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**Original investigation**

# The genus *Akodon* (Muroidea: Sigmodontinae) in Misiones, Argentina

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## Abstract

Our understanding of the rodent diversity from the Argentinean Atlantic rainforest and its surrounding environments (Misiones Province) is still relatively poor. Here we present an update on the species inhabiting Misiones of the genus *Akodon*. Integrated analyses of morphology, chromosomal and molecular data allow us to document the existence of four species of *Akodon* in the province. One of these is apparently undescribed, and is known only from one locality in the "campos" phytogeographic unit of southern Misiones. A second species, *A. montensis*, has a large distribution and is one of the dominant sigmodontine species in primary and secondary forest. *Akodon* sp. 2, previously reported as either *A. serrensis* and *A. paranaensis*, is known from only one locality at the northeast of the province, where it is sympatric with *A. montensis*. Also in sympatry with *A. montensis* at one locality in central Misiones there is a similar species with a gall bladder referred here to *A. cursor*. Finally, the previous reference of one specimen to *A. serrensis* must be discarded due to the referred specimen is lost, and the data at hand are insufficient to corroborate the identity of the specimen under question. As Misiones has the largest continuous patches of southern interior Atlantic rainforest remaining in Argentina we pose comments on the conservation significance of our study.

**Key words:** Rodentia, Muridae, Neotropics, taxonomy, conservation

## Introduction

Misiones is a small (29 801 km$^2$) province located in northeastern Argentina. It is characterized by a humid subtropical climate; rains reach 2000 mm annually and the average temperature is 20 °C (BERTONATTI and CORCUERA 2000). Biogeographically Misiones is interesting because, located in the center of the La Plata river basin, it contains the southern part of the Atlantic Rainforest. Moreover, currently the largest continuous remnants of this unique forest are those located in Misiones. Forty-five percent of the original forest cover is still preserved in Misiones, whereas this number drastically falls to less than 12% in Paraguay (DPNVS 1998) and 4% in Brazil (LACLAU 1994). The mammal diversity of Misiones is high with more that 120 mammal species known (GIRAUDO et al. 2002). However, as we show below, much

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remains to be learned about the local mammal fauna.
In this contribution we shed new light on the *Akodon* species from the Misiones Province. Our study is aimed to clarify those species that inhabit the province, identify their distribution, and provide preliminary data about their evolutionary history.

## Material and methods

We studied 79 specimens of *Akodon* from Misiones (Argentina) that were live trapped, as well as 7 batches of remains recovered from owl pellets. This material is or will be deposited in the following Argentinean collections: Museo de La Plata (MLP, and field numbers C, and UP); Museo de Ciencias Naturales y Tradicional de Mar del Plata "Lorenzo Scaglia", Colección Mamíferos (MMP-Ma); Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN); Colección Félix de Azara (CFA); and Colección del Instituto de Limnología "Raúl Ringuelet" (ILPLA). Numbers before each locality refer to their positions as mapped in figure 1. *Akodon montensis:* Department of Capital, (**1**) Santa Inés [S 27°31′ W 55°52′]: cranial remains from owl pellets; Department of Cainguas, (**2**) Reserva Privada UNLP "Valle del Arroyo Cuña Pirú" [S 27°05′ W 54°57′]: ILPLA 054, 079, 093, 118, 122, 132, 206, 216, 218, 219, 220, 221, 224, 225, 226, 227, 228, 230, 231, 257, 258, 259, MLP 30.IV.97.02, 30.IV.97.05, 30.IV.97.18, 30.IV.97.19, 30.IV.97.23, 30.IV.97.31, 30.IV.97.34, 30.IV.97.35, 30.IV.97.39, 30.IV.97.44, 30.IV.97.45, 30.IV.97.50, 30.IV.97.53, 30.IV.97.71, 30.IV.97.76, 30.IV.97.78; Department of Candelaria, (**3**) Santa Ana [S 27°59′ W 55°31′]: ILPLA 061; Department of Concepción, (**4**) Concepción de la Sierra [S 27°59′ W 55°36′]: CFA 00439, 01799, 01800, 01801, 01802, 01803, 02177; Department of El Dorado, (**5**) El Dorado Km 11 [S 26°24′ W 54°34′]: cranial remains from owl pellets; Department of General Manuel Belgrano, (**6**) Parque Provincial Islas Malvinas, 15 km N río Urugua-í [S ~25°50′ W ~54°10′]: MMP-Ma 2418, 2420, 2422, (**7**) General Manuel Belgrano [S 26°03′ W 53°47′]: MACN 18923; Department of Iguazú, (**8**) Puerto Península [S 25°41′ W 54°39′]: MLP 24.VIII.00.16, 24.VIII.00.17, 24.VIII.00.23, 24.VIII.00.29; Department of Libertador General San Martín, (**9**) Arroyo Garuhapé [S 26°48′ W 54°55′]: cranial remains from owl pellets; Department of Oberá, (**10**) 11 de noviembre, San Martín de Tours [S 27°27′ W 55°20′]: cranial remains from owl pellets; Department of San Ignacio, (**11**) desembocadura del Arroyo Yabebyrí [S 27°17′ W 55°32′]: cranial remains from owl pellets, (**12**) Parque Provincial Teyú Cuaré [S 27°17′ W 55°35′]: cranial remains from owl pellets; Department of San Javier, (**13**) San Javier [S 27°53′ W 55°08′]: CFA 00481, 00483, 00484, 00487; Department of San Pedro, (**14**) San Pedro [S 26°38′ W 54°07′]: MACN 15462. *Akodon* cf. *A. cursor*: Department of Cainguas, (**2**) Reserva Privada UNLP "Valle del Arroyo Cuña Pirú" [S 27°05′ W 54°57′]: C 024, 070, and MLP 5.XII.01.34. *Akodon* sp. 1: Department Capital, (**1**) Santa Inés [S 27°31′ W 55°52′]: UP 003, 005, 006, 007, 008, 011, 016, 020, 021, 026, 027, 028, 029, and 031 and cranial remains from owl pellets. *Akodon* sp. 2: Department of General Manuel Belgrano, (**6**) Parque Provincial Islas Malvinas, 15 km N río Urugua-í [S ~25°50′ W ~54°10′]: MMP-Ma 2421. In addition, we carried out comparisons with specimens of *Akodon* belonging to species inhabiting nearby areas in Argentina, Brazil, Paraguay, and Uruguay. Among those we studied are the type series of *Akodon sanctipaulensis* in the Field Museum of Natural History, USA (FMNH), *Akodon lindberghi*, temporarily deposited at the FMNH but belonging to the Museu Nacional of Rio de Janeiro, Brasil (MN), and series of *A. montensis* and *A. azarae* housed at the University of Michigan Museum of Zoology, USA (UMMZ and field numbers GD). Finally, the specimens from Misiones were compared with the published descriptions of *Akodon reigi* (GONZÁLES et al. 1998) and *A. paranaensis* (CHRISTOFF et al. 2000). Craniodental descriptions were made following the nomenclature of REIG (1977, 1987). Measurements were taken with a digital caliper following CHRISTOFF et al. (2000).
The following specimens were karyotyped following standard methods (FORD and HAMERTON 1956): *Akodon* sp. 1: UP 003 and UP 031 (locality 1); *A. montensis*: 97092410 and 97092411 (locality 2).
Molecular analyses were based on complete (1 140 base pairs) or nearly complete (801 bp) cytochrome b gene sequences taken from GenBank and obtained by us. We sequenced the following individuals: *A.* sp. 1: UP 007 and 008 (locality 1); *A.* sp. 2: MMP-Ma 2421; *A. montensis*: 15030003, 15030014, MLP 24.X.01.4, 24.X.01.5, 24.X.01.6, and 24.X.01.7 (locality 2). We amplified and sequenced the cytochrome b gene sequences reported in this study in two fragments using primers located both internally and in the flanking regions of the gene (MVZ 05–MVZ 16 and MVZ 103–MVZ 14, SMITH and PATTON 1993; SMITH pers. comm.). Negative controls were included in all

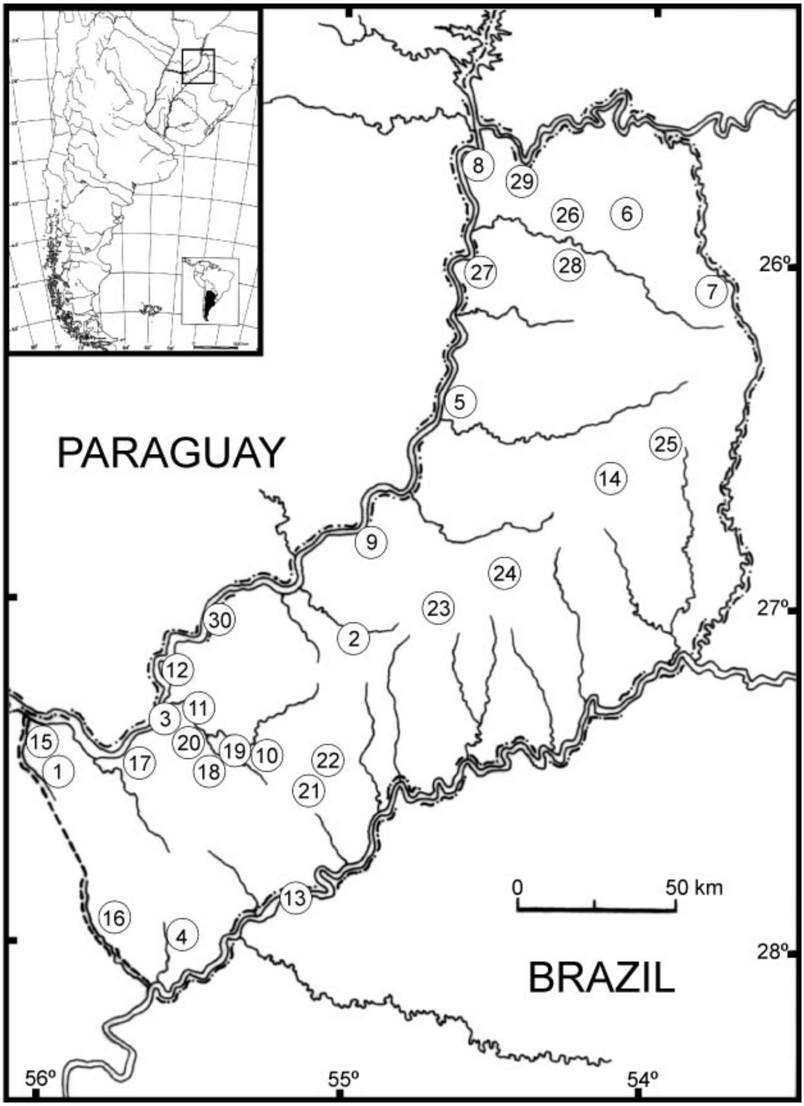


**Fig. 1.** Recording localities of the genus *Akodon* in Misiones Province, Argentina. For names and descriptions of localities 1 to 14 refer to the Material and methods section. Localities 1, 2, 4, 5, 8, 9, 10, 11, and 13, are reported for the first time in this study. Localities 15 to 30 correspond to additional records of *A. montensis* taken from the literature as follows: 15. Arroyo Itaembé Mini, puente Ruta 12 (S 27°26′ W 56°00′; MASSOIA 1983); 16. Apóstoles (S 27°55′ W 55°45′; MASSOIA et al. 1989 a); 17. Arroyo San Juan (S 27°25′ W 55°39′; MASSOIA 1993); 18. Bonpland (S 27°29′ W 55°28′; MASSOIA et al. 1989 d); 19. Colonia Martires (S 27°26′ W 55°23′; MASSOIA 1993); 20. Arroyo Yabebyrí (S 27°17′ W 55°31′; MASSOIA et al. 1989 c); 21. Los Helechos (S 27°33′ W 55°04′; MASSOIA et al. 1989 b); 22. Campo Ramón (S 27°28′ W 54°59′; MASSOIA 1988); 23. Dos de Mayo (S 27°02′ W 54°38′; MASSOIA 1974); 24. Cuartel Río Victoria (S 26°46′ W 54°18′; MASSOIA 1974); 25. Tobuna, ruta 14 km 352 (S 26°28′ W 53°53′; MASSOIA and FORNES 1962); 26. Río Urugua-í, 30 km de Puerto Libertad Iguazú (S 25°55′ W 54°18′; MASSOIA et al. 1987); 27. Puerto Esperanza (S 26°01′ W 54°39′; MASSOIA 1993); 28. Gobernador J. J. Lanusse (S 25°28′ W 54°16′; MASSOIA 1993); 29. Parque Nacional Iguazú (S 25°42′ W 54°25′; CRESPO 1982); 30. Puerto Gisela (S 27°01′ W 55°26′; REIG 1987).

experiments. Dye-labelled PCR products were cleaned in Sephadex columns and sequenced using an ABI 377 automatic sequencer. In all cases both heavy and light DNA strands were sequenced and compared. Sequence alignment was done using the program Clustal X (THOMPSON et al. 1997) and by eye. Maximum parsimony (MP) was the optimisation algorithm used to generate hypotheses of phylogenetic relationships among sigmodontine sequences. In all cases character were treated as unordered and equally weighted. PAUP* 4 (SWOFFORD 2000) was used to perform 200 replicates of traditional heuristic searches with random addition of sequences and tree bisection-reconnection branch swapping. We performed 500 bootstrap (FELSENSTEIN 1985) replications, each with three replicates of random sequence addition.

## Results

Our data document the existence of four species of *Akodon* for the Province of Misiones, Argentina. One species is apparently new and another is new for the province. The other two species have been recorded for the province before, but we disagree with the identification of one of these. Below we present an account for each of these four species. At the end of this section we pose comments on a species cited to occur in Misiones but for what there is no evidence to document its record.

### *Akodon montensis* Thomas, 1913 (Fig. 2 a; Tab. 1)

*Akodon arviculoides montensis* sensu MASSOIA and FORNES (1962)
*Akodon cursor* sensu MASSOIA (1980)
*Akodon cursor montensis* sensu REIG (1987)
*Akodon cursor* sensu LIASCOVICH and REIG (1989)
*Akodon cursor cursor* sensu MASSOIA (1993)
*Akodon cursor cursor* sensu CHEBEZ and MASSOIA (1996)

We identified specimens from Misiones with this species mainly on the basis of morphologic characters, although we also employed chromosomal and molecular data in some cases. These specimens are morphologically indistinguishable from Brazilian and Paraguayan specimens referred to *A. montensis*, including those from the type locality of the species. CHRISTOFF (1997) presented the most detailed description of this species, whereas MASSOIA and FORNES (1962) described Argentinean specimens, including some of those studied here. We karyotyped two specimens from Reserva Privada UNLP "Valle del Arroyo Cuña Pirú" in central Misiones. These specimens showed one of the diploid complements (2 n = 24) assigned to the species (GEISE et al. 1998). Further, six specimens from Valle del Arroyo Cuña Pirú were sequenced for the first 801 base pairs of the cytochrome b gene. Among these individuals three different haplotypes were recovered. Four specimens shared one haplotype, whereas the other two specimens each had a different haplotype. These three haplotypes are very similar, differing only in 2 or 4 substitutions (0.25–0.50%). At the same time, these haplotypes are very similar to those found in Paraguayan populations of *A. montensis*, including from the type locality of the species. The number of substitutions among Cuña Pirú and Paraguayan haplotypes range from 1 to 9 (0.13–1.12%). Moreover, the haplotypes recovered from Cuña Pirú specimens do not form a monophyletic group with respect to those haplotypes found in Paraguayan and Brazilian populations (results not shown). All evidence reinforces our idea, in agreement with MASSOIA and FORNES (1962) and LIASCOVICH and REIG (1989), that Misiones is inhabited by specimens of the one species that also inhabits Brazil and Paraguay, and currently known as *A. montensis.*

*A. montensis* has been recorded in 30 localities in the Province of Misiones (Fig. 1). This species is also distributed in southeastern Brazil (GEISE et al. 2001) and most of eastern Paraguay (GAMARRA DE FOX and MARTIN 1996). The type locality of this species is Sapucái, Paraguay (see THOMAS 1913) and not Misiones, Argentina, as stated in RIEGER et al. (1995). The distribution of *A. montensis* in Argentina is marginal. Besides Misiones the species extends west

**Table 1**. Measurements (in mm) and weight (in g) of samples of *Akodon* from Misiones Province, Argentina (1–4) and additional forms discussed in the text (5–8). Sample sizes ( ), means, standard deviations (±), and minimum – maximum are given for each measurement.

| | 1 *Akodon montensis*[1] | 2 *Akodon* cf. *A. cursor* | 3 *Akodon* sp. 1 | 4 *Akodon* sp. 2 | 5 *Akodon reigi*[2] | 6 *Akodon paranaensis*[3] | 7 *Akodon serrensis*[4] | 8 *Akodon "serrensis"*[5] |
|---|---|---|---|---|---|---|---|---|
| Head and body length | (21) 112.0 ± 8.9 93–125 | (3) 106.3 ± 6.1 101–113 | (7) 93.7 ± 9.8 82–109 | 122.0 | (8) 109.6 ± 18.9 92–150 | (19) 109.8 ± 2.1 92.9–125.3 | 97.6 | 101.0 |
| Tail length | (25) 89.1 ± 8.7 65–103 | (3) 83.7 ± 3.5 80–87 | (8) 62.2 ± 3.7 58–69 | 78.0 | (8) 89.2 ± 6.4 79–97 | (19) 83.1 ± 1.2 71.8–89.2 | 84.8 | 84.0 |
| Ear length | (21) 18.2 ± 0.8 16.0–19.5 | (3) 17.3 ± 0.6 17–18 | (3) 12.0 ± 0 12–12 | 18.0 | (7) 17.8 ± 1.0 16–19 | (19) 17.2 ± 0.3 12.8–19.7 | 15.2 | 18.0 |
| Hind-foot length (with claw) | (25) 25.0 ± 1.6 21–28 | (3) 25.3 ± 0.6 25–26 | (10) 17.6 ± 0.7 17–19 | 21.0 | (8) 24.8 ± 1.6 23.0–27.6 | (18) 22.8 ± 0.2 21.6–23.8 | 23.3 – | 24.0 – |
| Weight (g) | (23) 44.1 ± 7.0 30–56 | (3) 28.7 ± 2.3 26–30 | (3) 18.7 ± 4.3 14.5–23.0 | 39.0 | – | – | – | – |
| Basilar length | (30) 23.1 ± 1.1 20.7–25.0 | 22.5 | (7) 17.8 ± 1.1 15.9–19.4 | 22.3 | – | (21) 23.1 ± 0.2 21.7–25.0 | 21.6 | – |
| Condyle-squamosal length | (30) 10.8 ± 0.5 9.9–11.8 | 10.6 | (6) 8.7 ± 0.4 8.1–9.2 | 10.1 | – | (21) 10.9 ± 0.1 10.3–11.7 | 10.4 | – |
| Incisive foramen length | (30) 6.9 ± 0.2 6.5–7.3 | 7.1 | (12) 5.6 ± 0.4 4.8–6.3 | 6.7 | (6) 6.8 ± 0.4 6.1–7.1 | (21) 6.9 ± 0.1 6.3–7.5 | 6.1 | 6.0 |
| Condyle zygomatic length | (30) 19.6 ± 0.8 17.8–21.2 | 19.3 | (7) 16.1 ± 0.8 14.8–17.1 | 19.2 | – | (21) 19.8 ± 0.2 18.6–21.3 | 18.3 | – |
| Rostral length | (30) 11.2 ± 0.5 10.0–12.1 | 11.4 | (12) 8.2 ± 0.4 7.2–8.8 | 10.8 | – | (21) 11.4 ± 0.1 10.6–12.3 | 10.8 | 8.6 |
| Diastema length | (30) 7.9 ± 0.4 7.0–8.7 | 7.8 | (12) 5.7 ± 0.4 4.9–6.2 | 7.7 | (6) 7.6 ± 0.3 7.3–8.0 | (21) 7.9 ± 0.1 7.2–8.4 | 7.3 | 7.3 |
| Zygomatic breadth | (30) 14.5 ± 0.6 13.4–15.8 | 14.7 | (12) 12.9 ± 2.8 10.9–21.6 | 14.7 | (5) 14.4 ± 0.4 13.8–15.0 | (21) 15.0 ± 0.1 14.1–16.1 | 14.5 | 11.0 |
| Least interorbital breadth | (30) 4.9 ± 0.2 4.5–5.3 | 5.0 | (12) 4.5 ± 0.1 4.4–4.7 | 5.1 | (6) 4.9 ± 0.2 4.8–5.1 | (21) 4.8 ± 0.0 4.5–5.1 | 5.4 | 5.0 |
| Breadth braincase | (30) 12.3 ± 0.3 11.5–13.0 | 12.5 | (10) 10.5 ± 0.1 10.4–10.7 | 12.0 | (6) 12.9 ± 0.3 12.5–13.4 | (21) 12.1 ± 0.1 11.5–12.6 | 11.9 | 12.1 |
| Rostral width | (30) 5.5 ± 0.3 5–6 | 5.3 | (12) 4.5 ± 0.1 4.2–4.7 | 5.5 | (6) 4.5 ± 0.2 4.3–4.8 | (18) 5.4 ± 0.1 4.9–6.0 | 5.2 | 4.3 |

**Table 1.** (Continue)

| | 1 *Akodon montensis* | 2 *Akodon* cf. *A. cursor* | 3 *Akodon* sp. 1 | 4 *Akodon* sp. 2 | 5 *Akodon reigi*[2] | 6 *Akodon paranaensis*[3] | 7 *Akodon serrensis*[4] | 8 *Akodon "serrensis"*[5] |
|---|---|---|---|---|---|---|---|---|
| Palatal bridge | (30) 3.5 ± 0.2 3.0–3.9 | 3.6 | (12) 3.1 ± 0.3 2.7–3.6 | 3.4 | – | (21) 3.6 ± 0.1 2.9–4.2 | 4.1 | 2.9 |
| Breadth of palatal bridge | (30) 3.05 ± 0.2 2.8–3.5 | 3.1 | (12) 2.4 ± 0.1 2.2–2.5 | 2.5 | (6) 2.7 ± 0.3 2.4–3.0 | (21) 2.9 ± 0.0 2.5–3.2 | 2.8 | – |
| Occipital condyle width | (30) 6.5 ± 0.2 6–7 | 6.7 | (6) 5.7 ± 0.2 5.5–6.1 | 6.5 | – | (20) 6.9 ± 0.0 6.5–7.1 | 6.4 | – |
| Breadth of M1 | (30) 1.2 ± 0.1 1.1–1.4 | 1.2 | (12) 1.1 ± 0.1 1.0–1.3 | 1.2 | – | (21) 1.2 ± 0.0 1.1–1.3 | 1.2 | – |
| Upper tooth-row alveolar length | (30) 4.3 ± 0.2 4.0–4.8 | 4.6 | (12) 3.9 ± 0.1 3.7–4.1 | 4.6 | (5) 4.6 ± 0.1 4.5–4.8 | (21) 4.8 ± 0.0 4.5–5.1 | 5.0 | 4.0 |

[1] Values corresponding to the population sample of Reserva Privada UNLP "Valle del Arroyo Cuña Pirú" (locality 2);
[2] after González et al. (1998);
[3] after Christoff et al. (2000);
[4] after Christoff et al. (2000);
[5] after Justo and De Santis (1977).

through gallery forest along the Parana river and in forest patches in the northern part of Corrientes Province. This range extension based on seven specimens (MLP 1.X.94.16, MLP 1.X.94.17, MLP 1.X.94.18, MLP 1.X.94.19, MLP 1.X.94.21, MLP 1.X.94.22,MLP 1.X.94.23) from Santa Tecla, ruta 12 km 1287, Ituzaingo Department. *Akodon montensis* also reaches the provinces of Chaco and Formosa (Massoia and Fornes 1962).

An interesting feature of *A. montensis* is that fertile XY females are known from natural populations (Fagundes et al. 2000). We are unaware of the existence of this type of female in populations from Misiones although insufficient numbers of individuals have been karyotyped.

The validity of *A. montensis* and its distinction from *A. cursor* (Winge, 1887) has been discussed for several years. The two species are virtually indistinguishable morphologically, and earlier authors (e.g., Reig 1987) considered them to be the same. Later, cytogenetic studies showed the existence of two distinct sets of diploid complements (2 = 24–25 and 2 n = 14–15), making clear the existence of two synmorphic species. As the 2 n = 14–15 karyotypes were found in the type locality of *A. cursor*, these diploid complements were assigned to this species; the 2 n = 24–25 found elsewhere was assigned to *A. montensis*. However, two factors had raised doubts on the proposed relationship among diploid number and species names. For one, specimens with a 2 n = 24 have also been found at the type locality of *A. cursor* (Geise et al. 2001), making the assignment of any karyotype to either species name arbitrary. Moreover, specimens from the type locality of *A. montensis* had not as yet been karyotyped, although P. Myers (pers. comm.) found only 2 n = 24 in specimens from 7 Paraguayan populations. However, DNA phylogenetic analyses clearly show, independently of the names, that both species are valid since both sets of karyomorphs form monophyletic groups (Geise et al. 2001). Moreover, in a more extensive DNA phylogenetic analysis (results not shown) a specimen (GD 513, to be catalogued at the University of

Michigan Museum of Zoology) from the type locality of *A. montensis* falls into the 2 n = 24–25 clade early identified by Geise et al. (2001). These data support the contention of others in associating the name *A. montensis* with the 2 n = 24–25 form, which we follow here. However, karyotypes from topotypical specimens of *A. montensis* are much needed.

### *Akodon* cf. *A. cursor* (Winge, 1887) (Fig. 2 b; Tab. 1)

As noted above, *Akodon cursor* is in craniodental and penial morphology and pelage color very similar to *A. montensis* (Rieger et al. 1995). However, according to L. Geise (pers. comm.) these two species can be easily differentiated by the presence of a gall bladder in *A. cursor* which is lacking in *A. montensis.* Furthermore, both species are easy to distinguish by karyotype and molecular analyses (Geise et al. 1998, 2001).

In the locality Reserva Privada UNLP "Valle del Arroyo Cuña Pirú" we have collected three specimens of an *A. cursor-montensis* morph with the gall bladder present. Therefore, we refer these three specimens to *A. cursor*. Unfortunately, these individuals were not karyotyped nor were tissue samples saved to further test these identifications. We have not yet attempted to amplify DNA from pieces of skin of any of these specimens.

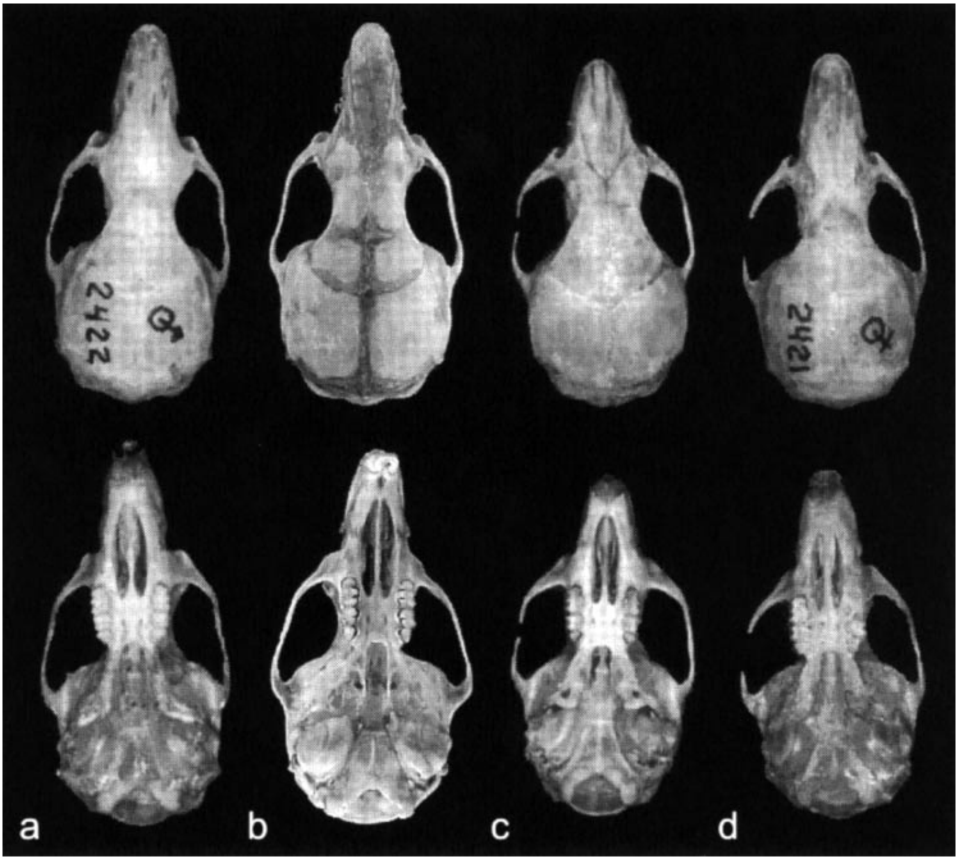


**Fig. 2.** Dorsal and ventral views of skull of adult specimens of the four species of *Akodon* known to inhabit the Misiones Province, Argentina. a) *Akodon montensis* (MMP-Ma 2422); b) *Akodon* cf. *A. cursor* (MLP 5.XII.01.34); c) *Akodon* sp. 1 (UP 08); d) *Akodon* sp. 2 (MMP-Ma 2421).

If our identification of these three animals is correct, then both *A. cursor* and *A. montensis* occur in sympatry in Reserva Privada UNLP "Valle del Arroyo Cuña Pirú," although *A. cursor* is far less common. Importantly, this locality is one of the few where both species are known to occur, thus reinforcing the value of this protected area. Both species are known to hybridize in nature (YONENAGA et al. 1975); however, among those specimens that were karyotyped we have not identified any hybrid.

The finding of *A. cursor* (sensu RIEGER et al. 1995) in Misiones is important for two reasons. First, it increases the number of mammal species known from Misiones and from Argentina. Second, it extends the known distribution of the species, until now restricted to the Brazilian Atlantic forest (CHRISTOFF 1997), further west into northeast Argentina. The Argentinean population is separated from the Brazilian ones by about 680 km, and further studies must be carried out to see if there are intermediate populations.

### *Akodon* sp. 1 (Fig. 2 c; Tab. 1)

We have registered the presence of an undescribed species of *Akodon* in the southern part of the Misiones Province. The formal description of this small representative of the genus *Akodon* will be presented elsewhere. Here we only present some features of it in order to facilitate its potential identification for other workers. Its dorsal pelage is dark gray with the tips of the hair agouti, whereas ventrally it is gray. The tail is short. The skull is slender, with a short rostrum and wide nasals. The zygomatic plate is very narrow, with a straight anterior border. The incisive foramina are short and do not pass the protocone of the M1. The anterior border of the mesopterygoid fossa is quadrate, and it is behind the posterior border of the M3.

Morphologically this species resembles *A. azarae* (Fischer, 1829), a species widely distributed in the Río de la Plata basin. However several pieces of evidence indicate that *A.* sp. 1 represents a different species. There are morphological features that differentiate both species. For instances, *A.* sp. 1 has a comparatively wider and shorter rostrum than *A. azarae*, broader nasals and a reduced zygomatic plate. In addition, *A.* sp. 1 has a diploid complement of 2 n = 36, whereas the *A. azarae* diploid number is 2 n = 37/38. We do not know if this difference has any biological significance, but it is remarkable that *A. azarae* shows uniformity in its chromosomal complement throughout its large range, with variations reported only in the sex determination system (BIANCHI and CONTRERAS 1967; LIZARRALDE et al. 1982; VITULLO et al. 1986; LISANTI et al. 2000). Both specimens of *A.* sp. 1 sequenced share the same cytochrome b gene haplotype. When this haplotype is compared with those recovered from *A. azarae* specimens from Argentina, Paraguay and Uruguay it differs by 10 to 10.86%. Moreover, in preliminary phylogenetic analyses based on these sequences, *A.* sp. 1 appears either as sister taxon of *A. azarae* or *A. lindberghi*, depending whether the analyses are based on 801 bases or the complete cytochrome b gene sequences, respectively. Also, *A.* sp. 1 is clearly distinct from other small species of *Akodon* inhabiting tropical and subtropical lowlands of east central South America in chromosomal, molecular, or morphological characters. For example, *A.* sp. 1 differs from *A. mystax* in karyotype and sequence (2 n = 44, BONVICINO et al. 1997; GEISE et al. 2001), from *A. lindberghi* in karyotype (2 n = 42; SVARTMAN and DE ALMEIDA 1994), and from *A. sanctipaulensis* in morphology (2 n unknown, no genetic information available).

*Akodon* sp. 1 is only known from Santa Inés, in southern Misiones Province (Fig. 1). This locality is placed in the "campos", a grassland formation that extends from southern Misiones to northern Corrientes Province (MARTÍNEZ CROVETTO 1963). At Santa Inés *A.* sp. 1 was trapped exclusively in grasslands that often surround forest patches. These grasslands are also inhabited by other sigmodontine rodents, in-

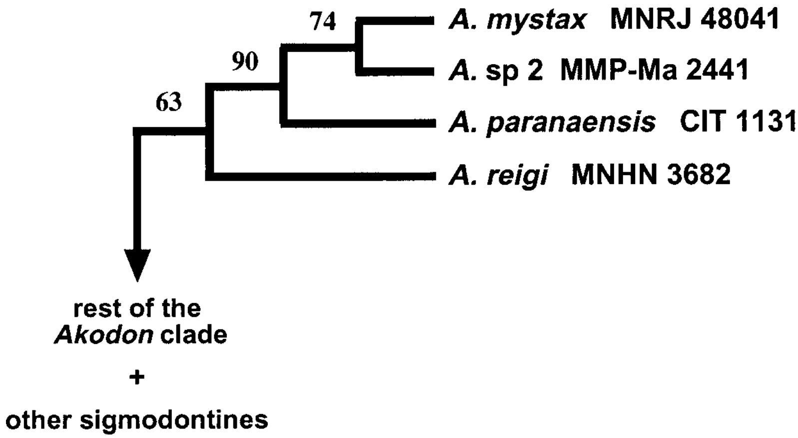


**Fig. 3.** Phylogenetic relationships among four forms of *Akodon* with 2 n = 44. The portrayed relationships are part of an extensive phylogenetic study of sigmodontine taxa. The maximum parsimony analysis was based on the first 801 bases of the cytochrome b gene where characters were treated as unordered and equally weighted. Numbers indicate the bootstrap (500 replications with 3 addition sequence replicates each) support value of the nodes at their right. All analyses were performed using PAUP* (Swofford 2000).

cluding *Calomys laucha*, *Oligoryzomys flavescens*, *O. nigripes*, *Oxymycterus rufus*, *Necromys temchuki* and *Bibimys chacoensis*. The other *Akodon* species known from the area, *A. montensis*, is restricted to forest patches along streams and rivers.

### *Akodon* sp. 2 (Fig. 2 d; Tab. 1)

*Akodon serrensis* sensu Liascovich and Reig (1989)
*Akodon paranaensis* sensu Christoff et al. (2000 (part))

The fourth *Akodon* species of Misiones is known only from one adult specimen (MMP-Ma 2421) from 15 km N of Uruguaí river, Parque Provincial Islas Malvinas (not from Puerto Peninsula as stated by Christoff et al. 2000). The taxonomic status of this specimen is not clear because the limited available evidence is inconclusive. Therefore we refer to it as *Akodon* sp. 2. The case of this specimen exemplifies the still confused taxonomy of sigmodontine rodents, and emphasizing the need for continued field and museum based research.

The specimen in question, MMP-Ma 2421, was originally referred as *Akodon serrensis* by Liascovich and Reig (1989). This assignment was mostly based on chromosomes. MMP-Ma 2421 has a 2 n = 44, a diploid complement at that time was believed to correspond to *A. serrensis* (Sbalqueiro et al. 1986). Later, Christoff et al. (2000) clarified the status of *A. serrensis* in regard to its morphological and chromosomal features, noting that the diploid complement of this species is 2 n = 46. Therefore, these authors corrected Liascovich and Reig's (1989) determination and assigned MMP-Ma 2441 to their new species, *A. paranensis* (Christoff et al. 2000). However, Christoff et al. (2000) did not note that González et al. (1998) already raised the possibility that the Misiones specimen belonged to their newly described species, *A. reigi*, which is morphologically similar and also has 2 n = 44.

A comparison of MMP-Ma 2441 with *A. reigi* and *A. paranaensis* as portrayed in their original descriptions (González et al. 1998; Christoff et al. 2000) indicates that the specimen from Misiones is indistinguishable from either of these two taxa. Among other features, the three forms (i. e., the specimen from Misiones, *A. reigi* and *A. paranaensis*) share the presence of a well developed ectolophid in the m1, a high zygomatic plate with a straight anterior bor-

**Table 2.** Pairwise comparisons of cytochrome b haplotypes (801 bp) recovered from *Akodon* forms with 2 n = 44. Numbers above de diagonal indicate observed number of nucleotide differences. Numbers below the diagonal indicate percentage of observed divergence. The sequence of *A. mystax* was retrieved from GenBank (accession number AF184054).

| | *A. paranaensis* | *A. mystax* | *A. reigi* | *A.* sp. 2 |
|---|---|---|---|---|
| *A. paranaensis* | | 23 | 41 | 77 |
| *A. mystax* | 2.87 | | 41 | 65 |
| *A. reigi* | 5.12 | 5.12 | | 83 |
| *A.* sp. 2 | 9.61 | 8.11 | 10.36 | |

der, marked similar external and skull measurements (Tab. 1), and a diploid complement of 2 n = 44.

We managed to sequence the first 801 base pairs of the cytochrome b gene from dry muscle attached to the skull of MMP-Ma 2441. The recovered haplotype is quite distinct from those of other *Akodon* species, including *A. paranaensis* and *A. reigi* (Tab. 2). However, in the phylogenetic analysis MMP-Ma 2441 falls into a well supported clade (Fig. 3) that includes *A. reigi*, *A. paranaensis and A. mystax*, which also has a 2 n = 44 (HERSHKOVITZ 1998). Interestingly, *A. mystax*, which is morphologically quite distinct from the rest of the forms in consideration, occupies an internal position in this clade. It appears as sister taxon of MMP-Ma 2441. In other words, there is evidence of an *A. reigi* like morph paraphyletic with respect to a much smaller *A. mystax* morph.

The evidence at hand could be taxonomically interpreted in different ways. We think that non-taxonomists will advocate a scenario where only one species is recognized to encompass the entire 2 n = 44 clade, because that way morphological diversity is underscored. Therefore, the first possibility is to follow the pattern of morphological variation to recognize two species within the 2 n = 44 clade: a larger species, *A. reigi*, paraphyletic with respect to a smaller one, *A. mystax*. Under this layout MMP-Ma 2441 from Misiones would constitute an Argentinean representative of *A. reigi,* with *A. paranaensis* as junior synonym. However, before formally suggesting the preceding scenario other factors must be considered first. For instance, an exhaustive morphological comparison covering type material of all involved species, as well as more specimens from Misiones, must be carried out. Second, comparisons of C and G banding patterns have to be performed to elucidate the extent of the karyotypic similarities among these 2 n = 44 forms. Third, phylogenetic analyses based on cytochrome b gene sequences should include more specimens, preferentially type or topotypical material as well as from geographically intermediate localities. Finally, the cytochrome b based topology must be further tested with phylogenetic analyses based on characters independent of the mitochondrial genome (e. g. morphology and/or nuclear sequences). A second taxonomic possibility is to validate as species each of the branches of the 2 n = 44 clade depicted in figure 3. This means the recognition of *A. mystax* and three morphologically indistinguishable species: *A. reigi*, *A. paranaensis*, and another represented by MMP-Ma 2441. This way no paraphyletic species is recognized. So far, this scenario is only supported by the substantial genetic divergence of the specimen from Misiones, an argument that a priori, and in spite of recent claims (e. g., BRADLEY and BAKER 2001), does not have a clear taxonomic meaning. Finally, an intermediate and less favored situation would be to recognize *A. mystax* and two synmorphic species, *A. reigi* and *A. paranaensis.* Here MMP-Ma 2441 would represent an Argentinean specimen of *A. paranaensis.* Since MMP-Ma is sister to *A. mystax*, one of the three species recognized under this arrangement would be paraphyletic, i. e., *A. para-*

*naensis* with respect to *A. mystax*. The foundation for this scenario rests on the differential support (measured as bootstrap values) of the nodes of the 2 n = 44 clade. The strongest supported node (90%) appears to be the one that represents the hypothetical common ancestor of *A. mystax*, MMP-Pa 2441, and *A. paranaensis*, whereas the weakest supported node (63%) of the 2 n = 44 clade is the one at its base, the one from which the *A. reigi* line branch off. In other words, of all members of the 2 n = 44 clade, *A. reigi* is the one whose identity as a member of this clade appears less supported. We tend to not embrace this scenario because its foundation is weak and seems more arbitrary than biologically sound.

Therefore, taking into account the above considerations, and until additional studies are carried out, we refer to the MMP-Ma 2441 specimen as *Akodon* sp. 2 and do not propose a formal synonymy of *A. paranaensis* and *A. reigi*.

According to information provided by the original collectors (Massoia et al. 1987), *Akodon* sp. 2 occurs in sympatry with *A. montensis* in Paranaense forest characterized by the presence of araucarias (*Araucaria angustifolia*) and palo rosa (*Aspidosperma polyneuron*). Coincidently, *A. paranaensis* inhabits similar forest characterized by araucarias (Christoff et al. 2000), whereas *A. reigi* was trapped on dense riparian forest.

### Unconfirmed Species

Justo and De Santis (1977) identified one specimen collected 32 km N of Bernado de Irigoyen, by the San Antonio River, as *A. serrensis serrensis*. This specimen, originally deposited in the Colección del Instituto Argentino de Investigaciones en Zonas Aridas, Mendoza (IADIZA-M 00667), is currently lost and all efforts to localize it in Argentinean collections have been fruitless. From the description and measurements given by Justo and De Santis (1977) it is not possible to assign IADIZA-M 00667 to *A. serrensis*. The comparative measurements (Tab. 1) indicate that the specimen in question belongs to a large *Akodon* species like *A. serrensis* but also *A. montensis*, *A. cursor*, and *A.* sp. 2, among others. However, at least two facts allow us to think that the assignment of IADIZA-M 00667 to *A. serrensis* is incorrect. First, the length of the upper molar series reported by Justo and de Santis (1977) falls outside the range of values reported for this character in *A. serrensis* (Christoff et al. 2000). Second, it is noticeable that Justo and de Santis (1977) did not mention the absence of the anteromedian flexus of the M1, a remarkable feature of *A. serrensis*. Therefore, we discard the record of *A. serrensis* for the mammal fauna of Misiones (and Argentina). It is worth noting that IADIZA-M 00667 came from the Araucaria forest district, one of the less surveyed biomes of Misiones. Finally, the reference of this specimen to *Thaptomys nigrita* stated by Galliari et al. (1996) was due to a confusion of the authors with the next specimen catalogued in the IADIZA collection (IADIZA-M 00668), which in fact is a specimen of *T. nigrita*.

## Discussion

Although Misiones is small with respect to the total continental surface of Argentina (0.8%), its mammal community is highly diverse, and certainly stands within the country by it uniqueness. Three of the four species of *Akodon* inhabiting Misiones are not known from elsewhere in Argentina. In addition, so far as is known one of these species (*Akodon* sp. 1), and perhaps a second one (*Akodon* sp. 2) are endemic for Misiones. Moreover, 11 other sigmodontine species from Misiones, including some of the most distinctive sigmodontine taxa (e. g., *Abrawayaomys ruschii*), are not known from other parts of Argentina. Among these are three recently described species belonging to the genus *Brucepattersonius* that are only know from Misiones (Mares and Braun 2000). Therefore, although it is clear that the extent of the mammal diversity of Misiones is still far from being well known, we can remark the uniqueness of this fauna in comparison to other parts of Argentina. As regards the conservation of the Argentinean mammal diversity, Misiones must be given high priority. However, attention has also to be paid to other areas with high levels of endemicity, such as the Yungas or the *Nothofagus* Andean forest.

The results of this study should be taken as a call of attention of the limited knowledge about the mammal fauna of northeastern Argentina, a situation also true for most of the country. Paradoxically the Misiones mammal fauna has been considered as one of the better known in Argentina (CHEBEZ and MASSOIA 1996).

Currently Misiones is facing a high rate of deforestation due to either agricultural practices or to the replacement of natural forest with exotic species (BERTONATTI and CORCUERA 2000). Misiones has a core of protected areas covering approximately 14.95% of the province (GIRAUDO et al. 2002). Populations of three of the four *Akodon* species known to occur in Misiones are located in protected areas. However, no studies have yet been conducted to assess the existence of different evolutionary significant units (ESU; MORITZ 1994 a, b) within each of these species. Therefore, some ESU may not be protected. In addition, no known population of *A.* sp. 1 is protected. This fact is extremely important because *A.* sp. 1, apparently endemic to Misiones, inhabits a type of habitat undergoing great human pressure.

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## Zusammenfassung

### Die Gattung *Akodon* (Muroidea: Sigmodontinae) in Misiones, Argentinien

Unser Verständnis der Diversität von Nagetieren in den argentinischen atlantischen Regenwäldern und den umliegenden Regionen (in der Provinz Misiones) ist noch verhältnismäßig begrenzt. Wir stellen neue Forschungsergebnisse über die Arten der Gattung *Akodon* vor, die in der Region Misiones vorkommen, und die eine der vielfältigsten sigmodontinen Nagergattung ist. Eine integrierte Analyse der morphologischen, chromosomalen und molekularen Daten ermöglicht es uns, die Existenz von vier Spezies von *Akodon* in der Provinz zu dokumentieren. Eine neue, unbeschriebene Art, *Akodon* sp. 1, ist bisher nur von einer Stelle in der pflanzengeografischen Region „campos" im südlichen Misiones bekannt. *A. montensis* hat eine große Verbreitung und ist eine der dominierenden Sigmodontinen im Primär- und Sekundärwald. *Akodon* sp. 2, bisher *A. serrensis* und *A. paranaensis* benannt, ist nur an einer Stelle im Nordosten der Provinz bekannt, in der sie mit *A. montensis* sympatrisch ist. Ebenfalls in Sympatry mit *A. montensis* gibt es eine ähnliche Spezies mit einer Gallenblase, die an einer Stelle im zentralen Misiones vorkommt. Wir nennen sie *A. cursor*. Schließlich muß die bisherige Zuordnung eines Exemplars zu *A. serrensis* aufgegeben werden, da es verloren gegangen ist und die vorhandenen Daten nicht ausreichen, um die Identität des Probenmaterials zu bestimmen. Da die Provinz Misiones die größten zusammenhängenden Flächen vom südlichen, atlantischen Regenwald einnimmt, diskutieren wir die Bedeutung unserer Studie für den Naturschutz. Schließlich betonen wir den Wert der Integration von unterschiedlichem Datenmaterial zur Systematisierung von Säugetieren.

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