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KARYOLOGY AND MORPHOMETRICS OF THREE SPECIES OF *AKODON* (MAMMALIA: MURIDAE) FROM NORTHWESTERN ARGENTINA

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ABSTRACT

Chromosomal and morphometric studies were conducted on a sample from an assemblage of *Akodon* spp. occurring in various patterns of sympatry from the provinces of Catamarca, Jujuy, Salta, and Tucumán, Argentina. Results showed three distinct morphometric groups based upon size. Size also varied with age, but there were no significant differences in measurements of males and females. The three morphometric groups have distinct karyotypes. *Akodon caenosus* Thomas is the smallest of the three, and has a karyotype of 2n = 34, FN = 40. *A. boliviensis tucumanensis* J. A. Allen is intermediate in size and has 2n = 40, FN = 40, 41. Three variations in centromeric position of the X chromosomes and two autosome arm numbers were found. *A. varius simulator*

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Thomas is the largest in size, has a distinctive white chin-spot, and has 2n = 41, 42 and FN = 42. Variation in diploid number is apparently due to centric fission or fusion.

INTRODUCTION

Neotropical murid rodents (sometimes treated as the family Cricetidae) include a group of vole-like pastoral species loosely allied as the akodonts. Most species are apparently insectivorous (Hershkovitz, 1966). Various authors have disagreed on the composition of the akodont group, both in terms of group membership and generic groupings of species (for example, Tate, 1932; Cabrera, 1961; Bianchi et al., 1971; Gardner and Patton, 1976). Cabrera (1961), in the latest comprehensive list of South American mammals, recognized eight genera (including *Scolomys* Anthony, *Oxymycterus* Waterhouse, and *Zygodontomys* J. A. Allen), consisting of 138 named forms of 59 species. Of these totals, the genus *Akodon* Meyen contained nine subgenera and 87 forms of 38 species. Bianchi et al. (1971) regarded eight of the nine subgenera of *Akodon* (*sensu* Cabrera, 1961) as separate genera (*Abrothrix* Waterhouse, *Akodon, Bolomys* Thomas, *Chroeomys* Thomas, *Hypsimys* Thomas, *Microxus* Thomas, *Thalpomys* Thomas, and *Thaptomys* Thomas). Excluding *Akodon* (*sensu stricto*), four of these are monotypic and the other three genera or subgenera each contain four species. Tate (1932), in the only other comprehensive account of akodonts, listed 15 genera (excluding *Scolomys* and *Zygodontomys*), and included the Central American genus *Scotinomys* in his akodont group. Hershkovitz (1966) placed *Abrothrix* (including *Microxus* as a synonym), *Lenoxus* Thomas, *Podoxymys* Anthony, and *Oxymycterus* in a separate group, the oxymycterines. Most authors have agreed that *Notiomys* Thomas and *Blarinomys* Thomas are other recognizable genera of the akodont group.

There has never been a comprehensive taxonomic review of the genera and species of akodont rodents, and a great many of the taxa are known only from restricted geographic areas or solely from their type localities. Consequently, our understanding of the number of species, their systematic relationships to each other, and the characters of value in recognizing species and defining higher taxa are still rudimentary.

Bianchi and co-workers and others have demonstrated great variation in chromosome structure and numbers, both within and between populations of akodonts (for example, see Bianchi et al., 1971, 1973, 1979; Yonenaga, 1972; Yonenaga et al., 1975; Gardner and Patton, 1976; Kiblisky et al., 1976; Spotorno and Fernandez, 1976). Although available karyotypic data for akodonts are still too fragmentary to be of much use in constructing phylogenies, they are becoming increasingly useful for making taxonomic determinations.

We undertook morphometric and karyotypic studies of populations of *Akodon* from the vicinity of San Miguel de Tucumán, Tucumán Province, Argentina, in order to clarify the nature and extent of structural variation apparent in our sample. During our studies we determined that our sample of *Akodon* could be sorted into three groups based upon external dimensions, color of pelage, and skull structure. In the process of identifying these three groups, we found it necessary to include in our analyses some specimens from neighboring areas. Herein we show correspondence in karyotypic and structural characters, supporting the hypothesis that three species of *Akodon* are represented in our samples.

MATERIALS AND METHODS

Numbers of individuals examined and localities of capture are listed in the Specimens Examined section (below). Skull characters were measured with dial calipers (accurate to 0.05 mm), and recorded to the nearest 0.1 mm. Standard external measurements were recorded to the nearest mm. Characters used in the morphometric analyses are listed in Tables 1 and 2. Methods of measuring skull characters were as follows:

Condyloincisive length.—Distance from occipital condyle to anterior face of incisor.

Least interorbital breadth.—Least distance across frontals in interorbital region.

Zygomatic breadth.—Greatest distance across skull, measured across zygomatic arches.

Greatest length of skull.—Greatest length from tip of nasals to back of occiput.

Breadth of braincase.—Greatest distance across braincase, measured immediately behind squamosal processes of the zygomatic arches.

Length of maxillary toothrow.—Alveolar length from front of M^1 to back of M^3.

Length of palate.—Distance from posterior margin of the alveolus of upper incisor to back of palatine at anterior border of the mesopterygoid fossa.

Length of mandibular toothrow.—Alveolar length from front of M_1 to back of M_3.

Length of diastema.—Distance from posterior margin of the alveolus of upper incisor to anterior alveolus of M^1.

Specimens were initially sorted into groups by sex and age classes for statistical analyses of morphometric traits. Age classes were arbitrarily defined by the amount of wear on the upper molars (Fig. 1). Individuals of the four age classes were treated separately in all univariate and multivariate analyses. Specimens were further sorted into three groups within sex and age classes, based upon overall size and the color of the chin (presence or absence of white hairs). The groups were then subjected to standard univariate analyses in order to detect significant ($P \leq 0.05$) differences between males and females. Statistical analyses employed the UNIVAR program, which is a sums of squares, simultaneous testing procedure (SS-STP, Gabriel, 1964), based upon a single-classification analysis of variance. Because no significant differences were noted between sexes within age and size groups, sexes were pooled for subsequent univariate and multivariate analyses.

All specimens, including those with missing values for some characters, were subjected to a discriminant function/canonical analysis (BMDP7M, Dixon and Brown, 1977). Individuals with missing values do not contribute to computation of variable means, F values, group linear classification functions, and associated statistics. Values are, however, estimated for missing characters, and statistics are calculated in order to classify these individuals with one of the established groups (Dixon and Brown, 1977; see Williams and Genoways, 1979, for further explanation of this type of analysis).

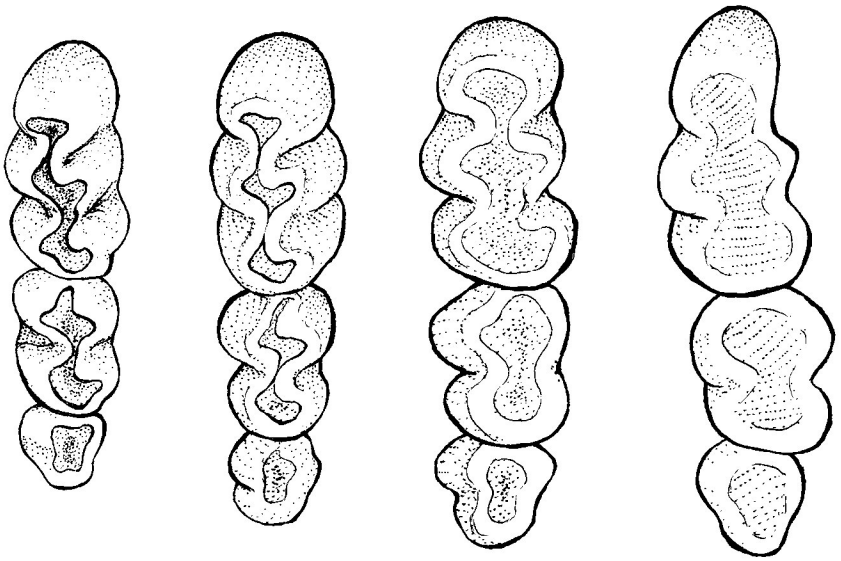


Fig. 1.—First upper molars of *Akodon* showing stages of wear corresponding to age classes used for grouping specimens for morphometric analysis. Age classes, from left to right, are: young; subadult; adult; old adult.

Standard *in vivo* chromosome preparations were made in the field, using the colchicine, hypotonic sodium-citrate, blaze-dry technique. Methods and karyologic nomenclature follow Patton (1967).

For clarity in the presentation of results, the names we use for the three phenetic groups are *Akodon boliviensis* Meyen, *A. caenosus* Thomas, and *A. varius* Thomas.

Collecting Sites

Specimens were collected from 10 localities in the provinces of Catamarca, Jujuy, Salta, and Tucumán, northwestern Argentina (see Specimens Examined section). All localities lie within a 350 km radius in the eastern Andean foothills; elevation ranges from about 700 to 1,100 m. Although 10 sites were examined, several of these shared various vegetational and climatological characteristics. Basically the localities were mesic forest sites, grassland-scrub sites, and riparian areas within dry regions.

One locality, Horco Molle, is located approximately 15 km W of the city of San Miguel de Tucumán, at an elevation of 700 m. The area is mostly Basal Subtropical Forest (Meyer and Weyrauch, 1966) with large trees such as *Phoebe porphyria, Terminalia triflora,* and *Jacaranda mimosifolia* and many other tree species (for example, *Tabebuia avellanedae, Cedrela lilloi,* and *Enterolobium contortisiliquum*). Many epiphytes are present and the forest is largely evergreen. The three species of *Akodon* herein considered were taken in second growth areas of the forest (for example along trails, creeks and roads). This site is similar to the Orán locality in north-central Salta Province which also supported three *Akodon* species (Fig. 2).

Fig. 2.—A mesic forest locality in north-central Salta Province along the Río Pescado. Here, *Akodon varius, A. boliviensis,* and *A. caenosus* occur in sympatry, particularly in areas of second growth vegetation such as that found along the riverbank.

Another major locality is El Cadillal, located approximately 25 km NE of San Miguel de Tucumán near the El Cadillal impoundment. The area is a mixture of cultivated fields, thorn scrub, and grassy fields (Fig. 3). Woody vegetation consists of *Acacia aroma, Piptadenia* spp., *Schinopsis haenkeana, Celtis spinosa, Prosopis alba,* and others. Most plants seldom exceed 5 m in height.

The third major site is along the Rio Andalgalá immediately N of Andalgalá, Catamarca Province (Fig. 4). This is a permanent water riverine forest within a broad xeric region known as the Monte (Morello, 1958). *Akodon boliviensis* and *A. varius* occur in

Fig. 3.—A grass-shrub community located near El Cadillal Reservoir in Tucumán Province. Common second growth plants, such as Castor beans (*Ricinus*) are visible in the photograph. All three species of *Akodon* occurred in this habitat.

the shrubby undergrowth along the river. Major trees are *Prosopis* sp., *Celtis* sp., and *Acacia* sp. This area is more fully described by Mares (1975, 1977).

RESULTS

Univariate Analysis

Eleven samples were analyzed using univariate statistical techniques (Table 1). The samples represented four age classes for two of the

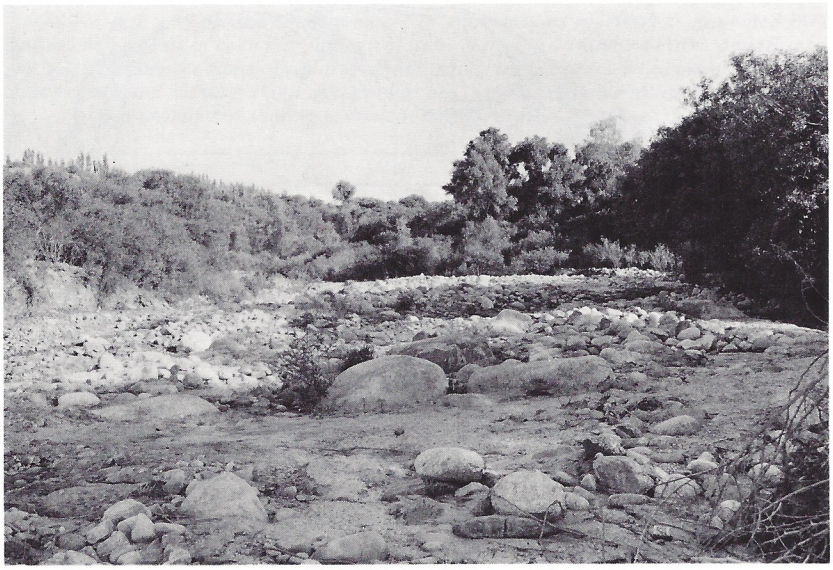


Fig. 4.—The Rio Andalgalá, in Catamarca Province immediately north of the town of Andalgalá. This site is a mesic refuge in the midst of the surrounding Monte Desert. *Akodon varius* and *A. boliviensis* are common in this habitat.

phenetic groups and three for the other phenetic group. The species that we consider to be *A. caenosus* lacked any individuals in the young age category.

The old and adult individuals of the phenetic group considered to represent *A. varius* averaged larger in all 14 measurements than members of *A. boliviensis* and *A. caenosus*. When samples of equivalent age were considered, *A. varius* averaged the largest, *A. boliviensis* averaged medium-sized, and *A. caenosus* always averaged the smallest in size (Fig. 5).

In breadth of braincase, the means of the four samples of *A. varius* form one nonoverlapping subset, the four samples of *A. boliviensis* form another, and the three samples of *A. caenosus* form a third. These differences are rather impressive considering that these samples represent different age groups. This means that young *A. varius* are significantly larger on the average than old *A. boliviensis* and that young *A. boliviensis* are significantly larger on the average than old *A. caenosus*.

In three measurements (length of hind foot, length of maxillary toothrow, and length of mandibular toothrow), the means of the three

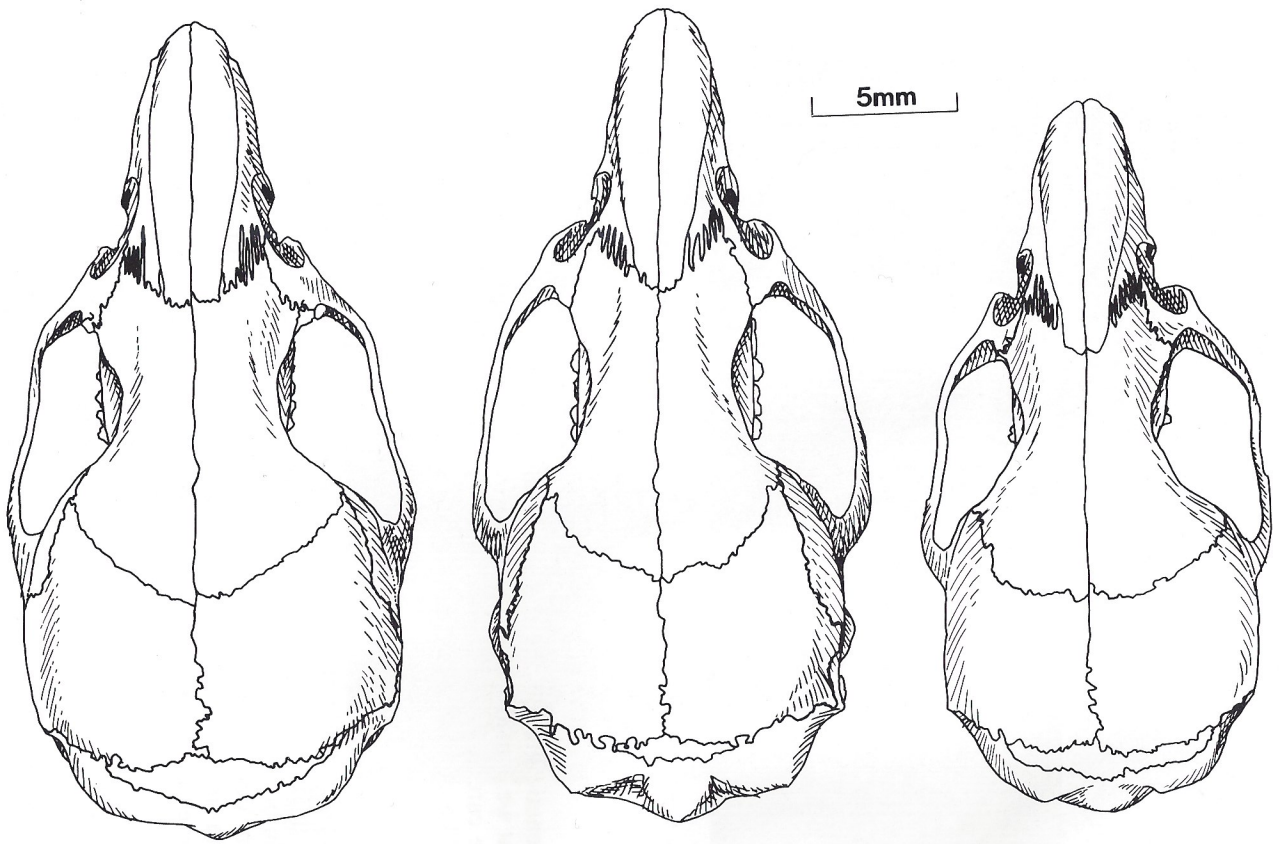


Fig. 5.—Skulls of young adult *Akodon varius* (left), adult *A. boliviensis* (middle), and adult *A. caenosus* (right). The animals differ in several cranial characters, but most noticeably in breadth of braincase and length of the maxillary and mandibular toothrows.

Table 1.—*Age groups and total numbers of each species of* Akodon *examined by a univariate analysis of each morphological trait. Means ± 2 standard errors and (Range) are given. Under the sums of squares-simultaneous testing procedure column (SS-STP), groups enclosed within a single vertical bar are indistinguishable at the* $P \leq 0.05$ *level, while groups not sharing a vertical bar differ significantly at that level.*

Species and age	N	Mean ± 2 SE	(Range)	SS-STP
		Length of head and body		
A. varius old	25	120.4 ± 3.88	(95–139)	|
A. varius adult	70	108.2 ± 2.23	(80–125)	|
A. boliviensis adult	7	107.3 ± 4.85	(101–120)	| |
A. boliviensis old	12	102.4 ± 6.04	(83–115)	| |
A. varius subadult	50	101.4 ± 2.33	(85–123)	| |
A. varius young	21	97.6 ± 3.58	(85–118)	|
A. boliviensis subadult	11	94.5 ± 5.43	(84–108)	|
A. caenosus old	2	93.5 ± 5.00	(91–96)	| |
A. caenosus adult	5	91.6 ± 7.79	(78–101)	| |
A. boliviensis young	6	89.0 ± 8.88	(75–104)	| |
A. caenosus subadult	10	78.5 ± 4.85	(65–94)	|
		Length of tail		
A. varius adult	68	84.1 ± 1.70	(69–101)	|
A. varius old	25	83.0 ± 2.87	(70–99)	|
A. varius subadult	48	74.6 ± 2.16	(61–99)	|
A. boliviensis old	12	73.3 ± 4.55	(58–83)	| |
A. boliviensis adult	7	73.2 ± 4.57	(65–82)	| |
A. varius young	21	70.3 ± 3.38	(60–87)	| |
A. boliviensis subadult	11	70.2 ± 4.14	(60–83)	| |
A. caenosus old	2	65.0 ± 12.00	(59–71)	| |
A. boliviensis young	6	64.0 ± 5.03	(58–75)	| |
A. caenosus adult	5	62.6 ± 2.50	(58–65)	| |
A. caenosus subadult	10	59.2 ± 2.21	(54–66)	|
		Length of hind foot		
A. varius adult	73	24.6 ± 0.25	(22.5–27.2)	|
A. varius old	25	24.1 ± 0.51	(21.3–26.4)	| |
A. varius subadult	50	23.7 ± 0.29	(21.5–26.0)	| |
A. varius young	21	23.1 ± 0.44	(21.4–24.3)	| |
A. boliviensis subadult	11	21.6 ± 0.45	(20.7–22.9)	| |
A. boliviensis old	12	21.4 ± 0.51	(20.0–22.7)	| |
A. boliviensis adult	7	21.3 ± 0.84	(19.0–22.6)	| |
A. boliviensis young	7	21.0 ± 0.80	(19.9–23.1)	| |
A. caenosus subadult	10	18.8 ± 0.52	(17.9–20.3)	|
A. caenosus adult	5	18.5 ± 0.44	(18.0–19.3)	|
A. caenosus old	2	18.4 ± 1.70	(17.6–19.3)	|

Table 1.—*Continued.*

Species and age	N	Mean ± 2 SE	(Range)	SS-STP
		Length of ear		
A. varius adult	73	20.5 ± 0.41	(17.0–27.2)	
A. varius subadult	49	19.2 ± 0.44	(16.3–23.5)	
A. varius old	25	19.1 ± 0.57	(16.6–21.9)	
A. varius young	21	18.3 ± 1.11	(15.4–23.8)	
A. boliviensis old	12	16.8 ± 0.56	(14.9–18.7)	
A. boliviensis subadult	11	16.5 ± 0.83	(14.5–18.3)	
A. boliviensis adult	7	16.4 ± 0.92	(14.4–18.3)	
A. boliviensis young	7	16.2 ± 0.99	(14.6–18.0)	
A. caenosus adult	5	14.4 ± 1.02	(12.7–15.4)	
A. caenosus subadult	10	14.3 ± 1.33	(9.2–16.6)	
A. caenosus old	2	14.0 ± 2.30	(12.8–15.1)	
		Weight		
A. varius old	25	46.7 ± 4.16	(22.5–59.0)	
A. varius adult	69	35.7 ± 2.01	(21.7–62.0)	
A. boliviensis old	12	33.2 ± 3.54	(20.0–40.2)	
A. boliviensis adult	7	32.5 ± 4.70	(27.5–42.0)	
A. varius subadult	45	28.5 ± 2.58	(17.5–59.0)	
A. boliviensis subadult	11	27.7 ± 4.50	(18.0–39.0)	
A. varius young	21	24.7 ± 3.71	(12.5–53.0)	
A. caenosus adult	5	20.5 ± 4.03	(14.5–26.3)	
A. caenosus old	2	19.7 ± 4.70	(17.3–22.0)	
A. boliviensis young	7	17.9 ± 2.98	(13.0–23.5)	
A. caenosus subadult	10	13.8 ± 1.94	(11.0–21.8)	
		Condyloincisive length		
A. varius old	19	27.3 ± 0.48	(24.6–28.7)	
A. varius adult	69	26.9 ± 0.21	(25.0–29.0)	
A. varius subadult	45	25.4 ± 0.35	(22.7–28.5)	
A. boliviensis old	12	24.7 ± 0.72	(22.2–27.6)	
A. varius young	17	24.1 ± 0.61	(21.6–27.2)	
A. boliviensis adult	7	23.9 ± 0.38	(23.3–24.5)	
A. boliviensis subadult	9	22.8 ± 0.42	(21.7–23.5)	
A. boliviensis young	3	21.0 ± 0.83	(20.2–21.5)	
A. caenosus adult	5	20.7 ± 0.62	(19.6–21.3)	
A. caenosus old	2	20.6 ± 1.00	(20.1–21.1)	
A. caenosus subadult	9	19.8 ± 0.28	(19.2–20.7)	
		Greatest length of skull		
A. varius old	20	28.8 ± 0.47	(26.6–30.5)	
A. varius adult	67	28.6 ± 0.21	(26.6–30.5)	
A. varius subadult	43	27.2 ± 0.29	(25.5–29.9)	
A. boliviensis old	12	26.3 ± 0.54	(24.3–28.1)	
A. varius young	17	26.0 ± 0.59	(23.8–28.9)	
A. boliviensis adult	7	25.5 ± 0.27	(25.1–26.0)	
A. boliviensis subadult	9	24.6 ± 0.45	(23.4–25.6)	
A. boliviensis young	3	23.3 ± 1.03	(22.3–23.9)	
A. caenosus adult	5	22.9 ± 0.77	(21.7–23.7)	
A. caenosus old	2	22.4 ± 0.00	(—)	
A. caenosus subadult	9	21.9 ± 0.47	(20.9–22.8)	

Table 1.—*Continued.*

Species and age	N	Mean ± 2 SE	(Range)	SS-STP
		Zygomatic breadth		
A. varius old	20	14.7 ± 0.18	(14.0–15.3)	
A. varius adult	68	14.6 ± 0.18	(13.5–16.7)	
A. varius subadult	43	13.9 ± 0.18	(12.8–15.5)	
A. varius young	13	13.3 ± 0.43	(12.2–15.0)	
A. boliviensis old	10	13.2 ± 0.61	(12.0–15.6)	
A. boliviensis adult	7	12.5 ± 0.20	(12.0–12.8)	
A. boliviensis subadult	6	12.4 ± 0.25	(12.1–12.9)	
A. boliviensis young	3	11.6 ± 0.35	(11.3–11.9)	
A. caenosus adult	4	11.3 ± 0.31	(10.9–11.6)	
A. caenosus old	2	11.2 ± 0.00	(—)	
A. caenosus subadult	8	10.7 ± 0.17	(10.3–11.0)	
		Interorbital breadth		
A. varius adult	73	5.1 ± 0.04	(4.8–5.5)	
A. varius old	25	5.1 ± 0.07	(4.8–5.6)	
A. varius subadult	50	5.0 ± 0.06	(4.5–5.5)	
A. varius young	21	4.9 ± 0.10	(4.5–5.2)	
A. boliviensis subadult	10	4.6 ± 0.07	(4.4–4.8)	
A. boliviensis old	12	4.6 ± 0.04	(4.5–4.7)	
A. boliviensis young	7	4.5 ± 0.13	(4.4–4.9)	
A. boliviensis adult	7	4.4 ± 0.15	(4.2–4.8)	
A. caenosus subadult	10	4.3 ± 0.07	(4.0–4.4)	
A. caenosus adult	5	4.1 ± 0.04	(4.1–4.2)	
A. caenosus old	2	4.1 ± 0.10	(4.0–4.1)	
		Breadth of braincase		
A. varius adult	70	12.5 ± 0.09	(11.8–13.4)	
A. varius subadult	45	12.4 ± 0.08	(11.7–12.9)	
A. varius old	20	12.4 ± 0.11	(12.0–12.8)	
A. varius young	18	12.2 ± 0.18	(11.2–12.9)	
A. boliviensis old	12	11.5 ± 0.21	(11.0–12.3)	
A. boliviensis adult	7	11.4 ± 0.22	(11.1–11.9)	
A. boliviensis young	3	11.4 ± 0.29	(11.2–11.7)	
A. boliviensis subadult	11	11.4 ± 0.15	(11.0–11.9)	
A. caenosus subadult	9	10.7 ± 0.25	(10.4–11.6)	
A. caenosus old	2	10.6 ± 0.10	(10.6–10.7)	
A. caenosus adult	5	10.5 ± 0.29	(10.2–11.0)	
		Length of maxillary toothrow		
A. varius old	24	5.0 ± 0.08	(4.6–5.5)	
A. varius adult	73	4.9 ± 0.03	(4.6–5.2)	
A. varius subadult	47	4.8 ± 0.05	(4.5–5.2)	
A. varius young	20	4.8 ± 0.07	(4.2–5.0)	
A. boliviensis old	12	4.5 ± 0.19	(4.1–5.4)	
A. boliviensis young	7	4.3 ± 0.09	(4.2–4.5)	
A. boliviensis adult	7	4.3 ± 0.10	(4.2–4.5)	
A. boliviensis subadult	11	4.3 ± 0.08	(4.1–4.5)	
A. caenosus adult	5	3.7 ± 0.14	(3.5–3.9)	
A. caenosus subadult	10	3.7 ± 0.09	(3.5–3.9)	
A. caenosus old	2	3.7 ± 0.30	(3.5–3.8)	

Table 1.—*Continued.*

Species and age	N	Mean ± 2 SE	(Range)	SS-STP
		Palatal length		
A. varius old	25	14.4 ± 0.23	(12.9–15.4)	
A. varius adult	73	14.1 ± 0.11	(13.3–15.2)	
A. varius subadult	49	13.4 ± 0.19	(11.7–15.1)	
A. boliviensis old	12	12.8 ± 0.47	(11.5–14.8)	
A. varius young	21	12.6 ± 0.35	(10.9–14.2)	
A. boliviensis adult	7	12.3 ± 0.32	(11.8–13.1)	
A. boliviensis subadult	10	11.8 ± 0.33	(10.8–12.5)	
A. boliviensis young	7	10.8 ± 0.81	(9.7–12.8)	
A. caenosus old	2	10.7 ± 0.30	(10.5–10.8)	
A. caenosus adult	5	10.6 ± 0.47	(10.0–11.3)	
A. caenosus subadult	10	10.3 ± 0.33	(9.7–11.4)	
		Diastema length		
A. varius old	25	7.8 ± 0.16	(6.7–8.4)	
A. varius adult	73	7.6 ± 0.08	(6.7–8.4)	
A. varius subadult	47	7.1 ± 0.14	(6.1–8.4)	
A. boliviensis old	12	6.8 ± 0.25	(6.0–7.9)	
A. varius young	21	6.8 ± 0.21	(5.8–7.8)	
A. boliviensis adult	7	6.6 ± 0.11	(6.4–6.8)	
A. boliviensis subadult	10	6.2 ± 0.18	(5.8–6.7)	
A. caenosus old	2	5.8 ± 0.10	(5.7–5.8)	
A. boliviensis young	7	5.7 ± 0.63	(4.8–7.2)	
A. caenosus adult	5	5.6 ± 0.31	(5.1–6.0)	
A. caenosus subadult	10	5.4 ± 0.19	(5.1–6.2)	
		Length of mandibular toothrow		
A. varius old	23	5.1 ± 0.08	(4.7–5.4)	
A. varius adult	73	5.0 ± 0.03	(4.7–5.3)	
A. varius subadult	46	4.8 ± 0.06	(3.8–5.2)	
A. varius young	20	4.7 ± 0.10	(4.1–5.0)	
A. boliviensis old	12	4.5 ± 0.13	(4.2–5.0)	
A. boliviensis young	7	4.3 ± 0.25	(4.0–5.0)	
A. boliviensis adult	7	4.3 ± 0.14	(4.1–4.6)	
A. boliviensis subadult	11	4.3 ± 0.10	(4.0–4.5)	
A. caenosus old	2	3.7 ± 0.20	(3.6–3.8)	
A. caenosus adult	5	3.7 ± 0.06	(3.6–3.8)	
A. caenosus subadult	10	3.7 ± 0.04	(3.6–3.8)	

samples of *A. caenosus* form a nonoverlapping subset. There is no overlap in the range of values for length of maxillary toothrow for *A. caenosus* and the other two species (3.5 to 3.9 versus 4.1 to 5.5 mm). There is overlap only at 3.8 mm for length of mandibular toothrow for these same groups (*A. caenosus*, 3.6 to 3.8, and *A. varius-boliviensis*, 3.8 to 5.4).

Table 2.—*Variables used in discriminant function analysis of Argentine* Akodon. *Characters are listed in order of their usefulness in distinguishing groups, with the character with the greatest between-group variance and the least within-group variance being selected first. Other traits are ranked using the same criteria. The statistics are recalculated at each step.*

Step	Character	F-value	U-statistic
1	Length of hind foot	54.55	0.2818
2	Interorbital breadth	23.75	0.2236
3	Length of head and body	16.16	0.1846
4	Palatal length	12.43	0.1605
5	Breadth of braincase	10.28	0.1417
6	Length of ear	8.80	0.1283
7	Zygomatic breadth	7.77	0.1165
8	Diastema length	7.00	0.1065
9	Length of maxillary toothrow	6.38	0.0984
10	Greatest length of skull	5.77	0.0946
11	Condylobasal length	5.39	0.0874
12	Length of mandibular toothrow	4.94	0.0856
13	Length of tail	4.56	0.0839

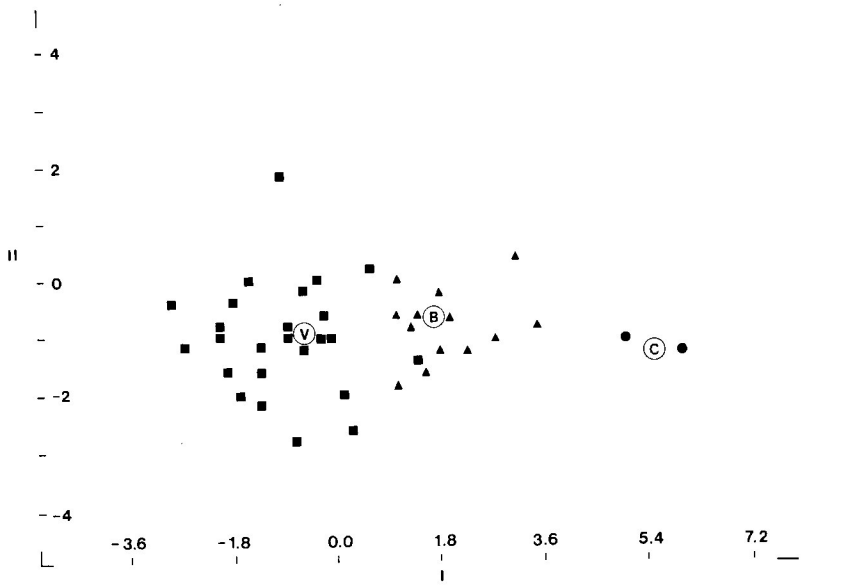
The old age category of *A. varius* was significantly larger in size than other samples in head-body length and weight. The samples of old and adult *A. varius* were significantly larger than all other samples in length of tail, condylobasal length, palatal length, and diastema.

Clearly, using univariate analysis, these three phenetic groups can be distinguished, especially when samples of equivalent age are considered.

In addition to the distinct differences in size of the three groups, the individuals of the sample we consider to be *A. varius* all have some white hairs on the chin. Some individuals have extensive white areas (hairs white to their bases) on the chin, throat, and chest; the amount being individually and perhaps geographically varible. Others have only a small, white spot on the chin. In contrast, specimens of *A. boliviensis* and *A. caenosus* have buffy or buffy-gray ventral parts without any white spots.

Multivariate Analysis

The same 11 samples used above were analyzed using discriminant function/canonical analysis. Characters utilized in this analysis are listed from the most useful to the least useful in discriminating groups (Table 2). Variate I accounts for 78.4% of the total dispersion, and Variate II accounts for 8.6%. The character with the highest positive canonical coefficient for Variable I was diastema length (0.262) and those with high negative values were interorbital breadth (−1.156) and


4
2
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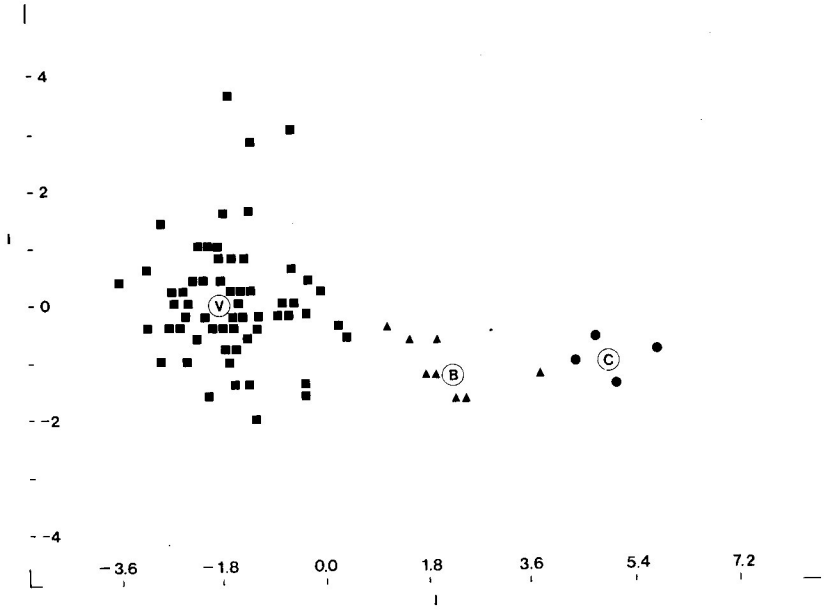
-4
-3.6
-1.8
0.0
1.8
3.6
5.4
7.2
V
B
C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-3.6
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V
B
C

Table 3.—*Chromosome characters for three species of* Akodon *from northwestern Argentina. A = acrocentric; BA = biarmed; FN = total number of autosomal arms; M = metacentric; SM = submetacentric; ST = subtelocentric.*

Species	N ♂	N ♀	2n	FN	Autosome structure A	Autosome structure BA	Gonosome structure X_1	Gonosome structure X_2	Gonosome structure Y
A. caenosus	1		34	40	24	8	ST		BA
A. caenosus		1	34	40	24	8	ST	ST	
A. boliviensis	3		40	41	35	3	A		BA
A. boliviensis		1	40	41	35	3	A	A	
A. boliviensis		2	40	41	35	3	A	M	
A. boliviensis		1	40	40	36	2	SM	A	
A. boliviensis		1	40	40	36	2	SM	SM	
A. boliviensis		2	40	40	36	2	SM	M	
A. varius	3		42	42	38	2	A		BA
A. varius		6	42	42	38	2	A	A	
A. varius	3		41	42	37	3	A		BA
A. varius		1	41	42	37	3	A	A	

length of maxillary toothrow (−0.278). In Variate II, high positive canonical coefficients were exhibited by interorbital breadth (1.838) and length of maxillary toothrow (0.600), and high negative values were exhibited by diastema length (−0.777) and palatal length (−0.355).

When all samples were plotted simultaneously on the first two canonical variates, there were no major isolated groups and the samples were extremely difficult to separate. However, when samples of equivalent age were compared the groups are easily separated (Fig. 6). This indicates that the groups seen with some of the individual characters are also revealed when all characters are considered simultaneously. This analysis also shows that it is important to consider the chronological age of specimens when making taxonomical determinations in the genus *Akodon*.

Karyotypic Analysis

Basic karyotypic data and a summary of variation in chromosome structure are presented in Table 3. Representative karyotypes are shown in Figs. 7, 8, and 9. Descriptions of karyotypes follow:

←

Fig. 6.—Two-dimensional plots of the first two canonical variables for old (upper) and adult (lower) individuals of three species of *Akodon* from northern Argentina. Squares equal *A. varius*; triangles equal *A. boliviensis*; circles equal *A. caenosus*. The open circles containing letters mark the positions of the sample means.

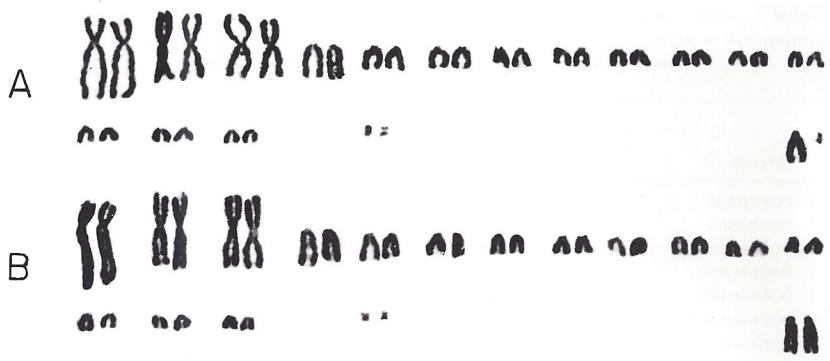

Fig. 7.—Karyotypes of *Akodon caenosus* from El Cadillal, Tucumán Province, Argentina. A = male CM 43381; B = female CM 43379. Sex chromosomes are the last pair at the lower right side of each karyotype.

Akodon caenosus (Fig. 7).—Karyotypic data were available for only two specimens. Both specimens had identical appearing autosomes consisting of a large, submetacentric pair (pair 1), two large metacentric pairs (pairs 2 and 3), one very small metacentric pair (pair 16), and 12 pairs of acrocentrics (pairs 4 through 15). The autosomes of pair 4 are considerably larger than pair 5. Pairs 5 through 15 formed an evenly graded series, making identification of homologs equivocal. The X chromosomes are medium-sized (similar in size to autosome pair 4), and subtelocentric. The Y chromosome is biarmed, and is similar in size and structure to autosome pair 16.

Akodon boliviensis (Fig. 8).—Two autosomal variants and three centromeric positions on the X chromosomes were noted among the 10 individuals examined (Table 3). Observed autosomal variation involved only pair 1. Six individuals are heteromorphic for pair 1, with one large acrocentric and one large subtelocentric chromosome (Fig. 8*a* and *b*). Four individuals are homomorphic for pair 1, exhibiting two large acrocentric chromosomes (Fig. 8*c*). In all six cases with heteromorphic pairs, the large biarmed element is approximately 145 to 150% of the length of the acrocentric member of the pair. Other autosomes form a graded series of acrocentrics from pairs 2 through 18. The smallest pair of autosomes are metacentric.

All of the seven females examined have X chromosomes of nearly equal lengths. Centromere positions varied, however, with acrocentric, submetacentric, and metacentric positions being represented in the sample. Two individuals have X chromosomes with the same centromere positions—acrocentric (not illustrated) and submetacentric

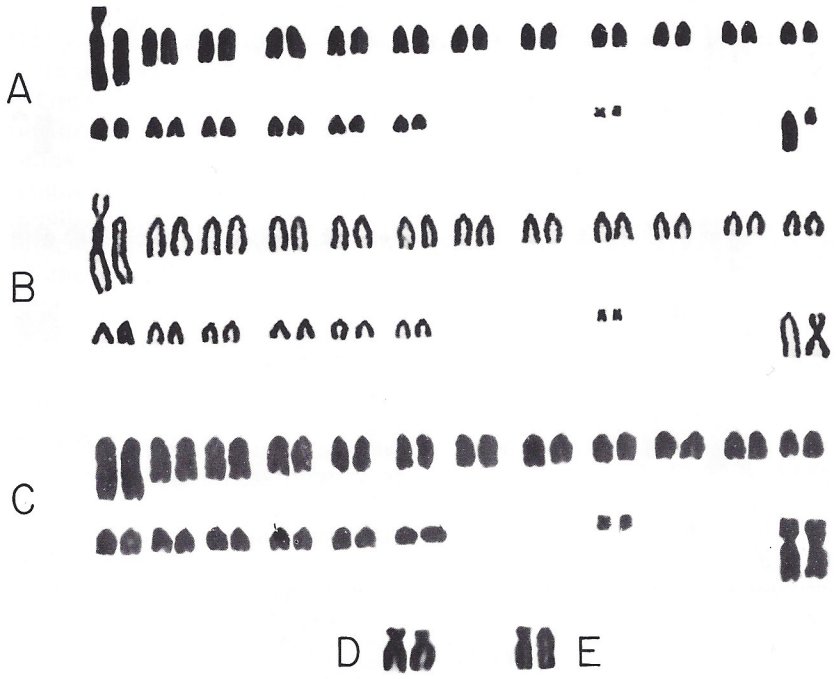

Fig. 8.—Karyotypes of *Akodon boliviensis tucumanensis* from Argentina. A = male CM 43183 and B = female CM 43182 from 3 km WNW Concepcion, Catamarca Province; C = female CM 43158 from Rio Andalgalá, 3.5 km NW Andalgalá, Catamarca Province; D = female CM 43382 from El Cadillal, Tucumán Province; E = female CM 43154 from El Potrero Dike, 13 km N Andalgalá, Catamarca Province. Sex chromosomes of A, B, and C are the pairs on the lower right sides of the karyotypes; for D and E, only the X chromosomes are presented—the autosomes are identical in structure to C.

(Fig. 8*d*). Two individuals have one acrocentric X and one metacentric X (Fig. 8*b*), two have a combination of metacentric and submetacentric (Fig. 8*c*), and one has a combination of submetacentric and acrocentric positions (Fig. 8*e*).

The three males examined have acrocentric X and small, biarmed Y chromosomes.

Akodon varius (Fig. 9).—Variations in autosome structure and numbers were noted. Nine individuals have terminal centromeres on autosome pair 1 (Fig. 9*a* and *b*), and a 2n of 42. Four individuals have one submetacentric and one acrocentric chromosome in pair 1 (Fig. 9*c*). Those individuals with a heteromorphic pair also have an un-

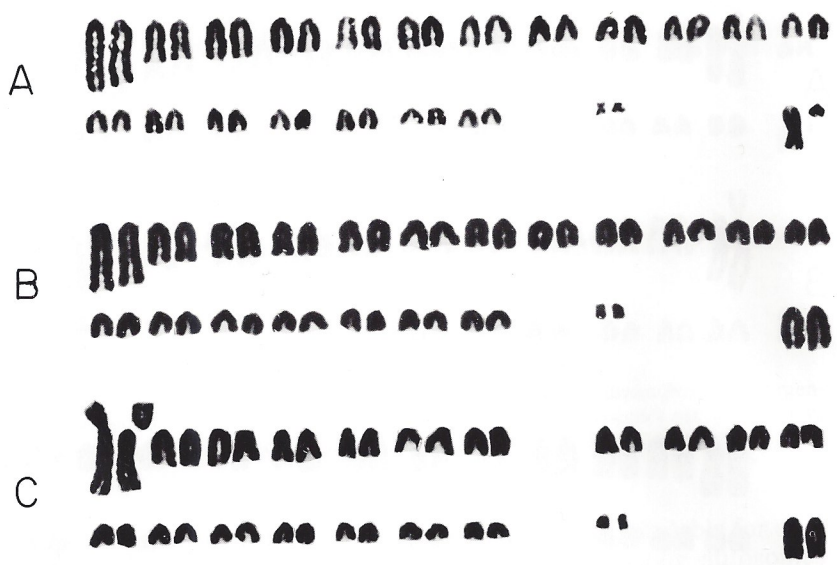

Fig. 9.—Karyotypes of *Akodon varius simulator* from Argentina. A = male CM 43385 from El Cadillal, Tucumán Province; B = female CM 43157 and C = female CM 43156 from Rio Andalgalá, 3.5 km NW Andalgalá, Catamarca Province. Sex chromosomes are the pairs on the lower right side of the karyotypes.

matched, medium-sized, acrocentric autosome and a 2n of 41. Other autosomes are acrocentric except for the smallest pair (pair 20), which are metacentric.

The X chromosomes are acrocentric and the Y is small and biarmed (submetacentric or subtelocentric).

DISCUSSION

The genus *Akodon* (*sensu lato*) contains a great number of named forms which exhibit a relatively high degree of structural uniformity. Most variation is slight, and involves continuous character gradients such as body size and proportions, size and robustness of claws, degree of procumbency of incisors, inflation of auditory bullae, length of pelage, degree of hypsodonty of molars, and others. The range of structural variation, while relatively small, is as great or greater within some species as between some genera (*sensu* Reig, as cited in Bianchi et al., 1971) of akodonts (see Thomas, 1916*a*). Although akodonts are quite similar to microtines (Muridae, Microtinae) in general appearance and superficial habits, their molars are not ever-growing and the

molar cusps quickly wear away. The amount of wear on the molars is a convenient guide to age classes, but the wear generally renders the teeth useless for identification of species.

Growth in most body dimensions of *Akodon* spp. appears to continue for considerable time after sexual maturity is attained (Table 1). Many dimensions representative of size, such as head and body length, length of hind foot, weight, greatest length of skull, condylobasal length, and zygomatic breadth vary significantly with age, and are typically unreliable for identifying species. Characters such as length of the maxillary toothrow, breadth of braincase, and interorbital breadth approach adult size earlier in ontogeny (Table 1) and vary less among the older age classes (that is, subadult, adult, and old adult), and hence are more reliable for identification of species. For pairs of species differing principally in size, characters such as the latter are generally useful for identification even when specimens of different ages are compared. External measurements and proportions are typically unreliable unless relative age can be determined. This is seldom possible with akodonts in the field, as pelage of subadults is generally not distinctive, and sexually active individuals may differ substantially in age.

Initial examination of the sample of *Akodon* reported on here suggested continuous variation in both body size and chromosome structure. It is apparent from the more detailed morphometric analyses, however, that three distinct phenetic groups are included. We believe that the evidence best supports a hypothesis that each group represents a different species.

This hypothesis is further supported by the karyotypic data (Table 3). Although karyotypes of additional specimens are needed to clarify the nature and extent of variation in chromosome structure, we are confident that additional data will not alter our general conclusions.

The differences in the basic *A. boliviensis* karyotype (2n = 40, FN = 40) and that of *A. caenosus* (2n = 34, FN = 40), can be explained solely by centric fission/fusion processes (Robertsonian variation). Bianchi et al. (1979) found continuous Robertsonian variation in *Akodon dolores* Thomas from 2n = 34 to 40 (FN = 44). Furthermore, they reanalyzed material previously reported (Bianchi et al., 1973) for *A. molinae* (Contreras), and found that chromosome arms of *A. dolores* and *A. molinae* were identical in G-banding patterns. Individuals of *A. molinae* have 2n = 42, 43, or 44, and FN = 44. No convincing evidence has been offered to indicate that *A. dolores* and *A. molinae* are separate species. Nevertheless, the range of Robertsonian variation exhibited by the *A. dolores/molinae* complex is pronounced, but none of our karyotypes of *A. caenosus, A. boliviensis,* or *A. varius* falls directly within that range. *Akodon caenosus* and *A. boliviensis* have

three to four fewer autosome arms (one pair of biarmed autosomes or two pairs of uniarmed autosomes), requiring different chromosomal rearrangements from a common ancestral karyotype for the two groups. Similarly, the karyotype of *A. varius* differs from *A. dolores* and *A. molinae* in having two less autosomal arms.

The origin of the biarmed autosome (pair 1) of *A. boliviensis* is assumed to have resulted from a Robertsonian process. The existence of specimens with the same diploid number (40) but with acrocentrics comprising pair 1, together with the fact that the long arms of pair 1 are the same size in all specimens, suggests that the variation in karyotypes derives from a combination of Robertsonian and deletion processes. The direction of the change (that is, fission or fusion) cannot be unequivocally determined. It seems more likely that a fission process, isolating the short-arm fragment from its centromere, would result in loss of the short arm during meiotic assortment; hence we favor this explanation. A fusion process would not disturb the integrity of the centromere of the unfused acrocentric element and its loss would not be expected. In either case, individuals with FN = 42 (biarmed elements in pair 1) should be present in the population. Their absence is not too surprising in view of the small sample size, but it is possible that individuals homozygous for the biarmed condition are not viable.

Bianchi et al. (1979) felt that their evidence from studies of *A. dolores* and *A. molinae* favored centric fissioning to explain similar polymorphisms in those species.

Variation in the X chromosomes of *A. boliviensis* seems to involve only inversions. All of the X chromosomes are the same relative length, regardless of centromere position. Bianchi et al. (1971) reported gross deletions from the X chromosomes of *Akodon azarae* and *A. boliviensis,* resulting in heteromorphic pairs of X's. The X chromosomes with deletions were small, with subterminal centromeres. We found no such variation in our sample of *A. boliviensis*.

We consider the Y chromosomes of *A. caenosus, A. boliviensis,* and *A. varius* to be biarmed. We doubt, however, that there is any difference in the structure of the Y chromosomes reported here and those of *A. boliviensis tucumanensis* and *A. varius simulator* described by Bianchi et al. (1971), who indicated the Y's were acrocentric. The Y is a very small chromosome, and the second arm is not apparent in all cells. Whether or not we have interpreted its structure correctly cannot yet be determined.

The karyotypes of *A. varius* present a different pattern of variation than that of *A. boliviensis* and *A. caenosus* (Table 3, Fig. 9). The basic karyotype appears to be 2n = 42, FN = 42, with all autosomes except the smallest pair (20) being acrocentric. Just as in *A. boliviensis,* heteromorphism was found in the largest autosome pair (pair 1, Fig. 9*c*).

Unlike *A. boliviensis,* however, there was an odd number of acrocentric autosomes, with an unmatched chromosome corresponding to the short arm of the biarmed member of pair 1 (positioned next to and above the acrocentric member of pair 1 in Fig. 9*c*). There are two plausible explanations for this chromosomal polymorphism: 1) a Robertsonian fusion or fission mechanism; or 2) a hybridization between individuals of *A. boliviensis* with a single biarmed chromosome in pair 1 (2n = 40, FN = 41) and *A. varius* with an acrocentric member in pair 1 (2n = 41, FN = 42). Such a mating would produce offspring with 2n = 41, FN = 42. Hybridization cannot be ruled out, but it seems less likely because it would appear to involve only individuals of *A. boliviensis* with an unmatched biarmed chromosome and with acrocentric X chromosomes. Until larger samples are obtained and further studies are carried out, this issue cannot be resolved.

The *A. varius* karyotypes differ from those reported by Bianchi et al. (1971) from Mendoza and Tucumán provinces, which had 2n = 40, FN = 40, with submetacentric X's and acrocentric Y's. We doubt that Bianchi et al.'s (1971) concept of *A. varius* is the same as ours. Gardner and Patton (1976) also reported a 2n = 40, FN = 40 karyotype for *A. varius* from Paraguay. Bianchi et al. (1971) presented a karyotype of *A. illuteus* (Thomas) from Villa Nougues, Tucumán Province, which appears identical to our *A. varius* karyotype in Fig. 9*c*. Villa Nougues is very near our two principal localities for *A. varius,* Horco Molle and El Cadillal, and the habitat is essentially identical to Horco Molle. It is also the type locality for *A. varius simulator* (Thomas, 1916*b*). Thomas (1925*b*) originally listed the type locality of *Abrothrix* (=*Akodon*) *illutea* as Concepción, 400 m, Tucumán Province. He later (Thomas, 1929) amended the type locality for *A. illuteus* to Aconquija, 3,000 to 4,000 m, Tucumán Province. Members of the *Abrothrix* group are distinguished by long pelage—they are basically adapted to cool and cold climates in southern Argentina and Chile, and in the high Andes in more subtropical and temperate latitudes. Perhaps Bianchi et al.'s (1971) identification is in error; most probably their specimen is *A. varius,* based upon its karyotype and the subtropical habitat at Villa Nougues. Further support for this opinion was offered by Spotorno and Fernandez (1976), who noted that karyotypes of *Abrothrix* and other akodonts adapted to cool or cold environments had high diploid numbers [>44, most with 52; for example, *A. jelskii* (Thomas), *A. longipilis* (Waterhouse), *A. olivaceus* (Waterhouse), and *A. xanthorhinus* (Waterhouse)]. This is not to imply that high diploid numbers are an adaptation to cold environments—rather, the true phyletic relationships among akodonts may cut across current taxonomic groups. Karyotypic, geographic, and environmental continuity among these species may express phyletic relationships.

Our knowledge of intra- and interpopulational variation, and variation within and among groups of akodont species, is too fragmentary to make generalizations about interspecific relationships. Indeed, at this stage we must concentrate on determining the number, distribution, and specific nomenclature of akodonts. From the several names that could potentially apply to the taxa in our study, we have chosen the three which most closely fit the species descriptions, geographic distributions, and habitats of the type localities. We expect that ultimately some of these names will be shown to be synonyms of earlier named and more widely-ranging species or subspecies.

Akodon caenosus Thomas, 1918, was originally described as a subspecies of *A. puer* (Thomas). The type locality is at León, 1,500 m, Jujuy Province, Argentina. Thomas (1920) subsequently elevated *caenosus* to species rank after examining additional specimens. Later, Thomas (1926) noted that some specimens he had included in an earlier characterization (1920) were instead *A. boliviensis tucumanensis*. Some measurments (in mm) of the holotype of *A. caenosus* (adult male) as presented by Thomas (1918), follow: lengths of head and body 82, tail 72, hind foot 20, ear 16 and skull (tip of nasals to back of interparietal) 18, zygomatic breadth 11.3, palatilar length 10.2, length of upper molar toothrow 3.6, length of nasals 9, and interorbital breadth 4.6. These measurements all fall within the range of values for *A. caenosus* in Table 1, except for interorbital breadth, which is 0.2 mm greater than the maximum recorded in our sample. The undersides of *A. caenosus* were characterized by Thomas (1918) as dull "pinkish buff." No other described taxon fits the physical description and corresponds with the geographic range and general habitat of our sample. We are confident that these specimens from Jujuy and Tucumán, Argentina are *A. caenosus*. We have no insight, however, into the species' wider distribution or broader systematic relationships.

Akodon boliviensis tucumanensis J. A. Allen, 1901 was described as a new species. The type locality is [San Miguel de] Tucumán, 450 m, [Tucumán Province], Argentina. Cabrera (1961) first treated *tucumanensis* as a subspecies of *A. boliviensis*. Selected measurements of the holotype (adult female), as given by Allen (1901), were: lengths of head and body 81, tail 59.5, hind foot 17.5, ear 15 and skull 24, zygomatic breadth 12, length of upper molar toothrow 4, length of nasals 8, interoribital breadth 5.2, and width of braincase 11.2. Overall, these measurements fit best with our sample of *A. boliviensis*, although some are slightly smaller and others are slightly larger than the ranges of values in our sample. Allen (1901) characterized the underparts as "buffy gray varying to strong buff," and, in another place in the description, as "pale buffy gray." This description corresponds closely to our sample of *A. boliviensis*. As the type locality is within 15 to 20

km, and is at essentially the same elevation as our principal collecting sites, we feel that there is little doubt about the identity of our sample.

Akodon varius simulator Thomas, 1916*b*, was also described as a distinct species. The type locality is Villa Nougues, San Pablo, 1,200 m, Tucumán Province, Argentina. Thomas (1925*a*) later indicated that *simulator* might be a subspecies of *A. varius* Thomas, 1902, from Tapacari, 3,000 m, west of Cochabamba, Bolivia. Subsequently, he (Thomas, 1926) used the trinomial *A. varius simulator* for specimens from Tucumán Province. Selected measurements (in mm) for the holotype (adult male), as recorded by Thomas (1916*b*), were: lengths of head and body 98, tail 79, hind foot 24, ear 18, skull 28.5, zygomatic breadth 14.7, palatilar length 12.6, length of upper molar toothrow 4.9, length of nasals 10.2, interorbital breadth 4.6, breadth of braincase 12.2. These measurements correspond with our sample of *A. varius* (Table 1).

Thomas (1916*b*) noted that the color of the ventral surface was "buffy or drabby whitish," and remarked on "its peculiar white chin" which he stated was unique (subsequently, he described other species with white chin spots). Our specimens correspond precisely with the description of *A. v. simulator,* leaving no doubt as to their identity.

SPECIMENS EXAMINED

Numbers of specimens examined cytologically are listed in parentheses immediately following total numbers of males and females examined. All specimens are deposited in the Section of Mammals, Carnegie Museum of Natural History.

Akodon caenosus (18).—ARGENTINA. *Jujuy*: Yala Lagunas Road, W of junction with Highway 9, 5 ♂, 2 ♀. *Tucuman*: El Cadillal, 3 (1) ♂, 2 (1) ♀; Horco Molle, 15 km W San Miguel de Tucumán, 3 ♂, 3 ♀.

Akodon boliviensis (59).—ARGENTINA. *Catamarca*: 0.5 mi N Andalgalá, 1 ♀, 3 km WNW Concepción, 1 (1) ♂, 1 (1) ♀; 3.5 mi N Andalgalá on Rio Andalgalá, 3 (1) ♀; El Potrero Dike, 13 km N Andalgalá, 1 (1) ♀; La Toma, 6.5 km N (by road) Highway 63 on La Toma Road, 1 ♂. *Salta*: Dept. Orán, 24 km N Agua Blanca, 9 (2) ♂, 9 (2) ♀. *Tucumán*: El Cadillal, 11 ♂, 14 (2) ♀; Horco Molle, 15 km W San Miguel de Tucumán, 2 ♂, 6 ♀.

Akodon varius (160).—ARGENTINA. *Catamarca*: 0.5 mi N Andalgalá, 5 ♂, 18 (2) ♀; 3.5 mi N Andalgalá on Rio Andalgalá, 2 (2) ♀; El Potrero Dike, 13 km N Andalgalá, 1 ♂; 23 km SW (by Road 60) Chumbicha, 1 (1) ♂; La Toma, 6.5 km N (by road) Highway 63 on La Toma Road, 2 (1) ♂. *Tucumán*: El Cadillal, 37 (4) ♂, 46 (3) ♀; Horco Molle, 15 km W San Miguel de Tucumán, 25 ♂, 23 ♀.

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