forms, with *A. boliviensis* restricted to high altitudinal grasslands in the extreme north of the region and *A. spegazzinii* extended over many habitats and large areas in south-central portions of the region. In spite of these differences, the genetic divergence between them was the smallest among all species pairs of the *A. boliviensis* group (Table 12). In addition, some overlap in morphological and morphometric characters was evident. Moreover, we could not evaluate the constancy of these differences because we failed to capture both species in sympatry. So, additional studies are needed in the north of the northwestern Argentinean region and in possible areas of sympatry to test the constancy of the observed differences here reported.

The taxonomic status of *A. tucumanensis*, *A. alterus*, and *A. leucolimnaeus* remained controversial despite the pioneering work by Myers *et al.* (1990). While all these forms were treated as subspecies or allied to *A. spegazzinii* by some authors (e.g. Myers *et al.* 1990; Díaz *et al.* 2000; Pardiñas *et al.* 2006; Jayat *et al.*, 2008a), others considered them as valid species (e.g. Barquez *et al.*, 1991; Mares *et al.*, 1997; Díaz, 1999; Díaz & Barquez, 2007; but see Galliari *et al.*, 1996 about the status of *A. tucumanensis*). In spite of the extended usage of the specific epithet *alterus* in previous works (e.g. Capllonch *et al.* 1997; Díaz *et al.* 1997; Mares *et al.* 1997; Díaz 1999; Díaz & Barquez 2007) none of these references was based on a detailed study of extensive topotypical series nor the use of molecular characters. Blaustein *et al.* (1992) were the only authors who tested the status of *alterus* (with respect to *tucumanensis*). However, they erroneously assumed that specimens from

El Infiernillo, Tucumán, belonged to *alterus*; then, they did not truly test the taxonomic status of *A. alterus*. They also failed to separate these specimens from *A. tucumanensis* from low altitude Yungas forest of Tucumán. In words of Blaustein *et al.* (1992, pag. 11) "... we believe that any conclusion on the taxonomic status of the two forms is untimely." The status of *A. leucolimnaeus* was even more dubious and, until the preliminary observations of Galliari *et al.* (1996), it was considered as a synonym of *Necomys lactens* (Cabrera, 1961; Reig, 1978, 1987; Mares *et al.*, 1997). However, Galliari *et al.* (1996) ranked *leucolimnaeus* as a valid species of *Akodon* (see also Musser & Carleton [2005] and Pardiñas *et al.* [2006]), view that contrasts with our results. All the available evidence indicates that the nominal forms *alterus*, *leucolimnaeus*, and *tucumanensis* must be considered junior synonyms of *A. spegazzinii*. Haplotypes from specimens coming from the type localities of these fall within the *spegazzinii* clade (Fig. 1). The genetic divergence among haplotypes of this clade is low (1.2% in average) and we found no clear morphological or morphometric differences among these forms. Most of the observed differences in coloration among populations may relate to the great environmental heterogeneity inhabited by *A. spegazzinii* (Fig. 10).

In the *A. boliviensis* clade, two haplotypes recovered from specimens from northern Salta were more closely related to the haplotype of a Peruvian specimen (MVZ 171607) than to those of other three Argentinean specimens (Fig. 1). This phylogeographic break, together with some morphological, morphometric and genetic differences between these two groups also suggest the possibility of unrecognized biological diversity within this group. This scenario is similar to that observed in *N. amoenus*, another highland inhabitant (D'Elía *et al.*, 2008). Notwithstanding, the studied material of *A. boliviensis* is scarce and the difference between both clades is moderate (2.1% of average genetic divergence), so we point that further research is needed on this area.

Myers *et al.* (1990) considered *A. caenosus* as a subspecies of *A. lutescens* (as *A. puer caenosus* in that publication). They highlighted subtle morphometric, morphologic, and cytogenetic characteristics that distinguished specimens from northwestern Argentina from those of Peru and Bolivia. Our phylogenetic analyses include haplotypes recovered from Argentinean specimens assignable to *caenosus* and a Peruvian specimen belonging to *lutescens*. These haplotypes form a paraphyletic group respect to *A. subfuscus* (Fig. 1). This topology, if *lutescens* and *subfuscus* are not to be considered conspecifics, suggests a specific status for *A. caenosus*. Moreover, the average genetic distance between the Peruvian haplotype of *lutescens* (MVZ 171612) and those from northwestern Argentinean specimens of *A. caenosus* is relatively high (3.5%); the average divergence value among specimens of *A. caenosus* is much lower (1%). Although, there are not clear morphological and morphometric differences among our material of *A. caenosus* and the values offered by Myers *et al.* (1990) for *A. lutescens*, the alternative position of considering *A. subfuscus* and *A. lutescens* conspecific seems less supported. These species differ by a substantially high (5.1%) average genetic distance. Furthermore Myers *et al.* (1990) detailed several morphological characters that distinguish *A. lutescens* from *A. subfuscus*.

Although we failed to obtain small specimens of *Akodon* from the type locality of *A. aliquantulus* (we studied ca. 100 individuals of *Akodon* from this locality and its surroundings and more than 390 from Tucumán province), its diagnosis does not permit us to distinguish the two type specimens from *A. caenosus*. Moreover, the haplotypes of three small *Akodon* sequenced from Catamarca and Tucumán were remarkably similar to haplotypes of *A. caenosus* topotypes (with average genetic distance lower than 1%). On these bases (see also our Species Account discussion above) we place *aliquantulus* under the synonymy of *A. caenosus*. This study corroborated the proposition of Jayat *et al.* (2007a) of placing *A. sylvanus* as a valid species of the *A. boliviensis* group. In the MP analysis *A. sylvanus* appears as the sister species of *A. polopi*; in accordance to low support of this clade (JK<50) it is not recovered in the BA where *A. polopi* is sister to the *A. boliviensis*-*A. spegazzinii* clade.

Akodon polopi, the new species here described, is a clearly distinct member of the *A. boliviensis* group, with several diagnostic characters coming from different sources of evidence; not surprisingly, it was early mentioned as a possible new subspecies by Elio Massoia or a new species (see Polop, 1989). This species, known only from high altitude grasslands of central Argentina, is the only species of the *A. boliviensis* group inhabiting the Sierras Grandes range, a medium altitude mountain system isolated (ca., 600 km) from the main

Andean chain by low elevation arid and semiarid environments. Data at hand are insufficient to pose a biogeographic scenario accounting for the diversification of *A. polopi* and the remainder species of the *A. boliviensis* group. Notwithstanding, Pampa de Achala has been mentioned as a biogeographic refuge and an area of endemism for other taxa (Polop, 1989, and references there).

Relationships among species of the *Akodon boliviensis* group are well resolved and mostly congruent among analyses. Differences relate to the position of *A. polopi* and *A. sylvanus*.

The present study, as several previous ones, reaffirms the phylogenetic legitimacy of both the *boliviensis* group and extends our knowledge of its contents, limits, and geographic ranges of its member species. However, we assert that additional research is still needed before an adequate picture of Andean *Akodon* can be acquired. In this line, more field work coupled with the study of specimen series housed in research institutions is essential.

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APPENDIX I

Specimens examined. Acronyms for institutions and personal catalogs are as follows. Argentina: Colección Mamíferos Lillo (CML), Tucumán; Colección de Mamíferos del Centro Nacional Patagónico (CNP), Puerto Madryn; Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (MACN), Buenos Aires. Bolivia: Colección Boliviana de Fauna (CBF), La Paz. USA: Museum of Vertebrate Zoology (MVZ), Berkeley. UK: Natural History Museum (BM). JPJ: field number of J. Pablo Jayat, to be deposited at CML; PEO-e: field number for owl pellets samples of Pablo E. Ortiz, to be deposited at Colección de Paleovertebrados Lillo (PVL), Tucumán. Localities are listed in alphabetic order. Genbank accession numbers for cyt b DNA sequences are provided between [] next to collection numbers of the specimens from where haplotypes were gathered.

Akodon albiventer (32). ARGENTINA: Jujuy Province: La Laguna, 4500 m, Sierra de Zenta, E de Maimará (MACN 27.102, 27.103, 27.105); Laguna de Pozuelos (MACN 19390, 19394, 19396, 19398, 19403 to 19407, 20288 to 20298, 20387); Sierra de Zenta, a 4500 m (MACN 31-113); Yavi Chico (MACN 36-456, 36466). Salta Province: Chorrillos, 4500 m (MACN 30-105, 30-106); Santa Rosa de Tastil (MACN 15639 to 15641).

Akodon aliquantulus (2). ARGENTINA: Tucumán Province: Las Agüitas, cumbre del Taficillo (CML 6121, 6122).

Akodon boliviensis (13). ARGENTINA: Salta Province: 1 km ENE de Rodeo Pampa, km 59 de Ruta Provincial N° 7, 3080 m (MACN 23507; JPJ 1330); Abra de Ciénaga Negra, aprox. 3 km al SE, 3090 m (MACN 23499, 23500; JPJ 724, 725, 728, 734, 735, 737, 739); Azul Cuesta, aprox. 9 km al S de Nazareno, 3286 m (MACN 23503); Pampa Verde, aprox. 8 km al OSO de Los Toldos y al S del Cerro Bravo, 2400 m (MACN 23504). PERU: Puno Department: 12 km S Santa Rosa (de Ayaviri), 3950 m (MVZ 171607).

Akodon budini (146). ARGENTINA: Jujuy Province: a 11 km de San Antonio, Cerro El Morado (CML 4605 to 4608, 4611); a 4 km al N de Tiraxi, sobre Río Tesorero, ruta 29 (CML 4613); Abra de Cañas (MACN 19487, 19488, 19490, 19496, 19497, 19502); Abra de Cañas, 1710 m, Parque Nacional Calilegua (MACN 19463, 19464, 19466, 19467); Abra de Cañas, Calilegua (MACN 19483, 19484, 19486, 19489, 19493 to 19495, 19498, 19499, 19501, 19503 to 19506, 20285); Abra de Cañas, El Monolito, 1700 m (CML 1789 to 1794, 1796, 1798 to 1802, 1806 to 1808); Abra de Cañas, El Monolito, 1707 m (CML 1775, 1776); Arroyo La Horqueta, 3 km al SE de las Lagunas de Yala (CML 4603); Cerro Hermoso (MACN 19475, 19477, 19479, 19482); Cerro Hermoso, Calilegua (MACN 19470, 19471, 19478, 19480, 19481); Cerro Hermoso, Parque Nacional Calilegua (MACN 19473, 19476); Cerro Morado, sobre Río Morado, 11 km al NW de San Antonio (CML 4604); El Duraznillo, Cerro Calilegua, 2600 m (CML 1738 to 1741, 1743 to 1751); León (MMPMa 8 specimens without numbers, 2192, 18.1.1.46); León, Arroyo La Tablada (MMPMa 1245, 1251, 1258, 1260); Tiraxi, ruta 29, sobre Río Tiraxi (CML 4612). Salta Province: aprox. 1.6 km al W de Los Toldos, sobre la senda a Santa Victoria, 1621 m (JPJ 1578 to 1582, 1587, 1591 to 1593, 1595, 1602, 1603, 1606, 1609, 1610, 1612, 1613, 1615, 1616, 1671 to 1676, 1681, 1682, 1687 to 1689, 1691, 1719, 1720, 1722, 1726 to 1728); aprox. 5 km (por ruta) al S de Los Toldos, sobre el camino a Vallecito, 1705 m (JPJ 1617, 1621, 1632, 1633, 1659, 1715); Los Helechos, P. N. Baritú, Fca. Jakulica, 1200 m (MACN 20666); P. N. Baritú, angosto Río Baritú, 1600 m (CML 5532; MACN 20662); P. N. Baritú, Fca. Jakulica, Los Helechos, 1200 m (CML 5524, 5526); P. N. Baritú, Fca. Jakulica, Sierra Las Pavas (CML 5529); P. N. Baritú, Sierra de Las Pavas, Fca. Jakulica, 1200 m (MACN 20667); Pampa Verde, aproximadamente 8 km al OSO de Los Toldos y al S del Cerro Bravo, 2400 m (MACN 23505; JPJ 351, 368).

Akodon caenosus (254). ARGENTINA: Catamarca Province: 6 km SW of hwy 9 on hwy 18, el. 5000' (CML 3304); aprox. 2 km al SE de Huaico Hondo, sobre Ruta Provincial N° 42, al E del Portezuelo, 1992 m (JPJ 398, 400, 408, 414, 417, 428, 429); Las Chacritas, aprox. 28 km al NNW de Singuil, sobre Ruta Provincial N° 1, 1888 m (JPJ 515, 517, 523, 533, 535, 542); unión entre las rutas provinciales N° 9 y 18, 3.4 km al S, sobre Ruta Provincial N° 18, 1529 m (MACN 23482, 23483; JPJ 3 to 5, 7, 8, 12, 14, 16 to 18, 20, 21, 23, 30, 32, 33, 36, 37, 39, 43, 1113 to 1115, 1120, 1123, 1133, 1134, 1142 to 1145, 1148, 1150, 1151). Jujuy Province: a 11 km de San Antonio, sobre Río Morado, Cerro El Morado (CML 4620 to 4622); Arroyo La Horqueta, 6 km al SE de las lagunas de Yala (CML 4958); Bárcena, aprox. 3 km al S, sobre Ruta Nacional N° 9, 1808 m (MACN 23494; JPJ 128, 129, 623, 627 to 629, 631, 634, 635, 641, 642, 648, 649, 654, 656, 658, 659, 666); Cerro Hermoso, Parque Nacional Calilegua (MACN 19474); Cerro Morado, sobre Río Morado, 11 km al NW de San Antonio (CML 4626, 4959, 4960); El Duraznillo, Cerro Calilegua, 2600 m (CML 1734); La Herradura, 12 km al SW de El Fuerte, sobre Ruta Provincial N° 6, 1428 m (JPJ 573, 574, 579, 581, 583, 585, 587, 588, 601, 603, 609, 612); León, Arroyo La Tablada (MMPMa 1241, 1243, 1254); Termas de Reyes, aprox. 15 km al N, sobre Ruta

Provincial N° 4 (JPJ 293, 309 to 314, 316-318, 328, 331, 332); Termas de Reyes, mirador, sobre Ruta Provincial N° 4 (JPJ 125 to 127, 299, 301, 305 to 307, 320, 323, 325 to 327); Tiraxi, 1.5 km al E, sobre ruta 29 (CML 4972 to 4974); Tiraxi, ruta 29, sobre Río Tiraxi (CML 4627, 4961 to 4966, 4968, 4969). Salta Province: 1 km ENE de Rodeo Pampa, km 59 de Ruta Provincial N° 7, 3080 m (MACN 23508; JPJ 1320, 1321); Campo Quijano (MACN 17492); Campo Quijano aprox. 5 Km al NO, Km 30 de la ruta Nacional 51 (Quebrada del Toro), alt. aprox. 1600 msnm (JPJ 95, 96, 99, 100, 105-108, 110, 134, 151); Cañadón Ojo de Agua, 10 km al Sur de Rosario de la Frontera (PEO-e 80); Cementerio de Rosario de La Frontera (PEO-e 135); Pampa Verde, aprox. 8 km al OSO de Los Toldos y al S del Cerro Bravo, 2400 m (MACN 23506; JPJ 337, 339, 341, 342, 345, 346, 348 to 349, 352, 355 to 357, 359, 360, 362-364, 366). Tucumán Province: Aconquija, a 3000 m (MACN 34-1127); aprox. 10 km al S de Hualinchay, sobre el camino a Lara, 2300 m (JPJ 492); aprox. 7 km al NO de la finca de la familia Usandivara, Altos de Medina, 1717 m (MACN 23510; JPJ 816, 836, 849); Concepción (MACN 29-353, 29-359, 33-381, 33-387, 33-396, 34-852, 34-912, 34-913, 34-918, 34-927, 34-964, 34-965, 34-967, 34-968, 34-1133, 37-737); Hualinchay, sobre el camino a Cafayate, 1861 (JPJ 172, 179 to 181, 184, 185, 192, 196, 197, 205-207, 210, 221, 222, 244); La Tranquera, límite N de Finca Los Chorrillos, sobre ruta provincial 205, 1426 m (JPJ 1771, 1772, 1774-1777, 1784 to 1787, 1791, 1883 to 1888, 1894, 1897, 1898, 1900 to 1903, 1905 to 1920, 1923 to 1928, 1930, 1931, 1933 to 1937); Reserva de la Florida, 7 km al W de Ibatín, sobre río Pueblo Viejo (CML 5014).

Akodon fumeus (83). ARGENTINA: Jujuy Province: Río Las Capillas, 15 km al N de Las Capillas, por ruta 20 (CML 5034, 5036 to 5042); Río Las Capillas, 15 km al N de Las Capillas, por ruta 20, 957 m (CML 4322, 4323). Salta Province: aprox. 1.6 km al W de Los Toldos, sobre la senda a Santa Victoria, 1621 m (JPJ 1583, 1588, 1594, 1596, 1599, 1600, 1604, 1605, 1614, 1679, 1680, 1683, 1692, 1693, 1721, 1724, 1725, 1730, 1731); aprox. 5 km (por ruta) al S de Los Toldos, sobre el camino a Vallecito, 1705 m (JPJ 1575, 1577, 1622, 1624 to 1629, 1631, 1634 to 1645, 1647 to 1650, 1654 to 1658, 1660 to 1670, 1694 to 1700, 1702, 1709 to 1713, 1716); Finca Alto Verde, 670 m (JPJ 1794 to 1797, 1799, 1800, 1802, 1803); Finca Jakulica, Sierra de Las Pavas (CML 5522); Parque Nacional Baritú, 700 m (MACN 20672); Parque Nacional Baritú, angosto Río Baritú, 1600 m (CML 5534, 5516; MACN 20663, 20664); Parque Nacional Baritú, Arroyo Santa Rosa, 900 m (MACN 20671); Parque Nacional Baritú, Baritú, 1600 m (CML 5539); Parque Nacional Baritú, boca Arroyo Santelmita (MACN 20673); Parque Nacional Baritú, cerro Chaguar, 1200 m (MACN 20679); Parque Nacional Baritú, desembocadura Arroyo Santelmita, 700 m (MACN 20674); Parque Nacional Baritú, Las Pavas, 1° angosto Río Pescado, finca Jakulica, 1200 m (MACN 20665); Parque Nacional Baritú, naciente Arroyo Santa Rosa, 900 m (CML 5535); Parque Nacional Baritú, nacientes Arroyo Santelmita (MACN 20670); Parque Nacional Baritú, nacientes Arroyo Santelmita, 900 m (MACN 20668); Parque Nacional Baritú, nacientes del Arroyo Santelmita, 900 m (CML 5512, 5533); Sierra Las Pavas, vecindades de Finca Jakulica (CML 5536); Vado de Arrazayal (CML 1071).

Akodon polopi, new species (52). ARGENTINA: Córdoba Province: Pampa de Achala (CUNRC 2805, 10145, 10178, 50151); Pampa de Achala, 2163 m (CUNRC 44748, 44749, 44750); Pampa de Achala, 2247 m (CUNRC 44744, 44745, 44747); Pampa de Achala, aprox. 6 km (por ruta 34) al E de la antenna repetidora La Posta, 2200 m (JPJ 2118, 2120, 2121, 2123, 2126 to 2135, 2139, 2141, 2143 to 2150, 2158 to 2160; CML 7672, 7673; CNP 1927, 1928; MACN 23486, 23487); Repetidora La Posta, Pampa de Achala, 2171 m (CNP 1500 to 1508).

Akodon simulator (303). ARGENTINA: Catamarca Province: Acceso sur a la ciudad de Catamarca, sobre ruta 38 (PEO-e 193); Agua del Gauchi, aprox. 1 km al E del Mogote Los Cocos, 2024 m (JPJ 1254, 1277, 1278, 1303); El Alamito, Campo del Pucará (CML 4633, 4634); El Espinillo, Campo del Pucará, Las Estancias (PEO-e 121); El Rodeo, 0.5 km W of Hwy 4, el. 4500 ft (CML 3365, 3366, 3369, 3370); Junta Suma, Las Estancias (CML 1755); Mogote Las Trampas, aproximadamente 15 km al NW de Chumbicha, 2300 m (JPJ 1418); unión entre las rutas provinciales N° 9 y 18, 3.4 km al S, sobre Ruta Provincial N° 18, 1529 m (JPJ 22, 27, 40, 1128, 1131, 1152, 1153). Jujuy Province: 12 km W de Fraile Pintado, sobre Río Ledesma (CML 4854); 13 km al SW de Yuto, sobre arroyo Yuto (CML 5054 to 5059); 2.5 km W El Bananal, 437 m (CML 4900 to 4906); a 11 km NW de San Antonio, sobre Río Morado, Cerro El Morado (CML 4635 to 4637); a 2.5 km del Arroyo Santa Rita, sobre camino a El Fuerte (CML 2040); Abra de Cañas, 1710 m, Parque Nacional Calilegua (MACN 19465); Abra de Santa Laura, sobre Ruta Nacional N° 9, 1397 m (CML 4887 to 4891, 4893); Aguas Negras (MACN 19460, 19461); Aguas Negras, Parque Nacional Calilegua, 600 m (MACN 19454); Arroyo El Cano, a 7 km del río El Saladillo (CML 4862); Caimancito (MACN 19455); Caimancito, 600 m, Parque Nacional Calilegua (MACN 19456, 19457); Caimancito, FCCNA, 700 m (MACN 30-306, 30-314, 30-315); Cerro Morado, sobre Río Morado, 11 km al NW de San Antonio (CML 4638 to 4651); El simbolar, 25 km al SW de Palma Sola (CML 1992, 1993, 2020, 2022 to 2024, 2044); Finca El Piquete (JPJ 1027, 1029, 1032); Finca FAMAT, aprox. 1.5 km al SW del portón de entrada de la finca, 406 m (JPJ 1961, 1962); Finca FAMAT, aprox. 3 km al SW del portón de entrada

de la finca, 400 m (JPJ 1957, 1960); Finca Las Moras, aprox. 6.5 km (por senda maderera) al SE de la entrada a la finca, 460 m (JPJ 1808); Finca Sauzalito, aprox. 1 km al E del cruce entre la ruta nacional 34 y el Río Yuto, 413 m (JPJ 1567); General San Martín (MACN 21026, 21028); La Herradura, 12 km al SW de El Fuerte, sobre Ruta Provincial N° 6, 1428 m. (JPJ 582, 608); La Mendieta (MACN 21039, 21040); Laguna La Brea (CML 4855 to 4859, 5044 to 5047); Laguna La Brea, sobre ruta 1, 3 km de Las Siete Aguas (CML 4860, 4861, 5048 to 5050, 5052); límite entre Salta y Jujuy, Abra de Santa Laura, sobre Ruta Nacional 9 (CML 4892, 4894, 4913); Mesada de Las Colmenas (MACN 19458, 19459); Parque Nacional Calilegua, bomba de YPF, en las márgenes del Arroyo Sauzalito (CML 2933 to 2935); Planta Caimancito, aprox. 700 m al E de la Batería, 498 m (JPJ 2047, 2052); Planta Caimancito, Batería, 535 m (JPJ 2049); Planta Caimancito, pozo 43, 560 m (JPJ 2048); Río Blanco, aprox. 9 km al E de San Antonio, sobre Río Blanco (CML 4895 to 4897); ruta 83, camino a Valle Grande, 9 km al N de San Francisco (CML 3747 to 3750, 5053); Tiraxi, 1.5 km al E, sobre ruta 29 (CML 4898); Yuto, INTA, 400 m (CML 4899). Salta Province: 1° angosto río Pescado, finca Jakulica, 650 m (MACN 20681); 27 km al O de Aguas Blancas (MACN 17517, 17530); 43.7 km al NW de ruta 50 y ruta provincial 18, camino a Isla de Cañas (CML 4925); Aguaray (MACN 3223); Aguaray, 600 m (MACN 3226, 3227); Aguaray. FCCNA, 700 m (MACN 30311, 30312); angosto Río Pescado (MACN 20684); aprox. 21 km (por ruta) al WNW de Vespucio, sobre el Río Seco, 532 m (JPJ 1495, 1506, 1510, 1485, 1488 to 1493, 1499, 1500, 1503 to 1505, 1507); aprox. 300 m al NE de la escuela Histórica San Pedrito, 1143 m (JPJ 1369); aprox. 35 km (por ruta) al NW de Vespucio, 635 m (JPJ 1547, 1552 to 1554, 1556); aprox. 36 km al NNW de Embarcación, Finca Río Seco, 611 m (JPJ 1942, 1944, 1945, 1948); Arroyo Salado, 7 km al E de Rosario de la Frontera, al lado del ACA (PEO-e 33); Barranca cerca de Ojo de Agua, 7 km al sudeste de Rosario de La Frontera (PEO-e 59); Cafayate (CML 852, 853); Campo La Peña, Cabeza de Buey (CML 720, 721, 794, 859); Campo Largo, km 74.5 de la ruta entre Acambuco y Campo Largo, 684 m (JPJ 1531); Campo Quijano (MACN 17504, 17505, 17518); Campo Quijano aprox. 5 Km al NO, Km 30 de la ruta Nacional 51 (Quebrada del Toro), alt. aprox. 1600 msnm (JPJ 109, 138); Cañadón Ojo de Agua, 10 km al Sur de Rosario de la Frontera (PEO-e 81); cementerio de Rosario de La Frontera (PEO-e 136); cerro Chaguar, Snias. del Porongal, 1200 m (MACN 20687); cerro Chaguar, Snias. Porongal, 1250 m (MACN 20688); desembocadura Arroyo Santelmita, 700 m (MACN 20690); El Corralito, aprox. 23 Km al SO de Campo Quijano, sobre ruta Nac. N° 51 (JPJ 146 to 148); Embarcación (MACN 16439); Finca Falcón, aprox. 3 km al NW del pozo de agua N° 5, cercanías del Río Seco, 704 m (JPJ 1358 to 1362, 1364, 1366, 1372, 1374 to 1376, 1378, 1379, 1383, 1387, 1388, 1392, 1395, 1396, 1401); finca Jakulica, 1° angosto río Pescado, 650 m (MACN 20679, 20680); finca Jakulica, 2° angosto río Pescado, 650 m (MACN 20686); finca Jakulica, casa vialidad, Río Pescado, 658 m (MACN 20685); finca Jakulica, Srras. de Las Pavas, cerca angosto río Pescado, 650 m (MACN 20682); Finca Río Seco, 40 km al N de Embarcación, 524 m (JPJ 1824 to 1826, 1838, 1840); nacimiento Quebrada Santa Rosa, 950 m (MACN 20689); P. N. Baritú, Las Juntas Lipeo-Bermejo (MACN 20678); Parque Nacional Baritú, Las Juntas (MACN 20677). Santiago del Estero Province: Bajada del Cuervo, 10 km al Sur de Termas de Río Hondo por río Dulce (PEO-e 101). Tucumán Province: 2 km al Sur de Gobernador Garmendia por ruta 34 (PEO-e 72); a 15 km de San Pedro de Colalao, sobre ruta hacia Hualinchay (CML 6107); aprox. 10 km al S de Hualinchay, sobre el camino a Lara, 2300 m (JPJ 437, 496, 1410); Burruyacu (MACN 19281, 19292 to 19298); Castillo de las Brujas, 15 km al sudeste de Amaicha del Valle (PEO-e 46); Cerro de Vipos, 1000 m (MACN 32-34 to 32-36); Cerro San Javier, 2300 m (MACN 26-134 to 26-138); Concepción (MACN 29-314, 29-373, 29-382, 29-385, 29-389, 29-392, 29-397, 29-401, 34-954); Cumbres de San Javier, Estación Biológica (MACN 17435, 17436); El Naranjal (MACN 17542); El Naranjal, ruta 307 (MACN 17561); Escuela de Agricultura de la UNT, Horco Molle (PEO-e 212); Horco Molle (MACN 19290); Hualinchay, sobre el camino a Cafayate, 1861 (JPJ 155, 174, 182, 186, 188, 201, 202, 204, 213, 214, 216, 224, 225, 231, 234, 246); Ing. San Pablo (MACN 17525, 17528); km 1315 de la ruta nacional N° 9, 700 m (JPJ 1750, 1752, 1753, 1755, 1756); La Tranquera, límite N de Finca Los Chorrillos, sobre ruta provincial 205, 1426 m (JPJ 1790, 1891, 1896, 1904, 1922, 1932); Parque Biológico Sierra de San Javier, área de la residencia universitaria, a metros del LIEY, 711 m (JPJ 1186, 1192, 1193); Reserva Provincial La Florida (CML 4924); Río Loro (MACN 17521, 17522); Río Salí (MACN 33-249); San Javier (MACN 17433); Villa Nougues, aprox. 2 km al N, sobre Ruta Provincial N° 338, a la altura de la antena repetidora del Canal 10 de televisión (JPJ 262, 265, 266, 280, 288).

Akodon spegazzinii (732). ARGENTINA: Catamarca Province: 6 km al sur de Buena Vista (PEO-e 190); Agua del Gauchi, aprox. 1 km al E del Mogote Los Cocos, 2024 m (JPJ 1233 to 1240, 1245, 1246, 1248, 1249, 1256, 1259, 1261 to 1268, 1282 to 1285, 1287, 1290, 1291, 1298 to 1302); aprox. 10 km al W de Los Varela, sobre Ruta Provincial N° 4, Sierra de Humaya, 2006 m (JPJ 1308, 1309); aprox. 2 km al SE de Huaico Hondo, sobre Ruta Provincial N° 42, al E del Portezuelo, 1992 m (JPJ 399, 401 to 403, 405 to 407, 409 to 411, 415, 416, 418, 422, 426, 427, 780, 783 to 789, 791 to 800, 803, 804, 806); Choya, 13 km NNW Andalgalá, el. 4000 ft (CML 3359); Cuesta del Clavillo, 5 km al SW de la banderita (CML 4064, 4065, 4956, 4957); El Bolsón, 2309 m (JPJ 2076, 2084, 2085); El Espinillo, Campo del Pucará, Las

Estancias (PEO-e 122); km 33 de la Ruta Provincial N° 47, al S de Capillitas, 2500 m (MACN 23476; JPJ 675, 678, 682, 684, 687, 689 to 691, 697 to 701, 708, 710 to 712, 714, 716, 717); Laguna Blanca, 3243 m (MACN 23477, 23478; JPJ 1842, 1843, 1845 to 1862, 1864 to 1866, 1868, 1869, 1876 to 1878); Las Chacritas, aprox. 28 km al NNW de Singuil, sobre Ruta Provincial N° 1, 1888 m (CNP 1493; JPJ 512 to 514, 516, 518, 519, 521, 522, 524, 528, 529, 531, 534, 537-540, 543 to 546, 548, 550, 554 to 559, 561, 562, 570, 571); Loma Atravesada, aprox. 3 km al NO del puesto de Leandro Vega, NO de Chumbicha (JPJ 1158, 1160, 1161, 1163 to 1166, 1171); Mogote Las Trampas, aprox. 15 km al NW de Chumbicha, 2300 m (CNP 1492; MACN 23479, 23480; JPJ 1419, 1429, 1437, 1438, 1443, 1462, 1465 to 1467, 1476); Río Vallecito, a 1500 m (MACN 50-424, 50-430, 50-435); unión entre las rutas provinciales N° 9 y 18, 3.4 km al S, sobre Ruta Provincial N° 18, 1529 m (JPJ 1121, 1125, 1135, 1141, 1155). Mendoza Province: Laguna Llacanelo, 1335 m (CNP 1897). Salta Province: aprox. 15 km al W de Escoipe, sobre Ruta Provincial N° 33, 2680 m (MACN 23496, 23497; JPJ 50, 52-56, 58, 59, 66, 69, 70, 76, 77, 80, 82, 83, 85, 88, 1033, 1036 to 1042, 1044, 1046, 1047, 1049 to 1051, 1053, 1058); aprox. 2 km al NNE de Cachi Adentro, sobre el camino a Las Pailas, 2567 m (JPJ 1199, 1203 to 1205); Arroyo Salado, 7 km al E de Rosario de la Frontera, al lado del ACA (PEO-e 34); Cachi Adentro, sobre Río Cachi, 2490 m (MACN 23495; JPJ 1194, 1209); Campo Quijano aprox. 5 Km al NO, Km 30 de la ruta Nacional 51 (Quebrada del Toro), alt. aprox. 1600 msnm (JPJ 139, 150); Cuesta del Obispo, aprox. 5 km al NE de Piedra del Molino, sobre Ruta Provincial N° 33, 3174 m (JPJ 1211, 1212); El Corralito, aprox. 23 km al SO de Campo Quijano, sobre ruta Nac. N° 51 (JPJ 143); La Poma, 3 km al este (PEO-e 197); Santa Rosa de Tastil (MACN 15642, 15643); Valle Encantado, Parque Nacional Los Cardones (PEO-e 111). Tucumán Province: 12 km W of Quebradita, Tafi del Valle, km 81 along Hwy 307 (CML 3455 to 3459); 2 km al Sur de Gobernador Garmendia por ruta 34 (PEO-e 73); Aconquija, 3000 m (MACN 34-851); Aconquija, a 3000 m (MACN , 29-285, 29-305, 29-306, 29-308, 29-310, , 29-316, 29-335 to 29-339, 29-350, 29-369 to 29-371, 29-378, 34-845, 34-859, 34-860, 34-884, 34-908, 34-910, 34-911, 34-915, 34-916, 34-922, 34-966, 34-1070, 34-1105, 34-1122, 34-1125, 34-1130); aprox. 10 km (por ruta) al NNW de Potrero de las Tablas, sobre la ruta entre Potrero de las Tablas y El Siambón, 900 m (JPJ 1516 to 1518, 1520 to 1522); aprox. 10 km al S de Hualinchay, sobre el camino a Lara, 2300 m (JPJ 430 to 434, 436, 438, 439, 448, 452, 454, 455, 457, 458, 462 to 464, 466, 477, 479, 480, 484 to 486, 489 to 491, 494, 497, 499, 500, 508, 754 to 759, 773, 971 to 976, 978, 980, 983 to 985, 988 to 991, 995, 996, 999, 1001 to 1004, 1006 to 1008, 1217 to 1219, 1223); aprox. 16 km de Hualinchay, sobre el camino a Lara, 2750 m (JPJ 741 to 745, 747, 750, 764, 766, 775, 778, 779); aprox. 7 km al NO de la finca de la familia Usandivara, Altos de Medina, 1717 m (MACN 23511; JPJ 808, 809, 811 to 815, 817, 819 to 823, 825 to 830, 833 to 835, 838, 840, 842 to 848, 850, 854, 855); Barranca de roedores fósiles, La Angostura (PEO-e 13, 26); Camino a Amaicha, km 83 (CML 698, 701, 710); Camino a Amaicha, Ruta Provincial 307, km 83 (CML 697); Camino a Villa Padre Monti, ruta 305 2 km al sur de Sunchal sobre río Calera (PEO-e 174); Campamento El Samay, Parque Provincial El Cochuna (CML 4170); Carapunco, km 81 de la Ruta Provincial N° 307, 2960 m (CNP 1491; JPJ 1065, 1067 to 1069, 1072 to 1074, 1076, 1077, 1079 to 1082, 1084 to 1098); Castillo de las Brujas, 15 km al sudeste de Amaicha del Valle (PEO-e 47); Cerro de Vipos, 1000 m (MACN 32-37, 32-38, 30-180, 30-182); Cerro de Vipos, 500 m (MACN 32-18 to 32-22); Cerro Muñoz (CML 669, 1928); Cerro San Javier, 2300 m (MACN 26-139); Concepción (MACN 29-278, 29-300, 29-319, 29-323, 29-325, 29-326, 29-328, 29-329, 29-331 to 29-333, 29-354, 29-355, 29-356, 29-360, 29-362, 29-368, 29-379, 34-865, 34-919, 34-924, 34-926, 34-929, 34-969, 34-971, 34-1136); Cumbre del Taficillo, al NE de Las Agüitas, Parque Biológico Sierra de San Javier (JPJ 111, 113, 115, 117, 119, 121); Cumbre del Taficillo, Las Agüitas, Parque Biológico Sierra de San Javier (CML 4038, 4041); desaguadero del dique La Angostura (PEO-e 18); Dique Escaba, 500 m al N, por ruta 358 (CML 4976, 4977); Dique Escaba, 700 m al NW del paredón (CML 4167); Dique San Ignacio (CML 2869); El Infiernillo (MMPMa 2374, 2378 to 2380, 2382, 2385, 2390, 2392, 2394); El Infiernillo, 3000 m (CML 691); El Infiernillo, km 83 along hwy 307, 10000 feet (CML 3468 to 3472); El Mollar (PEO-e 9); El Naranjal (MACN 17536); El Rincón, vertiente oeste de la Loma Pelada, Valle de Tafi (PEO-e 161); Escuela de Agricultura de la UNT, Horco Molle (PEO-e 211); Horco Molle (CML 2815); Hualinchay, sobre el camino a Cafayate, 1861 (JPJ 157, 160, 162, 164, 165, 171, 177, 193, 211, 226, 233, 237, 238, 241, 248, 250 to 252); Infiernillo, 3000 m (CML 692); Jardín del Instituto Lillo, Miguel Lillo y San Lorenzo, San Miguel de Tucumán (PEO-e 89, 157); La Aguadita (CML 4941 to 4944); La Cruz, Cumbre del Taficillo, Parque Biológico Sierra de San Javier, 1907 m (CNP 1490; MACN 23512; JPJ 856 to 862, 864 to 869, 871 to 893, 895 to 898, 900 to 910, 912 to 919); La Florida (Reserva)- Pueblo Viejo (CML 6090); La Tranquera, límite N de Finca Los Chorrillos, sobre ruta provincial 205, 1426 m (JPJ 1773, 1890, 1895); Las Agüitas, cumbre del Taficillo (CML 4018, 4022, 4023, 4025, 4027 to 4029, 4031, 4033 to 4035, 4037, 4040, 4042); Parque Biológico Sierra de San Javier, área de la residencia universitaria, a metros del LIEY, 711 m (MACN 23515); Parque Provincial El Cochuna (camping) (CML 4979); Parque Provincial El Cochuna, aprox. Km 40, ruta provincial 48 (CML 2916 to 2920); Piedras Coloradas, sobre ruta 307, km 21 (CML 4108); Plaza Belgrano, San Miguel de Tucumán (PEO-e 42); Quebrada Cainzo (CML 1630); Quebrada de Los Sosa, 700 m (MACN 20342); Reserva Arqueológica La Bolsa, al lado ruta 307 km 77 (PEO-e 24);

Reserva de la Florida, 7 km al W de Ibatín, sobre río Pueblo Viejo (CML 5007 to 5013, 5015 to 5018); Reserva la Florida, 7 km al O. de Ibatín, sobre Río Pueblo Viejo (CML 5007, 5009, 5010); Reserva La Florida, Pueblo Viejo (CML 6089 to 6091); Reserva Provincial Aguas Chiquitas (CML 4989); Reserva Provincial Aguas Chiquitas (El Cadillal) (CML 6009, 6011, 6016); Reserva Provincial Aguas Chiquitas, Arroyo Aguas Chiquitas (CML 4988, 4990); Reserva Provincial Aguas Chiquitas, El Cadillal (CML 4884, 4982, 4983, 4985, 4986); Reserva Provincial La Florida-Pueblo Viejo, sobre el Río Pueblo Viejo (CML 5004 to 5006); Reserva Provincial Los Sosa, camino a Tafí, ruta 307, km 35, campamento Vialidad (CML 4096, 4100); Reserva Provincial Los Sosa, El Indio, Río Los Sosa, Ruta 307 (CML 6039, 6040, 6042); Reserva Provincial Santa Ana, sobre Río El Saltón (CML 6030, 6031, 6047, 6068 to 6070, 6072, 6074, 6078, 6081); Ruta 307, km 72 (MMPMa 2381, 2384, 2395); Ruta 307, km 84, 3000 m (El Infiernillo) (CML 4630 to 4632); Ruta 307, km 84, 3000 m, El Infiernillo (CML 3773); San Miguel de Tucumán (MACN 17519); Sierra Aconquija, 3000 m (MACN 29-284); Sierra de Vipos, a 1000 m (MACN 30-181); Sobre Ruta 307, km 72 (MMPMa 2383, 2386, 2388, 2393); Tafí del Valle (CML 2058, 2061); Tafí del Valle, 2500 m (CML 934); Tafí del Valle, km 83, 2900 m (CML 1837); Tafí del Valle, La Quebradita, casa de Rubén (CML 3791); Tafí Viejo, 1000 m (MACN 33-231, 33-232); Tapia (CML 325, 332); Toma de agua Los Reales, aprox. 8 km al NW del Complejo Pueblo Viejo, 1065 m (JPJ 1477, 1478); Unión ruta 304 y río Tajamar, 2 km al norte de Benjamín Aráoz (PEO-e 65); Villa Nougés (CML 2774, 2789); Villa Nougés, 1388 m (CML 2770, 2773, 2790 to 2801, 2803, 5021); Villa Nougés, aprox. 2 km al N, sobre Ruta Provincial N° 338, a la altura de la antena repetidora del Canal 10 de televisión (JPJ 257, 261, 263, 264, 267 to 273, 281, 283 to 287, 289); Zanja del Chivo, La Angostura (PEO-e 2); Zanjón de Tafí, 2 km al sudoeste de Tafí del Valle (PEO-e 179).

Akodon sylvanus (81). ARGENTINA: Jujuy Province: a 2.5 km del Arroyo Santa Rita, sobre camino a El Fuerte (CML 2039); El Simbolar, 25 km al SW de Palma Sola (CML 1984 to 1988, 1990, 1991, 1994, 1996, 1997, 2019, 2027 to 2029, 2031 to 2036, 2099 to 2101, 2103, 2105, 2108, 2110 to 2112); Finca El Piquete, márgenes del Río Volcán, aprox. a 5 km del cruce del Río Tamango y la senda maderera, 973 m (MACN 23490); Finca El Piquete, márgenes del Río Volcán, aprox. a 5 km del cruce del Río Tamango y la senda maderera, 973 m (JPJ 1107); La Antena, Sierra del Centinela, al S de El Fuerte, 2350 m (CNP 1482; MACN 23491, 23493; JPJ 926 to 932, 934, 935, 937 to 939, 941 to 951, 959, 960); La Herradura, 12 km al SW de El Fuerte, sobre Ruta Provincial N° 6, 1428 m (CNP 1485; JPJ 576 to 578, 580, 584, 586, 589, 590, 592 to 594, 596, 600, 602, 604 to 606, 611, 615).

Akodon toba (12). ARGENTINA: Jujuy Province: Finca El Talar, aprox. 10 km al SSE de El Talar, 347 m (JPJ 1950, 1951). Salta Province: 17 km al E de Santo Domingo (CML 3017 to 3020); Finca Los Colorados, 17 km al E de Santo Domingo (CML 5192).

APPENDIX II

Gazetteer of localities.

- 1—Campo Largo, km 74.5 de la ruta entre Acambuco y Campo Largo, 684 m (Gral. José de San Martín, Salta) 22° 1' 42.96" S, 63° 55' 37.2" W.
- 2—Yavi Chico (Yavi, Jujuy) 22° 6' S, 65° 28' W.
- 3—1 km ENE de Rodeo Pampa, km 59 de Ruta Provincial N° 7, 3080 m (Santa Victoria, Salta) 22° 14' 47.7" S, 65° 3' 4.3" W.
- 4—Aguaray (Gral. José de San Martín, Salta) 22° 16' S, 63° 46' W.
—Aguaray, 600 m.
—Aguaray. FCCNA, 700 m.
- 5—Aprox. 1.6 km al W de Los Toldos, sobre la senda a Santa Victoria, 1621 m (Santa Victoria, Salta) 22° 16' 41.2" S, 64° 42' 45.9" W.
- 6—Pampa Verde, aprox. 8 km al OSO de Los Toldos y al S del Cerro Bravo, 2400 m (Santa Victoria, Salta) 22° 17' S, 64° 48' W.
- 7—Finca Falcón, aprox. 3 km al NW del pozo de agua N 5, cercanías del Río Seco, 704 m (Gral. José de San Martín, Salta) 22° 18' 41.4" S, 63° 58' 7.1" W.
- 8—Aprox. 5 km (por ruta) al S de Los Toldos, sobre el camino a Vallecito, 1705 m (Santa Victoria, Salta) 22° 19' 5.7" S, 64° 43' 8.3" W.
- 9—Laguna de Pozuelos (Santa Catalina, Rinconada and Yavi, Jujuy) 22° 21' 47.9" S, 66° 0' 9.3" W.
- 10—Aprox. 300 m al NE de la escuela Histórica San Pedrito, 1143 m (Gral. José de San Martín, Salta) 22° 22' 57.6" S, 64° 0' 4.8" W.
- 11—Aprox. 35 km (por ruta) al NW de Vespucio, 635 m (Gral. José de San Martín, Salta) 22° 25' 41.3" S, 63° 59' 42.2" W.
- 12—P. N. Baritú, Las Juntas Lipeo-Bermejo (Santa Victoria, Salta) 22° 26' S, 64° 31' W.
—Parque Nacional Baritú, Las Juntas.
- 13—P. N. Baritú, angosto Río Baritú, 1600 m (Santa Victoria, Salta) 22° 30' 25.5" S, 64° 45' 34.5" W.
-Parque Nacional Baritú, angosto Río Baritú, 1600 m.
-Parque Nacional Baritú, Baritú, 1600 m.
- 14—Desembocadura Arroyo Santelmita, 700 m (Santa Victoria, Salta) 22° 31' 1.5" S, 64° 35' 55.5" W.
-Parque Nacional Baritú, boca Arroyo Santelmita.
-Parque Nacional Baritú, desembocadura Arroyo Santelmita, 700 m.
- 15—Aprox. 21 km (por ruta) al WNW de Vespucio, sobre el Río Seco, 532 m (Gral. José de San Martín, Salta) 22° 31' 56.7" S, 64° 0' 11.4" W.
- 16—Azul Cuesta, aprox. 9 km al S de Nazareno, 3286 m (Santa Victoria, Salta) 22° 31' 58.8" S, 65° 6' 59.2" W.
- 17—Cerro Chaguar, snias. del Porongal, 1200 m (Santa Victoria, Salta) 22° 33' 25.5" S, 64° 35' 34.5" W.
—Cerro Chaguar, snias. Porongal, 1250 m.
—Parque Nacional Baritú, cerro Chaguar, 1200 m.
- 18—Parque Nacional Baritú, nacientes Arroyo Santelmita (Santa Victoria, Salta) 22° 33' 40.5" S, 64° 36' 37.5" W.
—Parque Nacional Baritú, nacientes Arroyo Santelmita, 900 m.
—Parque Nacional Baritú, nacientes del Arroyo Santelmita, 900 m.
- 19—Nacimiento Quebrada Santa Rosa, 950 m (Santa Victoria, Salta) 22° 34' 40.5" S, 64° 35' 55.5" W.
—Parque Nacional Baritú, Arroyo Santa Rosa, 900 m.
—Parque Nacional Baritú, nacimiento Arroyo Santa Rosa, 900 m.
- 20—Los Helechos, P. N. Baritú, Fca. Jakulica, 1200 m (Santa Victoria, Salta) 22° 39' 43.5" S, 64° 31' 58.5" W.
—P. N. Baritú, Fca. Jakulica, Los Helechos, 1200 m.
—P. N. Baritú, Sierra de Las Pavas, Fca. Jakulica, 1200 m.
- 21—Finca Jakulica, Sierra de Las Pavas (Santa Victoria, Salta) 22° 40' 7.5" S, 64° 34' 31.5" W.
—P. N. Baritú, Fca. Jakulica, Sierra Las Pavas.
—Sierra Las Pavas, vecindades de Finca Jakulica.
- 22—Parque Nacional Baritú, Las Pavas, 1 angosto Río Pescado, finca Jakulica, 1200 m (Santa Victoria, Salta) 22° 40' 10.5" S, 64° 33' 52.5" W.

- 23—finca Jakulica, casa vialidad, Río Pescado, 658 m (Santa Victoria, Salta) 22° 40' 40" S, 64° 29' 5.3" W.
- 24—1 angosto río Pescado, finca Jakulica, 650 m (Santa Victoria, Salta) 22° 40' 57" S, 64° 34' 40.9" W.
- Angosto Río Pescado.
- Finca Jakulica, 1 angosto río Pescado, 650 m.
- Finca Jakulica, 2 angosto río Pescado, 650 m.
- Finca Jakulica, srras. de Las Pavas, cerca angosto río Pescado, 650 m.
- 25—Vado de Arrazayal (Orán, Salta) 22° 40' 58.8" S, 64° 36' 0" W.
- 26—27 km al O de Aguas Blancas (Orán, Salta) 22° 45' S, 64° 40' W.
- 27—Finca Río Seco, 40 km al N de Embarcación, 524 m (Gral. José de San Martín, Salta) 22° 51' 6.3" S, 64° 4' 45.5" W.
- 28—Aprox. 36 km al NNW de Embarcación, Finca Río Seco, 611 m (Gral. José de San Martín, Salta) 22° 53' 35.4" S, 64° 8' 7" W.
- 29—43.7 km al NW de ruta 50 y ruta provincial 18, camino a Isla de Cañas (Orán, Salta) 23° 0' S, 64° 33' W.
- 30—Embarcación (Gral. José de San Martín, Salta) 23° 13' S, 64° 6' W.
- 31—Finca Alto Verde, 670 m (Orán, Salta) 23° 13' 38.4" S, 64° 32' 35" W.
- 32—Abra de Ciénaga Negra, aprox. 3 km al SE, 3090 m (Orán, Salta) 23° 19' 49" S, 64° 53' 32" W.
- 33—2.5 km W El Bananal, 437 m (Ledesma, Jujuy) 23° 33' S, 64° 32' W.
- 34—El Duraznillo, Cerro Calilegua, 2600 m (Valle Grande, Jujuy) 23° 34' S, 64° 53' W.
- 35—Cerro Hermoso (Ledesma, Jujuy) 23° 34' S, 64° 51' W.
- Cerro Hermoso, Calilegua.
- Cerro Hermoso, Parque Nacional Calilegua.
- 36—La Laguna, 4500 m, Sierra de Zenta, E de Maimar (Tilcara, Jujuy) 23° 35' S, 65° 18' W.
- Sierra de Zenta, a 4500 m.
- 37—Ruta 83, camino a Valle Grande, 9 km al N de San Francisco (Valle Grande, Jujuy) 23° 35' S, 64° 58' W.
- 38—Finca FAMAT, aprox. 1.5 km al SW del portón de entrada de la finca, 406 m (Ledesma, Jujuy) 23° 37' 38.3" S, 64° 31' 5.1" W.
- 39—Planta Caimancito, pozo 43, 560 m (Ledesma, Jujuy) 23° 38' 30.9" S, 64° 36' 26.7" W.
- 40—Yuto, INTA, 400 m (Ledesma, Jujuy) 23° 38' 40.5" S, 64° 28' 13.5" W.
- 41—Planta Caimancito, Batería, 535 m (Ledesma, Jujuy) 23° 38' 40.7" S, 64° 36' 11.9" W.
- 42—Planta Caimancito, aprox. 700 m al E de la Batería, 498 m (Ledesma, Jujuy) 23° 38' 41.7" S, 64° 35' 54.1" W.
- 43—13 km al SW de Yuto, sobre arroyo Yuto (Ledesma, Jujuy) 23° 38' 46.5" S, 64° 32' 34.5" W.
- 44—Parque Nacional Calilegua, bomba de YPF, en las márgenes del Arroyo Sauzalito (Ledesma, Jujuy) 23° 38' 52.5" S, 64° 34' 55.5" W.
- 45—Finca FAMAT, aprox. 3 km al SW del portón de entrada de la finca, 400 m (Ledesma, Jujuy) 23° 38' 53.4" S, 64° 31' 53.9" W.
- 46—Finca Sauzalito, aprox. 1 km al E del cruce entre la ruta nacional 34 y el Río Yuto, 413 m (Ledesma, Jujuy) 23° 39' 4.7" S, 64° 32' 2.8" W.
- 47—Finca El Talar, aprox. 10 km al SSE de El Talar, 347 m (Santa Bárbara, Jujuy) 23° 39' 7.8" S, 64° 20' 33.2" W.
- 48—Abra de Cañas (Valle Grande, Jujuy) 23° 40' S, 64° 54' W.
- Abra de Cañas, 1710 m, Parque Nacional Calilegua.
- Abra de Cañas, Calilegua.
- Abra de Cañas, El Monolito, 1700 m.
- 49—Mesada de Las Colmenas (Ledesma, Jujuy) 23° 42' S, 64° 52' W.
- 50—Caimancito (Ledesma, Jujuy) 23° 44' S, 64° 36' W.
- Caimancito, 600 m, Parque Nacional Calilegua.
- Caimancito, FCCNA, 700 m.
- 51—Aguas Negras (Ledesma, Jujuy) 23° 45' S, 64° 56' W.
- Aguas Negras, Parque Nacional Calilegua, 600 m.
- 52—General San Martín (Ledesma, Jujuy) 23° 48' 13.5" S, 64° 46' 49.5" W.
- 53—Finca Las Moras, aprox. 6.5 km (por senda maderera) al SE de la entrada a la finca, 460 m (Santa Bárbara, Jujuy) 23° 49' 38.8" S, 64° 31' 33.5" W.
- 54—Laguna La Brea (Santa Bárbara, Jujuy) 23° 51' 30.9" S, 64° 26' 14.8" W.

- Laguna La Brea, sobre ruta 1, 3 km de Las Siete Aguas.
- 55—12 km W de Fraile Pintado, sobre Río Ledesma (Ledesma, Jujuy) 23° 57' 34.5" S, 64° 55' 1.5" W.
- 56—Tiraxi, 1.5 km al E, sobre ruta 29 (Dr. Manuel Belgrano, Jujuy) 23° 59' S, 65° 19' W.
- Tiraxi, ruta 29, sobre Río Tiraxi.
- 57—A 4 km al N de Tiraxi, sobre Río Tesorero, ruta 29 (Capital, Jujuy) 23° 59' S, 65° 18' W.
- 58—Bárcena, aprox. 3 km al S, sobre Ruta nacional N° 9, 1808 m (Tumbaya, Jujuy) 24° 0' 2" S, 65° 26' 51.6" W.
- 59—Río Las Capillas, 15 km al N de Las Capillas, por ruta 20 (Dr. Manuel Belgrano, Jujuy) 24° 1' 46.5" S, 65° 6' 13.5" W.
- Río Las Capillas, 15 km al N de Las Capillas, por ruta 20, 957 m.
- 60—León (Dr. Manuel Belgrano, Jujuy) 24° 2' 7.5" S, 65° 26' 1.5" W.
- León, Arroyo La Tablada.
- 61—Arroyo La Horqueta, 6 km al SE de las lagunas de Yala (Capital, Jujuy) 24° 7' S, 65° 25' W.
- 62—Arroyo La Horqueta, 3 km al SE de las Lagunas de Yala (Capital, Jujuy) 24° 7' S, 65° 27' W.
- 63—Termas de Reyes, aprox. 15 km al N, sobre Ruta Provincial N° 4 (Dr. Manuel Belgrano, Jujuy) 24° 7' 4.5" S, 65° 29' 19.5" W.
- 64—El simbolar, 25 km al SW de Palma Sola (Santa Bárbara, Jujuy) 24° 8' 34.5" S, 64° 24' 16.5" W.
- 65—Termas de Reyes, mirador, sobre Ruta Provincial N° 4 (Dr. Manuel Belgrano, Jujuy) 24° 9' 46.5" S, 65° 29' 58.5" W.
- 66—Finca El Piquete (Santa Bárbara, Jujuy) 24° 10' 30.5" S, 64° 34' 20.1" W.
- 67—Finca El Piquete, márgenes del Río Volcán, aprox. a 5 km del cruce del Río Tamango y la senda maderera, 973 m (Santa Bárbara, Jujuy) 24° 11' 8.3" S, 64° 33' 34.2" W.
- 68—Chorrillos, 4500 m (Los Andes, Salta) 24° 15' S, 66° 25' W.
- 69—A 2.5 km del Arroyo Santa Rita, sobre camino a El Fuerte (Santa Bárbara, Jujuy) 24° 15' 28.5" S, 64° 25' 10.5" W.
- 70—La Antena, Sierra del Centinela, al S de El Fuerte, 2350 m (Santa Bárbara, Jujuy) 24° 17' 56.46" S, 64° 23' 9.3" W.
- 71—La Herradura, 12 km al SW de El Fuerte, sobre Ruta Provincial N° 6, 1428 m (Santa Bárbara, Jujuy) 24° 18' 5.7" S, 64° 29' 38.7" W.
- 72—La Mendieta (San Pedro, Jujuy) 24° 19' S, 64° 58' W.
- 73—Cerro Morado, sobre Río Morado, 11 km al NW de San Antonio (San Antonio, Jujuy) 24° 19' 12" S, 65° 24' 0" W.
- A 11 km de San Antonio, sobre Río Morado, Cerro El Morado.
- A 11 km NW de San Antonio, sobre Río Morado, Cerro El Morado.
- A 11 km de San Antonio, Cerro El Morado.
- 74—Río Blanco, aprox. 9 km al E de San Antonio, sobre Río Blanco (El Carmen, Jujuy) 24° 24.8' S, 65° 22.5' W.
- 75—Santa Rosa de Tastil (Rosario de Lerma, Salta) 24° 27' 20.88" S, 65° 57' 33.01" W.
- 76—Abra de Santa Laura, sobre Ruta nacional N°9, 1397 m (El Carmen, Jujuy) 24° 29.9' S, 65° 18.4' W.
- Límite entre Salta y Jujuy, Abra de Santa Laura, sobre Ruta Nacional 9.
- 77—Arroyo El Cano, a 7 km del río El Saladillo (El Carmen, Jujuy) 24° 32' S, 64° 52' W.
- 78—La Poma, 3 km al este (La Poma, Salta) 24° 42' 49.5" S, 66° 9' 58.5" W.
- 79—Finca los Colorados, 17 km al E de Santo Domingo (Anta, Salta) 24° 43' S, 63° 17' W.
- Los Colorados, 17 km al E de Santo Domingo.
- 17 km al E de Santo Domingo.
- 80—Campo La Peña, Cabeza de Buey (General Güemes, Salta) 24° 47' S, 65° 1' W
- 81—Campo Quijano aprox. 5 Km al NO, Km 30 de la ruta Nacional 51 (Quebrada del Toro), alt. aprox. 1600 m (Rosario de Lerma, Salta) 24° 53' S, 65° 40' W.
- 82—Campo Quijano (Rosario de Lerma, Salta) 24° 54' S, 65° 38' W.
- 83—El Corralito, aprox. 23 Km al SO de Campo Quijano, sobre ruta Nac. N° 51 (Rosario de Lerma, Salta) 24° 58' S, 65° 48' W.
- 84—Aprox. 2 km al NNE de Cachi Adentro, sobre el camino a Las Pailas, 2567 m (Cachi, Salta) 25° 5.03' S, 66° 11.99' W.
- 85—Cachi Adentro, sobre Río Cachi, 2490 m (Cachi, Salta) 25° 5' 52.1" S, 66° 11' 37.8" W.
- 86—Aprox. 15 km al W de Escoipe, sobre Ruta Provincial N° 33, 2680 m (Chicoana, Salta) 25° 10' 26.76" S, 65° 49' 31.29" W.
- 87—Cuesta del Obispo, aprox. 5 km al NE de Piedra del Molino, sobre Ruta Provincial N° 33, 3174 m (Chicoana, Salta)

- 25° 10' 35.82" S, 65° 51' 4.44" W.
- 88—Valle Encantado, Parque Nacional Los Cardones (Chicoana, Salta) 25° 11' 48.48" S, 65° 50' 33.93" W.
- 89—Cementerio de Rosario de La Frontera (Rosario de La Frontera, Salta) 25° 47' 49.5" S, 64° 58' 41.5" W.
- 90—Arroyo Salado, 7 km al E de Rosario de la Frontera, al lado del ACA (Rosario de La Frontera, Salta) 25° 49' 54.8" S, 64° 56' 17.7" W.
- 91—Barranca cerca de Ojo de Agua, 7 km al sudeste de Rosario de La Frontera, 953 m (Rosario de La Frontera, Salta) 25° 53' 25" S, 64° 57' 49.8" W.
- 92—Cañadón Ojo de Agua, 10 km al Sur de Rosario de la Frontera, 979 m (Rosario de La Frontera, Salta) 25° 53' 59.5" S, 64° 57' 42.8" W.
- 93—Cafayate (Cafayate, Salta) 26° 6' S, 65° 57' W.
- 94—La Tranquera, límite N de Finca Los Chorrillos, sobre ruta provincial 205, 1426 m (Burruyacu, Tucumán) 26° 16' 34.3" S, 64° 59' 0.9" W.
- 95—Hualinchay, sobre el camino a Cafayate, 1861 (Trancas, Tucumán) 26° 18' 21.3" S, 65° 36' 45.8" W.
- 96—A 15 km de San Pedro de Colalao, sobre ruta hacia Hualinchay (Trancas, Tucumán) 26° 18' 21.3" S, 65° 36' 45.8" W.
- 97—Aprox. 10 km al S de Hualinchay, sobre el camino a Lara, 2300 m. (Trancas, Tucumán) 26° 19' 20.2" S, 65° 36' 45.5" W.
- 98—Aprox. 16 km de Hualinchay, sobre el camino a Lara, 2750 m (Trancas, Tucumán) 26° 19.53' S, 65° 38.85' W.
- 99—Aprox. 7 km al NO de la finca de la familia Usandivara, Altos de Medina, 1717 m (Burruyacu, Tucumán) 26° 23' 13.74" S, 65° 5' 21.48" W.
- 100—Burruyacu (Burruyacu, Tucumán) 26° 30' S, 64° 45' W.
- 101—Laguna Blanca, 3243 m (Belén, Catamarca) 26° 32' 33.5" S, 66° 55' 57.6" W.
- 102—Unión ruta 304 y río Tajamar, 2 km al norte de Benjamín Aráoz, 543 m (Burruyacu, Tucumán) 26° 32' 49.4" S, 64° 46' 57.6" W.
- 103—2 km al Sur de Gobernador Garmendia por ruta 34 (Burruyacu, Tucumán) 26° 34' 35.7" S, 64° 33' 42.3" W.
- 104—Tapia (Trancas, Tucumán) 26° 35' 29.4" S, 65° 16' 40.2" W.
- 105—Reserva Provincial Aguas Chiquitas (Burruyacu, Tucumán) 26° 36' 19.3" S, 65° 9' 59" W.
- Reserva Provincial Aguas Chiquitas, Arroyo Aguas Chiquitas.
- Reserva Provincial Aguas Chiquitas (El Cadillal).
- Reserva Provincial Aguas Chiquitas, El Cadillal.
- Río Loro.
- 106—Camino a Villa Padre Monti, ruta 305, 2 km al sur de Sunchal sobre río Calera, 657 m (Burruyacu, Tucumán) 26° 37' 57.4" S, 65° 3' 13.2" W.
- 107—km 1315 de la ruta nacional N° 9, 700 m (Tafí Viejo, Tucumán) 26° 38' 20.6" S, 65° 14' 21.6" W.
- 108—Castillo de las Brujas, 15 km al sudeste de Amaicha del Valle (Tafí del Valle, Tucumán) 26° 38' 58.5" S, 65° 50' 34.5" W.
- 109—La Cruz, Cumbre del Taficillo, Parque Biológico Sierra de San Javier, 1907 m (Tafí Viejo, Tucumán) 26° 41' 11.7" S, 65° 19' 56.4" W.
- Cerro San Javier, 2300 m
- 110—Cumbre del Taficillo, al NE de Las Agüitas, Parque Biológico Sierra de San Javier (Tafí Viejo, Tucumán) 26° 41' 51.7" S, 65° 20' 20.4" W.
- 111—Cumbre del Taficillo, Las Agüitas, Parque Biológico Sierra de San Javier (Tafí Viejo, Tucumán) 26° 42' S, 65° 21' W.
- Las Agüitas, cumbre del Taficillo.
- La Aguadita.
- 112—Tafí Viejo, 1000 m (Tafí Viejo, Tucumán) 26° 43' 51.8" S, 65° 18' 22.5" W.
- 113—Ruta 307, km 84, 3000 m (El Infiernillo) (Tafí del Valle, Tucumán) 26° 44' 19.5" S, 65° 45' 52.5" W.
- Ruta 307, km 84, 3000 m, El Infiernillo
- 114—El Infiernillo, km 83 along hwy 307, 10000 feet (Tafí del Valle, Tucumán) 26° 44' 37.5" S, 65° 45' 19.5" W.
- Camino a Amaicha, Ruta Provincial 307, km 83.
- Tafí del Valle, km 83, 2900 m.

- Camino a Amaicha, km 83.
 —El Infiernillo, 3000 m.
 —Infiernillo, 3000 m.
 —El Infiernillo.
- 115—12 km W of Quebradita, Tafí del Valle, km 81 along Hwy 307 (Tafí del Valle, Tucumán) 26° 45' 18.93" S, 65° 44' 38.68" W.
- Carapunco, km 81 de la Ruta Provincial N° 307, 2960 m.
- 116—Parque Biológico Sierra de San Javier, área de la residencia universitaria, a metros del LIEY, 711 m (Yerba Buena, Tucumán) 26° 46' 36" S, 65° 19' 31" W.
- 117—Escuela de Agricultura de la UNT, Horco Molle (Yerba Buena, Tucumán) 26° 46' 47" S, 65° 19' 27.7" W.
- 118—Reserva Arqueológica La Bolsa, al lado ruta 307, km 77 (Tafí del Valle, Tucumán) 26° 47' S, 65° 43' W.
- 119—Horco Molle (Yerba Buena, Tucumán) 26° 47' 38.4" S, 65° 18' 57.6" W.
- 120—San Javier (Yerba Buena, Tucumán) 26° 47' 52.48" S, 65° 21' 35.52" W.
- 121—aprox. 10 km (por ruta) al NNW de Potrero de las Tablas, sobre la ruta entre Potrero de las Tablas y El Siambón, 900 m (Lules, Tucumán) 26° 48' 33.7" S, 65° 27' 0.5" W.
- 122—Ruta 307, km 72 (Tafí del Valle, Tucumán) 26° 48' 52.5" S, 65° 43' 25.5" W.
- Sobre ruta 307, km 72.
- 123—San Miguel de Tucumán (Capital, Tucumán) 26° 49' 30.3" S, 65° 12' 45.9" W.
- 124—Jardín del Instituto Lillo, Miguel Lillo y San Lorenzo, San Miguel de Tucumán (Capital, Tucumán) 26° 49' 50.8" S, 65° 13' 17.7" W.
- 125—Plaza Belgrano, San Miguel de Tucumán, 440 m. (Capital, Tucumán) 26° 50' 14.7" S, 65° 12' 59.1" W.
- 126—Tafí del Valle, La Quebradita, casa de Rubén (Tafí del Valle, Tucumán) 26° 50' 31.1" S, 65° 42' 38.6" W.
- 127—Villa Nougues, aprox. 2 km al N, sobre Ruta Provincial N° 338, a la altura de la antena repetidora del Canal 10 de televisión (Lules, Tucumán) 26° 50' 33.9" S, 65° 22' 59.82" W.
- 128—Tafí del Valle, 2500 m (Tafí del Valle, Tucumán) 26° 50' 37.5" S, 64° 42' 34.5" W.
- 129—Villa Nougues (Lules, Tucumán) 26° 50' 55.5" S, 65° 23' 19.5" W.
- Villa Nougues, 1388 m.
- 130—Zanjón de Tafí, 2 km al sudoeste de Tafí del Valle (Tafí del Valle, Tucumán) 26° 51' 43" S, 65° 43' 6" W.
- 131—Ing. San Pablo (Famaillá, Tucumán) 25° 51' 43.5" S, 65° 18' 34.5" W.
- 132—Tafí del Valle (Tafí del Valle, Tucumán) 26° 52' S, 65° 41' W.
- 133—Cerro Muñoz (Tafí del Valle, Tucumán) 26° 53' S, 65° 50' W.
- 134—Desaguadero del dique La Angostura (Tafí del Valle, Tucumán) 26° 56' 13.5" S, 65° 40' 58.5" W.
- 135—El Mollar (Tafí del Valle, Tucumán) 26° 56' 23.6" S, 65° 42' 30.2" W.
- 136—La Angostura (Tafí del Valle, Tucumán) 26° 56' 25.5" S, 65° 42' 10.5" W.
- Barranca de roedores fósiles, La Angostura.
- 137—El Rincón, vertiente oeste de la Loma Pelada, Valle de Tafí (Tafí del Valle, Tucumán) 26° 56' 22.5" S, 65° 46' 22.5" W.
- 138—Zanja del Chivo, La Angostura (Tafí del Valle, Tucumán) 26° 56' 46.5" S, 65° 40' 4.5" W.
- 139—Reserva Provincial Los Sosa, camino a Tafí, ruta 307, km 35, campamento Vialidad (Monteros, Tucumán) 27° 0' 48.3" S, 65° 39' 36.7" W.
- 140—El Bolsón, 2309 m (Belén, Catamarca) 27° 1' 28.8" S, 66° 45' 39.8" W.
- 141—El Naranjal, ruta 307 (Monteros, Tucumán) 27° 2' S, 65° 41' W.
- El Naranjal.
- 142—Reserva Provincial Los Sosa, El Indio, Río Los Sosa, Ruta 307 (Monteros, Tucumán) 27° 3' 23.3" S, 65° 40' 13.5" W.
- 143—Piedras Coloradas, sobre ruta 307, km 21 (Monteros, Tucumán) 27° 4' S, 65° 40' W.
- 144—Quebrada de Los Sosa, 700 m (Monteros, Tucumán) 27° 5' 41.5" S, 65° 39' 19.5" W.
- 145—Toma de agua Los Reales, aprox. 8 km al NW del Complejo Pueblo Viejo, 1065 m (Monteros, Tucumán) 27° 6' 56.5" S, 65° 46' 25.9" W.
- 146—La Florida (Reserva)—Pueblo Viejo (Monteros, Tucumán) 27° 9' 10.5" S, 65° 43' 31.5" W.
- Reserva Provincial La Florida-Pueblo Viejo, sobre el Río Pueblo.

- 147—Reserva de la Florida, 7 km al W de Ibatín, sobre río Pueblo Viejo (Monteros, Tucumán) 27° 12' 10.5" S, 65° 38' 58.5" W.
- Reserva la Florida, 7 km al O de Ibatín, sobre Río Pueblo Viejo.
- 148—Parque Provincial El Cochuna, aprox. Km 40, ruta provincial 48 (Chicligasta, Tucumán) 27° 19' 19.5" S, 65° 55' 34.7" W.
- Campamento El Samay, Parque Provincial El Cochuna.
- Parque Provincial El Cochuna (camping).
- 149—Concepción (Chicligasta, Tucumán) 27° 20' S, 63° 35' W.
- 150—Río Vallecito, a 1500 m (Andalgalá, Catamarca) 27° 20' S, 6° 6' 0" W.
- 151—Cuesta del Clavillo, 5 km al SW de la banderita (Andalgalá, Catamarca) 27° 20' 48.6" S, 65° 58' 20.1" W.
- 152—Km 33 de la Ruta Provincial N° 47, al S de Capillitas, 2500 m (Andalgalá, Catamarca) 27° 25' S, 66° 25' W.
- 153—Reserva Provincial Santa Ana, sobre río El Saltón (Río Chico, Tucumán) 27° 27' S, 65° 45' W.
- 154—Bajada del Cuervo, 10 km al Sur de Termas de Río Hondo por río Dulce (Río Hondo, Santiago del Estero) 27° 28' 41.7" S, 64° 47' 25.1" W.
- 155—El Alamito, Campo del Pucará (Andalgalá, Catamarca) 27° 29' S, 66° 2' W.
- 156—Choya, 13 km NNW Andalgalá, el. 4000 ft. (Andalgalá, Catamarca) 27° 32' S, 66° 24' W.
- 157—6 km al S de Buena Vista, 1669 m (Andalgalá, Catamarca) 27° 33' 44" S, 66° 1' 42.3" W.
- 158—El Espinillo, Campo del Pucará, Las Estancias (Andalgalá, Catamarca) 27° 35' 25.5" S, 66° 8' 34.5" W.
- 159—Dique Escaba, 500 m al N, por ruta 358 (Alberdi, Tucumán) 27° 38' 51.7" S, 65° 46' 28.7" W.
- 160—Dique Escaba, 700 m al NW del paredón (Alberdi, Tucumán) 27° 39' 18.3" S, 65° 45' 57.2" W.
- 161—Las Chacritas, aprox. 28 km al NNW de Singuil, sobre Ruta Provincial N° 1, 1888 m (Ambato, Catamarca) 27° 42' 24.2" S, 65° 54' 40.6" W.
- 162—Dique San Ignacio (La Cocha, Tucumán) 27° 44' S, 65° 40' W.
- 163—Unión entre las rutas provinciales N 9 y 18, 3.4 km al S, sobre Ruta Provincial N° 18, 1529 m (Paclín, Catamarca) 27° 49' 48.3" S, 65° 47' 53.3" W.
- 164—6 km SW of hwy 9 on hwy 18, el. 5000' (Ambato, Catamarca) 27° 52' S, 65° 48' W.
- 165—Aprox. 10 km al W de Los Varela, sobre Ruta Provincial N° 4, Sierra de Humaya, 2006 m (Ambato, Catamarca) 27° 56' 12.1" S, 65° 56' 52.8" W.
- 166—El Rodeo, 0.5 km W of Hwy 4, el. 4500 ft. (Ambato, Catamarca) 28° 13' 41.9" S, 65° 52' 52.3" W.
- 167—Aprox. 2 km al SE de Huaico Hondo, sobre Ruta Provincial N° 42, al E del Portezuelo, 1992 m (Valle Viejo, Catamarca) 28° 25' 10.9" S, 65° 32' 40.5" W.
- 168—Acceso sur a la ciudad de Catamarca, sobre ruta 38, 495 m (Capital, Catamarca) 28° 30' 14" S, 65° 46' 54" W.
- 169—Otro Cerro, 3000 m, 18 km al NNW de Chumbicha (Capayán, Catamarca) 28° 39' 19.5" S, 66° 14' 49.5" W.
- 170—Mogote Las Trampas, aprox. 15 km al NW de Chumbicha, 2300 m (Capayán, Catamarca) 28° 44' 30.66" S, 66° 19' 14.05" W.
- 171—Agua del Gauchi, aprox. 1 km al E del Mogote Los Cocos, 2024 m (Capayán, Catamarca) 28° 46' 52" S, 66° 18' 43" W.
- 172—Loma Atravesada, aprox. 3 km al NO del puesto de Leandro Vega, NO de Chumbicha (Capayán, Catamarca) 28° 47' 38.11" S, 66° 18' 26.24" W.
- 173—Cuesta La Cébila, a km de Chumbicha, sobre ruta 60 (Capital, La Rioja) 28° 50' S, 66° 24' W.
- 174—Trampasacha, 614 m (Capayán, Catamarca) 28° 50' 0" S, 66° 18' 21" W.
- 175—Pampa de Achala, aprox. 6 km (por ruta 34) al E de la antena repetidora La Posta, 2300 m (San Alberto, Córdoba) 31° 36' 44.5" S, 64° 48' 48.7" W.
- 176—Repetidora La Posta, Pampa de Achala, 2171 m (San Alberto, Córdoba) 31° 37' 2.5" S, 64° 52' 16.8" W.
- 177—Pampa de Achala, 2163 m (San Alberto, Córdoba) 31° 37' 41" S, 64° 52' 27.3" W.
- 178—Pampa de Achala (San Alberto, Córdoba) 31° 40' S, 64° 50' W.
- 179—Pampa de Achala, 2247 m (San Alberto, Córdoba) 31° 46' 49.8" S, 64° 49' 39.5" W.
- 180—Cerro de Oro (Río Cuarto, Córdoba) 32° 36' 17.4" S, 64° 53' 58.5" W.
- 181—Puesto Gonzalez (Río Cuarto, Córdoba) 32° 33' 58.2" S, 64° 52' 40.4" W.
- 182—La Ventana (Río Cuarto, Córdoba) 32° 37' 58.3" S, 64° 53' 43.9" W.

No specific localities

- Aconquija, 3000 m (Chicligasta, Tucumán)
- Cerro de Vipos, 1000 m (Trancas, Tucumán)
- Cerro de Vipos, 500 m (Trancas, Tucumán)
- Near Cuchilla Nevada, 1700-1800 m (Cruz del Eje, Córdoba)
- Parque Nacional Baritú, 700 m (Santa Victoria, Salta)
- Quebrada Cainzo (Tafí Viejo, Tucumán)
- Reserva Provincial La Florida (Monteros, Tucumán)
- Río Salí (Tucumán)
- Sierra Aconquija, 3000 m (Tucumán)
- Sierra de Vipos, a 1000 m (Tucumán)
- SW of Pampa de San Luis, 1900 m (Cruz del Eje, Córdoba)

Not found localities

- Cumbres de San Javier, Estación Biológica (Yerba Buena, Tucumán)
- Junta Suma, Las Estancias (Andalgalá, Catamarca)