

## A NEW SPECIES OF *AKODON* (RODENTIA, CRICETIDAE) FROM THE NORTHERN CAMPOS GRASSLANDS OF ARGENTINA

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Integrated analyses of morphological, chromosomal, and molecular data resulted in the description of a new species of the genus *Akodon*, endemic to the Northern Campos in southern Misiones, Argentina. The new species presents a unique combination of characters, including a narrow zygomatic plate almost without a free upper border, short rostrum, short tail (40% of the head–body length), small and flat auditory bullae, diploid complement of  $2n = 36$ , and several molecular synapomorphies. Phylogenetic analysis, based on cytochrome-*b* gene sequences, indicates that the Brazilian species *Akodon lindberghi* is sister to the new species, although this relationship is weakly supported. We comment on the conservation significance of our study, considering that these perisylvan grasslands are suffering substantial human disturbance by agriculture and burning practices.

Key words: *Akodon*, conservation, Neotropics, Northern Campos, Rodentia, Sigmodontinae, taxonomy

Cricetid rodents of the subfamily Sigmodontinae (sensu Reig 1984) constitute one of the most diverse groups of neotropical mammals. Remarkably, sigmodontine diversity is still being discovered at a high rate; 1 or 2 new living taxa are described each year (Patterson 2000). One of the genera in which new species are being described with regularity is *Akodon* (e.g., Braun et al. 2000; Díaz et al. 1999; González et al. 1998). *Akodon* is the type genus of the tribe Akodontini and is one of the most diverse and widely distributed within the entire sigmodontine radiation.

The alpha taxonomy of the genus *Akodon* has followed the classic stages in our knowledge of South American mammals. Most binomials were proposed during the discovery era, as characterized by the work of Oldfield Thomas in the late 1800s to very early 1900s, followed by a period of descriptive stasis that lasted about 50 years. During the latter period, the development of the biological species concept promoted the merger of former species into poorly characterized polytypic species, as culminated in the catalog of Cabrera (1961). Later, reviews undertaken by different authors significantly clarified the boundaries of certain species and species groups, in

particular of those from the Andes and semiarid regions (Braun et al. 2000; Díaz et al. 1999; Myers 1989; Myers and Patton 1989; Myers et al. 1990).

Some years later researchers also focused on *Akodon* species distributed in open and forested areas of eastern South America (e.g., Christoff et al. 2000; González et al. 1998; Hershkovitz 1990, 1998; Liascovich and Reig 1989; Pardiñas et al. 2003). Although these studies do not have the revisionary scope of those studies focused on species from western South American (e.g., Myers et al. 1990), they provided valuable information about the distribution, taxonomy, and natural history of several forms. Studies on Brazilian taxa have had a marked, and sometimes exclusive, cytogenetic approach, which has revealed great chromosomal diversity (Fagundes et al. 1998; Geise et al. 1998; Maia and Langguth 1981; Sbalqueiro and Nascimento 1996; Silva and Yonenaga-Yassuda 1998). Chromosomal analysis combined with other approaches (e.g., Geise et al. 2001; Pardiñas et al. 2003; Rieger et al. 1995) have resulted in a better understanding of the evolutionary history of the genus and have helped to clarify several taxonomic issues.

Herein we describe a new species of *Akodon* exclusively known from the southern portion of Misiones Province, Argentina. This region belongs to a particular biome characterized by tall grasslands in a perisylvan environment, known as Northern Campos (Giraud et al. 2003a). The description of this new species is based on morphological, karyological, and molecular data. Its comparison extends to phylogenetically related species and to similar-sized taxa that inhabit close

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tropical and subtropical lowlands of northeastern Argentina, eastern Paraguay, and southern Brazil.

## MATERIALS AND METHODS

Specimens of the new species described here were trapped with snap traps and recovered from owl pellets. Animal care and use procedures followed guidelines approved by the American Society of Mammalogists (Animal Care and Use Committee 1998). Voucher specimens, tissue samples, and cell suspensions are deposited in the Centro Nacional Patagónico, Puerto Madryn, Argentina (CNP); Laboratorio de Genética Evolutiva y Molecular, Facultad de Ciencias Exactas, Químicas y Naturales, Universidad Nacional de Misiones, Argentina; Facultad de Ciencias, Universidad de la República, Montevideo, Uruguay (ZVC-M); and the University of Michigan Museum of Zoology, Ann Arbor, Michigan (UMMZ). For comparisons, we examined *Akodon azarae*, *A. mystax*, *A. lindberghi*, *A. montensis*, and *A. sanctipaulensis*. These species were selected on the basis of the results of the phylogenetic analysis (see below) and geographic distribution. All specimens examined in this paper are listed in Appendix I.

External and craniodental morphologies were assessed by following Myers et al. (1990). Dental descriptions follow Reig (1977). A morphometric analysis was conducted based on 5 external measurements and 19 cranial and dental measurements (recorded with digital caliper to the nearest 0.01 mm). The latter were taken according to Myers et al. (1990). The list of recorded dimensions and sample sizes are provided in Appendix II. Statistical analyses included univariate descriptive values for all measurements (Appendix II) and a principal components analysis (PCA). The PCA was performed over a subset of 9 dimensions (zygomatic breadth, interorbital constriction, braincase breadth, nasal length, incisive foramen length, mesopterygoid fossa width, breadth of zygomatic plate, rostral width, and maxillary tooththrow length; see Appendix II) including only adult specimens (age class 3 sensu Myers et al. 1990) without missing values ( $n = 42$ ). Principal components were extracted from a variance-covariance matrix and computed by using the craniodental variables after transformation to their natural logarithms. Statistical analyses were made with the program STATISTICA (www.statsoft.com).

One female (CNP 738) and 1 male (ZVC-M 3805) of the new species were karyotyped by using standard chromosomal techniques. Mitotic metaphases from bone marrow were obtained in the field by following a colchicine-hypotonic technique (Verma and Babu 1995). Bone marrow was incubated in 0.1 ml (0.05%) of colchicine plus 9.9 ml of KCl (0.075 M) for 40 min at 37°C and subsequently fixed in 3:1 methanol:glacial acetic acid. Nondifferential chromosome staining was performed in phosphate-buffered Giemsa stain (pH = 6.8).

Genetic variation and phylogenetic analyses were based on cytochrome-*b* gene (*Cytb*) sequences generated by us herein and in a related study (Pardiñas et al. 2003), and taken from GenBank (accession numbers provided in "Specimens examined"). Three specimens (CNP 739, CNP 741, and CNP 742) of the new species, including the holotype, were sequenced. We also acquired sequences from 2 specimens of *A. azarae* (CNP 751 and GD 327). Sequences were obtained by following protocols detailed in D'Elía et al. (2003) and were deposited in GenBank (accession numbers AY702963–AY702968). The data set contained 1 specimen of each *Akodon* species available in GenBank. Following D'Elía (2003), who has shown that the species assigned to *A. serrensis* does not belong to the genus *Akodon*, we have not included a representative of this taxon. The exception to the pattern of including 1 specimen per species were the species described herein and *A. azarae*, a taxon morphologically

similar to the targeted species and that may be a complex of >1 species. All taxa genetically analyzed and the source and length of their *Cytb* sequence are listed in Appendix I.

Sequence alignment was done with the program Clustal X (Thompson et al. 1997) by using the default values for all alignment parameters. Percentage of observed sequence divergence was estimated with PAUP\* (Swofford 2000), ignoring those sites with missing data. Aligned sequences were subjected to maximum-parsimony (Farris 1982; Kluge and Farris 1969) and maximum-likelihood analyses (Felsenstein 1981). In the maximum-parsimony analysis characters were treated as unordered and equally weighted. PAUP\* (Swofford 2000) was used to perform 200 replicates of heuristic searches with random addition of sequences and tree bisection-reconnection branch swapping. To polarize character state transformations we included as outgroups (Nixon and Carpenter 1993) haplotypes of *Deltamys* and *Necomys*, 2 genera that belong to the *Akodon* division (sensu D'Elía 2003) of the tribe Akodontini. Two measures of clade support were calculated. We performed 1,000 parsimony jackknife (Farris et al. 1996) replications with 5 additional sequence replicates each and the deletion of one-third of the character data. Branches with <50% of support were allowed to collapse. Bremer support values (Bremer 1994) were computed for each node in PAUP\* by using command files written in TreeRot version 2 (Sorenson 1999). Maximum-likelihood analysis was conducted in PAUP\* (Swofford 2000) with 5 replicates of heuristic searches with random addition of sequences, under the GTR+G+I (Rodríguez et al. 1990) evolutionary model with the following parameters: A = 0.3270, C = 0.3098, G = 0.0947, T = 0.2685; percentage of invariable sites = 0.5473;  $\gamma = 1.4153$ . The model mentioned and its parameters were determined by using Modeltest 3.5 (Posada and Crandall 1998) by evaluating the likelihood of various substitution models optimized on a neighbor-joining tree (Saitou and Nei 1987) calculated from Jukes-Cantor corrected distances (Jukes and Cantor 1969).

## RESULTS

In 2000, while analyzing osteological remains from owl pellets collected at Estancia Santa Inés, southern Misiones Province (Argentina), we found several specimens of the genus *Akodon*, which although similar to those belonging to *A. azarae* could not be referred to this species. This undescribed taxon was one of the most common prey items of the barn owl (*Tyto alba*), reaching 30.7% of a sample of 182 individuals recovered in this locality. The same is true for an owl pellet sample collected at Parada Leis (Argentina, near Estancia Santa Inés) where the undescribed taxon represented 23% of 149 consumed micro-mammals. Preliminary qualitative comparisons with species from tropical and subtropical lowlands, including *A. azarae*, *A. lindberghi*, *A. sanctipaulensis*, and species of the *A. cursor* species group (sensu Rieger et al. 1995), suggested that the specimens in question belong to an undescribed species of *Akodon*. Trapping was then conducted to obtain complete specimens necessary for more detailed systematic analyses.

*Morphological results.*—Principal components analysis results (Fig. 1; Table 1) showed that this undescribed taxon is distinguishable from the other species to which it was compared. The 1st principal component (39.02% of the variance) shows a contrast between this undescribed taxon, *A. lindberghi*, and *A. sanctipaulensis*, and *A. azarae*. The latter has a larger maxillary tooththrow length and nasal length, wider

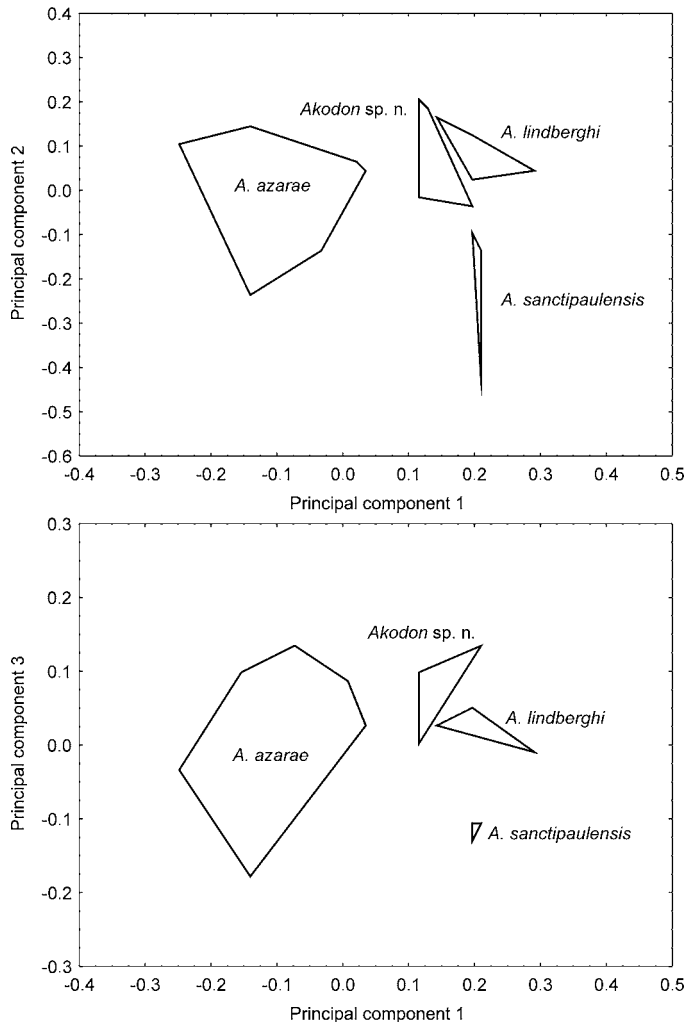


FIG. 1.—Specimen scores of individual *Akodon* ( $n = 42$ ) for principal components (top) 1 and 2 and (bottom) 1 and 3 extracted from the variance-covariance matrix of 9 craniodental dimensions (see text and Table 1).

breadth of zygomatic plate, and narrower interorbital constriction. The 3rd principal component discriminates this undescribed taxon from *A. sanctipaulensis*, which has a shorter incisive foramen length. In both graphs, individuals of this undescribed taxon appear in a cloud that is near but does not overlap with that of individuals of *A. lindberghi*.

**Karyotypic results.**—The undescribed taxon shows a diploid complement of  $2n = 36$ . This diploid number, as far as we know, has been cited only in 1 other instance within the genus *Akodon*. Brum-Zorrilla et al. (1985) reported the existence of Uruguayan specimens of *A. azarae* with  $2n = 36$  and  $2n = 38$ . Unfortunately, they did not provide the number of specimens with  $2n = 36$ , the frequency of this cytotype, its geographic distribution, or its fundamental number (FN), nor did they illustrate it. Argentinean specimens of *A. azarae* show  $2n = 37$  or  $38$ , depending on whether females are XO or XX, respectively (Bianchi et al. 1971; Lisanti et al. 2000). In addition to the differences in chromosome numbers, the karyotype of Argentinean specimens of *A. azarae* is clearly

TABLE 1.—Results of principal components (PC) analysis of craniodental measurements of adult specimens of *Akodon* (age class 3,  $n = 42$ ).

Variable	Pearson correlations		
	PC1	PC2	PC3
Zygomatic breadth	-0.49	-0.59	-0.02
Interorbital constriction	0.67	-0.34	-0.21
Braincase breadth	0.14	-0.55	-0.43
Nasal length	-0.61	-0.55	-0.54
Incisive foramen length	-0.24	-0.32	0.49
Mesopterygoid fossa width	0.41	-0.88	0.16
Breadth of zygomatic plate	-0.95	-0.16	0.17
Rostral width	-0.54	-0.31	0.45
Maxillary tooththrow length	-0.41	-0.29	-0.08
Eigenvalue	0.017	0.014	0.005
% of variance	39.0	31.9	10.5

distinct from that of this undescribed taxon; the former has only 1 pair of biarmed autosomes whereas the latter has 4. Future studies are needed to corroborate the existence of Uruguayan specimens of *A. azarae* with  $2n = 36$  and to assess the similarity of this putative cytotype and the new species described here.

**Phylogenetic results.**—The maximum-parsimony analysis recovered 3 shortest trees (1,763 steps; consistency index [CI] = 0.337; retention index [RI] = 0.509), the consensus of which is shown in Fig. 2. This undescribed taxon appears as sister to *A. lindberghi*; however, this relationship is only weakly supported (jackknife = 56; Bremer support value = 4). Four, 16, and 48 additional steps are needed to group this undescribed taxon with *A. azarae*, *A. montensis*, and *A. mystax*, respectively. At least 35 additional steps are needed to make *A. azarae* paraphyletic with respect to this undescribed taxon. In regard to this undescribed taxon, the maximum-likelihood analysis provided similar results (tree score: In likelihood = 8,710.93779; tree not shown) to that of the maximum-parsimony analysis: this undescribed taxon and *A. lindberghi* are sister taxa. The main difference between the 2 phylogenetic analyses appears in regard to the monophyly of *Akodon*: it appears paraphyletic to 1 outgroup (*Deltamys* or *Necromys*). Because this study was not designed to test akodontine generic limits we do not further discuss this issue and refer the reader to D'Elfa (2003), D'Elfa et al. (2003), and M. Smith and J. Patton (in litt.).

**Genetic comparisons.**—The observed genetic distance between the undescribed taxon and *A. lindberghi*, its sister taxon, is 10.1%. This value is one of the largest observed among pairs of sister species of *Akodon* (average for 8 comparisons = 5.9%; range 1.1% for the *A. molinae*–*A. dolores* pair to 11.2% for the *A. mimus*–*A. siberiae* pair).

## DISCUSSION

The morphological, cytogenetic, and genetic analyses provide unambiguous evidence indicating that the specimens in question belong to an undescribed species of the genus *Akodon*. The new species is qualitatively distinct from *A. cursor*, *A. montensis*, and *A. serrensis*. Although morphologically similar to *A. lindberghi*,

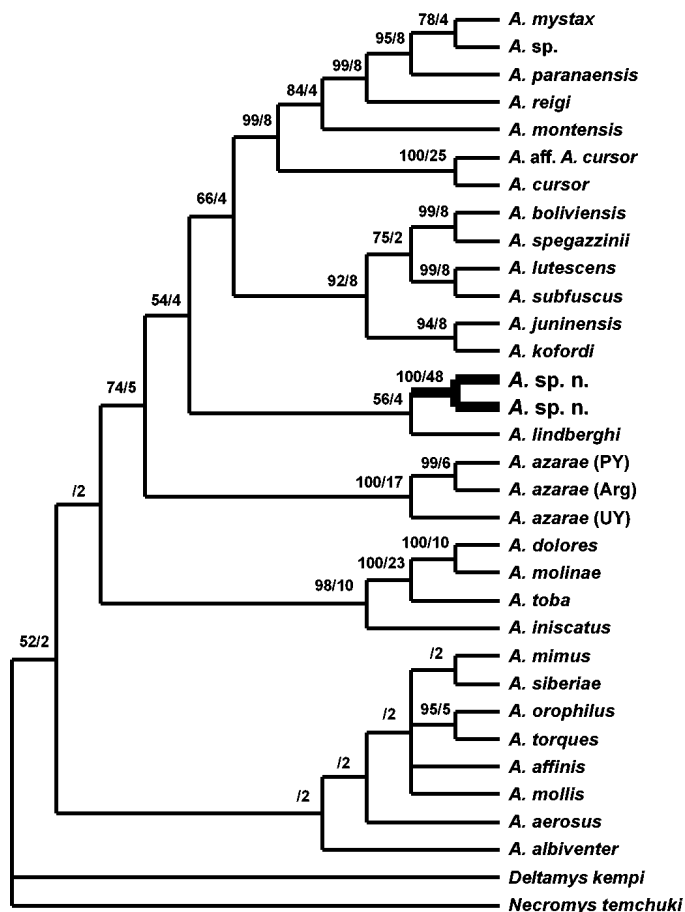


FIG. 2.—Strict consensus tree of the 3 most-parsimonious trees (length = 1,763 steps, consistency index [CI] = 0.337, retention index [RI] = 0.509) obtained in the maximum-parsimony analysis of cytochrome-*b* gene sequences. Numbers above branches indicate parsimony jackknife (to left of slash) and Bremer support (to right of slash) values of the nodes. Only jackknife values above 50% are shown. Branches leading to haplotypes of the new species of *Akodon* are thicker than those leading to haplotypes of the remaining *Akodon* species. Abbreviations indicate geographic origin of specimens of *A. azarae*: PY, Paraguay; Arg, Argentina; and UY, Uruguay.

its sister species (Fig. 2), and *A. azarae*, the 3 species clearly differentiate in a PCA of external and cranial dimensions (Fig. 1; Table 1). Moreover, the new species also shows a set of diagnostic features including cranial characters, such as a short rostrum and a very narrow zygomatic plate, a short tail, a distinct diploid complement ( $2n = 36$ ) for *Akodon*, as well as several molecular synapomorphies. Finally, although degree of DNA sequence divergence is not a good indicator of specific status (Ferguson 2002), it is interesting to note that the undescribed taxon recorded at Estancia Santa Inés is quite distinct from the other *Akodon* species for which data are available. Observed genetic distances for *Cytb* range from 10.01% (*A. lutescens* and *A. lindberghi*) to 15.09% (*A. siberiae*).

Based on these results and our assessment of qualitative characters, we recognize a new species of *Akodon* that we describe as follows.

#### *Akodon philipmyersi*, new species

*Holotype*.—CNP 739, adult male, collected by U. Pardiñas on 16 March 2001 (original field number UP 005), skin, skull, skeleton, and tissues in alcohol.

*Type locality*.—ARGENTINA: Province of Misiones, Department of Posadas, Estancia Santa Inés, Ruta No. 105 km 10 (27°31'32"S, 55°52'19"W, 95 m; Fig. 3).

*Diagnosis*.—A member of the subfamily Sigmodontinae (sensu Reig 1980) distinguishable from all other species of *Akodon* by the following combination of characters: size small (condyloincisive length <24 mm, zygomatic breadth <13 mm, maxillary tooththrow length <4.10 mm), short tail (40% of head and body length), short rostrum (incisive foramen length 5.6 mm of mean), nasals short and wide almost covering the rostrum in dorsal view, zygomatic plate very narrow almost without free upper border, mesopterygoid fossa wide with a median palatine process in the anterior border, interorbital constriction wide (4.3–4.6 mm), auditory bulla medium in size; the molecular synapomorphies are listed in Table 2 (note that sequences of several *Akodon* species were not analyzed). Diploid number ( $2n$ ) for *Akodon philipmyersi* is 36.

*Measurements of holotype*.—External measurements (in mm): length of head and body, 93; tail length, 58; length of hind foot (without claw), 17; length of hind foot (with claw), 19; ear length, 12. Weight (in g): 23. Cranial measurements (in mm): condyloincisive length, 22.31; zygomatic breadth, 12.46; braincase breadth, 10.67; interorbital constriction, 4.65; rostral length, 8.23; rostral width, 4.69; nasal length, 8.23; length of orbit, 7.93; diastema length, 6.11; maxillary tooththrow length, 3.95; length of incisive foramen, 5.92; width of tooththrow, 4.73; width across occipital condyle, 5.51; length of basioccipital at midline, 3.64; breadth of mesopterygoid fossa, 1.46; breadth of zygomatic plate, 2.14; cranial depth, 9.19; breadth of 1st upper molar, 1.21; and mandible length without incisor, 11.73. See Appendix II for paratype measurements.

*Paratypes*.—Thirteen livetrapped specimens collected at the type locality (CNP 738, CNP 740, CNP 741, CNP 742, CNP 743, CNP 744, CNP 745, CNP 746, CNP 747, CNP 748, CNP 749, UMMZ 176194, and ZVC-M 3805).

*Other referred specimens*.—Two sets of cranial remains recovered from owl pellets at the type locality (CNP 750) and Parada Leis (CNP 752).

*Distribution*.—In addition to the type locality, *A. philipmyersi* is known from Parada Leis (27°37'S, 55°49'W, 109 m, Department of Capital, Province of Misiones), about 10 km south of Estancia Santa Inés.

*Etymology*.—Dedicated to Philip Myers (University of Michigan Museum of Zoology) for his key contributions to the understanding of the taxonomy and systematics of the genus *Akodon*.

*Morphological description*.—Small representative of the genus with short limbs and tail. Back covered by soft and moderately long (mean length 10 mm) hair. Pelage at base obscure gray and agouti at distal end (about 4 mm); venter gray cream due to pheomelanin restricted to distal 2 mm of the hair. Dorsal and ventral coloration not markedly distinct. Ears

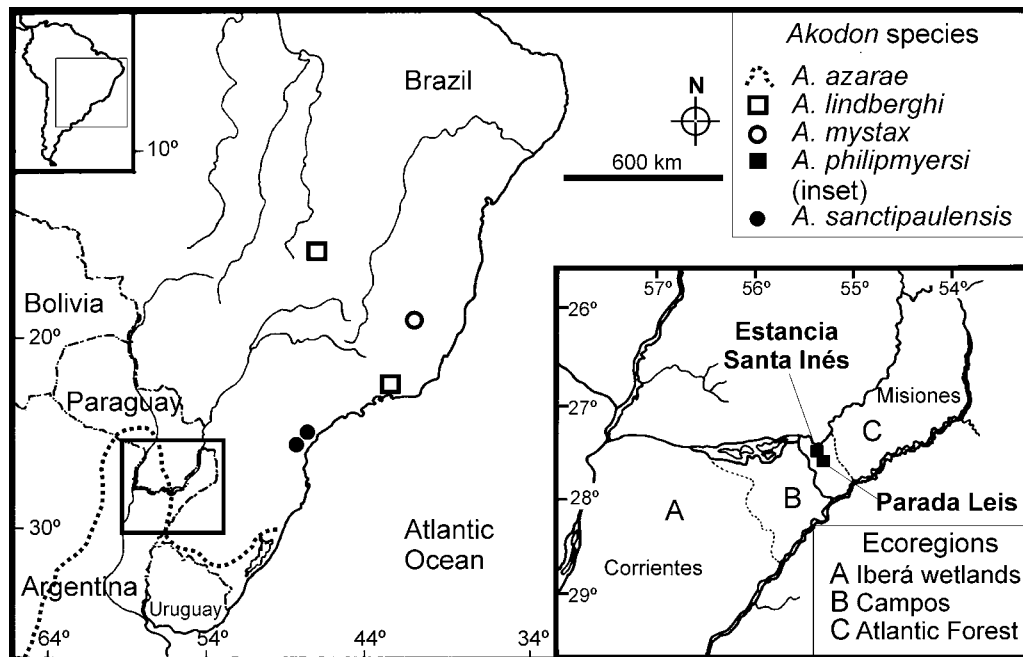


FIG. 3.—Localities and distributions in Argentina, Brazil, Paraguay, and Uruguay of *Akodon* species analyzed in this study. In the main map, the dotted line roughly indicates the northern limit of distribution of *A. azarae*.

prominent and membranous, and covered by delicate and short hair. Fore and hind feet covered dorsally by short whitish hair. Manus claws very short, whereas those on the pes reach 2 mm. Mystacial vibrissae short and not reaching ears; carpal vibrissae not surpassing claws. Tail entirely covered by short and delicate hair; dorsally dark and ventrally cream to whitish. Tail scales small, regular, and visible to the naked eye. Juveniles darker than adults, especially on belly, due to lack of the pheomelanin end of the hair.

Skull delicate, with a slightly domed profile, short rostrum, and rounded braincase (Fig. 4). Nasals short, flat, and wide, covering almost all the rostrum area in dorsal view, acuminate in their anterior end (Fig. 5a), and extending well beyond the premaxilla–frontal suture. Nasofrontal suture V- or U-shaped. Frontal sinuses moderately inflated. Interorbital region wide, with an almost undistinguishable constriction, and with smooth frontal borders. Coronal suture typically open V-shaped (Fig. 5b). Interparietal variable in size, but often reduced. Foramen magnum large and occipital condyles not conspicuous. Zygomatic plate medium in height, narrow, with upper free border extremely reduced and anterior border straight (Fig. 5c). Zygomatic notch inconspicuous. Zygomatic arches weak, diverging at posterior end. Incisive foramina large and wide, posterior ends reaching protocones of the M1. Palate flat and wide, without pronounced traits except 2 palate fissures at side of M2. Mesopterygoid fossa wide, with anterior border reaching posterior face of M3; anterior portion lire-shaped, with a small but clearly present median palatine process (Fig. 5e). Roof of mesopterygoid fossa presenting open sphenopalatine vacuities. Pterygoids medium in size and divergent at posterior end. Parapterygoid fossae well excavated and subequal in size with respect to mesopterygoid fossa. Auditory bullae of medium size,

with a short but wide eustachian tube. Basioccipital wide and excavated. A conspicuous posterior opening of the alisphenoid canal present, with a weak groove for infraorbital artery. Squamosal–alisphenoid region characterized by a foramen ovale divided by a consistently present alisphenoid strut, and a reduced anterior opening of the alisphenoid canal. A well-expressed trough for masticatory–buccinator nerve present in all individuals examined, sometimes ending in a small foramen; squamosoalisphenoid grooves also visible, confluent with the sphenofrontal foramina (Fig. 5f). Inferred carotid circulatory pattern of “pattern 1” (sensu Voss 1988), the widespread condition recorded for the genus (Myers et al. 1990). Hamular process short and with wide posterior end, resulting in a reduced subsquamosal fenestra (Fig. 5d). Tegmen tympani contacting, but not overlapping, the squamosal bone.

Mandible delicate and short (Fig. 4). Anterior point of diastema located below alveolar plane. Posterior face of diastema abrupt and mental foramen visible from labial view. Masseteric crest not evident, and upper and lower ridges meeting in a short section at mental foramen level. Capsular projection inconspicuous, lying at base of coronoid process. Condylod process short, wide, and slightly inclined inward. Angular process short and forms a well-developed inferior shelf, which bends outward distally. Lunar notch well developed. Coronoid process thin but large and inflected well forward; in some individuals distal end higher than condylod process.

Teeth of typical *Akodon* pattern (Fig. 6). Upper incisors orange and slightly opistodont; lower incisors much paler. Upper molars crested, with lingual cusps higher than labial ones. The arrangement of main cusps alternate. M1 with well-developed anteromedian flexus, dividing the procingulum in 2 conules; anterolingual conule slightly larger than anterolabial.

**TABLE 2.**—Molecular synapomorphies of *Akodon philipmyersi*, new species, as revealed by maximum-parsimony analysis of cytochrome-*b* gene (*Cytb*) sequences (1,140 base pairs). Molecular transformations were optimized on a strict consensus tree of the 3 most-parsimonious trees (1,763 steps; consistency index [CI] = 0.337) resulting from the analysis of the *Cytb* matrix. Fifty-nine fixed derived character states were found in *A. philipmyersi*. Of these, 11 derived character states, which are indicated by asterisks, have not evolved independently in any species of *Akodon* (3 of these 11 characters have CI < 1 because the character state present in *A. philipmyersi* also has evolved independently in at least 1 of the outgroups). The remaining 48 derived character states of *A. philipmyersi* also have appeared secondarily in at least 1 species of *Akodon*.

	Nucleotide position	Codon position	Character state in <i>A. philipmyersi</i>	Character CI
1	24	3	T	0.2
2	61	1	T	0.25
3	111	3	C	0.2
4	120	3	T	0.25
5	156	3	T	0.29
6	219	3	G	0.33
7	234	3	G	0.5
8	*237	3	T	1
9	246	3	G	0.5
10	252	3	C	0.2
11	261	3	T	0.17
12	282	3	C	0.17
13	312	3	T	0.17
14	321	3	C	0.17
15	333	3	G	0.5
16	342	3	T	0.33
17	363	3	A	0.33
18	417	3	T	0.182
19	438	3	T	0.11
20	473	2	A	0.18
21	*489	3	G	1
22	501	3	T	0.5
23	525	3	T	0.6
24	576	3	T	0.5
25	585	3	C	0.14
26	*588	3	T	1
27	589	1	T	0.33
28	615	3	T	0.29
29	636	3	T	0.33
30	708	3	T	0.67
31	709	1	C	0.33
32	*712	1	A	0.5
33	*721	1	G	1
34	*723	3	C	0.67
35	724	1	C	0.33
36	756	3	T	0.5
37	783	3	C	0.22
38	807	3	G	0.2
39	906	3	G	0.33
40	*939	3	G	1
41	*945	3	G	0.5
42	981	3	C	0.17
43	1,002	3	T	0.33
44	1,014	3	C	0.25
45	1,020	3	T	0.17
46	1,032	3	G	0.25
47	1,046	2	T	0.17
48	1,053	3	G	0.5
49	1,059	3	T	0.17

**TABLE 2.**—Continued.

	Nucleotide position	Codon position	Character state in <i>A. philipmyersi</i>	Character CI
50	*1,065	3	G	1
51	1,066	1	G	0.33
52	1,077	3	T	0.5
53	1,083	3	T	0.17
54	1,086	3	C	0.11
55	*1,088	2	C	1
56	*1,101	3	C	1
57	1,102	1	A	0.33
58	1,116	3	T	0.5
59	1,125	3	C	0.25

Anteroloph and mesoloph present, showing a tendency to coalesce with paracone and metacone, respectively. Hypoflexus wide and posteriorly directed. M2 rectangular in outline, with an anteroloph moderately developed and a reduced mesoloph. Para- and metacone subequal. M3 displaying cylindrodont pattern, with a reduced hypoflexus; mesoflexus persisting as a small fossette. Lower molars crested and transversally compressed. First lower molar (m1) having well-developed anteromedian flexid present; anterolabial and anterolingual conulids subequal and rounded, determining a well-developed procingulum. Anterolabial cingulum present but not well developed. A reduced mesolophid and a small ectolophid present; posterolophid is evident. Second lower molar (m2) having subequal proto- and hypoconid, absent mesolophid; posterolophid well developed. Third lower molar (m3) large, slightly shorter than m2 in adult individuals; hypoflexid wide.

*Akodon philipmyersi* has, based on 5 individuals (CNP 739, CNP 740, CNP 741, CNP 742, and CNP 747), 13 thoracic ribs, 12 or 13 thoracic vertebrae, 6 lumbar vertebrae, and 22 or 23 caudal vertebrae.

**Karyological data.**—The karyotype (2n = 36, FN = 42) contains 3 pairs of large biarmed autosomal chromosomes (pairs 1–3), 14 pairs of small autosomal chromosomes (all telocentrics except pair 4, which is biarmed), a telocentric X chromosome, and a telocentric Y slightly smaller.

**Molecular variation.**—Observed intrapopulation variation in *A. philipmyersi* is minimal. Sequences were obtained from 3 specimens: for both CNP 739 and CNP 742 the entire *Cytb* was sequenced (1,140 base pairs [bp]), whereas for CNP 741 only the first 801 bp of the gene were obtained. Haplotypes of CNP 739 and CNP 742 differ only at position 1,107 (character states: T for CNP 739 and C for CNP 742). The sequence of CNP 741 is indistinguishable from those of the other 2 specimens; sequences of the 3 specimens are identical in their first 801 bp.

**Comparisons.**—The only species of *Akodon* sympatric with *A. philipmyersi* is *A. montensis* Thomas, 1913. *Akodon montensis* is distinguishable by its large size, dark coloration, robust skull, large rostrum and teeth, and 2n = 24 (see Pardiñas et al. 2003). *Cytb* haplotypes of *A. philipmyersi* and *A. montensis* diverge by 11.32–11.40%.

Four small-sized species of *Akodon* inhabit tropical and subtropical lowlands of southeastern South America. Of these,



FIG. 4.—*Akodon philipmyersi*, new species (holotype, CNP 739): dorsal (upper left), ventral (upper right), and lateral (middle) views of skull and labial view (bottom) of mandible. Scale bar = 5 mm.

2 are morphologically similar to *A. philipmyersi*, and 2 are different. The former are *A. azarae* (Fischer, 1829) and *A. lindberghi* Hershkovitz, 1990; the latter are *A. mystax* Hershkovitz, 1998, and *A. sanctipaulensis* Hershkovitz, 1990.

The widespread *A. azarae* is in general larger than *A. philipmyersi* (Appendix II), with a more robust and larger skull, particularly in the braincase region. The interorbital constriction of *A. azarae* is defined clearly with the frontals divergent at

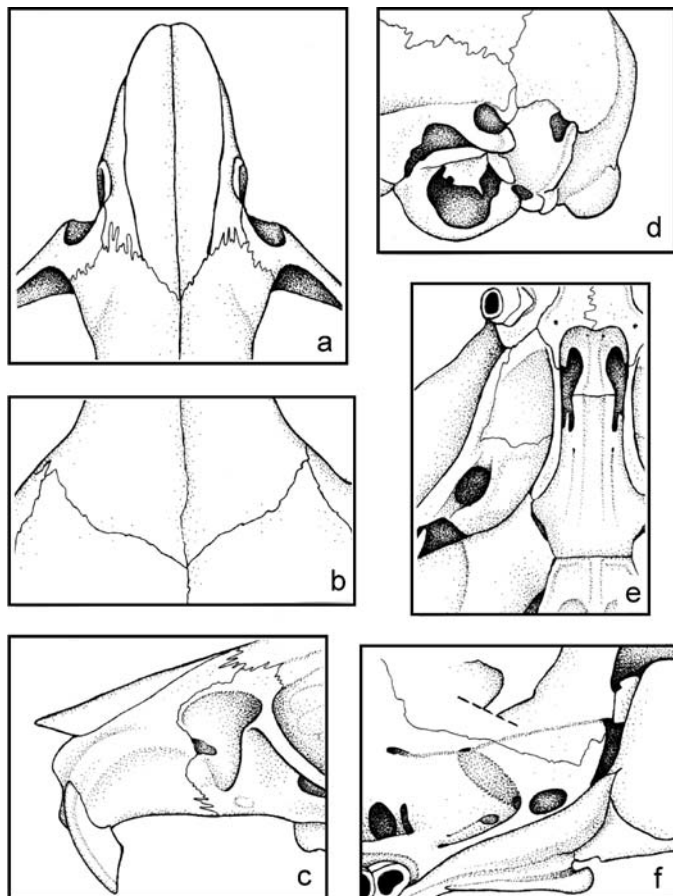


FIG. 5.—Selected morphological traits of *Akodon philipmyersi*, new species: a) nasals and rostrum in dorsal view (CNP 739), b) frontoparietal suture (CNP 739), c) rostrum and zygomatic plate in lateral view (CNP 740), d) auditory region in lateral view (UMMZ 176194), e) mesopterygoid and parapterygoid regions in ventral view (CNP 740), and f) alisphenoid region in midlateral view (CNP 740).

their posterior end. The nasals are subparallel and the nasofrontal suture is W-shaped (versus V- or U-shaped in *A. philipmyersi*). The free upper border of the zygomatic plate is well developed. The coronal suture is U-shaped. The mesopterygoid fossa is narrower than in *A. philipmyersi*, in general without a median palatine process. The parapterygoid fossa is reduced proportionally and well divergent. The auditory bullae are larger than in *A. philipmyersi*. Molars of *A. azarae* are more robust and transversally expanded than those of *A. philipmyersi*. In addition, a more hypsodont condition is evident in *A. azarae*. Externally, the dorsal coloration of *A. azarae* is darker. The scales of the tail are larger than those found in *A. philipmyersi*. The basic karyotype of *A. azarae* has  $2n = 38$ . However, females with  $2n = 37$  have been reported in Argentinean populations (Bianchi and Contreras 1967; Vitullo et al. 1984) and  $2n = 36$  exists for specimens from Uruguay (Brum-Zorrilla et al. 1985). *Cytb* haplotypes of *A. philipmyersi* and *A. azarae* differ by 10.86–12.03% depending on whether haplotypes are from specimens in Buenos Aires province, Argentina (801 bp), or from Paraguay (1,140 bp).

*Akodon lindberghi*, distributed in the Brazilian Cerrado biome (Geise et al. 1996), is the *Akodon* species that morphologically most closely resembles *A. philipmyersi*. However, *A. lindberghi* has a rather longer tail (70% of the head and body length) and its pelage is long and soft. Cranially, *A. lindberghi* differs imperceptibly by a wider and longer incisive foramina, a wider interorbital constriction, a narrower zygomatic plate, and a narrower and U-shaped mesopterygoid fossa. The diploid number of *A. lindberghi* is 42 (Geise et al. 1996; Svartman and Almeida 1994). *Cytb* haplotypes of *A. philipmyersi* and *A. lindberghi* diverge 10.09–10.19%.

*Akodon mystax*, which was described from the forests of Caparaó National Park (Minas Gerais, Brazil) at 2,300–2,700 m (Hershkovitz 1998), is a small *Akodon*, with noticeably long (about 12-mm) and soft back hairs and hairy tail. Cranially, *A. mystax* displays trenchant differences with respect to *A. philipmyersi*; the rostrum is not anterior–posteriorly compressed (more similar to *A. azarae*), nasals are long, region of the interorbital constriction is tubular, coronal suture is straighter, interparietal is reduced, occipital is more rounded, zygomatic plate has the upper free border inclined with respect to anteorbital bridge, and hamular process is short and expanded reducing the subsquamosal foramen to a fissure. Ventrally, incisive foramina is long and reaches the hypocone of M1, and the anterior border of mesopterygoid fossa is close to posterior face of M3, determining a short palate. Molars are more robust than in *A. philipmyersi*, wider and crested; the M3 hypoflexid is not reduced. *A. mystax* has  $2n = 44$  (Bonvicino et al. 1997). *Cytb* haplotypes of *A. philipmyersi* and *A. mystax* diverge 11.58–11.66%.

Although *A. sanctipaulensis* originally was described as a member of *A. boliviensis* size-group (sensu Hershkovitz 1990), the holotype and most of the type series are young or immature specimens. Adult individuals are larger than *A. philipmyersi*. *A. sanctipaulensis*, which is known exclusively from southeastern Brazilian state of San Pablo, is a sorcidlike akodont, with a hispid pelage and short (approximately 7-mm) back hairs. *A. sanctipaulensis* is easily distinguishable from *A. philipmyersi* by a greater overall size, including a wide interorbital constriction (5.44 mm) and a maxillary tooththrow length  $> 4.8$  mm. In addition, the anterior border of the mesopterygoid fossa of *A. sanctipaulensis* is U-shaped (without palatine median process), and the zygomatic plate is similar to that of *A. mystax*. No chromosomal data are available for this species. The divergence of *Cytb* haplotypes of *A. philipmyersi* and *A. sanctipaulensis* is unknown because no specimen of the latter species has been sequenced.

*Natural history.*—*Akodon philipmyersi* is found in natural grasslands of southern Misiones Province, some of which have been converted to yerba mate (*Ilex paraguayensis*) fields. Specimens were obtained at night in a portion of the field covered by tall (2-m) gramineous vegetation. Of the 14 trapped individuals, reproductive condition was recorded for 12. Of these, 4 females were pregnant (with  $\leq 3$  embryos) and 6 males had scrotal testes ( $\leq 5$  mm in length). Examination of these data indicates that the species is reproductively active by the end of the summer season (March).



Other small mammals trapped syntopically with *A. philipmyersi* were the sigmodontines *Calomys laucha*, *Necomys temchuki*, *Oligoryzomys flavescens*, *Oligoryzomys nigripes*, and *Oxymycterus rufus*, and the marmosine *Monodelphis dimidiata*. In owl pellets we also recorded *Bibimys chacoensis*, *Cavia aperea*, *Euryzgomatomys spinosus*, and *Holochilus brasiliensis*. *A. philipmyersi* is sympatric, but not syntopic, with *A. montensis*. The latter inhabits gallery forest along creeks and streams.

**Phylogenetic relationships.**—*Akodon philipmyersi* is sister to *A. lindberghi*; although this relationship is weakly supported (Fig. 2; jackknife = 56; Bremer support value = 4), and as such should be tested with further analysis (i.e., addition of more characters, taxa, or both), it is still of interest for 2 reasons. First, in a phylogenetic analysis (M. Smith and J. Patton, in litt.) *A. lindberghi* was found to be 1 of 6 species without clear phylogenetic relationships. Thus, the discovery of *A. philipmyersi* shed new light onto the sister relationship of *A. lindberghi*. Future research will clarify the extent to which the inclusion in upcoming phylogenetic analyses of species would help to stabilize other parts of the *Akodon* tree. Second, morphologically *A. philipmyersi* mostly resembles *A. lindberghi*. Both species are allopatrically distributed in open environments that are separated by the Atlantic Forest. Future research would test if the inferred cladogenetic event was mediated by the fragmentation of a previously continuous open environment or if the history of these taxa is more complex. The *A. philipmyersi*–*A. lindberghi* clade is sister to a large clade composed by the *A. boliviensis* and *A. cursor* groups (see M. Smith and J. Patton, in litt.).

**Final considerations.**—*Akodon philipmyersi* is known from only 2 localities in the Northern Campos of southern Misiones. *Akodon* species recorded in this ecoregion are *A. azarae*, restricted to the southwest margin, and *A. philipmyersi* (in the northeast); *A. montensis* also is present but exclusively inhabits gallery forests and forest patches. *A. philipmyersi* is the only known Northern Campos mammal endemic.

The Northern Campos, situated between the Ibera Wetlands and the Espinal to the west and the Atlantic Forest to the east (Fig. 3, inset), is a florist district developed in a smoothly undulating region with lateritic soils and grasslands dominated by *Aristida pallens*, *Andropogon lateralis*, and *Elionurus muticus* (Cabrera 1976; Fontana 1996; Martínez Crovetto 1963). Although the Northern Campos covers only 0.7% of the Argentinean continental surface, this biome supports an outstanding biological diversity (Fontana 1993; Giraudo et al. 2003a). Biogeographically, the Northern Campos micromammal assemblages represent a mixture between temperate species (e.g., *Calomys laucha*, *Oligoryzomys flavescens*, *Oxymycterus rufus*, and the marmosine *Monodelphis dimidiata*), and tropical species (e.g., *Bibimys chacoensis* and *Thaptomys nigrita*).

Human disturbance over the Northern Campos began as early as the 16th century. At present, extensive yerba mate and tea plantations, forestation with exotic tree species (*Pinus* and *Eucalyptus*), cattle raising, and indiscriminate burn practices have changed the vegetational composition of this region. The local extinction of some large-mammal species is a fact (e.g.,

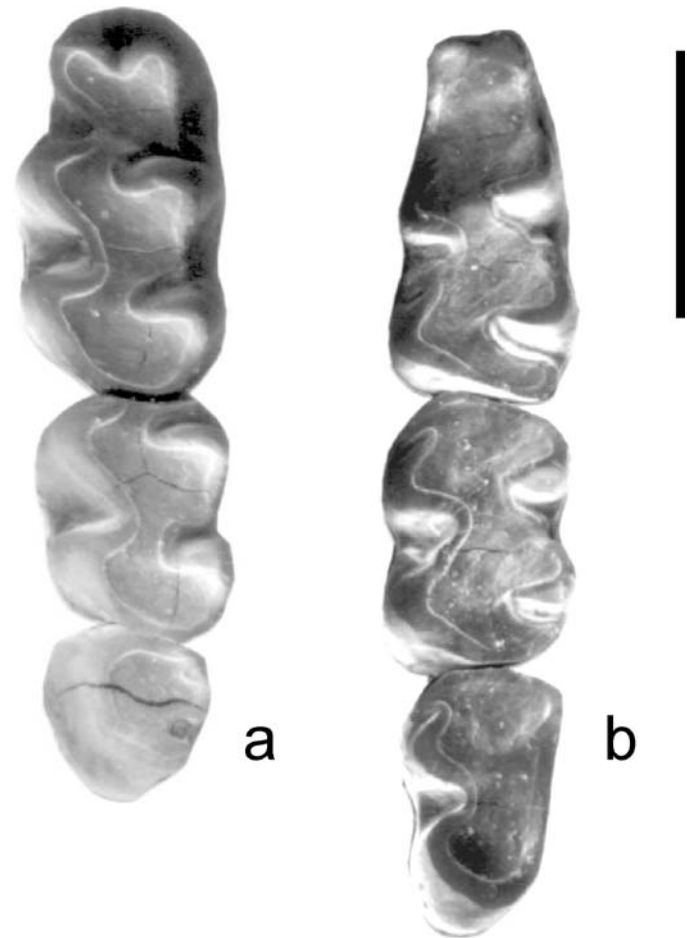


FIG. 6.—*Akodon philipmyersi*, new species (CNP 750): occlusal views of a) upper and b) lower right molar series. Scale bar = 1 mm.

*Blastocerus dichotomus*, *Myrmecophaga tridactyla*, *Panthera onca*, *Ozotoceros bezoarticus*, and *Pteronura brasiliensis*; see Giraudo et al. 2003a), but nothing is known about the status of small-mammal populations. At Estancia Santa Inés, *A. philipmyersi* was trapped mainly in a grid closed to agricultural activities, where grasslands cover all the ground. Protected areas in the Northern Campos are scarce and reduced in surface, totaling no more than 1,500 ha (0.4% of its surface—Giraudo et al. 2003b). In fact, no protected population of *A. philipmyersi* is known. The discovery of a new mammal species endemic to the Northern Campos should be taken as a call for attention to the need for intensifying conservation efforts of this particular biome.

Owl pellet analyses have been the usual and practically only source of information about small-mammal assemblages in Misiones Atlantic Forest and surrounding open biomes during the last 2 decades (Massoia 1993). Clearly, this method provides valuable information for several purposes, but we emphasize the need for additional active trapping as a critical step in obtaining an adequate knowledge of Misiones small-mammal assemblages.

## RESUMEN

Un análisis combinado de información morfológica, cromosómica y molecular nos ha permitido reconocer y describir una

nueva especie del género *Akodon* (Rodentia, Cricetidae), endémica de los Campos del sur de Misiones (Argentina). Esta nueva especie puede ser diferenciada por un conjunto de caracteres que incluyen una placa cigomática muy estrecha y casi sin borde superior libre, un rostro corto, una cola corta (40% del largo combinado cabeza–cuerpo), bullas auditorias pequeñas y achatadas, un complemento diploide ( $2n = 36$ ) y varias sinapomorfías moleculares. El análisis filogenético, basado en secuencias de citocromo *b*, muestra a la especie brasileña *A. lindberghi* como hermana del nuevo taxón aquí descrito, si bien esta relación está débilmente apoyada. Finalmente, destacamos la significación a nivel de conservación de nuestro estudio, considerando que los pastizales periselváticos donde se registra la nueva especie están sufriendo un disturbio antrópico muy importante por prácticas agrícolas e incendios.

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## APPENDIX I

*Specimens examined.*—Acronyms for institutions are as follows: Facultad de Ciencias, Universidad de la República, Montevideo, Uruguay (ZVC-M); Colección del Instituto de Limnología “Raúl Ringuelet,” Buenos Aires, Argentina (ILPLA); Colección de Mamí-

feros del Centro Nacional Patagónico, Puerto Madryn, Argentina (CNP); Museo de La Plata, La Plata, Argentina (MLP); Museo de Ciencias Naturales y Tradicional de Mar del Plata “Lorenzo Scaglia,” Mar del Plata, Argentina (MMP-Ma); Museo Argentino de Ciencias Naturales “Bernardino Rivadavia,” Buenos Aires, Argentina (MACN); Museu Nacional de Rio de Janeiro, Rio de Janeiro, Brazil (MN); the University of Michigan Museum of Zoology, Ann Arbor, Michigan (UMMZ); and the Field Museum, Chicago, Illinois (FMNH); GD: field number of Guillermo D’Elía, to be deposited at the Colección de Mamíferos, Facultad de Ciencias, Universidad de la República, Montevideo, Uruguay. Localities are listed in alphabetic order. A single asterisk (\*) indicates specimens measured (Appendix II); double asterisks (\*\*) indicate specimens included in PCA. Specimens used in the phylogenetic analysis are identified by their GenBank accession number after the collection number. Unless noted, all sequences are 1,140 bp in length.

*Akodon aerosus* (1).—PERU: Cuzco: 72 km NE Paucartambo (MVZ 171679: M35703).

*Akodon aff. A. cursor* (1).—BRAZIL: Bahia: Estação Experimental Djalma Bahia (EDH 30: AF184053).

*Akodon affinis* (1).—COLOMBIA: Risaralda: Corregimiento La Florida (ICN 16547: AY196164).

*Akodon albiventer* (1).—CHILE: Tarapacá: Parinacota (FMNH 129978: AY494838).

*Akodon azarae* (67).—ARGENTINA: Buenos Aires: Hudson (MLP 8.IV.97.47\*, MLP 8.IV.97.46\*), Hurlingham (UMMZ 109223\*\*, UMMZ 111009\*\*), La Matanza (UMMZ 110445\*), Ciudad de Buenos Aires (UMMZ 111010\*\*), Canal Arana y Arroyo Mendez Chico (MLP 5.IV.02.1\*\*), La Balandra (MLP 8.VIII.00.9, MLP 8.VIII.00.11\*\*, MLP 8.VIII.00.7\*\*, MLP 8.VIII.00.12\*\*), Monte Veloz (MLP 15.V.97.10\*, MLP 15.V.97.15\*, MLP 15.V.97.38\*, MLP 15.V.97.03\*, MLP 15.V.97.07\*, MLP 15.V.97.22, MLP 15.V.97.21, MLP 15.V.97.09, MLP 15.V.97.28\*, MLP 15.V.97.04\*\*, MLP 15.V.97.05\*\*), Parque Provincial Ernesto Tornquist, Sierra de La Ventana (MLP 29.XII.00.14, MLP 16.V.01.5, MLP 14.IX.99.70, MLP 5.II.96.73, MLP 5.II.96.40, MLP 16.V.01.5\*, MLP 5.II.96.41, MLP 14.IX.99.70\*\*), Punta Indio (CNP 751: AY702963), Punta Lara (MLP 5.VI.00.5\*\*, MLP 10.VIII.00.6\*\*, MLP 5.II.92.10\*\*, MLP 5.II.96.40\*\*, MLP 5.II.96.41\*\*, MLP 5.II.96.73\*\*), Punta Piedras (MLP 3.IX.01.19\*\*, MLP 10.IX.01.3\*\*), Arroyo Zabala, San Cayetano (MLP 9.V.01.11), Isla Talavera (MLP 29.XII.00.13), Arroyo Brusquitas (MLP 1.X.70.12), Balneario San Antonio (MLP 14.IX.99.47). Entre Ríos: Arroyo Perucho Verna (MLP 7.IV.99.14, MLP 11.08.99.21, MLP 11.08.99.9, MLP 8.V.00.3\*\*, MLP 11.08.99.18, MLP 11.08.99.4, MLP 11.VIII.99.22\*\*, MLP 8.V.00.6\*\*), Paraná (MACN 18594\*\*, MACN 17788\*\*, MACN 14906\*, MACN 14907), Villa Elisa (MLP 27.XII.01.30\*\*). PARAGUAY: Presidente Hayes: 15.5 km NNW Chaco-i (UMMZ 126070\*). Misiones: costa del Río Tebicuary (UMMZ 174823\*\*), Ñeembucu: Estancia Santa Teresa (UMMZ 175996\*\*, UMMZ 174997\*\*, UMMZ 174998\*\*), Estancia Yacare (UMMZ 174832\*, UMMZ 175000\*\*, UMMZ 175001). Paraguari: costa del Río Tebicuary (UMMZ 174872\*\*). URUGUAY: San José: Kiyu (GD 327: AY702964). PARAGUAY: Ñeembucu: 5.8 km by road NE Pilar (UMMZ 134443: U03529).

*Akodon boliviensis* (1).—PERU: Puno: 12 km S Santa Rosa (MVZ 171607: M35691).

*Akodon cursor* (1).—BRAZIL: São Paulo: Estação Biológica de Boracéia (MZUSP 29257: AF184051).

*Akodon dolores* (1).—ARGENTINA: San Luis: Papagayos (UP PY16: AY273904).

*Akodon iniscatus* (1).—ARGENTINA: Río Negro: 10 km S Comallo (MVZ 182655: AY273917).

*Akodon juninensis* (1).—PERU: Junin: 22 km N La Oroya (MVZ 173038: M35698).

*Akodon kofordi* (1).—PERU: Puno: Agualani (MVZ 171665: M35697).

*Akodon lindberghi* (5).—BRAZIL: Distrito Federal: Parque Nacional de Brasília (FMNH 128292\*\* [holotype], FMNH 128293\*\*, FMNH 128295\*\*, FMNH 128298\*\*). Minas Gerais (MN 48026: AF184057).

*Akodon lutescens* (1).—PERU: Puno: 12 km S Santa Rosa (MVZ 171612: M35693).

*Akodon mimus* (1).—PERU: Puno: 14 km W Yanahuaya (MVZ 171752: M35710).

*Akodon molinae* (1).—ARGENTINA (AK 222: AY494839).

*Akodon mollis* (1).—PERU: Piura: “Machete” on Zapalache Carmen trail (LSUMZ 27007: U03546).

*Akodon montensis* (46).—ARGENTINA: Misiones: 15 km N Uruguá River, Parque Provincial Islas Malvinas (MMP-Ma 2418, MMP-Ma 2420, MMP-Ma 2422), Reserva Privada UNLP “Valle del Arroyo Cuña Pirú” (ILPLA 226, ILPLA 132, ILPLA 227, ILPLA 228, ILPLA 216, ILPLA 118, ILPLA 122, ILPLA 220, ILPLA 224, ILPLA 231, ILPLA 093, ILPLA 258, ILPLA 259, ILPLA 206, ILPLA 257, ILPLA 219, ILPLA 221, ILPLA 079, ILPLA 230, ILPLA 218, ILPLA 225, ILPLA 054, MLP 30.IV.97.34, MLP 30.IV.97.71, MLP 30.IV.97.31, MLP 30.IV.97.18, MLP 30.IV.97.78, MLP 30.IV.97.19, MLP 30.IV.97.50, MLP 30.IV.97.39, MLP 30.IV.97.76, MLP 30.IV.97.45, MLP 30.IV.97.44, MLP 30.IV.97.05, MLP 30.IV.97.02, MLP 30.IV.97.53, MLP 30.IV.97.35, MLP 30.IV.97.23), Puerto Península (MLP 24.VIII.00.16, MLP 24.VIII.00.17, MLP 24.VIII.00.23, MLP 24.VIII.00.29). PARAGUAY: Paraguari: Sapucái (UMMZ 174969: AY195864).

*Akodon mystax* (2).—BRAZIL: Minas Gerais: Pico da Bandeira, Arrozal (MN 31910 [holotype]). Río de Janeiro (MN 48041: AF184054).

*Akodon orophilus* (1).—PERU: Junin: 16 km NNE Palca (MVZ 173057: M35699).

*Akodon paranaensis* (1).—BRAZIL: Río Grande do Sul: Venancio Aires (CIT 1131: AY195866).

*Akodon philipmyersi, new species* (14).—ARGENTINA: Misiones: Estancia Santa Inés (CNP 738\*, CNP 739\*\* [holotype]: AY702965, CNP 740\*\*, CNP 741\*: AY702967 [801 bp], CNP 742\*\*: AY702966, CNP 743\*, CNP 744\*, CNP 745\*, CNP 746\*, CNP 747, CNP 748\*, CNP 749\*, UMMZ 176194\*\*, ZVC-M 3805\*\*, and cranial remains from owl pellets [CNP 750]), Parada Leis (cranial remains from owl pellets [CNP 752]).

*Akodon reigi* (1).—URUGUAY: Lavalleja: Paso Averías (MNHN 3682: AY195865).

*Akodon sanctipaulensis* (4).—BRAZIL: São Paulo: Primeiro Morro (FMNH 94514, FMNH 94515, FMNH 94516\*\* [holotype]), Quadro Ponteadó (FMNH 94513\*\*).

*Akodon siberiae* (1).—BOLIVIA (NK 12801: AY273909).

*Akodon sp.* (1).—ARGENTINA: Misiones: Parque Provincial Islas Malvinas (MMP-Ma 2221: AY702968 [801 bp]).

*Akodon spagazzinii* (1).—ARGENTINA: Córdoba: Pampa de Achala (UP AC008: AY196165).

*Akodon subfuscus* (1).—PERU: Arequipa: 15 km S Callalli (MVZ 174109: M35695).

*Akodon toba* (1).—PARAGUAY: Presidente Hayes: 9 km NE Juan de Zalazar (UMMZ 133965: U03527).

*Akodon torques* (1).—PERU: Cuzco: 32 km NE Paucartambo (MVZ 17120: M35700).

*Deltamys kempfi* (1).—URUGUAY: San José: Ruta 1 sobre Arroyo Cufre (MNHN 4151: AY195862).

*Necomys temchuki* (1).—ARGENTINA: Misiones: Estancia Santa Inés (UP 22: AY273914).

## APPENDIX II

External and cranial measurements (in millimeters) and weight (in grams) of *Akodon philipmyersi*, new species, from Argentina (Estancia Santa Inés, Misiones Province) and other similar-sized species of *Akodon*.

	<i>Akodon philipmyersi</i> , new species				<i>Akodon lindberghii</i> <sup>a</sup>				<i>Akodon sanctipaulensis</i> <sup>b</sup>				<i>Akodon mystax</i> <sup>c</sup>				
	n	$\bar{X} \pm SD$	Range	n	$\bar{X} \pm SD$	Range	n	$\bar{X} \pm SD$	Range	n	$\bar{X} \pm SD$	Range	n	$\bar{X}$	n	$\bar{X}$	Range
Length of head and body	7	92.00 ± 12.75	70.00–109.00	40	90.95 ± 10.22	76.00–117.00	6	90.33 ± 3.08	56.00–66.00	4	93.00 ± 7.53	86.00–100.00	11	95.0	11	95.0	85.0–101.0
Tail length	9	60.67 ± 6.16	47.00–69.00	40	70.10 ± 7.30	60.00–88.00	6	62.83 ± 3.66	56.00–66.00	4	72.00 ± 7.75	63.00–81.00	11	67.0	11	67.0	63.0–73.0
Ear length	4	11.75 ± 0.50	11.00–12.00	38	13.18 ± 1.07	11.00–15.00	6	13.33 ± 0.52	13.00–14.00	4	15.50 ± 1.73	13.00–17.00	11	13.0	11	13.0	12.0–14.0
Length of hind foot with claw	11	17.55 ± 0.69	17.00–19.00	32	21.08 ± 0.93	19.50–23.00	6	18.67 ± 0.52	18.00–19.00	4	23.83 ± 0.89	23.00–25.00	11	19.0	11	19.0	17.0–22.0
Length of hind foot without claw	11	15.68 ± 0.60	15.00–17.00	28	18.79 ± 0.77	17.50–21.00											
Weight	3	18.67 ± 4.25	14.50–23.00	30	21.44 ± 4.65	15.00–33.20	4	18.00 ± 2.45	16.00–21.00								
Condylolincisive length	7	21.60 ± 1.09	19.88–23.24	43	23.31 ± 1.08	20.87–25.60	5	22.50 ± 0.51	21.70–22.90								
Zygomatic breadth	13	12.05 ± 0.49	10.90–12.66	43	12.34 ± 0.55	10.70–13.33	6	11.93 ± 0.41	11.20–12.40								
Braincase breadth	11	10.58 ± 0.09	10.40–10.70	43	10.97 ± 0.31	10.22–11.97	6	11.08 ± 0.10	10.90–11.20								
Interorbital constriction	13	4.50 ± 0.09	4.33–4.65	43	4.22 ± 0.18	3.76–4.59	6	4.73 ± 0.12	4.60–4.90								
Rostral length	13	8.15 ± 0.39	7.20–8.79	43	8.90 ± 0.58	7.56–10.21											
Rostral width	13	4.53 ± 0.14	4.24–4.74	43	4.59 ± 0.27	4.03–5.20	5	4.42 ± 0.08	4.30–4.50								
Nasal length	10	8.19 ± 0.44	7.36–8.99	43	9.18 ± 0.62	7.90–10.70	6	8.03 ± 0.41	7.30–8.40								
Orbital length	13	7.81 ± 0.45	6.92–8.50	43	8.56 ± 0.38	7.86–9.36											
Diastema length	13	5.75 ± 0.37	4.85–6.23	43	6.35 ± 0.40	5.65–7.12	5	5.98 ± 0.44	5.20–6.30								
Maxillary toothrow length	13	3.91 ± 0.09	3.73–4.08	43	4.08 ± 0.16	3.68–4.44	6	4.02 ± 0.10	3.90–4.10								
Incisive foramen length	13	5.57 ± 0.35	4.83–6.33	43	5.93 ± 0.36	5.14–6.62	6	6.13 ± 0.40	5.60–6.70								
Alveolar width	12	4.63 ± 0.15	4.41–4.88	43	4.76 ± 0.35	2.78–5.33											
Occipital condyle width	7	5.71 ± 0.22	5.51–6.11	43	5.94 ± 0.21	5.26–6.41											
Basioccipital length	7	3.52 ± 0.17	3.28–3.78	42	3.76 ± 0.30	2.96–4.34											
Mesopterygoid fossa width	9	1.34 ± 0.18	1.09–1.64	42	1.37 ± 0.10	1.13–1.57	5	1.26 ± 0.17	1.00–1.40								
Breadth of zygomatic plate	13	1.97 ± 0.13	1.61–2.14	43	2.25 ± 0.16	1.92–2.58	6	1.78 ± 0.16	1.50–1.90								
Cranial depth	6	9.16 ± 0.23	8.87–9.43	43	9.46 ± 0.29	8.97–10.24											
Breadth of 1st upper molar	13	1.11 ± 0.07	1.02–1.27	42	1.15 ± 0.05	1.05–1.28											
Mandible length without incisor	12	11.38 ± 0.39	10.71–11.98	40	12.58 ± 0.52	11.40–13.53	6	14.57 ± 0.71 <sup>d</sup>	13.20–15.00								

<sup>a</sup> After Hershkovitz (1990; table 3:8).

<sup>b</sup> External measurements after Hershkovitz (1990; table 4:26); cranial measurements from holotype FMNH 94516.

<sup>c</sup> External measurements after Hershkovitz (1998; table 7:222); cranial measurements from holotype MN 31910.

<sup>d</sup> Measurement includes the incisor.