

MISCELLANEOUS PUBLICATIONS
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, NO. 177

**A Review of the *Boliviensis* Group of
Akodon (Muridae: Sigmodontinae), with
Emphasis on Peru and Bolivia**

by

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MUSEUM OF ZOOLOGY, THE UNIVERSITY OF MICHIGAN
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ABSTRACT

Myers, P., J. L. Patton, and M. F. Smith. 1990. A review of the boliviensis group of *Akodon* (Muridae: Sigmodontinae), with emphasis on Peru and Bolivia. *Misc. Publ., Mus. Zool., Univ. Michigan.* 177:1-104, figs. 1-29. We recognize the *Akodon boliviensis* group as an informal assemblage of species including *Akodon boliviensis* (western Bolivia and Puno Department, Peru), *Akodon puer* (subspecies *caenosus* in northwestern Argentina and southern Bolivia, *puer* in central Bolivia, and *lutescens* in Puno Department, Peru and La Paz Department, Bolivia), *Akodon subfuscus* (subspecies *subfuscus* in southeastern Peru and La Paz Department, Bolivia; also a new subspecies from southwestern Peru), and *Akodon* n. sp. (central Peru). We further suggest that *Akodon spegazzinii* (subspecies *spegazzinii* and *tucumanensis*) from northern Argentina may be a member of this group. *Akodon pacificus* is shown to be a synonym of *A. boliviensis*. The *boliviensis* group is diagnosed by a combination of characters including small size, delicate cranium, narrow and straight-sided mesopterygoid fossa, hourglass-shaped interorbital region, and dull brown fur without contrastingly colored areas.

Descriptions of included species and subspecies are provided. Traditional cranial, dental, and external characters are used in combination with electrophoresis and anatomical features of the soft palates, male reproductive tracts, and hind feet to recognize and diagnose species. Treatment of age-related variation is particularly important to distinguish these species; we document qualitative and quantitative changes in cranial morphology with age (toothwear class) and use regression to allow comparison of individuals of different ages.

We tentatively propose that *subfuscus*, *puer*, and the new species form a clade with *boliviensis* as its sister group. This hypothesis cannot be subjected to formal test, however, until the condition of relevant characters in potential outgroups is better understood.

Key words: *Akodon*, *boliviensis*, *puer*, *caenosus*, *lutescens*, *subfuscus*, *pacificus*, *tucumanensis*, *spegazzinii*, *alterus*, *azarae*, *juninensis*, *arequipae*, *Peru*, *Bolivia*, *Argentina*, *Rodentia*, *Sigmodontinae*, *South America*, *systematics*, *taxonomy*, *electrophoresis*, *ontogenetic variation*.

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INTRODUCTION

The genus *Akodon* is one of the largest, most complex, and taxonomically most poorly understood groups of South American muroid rodents. Over 90 taxa were assigned to the genus by Tate (1932), while Ellerman (1941) allocated 85 names to 62 species in *Akodon*. More recently, Cabrera (1961) recognized only 38 species of *Akodon*, 21 within the nominate subgenus, and Honacki *et al.* (1982) reduced the number of species to 33, an estimate that is clearly conservative.

Within *Akodon*, a number of subgroups have been identified. Some have been recognized formally as subgenera (see recent summaries in Honacki *et al.*, 1982, and Reig, 1987), while others have been given the informal status of species groups—assemblages of morphologically similar and possibly related species (*e.g.*, Myers, 1989; Myers and Patton, 1989a; Hershkovitz, in manuscript). The composition of these groupings varies considerably from author to author, and few analyses of species limits and geographic variation have been undertaken for any of the taxa recognized within these groups (for exceptions, see Myers, 1989, and Macedo and Mares, 1987). The lack of adequate descriptions of species and the resulting lack of agreement as to the limits and relationships of species within *Akodon* have been an impediment to investigations of virtually all aspects of the biology of these common animals, including their ecology, behavior, cytology, and physiology as well as systematics and biogeography.

In this paper, we focus on the characterization and diagnosis of members of what we refer to as the “*boliviensis* group” of species of the nominate subgenus *Akodon*. This group includes the type species of the genus, *Akodon boliviensis* Meyen 1833, a taxon that we shall demonstrate is, as currently viewed, a composite of several sympatric or contiguously allopatric species. Members of this group are small, brown mice with delicate skulls that inhabit grasslands at high elevation in the Altiplano from central Peru to northwestern Argentina, and perhaps into the pampas of central Argentina at lower elevations. Our emphasis in this paper is on the northern areas occupied by the *boliviensis* group, mainly central and southern Peru and adjacent areas in Bolivia. This is the area where our own fieldwork has centered and where the largest series of specimens are available for examination. We shall refer, however, to samples from other areas in southern Bolivia and northern Argentina.

Our goal in this paper is to characterize species limits rather than to elucidate phylogenetic relationships among the species recognized or between this “group” and others within the genus. In characterizing the *boliviensis* complex, we do not necessarily imply that the group is a monophyletic assemblage, or that the taxa we consider as members are the only ones. Decisions with regard to these points must await a more thorough evaluation of the genus and its component parts.

Ellerman (1941) also referred to an assemblage of species in the subgenus *Akodon* as the “*boliviensis* group.” Our usage of this term, however, is

more restricted. Ellerman placed fully two-thirds of all species he recognized in the subgenus *Akodon* in this group and contrasted it only with an *Akodon* "urichi" species complex. Hershkovitz (in manuscript) uses "bolivien-sis group" to refer to 11 species of the subgenus *Akodon* united by small size. Our usage is similar to his, but he includes several species we have not studied.

METHODS AND MATERIALS

Our analyses include the standard ones traditionally used to define rodent taxa (qualitative and quantitative description of the external body, pelage, cranium, and teeth), but we also rely heavily on variation in aspects of the internal soft anatomy (particularly the alimentary canal and male reproductive system), comparative karyology, and on examination of electromorphic characters from representative geographic samples of each taxon we recognize. The methods used for each aspect of the study are defined here, and a list of all specimens examined is given in Appendices I and II.

In all sections that follow, we usually refer to members of the genus *Akodon* by their specific epithet alone for convenience and brevity. Reference to members of other genera will be by the full binomial.

CRANIAL AND EXTERNAL MORPHOLOGY

Specimens from the following museums were examined: American Museum of Natural History (AMNH); Academy of Natural Sciences, Philadelphia (ANSP); British Museum (Natural History) (BMNH); Carnegie Museum of Natural History (CM); Field Museum of Natural History (FMNH); The Museum, Michigan State University (MSU); Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); University of Michigan Museum of Zoology (UMMZ); Zoological Museum, University of Montana (UMZ); Museum of Southwestern Biology, University of New Mexico (MSB); Swedish Royal Natural History Museum (RNHMS); and U.S. National Museum of Natural History (USNM).

Four external and 20 cranial dimensions were recorded for each specimen. Cranial dimensions were measured to 0.1 mm by means of dial or digital calipers. Each measurement is given with the abbreviation used in the text and figures, as follows:

Total length, TOTAL: taken from skin tag.

Tail length, TAIL: taken from skin tag.

Hind foot length, HF: taken from skin tag.

Ear length, EAR: taken from skin tag.

Condylolincisive length, CIL: distance from anterior edge of upper incisors to posterior face of occipital condyles.

Zygomatic breadth, ZB: greatest distance between the outside margins of the zygomatic arches (in *Akodon*, usually near the squamosal root).

Braincase breadth, BB: greatest breadth of the braincase at a point just superior to the zygomatic root of the squamosal.

Interorbital constriction, IOC: least distance across the interorbital region.

Rostral length, RL: diagonal distance from the anterior margin of the orbit to the anterior tip of the nasals.

Nasal length, NL: length of the nasal bones measured at the midline.

Rostral width, RW: breadth of the rostrum across the nasolacrimal capsules.

Mid-rostral width, RW2: breadth of the rostrum measured at the top of the arc formed by the roots of the incisors as they pass posteriorly. This arc is visible as a raised curve along the rostral walls.

Orbital length, OL: the greatest longitudinal distance across the inside of the orbit.

Diastema length, DL: length of the diastema from the posterior margin of the upper incisors to the anterior margin (root) of M¹.

Maxillary toothrow length, MTRL: greatest length of the upper tooth row taken at the alveolus.

Incisive foramen length, IFL: greatest length of the incisive foramen.

Alveolar width, AW: width of the palate measured across the labial margins of the alveoli of right and left M¹s.

Occipital condyle width, OCW: width across the occipital condyles.

Mastoid breadth, MB: breadth of the braincase measured across the mastoid processes.

Basioccipital length, BOL: length of the basioccipital along the ventral midline of the cranium.

Mesopterygoid fossa length, MFL: length from the anteriormost palatal margin to the posterior extent of the hamular processes.

Mesopterygoid fossa width, MFW: width of the fossa at the point where the palatines contact the pterygoids (in these species, approximately halfway down the length of the mesopterygoid fossa).

Zygomatic plate depth, ZP: greatest longitudinal distance, taken at approximately mid-height.

Cranial depth, CD: depth of skull, measured by placing the skull on a glass slide, measuring the distance from the bottom of the slide to the top of the cranial vault, and subtracting the thickness of the slide.

Statistical calculations were performed using the Michigan Interactive Data Analysis System (MIDAS). Descriptions of specific techniques used are provided below, as are the variables included in each analysis. Capitalized color terms are from Ridgway (1912).

AGE AND SIZE

The relative age of each specimen was estimated by the wear on its teeth. Specimens were placed in one of five age (toothwear) classes established following Myers (1989). Briefly, age classes 1 and 2 comprise young animals with unworn or lightly worn teeth. Age classes 3 to 5 are made up of individuals with progressively more worn teeth, with the extreme (age class 5) made up of those individuals with completely featureless, "dished out" molars. Sexual maturity appears to be attained by most animals during age class 2.

Most cranial dimensions increase throughout the lives of these animals, and inevitable differences in age composition complicate comparisons of populations. Most variables, however, appear to increase in an approximately linear fashion between age (toothwear) classes 2 and 5 (this pattern is discussed under Age Variation, p. 25), suggesting that regression might be used to "adjust" the measurements of each specimen statistically so that all individuals appear as if they were measured at the same age class. To accomplish this for each taxon, we regressed measurements for each variable on age (age classes 2–5) and used the resulting regression coefficients to adjust measurements of each specimen to a single age class (we arbitrarily chose age class 4). No adjustment was made for variables with nonsignificant regression slopes. These age-corrected measurements of individuals were then used when appropriate to compare populations within a species, and the age-corrected measurements presented below can be interpreted as an estimate of each measurement in animals of age class 4.

The advantage of this technique is that it permits simultaneous quantitative comparison of individuals that differ in age, insofar as age is reflected by toothwear class. It fails when size does not increase approximately linearly with toothwear class. Nonlinear increase in size with increasing age class was found consistently in only one of the taxa treated below, and the treatment of those samples will be described in the discussion of that taxon (a new subspecies of *Akodon subfuscus* from western Peru). The method also requires a reasonable total number of specimens, distributed similarly in each taxon among the four included age classes, for estimating the slope of each measurement on age. For most but not all taxa, the majority of individuals fell into classes 3 and 4. To insure that unequal representation of age classes in different samples introduced no bias into the procedure for age correction, we restricted the number of specimens in each age class of each taxon to the number of specimens present in the age class that contained the fewest individuals. Thus, if age class 5 contained only 17 individuals, we randomly selected 17 individuals each from age classes 2, 3, and 4, and performed the regression of each variable on age class using these $17 \times 4 = 68$ individuals. The resulting regression coefficients were then used to adjust the measurements of each variable for *all* specimens of that taxon.

As a check on the effectiveness of the technique in reducing age-related

TABLE 1.—Percent variation explained by toothwear class before and after age correction. Asterisks indicate significance levels for differences among toothwear classes for each measurement (ANOVA; * $p < 0.05$; ** $p < 0.01$). The percentages given are for *Akodon boliviensis*, age classes 2-5 ($n = 367$).

	before	after
CIL	68.5**	4.3**
ZB	51.8**	0.5
BB	4.0**	1.3
IOC	2.2*	0.0
RL	66.8**	1.5
NL	58.7**	0.0
RW	45.8**	0.9
RW2	37.6**	0.4
OL	57.1**	4.7**
DL	61.0**	3.1*
MTRL	20.6**	1.3
IFL	43.5**	0.8
AW	33.2**	0.7
OCW	7.3**	0.0
MB	27.6**	4.3**
BOL	50.2**	1.6
MFL	48.8**	0.1
MFW	6.1**	1.5
ZP	44.8**	0.0
CD	5.8**	0.0

variation, we performed analyses of variance for each measurement for each taxon before and after age adjustment took place (Table 1, Fig. 1). Means for each age class were compared. Before adjustment, up to nearly 70% of the variation in each measurement could be attributed to age class. Values over 50% were common. After adjustment, this value fell to between 0% and 5%, and differences among age classes were usually not statistically significant. The growth pattern of typical measurements and the effectiveness of the adjustment in eliminating variation attributable to age is shown in Fig. 1.

Our use of this technique will be discussed further in the section on Sex and Age Variation, p. 25, and in the accounts of species.

ALIMENTARY CANAL AND MALE REPRODUCTIVE ORGANS

Dissections were made of specimens preserved in formalin and stored in alcohol to describe the rugae of the soft palate and the morphology of the stomach. Terminology follows Carleton (1973, 1980). Similarly, the reproductive tracts of adult males were dissected to describe the anatomy of the accessory reproductive glands, following Voss and Linzey (1981). Penial morphology was examined both from study skins and from specimens maintained in fluid. The methods for treatment of either type differed, as follows:

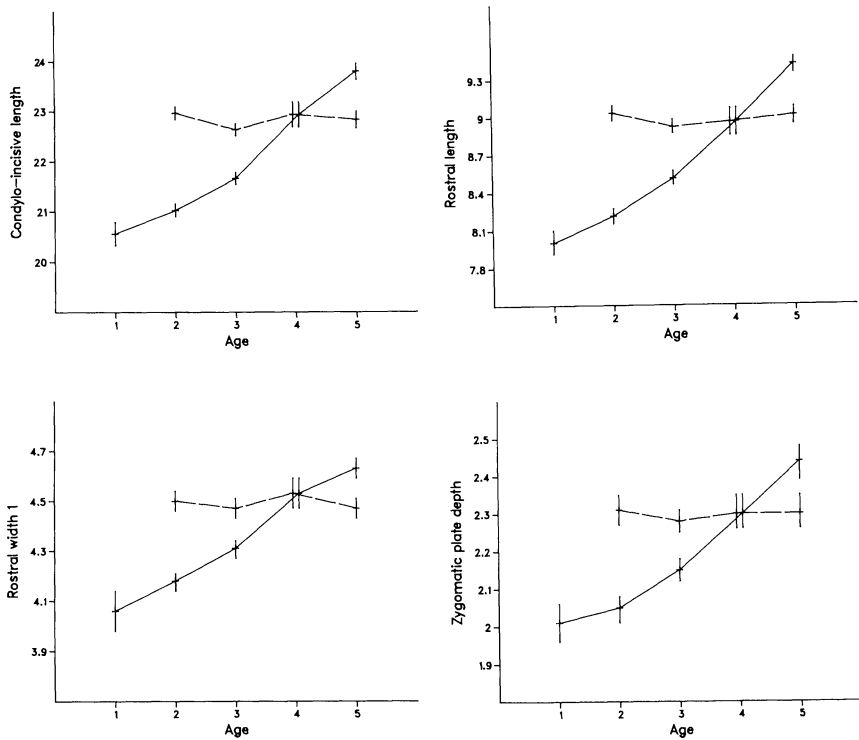


FIG. 1. Size *vs.* age (toothwear class) for four cranial dimensions. Solid curve for each plot shows average value of the measurement for each age class; dashed curve shows means after adjusting values to remove the effect of increasing age (toothwear class). See text for explanation.

For specimens preserved in fluid, the glans was dissected carefully from the prepuce, stained lightly (1–3 hours) with 0.3% alizarin, and photographed using a Wild M-7 stereozoom microscope and Kodak Panatomic-X film. Dissected glandes were maintained in 70% ethanol. Material processed in this fashion retains its natural shape and remains pliable, the epidermis remains intact, and all external and crater structures are made readily visible by superficial staining. These specimens permit detailed observations free of the distortion that normally results from clearing and staining dried phalli. Observations included general glans shape, surface features such as grooves and spines, details of the crater lip area, height of the lateral and medial bacular mounds, and characteristics of the urethral flaps and dorsal papilla (for terminology, see Hooper and Musser, 1964; Lidicker, 1968).

Dried phalli were removed from skins and soaked in distilled water from one to three days to reconstitute them. They were then lightly stained with alizarin, as above, and observations of surface features were made. The reconstituted organ retains much of its natural shape when compared to

those originally preserved in formalin, but details are less readily observable as the epidermis sloughs easily and warping is likely.

After initial observation, the glans was cleared in 0.2% KOH for from one to four days, stained in 0.3% alizarin, and then passed through daily soakings in 25%, 50%, and 75% glycerin prior to storage in glycerin with thymol crystals added to prevent mold growth. All observations on the baculum were made from these cleared specimens.

KARYOLOGY

Chromosome preparations were made using modifications of the basic colchicine and hypotonic citrate technique of Patton (1967). For specimens karyotyped prior to 1984, slides were made in the field by flame drying; more recent materials were prepared from cell suspensions that had been fixed in Carnoy's solution and frozen in liquid nitrogen in the field. Frozen specimens were brought to the laboratory where slides were prepared by air drying. These slides were stained either with Giemsa or Wright's stain.

ELECTROPHORESIS

Tissue samples from 506 specimens representing 30 populations of the *boliviensis* complex were available for analysis using horizontal starch-gel electrophoresis. In addition, eight specimens of *Bolomys amoenus* were used as an outgroup taxon (Patton *et al.*, 1989).

Twenty-one enzymes and other proteins encoded by 26 presumptive gene loci were examined for all populations and taxa, except that 120 individuals from Santa Rosa [de Ayaviri] (Puno Department, Peru) collected in 1986 were examined only for the subset of loci that differentiate the two taxa that occur sympatrically at that locality (see below). Aqueous extracts of kidney were used for all systems studied; enzymes and other proteins examined, and the gel running conditions, are given in Patton *et al.* (1989). Alleles are designated by their mobility relative to the most common allele at each locus, which was set at 100.

Estimates of genetic divergence among populations and taxa were made using the genetic distance measures of Nei (1972), corrected for small sample size (Nei and Roychoudhury, 1974; Nei, 1978), and of Rogers (1972). Patterns of phenetic similarity among taxa were examined by UPGMA clustering (Sneath and Sokal, 1973); phylogenetic trees were constructed by the Wagner distance algorithm (Farris, 1972), based on Rogers' $D(D_R)$, with *Bolomys amoenus* as outgroup. Estimates of genic heterozygosity were obtained from the electromorphic genotypes by direct count for each locus and were averaged across loci for population estimates of individual variability. Deviations from values expected if allele frequencies are in Hardy-Weinberg equilibrium were examined by Chi-square tests for all localities where the total sample size was greater than 20. All calculations of genetic distance, variability measures, and Hardy-Weinberg deviations

were performed using the BIOSYS-1 program (Swofford and Selander, 1981) on an IBM 4341 mainframe computer, as were construction of UPGMA and Wagner trees.

MEMBERS OF THE *AKODON BOLIVIENSIS* COMPLEX

By most current views, a single species of small, brown *Akodon* inhabits the high Altiplano grasslands of southern Peru (see, for example, Pearson, 1982) and Bolivia (Anderson, 1985). This species is referred to as *Akodon boliviensis* Meyen, the type species of the genus *Akodon*. We began our studies of the akodont rodents of southern Peru accepting this assumption. Based initially on preliminary comparative electromorphic studies, however, we came to realize that several species masquerade under the name *boliviensis* in central and southern Peru, and probably throughout Bolivia and adjacent Argentina. As will be shown, several of these species can be assigned to currently recognized names such as *boliviensis*, *puer*, and *subfuscus*. At least one, however, appears to lack an available name and is described below.

At this point, we provide the initial and subsequent electrophoretic evidence that documents the existence of several taxonomic units within this group. In subsequent sections, we describe elements of morphology that are shared by all members of the group, justify the assignment of existing names to each taxon (when possible), and characterize each taxon as it occurs in Peru and/or adjacent parts of Bolivia (the area of principal focus of this paper). The distribution of each taxon will be outlined insofar as it is known, and each taxon will be described in morphological, chromosomal, and genetic terms. We shall also suggest how certain forms from southern Bolivia and Argentina might be associated with this complex.

ELECTROMORPHIC DIFFERENTIATION

Allele frequencies were compiled for samples representing each taxon of the *boliviensis* complex in Peru (these data are available by request to J. L. Patton). A UPGMA phenogram and a distance Wagner tree, based on Rogers' D_R calculated for all pairs of populations, are presented in Figs. 2A and B, respectively. These figures strongly suggest that the populations fall into several distinct groups or taxa. The levels of genetic differentiation for pairs of populations within and among these groups, also based on Rogers' D_R , are given in Table 2.

We assign the names *boliviensis*, *puer*, and *subfuscus* to three of the four groups of populations in Fig. 2; the fourth group is currently unnamed. Below, we justify these assignments and provide a name for the fourth group.

Within each of these groups, most genetic distances range from 0.03 to 0.05, with a maximum distance between any pair of populations equal to

0.086 (Table 2). These values are characteristic of differentiation at the level of local populations for most other rodent species (Awise and Aquadro, 1982; Nevo, 1978). The average level of differentiation for pairs in which each population represents a different group, however, is considerably higher, ranging from 0.10 to 0.18 (minimum 0.06; Table 2). These levels are characteristic of differences found between species of a genus, although at the low end of the range of divergences.

In comparing these taxa, it is apparent that the group comprising samples of the undescribed taxon from central Peru is the most strongly differentiated. This is a result of the fixation of unique alleles at both the Ck-1 and Icd-1 loci, which greatly inflates the D_R (0.409) of these populations relative to the outgroup taxon (*Bolomys amoenus*) compared with that distance for the groups in which these alleles are not present (D_R between 0.295 and 0.352). The other three groups differ from one another by similar amounts, except that the *subfuscus-puer* distance is only about one-half that found between any other combination (Table 2). Each of these four taxa contains a moderate number of unique alleles relative to the total number present: *boliviensis* 4/39 unique; *subfuscus* 9/45; *puer* 4/36; and the undescribed species, 3/28.

Do these four groups represent distinct biological species? We accept as demonstration of probable specific separation of two taxa their coexistence in sympatry or contiguous allopatry without evidence of gene flow between them. Two of the taxa, *boliviensis* and *puer*, are sympatric yet maintain fixed allelomorphous differences over a large area in the department of Puno of southern Peru, suggesting that they are indeed distinct species. Separation at the level of species is also suggested for *subfuscus* and the undescribed taxon from central Peru, as these two are found in sympatry near Puquio in Ayacucho Department. Finally, *subfuscus* lives in very close geographic proximity to both *boliviensis* and *puer* in northern Puno and southern Cusco, suggesting that it is fully separated from those taxa, even though we know of no areas of actual contact (the morphological evidence of distinctiveness will be discussed in the species accounts that follow).

To illustrate the degree to which *boliviensis* and *puer* maintain their distinctiveness in sympatry, we tested for Hardy-Weinberg equilibrium at those sample localities where both taxa occur and where the sample size for each was greater than 5: Pucará, *puer* $n = 23$ and *boliviensis* $n = 14$; Santa Rosa, subdivided by year of collection, *puer* $n = 6$ and *boliviensis* $n = 19$ in 1985, *puer* $n = 17$ and *boliviensis* $n = 102$ in 1986. Chi-square analyses were performed for members of each suspected taxon at a locality separately, and then they were repeated, with members of both taxa pooled at each locality. Variable loci with rare alleles were excluded. The results are given in Table 3. As is clearly evident, allele frequencies at none of the loci deviate from Hardy-Weinberg equilibrium when each taxon is considered alone, but most show significant heterozygote deficiencies when individuals of both taxa are pooled. This is *prima facie* evidence that these two taxa maintain separate gene pools in areas of sympatry.

The general level and pattern of genetic differentiation among *boliviensis*, *puer*, *subfuscus*, and the fourth group support the hypothesis that each represents a distinct species. The level of genetic distance between sympatric *boliviensis* and *puer* is on the same order as is that between any combination of *boliviensis*, *subfuscus*, and the undescribed species from central Peru; only the combination of *subfuscus* and *puer* exhibits a lower degree of divergence (Table 2).

Akodon boliviensis GROUP

DIAGNOSIS.—Members of this group can be distinguished from all other *Akodon* or akodont species by the following combination of characters: small size (range of mean head-body length among species, 80.5–90.9 mm; hind foot length, 18.7–21.2 mm; maxillary tooth row length, 3.5–4.1 mm); interorbital region hourglass-shaped and with rounded edges (not beaded; edges may be squared in the posterior part of the orbit in old animals); mesopterygoid fossa narrow and straight-sided, with the sides parallel or gradually diverging posteriorly; bullae not unusually enlarged; overall color medium brown dorsally (usually with olivaceous tones) and buffy or grayish ventrally, pattern rather uniform and without contrasting areas of differently colored fur; yellowish eyering weakly expressed but usually distinct.

DISTRIBUTION.—Species of the *boliviensis* group are found in Peru from the western slopes of the Andes in Ancash Department southward along the western and central Andes to Tacna Department, and in the eastern Andes from Apurimac to Puno departments. Most localities are in grasslands between 2500 m and 4500 m elevation. The group is known from scattered localities in the Andes and Altiplano of Bolivia also at elevations usually above 2500 m. Representatives occur in western Argentina at least as far south as Catamarca Province; Argentine populations are known from elevations between 300 m and 3000 m.

GENERAL DESCRIPTION.—In this section, we describe a number of morphological features of members of the *boliviensis* group. Some of these features are mentioned to present an overall impression of these mice; others are described either because they may help distinguish the group from other sigmodontines, or because they may play a role in the description of individual species that follows. Unfortunately, the distributions of these characteristics among other members of the genus or subfamily are incompletely known, so that while they are descriptive, they neither can

FIG. 2. Relationships among populations of four species of the *boliviensis* group of *Akodon*, based on Rogers' genetic distance and rooted by specifying *Bolomys amoenus* as an outgroup. Numbers to the right of each tree refer to samples listed in Appendix I. A. UPGMA phenogram. The stippled boxes at basal nodes represent approximate 95% confidence limits. $r_{cc} = 0.972$. B. Wagner distance tree. Total tree length = 0.056; $F = 4.703$, $r_{cc} = 0.982$.

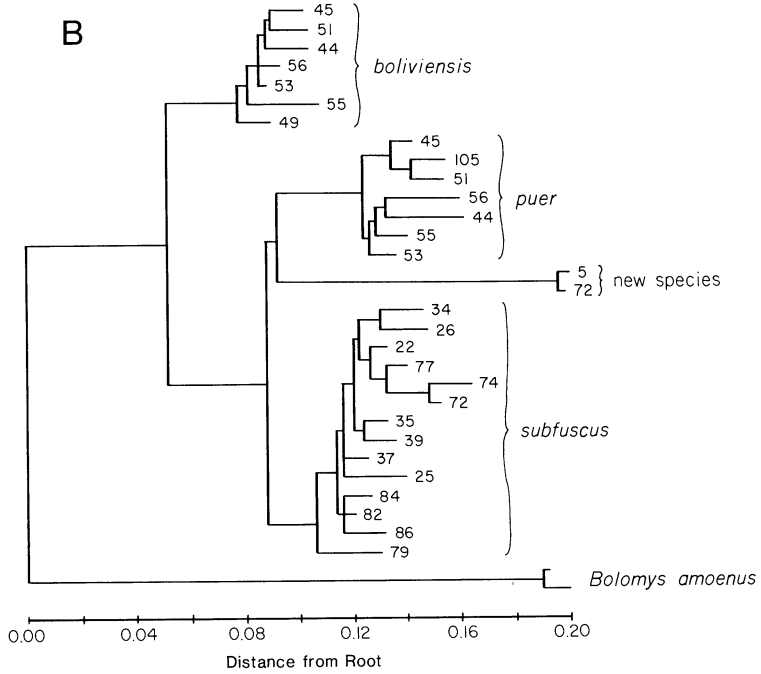
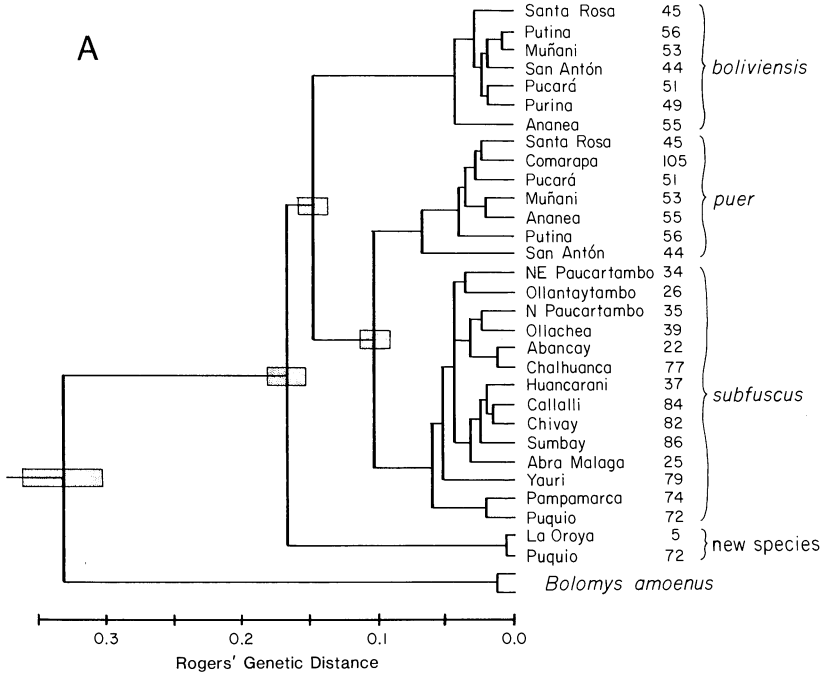


TABLE 2.—Summary of Rogers' genetic distances (D_R) among populations and species of the *Akodon boliviensis* complex.

	number of comparisons	mean \pm SD D_R	range D_R
within taxa:			
<i>boliviensis</i>	7	0.030 \pm 0.013	0.008-0.062
<i>puer</i>	7	0.045 \pm 0.019	0.021-0.086
<i>subfuscus</i>	14	0.046 \pm 0.016	0.011-0.082
new species	2	0.005	---
between taxa:			
<i>boliviensis-puer</i>		0.156 \pm 0.019	0.129-0.202
<i>boliviensis-subfuscus</i>		0.141 \pm 0.018	0.105-0.178
<i>boliviensis-new species</i>		0.177 \pm 0.010	0.163-0.194
<i>puer-subfuscus</i>		0.101 \pm 0.019	0.060-0.145
<i>puer-new species</i>		0.170 \pm 0.020	0.146-0.213
<i>subfuscus-new species</i>		0.152 \pm 0.015	0.139-0.189

TABLE 3.—Deviations from Hardy-Weinberg equilibrium for variable loci at two localities of sympatric contact between *Akodon boliviensis* and *A. puer* in Puno Department, Peru. For each locality, the two taxa are examined separately and pooled.

locality/ combination	number of individuals	number of loci	number of heterozygote deficiencies ($p < 0.05$)
Santa Rosa (45): 1985			
<i>boliviensis</i>	19	5	0
<i>puer</i>	6	4	0
pooled		7	6*
Santa Rosa (45): 1986			
<i>boliviensis</i>	102	5	0
<i>puer</i>	17	4	0
pooled		7	6*
Pucará (51): 1986			
<i>boliviensis</i>	14	4	0
<i>puer</i>	23	6	0
pooled		6	4†

*6PGD, with a rare allele in *boliviensis*, is not in statistical deviation when pooled.

†MPI and PGM do not exhibit heterozygote deficiency. MPI has two rare alleles in *boliviensis* not found in *puer*; for PGM, the allele frequencies are similar between the two species at this locality.

be used to diagnose the group formally nor as an argument for its monophyly.

External characters. Members of the *boliviensis* group are small, brownish mice (140–160 mm total length) with relatively short tails (60–70 mm), medium-sized hind feet (18–22 mm), and small, furry ears. In general, they resemble North American arvicolines in their external appearance.

The dorsal pelage of members of this group varies considerably both among and within taxa, but it is always some shade of brown tinged olivaceous or gray. The dorsal fur averages 8–12 mm long over the rump and is fine and dense. This color is distributed more or less uniformly across the back from rump to crown. The dorsal pelage always appears lightly to heavily streaked with black due to numbers of mostly black or dark brown guard hairs. These hairs are long, extending beyond the level of the fur hairs by 3 mm or more (with considerable variation in this distance among taxa). The tips of these hairs are usually gray or faintly buffy, paler than the main shaft of the hair; this pale zone is no more than 1–2 mm long. Fur hairs are agouti, with gray bases, a single brown pheomelanin band, and a black tip. The pheomelanin bands average 1–2 mm long. Variation in the length and hue of these bands is largely responsible for variation in dorsal color, with the concentration of guard hairs also playing an important role. The length of the black tips on fur hairs is highly variable (probably as a result of wear) but always less than 1 mm.

The color and color pattern of the flanks are generally similar to the dorsum. Flank color is usually somewhat paler than dorsal color and appears less heavily streaked due to a decrease in the number of guard hairs. Cheeks are buffy but streaked with black. Pale hairs circle the eyes in each species, giving the appearance of narrow yellow eyerings, but the conspicuousness of these rings varies considerably among taxa.

Ventrally, most hairs are slate gray for at least half their length. Most are tipped with gray, buff, or orangish bands, depending on the species and population. The color of the inguinal area in some individuals appears more intense than on the rest of the venter, in part due to lengthening of the pheomelanin or gray hair tips. The pattern of hairs on the throat is the same as on the chest. The chin sometimes has a small area of monocolored, white hairs, which may be difficult to see on dried skins but is obvious on live or fluid-preserved specimens.

Immature (age class 1) animals share the same color and color pattern as adults. Their pelage is not slaty, as it is in many other sigmodontines. Individual hairs may be shorter than in adults and may appear woollier, but in general the differences are slight.

The vibrissae of members of the *boliviensis* group are relatively short and sparse compared to those of other sigmodontines, and we found no consistent differences in number or arrangement among taxa of the group. As is usual for *Akodon*, the more ventral mystacial vibrissae are white and the more dorsal are dark (terminology follows Brown, 1971; Brown and Yalden, 1973). Most of these vibrissae do not reach the level of the ears when

folded caudally on dried skins. One or two superciliary and genal-1 vibrissae are present, but they are short and in fact barely distinguishable from guard hairs. A few white interramal vibrissae also can usually be seen. Ulnar carpal vibrissae are present on the forelimbs, but like the superciliary and genal series, are scarcely different from guard hairs.

The ears of all members of the *boliviensis* group are short, rounded, densely clothed with agouti hairs on their inner surfaces and with agouti or blackish hairs posteriorly. In no case is the fur in front of or immediately posterior to the ears contrastingly colored.

Both fore and hind feet are whitish or pale buff on their dorsal surfaces. In almost all cases the hairs are monocolored (not agouti). Tufts of white hairs surround the claws but do not extend much beyond them. The tarsal pads and relative proportions of the toes are described below.

Members of the *boliviensis* group generally have relatively short tails, averaging 70–80% of the head-body length. The tails are sharply bicolored, with the black dorsal band confined to a narrow stripe usually no more than 1–2 mm wide (but in some cases occupying nearly half the surface of the tail). The tails are lightly to heavily invested with hairs, which extend the length of from 2 to 4 scales. We note some variation among taxa in these characteristics.

Cranial characters (Figs. 3–6, Table 4; terminology follows Carleton, 1980; Musser, 1981; Wahlert, 1985; Voss, 1988). The crania of members of the *boliviensis* group possess few features that distinguish them strongly from other *Akodon*. In dorsal view the rostrum appears short and of average width for the genus. The posterior ends of the nasals, which are usually rounded or squared, terminate at the same level as the premaxillae or slightly posterior to them. The zygomatic notches vary from narrow and shallow (the usual condition for *Akodon*) to relatively broad, and, as is commonly the case among akodonts, they deepen and broaden noticeably with age (see below). The zygomatic arches tend to flare laterally slightly to sharply, with variation attributable both to age and taxon. They are slender to moderately robust. In older animals the arches tend to run parallel in their midsections, while in younger animals they converge anteriorly. Lacrimals can usually be found in cleaned skulls of most taxa of the group; they vary considerably in size among taxa. The frontal sinuses are slightly but usually not conspicuously swollen. The interorbital region is usually narrow and smoothly hourglass-shaped, with dorsolateral margins that are rounded anteriorly but that may be squared posteriorly, especially in older animals. Sharp ridges or beads that overhang the orbits, however, do not occur. The fronto-parietal suture forms a smooth crescent. The interparietal is of medium size in young animals, at most 5–6 mm in breadth and 2 mm long. It decreases in size with age and is sometimes completely obscured in old individuals. Temporal and mastoid ridges are usually present, weakly developed and inconspicuous in young animals but often moderately pronounced in older ones. These vary among taxa in prominence.

TABLE 4.—Measurements of taxa of the *Akodon boliviensis* group (age classes 3-5). For each measurement, mean, standard deviation (in parentheses), and sample size are given. *Akodon* new sp. and *A. subfuscus* new ssp. are described below.

	<i>bolivi-</i> <i>ensis</i>	<i>spagazzinii</i>	<i>puer</i> <i>puer</i>	<i>puer</i> <i>caenosus</i>	<i>puer</i> <i>lutescens</i>	<i>subfuscus</i> <i>subfuscus</i>	<i>subfuscus</i> new ssp.	new sp.
TOTAL	155.7 (13.64) 235	165.5 (14.51) 57	152.7 (13.23) 31	148.9 (13.18) 34	139.2 (11.98) 42	159.6 (11.83) 184	143.0 (13.17) 169	149.4 (13.09) 68
TAIL	64.6 (5.64) 235	69.7 (7.31) 57	68.0 (5.81) 31	60.6 (4.68) 34	59.0 (5.95) 42	68.2 (5.59) 184	63.9 (5.14) 169	61.8 (5.44) 69
HF	21.1 (1.08) 239	21.1 (1.38) 59	19.0 (2.02) 31	18.7 (0.75) 34	18.5 (0.93) 41	20.6 (0.97) 185	20.4 (3.92) 175	19.5 (1.28) 70
EAR	13.7 (1.00) 209	15.6 (1.72) 59	14.0 (1.13) 30	14.0 (1.73) 23	12.4 (0.99) 42	13.8 (0.95) 143	13.4 (0.79) 169	12.2 (1.87) 70
CIL	22.40 (1.20) 289	23.09 (0.95) 60	21.33 (0.92) 35	20.65 (0.94) 34	20.66 (0.99) 52	22.17 (1.00) 218	21.04 (1.24) 196	20.06 (0.92) 82
ZB	12.29 (0.52) 295	12.45 (0.45) 61	11.66 (0.41) 36	11.23 (0.48) 33	11.17 (0.41) 52	12.06 (0.46) 221	11.57 (0.44) 196	11.65 (0.41) 82
BB	11.21 (0.28) 294	11.40 (0.36) 60	10.91 (0.29) 36	10.53 (0.29) 34	10.51 (0.22) 51	11.14 (0.33) 221	10.83 (0.25) 196	10.92 (0.22) 81

TABLE 4, continued.

	<i>bolivi- ensis</i>	<i>spgazzinii</i>	<i>puer puer</i>	<i>puer caenosus</i>	<i>puer lutescens</i>	<i>subfuscus subfuscus</i>	<i>subfuscus new ssp.</i>	new sp.
IOC	4.21 (0.15) 298	4.54 (0.18) 62	4.38 (0.18) 36	4.21 (0.17) 35	4.19 (0.14) 52	4.38 (0.16) 220	4.23 (0.14) 196	4.32 (0.16) 83
RL	8.82 (0.51) 294	9.21 (0.48) 58	8.40 (0.42) 35	8.15 (0.52) 34	8.18 (0.48) 50	8.85 (0.46) 215	8.24 (0.51) 194	8.76 (0.40) 78
NL	8.83 (0.54) 295	9.12 (0.50) 58	8.59 (0.50) 35	8.36 (0.50) 34	8.15 (0.56) 50	8.77 (0.52) 214	8.15 (0.58) 194	8.83 (0.44) 78
RW	4.44 (0.25) 298	4.67 (0.25) 62	4.34 (0.23) 36	4.19 (0.22) 35	4.12 (0.25) 52	4.52 (0.21) 220	4.42 (0.28) 196	4.51 (0.21) 82
RW2	3.74 (0.21) 298	3.92 (0.23) 62	3.69 (0.20) 36	3.62 (0.19) 35	3.59 (0.23) 52	3.83 (0.19) 220	3.65 (0.21) 196	3.73 (0.17) 82
OL	8.12 (0.45) 297	8.12 (0.32) 62	7.59 (0.36) 36	7.49 (0.33) 34	7.40 (0.37) 52	7.89 (0.36) 220	7.48 (0.40) 196	7.86 (0.31) 82
DL	6.20 (0.44) 298	6.37 (0.38) 62	5.81 (0.34) 36	5.61 (0.39) 35	5.61 (0.36) 52	6.21 (0.37) 221	5.80 (0.42) 196	6.22 (0.40) 81
MTRL	4.02 (0.16) 300	4.21 (0.18) 62	3.71 (0.17) 36	3.59 (0.11) 35	3.56 (0.10) 52	3.83 (0.18) 221	3.70 (0.14) 196	3.74 (0.14) 83

IFL	5.17 (0.38) 298	5.90 (0.35) 61	5.33 (0.31) 36	5.14 (0.36) 33	4.68 (0.37) 52	5.44 (0.40) 221	5.18 (0.35) 195	5.39 (0.35) 81
AW	4.83 (0.23) 296	4.99 (0.27) 61	4.68 (0.19) 36	4.59 (0.24) 33	4.52 (0.20) 52	4.85 (0.23) 221	4.67 (0.23) 194	4.62 (0.19) 82
OCW	6.06 (0.20) 288	6.14 (0.17) 58	5.86 (0.23) 34	5.76 (0.22) 33	5.78 (0.20) 52	6.02 (0.20) 216	5.93 (0.20) 195	5.98 (0.15) 80
MB	10.79 (0.35) 288	11.02 (0.39) 61	10.51 (0.35) 35	10.18 (0.42) 34	10.20 (0.27) 52	10.73 (0.32) 219	10.47 (0.35) 195	10.65 (0.25) 82
BOL	3.47 (0.31) 288	3.72 (0.26) 59	3.45 (0.28) 34	3.27 (0.24) 34	3.25 (0.24) 52	3.43 (0.30) 219	3.32 (0.27) 195	3.41 (0.21) 81
MFL	3.66 (0.25) 279	3.77 (0.23) 35	3.60 (0.23) 29	3.52 (0.29) 15	3.31 (0.24) 51	3.64 (0.31) 210	3.46 (0.27) 192	3.79 (0.28) 79
MFW	0.95 (0.12) 295	1.12 (0.17) 60	1.04 (0.16) 29	1.00 (0.14) 34	0.99 (0.13) 51	1.13 (0.17) 221	0.87 (0.19) 196	1.14 (0.16) 82
ZP	2.25 (0.21) 298	2.24 (0.16) 62	2.13 (0.21) 36	1.99 (0.15) 35	2.10 (0.16) 52	2.06 (0.17) 221	1.94 (0.18) 196	1.86 (0.17) 82
CD	9.33 (0.33) 288	9.43 (0.29) 61	8.88 (0.21) 34	8.58 (0.31) 32	8.72 (0.27) 52	9.14 (0.32) 216	9.09 (0.28) 194	9.07 (0.23) 81

Laterally, the profile of the dorsal surface of the cranium is strongly curved in age classes 1 and 2, but the curvature gradually decreases with age (see below). The paths of the incisor roots through the rostrum are clearly visible as raised channels on the lateral surfaces of the premaxillae. The posterior end of each channel, at the nasolacrimal capsule, is slightly to moderately swollen. In it a nasolacrimal foramen is present; its opening faces posterodorsally and is about the length of M^2 . Each zygomatic arch droops distinctively in its midsection to about the level of the molar toothrow (Fig. 3). The zygomatic plate (Fig. 4) is neither especially narrow (as it is in *Akodon torques* or *Microxus mimus*) nor especially broad (as in *Akodon albiventer*). Its ventral root is directly beneath or slightly anterior to the dorsal root, so that the plate is oriented either vertically or slopes gently forward from top to bottom. The anterior margin of the zygomatic plate is flat or slightly concave. The dorsal portion of the zygomatic plate includes a well-developed lip of bone that forms the lateral margin of each zygomatic notch.

The infraorbital foramen is a conspicuous opening for the passage of nerves and muscles that run between the zygomatic plate and the rostrum. In the *boliviensis* group, as in other *Akodon*, it is typically muroid in form, of medium size for the group, and with the dorsal portion considerably broader than the middle or ventral.

Within the orbit, the optic foramen is larger in diameter than M^3 , but slightly to substantially smaller than the anterior alar fissure. There is a single ethmoid foramen and a single supraorbital foramen (which lies within the orbit, beneath the supraorbital margins). The supraorbital artery leaves a distinct indentation, the squamoso-alisphenoid groove, along the alisphenoid between the bullae and the sphenofrontal foramen. An alisphenoid strut usually separates the buccinator-masticatory foramen from the foramen ovale accessorius, although this strut is missing in some individuals. As it exits its foramen, the buccinator nerve passes through a deep groove running dorsally along the posterior orbit. The foramen ovale accessorius and opening of the transverse canal are similar in diameter and about the size of M^3 or slightly larger. A sphenopalatine foramen is open and large in old animals, but in younger ones (age classes 1-3) it is usually obscured by bone surrounding the molar roots. When open, it is about the length of M^2 .

A particularly useful character in distinguishing certain species of this group concerns the alisphenoid. In these species and other *Akodon*, a part of the alisphenoid (referred to below as the posterior ascending process) projects dorsally as a narrow band running between the squamosal and bulla. This band varies considerably in development among species, sometimes extending dorsally at least to the point where the squamoso-alisphenoid groove can be seen to meet the bulla, and sometimes terminating well ventral to the groove (Fig. 5).

Posterior to the orbit and dorsal to the bullae, the postglenoid foramina are of medium size for the genus and slightly larger than the subsquamosal

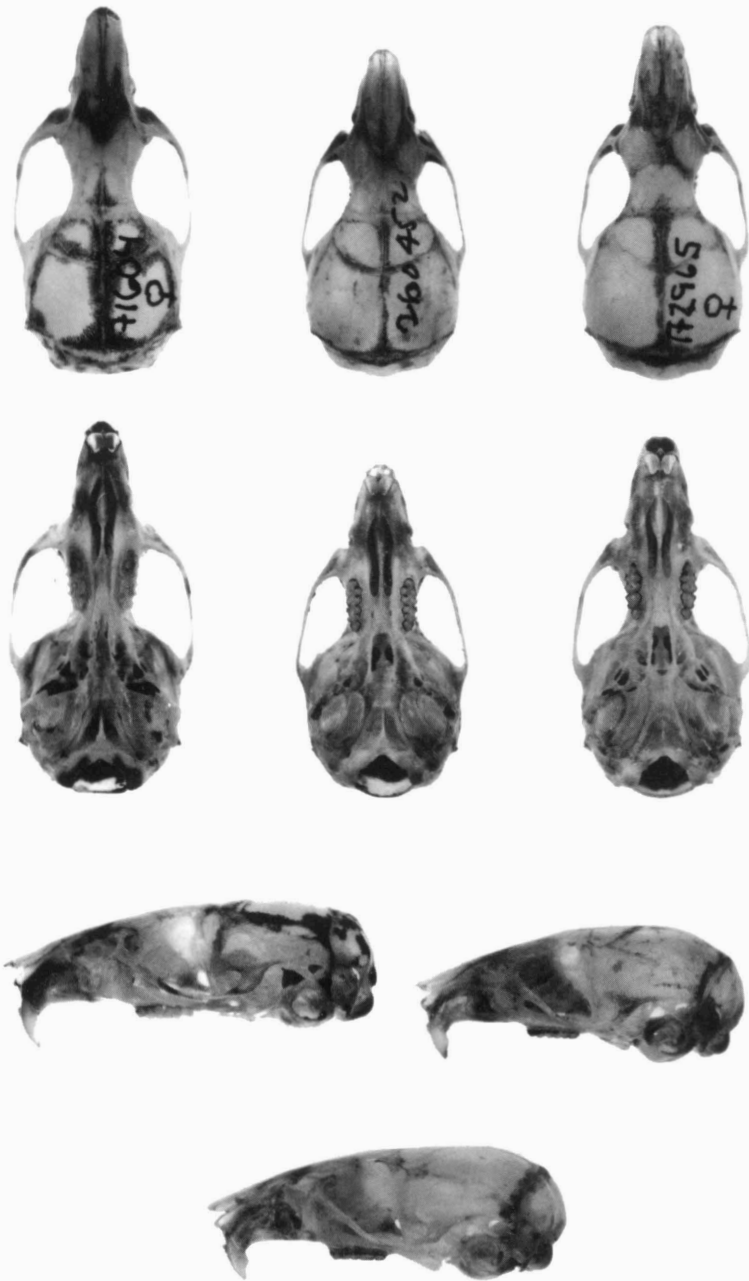


FIG. 3. Dorsal, ventral, and lateral views of crania of several members of the *Akodon boliviensis* group. First and second rows, dorsal and ventral views of *A. boliviensis* (left), *A. puer* (center), *A. subfuscus* (right). Third and fourth rows, *A. boliviensis* (left), *A. puer* (right), *A. subfuscus* (bottom).

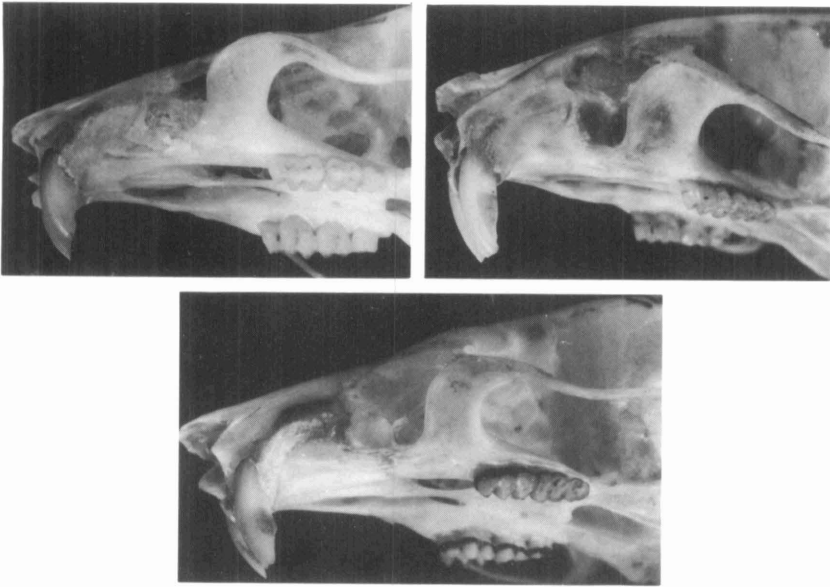


FIG. 4. Zygomatic plate of *Akodon boliviensis* (MVZ 171603, left), *A. torques* (UMMZ 160501, center), and *A. albiventer* (UMMZ 155939, right).

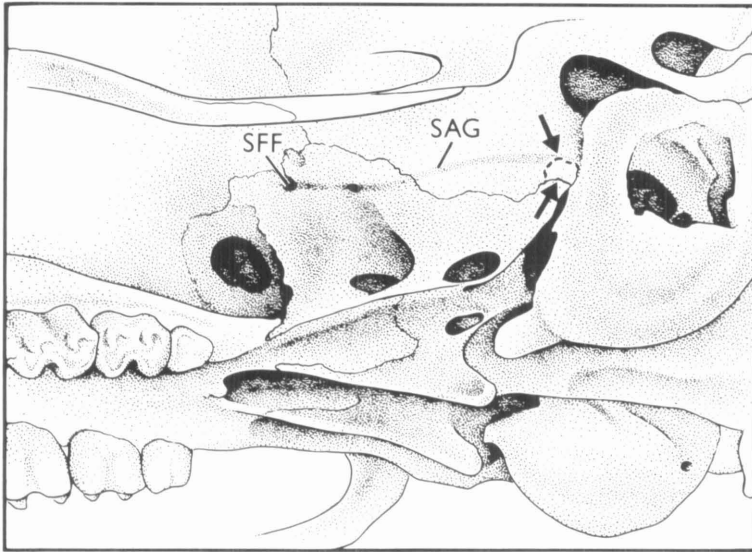


FIG. 5. Variation in the posterior ascending process of the alisphenoid (SFF, sphenofrontal foramen; SAG, squamoso-alisphenoid groove). In *Akodon boliviensis*, the process usually extends dorsally to or beyond the level of the supraorbital artery (seen as a distinct groove [stippled] between the bulla and sphenofrontal foramen). This condition is indicated by the

foramina, but some variation in size occurs among species and is discussed below. The two foramina are separated by a strut of bone, the hamular process of the squamosal or tympanic hook, which varies in thickness and perhaps shape among taxa of the *boliviensis* group.

Ventrally, the incisive foramina are long and narrow, ending posteriorly at about the level of the protocone of M^1 . The palate is shallowly to moderately deeply grooved and marked by a single pair of anterior and usually one pair of posterior palatine pits. Its posterior end (anterior margin of the mesopterygoid fossa) is smoothly rounded or squared, sometimes with a small median spine (Fig. 6). The mesopterygoid fossa is narrow and has straight sides, with the sides either parallel or gradually diverging posteriorly. This conformation distinguishes members of the *boliviensis* group from most (but not all) other *Akodon*, which usually have a broader mesopterygoid fossa with parallel or lyre-shaped sides. Sphenopalatine vacuities are generally present but vary in size. The parapterygoid plates are moderately to deeply excavated and have straight to slightly convex lateral margins. At the posterior ends of these plates, the foramina ovale vary from being larger in diameter than M^3 to being almost closed over by bone; just anterior to the bullae, the median lacerate foramina also vary considerably in size.

In the region of the bullae and posterior part of the cranium, the stapedia foramina are large. This, with the presence of sphenofrontal foramina and squamoso-alisphenoid grooves, corresponds to the pattern of cranial circulation Carleton (1980) described as "character state 0" or Voss (1988) referred to as "pattern 1." Hypoglossal and jugular foramina are present and well separated. Stylomastoid foramina are also present and large. Well-formed paroccipital processes are present and project ventrally a distance approximately equal to the diameter of M^3 .

The tympanic bullae are similar to those of most other *Akodon*. They are of medium size, flask-shaped, and with broad and short eustachian tubes. The periotic is visible on the posterior surface of the skull. It appears to be thin and is pierced by a single, large, dorsally-placed fenestra. Ventrally, the petrosal part of the bulla is exposed as a wedge-shaped band between the basioccipital and ectotympanic, beginning at about the opening of the carotid canal and broadening posteriorly. By the posterior end of the bulla it occupies one-third to one-half the dorsoventral height of that structure. Within the bulla, a large orbicular process can usually be seen on the malleus.

The mandibles of members of the *boliviensis* group resemble those of most other *Akodon*. The rami are delicate and not especially deep. The coronoid process above each ramus is falciform and delicate. Its dorsal border lies at about the same level as the condyloid process. The sigmoid notch separating coronoid and condyloid processes on each ramus is fairly shallow and narrow, resembling that of phyllotine rodents (see Hershkovitz, 1962) more closely than that of ichthyomines (see Voss, 1988). The angular process is strongly developed, intermediate in size between coronoid

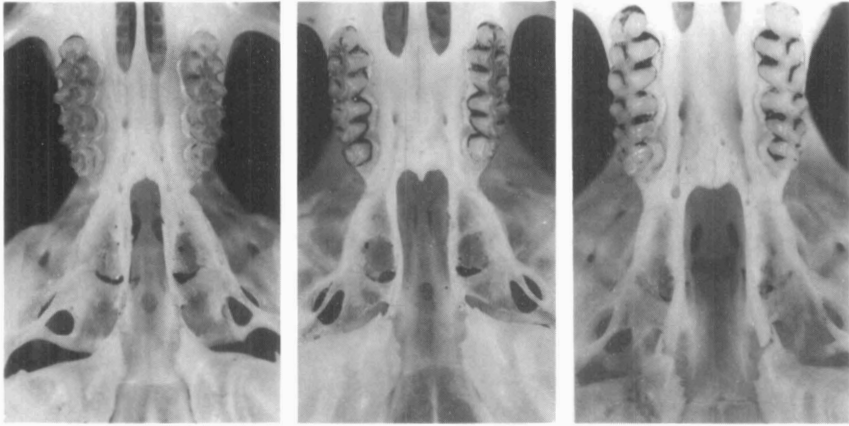


FIG. 6. Mesopterygoid region of *Akodon boliviensis* (MVZ 171605, left), *A. kofordi* (MVZ 171666, center), and *A. dayi* (AMNH 262732, right).

and condyloid processes, and its thickened ventral border is strongly reflected medially. On the ramus, the inferior masseteric ridge is raised and sometimes appears rugose, especially in old individuals. Posteriorly, the root of the incisor forms a conspicuous capsular process; this is not as large, however, as in many other sigmodontines. The mental and mandibular foramina are large, and both appear to have single openings.

Dental characters (terminology following Reig, 1977). *Akodon* teeth are frustrating to study because they wear rapidly, and as they wear they lose much of their occlusal topology. Even relatively young animals in age class 2 and 3 have lost many of the smaller lophs and flexi that can be seen on the teeth of unweaned or recently weaned animals. This is particularly the case for the upper and lower third molars, which appear completely "dished" and without surface structure in all but the youngest individuals. As a result, our description of the details of the teeth of each member of the *boliviensis* group is based on relatively few young animals and should be considered tentative, particularly with respect to the frequency of occurrence of individual structures.

The upper and lower incisors of members of the *boliviensis* group are delicately constructed and lack any trace of grooves on the anterior surface. The upper incisors are approximately orthodont in orientation.

As in other *Akodon*, the first upper molar of members of the *boliviensis* group appears to have six main cusps. The anterior pair, the anterolingual and anterolabial conules, are separated by a usually deep anteromedian flexus and are approximately equal in size. They sit opposite one another on the tooth. The next pair, the protocone and paracone, are equal in size but diagonally arranged, with the protocone anterior to the paracone. Similarly, the third pair, the hypocone and metacone, are equal in size to each other (and to the protocone/paracone) and diagonally arranged, with the hypocone anterior.

The presence and size of secondary cusps and lophs on the M^1 s is rather variable. On the labial side of the tooth, a parastyle and anteroloph are usually found between the anterolabial conule and the paracone. On the opposite side, between the anterolingual conule and protocone, the proto-style that is seen in some sigmodontines is almost always absent. A mesoloph and mesostyle are usually present and conspicuous between the paracone and metacone, and an enterostyle is occasionally found between the protocone and hypocone. A posteroloph is almost always present along the posterior border of the tooth, but the posteroflexus that separates it from the metacone is shallow, so that the posteroloph is small and appears poorly defined.

The anterior border of the M^2 lacks an anterolingual conule. A conspicuous cingulum, perhaps homologous with the anterolabial conule, runs from the midline of the tooth to the labial border. Protocone, paracone, hypocone, and metacone are as in M^1 . Also as in M^1 , M^2 usually has a mesoloph and/or mesostyle, usually lacks an enterostyle, and has a small and poorly defined posteroloph.

The third upper molar varies considerably in morphology among the taxa of the *boliviensis* group, and its morphology will be described in the account of each species. In its most complex form it is large, over half the length of M^2 , and has a well-defined metaflexus and hypoflexus, giving it a distinctive "8" shape. At the other extreme it is considerably smaller than half the size of M^2 and is oval in outline.

The first lower molar, like the first upper, has six major cusps. The anterior pair, the anterolabial conulid and anterolingual conulid, are opposite one another and separated by a conspicuous anteromedian flexid. The anterolingual conulid is equal to or slightly smaller than the anterolabial one. The next pair of major cusps, the protoconid and metaconid, are arranged diagonally with the metaconid slightly anterior to the protoconid. They are approximately equal in size. The third pair, the entoconid and hypoconid, are also arranged diagonally with the entoconid slightly anterior. They are approximately equal in size.

Between the anterolabial conulid and protoconid can usually be found a small protostylid, often connected to the anterior mure by a well-developed loph. On the lingual side of the tooth, between anterolingual conulid and metaconid, a metastylid is occasionally present but if so, tiny in size. An ectostylid can often be found between protoconid and hypoconid, but it also is usually tiny. Opposite it, between metaconid and entoconid, a tiny mesostylid is occasionally present.

On the posterior part of the tooth, a deep posteroflexid separates a conspicuous posterolophid from the rest of the tooth. This structure, while relatively large, lacks any recognizable posterostylid.

The second lower molar contains four major cusps arranged in two pairs, presumed to be the protoconid-metaconid and hypoconid-entoconid. These are arranged diagonally with the lingual member of each pair slightly anterior to the labial. The anterolingual conulid is always missing,

while a distinctive cingulid, running from the middle of the anterior face of the tooth to the labial margin (perhaps a homologue of the anterolabial conulid) is sometimes present. A small ectostylid is sometimes found between protoconid and hypoconid; the mesostylid is missing or if present, is tiny. As in M_1 , a posteroflexid is present and defines a conspicuous posterolophid.

The third lower molar is reduced, but not as much so as the third upper molar. As in M_2 , four cusps are present. The posterolophid is missing, however, so that the tooth has an "8" shape. A trace of an anterolabial cingulid is sometimes seen.

Female reproductive tract. Females have four pairs of nipples, two each in the axillary and inguinal regions. The uterus is duplex, and large preputial glands lie on each side of the clitoris. These features are common to most *Akodon* (e.g., Myers, 1989).

Male accessory glands. Fluid-preserved specimens are available for representatives of *boliviensis*, *subfuscus*, and the undescribed species from central Peru described below. These have the standard akodontine complement of accessory glands as described by Voss and Linzey (1981). These include single pairs of large preputial, bulbourethral, vesicular, and ampullary glands; a double pair of ventral prostates; and unpaired dorsal and anterior prostates. The medial ventral prostates are small, as is characteristic of *Akodon* in general, although in the materials available to us they appear to vary somewhat in size among taxa. The vesicular glands of each of these three taxa are generally lobed medially and along their greater curvatures but differ in details of surface structure.

Glans penis and baculum. In general, both the phallus and baculum are as described for *Akodon* by Hooper and Musser (1964:23): "glans externally plain, with middorsal and midventral troughs but no more than traces of parotoid lobes, its spiny investiture as in *Oryzomys*; bacular mounds erect, the medial one longer, but no larger in diameter, than the lateral pair; that pair closely appressed to the medial; . . . dorsal papilla spinous, at least apically; . . . urethral flap relatively long and divided in its distal one-half or three-fourths into two attenuate erect processes; ventral face of the flap spinous in most if not all species." Differences among taxa will be discussed below.

The baculum is shorter than the glans and divided into a proximal bony element with a straight shaft and flared base, and a well-developed tridigitate distal cartilaginous element. Departures from this general condition that differentiate species of the *boliviensis* group are also given below under each account.

Stomach. Stomachs of the members of the *boliviensis* group have the basic unilocular and hemiglandular anatomical design that characterizes all known *Akodon* (following Carleton, 1973; and personal observations). The incisura angularis is shallow in all specimens; the bordering fold has its origin either just medial to the incisura angularis (*boliviensis*) or caudal to it (*subfuscus*, *puer*, and the undescribed taxon from central Peru); and the

bordering fold courses in a straight line to separate the corpus from the antrum of the stomach.

Palatal rugae (Fig. 7). Two complete (diastemal) and four incomplete (interdental) palatal rugae (terminology following Carleton, 1980) characterize all *Akodon* that we have examined to date, including *boliviensis*, *puer*, *subfuscus*, and the undescribed species. Differences in the shape of these ridges that characterize each species based on material available are noted in the individual accounts, below.

Plantar surfaces of feet (Fig. 8). The plantar surfaces of the fore and hind feet are similar in all *Akodon* (*s.s.*) examined to date. The three interdigital and two metacarpal pads on the manus do not differ in size or position among the species of the *boliviensis* group examined. All individuals have a reduced pollex that lacks a claw, a condition typical of most muroid rodents. Six separate tubercles are present on the hind foot (terminology follows Brown and Yalden, 1973). Two of these are on the metatarsal pad and four (the interdigitals) are at the base of the digits. In all four species of the *boliviensis* complex, the lateral metatarsal tubercle (hypothenar, LMT) is relatively large, nearly subequal in size to the interdigital tubercles. The distal edge of the medial metatarsal tubercle (thenar, MMT) typically just reaches the LMT and is positioned approximately midway along the sole of the foot. The hallux in all species is well developed, and the fifth toe is long, with its fleshy tip extending well beyond the base of digits 2-4.

Karyotype. The diploid number is either 34 or 40, and the number of autosomal arms is 40 or 42. The autosomal complement of the $2n=40$, $FN=40$ karyotype includes one pair of very small metacentric elements, with the remaining chromosomes consisting of a single pair of large acrocentrics and 17 pairs of acrocentrics that grade evenly in size from medium to small. The $2n=34$ karyotype differs by possessing three pairs of large biarmed and six fewer uniarmed elements than in the $2n=40$ karyotypes. The morphology of the X and Y chromosomes vary among the species in the group (see accounts, below).

SEX AND AGE VARIATION

In studying the morphology of the species of this group, as in any taxonomic study of mammals, we had to recognize and take into account two potentially important sources of variation that are unrelated to differences among the groups studied, variation due to sexual dimorphism and variation due to growth (age). Several common patterns have emerged from these studies; these will be documented here, and differences among taxa will be explored in the species accounts that follow.

AGE VARIATION.—*Quantitative analysis*. Individuals of each taxon continue to increase in most cranial dimensions as long as they live. Plots of variable measurements against age class fell into three general categories. In the first, size continued to increase at a rapid rate even between the

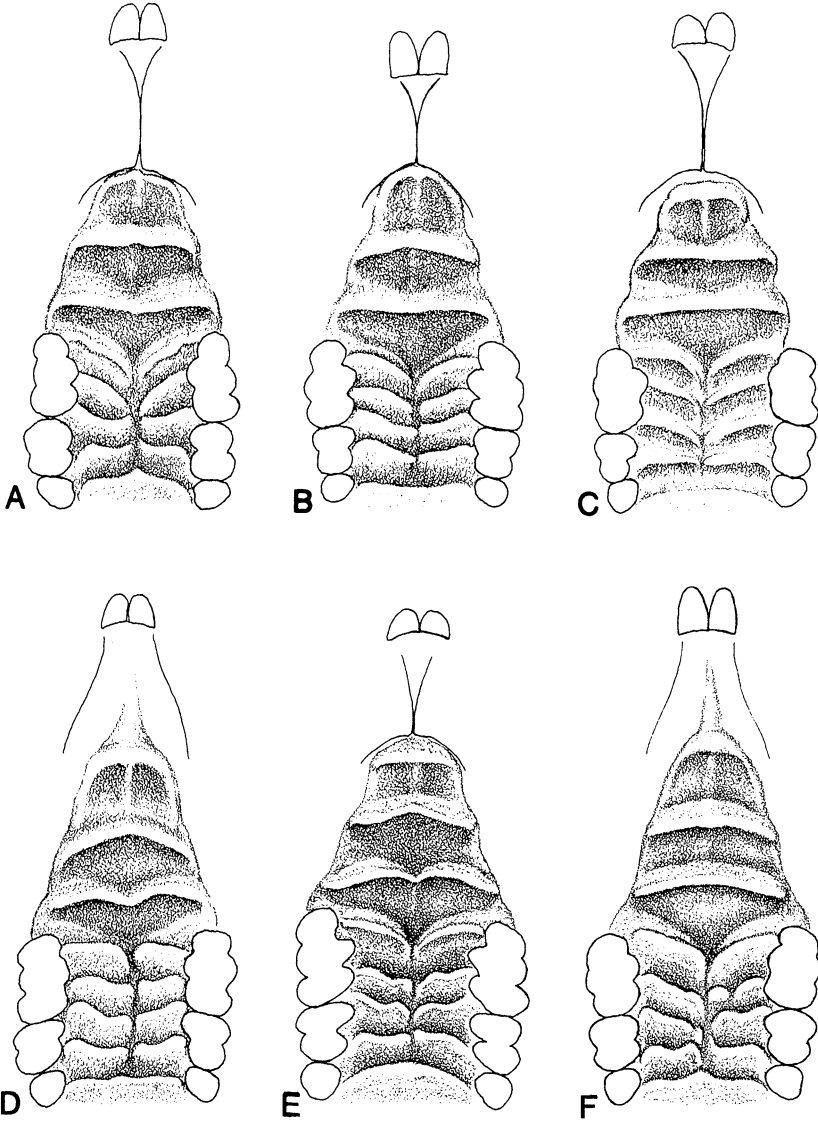
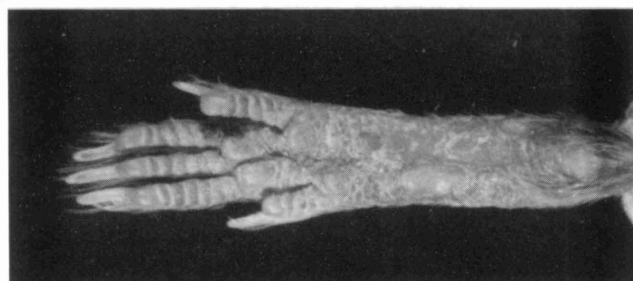


FIG. 7. Palatal rugae of members of the *Akodon boliviensis* group. A. *A. boliviensis* (MVZ 172380). B. *A. puer puer* (AMNH 260447). C. *A. puer lutescens* (MVZ 172382). D. *A. subfuscus subfuscus* (MVZ 172368). E. *A. subfuscus* new subspecies (MVZ 174366). F. *A.* new species (AMNH 232641).

FIG. 8. Details of the plantar surface of the left hind foot of five taxa of the *Akodon boliviensis* group: A. *A. boliviensis* (MVZ 173641). B. *A. puer lutescens* (MVZ 172382). C. *A. puer puer* (AMNH 260451). D. *A. subfuscus subfuscus* (MVZ 172365). E. *A.* new species (AMNH 232641).



oldest age classes, 4 and 5 (Fig. 1). Most variables representing cranial lengths fell into this category, including CIL, RL, NL, OL, DL, IFL, BOL, ZP, and MFL. Other variables with this growth form were RW, RW2, and AW. TOTAL, TAIL, and EAR also appeared to grow continuously.

In a few variables, growth appeared to slow somewhat in mice of age classes 4 and 5. These included variables representing the breadth of the braincase and orbit (BB, IOC, MB, OCW), the toothrow, and the hind foot. Total growth in these measurements (*i.e.*, size at age class 2 compared to size at age class 5) was generally much less than in the first category. While size in these measurements did not change linearly with age, the deviation from linearity was generally small, and age adjustment was carried out as described above.

A third group of measurements scarcely changed with age. This group included width of the mesopterygoid fossa (MFW) and cranial depth (CD). Age adjustment had no effect on these measurements.

These patterns are striking and crucial to recognize if comparisons are to be made among populations that differ in age structure, but viewed independently they give an incomplete picture of the relative importance of growth in each dimension in determining the overall change in cranial size. To investigate this aspect of growth in each species, we performed principal components analysis for each taxon, based on variance-covariance matrices and using log transformed data (Bookstein *et al.*, 1985). The loadings for the first component were mostly positive and generally varied within a fairly narrow range, suggesting that this component could be interpreted as representing variation in overall size. If most size variation is due to growth, as seems reasonable in a sample that includes animals ranging from recently dispersed young to individuals whose teeth are worn to the gums (the correlation between age class and score on this axis is given in Table 5 for each species), then the loadings on PC1 estimate allometric coefficients of each variable on growth when they are rescaled so that their squares sum to the number of variables (Strauss and Fuiman, 1985).

These allometric coefficients are presented in Table 6. Measurements that consistently grew with strongly positive allometry (coefficients > 1.10) included length measurements from the entire skull (CIL) and especially from the anterior part of the cranium (RL, NL, DL, IFL, ZP), and also a measure of basicranial length (BOL). Measurements that grew slowly (coefficients consistently < 0.90) included ZB, most dimensions of the braincase (BB, MB, OCW, CD), IOC, and those involving the toothrow (AW, MTRL). Measurements of rostral breadth (RW, RW2) had coefficients near unity, as did OL.

Generally, these species of *Akodon* are relatively similar in their patterns of allometric growth, although occasionally species exhibit quite different coefficients for individual measurements. These differences are difficult to interpret, however, because confidence intervals for the allometric coefficients were not available.

TABLE 5.—Correlation between first principal component scores and toothwear class. *Akodon* new sp. and *subfuscus* new ssp. are described below.

Taxon	<i>n</i>	<i>r</i>
<i>boliviensis</i>	322	0.78
<i>puer lutescens</i>	70	0.80
<i>s. subfuscus</i>	219	0.49
<i>subfuscus</i> new ssp.	224	0.76
new sp.	89	0.73

To compare these differences, we computed coefficients of vector correlation for all pairwise comparisons of the PC1 scores on which Table 6 is based. These coefficients, calculated as the inner product of the variable loadings, are the cosine of the angle between each pair of vectors (Morrison, 1967; Voss, 1988). A value of unity indicates that the vectors are parallel, while a value of zero results when they are orthogonal. In each comparison, the coefficients were 0.96–0.99, indicating that the vectors for each of the *Akodon* species appear to be nearly parallel. This suggests that growth in cranial dimensions is very similar among these species.

The finding that measures associated with lengths of the anterior part of the skull in these taxa tended to increase most rapidly with age is in agreement with results for other muroid species (Moore, 1981; Dos Reis, 1985; Voss, 1988; Myers, 1989). The continuing growth of basioccipital length and its strongly positive allometry may be related to the tendency of the skulls to flatten in lateral view (*i.e.*, for the degree of basicranial flexure to decrease) as animals age (see below). This pattern is also consistent with the low allometric coefficients for cranial depth for all species.

Qualitative variation (Fig. 9). Most changes in the general appearance of crania related to age can be anticipated from the patterns of quantitative variation documented above. Skulls increase substantially in length and somewhat less in breadth. Growth is most noticeable in the anterior part of the skull. The rostrum of older animals appears distinctly longer and proportionately narrower than that of younger animals, the zygomatic plate deepens, and the distance across the zygomatic arches increases.

Several other changes common to all of the taxa in this study are not shown by the analysis of measurements, although they are conspicuous in an age-ordered series of crania. On the dorsal skull, the zygomatic notches broaden due to the outward flaring of their anterolateral margins. The distance between the zygomatic arches also increases and, as a result of their increasing distance from the orbit and perhaps changes in the angles the roots form with the cranium, the arches appear to flare laterally. There is a striking decrease in the area of the interparietal. Temporal ridges develop as thickenings running posteriorly from the orbits along the parietal-squamosal border; they terminate in mastoid ridges that run dorsoventrally along the border formed between the squamosal and occipitals. These ridges increase in size and conspicuousness as animals age. On the

TABLE 6.—Allometric coefficients describing cranial growth. The principal component analysis is described in the text*. Names of taxa are as in Table 4, except *Akodon aerosus* (specimens from Puno Dept., Peru), which are included for comparison.

	<i>bolivi-ensis</i>	<i>puer lutescens</i>	<i>subfuscus subfuscus</i>	<i>subfuscus new ssp.</i>	new sp.	<i>aerosus</i>
CIL	1.25	1.13	General length 1.15	1.43	1.34	1.20
RL	1.40	1.91	Anterior skull length 1.39	1.48	1.46	1.06
NL	1.47	2.20	1.50	1.85	1.46	1.38
DL	1.86	1.83	1.63	2.10	2.74	1.74
IFL	1.71	1.79	1.65	1.62	2.54	3.31
ZP	2.83	2.03	2.03	2.52	3.54	1.97
MTRL	0.25	0.14	Toothrow 0.52	0.23	0.08	0.14
AW	0.49	0.68	0.86	0.60	0.48	0.53
BOL	2.81	1.61	Basicranial length 3.02	1.98	1.15	2.04
BB	0.04	0.06	Braincase and occipital region 0.14	0.03	0.10	0.14
MB	0.21	0.27	0.26	0.35	0.06	0.43
OCW	0.08	0.11	0.25	0.16	0.12	0.17
CD	0.07	0.18	0.22	0.12	0.05	0.27
OL	1.00	0.96	0.88	0.92	0.95	0.82

ZB	0.65	0.47	Breadth of anterior skull			0.66	0.88
RW	1.02	1.27	0.72	0.51	0.95	0.94	
RW2	0.79	1.19	0.77	1.20	0.31	0.72	
			0.76	0.88			
IOC	0.06	0.17	Other breadth measurements			0.01	0.25
<i>n</i>	322	70	0.26	0.04	89	123	
% Variance explained	69.1	64.5	219	224	61.5	52.7	
			57.4	68.1			

*Coefficients are based on age classes 2-5 due to the small number of individuals available in age class 1, and measurements of the mesopterygoid fossa were omitted due to the large number of specimens for which they were missing.

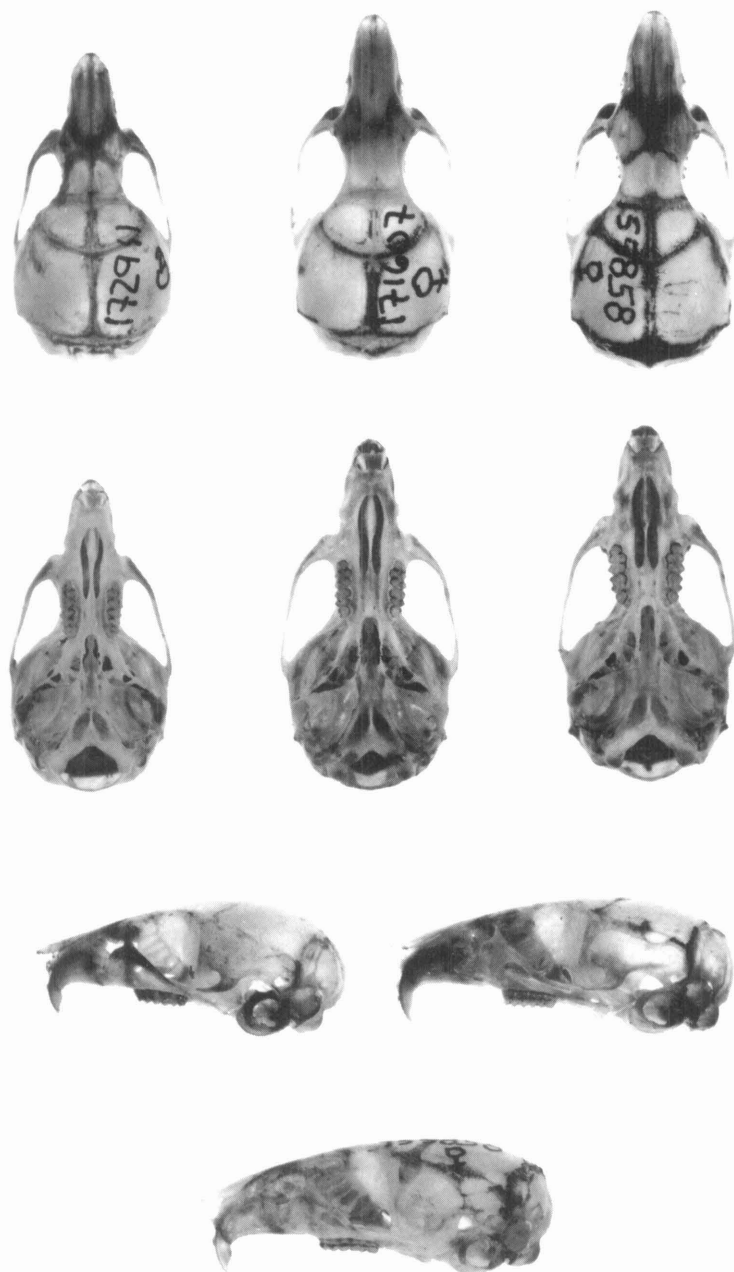


FIG. 9. Age variation in crania of *Akodon boliviensis*. First and second rows, dorsal and ventral views of MVZ 172911 (left, age class 1); MVZ 171602 (center, age class 3); UMMZ 155858 (right, age class 5). Third and fourth rows, lateral views of MVZ 172911 (left), MVZ 171602 (right), and UMMZ 155858 (bottom).

lateral surface of the cranium, the tympanic hook becomes noticeably thicker. The profile of the skull as seen from the side flattens, as already mentioned, especially in the oldest animals. Finally, on the ventral surface, the palate becomes more conspicuously grooved in older animals, and posterior to it the parapterygoid plates become more deeply excavated.

SEXUAL DIMORPHISM.—Males tend to average 1–2% larger than females in most cranial dimensions. This difference was significant when all variables were considered simultaneously in *A. boliviensis* (MANOVA, $F=1.675$, $df=20,226$, $p<0.040$) and populations of *subfuscus* from Arequipa Department, Peru ($F=2.792$, $df=20,133$, $p<0.001$), but not *puer lutescens* ($F=0.654$, $df=20,27$, $p=0.83$), *subfuscus* populations from Cusco and Puno departments in Peru ($F=0.953$, $df=20,154$, $p=0.52$), or the new species described below from central Peru ($F=1.630$, $df=20,40$, $p=0.09$). We noted no tendency for particular measurements to be consistently more dimorphic than others. We conclude that sexual dimorphism in these mice is slight and certainly less important as a source of within-species variability than age variation (even among the adult age classes) or in most cases geographic variation (see below).

COMPARISONS WITH OTHER SYMPATRIC *Akodon*

Many species of the genus *Akodon* are similar in cranial and external morphology and can be extremely difficult to distinguish. Further, most descriptions in the literature are sketchy at best. For these reasons, we begin by comparing members of the *boliviensis* group with other *Akodon* and members of certain related genera that resemble *Akodon* and have overlapping distributions.

In general, the *boliviensis* group includes the smallest members of the genus within any sympatric assemblage of akodonts. Other akodonts from central Peru south into northwestern Argentina that approach members of the *boliviensis* group in size include *albiventer*, *andinus*, *fumeus*, *kofordi*, *mollis*, *sylvanus*, and *Bolomys amoenus*; others, such as *aerosus*, *siberiae*, *simulator*, *torques*, *varius*, *Microxus mimus*, and *Chroecomys jelskii* are considerably larger and/or quite distinct in color and color pattern. Selected measurements of a few individuals from populations of these taxa are given in Table 7.

Akodon aerosus Thomas (Fig. 10A) occurs in close elevational proximity to *subfuscus* in the Sangabán Valley of northern Puno Department, Peru, and probably in nearby La Paz Department, Bolivia. It occupies upper montane forests (at elevations below those of *torques* on the eastern Andean slope in southern Peru) and ranges in the eastern Andes at least from Ecuador to central Bolivia. Compared to members of the *boliviensis* group, *aerosus* from southern Peru and Bolivia is much larger in body size and has a nearly naked but moderately long tail. It is uniformly darkly colored, typically a deep blackish or reddish brown dorsally and also dark ventrally, with gray-based but buffy-tipped hairs. It lacks an eyering. The skull is

TABLE 7.—Measurements of some species of akodonts whose ranges overlap those of members of the *Akodon boliviensis* group. Each sample combines individuals in age classes 3-5. For each measurement, mean, standard deviation (in parentheses), and sample size are given.

	<i>aerosus</i>	<i>albi- venter</i>	<i>andinus</i>	<i>dayi</i>	<i>fumeus</i>	<i>ko- fordi</i>	<i>mollis</i>	<i>sibe- rae</i>	<i>simu- lator</i>	<i>syl- varius</i>	<i>torques</i>	<i>varius</i>	<i>Bolomys amoenus</i>	<i>Microtus mimus</i>	<i>Chrooomys jelskii</i>
TOTAL	190.2 (13.31) 131	171.8 (6.80) 5	137.3 (7.23) 11	197.1 (14.30) 35	171.2 (12.64) 32	173.9 (7.52) 16	169.8 (14.00) 17	191.1 (12.01) 7	192.7 (14.02) 112	193.7 (8.02) 3	195.3 (15.93) 149	193.5 (13.57) 25	161.3 (4.16) 3	194.4 (9.17) 111	179.0 (7.07) 4
TAIL	84.4 (7.05) 139	70.6 (8.62) 5	51.7 (5.02) 11	79.3 (8.11) 35	76.2 (5.67) 32	77.6 (5.14) 16	72.0 (8.54) 17	89.1 (8.76) 7	81.6 (7.13) 112	85.0 (9.54) 3	91.3 (6.56) 149	84.8 (7.70) 25	68.0 (1.00) 3	96.0 (6.62) 111	78.8 (6.40) 4
HF	24.5 (1.16) 139	20.2 (0.45) 5	19.7 (1.27) 11	26.0 (1.51) 35	21.4 (1.44) 32	22.5 (0.97) 16	20.4 (1.77) 17	24.1 (0.99) 8	24.1 (1.69) 112	22.3 (0.58) 3	24.5 (4.33) 151	23.4 (1.85) 28	21.3 (0.58) 3	24.3 (0.97) 113	24.5 (2.52) 4
CIL	25.62 (1.09) 130	23.67 (0.37) 6	21.62 (0.52) 11	27.70 (1.11) 31	23.48 (0.85) 35	23.15 (0.70) 17	23.14 (0.76) 33	24.88 (0.49) 10	26.70 (1.11) 107	25.20 (0.66) 3	24.40 (0.73) 151	26.80 (0.93) 25	24.32 (0.57) 3	24.51 (0.57) 118	25.31 (0.85) 4
ZB	14.43 (0.61) 139	13.11 (0.28) 6	12.44 (0.23) 11	15.20 (0.78) 35	12.81 (0.38) 34	12.65 (0.36) 17	12.54 (0.40) 33	13.76 (0.31) 11	14.50 (0.58) 107	13.23 (0.47) 3	13.39 (0.42) 152	14.60 (0.43) 24	13.81 (0.17) 3	13.39 (0.38) 119	14.05 (0.61) 4
BB	12.92 (0.35) 138	11.67 (0.25) 6	11.81 (0.23) 4	12.50 (0.24) 23	11.68 (0.21) 33	11.46 (0.21) 17	11.61 (0.26) 33	12.36 (0.34) 11	12.40 (0.30) 98	11.90 (0.10) 3	12.36 (0.30) 152	12.80 (0.38) 13	11.43 (0.13) 3	12.08 (0.32) 118	12.80 (0.34) 4
IOC	5.49 (0.22) 145	4.64 (0.10) 6	4.37 (0.11) 11	5.20 (0.26) 43	4.75 (0.16) 36	4.67 (0.10) 17	5.04 (0.22) 33	5.15 (0.16) 11	5.10 (0.18) 121	4.87 (0.15) 3	5.33 (0.15) 152	5.10 (0.16) 29	4.35 (0.09) 3	5.64 (0.17) 119	4.80 (0.13) 4
NL	10.55 (0.54) 143	9.02 (0.94) 6	8.67 (0.15) 11	11.20 (0.69) 42	9.76 (0.38) 35	9.80 (0.45) 17	9.72 (0.55) 33	10.50 (0.59) 11	10.60 (0.61) 113	10.23 (0.60) 3	10.32 (0.44) 151	10.80 (0.52) 27	8.07 (0.12) 3	11.14 (0.51) 117	9.96 (0.40) 4

MTRL	4.59	4.07	3.48	4.80	4.07	3.95	4.08	4.81	4.80	4.40	4.34	4.80	4.12	4.58	4.19
	(0.20)	(0.13)	(0.18)	(0.17)	(0.17)	(0.12)	(0.12)	(0.20)	(0.21)	(0.10)	(0.19)	(0.19)	(0.12)	(0.17)	(0.07)
	144	6	11	42	36	17	33	11	119	3	152	29	3	118	4
IFL	6.00	5.68	4.86	6.80	5.94	5.73	5.40	6.37	6.90	6.73	5.95	6.50	5.63	5.71	6.26
	(0.44)	(0.22)	(0.26)	(0.34)	(0.33)	(0.28)	(0.31)	(0.23)	(0.40)	(0.25)	(0.30)	(0.26)	(0.35)	(0.30)	(0.33)
	145	6	11	43	36	17	33	11	117	3	152	29	3	119	4
MFW	1.92	1.46	1.54	1.71	1.54	1.19	1.57	1.67				1.45	1.45	1.66	1.34
	(0.18)	(0.08)	(0.09)	(0.16)	(0.17)	(0.12)	(0.15)	(0.15)				(2.10)	(0.05)	(0.15)	(0.13)
	141	6	11	8	35	17	33	11			152	6	3	118	4
ZP	2.34	2.54	2.16	2.00	2.17	2.30	2.89	2.12	2.90	2.40	1.98	2.80	2.68	1.71	2.16
	(0.20)	(0.10)	(0.06)	(0.25)	(0.17)	(0.10)	(0.26)	(0.13)	(0.23)	(0.10)	(0.18)	(0.21)	(0.11)	(0.17)	(0.17)
	145	6	11	43	36	17	33	11	120	3	152	29	3	119	4

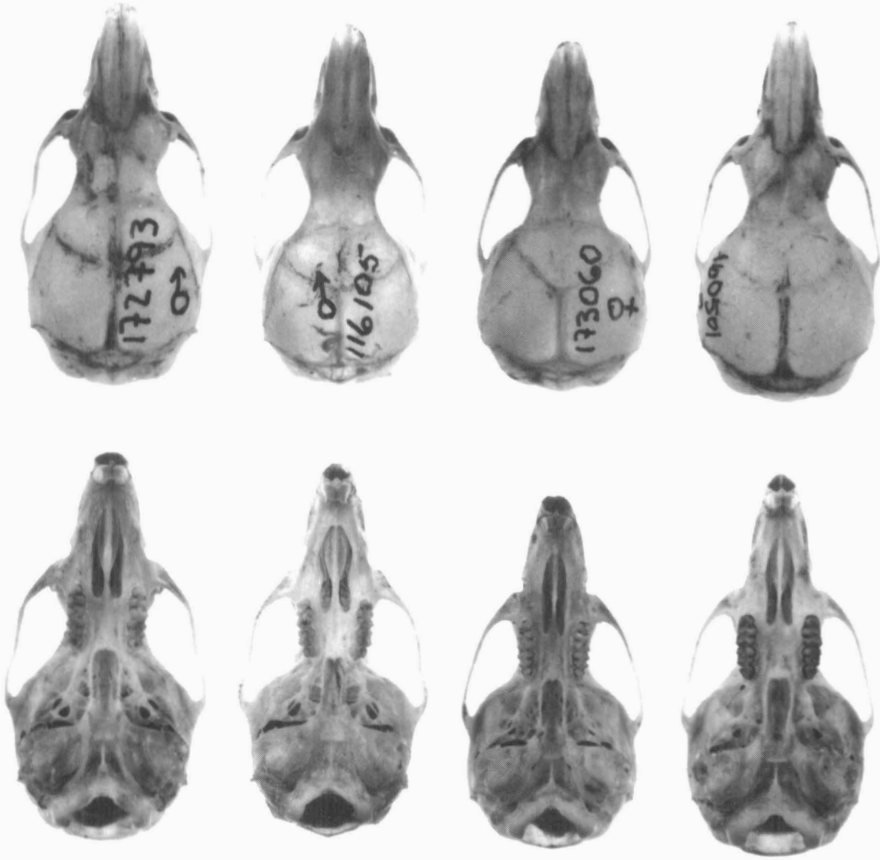


FIG. 10. Dorsal and ventral views of crania of some akodonts. A. From left to right, *Akodon aerosus* (MVZ 172793), *A. kofordi* (MVZ 116105), *A. mollis* (MVZ 173060), and *A. torques* (UMMZ 160501).

strongly built, with a short and broad rostrum, very broad interorbital region, vertical and wide zygomatic plate, broad mesopterygoid fossa, and long maxillary tooth row.

Akodon albiventer Thomas (Fig. 10B; we include *berlepschii* Thomas) ranges widely across the southern Altiplano from the Cordillera Occidental in Arequipa and Tacna departments in Peru to Salta in northern Argentina and also to northern Chile. In Peru, it prefers dense tola shrubs or rock walls (Pearson, 1951). It is a mouse of moderate to small size (similar to *boliviensis*), with comparatively short and coarse fur. The dorsal pelage is dark gray sprinkled with silver in northern localities, paler yellow brown in more southern ones, while the ventral pelage is pale and strongly contrasts with the dorsal. The skull is about the size of that of *boliviensis*, but

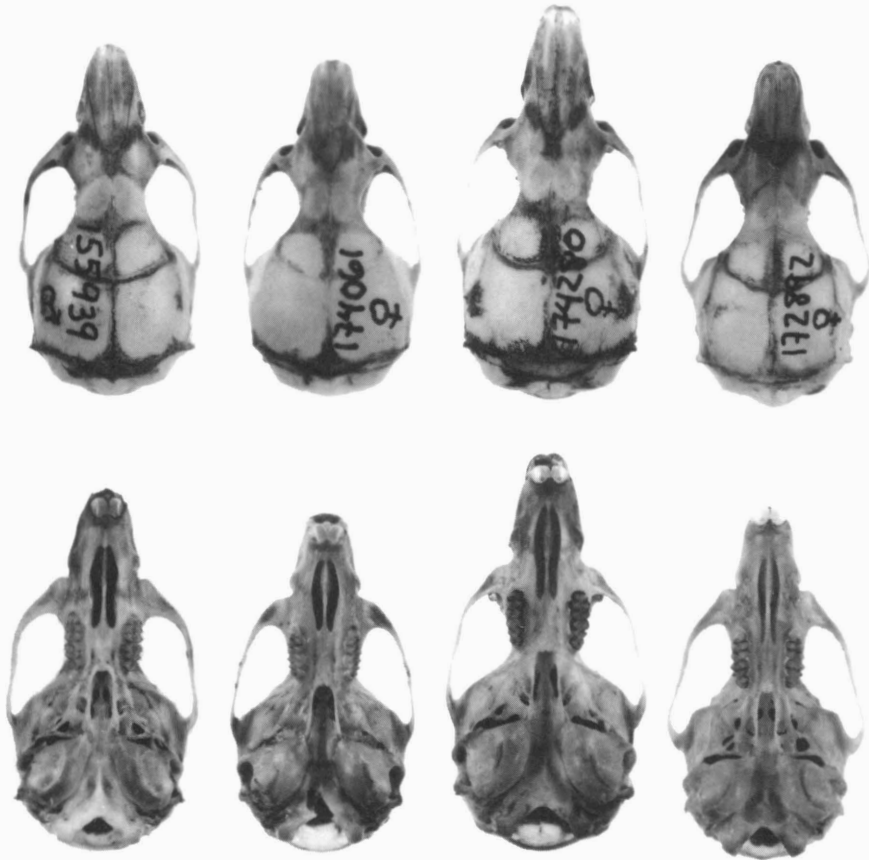


FIG. 10B. From left to right, *Akodon albiventer* (UMMZ 155939), *A. andinus* (MVZ 174061), *Chroeamys jelskii* (MVZ 174280), and *Bolomys amoenus* (MVZ 172892).

with shallower and narrower zygomatic notches, much larger tympanic bullae, shorter maxillary toothrows, and more proodont upper incisors.

Akodon andinus (Philippi) (Fig. 10B) is a denizen of the higher elevations of the Altiplano from southern Peru to northwestern Argentina. It is found in open habitats of sparse and low-stature bunchgrass and small shrubs on hard soil pavements, in contrast to the denser and lush swales of bunchgrass and tola shrublands characteristic of species of the *boliviensis* group (Pearson, 1951). This species is readily distinguished by its usually slightly smaller body size (shorter body and tail length); usually whitish as opposed to yellowish undertones to both dorsal and ventral color (some specimens from Arequipa Department, however, tend to be yellowish and similar in body color to members of the *boliviensis* group); white rather than yellow eyering; small but distinct white postauricular patches; broad and well-haired hind feet; furry tail; distinctive skull with short rostrum, broad

braincase, and enlarged, globular bullae; elongate and tapering rather than barrel-shaped phallus; and $2n = 52$ rather than $2n = 40$ or less diploid complement.

Akodon dayi Osgood is a large *Akodon* known primarily from damp forests at intermediate and low elevations in Bolivia. It resembles *Akodon varius* and *A. simulator* in many features of cranial and external morphology (Myers, 1989). Its large size (MTRL averages 4.8 mm), pronounced supraorbital ridges, and short and broad rostrum immediately distinguish it from members of the *boliviensis* group.

Akodon fumeus Thomas is known from the eastern Andean slopes at the moist grassland-elfin forest interface in extreme southern Peru and Bolivia. It shares general size, cranial, and pelage color characteristics with *mollis* (with which it has been linked by Cabrera, 1961; Gyldenstolpe, 1932; Myers and Patton, 1989a; and Hershkovitz, in manuscript) and can be distinguished from sympatric or contiguous populations of the *boliviensis* group by the basic characteristics listed under *mollis*, below. It occurs at slightly lower elevations than the *boliviensis* group species on the eastern slope (Myers and Patton, 1989a).

Akodon kofordi Myers and Patton (Fig. 10A) is known from the Limbani and Marcapata drainages of southeastern Cusco and Puno departments, Peru. It is very similar to *fumeus* and *mollis* but can be distinguished from those species by the combination of its lyre-shaped mesopterygoid fossa, M^1 with an island apparently formed from part of the paraflexus, olivaceous pelage, and unicolored tail. It occurs sympatrically or nearly sympatrically with *subfuscus*, and in fact the series of "topotypes" listed in the description of *subfuscus* (Osgood, 1944) contains several examples of *kofordi*. The two can be distinguished by *kofordi*'s broader mesopterygoid fossa, M^1 with an island, unicolored tail, and dark feet.

Akodon mollis Thomas (Fig. 10A), an inhabitant of the montane regions and Pacific lowlands from central Peru northward, is very similar to members of the *boliviensis* group, with which it may occur sympatrically in the southern part of its range. It is somewhat larger in all external and most cranial dimensions, with longer maxillary toothrow (average 4.1 mm *vs.* 3.7 mm), darker dorsal and ventral color, brown rather than yellowish pinna and shorter pale tips to the ventral fur. In most individuals of *mollis*, the mesopterygoid fossa is conspicuously broader than in *boliviensis* or its allies. Where sympatric with an undescribed member of the *boliviensis* group (described below) in central Ancash department, *mollis* occurs in denser shrub habitats on moister slopes with better drained soils (field notes of Carl Koford in MVZ files). In central Junín Department, *mollis* occurs at lower elevations than this undescribed species (below about 3000 m) along transects on the eastern slope.

Akodon siberiae Myers and Patton is a newly described species, similar to *Akodon budini* of northern Argentina. It has been collected in the elfin forests of the departments of Cochabamba and Santa Cruz, Bolivia, where it is sympatric with *Akodon fumeus* and *Microxus mimus* and narrowly ecologi-

cally segregated from *Akodon puer* (which occurs in grasslands at higher elevations, contiguous with elfin forests; Myers and Patton, 1989b). From *puer*, *siberiae* differs by its large overall size, dark blackish-brown coloration, lack of an eyering, large skull with long palate, flat profile, rounded but very broad braincase, rounded but broader interorbital region, shallow but broad zygomatic notches, narrow but relatively vertical zygomatic plates, weak and not flared zygomatic arches, and long incisive foramina.

Akodon simulator Thomas is a member of the "varius" group (Myers, 1989). It is a large, gray or brown mouse with prominent buffy eyerings and cheeks, divergent and squared interorbital region, broad rostrum, well-developed temporal and mastoid ridges, long palate, and deep and broad zygomatic notches. It is found in sympatry with two members of the *boliviensis* complex in northwestern Argentina (Barquez *et al.*, 1980).

Akodon sylvanus Thomas is probably close to *mollis* and *fumeus*, although others have considered it to be related to *A. azarae* (e.g., Thomas, 1921; Cabrera, 1961). The type locality is in "thick damp woods at 1200 to 2000 metres" in Jujuy Province, Argentina, and it has also been reported from Tarija Department, Bolivia (Thomas, 1926a). We have examined three specimens from El Simbolar, Jujuy (CM 43392, 43394, and 43396) that are probably this species. They are approximately the size of *mollis*, slightly larger than *boliviensis*. Dorsally, they are dark gray-olivaceous, much darker than most *boliviensis*-group species. The tops of their feet are clothed with dark hairs, unlike any member of the *boliviensis* group. The tail is only weakly bicolored, and the chin and throat lack any all-white hairs. The cranium is similar to that of *mollis* in general conformation. The foramina ovale are unusually large, and the bullae also appear larger than usual for the genus. Compared to typical *boliviensis*, these specimens are larger, have proportionately larger teeth, a wider mesopterygoid fossa, and a longer rostrum.

Akodon torques (Thomas) (Fig. 10A) inhabits the upper elfin forest on the eastern slope of the Andes in Ayacucho and Cusco departments in southern Peru at elevations from about 2000 m to 3500 m. It is sympatric with *subfuscus* in these regions but segregated by habitat, being found most commonly in the dense moss mats under canopies formed by trees or large shrubs, while *subfuscus* is present in adjacent clumps of tall, lush bunchgrass. This species is considerably larger in overall size than *subfuscus*, with a nearly naked, much longer tail (approximately 98% of head-body length, compared to 76% for *subfuscus*). It is rather uniformly dark gray brown above and below, and it lacks a distinct eyering. The skull is much larger, with a more elongate rostrum; a narrow, posteriorly slanting zygomatic plate; and a much longer maxillary toothrow.

Akodon varius Thomas is a large, brownish mouse, heavily streaked with gray and with pale eyerings. Its skull has pronounced supraorbital ridges that form sharply squared sides over the interorbital region, a rather short and broad rostrum with short incisive foramina and diastema, and a long maxillary tooth row. It occurs along the eastern Andean escarpment in

Bolivia, from Cochabamba probably to Tarija Department (Myers, 1989), but usually at lower elevations than members of the *boliviensis* group.

Bolomys amoenus Thomas (Fig. 10B) is sympatric with *Akodon boliviensis*, *puer*, and *subfuscus* in the high elevation grasslands of the departments of Cusco, Puno, Arequipa, Moquegua, and Tacna in Peru, and in adjacent Bolivia. It is easily distinguished by its somewhat larger size; short and coarse fur; long claws on the fore feet; distinct yellow-orange suffusion dorsally, particularly around the face, eyes, legs, feet, and tail, contrasting with a white venter; and cranium with short rostrum but strongly proodont incisors.

Chroemys jelskii Thomas (Fig. 10B) is also a resident of the high elevation grasslands of the Altiplano, from Pasco Department in central Peru to northwestern Argentina (Sanborn, 1947). It is sympatric with each of the four Peruvian and Bolivian species of the *boliviensis* group at some point in its extensive range. It is readily distinguished from these species, however, by its larger size and highly distinctive pelage color and color pattern. In central Peru, *C. jelskii* is gray above with orange-tipped hairs, a paler buffy venter, and with an orange nose, face, ears, feet, and tail. In southern Peru, members of this species have chocolate brown to reddish brown upperparts, white underparts, with an orange nose and orange tinge on the feet, but with very distinctive white thighs, pinnae, and postauricular patches that are usually confluent with white cheeks and throat. Cranially, *C. jelskii* can be distinguished from members of the *boliviensis* group by its large size, broad mesopterygoid fossa, no alisphenoid strut, relatively large bullae, and numerous other characteristics.

Microxus mimus (Thomas), like *Akodon torques*, inhabits the upper elfin forests on the eastern Andean slopes. It replaces *torques* geographically in these habitats from Puno Department of Peru to eastern Cochabamba Department in Bolivia. *Microxus mimus* is a mouse of moderate size and uniformly gray-brown color above and below, without an eyering, and with an absolutely and proportionately long tail (usually longer than the head-body length). Its skull is gracile and has a very elongated rostrum and narrow, posteriorly slanting zygomatic plates. Virtually all of its features are accentuations of those described above for *torques*. It is currently known to be sympatric, but segregated by habitat, with *puer* in east-central Bolivia but not elsewhere along the eastern slope.

Other named forms of *Akodon* that have been identified in the geographic area encompassed by this study are treated in the accounts that follow. Included among these are *alterus* Thomas, *azarae* (Fisher), *caenosus* Thomas, *lutescens* J. A. Allen, *pacificus* Thomas, *spegazzinii* Thomas, and *tucumanensis* J. A. Allen.

ACCOUNTS OF SPECIES

We begin our discussion of species of the *Akodon boliviensis* group with the description of a new species from central Peru. We then provide

emended diagnoses, descriptions, and discussions of variation for the species *A. boliviensis* (the type species of *Akodon*), *A. puer* (including *A. p. lutescens* and *A. p. caenosus*), and *A. subfuscus* (including the description of a new subspecies).

Recent collections from Junín and Ayacucho departments include an *Akodon* that is very similar morphologically to members of the *boliviensis* group from nearby areas in Ayacucho and Apurímac departments, but that stands out electromorphically. Further collecting and study has shown that this form differs morphologically from all other *Akodon* in ways that are consistent but often subtle. We name this form

Akodon juninensis new species

HOLOTYPE.—MVZ 173044; adult female (age class 3–4); skin, skull, and tissues; collected 7 August 1986 by J. L. Patton, original no. 13390.

TYPE LOCALITY.—22 km N La Oroya (by road), Depto. Junín, Peru, 4040 m (at the junction of roads to Junín [Hwy 3] and Tarma [Hwy 20]).

DIAGNOSIS.—*Akodon juninensis* is a species of the *boliviensis* group characterized by the following combination of characteristics: overall size intermediate (Table 4); zygomatic notches small and shallow; zygomatic plates narrow; posterior ascending process of the alisphenoid usually contacting the squamoso-alisphenoid groove; postglenoid and subsquamosal foramina small; foramen ovale completely or almost completely walled over by bone; small but distinct metaflexus on M³; anteromedian flexus on M¹ usually shallow; phallus with a moderately well-developed crater rim and relatively short urethral flaps; uniquely fixed alleles at two allozyme loci (Ck-1 and ICD-1) (see above, p. 9).

RANGE.—*Akodon juninensis* is known from elevations above 2700 m in the central Peruvian departments of Ancash, Junín, and Lima on both eastern and western escarpments of the Andes, south on the Pacific slope to south-central Ayacucho (Figs. 11, 12).

DESCRIPTION.—*External characters.* The dorsum is medium brown to pale olivaceous, heavily lined with black. Fur hairs average 10–11 mm long in the midrump region. Pheomelanin bands on individual fur hairs are 1.0–1.5 mm long and Warm Buff to Ochraceous Buff (depending on the population). Black guard hairs are moderately dense and long, projecting 5–7 mm beyond the level of the fur on the rump. In the midventral region approximately 80% of each hair is slate gray, with the tips whitish or buffy. The inguinal region appears similar to the midventral area. Hairs on the chin and sometimes the upper throat are monocolored and white.

As in other members of the group, the ears of *juninensis* are densely furry, with individual hairs agouti; the vibrissae are short and relatively inconspicuous; and a yellowish eyering is present (but inconspicuous compared to that of most other members of the group).

The tail is densely furred and sharply bicolored; the dark stripe occupies the dorsal one-third of the circumference of the tail. Individual hairs on

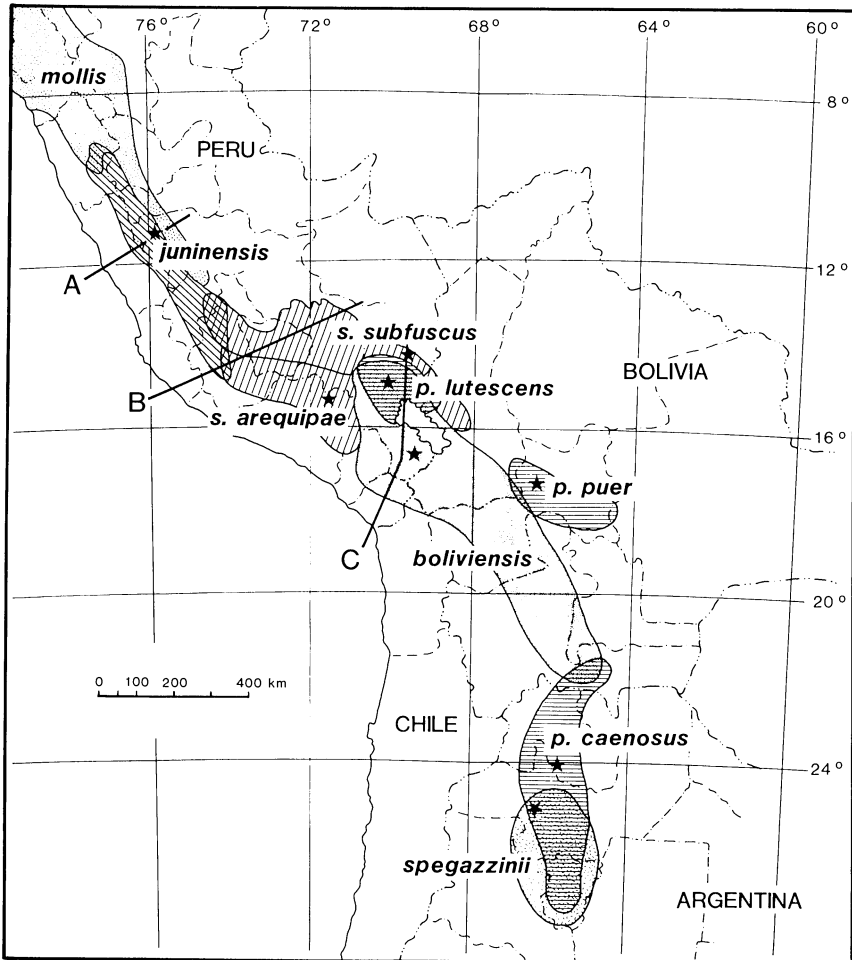


FIG. 11. Distribution of the species of the *Akodon boliviensis* group. The geographic relationship of members of this group to *A. mollis* in central Peru is also indicated. Lines A through C refer to the elevational profiles of species distribution in Fig. 12.

the tail run the length of 2.5–3 scales. The length of the tail is approximately 71% of the head-body length.

Cranial characters (Fig. 13). Dorsally, the cranium appears relatively narrow (Table 4). The zygomatic notches of *juninensis* seem especially narrow compared to those of other species of the *boliviensis* group, appearing compressed, but this difference can only be appreciated if individuals of the same age are compared, and the difference appears less in older individuals. The interorbital region is hourglass-shaped; its sides are rounded anteriorly to squared or nearly squared in the posterior part of the orbit. Lacrimals are usually present but very small. The zygomatic arches are

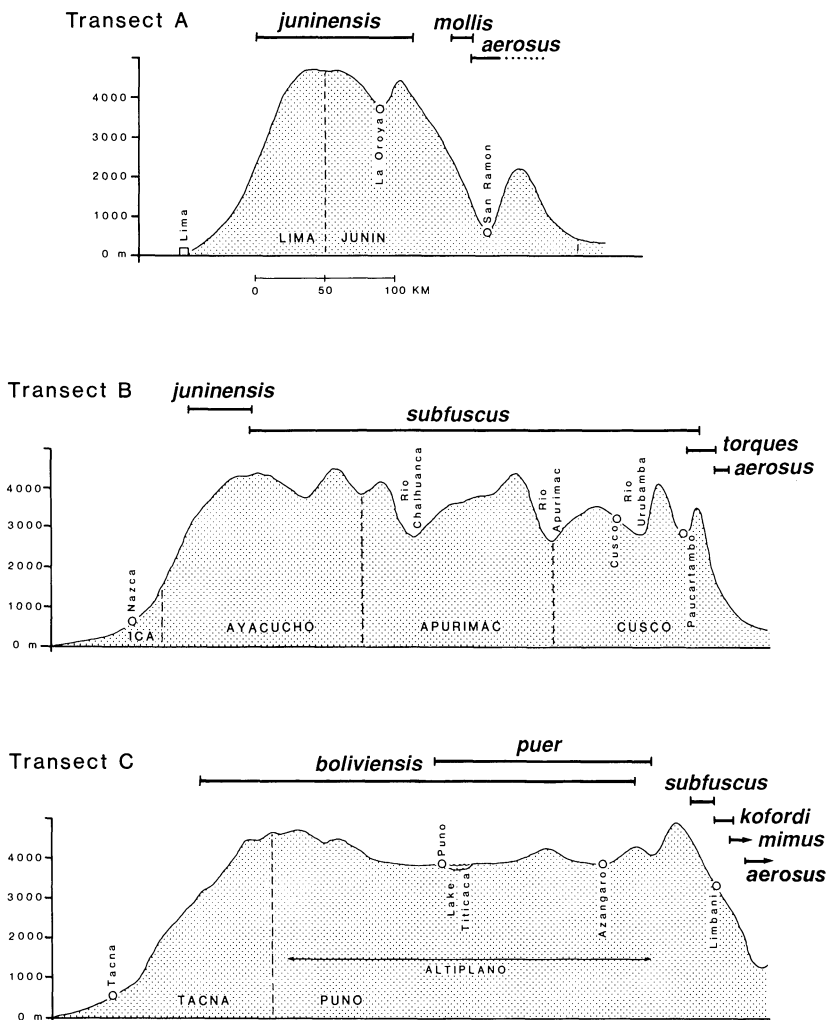


FIG. 12. Elevational and horizontal distributions of species of *Akodon* along three west to east transects from central to southern Peru (see Fig. 11). Elevational topography is provided, as are department boundaries, major drainages, and large cities. Altiplano species have very broad horizontal distributions; those on the eastern slope, in contrast, have very narrow elevational limits.

only slightly flared and ZB is correspondingly small. Temporal and mastoid ridges are absent or weakly developed.

The transverse section of the skull at the level of interorbital constriction is rounded, so that a skull placed on its dorsal surface tends to roll onto its side.

In lateral view, the dorsal profile of the cranium is relatively flat to gently rounded. The zygomatic plates appear more reclined and somewhat narrower than is usual for the group. The posterior ascending process of the alisphenoid reaches dorsally to or almost to the squamoso-alisphenoid

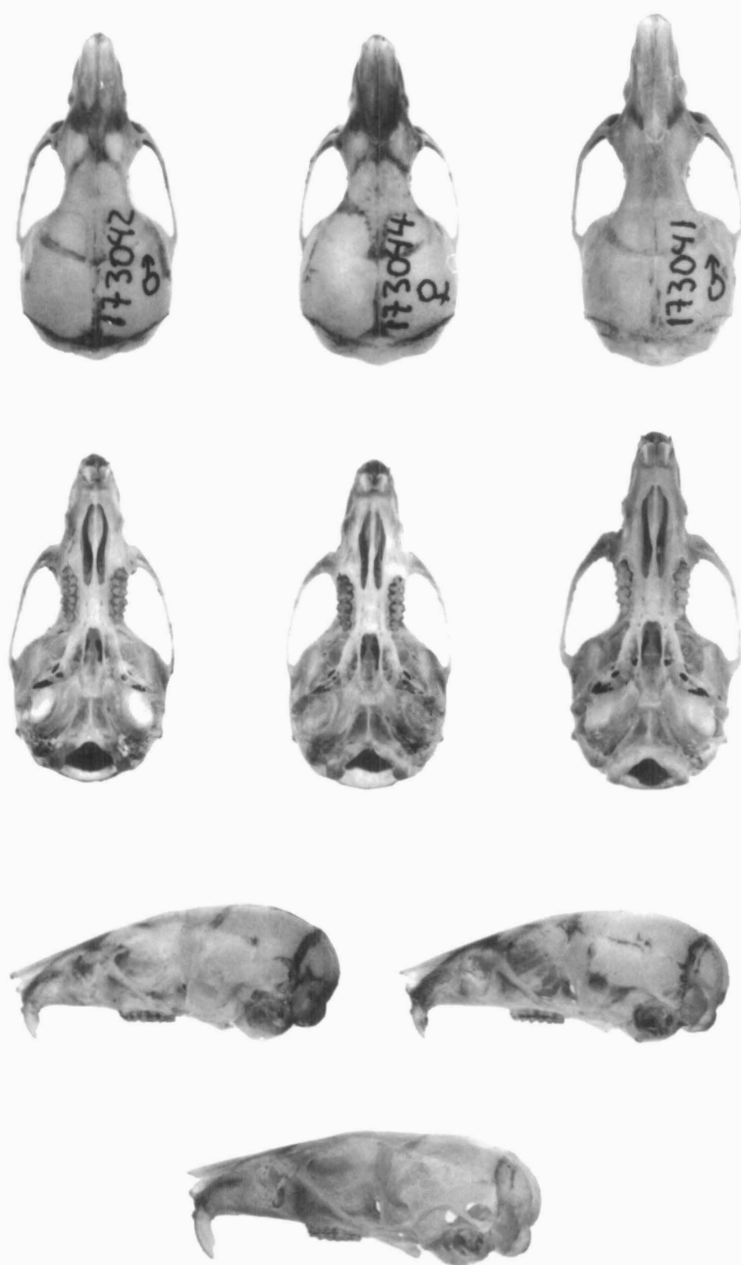


FIG. 13. Crania of *Akodon juninensis*. First and second rows, dorsal and ventral views of (left) MVZ 173042 (age class 2), (center) MVZ 173044 (age class 3), and (right) MVZ 173041 (age class 5). Third and fourth rows, lateral views of MVZ 173042 (left), MVZ 173044 (right), and MVZ 173041 (bottom).

groove. Both the postglenoid and subsquamosal foramina tend to be smaller than in other members of the group, but like-age animals must be compared for this to be appreciated. The tympanic hook is slender to medium-sized.

Useful characteristics on the ventral surface of the cranium include the following: the palate is deeply grooved; the mesopterygoid fossa is broad (Table 4) with the anterior end usually gently rounded to squared and lacking a median spine; the foramina ovale are very small, at most attaining the size of M^3 and sometimes completely closed by bone; the median lacerate foramina are unusually narrow; and the sphenopalatine vacuities are of average size for the group.

Akodon juninensis appears to differ slightly from other members of the group in the allometric coefficients describing cranial growth (Table 6). It has unusually large coefficients for measurements of anterior length (DL, IFL, ZP), and strikingly small coefficients for other measurements, including BOL and two measurements of cranial breadth, MB and RW2. These coefficients appear to describe a pattern in which crania become relatively longer and narrower as they age compared to the crania of other members of the group.

Dental characters (Fig. 14). Most characteristics of the upper molars are as described for the group. The following attributes stand out: (1) M^3 is small, and at least in young animals with unworn or moderately worn teeth, the metaflexus is shallow (but usually present); (2) while an anteromedian flexus on M^1 is always present, it is often unusually shallow (particularly in specimens from Lima and Ancash); (3) M^1 always lacks a metalophule (*vs.* sometimes present in the other species of the group).

The molars of the lower jaw are as described for the group.

Accessory glands. The male accessory reproductive glands are as described for the group. The medial prostates tend to be unusually small, however, and the surface of the vesicular glands lacks the knobs that are characteristic of some species.

Phallus and baculum (Fig. 15). The shaft is sub-cylindrical with nearly parallel sides and a convex dorsal profile. Weakly developed ventral and dorsal grooves are present and confluent with the crater lip. The crater lip is only weakly expressed, and it surrounds the entire opening; a small but clearly visible dorsal notch is present, but ventral and lateral notches are absent. The epidermal spines are small, fine, dense, grade to a smaller size distally, and are imbedded in individual but shallow pits. The epidermal surface appears smooth. Both lateral and medial bacular mounds extend above the crater rim, with the lateral mounds situated slightly ventrad to the medial one. The urethral flaps are long, tapering, with well-separated tips lacking noticeable lateral spines; they reach the level of the crater lip but do not extend beyond it. The dorsal papilla is well developed and elongate in shape. It has a distinctly tapering tip, which is surrounded by folds of tissue that extend from the medial bacular mound to the inner crater wall only at its base, and the tip ends in a distinct spine. The phallus

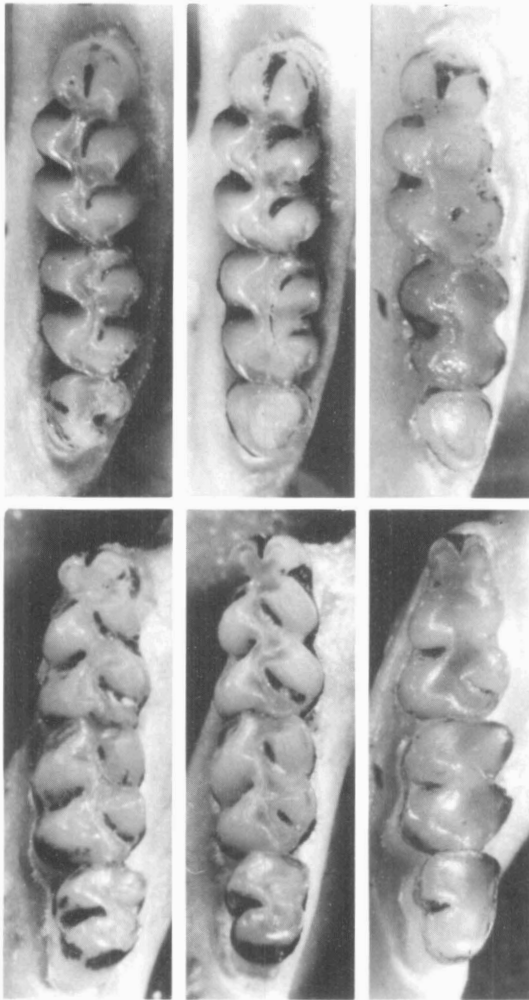


FIG. 14. Molars of *Akodon juninensis*. Upper left molars on top; lower left molars on bottom. From left to right, AMNH 231351 (age class 2), AMNH 231359 (age class 3), MVZ 173038 (age class 4).

of *juninensis* is similar to that of *subfuscus* or *puer*, described below, differing only in the presence of a distinct dorsal notch, a narrow rim that circumscribes the entire crater, the lack of urethral flaps that are exposed distally beyond the lip, and the somewhat more ventrally located lateral bacular mounds.

The proximal baculum is short, with a stout central shaft and a laterally flared base as in other members of the group. A distinct medial notch is present in the base in ventral view. Laterally, the shaft is straight. The distal baculum is tridigitate and cartilaginous, with the lateral digits about

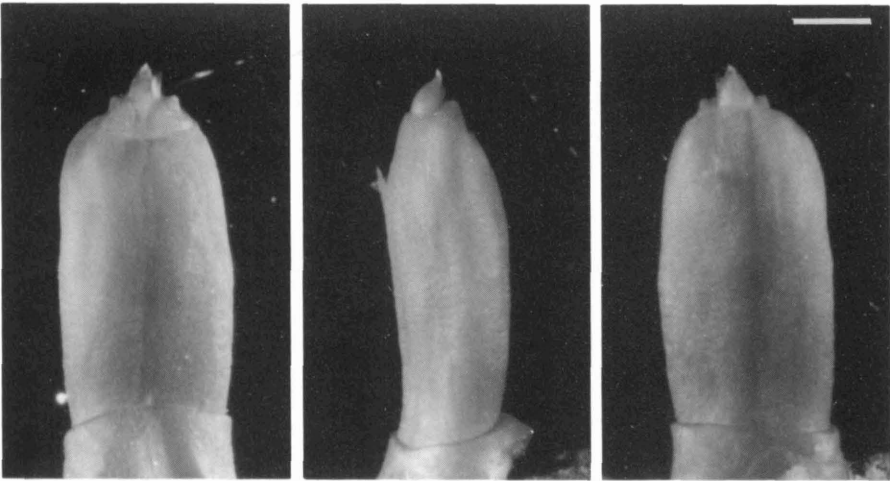


FIG. 15. Ventral, right lateral, and dorsal views of the phallus of *Akodon juninensis* (AMNH 232640); line = 5 mm.

three-fourths the length of the medial one. The proximal baculum averages 2.09 times the length of the distal component (range 1.98–2.23).

Palatal rugae (Fig. 7). The diastemal rugae are complete but both are slightly arched at the midline, and the second ridge lacks a medial notch. All four interdental rugae are incomplete. The first three have straight edges, but each slopes posteriorly towards the midline.

Karyotype. $2n = 40$, $FN = 40$. Karyotypes of this species were prepared by field parties led by Carl Koford in 1969. The description that follows is based on photographs in the MVZ files.

The autosomal complement of *juninensis* is composed of 18 pairs of acrocentrics, one of which is distinctly larger than the remainder, while the remainder grade evenly in size from medium to small. There is also one pair of small metacentrics. The X chromosome must be an acrocentric, as the only biarmed elements present are the small metacentric pair. The morphology of the Y chromosome is unknown as only females have been examined.

HABITAT.—*Akodon juninensis* primarily occupies clumps of dense bunchgrass at elevations above 3800 m in well-drained and fine-grained soils. In the highlands of central Ancash, Carl Koford (unpublished field notes) noted a distinct habitat separation between this species and specimens we allocate to *Akodon mollis*, with *mollis* found in denser shrub habitats on moister slopes with better drained soils. On the western slope in Lima Department, *juninensis* extends down into the sparse perennial forests at elevations as low as 2700 m. This species is also sympatric with *Chroecomys jelskii* in Junín Department, with the latter preferring denser grass-rock areas.

Other sigmodontines known to co-occur with this species are *Auliscomys*

TABLE 8.—Geographic variation in *Akodon juninensis**†‡. Distances between regions were not calculated due to the small number of specimens in the Ayacucho sample.

	Ancash	Lima/ Junín	Ayacucho
CIL	22.62	22.50	23.35
ZB	11.77	11.81	12.31
BB	10.80	10.95	11.08
IOC	4.42	4.31	4.34
RL	9.10	8.95	9.19
NL	9.03	8.98	9.25
RW	4.42	4.57	4.84
RW2	3.72	3.77	3.99
OL	8.08	7.98	8.27
DL	6.41	6.40	6.77
MTRL	3.69	3.76	3.75
IFL	5.52	5.52	5.83
AW	4.73	4.67	4.82
OCW	6.00	6.01	5.88
MB	10.51	10.67	10.53
BOL	3.62	3.48	3.57
MFW	1.21	1.20	1.15
ZP	1.92	1.91	2.21
CD	9.18	9.07	9.15
<i>n</i> =	6	70	3

*The regions are defined as follows (numbers refer to locality numbers in Appendix I): Ancash, 1-3; Lima/Junín, 4-10; Ayacucho, 11, 72.

†The columns present "age corrected" mean values (mm) for measurements from specimens representing each regional sample. MFL was omitted due to the large number of missing values.

‡The overall test for equality of means (maximum likelihood ratio criteria, Rao, 1973) is significant (MANOVA, $df=38,116$; $F=1.7998$, $p<0.01$).

pictus, *Phyllotis andium* and *darwini*, *Calomys sorellus*, *Neotomys ebriosus*, and species of *Oligoryzomys*.

GEOGRAPHIC VARIATION (Table 8).—Samples from eastern Lima Department were combined with those from adjacent areas of Junín Department and compared with those from Ancash and Ayacucho departments. Minor but statistically significant differences were noted in age-corrected cranial dimensions. Three specimens from the southern part of the range of *juninensis* (Huancavelica and Ayacucho departments) averaged slightly larger in most dimensions but otherwise did not differ from specimens elsewhere in the range.

The color and color patterns of individuals from each population were similar.

COMPARISONS.—Within the *boliviensis* group, the most useful qualitative characteristics for distinguishing *juninensis* and *boliviensis* are the narrow zygomatic notches, narrow zygomatic plates, small foramina ovale, and distinctive M^3 s of *juninensis*. *Akodon juninensis* differs from Peruvian *puer*

and *subfuscus* in having slightly larger overall size and narrower cranium, small foramina ovale, small subsquamosal foramina, and phallus with a dorsal notch on the crater lip, as well as by electromorphic characters. These differences are discussed further in the species accounts that follow.

Akodon juninensis can easily be distinguished from akodonts not included in the *boliviensis* group by a combination of the small size, dull color, and relatively narrow and straight-sided mesopterygoid region of *juninensis*. The most difficult distinction is with *A. mollis*, with which it may occur in sympatry or near sympatry. From *mollis*, *juninensis* can be distinguished by its smaller overall size (maxillary tooth row length averages 3.71 mm vs. 4.11 mm for samples of *mollis* in Junin Department); narrower mesopterygoid fossa (MFW 1.14 mm for *juninensis*, 1.57 mm for *mollis*); and by its pelage, which in *juninensis* is paler dorsally, more yellow than deep brown, with agouti hairs in the pinnae appearing strongly yellowish (giving the ears a yellow rather than brown appearance), and paler ventrally as a result of less of the gray base of each hair showing through. Chromosomally, this species has $2n = 40$ while sympatric or nearly sympatric *mollis* has $2n = 22$.

REMARKS.—Thomas (1926b:317) allocated specimens of this species from Hacienda Atocsaico and from Oroya, Junin Department, to *Akodon puer*, remarking on features distinguishing it from *A. mollis*, including "... smaller size, yellower colour, and very small teeth." While we have not examined these particular specimens, they doubtless belong to *juninensis*, not *puer*.

Akodon boliviensis, the type species of the genus *Akodon*, was first described in 1833 by F. J. F. Meyen in a brief account. The description gives some external measurements and information on color, and it is accompanied by a rough drawing of the mouse, its feet, and its molars. The type locality is given as the Peruvian Indian village of Pichu-pichun, at an elevation of 14000 feet. No holotype is mentioned in the account, and we are not aware of any having been designated.

Size, color, and elevation at the locality of capture clearly suggest that the mouse is a member of the group of mice defined above. Can this name be assigned with confidence to any one of the species that we recognize? Two arguments suggest that it can.

First, as far as is known, only one species of the group is found at the type locality. Most earlier authors assumed this place to be Mt. Pichu-Pichu, near Mount Misti, to the northeast of Arequipa in Arequipa Department (e.g., Thomas, 1901; Gyldenstolpe, 1932; Tate, 1932). Sanborn (1950:11-12), however, after careful inquiry, ascertained that Pichu-pichun is a small hacienda near the village of Huacullani, located south of Lake Titicaca in the province of Chucuito of southern Puno Department (listed as "Pichupichuni, 12600 ft., 5 mi NW Huacullani" by Pearson [1958]; Huacullani is at approximately 16°38'S and 69°19'W on the 1983 Mapa Físico Político of the Departamento de Puno, Instituto Geográfico

Militar, Lima). Two members of the *boliviensis* complex are known from high elevations in central and southern Puno Department. Only one has been taken within 100 km of Pichu-pichun, however, and it would seem reasonable to assign the name to it.

Secondly and more critically, the drawing of the molars that accompanies Meyen's description clearly depicts a bilophodont third upper molar with strongly developed metaflexus and hypoflexus. This is an unusual condition for the genus *Akodon*. It characterizes one member of the *boliviensis* complex, the same species that is known from the vicinity of Pichu-pichun. This form is relatively large bodied and has a long toothrow. Its external measurements are consistent with those given by Meyen. These observations lead us to assign the name *boliviensis* to the following taxon:

Akodon boliviensis Meyen

Akodon boliviense Meyen, 1833; Nova Acta Acad. Leop.-Car., 16:600 (type description).

Akodon boliviense, Tschudi, 1845; Fauna Peruana, 1844:177.

Akodon boliviensis, Trouessart, 1898; Catal. Mammal., 2:535.

Akodon pacificus Thomas, 1902; Ann. Mag. Natur. Hist., ser. 7, 9:135 (type locality: La Paz, W. Bolivia).

HOLOTYPE.—None identified by Meyen.

TYPE LOCALITY.—“Auf der Hochebene von Hochperu, in dem Indianerdorfe Pichu-pichun, auf einer Höhe von 14000 Fuss gefangen.”

EMENDED DIAGNOSIS.—*Akodon boliviensis* is a large species of the *boliviensis* group. The head-body length of adults averages 91.0 mm, the hind foot 21.2 mm, the condyloincisive length 22.44 mm, and the maxillary tooth row length 4.01 mm (range 3.7–4.4 mm). *Akodon boliviensis* is distinguished by its broad (but nevertheless shallow) zygomatic notches, moderately broad braincase, and relatively strongly developed temporal and mastoid ridges. In most individuals the posterior ascending process of the alisphenoid projects dorsally in *boliviensis* at least to the squamoso-alisphenoid groove. Relative to its large size, *boliviensis* also appears to have a narrow interorbital region and broad zygomatic plates compared to other members of the group. Finally and perhaps most distinctively, *boliviensis* has strongly bilophodont third molars above and below.

RANGE (Figs. 11, 12).—Distributed largely in the drier southern half of the Altiplano in Puno Department west and south of Lake Titicaca to the western Andean slopes in Moquegua and Tacna departments in Peru, at elevations above 3700 meters. The distribution of *boliviensis* in Bolivia is poorly understood, but spotty records are available from the highlands of that country south to Tarija Department. This species may also extend into the highlands of northwestern Argentina, in the provinces of Jujuy, Salta, Tucumán, and Catamarca as the named forms *spgazzinii* Thomas, *tucumanaensis* J. A. Allen, and *alterus* Thomas, although at present it is not clear that these populations are conspecific with true *boliviensis* (see below).

DESCRIPTION.—*External characters.* Dorsally, individual *boliviensis* from southern Peru are pale brown, tinged olivaceous. The pelage is uniformly colored across the back and crown, appearing to be lightly streaked with black due to moderate numbers of long, black or dark brown guard hairs. Pheomelanic bands on the fur hairs are about 2 mm long and near Yellow Ochre or Antimony Yellow. The dorsal fur averages 11 mm long over the rump and is particularly fine and dense. Guard hairs are especially long, extending beyond the level of the fur hairs by 5 mm or more. Color and pattern of the flanks are similar to the dorsum. The yellow eyerings are narrow but conspicuous. On the venter, hairs are buffy tipped for about one-fourth of their length, with their tips similar in color to the pheomelanin of the dorsum. The inguinal area in some individuals appears especially dark, almost rufous. A small patch of white fur occurs at the apex of the chin; this may not, however, be visible on dried skins due to distortion associated with drying.

Akodon boliviensis has a sharply bicolored tail, with the dorsal band occupying about one-third the circumference of the tail (1–2 mm wide). The tail appears heavily invested with hairs (relative to most other *Akodon*); these hairs extend about the length of 3–4 scales. The tail averages about 65 mm in adults (age classes 3–5), or about 71% of head-body length.

Cranial characters (Figs. 3–6, 16; Table 4). Most characteristics of the crania of *boliviensis* are as described above in the description of the *boliviensis* group. They differ, however, from crania of other members of the group in several ways. In dorsal view, the zygomatic notches are unusually broad (and indeed, broader relative to the size of the cranium than those of most members of the genus). These notches broaden and deepen substantially with age, so it is essential to compare animals of similar toothwear class. The zygomatic arches tend to flare laterally more than in other members of the group and ZB is correspondingly large. Lacrimals are usually present in cleaned skulls and unusually large. The interorbital region is narrow, and its posterior margins have a greater tendency to be sharply squared than is usually the case within the *boliviensis* group. Temporal and mastoid ridges are also unusually strongly developed, especially in older animals.

Laterally, the dorsal profile of the cranium is relatively flat, especially in older individuals. The zygomatic plates are relatively broad, and their anterior face tends to be vertical. The posterior ascending process of the alisphenoid projects dorsally at least to the squamoso-alisphenoid groove. The postglenoid foramen is of medium size for the group and is slightly larger than the subsquamosal foramen. The tympanic hook appears stout (Fig. 16).

On the ventral surface of the cranium, the incisive foramina are long and narrow. The palate is moderately deeply grooved. The anterior margin of the mesopterygoid fossa is usually squared and often has a small median spine (Fig. 6). The mesopterygoid fossa is especially narrow, and the sphenopalatine vacuities are open and broad, but the presphenoid is

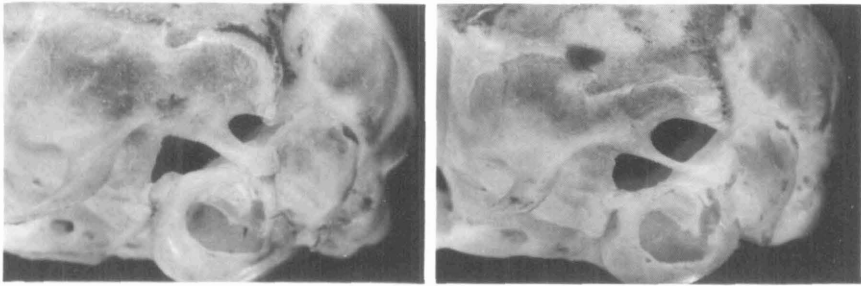


FIG. 16. Tympanic hook (hamular process) of *Akodon boliviensis* (MVZ 171603, left) and *A. puer lutescens* (MVZ 171614, right).

usually wider at the level of the vacuities than the breadth of the individual vacuity on either side. The foramina ovale are substantially larger in diameter than M^3 , while the median lacerate foramina are about as long and wide as M^1 .

Dental characters (Fig. 17). In the upper teeth of the youngest specimens we examined, M^1 always had a well-formed parastyle but lacked a proto-style. A mesostyle was also present but rather small, and a metalophule was occasionally present. A few specimens had a suggestion of an enteroloph or enterostyle, but in most the lingual face of the hypocone was smooth. In M^2 , an anterior cingulum was always present. A mesostyle was present, but both enterostyle and metalophule were lacking.

The M^3 of *boliviensis* is unique among members of the *boliviensis* group. Among the young animals we examined, it was invariably large and complex compared to that of other members of the group (and indeed, the genus), averaging about half the length of M^2 . A distinct anteroloph was present in at least some very young animals (age class 1), and in all but the oldest, major folds, probably the metaflexus plus hypoflexus, partly divided the tooth near or just posterior to its middle, making it distinctively "8"-shaped. The tooth always lacked a posteroloph.

The lower teeth resemble those of other members of the group. In M_1 , a protostylid was present but sometimes small, and the metastylid was always absent. In both M_1 and in M_2 , an ectostylid and mesostylid were sometimes present but always tiny.

In its unworn condition, M_3 is long, about two-thirds to three-fourths the length of M_2 . As in M^3 , the tooth was conspicuously "8"-shaped in all young specimens examined; this shape, however, is found in all species of the group. A trace of an anterior cingulid was seen in a few specimens.

Male accessory glands. The male accessory glands are as described above for the *boliviensis* group. They differ from those of *juninensis* and *subfuscus* in that (1) the medial ventral prostates are larger, and (2) distinctive knobs are present on the surface of the vesicular glands.

Phallus and baculum (Fig. 18). The glans penis is short and stocky, somewhat barrel-shaped and with the dorsal surface convex in lateral profile.

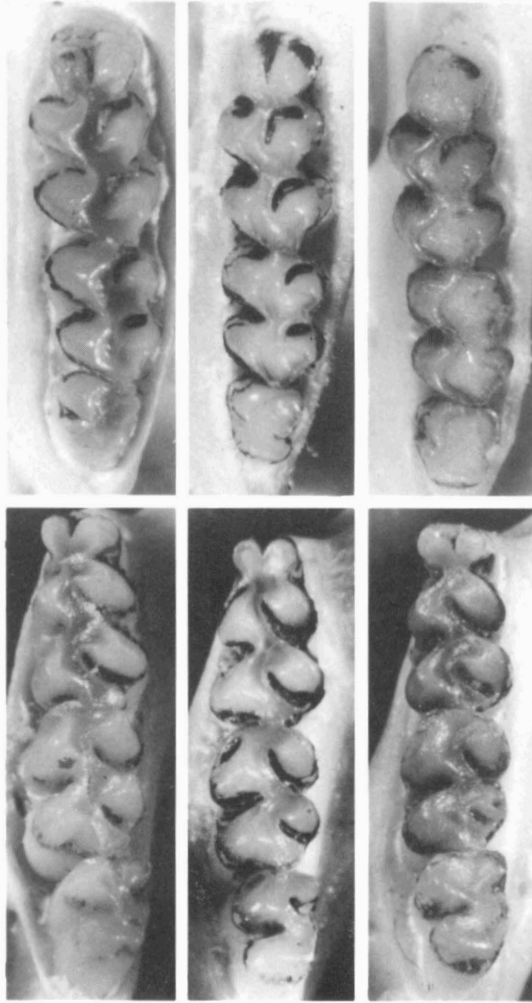


FIG. 17. Molars of *Akodon boliviensis*. Upper left molars on top; lower left molars on bottom. From left to right, MVZ 172916 (age class 2), MVZ 172901 (age class 3), MVZ 171602 (age class 4).

Ventral and dorsal grooves are well developed and confluent with the crater lip; the ventral groove has a distinct excrescence of tissue. Epidermal spines are moderately large and dense. They are deeply imbedded in individual pits, giving the epidermis a very rugose appearance in contrast to the tiny spines and seemingly smooth surface of *juninensis*. They grade in size from larger proximally to distinctly smaller distally. The area of the crater lip is thick, highly crenulated, and sharply set off from the spinous epithelium by a distinct fold. Both a ventral and dorsal notch are present in the crater lip, but neither is confluent with the corresponding ventral or dorsal grooves. A pair of lateral notches is also present. Only the medial

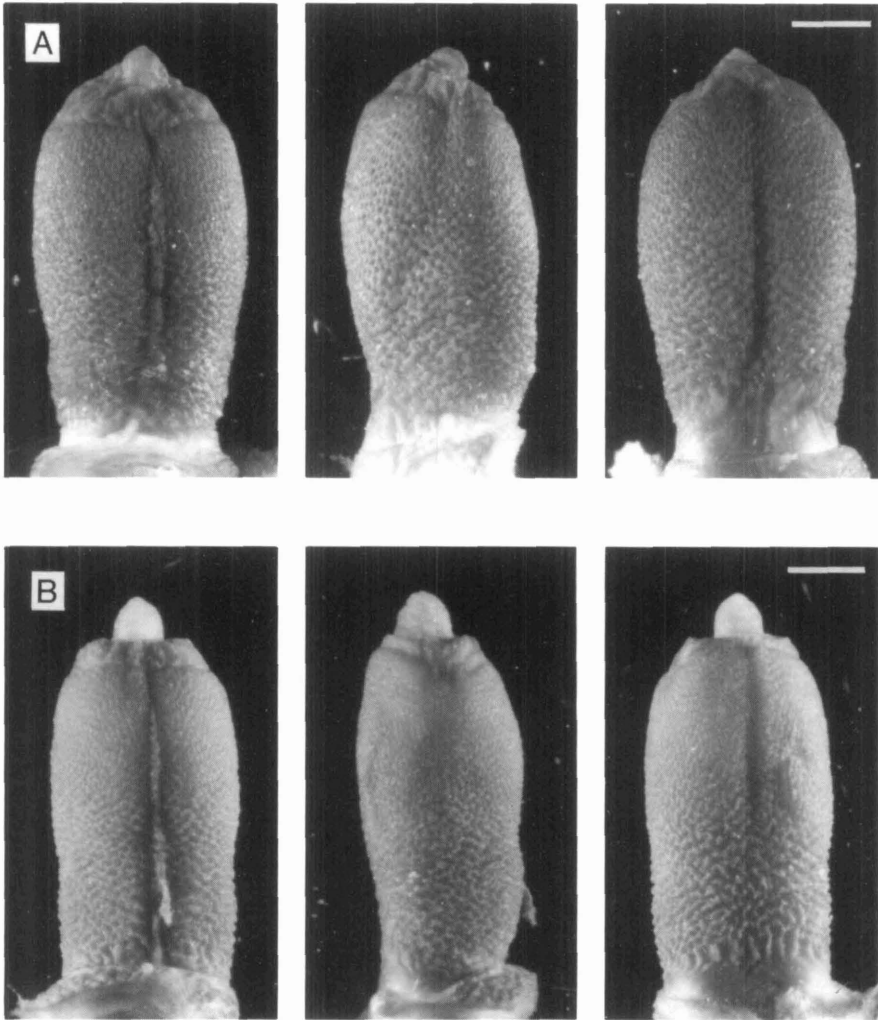


FIG. 18. Ventral, right lateral, and dorsal views of the phallus of *Akodon boliviensis*. A. Peru: Puno (MVZ 172379). B. Bolivia: Oruro (UMMZ 156285). Line = 5 mm.

bacular mound extrudes beyond the crater rim and is thus visible externally; its tip projects straight outward from the glans, as opposed to curving either ventrally or dorsally. Urethral flaps are well developed and large. They are located wholly within the crater and taper distally, with their tips well separated. Three weakly developed spines are present on each flap near the tip. The dorsal papilla is well developed, thick, and spatulate; it is totally surrounded by tissue folds connecting the medial bacular mound with the inner crater wall.

The proximal baculum is short and stout, with a laterally flared base. The base has a distinct proximal flange with a median notch; the shaft is

thick and rather straight, convex ventrally only near the tip; and the cartilaginous distal baculum is well developed, with the lateral digits about three-fourths the length of the median digit. The proximal baculum averages 2.21 times the length of the distal baculum (range 2.00–2.37).

Palatal rugae (Fig. 7). The first diastemal ruga is nearly straight transversely but with a slight peak at the midline; the second diastemal ruga is also straight transversely. Of the interdental rugae, the first two slope sharply posteriorly towards the midline; the posterior two are relatively straight.

Karyotype (Fig. 19A). $2n=40$, FN=40–42. Karyotypes of specimens belonging to this species have been described by Gardner and Patton (1976) and Barquez *et al.* (1980). The diploid number is 40 in all populations, but variation exists among geographic regions as to details of both autosomal and sex chromosomal morphology, as follows.

In Puno Department, Peru, the karyotype has $2n=40$, FN=40. The autosomal complement consists of 18 pairs of unarmed elements, one of which is distinctly larger than the others, while the remainder grade evenly in size from medium to small. One pair of small metacentric elements is also present. The X chromosome is of medium size and subtelocentric, the Y is small and submetacentric but larger than the smallest acrocentric autosome.

Specimens from Tacna Department, Peru, also have $2n=40$, but the FN is 42. There are 17 pairs of unarmed elements, with one distinctly larger than the rest and the remainder grading evenly in size from medium to small. In addition, one pair of subtelocentrics is exceptionally large and there is a single pair of very small metacentrics. The X chromosome is a large subtelocentric, and the Y is a small submetacentric. This karyotype differs from the first primarily by its possession of the single large subtelocentric pair, and hence a higher FN by two.

Finally, specimens allocated to *boliviensis tucumanensis* from northwestern Argentina by Barquez *et al.* (1980) have a basic karyotype apparently identical to those from Puno, but they are heteromorphic in both the largest autosomal pairs, which may be acrocentric or subtelocentric, and in the X chromosome, which may also be subtelocentric or acrocentric. As described below, however, we suspect that these populations are not conspecific with true *boliviensis*.

HABITAT (Fig. 20A,B).—The habitat of *Akodon boliviensis* in Peru has been described by Pearson (1951) and Pearson and Ralph (1978). This species is most common in dense bunchgrasses (*Stipa* and *Festuca*), where it forms distinct runways within and between grass clumps. It is also common where rocks or shrubs are interspersed among the grasses, and it is readily trapped along rock walls of corrals or houses where there are clumps of grasses.

Akodon boliviensis may be sympatric with up to four other akodont species, depending upon the locality. In central and northern Puno in the Lake Titicaca Basin, it co-occurs with *Akodon puer*, *Chroemys jelskii*, and

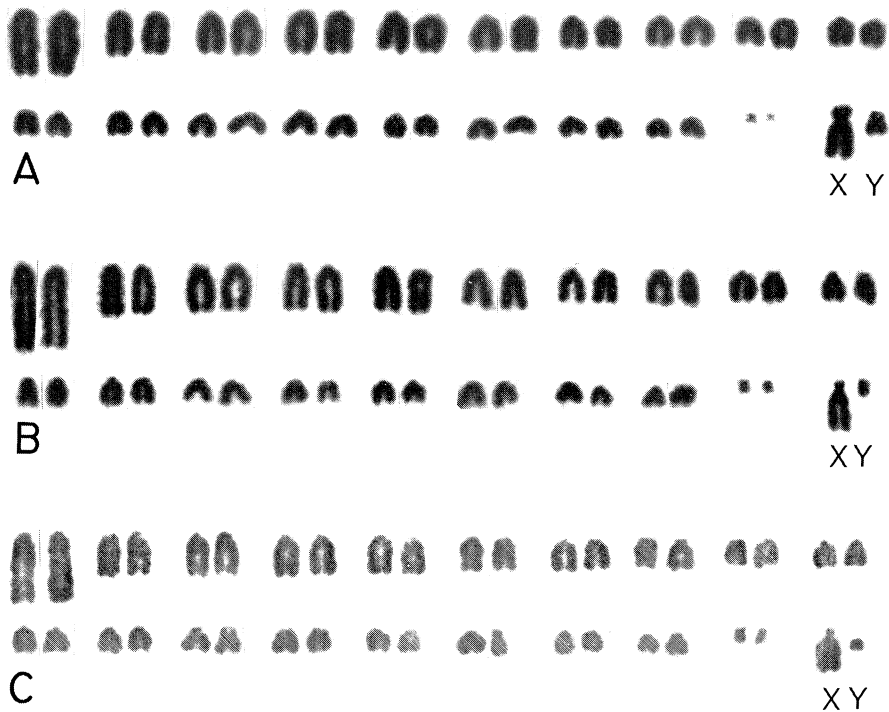


FIG. 19. Non-differentially stained karyotypes of three species of the *Akodon boliviensis* group: A. *A. boliviensis* (male, MVZ 172943). B. *A. puer lutescens* (male, MVZ 173021). C. *A. subfuscus subfuscus* (male, UMMZ 160531).

Bolomys amoenus, sharing the bunchgrass and tola habitat with *amoenus* and the rocky-grassy areas with *jelskii*. *Akodon boliviensis* and *puer* are both found in bunchgrass associations, but where they are sympatric they are sharply segregated by habitat. *Akodon puer* is found almost exclusively in the coarser, more spiny *Festuca*, which characterizes the well drained, harder soils of slopes; *boliviensis*, on the other hand, is extremely abundant in the softer *Stipa* found in the deeper, more friable soils of the lower bajadas and swales (Fig. 20B).

In the drier regions of southern Puno and on the western Andean slope, *boliviensis* co-occurs with *Akodon albiventer*, *A. andinus*, *Bolomys amoenus*, and *Chrocomys jelskii*. As noted by Pearson (1951), *andinus* is a denizen of higher elevations in very open, sparse grassland-tola habitats.

Other sigmodontine associates of *Akodon boliviensis* in southern Peru include *Auliscomys pictus*, *Auliscomys sublimus*, *Phyllotis darwini*, *Phyllotis osilae*, *Phyllotis magister*, *Calomys lepidus ducillus*, *Calomys sorellus*, *Eligmodontia typus*, *Galenomys garleppi*, *Andinomys edax*, *Neotomys ebriosus*, *Chinchillula sahamae*, and species of *Oligoryzomys*.

GEOGRAPHIC VARIATION.—In Peru, specimens of *boliviensis* from relatively wet areas north and northeast of Lake Titicaca (Central Puno; Table



FIG. 20. Puna grassland habitat of *Akodon boliviensis* and *A. puer lutescens* in the Altiplano of northern Puno Department, Peru, where the two species occur sympatrically (*páramo muy húmedo subtropical* of the Holdridge system; Tosi, 1960). A. 4.5 km NE San Antón, 400 m, along the Río Carabaya. B. 12 km S Santa Rosa [de Ayaviri], 3960 m. At this locality, *A. boliviensis* occurs primarily in the dense mats of *Stipa* (extending from the lower right-hand corner to the middle of the photograph), while *A. puer lutescens* is restricted to the coarser and more open clumps of *Festuca* on the hillsides. Two other akodontines, *Bolomys amoenus* and *Chroemys jelskii*, were also collected at both localities.

9) tend to be 2–4% smaller in age-adjusted cranial dimensions than specimens from the drier areas west and south of the lake in Puno Department. There is no detectable difference in color between individuals from these two areas. Those from the arid western Andean slope above Tarata (Tacna Department) also average about 3% smaller than those from southern Puno; they also tend to differ slightly from Puno animals in some proportions. These specimens are also grayer on the dorsum and especially on the venter, due to a large increase in the proportion of black guard hairs plus distinctly paler pheomelanin bands (Antimony Yellow). Four specimens from Moquegua are the most distinctive; these average 5–6% larger than those in neighboring Tacna, and they have especially long rostra and maxillary tooththrows. These specimens are relatively old individuals, however (age classes 4–5), which may account for the difference in overall size and rostral size, but not tooththrow length. They do not differ from Puno specimens in color.

A few specimens are available from Bolivia. Those from La Paz, Oruro, and Potosí departments (Western Bolivia; Table 9) are similar in size and color to specimens from Puno. On average, specimens from Tarija Department, Bolivia, are darker and smaller than Puno specimens, but the differences are slight. These specimens from Tarija are discussed on p. 61.

To summarize and test the significance of these differences in cranial dimensions, we calculated Mahalanobis distances based on 19 age-corrected cranial dimensions (mesopterygoid fossa length was omitted due to the large number of crania with broken pterygoid wings) and performed a multivariate analysis of variance (Willig *et al.*, 1986). The results are given in Table 9. They indicate that the four animals from Moquegua are indeed the most distinctive, followed by specimens from Tarija, and that the differences among the other populations are statistically significant but relatively small.

COMPARISONS.—*Akodon boliviensis* differs from *juninensis* by having broad zygomatic notches, well-developed temporal and mastoid ridges, a well-developed hypoflexus and metaflexus on M^3 , a large foramen ovale, large postglenoid and subsquamosal foramina, a ventral as well as dorsal notch on the crater lip of the phallus, and numerous other characteristics. It is compared to other members of the *boliviensis* group in the accounts of those species, below. *Akodon boliviensis* can be distinguished from all other *Akodon* by the combination of its dull pelage, small size, distinctive mesopterygoid fossa, and other characteristics given under the general description of the *boliviensis* group.

REMARKS.—*Akodon pacificus* Thomas was described with its type locality La Paz, Bolivia. The holotype appears to be an old individual of *boliviensis*. The edges of the interorbital region are more square-sided and divergent than average for this species, but they fall within the range of variation of *boliviensis* from Peru. In all cranial dimensions, the holotype of *pacificus* agrees well with Peruvian *boliviensis* and, in fact, cannot be distinguished from them on the basis of discriminant analysis of cranial measurements.

TABLE 9.—Geographic variation among regional samples of *Akodon boliviensis**†. A. "Age corrected" mean values (mm) for measurements from specimens representing each region. B. Mahalanobis distances (based on "age-corrected" measurements) describing the overall morphological differences among regions‡.

A.						
	Central Puno	Southern Puno	Tacna	Moquegua	Western Bolivia	Tarija
CIL	22.77	22.95	22.53	23.13	22.83	22.07
ZB	12.43	12.52	12.17	12.64	12.41	12.13
BB	11.21	11.30	11.09	11.44	11.30	11.24
IOC	4.18	4.32	4.25	4.34	4.30	4.20
RL	8.96	9.03	8.85	9.15	8.96	8.75
NL	8.93	9.06	8.77	9.45	8.99	9.00
RW	4.43	4.59	4.54	4.88	4.68	4.59
RW2	3.73	3.83	3.83	3.82	3.86	3.98
OL	8.83	8.21	8.07	8.25	8.21	7.89
DL	6.37	6.31	6.11	5.97	6.30	6.09
MTRL	4.01	4.08	4.02	4.33	4.09	4.05
IFL	5.17	5.42	5.23	5.64	5.55	5.43
AW	4.84	4.92	4.81	5.15	4.95	4.99
OCW	6.07	6.13	6.03	6.21	6.17	6.03
MB	10.70	11.15	10.96	11.11	11.12	10.95
BOL	3.50	3.66	3.48	3.75	3.79	3.54
MFW	0.98	0.92	0.95	0.99	0.91	0.96
ZP	2.30	2.27	2.32	2.34	2.34	2.23
CD	9.36	9.41	9.07	9.16	9.36	9.62
<i>n</i> =	221	59	25	4	10	17
B.						
	Central Puno	Southern Puno	Tacna	Moquegua	Western Bolivia	
S. Puno	7.99					
Tacna	9.06	4.68				
Moquegua	33.82	19.88	24.41			
W. Bolivia	14.05	3.61	9.26	17.29		
Tarija	23.84	13.82	21.46	31.55	10.67	

*MFL was omitted due to the large number of missing values.

†The regions are defined as follows (numbers refer to locality numbers in Appendix I): Central Puno, 43-46, 49-58; Southern Puno, 60-69, 64a, 65, 67a; Tacna, 91; Moquegua, 90; Tarija, 110; Western Bolivia, 96-98, 107-109.

‡All distances are statistically significant at $p < 0.0001$ except Southern Puno-Western Bolivia ($p = 0.072$), and the overall test for equality of means (maximum likelihood ratio criteria, Rao, 1973) is also significant (MANOVA, $df = 95, 1523$; $F = 8.3438$, $p < 0.0001$).

As a consequence, we treat Thomas's *pacificus* as a junior synonym of Meyen's *boliviensis*. Specimens from Cochabamba Department assigned by Thomas to *pacificus* in the description of that species are probably *Akodon puer*, described in the next account (p. 63).

Akodon spegazzinii was described by Thomas (1897) from the lower Cachi River in Salta Province, Argentina. It has been considered a subspecies of

A. boliviensis by later authors (e.g., Cabrera, 1961). Similarly, *Akodon tucumanensis*, from Tucumán, Tucumán Province, Argentina (Allen, 1901) has also been considered a southern population of *boliviensis* (but see Hershkovitz, in manuscript). The type localities of these two taxa, which are both at relatively low elevation (*tucumanensis*, 450 m; *spgazzinii* unknown, but probably under 2000 m), lie in adjacent valley systems and within about 200 km of one another.

Specimens available to us from immediately north and south of Tucumán appear very dark, with strongly rufous tones, and with the ventral pelage scarcely different from the dorsal. They agree with the description of *tucumanensis* and undoubtedly represent that taxon. They differ sharply in color from mice from the Cachi Valley in Salta Province, which we take to represent *spgazzinii*. Specimens from the Cachi Valley are substantially paler than *tucumanensis*; they have an olivaceous rather than rufous cast to the dorsal pelage; and their dorsal pelage is somewhat more sharply distinct from their ventral pelage than is the case for *tucumanensis*. Populations with this color extend south in the same valley system and on adjacent hills at least as far as Tafi del Valle, Tucumán Province, about 50 km W of Tucumán. Collections from the vicinity of Tafi del Valle contain both color forms.

Do *spgazzinii* and *tucumanensis* represent the same species? While the difference in color between members of these two taxa is striking, we see no consistent differences between them in cranial size or morphology (Fig. 21; Table 4). Few specimens, however, are available to us, and we are unable to compare soft anatomical structures, karyotypes, or electromorphs from specimens representing each population. For the present, lacking convincing evidence to the contrary, we prefer to consider them conspecific.

Do *spgazzinii* and *tucumanensis* represent southern populations of *boliviensis*? Skins of *spgazzinii* are virtually indistinguishable from those of Peruvian *boliviensis*, while as noted those of *tucumanensis* are sharply different in hue (but similar in color pattern). The crania of all three taxa appear similar in general shape, and in particular share the distinctively broad, shallow zygomatic notches of *boliviensis*. Skulls of *spgazzinii* and *tucumanensis*, however, are 5–10% larger in most dimensions (Table 4). Moreover, the incisive foramina of *spgazzinii* and *tucumanensis* are strikingly longer than those of *boliviensis* (average 5.9 mm vs. 5.1 mm), and the palate is correspondingly shorter. Further, the mesopterygoid fossa appears wider and more parallel-sided in *spgazzinii* and *tucumanensis* than in *boliviensis*, and M^3 in both *spgazzinii* and *tucumanensis* is oval, lacking the lateral indentations of the M^3 s of *boliviensis*.

Northwestern Argentina and southern Peru are separated by a considerable distance, and questions regarding the distinctiveness of these two taxa might best be resolved by examining specimens from intermediate localities. Unfortunately, few are available. As noted above, we have examined three specimens of *boliviensis* from La Paz Department, six from localities

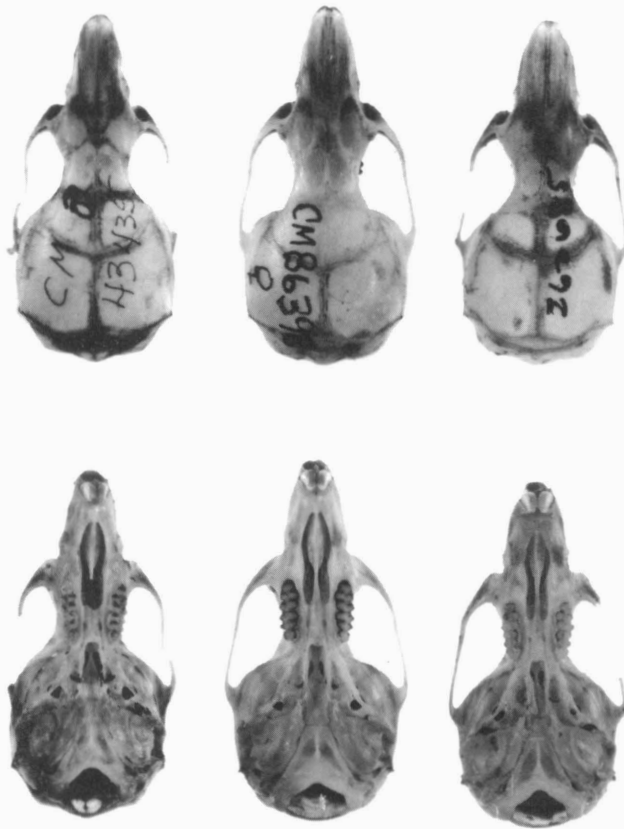


FIG. 21. Dorsal and ventral views of crania of *Akodon spagazzinii* (CM 43435, left), *A. tucumaniensis* (CM 86398, center), and *A. boliviensis* from southern Bolivia (AMNH 262685, right).

in Oruro Department, and one from Potosí Department, all in Bolivia. All closely resemble typical *boliviensis* in most respects, including size, development of the temporal and mastoid ridges, size of lacrimals, breadth and conformation of the zygomatic notches, and at least a trace of a hypoflexus and metaflexus on M^3 . Eighteen specimens are available from Iscayachi, Tarija Department, in southern Bolivia. These specimens resemble *boliviensis* strongly in most characteristics and we tentatively assign them to that species. Resemblances include the overall shape of the cranium, and in particular, the broad zygomatic notches, medium to large lacrimals, medium to broad tympanic hook, posterior ascending process of the alisphenoid that always reaches the level of the alisphenoid canal, and relatively well-developed temporal and mastoid ridges. The male phallus is also very similar to that of Peruvian *boliviensis*. Specimens from Tarija, however, are slightly smaller than Peruvian specimens of *boliviensis*. Also, the presence

and development of the hypoflexus and metaflexus on M^3 varies among individuals and is sometimes completely lacking. Certainly, however, none approaches the size of *spgazzinii* or *tucumanensis*, nor does any have an elongated incisive foramen or shortened palate that would suggest that these southern Bolivian animals are in any way intermediate between typical *boliviensis* and *spgazzinii* or *tucumanensis*.

A final difference between members of these taxa concerns their habitats. Collections of *boliviensis* are typically from high elevations. In Peru, the species is known only above 3000 m, and the southernmost populations that may represent this taxon in Tarija are from 3450 m. The collections of *spgazzinii* and *tucumanensis* available to us, in contrast, are mostly from between 400 and 1000 m, a striking difference in elevation.

Clearly, more work is needed on the Bolivian and Argentine representatives of this group. The evidence at present suggests that *boliviensis* extends through La Paz, Oruro, and Potosí departments, and probably to southern Bolivia in Tarija Department. The connection between *boliviensis* and *spgazzinii* plus *tucumanensis* is tenuous, however, and for the present we consider these taxa to comprise three subspecies placed in two species (*boliviensis*, *spgazzinii spgazzinii*, *spgazzinii tucumanensis*).

Akodon alterus Thomas, another taxon often considered to be a subspecies of *boliviensis*, was described from "Otro Cerro," probably in La Rioja Province, Argentina, at an elevation of 3000 m. Thomas also assigned specimens from Chumbicha, Catamarca, to this taxon. According to Thomas, the skull of *alterus* is very much like that of *spgazzinii* but with a long incisive foramen. The primary difference between the two species is in color, *alterus* being "readily distinguishable from the older known species by the absence of a strong yellowish or buffy suffusion in the fur." Instead, *alterus* is "between 'buffy brown' and 'Saccardo's umber' of Ridgway."

According to the collector, Budin (as reported by Thomas, 1919), Otro Cerro was reached by travelling about 30 miles west from Chumbicha, which lies in the Sierra de Ambato, across the Cerro to another range of hills for which he could find no recognized name, but which Thomas presumed to be the Cerro Nunorca. This mountain is probably within a range (for which we also have not found a name) that runs NNW from the Sierra de Valasco, originating just west of La Rioja. It is separated from the Sierra de Ambato by a narrow valley under 700 m elevation.

We have examined a single specimen of the *boliviensis* group from La Merced, Catamarca Province, that may represent *alterus*. Like Chumbicha, La Merced lies in the Sierra de Ambato, approximately 90 km N of that town. Cranially, this specimen is similar to specimens of *spgazzinii* of the same age, but it is somewhat broader across the braincase. Its color is intermediate between that of *tucumanensis* and *spgazzinii*, generally brown to pale fulvous dorsally and with buffy tips on the ventral hairs. If this specimen is true *alterus*, then it seems likely that *alterus* is properly allied with *spgazzinii* and *tucumanensis*. Questions regarding its distinctiveness, however, must await additional specimens and study.

Finally, we point out that *Akodon azarae*, a species of wide distribution in the lowlands of Argentina, Uruguay, and Paraguay, is very similar in many aspects of cranial and external morphology with both *boliviensis* and *spgazzinii*. Descriptions of soft anatomical structures and electromorphic characters, as well as additional collections from Argentina and Bolivia, are needed to resolve the relationships of these three taxa.

Akodon puer Thomas

Hesperomys (Habrothrix) xanthorhinus Thomas, 1884; Proc. Zool. Soc. London, 1884:450 (not Waterhouse, 1837).

Akodon puer Thomas, 1902; Ann. Mag. Natur. Hist., ser. 7, 9:136 (original description).

Akodon caenosus Thomas, 1918; Ann. Mag. Natur. Hist., ser. 9, 1:189.

Akodon lutescens J. A. Allen, 1901; Bull. Amer. Mus. Natur. Hist., 14:46.

HOLOTYPE.—BMNH 2.1.1.78; adult female (age class 4); skin and skull; collected 15 July 1901 by P. O. Simons, original number 1501.

TYPE LOCALITY.—Choquecamate, Cochabamba Dept., Bolivia, 4000 m (approximately 16°55'S and 66°37'W, "... in the high paramos north and northwest of Cochabamba, surrounding on the west and south the sources of the Río Secure ...," p. 126).

EMENDED DIAGNOSIS.—*Akodon puer* is the smallest member of the *boliviensis* group (hind feet 21 mm or less, maxillary tooth row averages 3.58 mm [range 3.3–3.8]). In addition to being small, *puer* is distinguished by a combination of especially shallow and narrow zygomatic notches; weakly developed temporal and mastoid ridges; large oval, postglenoid, and sub-squamosal foramina; delicate tympanic hook; posterior ascending process of the alisphenoid almost never reaching the squamoso-alisphenoid groove; and M³ either entirely without lateral indentations (not "8"-shaped) or lateral indentations present but shallow.

RANGE (Figs. 11, 12).—*Akodon puer* is known from the high elevation Altiplano of the Andes, from Puno Department in Peru south through La Paz and Cochabamba departments of Bolivia, and from the mountainous regions of northwestern Argentina in the provinces of Jujuy, Salta, Tucumán, and Catamarca.

Geographically separated populations of *puer* differ substantially to an extent that we believe requires formal recognition of subspecies. We begin by giving a general description encompassing all populations of the species that we examined. We then treat three subspecies, *A. p. puer*, *A. p. caenosus*, and *A. p. lutescens*.

DESCRIPTION.—*External characters.* The dorsal coloration is medium brown to slightly olivaceous brown across the back and top of the head, becoming slightly darker in older animals. The pheomelanin bands of the dorsal fur hairs are 1.5–2 mm long and vary geographically in color (described below). The dorsal pattern merges gradually with the ventral one, which is made up of individual hairs with slaty bases and buffy or grayish

tips. The inguinal region resembles the rest of the venter or is slightly paler (less gray) in appearance. The chin may have a few all-white hairs, but if so the area covered is small.

The tail is bicolored, with a narrow dark stripe that occupies one-fourth to one-third of its circumference. The tail appears rather hairy, with individual hairs near its base the length of two to three scales. It averages about 74% of the length of the head plus body.

Cranial characters (Figs. 3, 5, 16; Table 4). Crania of *puer* closely resemble those of *boliviensis* in most respects. As noted above, they are small compared to those of other members of the group. Dorsally, they are characterized by an inconspicuous lacrimal (often missing in cleaned skulls); zygomatic arches that flare weakly laterally; shallow and laterally compressed zygomatic notches; interorbital region that appears broad relative to the small size of the skull; and a proportionately large interparietal.

When the crania of old (age class 4 or 5) individuals are viewed from the side, they seem to be less flattened in dorsal profile than in other *boliviensis* group species. The zygomatic plates are slender and their anterior faces are either oriented vertically or very slightly reclining. Postglenoid and subsquamosal foramina are relatively large. In most populations the tympanic hook is relatively narrow and delicate (Fig. 16), and the posterior ascending process of the alisphenoid does not reach the level of the squamoso-alisphenoid groove (Fig. 5).

Ventrally, the palate appears broad (relative to the size of the skull) and only shallowly grooved; the posterior end of the palate (anterior border of mesopterygoid fossa) is strongly squared in most populations and usually bears a median spine; the sphenopalatine vacuities, foramina ovale, and median lacerate foramina are large; the mesopterygoid fossa is exceedingly narrow; and lateral edges of the parapterygoid plates are straight or only slightly convex. The length of the incisive foramina varies geographically from very short to about average for the group.

Dental characters (Fig. 22). The teeth of *puer* resemble those of *boliviensis*. Two conspicuous characteristics of *puer*, however, are (1) the length of the maxillary toothrow is short, less than 3.7 mm in most populations (*cf.* usually over 3.8 for *boliviensis*), and (2) M³ lacks a deep hypoflexus and metaflexus, so that the perimeter of the surface of M³ in *puer* is usually an uninterrupted oval.

Phallus and baculum. Only reconstituted dried phalli were available for examination. The features visible on such specimens indicate, however, that the basic components of the glans of *puer* are similar to those of *subfuscus*, which is described in detail under that species.

The proximal baculum is rather short and stocky, with a laterally flared base that lacks a medial flange and usually has a shallow medial notch. The shaft is thick and straight in lateral aspect. The cartilaginous distal baculum is well developed, with the lateral digits about three-fourths the length of the medial one. The height of the distal part of the baculum relative to that of the proximal part is highly variable among specimens. For example,

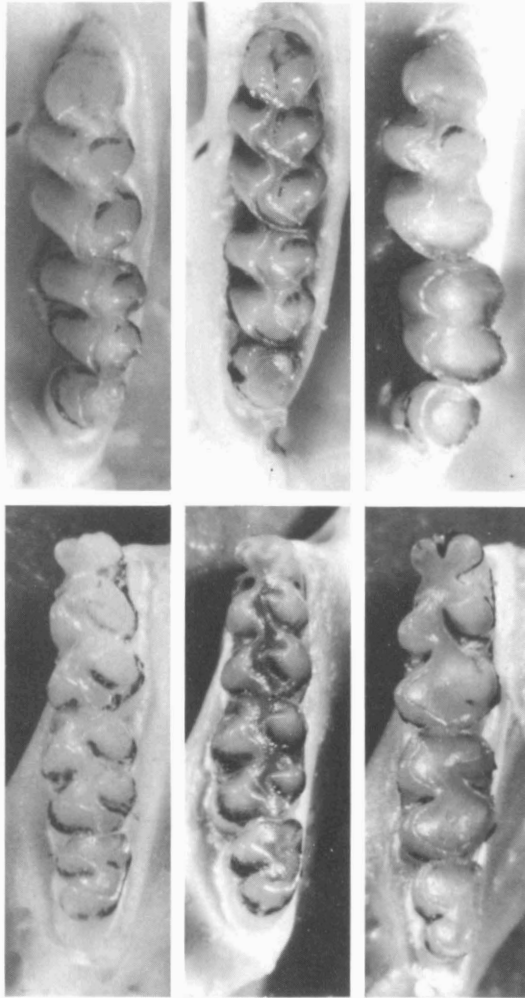


FIG. 22. Molars of *Akodon puer lutescens*. Upper molars on top; lower molars on bottom; both photographs are of the left side of the jaw. From left to right, MVZ 171612 (age class 2), MVZ 173031 (age class 3), MVZ 173034 (age class 4).

in specimens representing populations in Puno Department, Peru, proximal length is 2.24 times distal length in a specimen from Santa Rosa, 2.12 times distal length (range 1.88–2.35) in two specimens from Pucara, and only 1.87 times that length in a specimen from Ananea.

HABITAT (Fig. 20).—*Akodon puer* inhabits puna grasslands at high elevations. Its habitat preferences in Peru are discussed above with those of *Akodon boliviensis*. *Akodon puer* occurs sympatrically with *Akodon boliviensis*, *Bolomys amoenus*, and *Chroemys jelskii* in southern Peru, and probably with *Akodon fumeus*, *Akodon siberiae*, and *Microxus mimus* in central Bolivia. Other sigmodontines with which it co-occurs in southern Peru include *Auliscomys*

pictus, *Phyllotis osilae*, *Phyllotis darwini*, *Calomys lepidus*, *Calomys sorellus*, *Chinchilla sahamae*, *Neotomys ebriosus*, and species of *Oligoryzomys*.

COMPARISONS.—*Akodon puer* is easily distinguished from *boliviensis* where it overlaps that species in Puno Department, Peru, by the following characteristics of *puer* (most of which are most readily apparent if animals of similar age are compared): (1) small size; (2) underparts tend to be whiter or grayer, due to whitish to pale yellow tips on the ventral hairs rather than buffy or ochraceous buffy tips as in *boliviensis*; (3) smaller, narrower zygomatic notches; (4) less strongly flared zygomatic arches; (5) more weakly developed temporal and mastoid ridges, especially in animals of age classes 3 and 4; (6) posterior ascending process of the alisphenoid rarely extending dorsally to the squamoso-alisphenoid groove; (7) M^3 a simple oval, with metaflexus and hypoflexus very shallow or absent; (8) lacrimal tiny or absent; (9) tympanic hook relatively delicate. It is important to note, however, that there is significant variation in some of these characteristics in areas where *boliviensis* does not occur; these modifications are described below in the accounts of subspecies.

Compared to *juninensis*, *puer* is slightly smaller, has a relatively broader cranium, larger foramina ovale, larger postglenoid and subsquamosal foramina, and its phallus lacks a dorsal notch. It further differs from *juninensis* in the electromorphic characters described under that species. *Akodon puer* is compared to other members of the *boliviensis* group in the accounts of those species, and to other *Akodon* in the general description of the *boliviensis* group.

GEOGRAPHIC VARIATION.—Individuals from Cochabamba Department, Bolivia, are assigned to *A. p. puer*. These animals are large and dark; some variation among populations of this subspecies is described below.

The name *Akodon lutescens* appears to apply to specimens from Puno Department, Peru and La Paz Department, Bolivia (near the Peruvian border) that are similar in shape and color pattern to typical *puer*, and which resemble very closely *puer* from the eastern border of Cochabamba Department in karyotype and electromorphic characters. They are distinctively smaller, however, than typical *puer*, paler in dorsal color, and differ in several details of cranial shape. The name *lutescens* is usually listed as a synonym or subspecies of *Akodon andinus* (but see Hershkovitz, in manuscript); we establish below that this is not correct.

Akodon caenosus, which has its type locality in northern Argentina, is clearly a close relative of *puer* and probably is conspecific with it, as suggested by O. A. Reig (in Vitullo *et al.*, 1986:73). Because of distinctive color and cranial features as well as different karyotypes (see below), we choose to recognize *caenosus* as a valid subspecies of *puer* even though we lack sufficient specimens to understand fully its evolutionary relationship with populations of *puer* from Peru and Bolivia.

Akodon puer puer Thomas

EMENDED DIAGNOSIS.—*Akodon p. puer* are distinctive among *puer* for the combination of large size, long rostra, long mesopterygoid foramina, especially long incisive foramina, and diploid chromosome number $2N = 40$.

RANGE.—High elevation grasslands of Cochabamba Department, Bolivia; elevational range above 2900 m in Bolivia.

DESCRIPTION.—*External characters.* The pelage of *p. puer* is generally brownish above with a faint olivaceous tinge. The upper surface of the crown and middorsal area are similarly colored and noticeably darker than the flanks. Midrump fur averages about 11 mm long, with guard hairs extending generally 5 mm beyond the level of the fur hairs. Pheomelanin bands on fur hairs are approximately Ochraceous-Buff and average 1.5 mm long. The ventral hairs are slate gray for two-thirds of their length and tipped with buffy or grayish.

The tail of *p. puer* appears relatively long, approximately 80% of head-body length. It is bicolored, and the dark dorsal stripe is wide, occupying from one-third to one-half of the circumference of the tail. Hairs at the base of the tail are short, the length of 2–2.5 scales.

Cranial characters (Fig. 23, Table 4). Members of populations of *p. puer* average 5% larger than those from other areas. The nominate subspecies is also notable for its long incisive foramina, relatively stout tympanic hook (but not as stout as in *boliviensis*), large braincase, less well-developed temporal ridges, more inflated frontal sinuses, and broader interorbital region. In most individuals the posterior ascending process of the alisphenoid does not reach the squamoso-alisphenoid groove.

Palatal rugae (Fig. 7). Both sides of the first diastemal ruga are straight but arched toward the midline; the second diastemal ruga is transversely straight. As in *boliviensis*, the first two interdental rugae are arched and slope posteriorly toward the midline.

Karyotype. $2n = 40$, $FN = 40$. The autosomal complement of *p. puer* consists of 18 pairs of uniarmed elements. Members of one pair are distinctly larger than members of the remaining pairs (about twice the size of the next largest), and the latter grade evenly in size from medium to small. One pair of small metacentrics is also present; these are about one-half the size of the smallest acrocentric autosome. The X chromosome is a medium subtelocentric and the Y is a small acrocentric, considerably smaller than the smallest uniarmed autosome.

GEOGRAPHIC VARIATION.—Minor differences, primarily in size, can be found among populations of *p. puer* in Cochabamba. Specimens were grouped into three regions (Table 10). Too few specimens were available for computation of age-corrected measurements or statistical comparison of regions by MANOVA. Comparison of animals in age classes 3 + 4, however, suggests that the most distinctive individuals are from grasslands above the elfin forest on the border between Santa Cruz and Cochabamba departments. These animals are slightly darker, especially mid-dorsally,

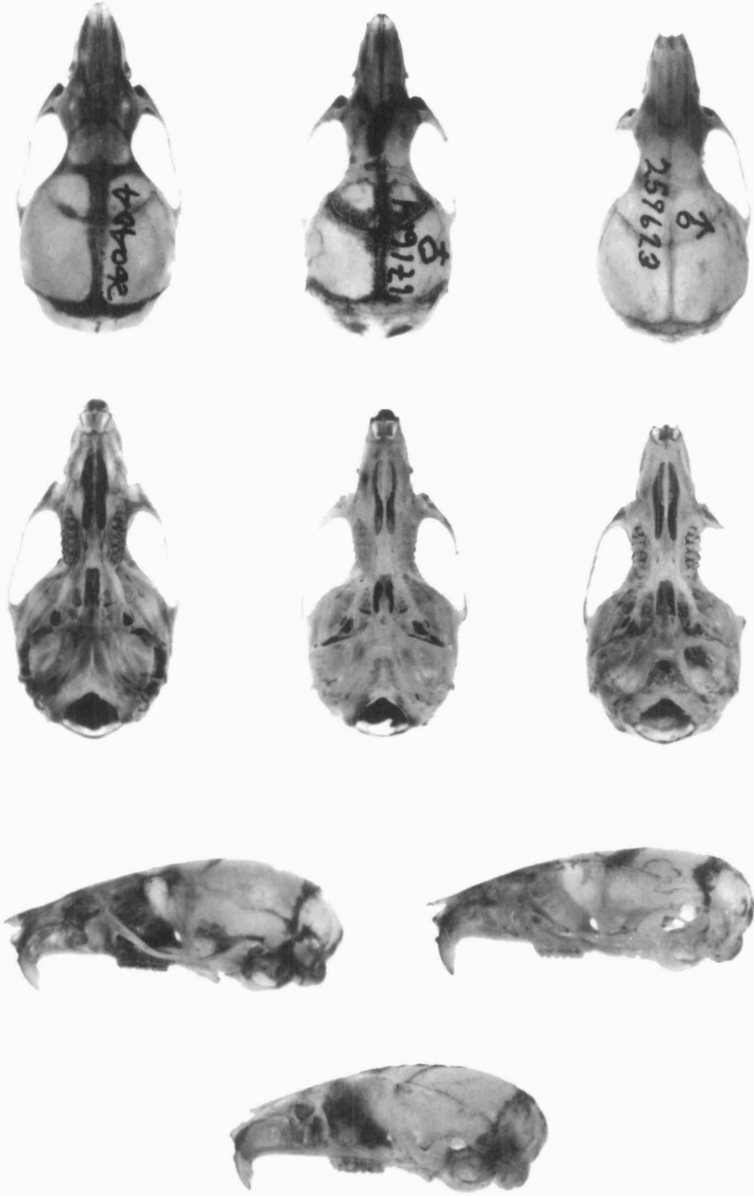


FIG. 23. Crania of *Akodon puer*. First and second rows, dorsal and ventral views of *A. puer puer* (AMNH 260404, left), *A. puer lutescens* (MVZ 171614, center), and *A. puer caenosus* (USNM 259623, right). Third and fourth rows, lateral views of *A. puer puer* (AMNH 260404, left), *A. puer lutescens* (MVZ 171614, right), and *A. puer caenosus* (USNM 259623, bottom).

TABLE 10.—Geographic variation in *Akodon p. puer**†.

	Western Cochabamba	Central Cochabamba	Comarapa
CIL	21.17	21.14	21.40
ZB	11.59	11.50	11.77
BB	10.75	10.85	11.01
IOC	4.25	4.38	4.43
RL	8.32	8.36	8.41
NL	8.56	8.62	8.56
RW	4.22	4.20	4.48
RW2	3.62	3.64	3.75
OL	7.47	7.54	7.64
DL	5.77	5.70	5.87
MTRL	3.57	3.71	3.77
IFL	5.13	5.32	5.41
AW	4.58	4.60	4.75
OCW	5.86	5.87	5.85
MB	10.26	10.63	10.53
BOL	3.43	3.52	3.38
MFL	3.42	3.57	3.63
MFW	0.96	1.02	1.06
ZP	2.05	2.09	2.20
CD	8.88	8.82	8.90
<i>n</i> =	8	11	16

*Regions are defined as follows (numbers refer to locality numbers in Appendix I): Western Cochabamba, 99–100; Central Cochabamba, 101–104; Comarapa, 105–106.

†Columns give mean values (mm) for measurements from specimens of age classes 3 and 4. "Age corrected" values and distances between regions were not calculated due to the small number of specimens in the sample.

than other *p. puer* we have examined. They have slightly broader zygomatic plates, broader rostra, broader palates, and shorter basioccipitals. These differences are slight, however (most measurements within about 5% of those of other specimens of *p. puer* from Cochabamba, including the holotype), and we tentatively consider these animals to be of that subspecies.

HABITAT.—Other species of sigmodontines reported by Thomas to occur at the type locality include *Phyllotis lutescens* (regarded by Pearson, 1958 and Hershkovitz, 1962, to be a synonym of *P. osilae*) and *Oxymycterus paramensis*. Populations from eastern Cochabamba are found in moist bunchgrass associations at elevations above the elfin forest. Here, these animals contact the ranges of *Akodon fumeus*, *A. siberiae*, *Microxus mimus*, and *Oxymycterus hucucha*, all akodontines that are denizens of the adjacent elfin forest.

COMPARISONS.—*Akodon p. puer* is compared to other species of *Akodon* in preceding sections. It is compared to other subspecies of *puer* above and in the sections that follow.

Akodon puer lutescens J. A. Allen

HOLOTYPE.—AMNH 16507; adult female; skin and skull fragments; collected Oct. 21, 1900 by H. H. Keays.

TYPE LOCALITY.—Tirapata, Peru (about 15,000 ft). Tirapata is in Puno Department about 50 km NW of Lake Titicaca.

EMENDED DIAGNOSIS.—This taxon resembles *p. puer* in most aspects of cranial shape and external morphology, but differs from all other *puer* by the following combination of characteristics: small size; short incisive foramina; small braincase; very delicate tympanic hooks; relatively strongly developed temporal ridges (especially in old animals); frontal sinuses not inflated; interorbital region narrow; diploid chromosome number $2N = 40$.

RANGE.—This subspecies is found in the high elevation grasslands of Puno Department, Peru, and La Paz Department, Bolivia, generally above 3800 m elevation.

DESCRIPTION.—*External characters.* *Akodon p. lutescens* is a small, pale olivaceous brown form generally similar in external appearance to *A. p. puer*. Skins are almost indistinguishable in color from those of sympatric *boliviensis* except for their paler, grayer venters. Individual fur hairs are approximately 10 mm long over the rump, and the guard hairs in that region project 5 mm or less over the surface of the back. The pheomelanin bands of individual rump hairs are long (1.5–2 mm) and approximately Antifmony Yellow. The fur is sparsely punctuated by black guard hairs. This combination of hairs gives an overall impression to the dorsum of pale grayish or olive brown, moderately heavily lined with black. The dorsal pattern extends well down the flanks, where it grades into the ventral pelage. An eyering is present and moderately conspicuous. Ventrally, the hairs are slate gray for one-half to two-thirds of their length, then tipped with either pale buff or gray. A few hairs on the chin and, in some specimens, the upper throat are monocolored and white.

On the tail, the hairs appear denser, longer, and generally more conspicuous in *lutescens* than in *puer*; most extend the distance of three scale lengths. Tail length is about 74% of head-body length. The tail is sharply bicolored, with a narrow dorsal stripe that covers from one-fourth to one-third of its circumference.

Cranial characters (Fig. 23). The cranium is similar to that of typical *p. puer*, except for its smaller size, shorter incisive foramina, and other differences noted above. The posterior ascending process of the alisphenoid was never seen to reach the squamoso-alisphenoid groove, and the tympanic hook was always very narrow and delicate. These differences are subtle, however, and can best be seen in comparisons of age-sorted material.

Male reproductive tract. No information is available concerning the anatomy of phallus, baculum, or accessory glands.

Palatal rugae (Fig. 7). The pattern of the rugae appears the same as in *p. puer*, except that the first diastemal ruga is transversely straight rather than arched toward the midline.

Karyotype (Fig. 19B). $2n=40$, $FN=40$. The karyotype appears identical to that of *A. p. puer*. It differs from that of *A. p. caenosus* as described under that subspecies.

HABITAT.—*Akodon puer lutescens* is a denizen of the puna grassland of the Altiplano (Fig. 20). Where sympatric with *boliviensis*, *lutescens* is found most commonly in *Festuca* bunchgrass on harder soils (see account of *boliviensis*, above).

GEOGRAPHIC VARIATION.—No variation in color was seen among populations of *p. lutescens*. Age-corrected samples from three regions in Puno Department were compared among themselves and with very small samples from southern Puno ($n=5$) and western La Paz ($n=2$). Significant geographic variation in size was found (Table 11) but is not easily interpreted. Clearly, the specimens from La Paz Department (Ulla Ulla) are large and have unusually long incisive foramina. They are more similar in these respects to *p. puer* from Cochabamba Department than to *p. lutescens*. Their color, however, is most like that of *p. lutescens*, and we refer them to that subspecies.

COMPARISONS.—Comparisons to sympatric *boliviensis* are made above under the general description of *puer*. *Akodon p. lutescens* differs from *p. puer* by being smaller and having shorter incisive foramina, paler color (especially the middorsal area, which is often very dark in *p. puer*), and other characteristics noted above. *Akodon p. lutescens* is compared with *p. caenosus* in the following account. Other akodonts occurring at high elevations in southern Peru are all distinguished by a combination of larger size and/or distinctive coloration, as outlined above in the description of the *boliviensis* group.

REMARKS.—Allen described *lutescens* as a small, "fulvous gray brown" mouse from the highlands of Puno Department, Peru. He did not compare it explicitly with any other Peruvian species, merely stating that it "appears to resemble in a general way other species of the soft-haired, dull-colored section of the genus," and noting that it "agrees with none of the described species in respect to details of size, coloration, and proportions." In his description of *Akodon boliviensis subfuscus*, Osgood (1944) noted that *lutescens* is "perhaps a synonym" of *boliviensis*. In the same paper he described *Akodon andinus polius* from neighboring Arequipa Department. Sanborn, in a brief note published in 1949, stated that "Dr. Osgood concluded that *polius* should be a synonym of *lutescens* which was a subspecies of *andinus*," a conclusion that appears to contradict Osgood (1944) and that is apparently based on notes Osgood left in trays of specimens identified as *polius*. Others (e.g., Cabrera, 1961; but see Hershkovitz, in manuscript) have followed this suggestion, listing *lutescens* as a subspecies of *andinus*.

We agree with Hershkovitz (in manuscript) that the true affinities of the taxon described as *lutescens* are not with *andinus* but with the *boliviensis* group, specifically, with *Akodon puer*. First, lack of any trace of whitish postauricular tufts exclude both the holotype and paratype of *lutescens* from *andinus*. These tufts are sometimes inconspicuous, but they are pre-

TABLE 11.—Geographic variation in *Akodon puer lutescens**†‡.

	South Puno	East Puno	Central Puno	Ulla Ulla
CIL	21.15	21.05	21.23	21.80
ZB	11.33	11.30	11.39	11.34
BB	10.38	10.55	10.56	10.73
IOC	4.14	4.18	4.23	4.25
RL	8.44	8.28	8.47	8.84
NL	8.50	8.24	8.48	8.94
RW	4.27	4.16	4.27	4.33
RW2	3.58	3.66	3.73	3.55
OL	7.76	7.53	7.59	7.70
DL	5.81	5.72	5.76	6.08
MTRL	3.55	3.57	3.66	3.49
IFL	4.89	4.76	4.80	5.35
AW	4.44	4.54	4.65	4.69
OCW	5.61	5.76	5.86	5.81
MB	10.41	10.15	10.37	10.63
BOL	3.52	3.36	3.31	3.53
MFW	0.91	1.05	0.99	0.93
ZP	2.21	2.08	2.22	1.96
CD	8.77	8.66	8.85	8.83
<i>n</i> =	5	34	32	2

*The columns give "age corrected" mean values (mm) for measurements from specimens representing each regional sample. MFL was omitted due to the large number of missing values.

†Regions are defined as follows (numbers refer to locality numbers in Appendix I): Southern Puno, 63; Eastern Puno, 45; Central Puno, 44, 48, 51, 53, 55; Ulla Ulla, 92.

‡The overall test for equality of means (maximum likelihood ratio criteria, Rao, 1973) is significant (MANOVA, $df=57,141$; $F=2.5363$, $p<0.001$).

sent on all *andinus* we have examined, including those from nearby Arequipa Department. The cranium of the holotype of *lutescens*, which might allow an unambiguous distinction between *andinus* and members of the *boliviensis* group, is unfortunately severely damaged, and the critical maxillary teeth are missing entirely. The cranium of the paratype of *lutescens*, however, is in good condition. It lacks the characteristic short, broad rostrum and enlarged bullae of *andinus*, and in all respects appears to belong to the *boliviensis* group.

Second, *lutescens* is allied with *puer* rather than *boliviensis*. The skins of both the holotype and paratype have pale buffy tips on the ventral fur rather than the more deeply buffy or fulvous tips that characterize *boliviensis*. Further, the hind feet of both specimens are small, 19 mm according to Allen, a measurement that lies within the range of hind foot measurements for *puer* but that is smaller than measurements of most *boliviensis*. The cranium of the paratype is very small, has an oval M³, MTRL 3.6 mm, a posterior alisphenoid extension that does not reach the squamoso-al-

isphenoid groove, and other characteristics that make it unambiguously *puer*.

We also note that Allen first presented the name of this taxon as "*lutesens*," but later in the description replaced that spelling with "*lutescens*." Allen did not explain the origin of the name, but presumably "*lutescens*" would be derived from the Latin meaning "yellow gray," while "*lutesens*" would come from the Greek for "bather." The former is an apt description of the dorsal color of the mouse; the latter appears to be nonsensical. Cabrera (1961) stated that *lutesens* was an apparent *lapsus* for *lutescens*, emended by Allen himself later on the same page. Other authors (e.g., Osgood, 1944; Sanborn, 1949) apparently shared the same opinion, and we concur.

Akodon puer caenosus Thomas

HOLOTYPE.—BMNH 18.1.1.38; adult male (age class 3); skin and skull; collected 21 August 1917 by E. Budin, original no. 22.

TYPE LOCALITY.—León, Prov. Jujuy, Argentina, 1500 m (24°03'S, 65°26'W).

EMENDED DIAGNOSIS.—*Akodon puer caenosus* is a small, dark race of *puer* found in the southern part of the species' range. It is notable for its small size (3–5% smaller in most dimensions than *p. puer*), relatively delicate cranium with especially small zygomatic notches, uniformly dark pelage, and diploid chromosome number $2N = 34$.

RANGE.—*Akodon p. caenosus* is found in the highlands of northwestern Argentina (Jujuy Province) and adjacent Tarija Department, Bolivia, and perhaps also in Salta, Tucumán, and Catamarca provinces, Argentina.

DESCRIPTION.—*External characters.* *Akodon p. caenosus* is similar in overall body size to Peruvian *p. lutescens*. The color of *p. caenosus* is very dark. In the individuals we examined, the pelage lacked the very dark middorsal area seen in most *p. puer*. Individual pheomelanin bands are 1.5–2 mm long and Ochraceous Buff. Guard hairs project about 3 mm above the surface of the rump in skins, compared to about 5 mm in *p. puer*, and they appear to be somewhat fewer in number. The dorsal pelage gradually merges into the ventral pelage. Ventral hairs are slate gray for about three-fifths of their length; the tips are strongly buffy. A few white hairs are present on the chins of specimens of *p. caenosus*, but most chin hairs are gray. As in the other subspecies, a distinct and fairly conspicuous ring of pale hairs is present around each eye.

The tail of *p. caenosus* averages 69% of the length of head and body, shortest of the subspecies. The width of the dorsal stripe is highly variable, occupying from one-fourth to one-half the circumference of the tail. Individual hairs near the base of the tail run the length of 2–2.5 scales.

Cranial characters (Fig. 23; Table 4). The skulls of *A. p. caenosus* are similar to those of other *puer*, except that *p. caenosus* tends to have slightly narrower zygomatic plates, slightly narrower zygomatic notches, and a slightly

shorter basioccipital. Ventrally, the anterior margin of the mesopterygoid fossa tends to be arched in *p. caenosus*; it is usually flat in *p. puer*. As with other taxa of this group, these differences are subtle; age-sorted series must be compared for them to be appreciated.

Male reproductive tract. No information is available.

Karyotype. $2n = 34$, $FN = 40$. The karyotype of topotypic specimens has been described by Vitullo *et al.* (1986), and of specimens from Tucumán Province, Argentina by Barquez *et al.* (1980). The autosomal complement contains three pairs of large and one pair of very small metacentrics, plus 12 acrocentric pairs that grade evenly in size from medium to small. The X chromosome is a medium-sized subtelocentric; the Y is a very small acrocentric in the Jujuy specimens, but is biarmed in those from Tucumán. Vitullo *et al.* (1986) reported a deleted X condition in some females. This karyotype differs from those described above for *p. puer* and *p. lutescens* by three Robertsonian whole-arm transpositions, rearrangements that produce the shift in diploid number but not number of autosomal arms.

GEOGRAPHIC VARIATION.—Specimens from the northern part of the range of this subspecies are substantially larger than specimens from Tucumán Province (Table 12).

COMPARISONS.—Comparisons to *boliviensis* and other *Akodon* are made above. In Argentina, *p. caenosus* is similar in shape and color to sympatric *A. spegazzinii* but much smaller in size; Barquez *et al.* (1980) provided comparisons of measurements for these two taxa. From *p. puer*, *p. caenosus* differs by its small size, narrow zygomatic plate and notches, uniformly dark coloration, and distinctive karyotype. Compared to *p. lutescens*, *p. caenosus* is distinguished by its long incisive foramina, darker color, and unique chromosome morphology.

Akodon subfuscus Osgood

Akodon boliviensis subfuscus Osgood, 1944; Field Mus. Natur. Hist., Zool. ser., 29:195 (original description).

HOLOTYPE.—FMNH 52558; adult male (age class 4); skin and skull; collected 29 September 1941 by C. C. Sanborn, original no. 2881.

TYPE LOCALITY.—Limbani, Puno, Inambari drainage, Peru, about 9000 feet.

EMENDED DIAGNOSIS.—*Akodon subfuscus* is an intermediate-sized member of the *boliviensis* group with the following combination of characters: narrow zygomatic notches; weakly developed temporal and mastoid ridges; large oval, postglenoid, subsquamosal, and median lacerate foramina; relatively large teeth (MTRL averages 3.74 mm); perimeter of the surface of M^3 usually oval, with a weakly developed metaflexus and/or trace of a hypoflexus sometimes present but never so deep as to give the tooth an "8" shape; glans penis with dorsal and (weak) ventral grooves, while the crater lip lacks dorsal, ventral, or lateral notches; second diastemal ruga with

TABLE 12.—Geographic variation in *Akodon puer caenosus**†.

	Tarija	Jujuy	Tucumán
CIL	20.92	20.75	20.10
ZB	11.28	11.33	10.97
BB	10.26	10.58	10.39
IOC	3.92	4.29	4.09
RL	8.20	8.21	7.84
NL	8.19	8.34	8.23
RW	4.07	4.19	4.07
RW2	3.54	3.64	3.50
OL	7.36	7.46	7.39
DL	5.56	5.70	5.36
MTRL	3.64	3.60	3.59
IFL	5.38	5.17	4.99
AW	4.44	4.62	4.44
OCW	5.79	5.81	5.67
MB	10.03	10.16	10.08
BOL	3.49	3.29	3.16
MFL	---	3.55	3.49
MFW	0.77	0.98	1.01
ZP	1.97	1.99	1.94
CD	8.18	8.60	8.38
<i>n</i> =	1	18	10

*Regions are defined as follows (numbers refer to locality numbers in Appendix I): Tarija, 111; Jujuy, 114, 115; Tucumán, 122-123, 126, 128.

†Columns give mean values (mm) for measurements from specimens of age classes 3 and 4. "Age corrected" values and distances between regions were not calculated due to the small number of specimens in the sample.

distinct notch; interdental rugae oriented approximately perpendicular to the toothrow. The distinctiveness of *subfuscus* is also clearly established by evidence from the distribution of electromorphs described on pp. 8-10.

RANGE (Figs. 11, 12).—*Akodon subfuscus* is widely distributed in the high elevations of southern Peru from the western Andean slopes in Ayacucho and Arequipa departments, east and south across the deeply dissected highlands of Apurimac and Cusco departments to the eastern Andean slopes in Cusco and Puno departments, and southward at least to western La Paz Department, Bolivia, at elevations above 2200 m. Its distribution in Bolivia is poorly known. In Peru, this species is replaced north of Ayacucho by *juninensis*, and in the Lake Titicaca Basin by both *puer* and *boliviensis*.

Two distinctive races of *subfuscus* live in southern Peru. One, *A. s. subfuscus*, is found along the eastern slope of the Andes in Cusco and Puno departments. The second, for which we shall provide a name below, is widely distributed in the central and western Andes of Cusco, Arequipa, Apurimac, and Ayacucho departments. As with *puer*, we first give a general description for the species, then treat each subspecies separately.

GENERAL DESCRIPTION.—*External characters.* Dorsally, *subfuscus* skins vary

from olivaceous to grayish brown and are heavily lined with black. The crown, middle of the back, and rump are uniformly colored. The pelage over the rump averages 11–13 mm long and the individual pheomelanic bands 1–2 mm long. These lengths, as well as the color of the pheomelanic bands, vary geographically and will be described further below. Buffy or yellowish hairs around the eyes form a faint eyering. The transition from dorsal to ventral pelage is gradual. The basal five-sixths of each ventral hair is slate gray and the tip dark buff to whitish, with variation among populations in tip color. The inguinal region resembles the rest of the venter or appears slightly paler. Most specimens have at least a small patch of all-white hairs on the chin.

The tail of *subfuscus* is sharply bicolored and moderately furry, with individual hairs running the length of 2–3 scales. The tail is long, averaging 75% to 81% of head-body length. The width of the middorsal stripe varies geographically from one-fourth to one-half the circumference of the tail.

Cranial characters. The skulls of *subfuscus* are very similar to those of Peruvian *puer*. They are small to intermediate in size (Table 4), the zygoma appear weakly flared, the zygomatic notches are narrow and shallow, the lacrimals appear small (if present at all), the sides of the interorbital region are usually rounded (sometimes squared posteriorly), and temporal and mastoid ridges are weakly expressed. From the side, the profile of the top of the skull is moderately curved, and the frontal region appears slightly swollen. The zygomatic plates are of average to slightly less than average breadth, and the tympanic hook is usually slender to only moderately stout. The posterior ascending process of the alisphenoid may or may not contact the squamoso-alisphenoid groove.

Ventrally, the incisive foramina are of average size for the group. The palate is shallowly to moderately deeply grooved. The posterior end of the palate (anterior border of the mesopterygoid fossa) is strongly squared and usually has a median spine. The mesopterygoid fossa is either especially narrow or of intermediate size compared to other members of the *boliviensis* group, depending on the population examined. The sides are straight to slightly convex. Foramina ovale, median lacerate foramina, and sphenopalatine vacuities are of medium size to large.

Dental characters (Fig. 24). The teeth of *subfuscus* are generally as described in detail for the *boliviensis* group. A well-developed parastyle and mesostyle are present on M^1 , a metalophule is usually present but tiny, and the enterostyle is absent. On M^2 , an anterior cingulum and mesostyle are present and conspicuous, while enterostyle and metalophule are usually missing entirely. As in *puer*, the M^3 tends to be small and less complex than in *boliviensis*, with the hypoflexus and metaflexus either absent or at most very shallow (*vs.* strongly developed in *boliviensis*).

On the lower jaw, *subfuscus* differs from *boliviensis* in that an ectostylid is often seen on M_2 and an anterior cingulid on M_3 (but these structures are not present on all specimens, nor is either invariably absent in *boliviensis*).

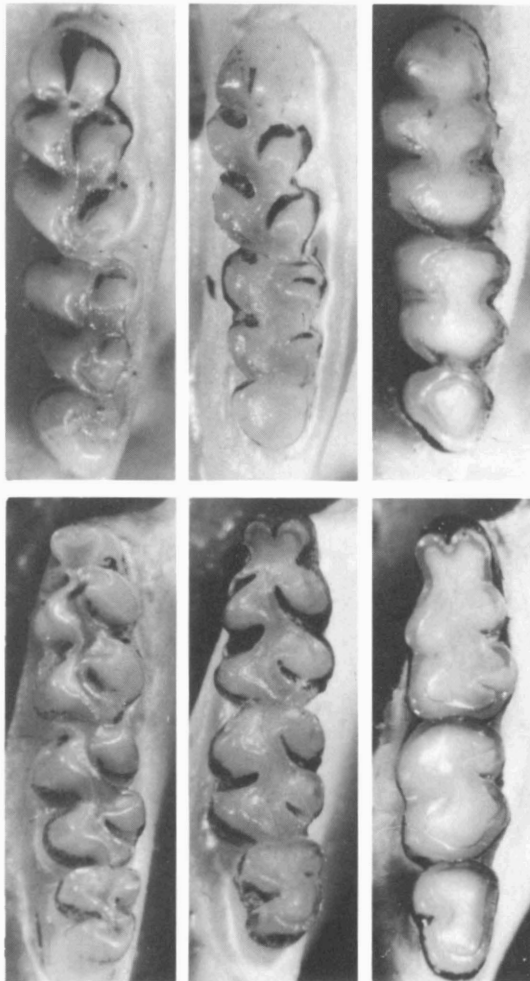


FIG. 24. Molars of *Akodon subfuscus*. Upper left molars on top; lower left molars on bottom. From left to right, MVZ 174254 (age class 1), MVZ 172991 (age class 3), UMMZ 160793 (age class 5).

Accessory reproductive glands. These structures are generally as described for the group. The medial ventral prostates are especially small, and the vesicular glands lack the distinctive knobs found in some species.

Phallus and baculum (Fig. 25). The glans is short and stout, sub-cylindrical, with the dorsum flat and venter convex in profile. A ventral groove is weakly developed and confluent with the crater lip; a dorsal groove is well developed and also confluent with the crater lip. Epidermal spines are very fine and short, averaging 0.07 mm long and 11 per millimeter along the ventral midline; they grade to a somewhat smaller size distally. The spines

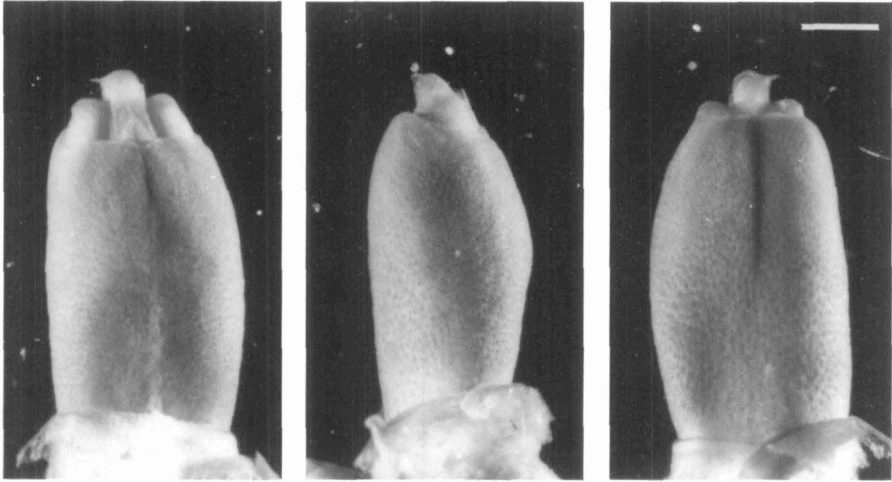


FIG. 25. Ventral, right lateral, and dorsal views of the phallus of *Akodon subfuscus*; line = 5 mm. The individual depicted (MVZ 174160) is a member of the subspecies of *subfuscus* described below.

are imbedded in very shallow individual pits; both the small size of the spines and the shallowness of the pits give the epidermis a distinctively smooth texture compared to that of *boliviensis*. The crater lip is very thin and only weakly distinguishable from the spinous epithelial body of the glans; it does not completely surround the crater. Neither ventral, dorsal, nor lateral notches are present. Both lateral and medial bacular mounds extrude distally from the crater rim; the medial mound is only slightly higher than the lateral ones, and its tip is curved dorsally rather than projecting straight outward from the glans as in *boliviensis*. Urethral flaps are long and well developed, taper distally, have well separated tips, and extend beyond the crater rim so as to be visible externally; no obvious spines or other ornamentation are present. The dorsal papilla is rather small and only its base is surrounded by folds of tissue extending from the medial mound to the inner crater wall; it is elongate in shape, with a distinctly tapering tip.

The proximal baculum is short and stocky, with a flared base that lacks a medial flange (except in one specimen from above Ollachea, Puno [MVZ 172982]), and with a distinct medial notch. The shaft is thick and straight in lateral aspect. The distal baculum is well developed, with the lateral digits about three-fourths the length of the medial one. The proximal baculum is relatively longer in specimens from the Sangabán valley (Puno Department) than those from either Cusco or Arequipa departments, averaging 2.33 times the distal bacular length (range 2.32–2.34) as opposed to 2.02 times that length in others (range 1.82–2.20).

Palatal rugae (Fig. 7). *Akodon subfuscus* has an arched first diastemal ruga with straight sides, a wavy second diastemal ruga with a distinct medial

notch, and interdental rugae that tend to be straight in their transverse portions. This pattern is the same in all *subfuscus* examined from eastern (Cusco Department) and western (Arequipa Department) segments of the range of this species.

Karyotype. $2n=40$, $FN=40$ (Fig. 19C). The autosomal complement is identical to that described above for *boliviensis* and *puer*. The X chromosome is a medium subtelocentric as in *puer*, but the Y is a very small acrocentric, equivalent in size to the small biarmed autosomal pair.

HABITAT.—As with all Peruvian and Bolivian members of the *boliviensis* group, *subfuscus* is a denizen of bunchgrass habitats in the high elevations of the Andes. It is particularly common in mixtures of grass clumps and shrubs or of grass and large exposed rocks, as along walls of corrals or houses, but where the soils are relatively soft and fine grained. Its ecological relationships with sympatric *Akodon andinus*, *Bolomys amoenus*, and *Chroecomys jelskii* are discussed above, p. 56.

In the western parts of its range in Peru, *A. subfuscus* co-occurs with a sigmodontine assemblage that includes *Auliscomys pictus* and *sublimus*, *Phyllotis darwini* and *magister*, *Calomys lepidus* and *sorellus*, *Neotomys ebriosus*, *Chinchillula sahamae*, and species of *Oligoryzomys*. In Cusco and Puno departments, *Akodon subfuscus* is sympatric with *Auliscomys pictus*, *Phyllotis darwini* and *osilae*, *Calomys sorellus*, *Chinchillula sahamae*, *Neotomys ebriosus*, *Oxymycterus paramensis*, *Microroryzomys altissimus*, and species of *Oligoryzomys*.

COMPARISONS.—This species is not known to occur in sympatry with either *boliviensis* or *puer*, although their respective ranges nearly meet along the border between Cusco and Puno departments in southern Peru, and along the crest of the Cordillera Carabaya in northern Puno Department (Figs. 11, 12). In these areas, *subfuscus* can be distinguished from either *boliviensis* or *puer* by a combination of the following differences (most of which can best be seen when animals of the same age class are compared). Compared to *boliviensis*, *subfuscus* is darker and has less complex M^3 s; less strongly developed cranial ridges; narrower zygomatic notches; first diastemal ruga arched and second ruga notched; and glans penis clothed with small spines, giving it a smooth (*vs.* shaggy) appearance. Compared to *puer*, with which it is most similar both morphologically and electromorphically, *subfuscus* from Puno Department can easily be recognized by its distinctly larger overall size (intermediate between *puer* and *boliviensis*) and much darker color. In general, the zygomatic notches in *subfuscus* average broader than in *puer*, and the teeth of *subfuscus* are distinctively larger. The bony palate also appears to be less deeply grooved in *subfuscus* than *puer*. Parapterygoid plates tend to be more deeply excavated in *subfuscus* (but old *puer* have more deeply excavated plates than young *subfuscus*), and the lateral margins of the plates tend to be more convex (especially in old individuals). The tympanic hook of *subfuscus* is usually stouter (but not as stout as in *boliviensis*). Individuals in most populations of *A. subfuscus* also differ from *puer* in that there is considerable variation in *subfuscus* as to whether the posterior ascending process of the alisphenoid contacts the

squamoso-alisphenoid groove (while it almost always does not in *puer*). Finally, the arched first diastemal ruga, notched second ruga, and relatively straight interdental rugae of *subfuscus* all serve to distinguish it from *puer*.

Akodon subfuscus is known to occur sympatrically with *Akodon juninensis* in Ayacucho Department, Peru. The morphological differences between these two species are subtle, and in fact the electromorphic characters described above provided the first evidence that two separate species might exist. *Akodon subfuscus* differs from *juninensis* by having on average a larger and relatively broader cranium, broader zygomatic plates, much larger foramina ovale, larger postglenoid foramina, M¹ with a relatively deep anteromedian flexus, and glans penis lacking a dorsal notch on the crater lip. The cranial characters in particular can only be appreciated if same-age individuals are compared. The soft palate of *subfuscus* also differs from that of *juninensis* in the same way as it differs from that of *puer*.

Akodon subfuscus also occurs sympatrically with *mollis*-like forms, and, in fact, the type series of *subfuscus* from the Limbani Valley in northern Puno includes several individuals of *Akodon kofordi*, a recently described species close to *A. fumeus* and perhaps *A. mollis* (Myers and Patton, 1989a). *Akodon subfuscus* differs from *kofordi* and its relatives, however, by usually being smaller and, in particular, by having a relatively narrow and parallel-sided mesopterygoid fossa (rather than broad and often lyre-shaped) and large sphenopalatine vacuities (Myers and Patton, 1989a).

GEOGRAPHIC VARIATION.—Samples of *A. subfuscus* were available from a number of localities in southern Peru. Specimens representing populations in the northeastern part of the range of this species (Puno, most of Cusco, and northern Apurimac, central Ayacucho, and eastern Huancavelica departments) were consistently darker and 5% larger than those from the southwestern and western part of the range (southern Cusco, Arequipa, southern Apurimac, and southern Ayacucho departments); these differences were statistically highly significant when individuals of the same toothwear class were compared (MANOVA, Age Class 3, $F=25.31$, $df=19,197$, $p<0.0001$; Age Class 4, $F=13.44$, $df=19,94$, $p<0.0001$; Age Class 5, $F=3.28$, $df=19,47$, $p<0.001$; comparisons not made of age-adjusted measurements for reasons described below). Based primarily on this difference, the electromorphic patterns described above, and on differences in coloration noted below, we formally recognize two subspecies of *Akodon subfuscus*, as follows:

Akodon subfuscus subfuscus Osgood

EMENDED DIAGNOSIS.—Populations assigned to *A. s. subfuscus* are distinctive for their very dark dorsal and ventral coloration and their overall large size.

RANGE.—The nominate subspecies is found along the eastern escarpment of the Andes between 1900 m and 4100 m elevation in Puno, Cusco,

northern Apurimac, central Ayacucho, and eastern Huancavelica departments, Peru (Fig. 11).

DESCRIPTION.—*External characters.* The overall color pattern is as described for the species. Dorsally, the fur is dark, appearing dark olivaceous brown. Fur hairs over the rump average 12–13 mm long. Pheomelanin bands on individual hairs in this area are 1.0–1.5 mm long and approximately Ochraceous Buff. Numerous black guard hairs are present; these project 5–6 mm beyond the ends of the fur hairs. Ventrally, Ochraceous Buff tips on the hairs give the pelage the appearance of being washed with buff. The chin has a large patch of monocolored white hairs.

The tail of *s. subfuscus* is long (75% of head-body length) and strongly bicolored, with the black stripe occupying one-third to one-half the circumference of the tail. The tail appears moderately hairy, with individual hairs the length of 2–3 scales.

Cranial characters. In shape, skulls of *s. subfuscus* are as described for the species. Individuals from these northeastern populations average 5–10% larger than individuals from other areas (Table 4, Fig. 26, and below).

Dental characters. The teeth are as described for the species, except that within the populations of *s. subfuscus* we sampled all individuals that could be scored had at least a trace of an ectostylid on both M_1 and M_2 and an anterior cingulid on M_3 .

HABITAT.—This subspecies inhabits lush bunchgrass and bunchgrass-shrub or bunchgrass-large rock associations above the elfin forest on the eastern Andean escarpment (Fig. 27).

COMPARISONS.—See the description of the next subspecies.

GEOGRAPHIC VARIATION (Table 13).—Some variation in color was noted among populations within the northeastern geographic unit of *s. subfuscus*. Specimens from the various drainages on the eastern slope in Cusco (Urubamba and Cosñipata) and Puno (Sangabán and Limbani, the latter including the holotype) are dark dorsally, with animals from the more northern drainages darkest, although only minimally different from those from the southern parts of the range. Specimens taken from the Sangabán drainage above Ollachea in Puno Department differ from all others in having whitish (rather than buffy) tips on their ventral hairs, giving their venters an overall pale grayish to faintly buffy cast (dark grayish and more strongly buffy in other samples). These specimens are also among the largest of the subspecies.

Specimens from the northeastern side of Lake Titicaca in La Paz Department, Bolivia, appear to be *s. subfuscus*, and we tentatively place them in this subspecies. They average about 6% larger in most cranial dimensions than individuals from elsewhere within the range of *s. subfuscus*. Their large size appears to represent the continuation of a northwest to southeast cline of increasing body size, beginning with the small animals of Arequipa and Ayacucho departments. The increase in the width of the mesopterygoid fossa is especially notable; it averages 17% larger in the specimens from La Paz compared to those from adjacent Peruvian populations, and



FIG. 26. Dorsal, ventral, and lateral views of crania of *Akodon subfuscus subfuscus* (MVZ 172966, left) and *A. subfuscus* *ssp. nov.*, described below (MVZ 174114, right).

FIG. 27. Habitat of *Akodon subfuscus subfuscus* at two localities on the eastern Andean slope, Cusco Department, Peru. A. Below Abra Acanacu, 32 km by road NE Paucartambo, 3140 m (contact between páramo muy húmedo subalpino subtropical and bosque pluvial montano subtropical; Tosi, 1960). *A. subfuscus* occurs in the grassland, *A. torques* is common in patches of elfin forest. B. Piri Valley, 26 km by road NW Ollantaytambo, 3770 m (bosque muy húmedo montano subtropical; Tosi, 1960). Highly disturbed bunchgrass and *Baccharis* shrub community amid human dwellings.

A



TABLE 13.—Geographic variation in *Akodon s. subfuscus**. A. "Age corrected" mean values (mm) for measurements from specimens representing each regional sample†. B. Mahalanobis distances describing the overall morphological differences among populations (based on "age-corrected" measurements)‡.

A.	Aya- cucho	Apur- imac	Uru- bamba	Paucar- tambo	Marca- pata	San- gabán	Lim- bani	Beni
CIL	22.73	21.94	22.33	21.79	22.87	22.47	22.34	23.42
ZB	11.99	11.99	12.15	11.76	12.32	12.21	12.14	12.64
BB	11.06	11.03	11.11	10.93	11.23	11.27	11.15	11.49
IOC	4.35	4.36	4.33	4.19	4.42	4.44	4.38	4.59
RL	8.93	8.65	8.87	8.55	9.25	9.16	9.04	9.31
NL	8.75	8.50	8.79	8.58	9.44	8.97	9.06	9.27
RW	4.62	4.53	4.53	4.47	4.59	4.60	4.48	4.63
RW2	3.91	3.84	3.76	3.78	3.88	3.86	3.76	4.11
OL	8.10	7.87	7.87	7.71	8.05	8.05	8.06	8.19
DL	6.42	6.10	6.23	6.17	6.50	6.27	6.38	6.61
MTRL	3.79	3.78	3.90	3.65	3.83	3.89	3.82	4.01
IFL	5.73	5.52	5.62	5.33	5.93	5.29	5.53	5.56
AW	4.85	4.87	4.86	4.58	4.94	5.03	4.87	5.08
OCW	6.03	5.97	5.98	5.86	6.07	6.09	6.07	6.26
MB	10.79	10.68	10.76	10.44	11.04	10.74	10.75	10.95
BOL	3.51	3.43	3.52	3.23	3.74	3.37	3.62	3.70
MFW	1.09	1.18	1.08	1.09	1.31	1.16	1.12	1.27
ZP	1.98	1.98	2.06	2.02	2.07	2.21	2.00	2.23
CD	9.07	9.09	9.20	8.80	9.31	9.43	9.15	9.21
n =	21	34	52	32	8	38	13	20

B.

	Ayacucho	Apurimac	Urubamba	Paucartambo	Marcapata	Sangabán	Limbani
Apurimac	5.05						
Urubamba	9.52	4.75					
Paucartambo	10.70	12.00	10.91				
Marcapata	14.43	10.50	9.47	19.53			
Sangabán	20.74	14.74	12.29	24.52	21.61		
Limbani	6.40	6.88	6.40	13.88	6.68	12.77	
Beni	15.42	15.21	15.55	21.78	18.72	15.27	13.28

*Regions are defined as follows (numbers refer to locality numbers in Appendix I): Urubamba, 23-32; Paucartambo, 33-37; Limbani, 40-42; Apurimac, 16-22; Ayacucho, 12-15; Marcapata, 38; Sangabán, 39; Beni, 93-95.

†MFL was omitted due to the large number of missing values.

‡All distances are statistically significant at $p < 0.0001$ except Marcapata-Limbani ($p = 0.62$), and the overall test for equality of means (maximum likelihood ratio criteria, Rao, 1973) is also significant (MANOVA, $df = 133, 1279$; $F = 7.2162$, $p < 0.0001$).

nearly 65% larger than those from Ayacucho and Arequipa departments in southwestern Peru. The status of Bolivian populations is questionable; additional material (including tissues for electrophoretic analyses) is needed to verify their relationship with *subfuscus*.

Akodon subfuscus arequipae new subspecies

HOLOTYPE.—MVZ 174114; young adult male (age class 3); skin, skull and tissues; collected on 10 July 1987 by J. L. Patton, original number 13645.

TYPE LOCALITY.—15 km S Callalli, Depto. Arequipa, Peru, elevation 4150 m.

DIAGNOSIS.—*Akodon s. arequipae* is a race of *subfuscus* characterized by its small size, pale pelage, and especially narrow mesopterygoid fossae.

RANGE.—*Akodon s. arequipae* is known from the central and western Andes of Cusco, Arequipa, southern Apurimac, and southern Ayacucho departments at elevations between 3200 and 4420 m.

DESCRIPTION.—*External characters.* The dorsal pelage appears grayish brown and rather pale, without striking olivaceous or brown tones. The fur averages 11–12 mm long in the mid-rump area, and pheomelanin bands appear longer than in *s. subfuscus*, averaging 1.5–2.0 mm. These bands are approximately Warm Buff. The ventral pelage is tipped whitish, grayish, or faintly buffy, never taking on the deep buffy, almost orange hues of the ventral pelage found on members of northeastern populations of *s. subfuscus*.

The tail is long (81% of head-body length) and sharply bicolored, with a narrow black dorsal stripe only one-fourth to one-third the circumference of the tail in width. Individual hairs from near the base of the tail run the length of 2.5–3 scales.

Cranial characters (Fig. 26). As noted above and in Table 4, specimens of *s. arequipae* are smaller on average than specimens of *s. subfuscus*. The difference in size is most notable in animals of age class 3 ($n=97$ *s. subfuscus*, $n=126$ *s. arequipae*), for which measurements of length such as condyloincisive length, rostral length, nasal length, orbital length, and others are from 5 to 10% larger in *s. subfuscus* than in *s. arequipae*. Width measurements tend to show less difference, with most no more than 5% larger in *s. subfuscus*. The most striking difference, however, is in mesopterygoid fossa width, in which *s. subfuscus* averages 26.9% broader than *s. arequipae*. Differences in size are less in older animals; in age class 4 ($n=87$ *s. subfuscus*, $n=35$ *s. arequipae*) most length measurements are 5–6% larger in *s. subfuscus* (breadth measurements remain 0–5% larger); the mesopterygoid fossa width in *s. subfuscus* averages 25.4% larger than in *s. arequipae*. In age class 5 ($n=35$ *s. arequipae*, $n=35$ *s. subfuscus*), all differences are under 4% except mesopterygoid width, for which *s. subfuscus* averages 10.5% greater.

Dental characters. In general, the teeth of *s. arequipae* are as described for the species. They differ from those of *s. subfuscus*, however, in that the

mesostylid on M_1 is usually tiny or absent (*vs.* usually large), and the mesostylid on M_2 is usually missing entirely. Further, most individuals examined appeared to lack an anterior cingulid on M_3 ($n=5$ of 6 examined), while all *s. subfuscus* young enough to show this structure ($n=6$) had at least a trace.

HABITAT.—*Akodon s. arequipae* is found in bunchgrass clumps associated with large shrubs and/or rocks in xeric western slope communities dominated by thorny shrubs and cacti (Fig. 28B). It also ranges in open llanos of bunchgrass and lower stature shrubs at higher elevations (Fig. 28A).

COMPARISONS.—Members of this subspecies differ from members of the nominate subspecies by being paler and smaller, and by having (on average) narrower mesopterygoid fossae. There is considerable geographic variation in electromorphic characters, but most *s. arequipae* populations possess the GOT-1^{131,100} and PGI¹⁶⁷ alleles, while *s. subfuscus* populations do not.

AGE VARIATION.—Specimens of *s. arequipae* differed from all other members of the *boliviensis* group in the relationship between toothwear class and cranial size. As described under Methods, in most taxa of the group measurements of cranial dimensions increased approximately linearly with increasing toothwear class. This pattern allowed the "adjustment" of all measurements taken from individuals in classes 2–5 to a common toothwear class. As long as the relationships are linear, and insofar as an individual's toothwear class reflects its age, this procedure results in age-corrected measurements and allows comparison of individuals whose actual age may not be the same.

Curiously, the relationship between toothwear class and several cranial measurements in *s. arequipae* was strongly curvilinear, in each case due to an unusual amount of growth between toothwear classes 4 and 5. The difference was so great that we were unable to transform the original values to linearity. For each variable, however, growth between classes 2–4 was approximately linear. The comparisons of age-adjusted measurements made below are based on these age classes only, and as is the case for other taxa, these age-adjusted measurements are used only for comparisons within the taxon on which the regression is based.

The reason for and taxonomic significance of this difference in the relationship between cranial size and the rate of erosion of the molar surface is unknown. Possible explanations include (1) growth actually accelerates between classes 4 and 5 in *s. arequipae* compared to others in the *boliviensis* group; (2) the rate at which teeth wear in older *s. arequipae* is slower, so that the difference in age between toothwear classes 4 and 5 is greater in *s. arequipae* than in other taxa of the group. A difference in the rate of toothwear might be due to dietary differences (*e.g.*, less reliance on abrasive foodstuffs in *arequipae*) or due to differences in the teeth themselves that make them less susceptible to wear. Why this might affect individuals in toothwear class 5 more than others is not known.

GEOGRAPHIC VARIATION.—Specimens from Arequipa and western Cusco

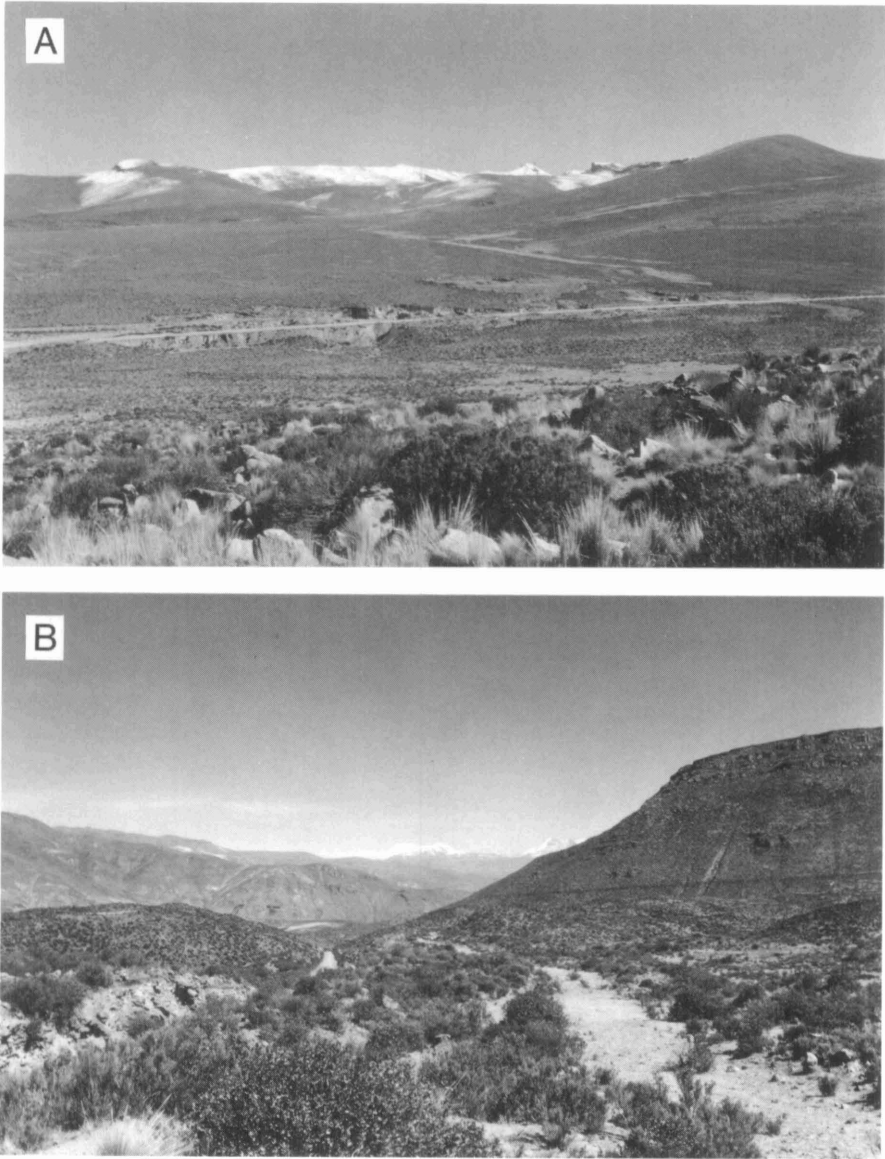


FIG. 28. Habitat of *Akodon subfuscus arequipae* at two localities in Arequipa Department, Peru. A. 2 km W Sumbay, 4200 m (*páramo húmedo subalpino subtropical*; Tosi, 1960). *A. subfuscus* and *Chroemys jelskii* are common inhabitants of the puno bunchgrass and tola shrub habitat in the foreground; *A. andinus* occurs in the dwarf shrub habitat on the slopes above the road that runs through the middle of the photograph. B. 1 km N Chivay, 3700 m (*maleza desértica montano*; Tosi, 1960). *A. subfuscus* is the only akodontine at this locality.

TABLE 14.—Geographic variation in *Akodon subfuscus arequipae**†. A. "Age corrected" mean values (mm) for measurements from specimens representing each regional sample. B. Mahalanobis distances (based on "age-corrected" measurements) describing the overall morphological differences among populations‡.

A.					
	South Ayacucho	South Apurimac	North Arequipa	Callalli	Arequipa
CIL	21.42	20.96	20.86	20.91	20.81
ZB	11.69	11.41	11.27	11.54	11.40
BB	10.93	10.74	10.65	10.83	10.90
IOC	4.29	4.24	4.13	4.21	4.27
RL	8.43	8.25	8.22	8.19	8.06
NL	8.10	7.98	8.28	8.14	7.97
RW	4.38	4.22	4.34	4.43	4.47
RW2	3.64	3.52	3.58	3.67	3.65
OL	7.51	7.35	7.39	7.39	7.48
DL	6.01	5.78	5.66	5.78	5.66
MTRL	3.77	3.74	3.62	3.68	3.71
IFL	5.51	5.41	5.03	5.14	5.13
AW	4.89	4.69	4.59	4.68	4.70
OCW	5.96	6.01	5.93	5.88	5.85
MB	10.49	10.36	10.47	10.51	10.38
BOL	3.36	3.19	3.31	3.34	3.31
MFW	0.86	0.93	0.99	0.79	0.85
ZP	1.99	1.98	1.92	2.01	1.81
CD	9.09	8.81	8.71	9.08	8.96
<i>n</i> =	27	6	10	118	28
B.					
	South Ayacucho	South Apurimac	North Arequipa	Callalli	
S. Apurimac	6.33				
N. Arequipa	22.30	17.16			
Callalli	11.64	16.06	9.95		
Arequipa	14.71	20.84	11.56	9.91	

*MFL was omitted due to the large number of missing values.

†Regions are defined as follows (numbers refer to locality numbers in Appendix I): South Ayacucho, 72-74; South Apurimac, 78-79; North Arequipa, 80-81; Callalli, 82-84; Arequipa, 85-89.

‡All distances are statistically significant at $p < 0.0001$ except South Ayacucho-South Apurimac ($p = 0.10$), and the overall test for equality of means (maximum likelihood ratio criteria, Rao, 1973) is also significant (MANOVA, $df = 76,656$; $F = 6.5789$, $p < 0.0001$).

departments appear slightly paler and grayer than those from Ayacucho, Apurimac, or Huancavelica departments.

Age-corrected cranial measurements were calculated as described above (age classes 2-4), and comparison of regional samples (Table 14) revealed significant differences among these groups. Specimens from the Acari river drainage in southern Ayacucho Department averaged 2-7% larger

than others, with the greatest differences found in IFL, DL, and AW. Specimens from near Cailloma, Arequipa Department (North Arequipa sample in Table 14), tended to have narrow crania, averaging 2–4% smaller than other *arequipae* in measurements such as ZB, BB, IOC, RW, RW2, and AW, as well as in IFL, ZP, and CD. These specimens also had markedly narrower mesopterygoid fossae, with MFW averaging only 12% smaller than in *s. subfuscus* (*vs.* 18–30% in other populations of *s. arequipae*; Table 14).

CONCLUSIONS

The species we treat here as members of the *boliviensis* group are exceedingly similar in virtually all aspects of their morphology and genetics, and it seems likely that they represent phylogenetically closely related entities. Nevertheless, we do not know at present if this group will prove to be monophyletic relative to the remaining species within the subgenus *Akodon*, or whether other currently recognized forms, or those awaiting discovery, will be found to be members of this group. Members of the *boliviensis* group probably have a close relationship to *Akodon mollis* (including *orophilus*, *orientalis*, and *altorum*), which replaces the *boliviensis* group geographically in northern Peru and Ecuador. Members of the *boliviensis* group also may have close relationships to *Akodon azarae* (including subspecies *bibianae* and *hunteri* [following Cabrera, 1961 and Massoia, 1971]) in northern Argentina, Uruguay, and Paraguay.

Within the *boliviensis* group as recognized here, *juninensis*, *subfuscus*, and *puer* appear more similar morphologically and we suspect more closely related to each other than to *boliviensis* itself. The first three species share contiguous or nearly contiguous ranges, with minimal or no geographic overlap, whereas *boliviensis* and *puer* are broadly sympatric and strongly segregated by habitat over most of Puno Department in Peru. Moreover, these three species share details of the cranium, teeth, and male phallus that set them apart from all other *Akodon*, including *boliviensis*, that we have examined. Shared cranial and dental features include the small M^3 without strongly developed hypoflexus or metaflexus, small and narrow zygomatic notches, weakly developed cranial ridges, moderately to very slender tympanic hook, and in general, small size and delicate construction. Shared features of the phallus include fine epidermal spines and a generally smooth appearance to the phallic epidermis, a sub-cylindrical shaft, very narrow crater lip area, lack of ventral and lateral crater notches, exposed lateral as well as medial bacular mounds, elongated and strongly tapering urethral flaps that are usually exposed distally, and a dorsal papilla that is only minimally imbedded in basilar tissue folds. We lack information, however, concerning the condition of most of these characteristics (especially soft anatomical structures) in outgroup species, so that at this time cladistic treatment of morphological characters is not possible.

The overall slightly greater similarity among *juninensis*, *subfuscus*, and *puer* does not, however, extend to all genetic distance measures based on the electromorphic analyses. *Akodon juninensis* is placed as a sister group to the other three species in the UPGMA phenogram (Fig. 2A); this is due to its possession of uniquely fixed alleles at two loci (while the other three species are likewise characterized by unique alleles, in no case are any of these fixed). In the Wagner tree (Fig. 2B), however, *juninensis* is placed with *puer* and then *subfuscus* relative to *boliviensis*, in agreement with our assessment of the morphological similarities of the four taxa.

There is no resolution at all of the phyletic relationships among these taxa when patterns of shared alleles are examined. There are a total of 59 alleles for the 26 loci examined among the four species, 22 of which are shared with an outgroup taxon, *Bolomys amoenus* (and thus are probably symplesiomorphic; see Table 2 and Patton *et al.*, 1989). Of the remaining 37 alleles, 20 are autapomorphic for individual species, four are synapomorphic to the four taxa relative to *Bolomys*, and the remainder are distributed among pairs or triplets of the four, with no fewer than one allele, nor more than three, linking any pair or triplet. The *boliviensis-subfuscus* pair is linked by three, *boliviensis-puer* by two, and the pairs *puer-subfuscus* and *subfuscus-juninensis* by one each. The triplet *puer-subfuscus-juninensis* shares but one allele, and that of *boliviensis-puer-subfuscus* shares three.

This pattern of allele sharing results in the following conclusions about relationships among these taxa: (1) the generally more divergent placement of *boliviensis* in both distance trees (Fig. 2) is a product of its larger number of high frequency unique alleles (3 of 4) and greater frequency differences for some alleles shared with other taxa; (2) *juninensis* has relatively large distances to other taxa because it has a low number of total alleles and is fixed for unique ones at two loci; and (3) cladistic relationships cannot be resolved with any confidence beyond a simple polychotomy relative to the outgroup taxon, *Bolomys amoenus*.

If the *boliviensis* group as we currently recognize it is indeed a monophyletic taxon, then the electromorphic data suggest the following with regard to the derivation of its species. First, the timing of differentiation and speciation was relatively recent. The level of divergence recorded among the four species is low but within the range of differences seen for other pairs of rodent species (see above and genetic distance summaries in Selander and Johnson, 1973; Nevo, 1978; and Avise and Aquadro, 1982). The electromorphic distance values across the range of each species are in the neighborhood of those values for local populations of other rodents. Second, the pattern of divergence appears to result from geographic splitting, or vicariance, of a once widely spread ancestral taxon, with each present species evolving *in situ* from this ancestral base. This seems particularly so for the triad of species *juninensis*, *subfuscus*, and *puer*, and their included races.

Finally, we offer some suggestions as to the direction that future research with these species should take. Most obviously from the accounts

presented above, the geographic limits and ecological relationships of *juninensis* and *subfuscus* need to be determined. Unfortunately, with the information available, these two forms are not easy to distinguish in the field. Similarly, additional fieldwork is needed across Abra La Raya, on the Cusco-Puno border, as well as across the Cordillera Carabaya in northern Puno Department, to determine the distributional, ecological, and genetical relationships between *subfuscus* and *puer*. These problem areas in Peru are reasonably well defined because of the extent of materials of all types available to us now. However, Bolivia and northwestern Argentina represent open domains for continued field work. It is difficult at the moment to identify specific areas that need more effort than others in these areas because good series of specimens, necessary for age-corrected comparisons, are few indeed. We believe it likely, however, that when levels of geographic analyses are carried out for these regions similar to those presented above for southern Peru, additional taxa of the *boliviensis* group will deserve recognition, and a reevaluation of our conclusions here will be necessary.

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APPENDIX I

GAZETTEER AND LIST OF SPECIMENS OF THE *Akodon boliviensis* GROUP EXAMINED

Localities are numbered below sequentially from north to south as shown in Fig. 29. For each locality, data include the species identification(s), museum repository (as identified in the Materials and Methods section), the number of specimens by sex that have been examined, and indication of specimens karyotyped [K] or examined biochemically by elec-

trophoresis [E]. A few specific localities could not be located; these are not mapped but are listed below. Other localities were not mapped because of close geographic proximity; these are listed under the same number below and on the map. Elevations have been converted to meters for all localities, even if given in feet on the original specimen labels.

PERU

ANCASH:

1. 2 km W Yupash [=Llupash], 3030 m (*juninensis*: 3 females, MVZ 139220–139222).
2. 25 mi S Huaras, 3790 m (*juninensis*: 2 females, MVZ 137958–137959).
3. 6 mi WSW Cahuel Tunnel (on rd to Chavin), 3940 m (*juninensis*: 1 male, MVZ 137947; 1 female, MVZ 137948).

JUNIN:

4. Near San Blas, 4250 m (*juninensis*: 1 male, UMMZ 120285).
5. 22 km N La Oroya, 4040 m (*juninensis*: 3 males [all E], MVZ 173041–173043; 3 females [all E], MVZ 173038, 173040, 173044).
6. 9.5 mi N La Oroya, 3950 m (*juninensis*: 14 males, AMNH 231317, 231324–231326, 231338, 231340, 231346, 231702, 231745, 231945, 232638–232641; 16 females, AMNH 231318, 231319, 231322, 231327–231329, 231331, 231332, 231334–231337, 231341, 231676, 231679, 231703).
7. Pomacocha, Yauli Valley, 4300 m (*juninensis*: 2 males, MVZ 137606, 137607; 2 females [both K], MVZ 137966, 137967).

LIMA:

8. 1.2 mi W Chinchán, 4730 m (*juninensis*: 2 males, AMNH 231349, 231352; 6 females, AMNH 231351, 231354, 231356–231359). 6.3 mi W Casapalca, 3900 m (*juninensis*: 23 males, AMNH 231363, 31374, 231377, 231379, 231381, 231383–231385, 231387, 231391, 231400, 231403, 231406, 231414, 231419, 231425, 231428, 231442, 231443, 231445, 231446, 232633, 232634; 10 females, AMNH 231382, 231386, 231399, 231402, 231407, 231409, 231411, 231427, 231429, 231438).
9. Villavista, 3700 m (*juninensis*: 1 female, MVZ 119929). San Mateo, 2900 m (*juninensis*: 1 male, MVZ 119928).
10. Zarate, 6 mi E Pueblo San Bartolomé, 2725 m (*juninensis*: 2 males, MVZ 119931, 119932; 1 female, MVZ 119930).

HUANCAVELICA:

11. Hda. Piso, Locroja (*juninensis*: 1 male, FMNH 75561).
12. Lircay (*subfuscus subfuscus*: 3 males, FMNH 75520, 75521, 75563; 3 females, FMNH 75522, 75562, 75564).

AYACUCHO:

13. 2 mi SE Huanta, 2775 m (*subfuscus subfuscus*: 2 males [both K], MVZ 141321, 141322).
14. Huanta (*subfuscus subfuscus*: 2 males, FMNH 75516, 75517; 2 females, FMNH 75518, 75519).
15. Pacaicasa, Ayacucho Basin, 2650 m (*subfuscus subfuscus*: 2 males, UMMZ 120274, 120276; 1 female, UMMZ 120275). Chunyacc, Ayacucho Basin, 3600 m (*subfuscus subfuscus*: 3 males, UMMZ 120277, 120278, 120281; 3 females, UMMZ 120279, 120280, 120282). Tucumacha, Ayacucho Basin, 4250 m (*subfuscus subfuscus*: 1 male, UMMZ 120284; 1 female, UMMZ 120283).
16. San Miguel Tambo (*subfuscus subfuscus*: 3 males, FMNH 75512–75514; 3 females, FMNH 75515, 75559, 75560).
17. Hda. Pajonal, Ocros, 2200 m (*subfuscus subfuscus*: 2 males, FMNH 75511, 75536; 1 female, FMNH 75558). Ocros, 3150 m (*subfuscus subfuscus*: 1 male, FMNH 75494; 3 females, FMNH 75492, 75493, 75495).

APURIMAC:

18. Uripa, Andahuaylas, 3100 m (*subfuscus subfuscus*: 1 male, FMNH 75557; 1 female, FMNH 75535).
19. Hda. La Laguna, Andahuaylas, 3040 m (*subfuscus subfuscus*: 4 males, FMNH 75529–75531, 75533; 4 females, FMNH 75528, 75532, 75553, 75554).

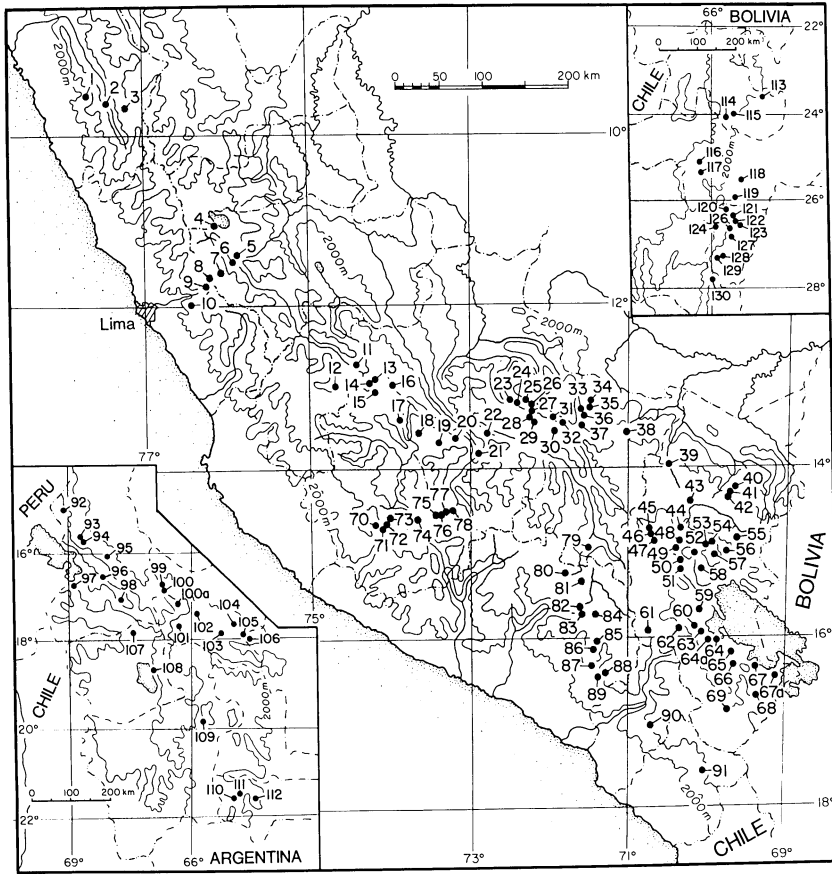


FIG. 29. Collecting localities for members of the *Akodon boliviensis* group. Localities are numbered as in the gazetteer (Appendix I). Elevational contours of 1000 and 3000 m are indicated.

20. Hda. Palmira, Andahuaylas, 2200 m (*subfuscus subfuscus*: 3 males, FMNH 75524–75526; 5 females, FMNH 75510, 75523, 75527, 75550, 75551). Hda. Mozobamba, Andahuaylas, 2300 m (*subfuscus subfuscus*: 1 male, FMNH 75556; 1 female, FMNH 75555; not located but presumed near Hda. Palmira).

21. Hda. Matara, Quebrada Matara, 1880 m (*subfuscus subfuscus*: 1 male, FMNH 52566; 2 females, FMNH 52567, 52568).

22. 28 km by rd NE Abancay, 3620 m (*subfuscus subfuscus*: 2 males [all E], MVZ 174237, 174238; 1 female [E], MVZ 174236).

Cusco:

23. Machu Picchu, 3640 m (*subfuscus subfuscus*: 1 male, UMZ 17019).

24. 20 km E Machu Picchu, 3725 m, 3880 m, 3940 m, 4060 m (*subfuscus subfuscus*: 4 males, FMNH 107803, 107805, 107810, 107817; 4 females, FMNH 107807, 107814, 107822, 107826).

25. Below Abra Málaga, 90 km SE by rd Quillabamba, 3540 m (*subfuscus subfuscus*: 1 male [E], MVZ 166721; 1 female [E], MVZ 166719; 2 males [both E], UMMZ 160530, 160531[K]).

26. 26 km NW by rd Ollantaytambo, 3700 m (*subfuscus subfuscus*: 6 males, MVZ 174223–174226 [all E], 174229[E], 174375; 8 females, MVZ 174227[E], 174228[E], 174231–174235 [all E], 174374). 55.4 km by rd N Calca, 3560 m (*subfuscus subfuscus*: 1 male, UMMZ 160793).

27. Ollantaytambo, 2800 m (*subfuscus subfuscus*: 3 males, USNM 194675, 194751, 194752; 4 females, USNM 194746, 194749, 194750, 194757).

28. Chospiyoc, 3030 m (*subfuscus subfuscus*: 1 male, USNM 194673; 1 female, USNM 194743).

29. Huarcocondo, 3330 m (*subfuscus subfuscus*: 3 males, USNM 43375, 43376, 43379; 2 females, USNM 43377, 43378).

30. Cusco, 3400 m (*subfuscus subfuscus*: 2 males, FMNH 52570, 52571; 2 females, FMNH 52569, 52572).

31. Hda. Urco, near Calca, 2880 m (*subfuscus subfuscus*: 4 males, FMNH 49686, 49690, 49691, 49693; 5 females, FMNH 49687-49689, 49692, 49694). Hda. Paullo Grande, Calca, 2900 m (*subfuscus subfuscus*: 2 males, FMNH 84420, 84421; 1 female, FMNH 84423).

32. Pisac, Ampay, 3000 m (*subfuscus subfuscus*: 2 males, FMNH 84419, 84424; 1 female, FMNH 84423).

33. 10 km N Paucartambo, 3150 m (*subfuscus subfuscus*: 1 female, MVZ 115661).

34. 32 km NE by rd Paucartambo, 3140 m (*subfuscus subfuscus*: 4 males [all E], MVZ 171571-171573, 171576; 5 females [all E], MVZ 171574, 171575, 171577-171579; 1 male [E], UMMZ 160805).

35. 20 km N by rd Paucartambo, 3580 m (*subfuscus subfuscus*: 7 males [all E], MVZ 171580-171583, 171586, 171588, 171589; 4 females, MVZ 171584[E], 171585[E], 171587[E], 172365).

36. Tres Cruces, 18 km N Paucartambo, 3610 m (*subfuscus subfuscus*: 1 male, MVZ 115663; 4 females, MVZ 115662, 115664-115666).

37. 5 km N Huancarani, 3870 m (*subfuscus subfuscus*: 9 males, MVZ 171590, 171593, 171594, 171597[E], 171599[E], 172366-172368, 172370; 7 females, MVZ 171591, 171592, 171595[E], 171596[E], 171598[E], 171600[E], 172369).

38. Ccolini, Marcapata, 3900 m (*subfuscus subfuscus*: 5 males, FMNH 75487-75491). Amacho, Marcapata, 2750 m (*subfuscus subfuscus*: 2 males, FMNH 75482, 75484; 2 females, FMNH 75485, 75486).

Not located. Fondo Perayoc (*subfuscus subfuscus*: 1 male, FMNH 83477).

PUNO:

39. 6.5 km SW Ollachea, 3350 m (*subfuscus subfuscus*: 25 males, MVZ 172964[E], 172967-172969 [all E], 172972[E], 172975[E], 172976[E], 172978[E], 172981-172985 [all E], 172987-172994 [all E], 173230, 173233, 173234, 173237; 16 females, MVZ 172965[E], 172966[E], 172970[E], 172971[E], 172973[E], 172974[E], 172977[E], 172979[E], 172980[E], 172986[E], 172995[E], 173229, 173231, 173232, 173235, 173236).

40. Limbani, 3350 m (*subfuscus subfuscus*: 3 males, FMNH 52558, 52563, 53137; 5 females, FMNH 52557, 52561, 52562, 53134, 53135; includes holotype).

41. 1 mi S Limbani, 3485 m (*subfuscus subfuscus*: 1 male, MVZ 116081; 2 females, MVZ 116082, 116083).

42. 4 mi SSW Limbani, 3940 m (*subfuscus subfuscus*: 1 male, MVZ 116085; 1 female, MVZ 116084).

43. 13 mi W and 2 mi N Crucero, 3940 m (*boliviensis*: 1 female, MVZ 116076). 39 km SE by rd Macusani, 4080 m (*puer lutescens*: 1 male, MVZ 172997; 1 female, MVZ 172996).

44. 4.5 km NE San Antón, 4000 m (*boliviensis*: 8 males, MVZ 172952[E], 172954[E], 173384[E], 173390-173392 [all E], 173394[E], 173461; 20 females [all E], MVZ 172951, 172953, 172955-172963, 173385-173389, 173393, 173395-173397. *puer lutescens*: 1 female [E], MVZ 173382).

45. 12 km S Santa Rosa [de Ayaviri], 3950 m (*boliviensis*: 89 males, MVZ 171602[E], 171606[E], 171608-171611 [all E], 171615[E], 171617[E], 171619[E], 171621[E], 171647[E], 171652-171656 [all E], 172371, 172372, 172379-172381, 172384, 172895[E], 172900[E], 172905[E], 172907[E], 172910-172912 [all E], 172917[E], 172919-172921 [all E], 172926[E], 172928[E], 172930[E], 172932-172936 [all E], 172938-172941 [all E,K], 172943[E,K], 172944[E,K], 172946[E,K], 173214[E], 173217[E], 173221[E], 173226[E], 173228[E], 173297[E], 173300[E], 173301[E], 173304[E], 173306[E], 173307[E], 173309[E], 173313[E], 173316[E], 173318[E], 173320[E], 173322[E], 173326[E], 173328[E], 173334[E], 173337-173344 [all E], 173350[E], 173352[E], 173354[E], 173355[E], 173360[E], 173361[E], 173364[E], 173377[E], 173381[E], 173553[E], 173556-173558 [all E]; 101 females, MVZ 171603-171605 [all E], 171607[E], 171616[E], 171618[E], 171620[E], 171624-171628 [all E], 171636[E], 171639[E], 171640[E], 171642[E], 171645[E], 171646[E], 171648-171651 [all E], 172373-172378, 172383, 172385, 172897-172899 [all E], 172903[E], 172904[E], 172906[E],

- 172908[E], 172909[E], 172913–172916 [all E], 172922–172925 [all E], 172927[E], 172929[E], 172931[E], 172942[E,K], 172945[E,K], 172947[E,K], 173212[E], 173213[E], 173216[E], 173218[E], 173220[E], 173222[E], 173224[E], 173225[E], 173227[E], 173296[E], 173299[E], 173302[E], 173303[E], 173305[E], 173308[E], 173310[E], 173312[E], 173314[E], 173315[E], 173317[E], 173319[E], 173321[E], 173323[E], 173325[E], 173327[E], 173329–173332 [all E], 173336[E], 173345–173349 [all E], 173351[E], 173353[E], 173357[E], 173359[E], 173363[E], 173376[E], 173378–173380 [all E], 173552[E], 173554[E], 173555[E], 173560[E], 173561[E].
- puer lutescens*: 14 males [all E], MVZ 171613, 171623, 171631, 171633, 171635, 171641, 171643, 171644, 172896, 172918, 173335, 173369, 173373, 173374; 27 females, MVZ 171601[E], 171612[E], 171614[E], 171622[E], 171629[E], 171630[E], 171632[E], 171634[E], 171637[E], 171638[E], 172382, 172937[E], 173215[E], 173223[E], 173298[E], 173324[E], 173333[E], 173356[E], 173358[E], 173365–173368 [all E], 173370–173372 [all E], 173375[E].
46. Chuquibambilla, 3940 m (*boliviensis*: 2 males, FMNH 49695, 49698; 2 females, FMNH 49696, 49697).
47. 25 km N Ayaviri, 3910 m (*boliviensis*: 2 males, MVZ 115667, 115668).
48. 5 mi S Asillo, 4545 m (*puer lutescens*: 2 females, MVZ 116077, 116078).
49. Hda. Purina, 7.5 km N and 1.7 km W Tirapata, 3940 m (*boliviensis*: 1 male [E], MVZ 172948; 2 females [both E], MVZ 172949, 172950).
50. 2 mi NNW Pucará, 3850 m (*boliviensis*: 1 male, MVZ 116079; 1 female, MVZ 116080). Tirapata, Peru (*puer lutescens*: 1 male, AMNH 16508).
51. 6 km S Pucará, 3850 m (*boliviensis*: 9 males [all E], MVZ 172998, 173002, 173004, 173012, 173019, 173246, 173406, 173407, 173412; 17 females [all E], MVZ 172999–173001, 173005, 173006, 173009, 173011, 173013, 173239, 173243, 173247, 173404, 173405, 173409–173411, 173416. *puer lutescens*: 17 males [all E], MVZ 173003, 173007, 173008, 173010, 173014, 173016, 173019, 173021, 173022[K], 173238, 173245, 173398, 173402[K], 173403, 173413, 173414, 173417; 13 females [all E], MVZ 173015, 173017, 173018[K], 173020, 173240–173242, 173244, 173248, 173399, 173401, 173408, 173415).
52. Azángaro, 4020 m (*boliviensis*: 1 male, FMNH 64339).
53. 3.6 km W Muñani, 3980 m (*boliviensis*: 3 males [all E], MVZ 173023, 173025, 173029; 6 females [all E], MVZ 173024, 173026–173028, 173030, 173031. *puer lutescens*: 2 males [both E], MVZ 173029, 173419; 3 females [all E], MVZ 173030, 173031, 173418[K]).
54. Hda. Checayani, 20 km NE Azángaro, 4000 m (*boliviensis*: 1 male, MVZ 136254).
55. 11 km W and 12 km S Ananea, 4200 m (*boliviensis*: 2 males [both E], MVZ 173033, 173421; 2 females [both E], MVZ 173032, 173420. *puer lutescens*: 4 males [all E], MVZ 173034–173037).
56. 6 km N Putina, 3900 m (*boliviensis*: 1 male [E], MVZ 171673; 3 females [all E], MVZ 171671, 171672, 171675. *puer lutescens*: 1 female [E], MVZ 171674).
57. Alta Calacala, 40 mi NE Juliaca, 4060 m (*boliviensis*: 1 male, MVZ 139540). Hda. Calacala, 7 mi SW Putina, 4000 m (*boliviensis*: 2 males, MVZ 114641, 116653; 2 females, MVZ 114640, 116654).
58. 3 mi NE Arapa, 3820 m (*boliviensis*: 1 male, MVZ 116652).
59. Hda. Umayo, 15 mi S Juliaca (*boliviensis*: 1 male, MVZ 116657; 3 females, MVZ 116655, 116656, 116658).
60. 15 km W Puno (*boliviensis*: 1 male, MVZ 115674).
61. 78 km W Puno, 4090 m (*boliviensis*: 1 male, MVZ 115675). 82 km W Puno, 4240 m (*boliviensis*: 2 males, MVZ 115677, 115767). Tincopalca, 50 mi W Puno, 4090 m (*boliviensis*: 1 male, MVZ 114649).
62. 13 mi W Vilque, 3940 m (*boliviensis*: 1 female, MVZ 115678).
63. 5 km W Puno (*puer lutescens*: 1 male, MVZ 115672; 1 female, MVZ 115673). 5 mi NW Puno (*boliviensis*: 1 female, AMNH 213575. *puer lutescens*: 2 males, AMNH 213574, 213578).
64. Chucuito, 3880 m (*boliviensis*: 1 male, FMNH 52564; 1 female, FMNH 52565).
- 64a. Hda. Collacachi, 5 km SW Chucuito, 3850 m (*boliviensis*: 4 males, FMNH 49684, 49699, 49700, 49702; 2 females, FMNH 49685, 49701).
65. Sorapa, near Río Ilave (*boliviensis*: 3 males, AMNH 91554, 91556, 91557; 2 females, AMNH 91558, 91559). 35 km S, 5 km W Ilave, 3790 m (*boliviensis*: 9 males, FMNH 107839, 107840, 107848, 107853, 107856, 107868, 107869, 107886, 107892; 13 females, FMNH 107829, 107830, 107834, 107841, 107845, 107852, 107858, 107863, 107865, 107877, 107882, 107889).
66. Hda. Pairumani, 24 mi S Ilave, 3940 m (*boliviensis*: 3 males, MVZ 114643, 114647, 116657; 7 females, MVZ 114642, 114644–114646, 116655, 116656, 116658).

67. 4 km E Juli, 3850 m (*boliviensis*: 1 male, MVZ 115670; 1 female, MVZ 115699).

67a. 6 mi S Yungayo, 3940 m (*boliviensis*: 2 males, FMNH 51290, 51291; 7 females, FMNH 51293–51299).

68. Huacullani, 3850 m (*boliviensis*: 7 males, FMNH 52542, 52544–52548, 52551; 3 females, FMNH 52549, 52550, 52552).

69. Mazocruz, Río Huanque, 3940 m (*boliviensis*: 3 males, MVZ 115671, 139226, 139227[K]; 3 females, MVZ 136256, 136257[K], 136258).

AYACUCHO:

70. 10 mi WNW Puquio, 3940 m (*subfuscus arequipae*: 1 female, MVZ 137974).

71. 18 km NW Puquio, 4090 m (*subfuscus arequipae*: 2 males, MVZ 115658, 115659).

72. 18 km E by rd Puquio, 3770 m (*juninensis*: 2 males [both E], MVZ 174261, 174265. *subfuscus arequipae*: 14 males [all E], MVZ 174249, 174252, 174254, 174256, 174258–174260, 174262–174264, 174266–174269; 7 females [all E], MVZ 174250, 174253, 174255, 174257, 174270–174272).

73. 9 mi NE Puquio, 4090 m (*subfuscus arequipae*: 1 male, MVZ 116011). 15 km NE Puquio, 4090 m (*subfuscus arequipae*: 1 male, MVZ 115657).

74. 4 km W Pampamarca, 4230 m (*subfuscus arequipae*: 1 male [E], MVZ 174246; 3 females [all E], MVZ 174245, 174247, 174248).

APURIMAC:

75. 40 km S Chalhuanca, 4390 m (*subfuscus arequipae*: 1 male, MVZ 115656).

76. 24 km S Chalhuanca, 3545 m (*subfuscus arequipae*: 2 males, MVZ 115654, 115655; 1 female, MVZ 115653).

77. 36 km S by rd Chalhuanca, 3510 m (*subfuscus arequipae*: 1 male [E], MVZ 174242; 5 females [all E], MVZ 174239–174241, 174243, 174244).

78. 22 km S Chalhuanca, 3240 m (*subfuscus arequipae*: 1 female [K], MVZ 136252).

CUSCO:

79. 16 km SE Yauri, 3960 m (*subfuscus arequipae*: 2 males [both E], MVZ 174221, 174222; 1 female [E], MVZ 174220).

AREQUIPA:

80. Cailloma, 4395 m (*subfuscus arequipae*: 3 males, FMNH 49681–49683; 1 female, FMNH 49680).

81. 20 km SE Cailloma, 4090 m (*subfuscus arequipae*: 9 males, FMNH 107745, 107747, 107750, 107751, 107766, 107768, 107770, 107772, 107777; 8 females, FMNH 107744, 107753, 107754, 107755, 107760, 107765, 107771, 107776).

82. 1 km N Chivay, 3700 m (*subfuscus arequipae*: 9 males [all E], MVZ 174199–174202, 174205, 174206, 174208, 174213, 174216; 12 females [all E], MVZ 174203, 174204, 174207, 174209–174212, 174214, 174215, 174217–174219). 5 km NNE Chivay, 3640 m (*subfuscus arequipae*: 6 males, FMNH 107701, 107703, 107719, 107721, 107723, 107727; 5 females, FMNH 107679, 107700, 107707, 107720, 107729).

83. 5 km S Chivay, 4120 m (*subfuscus arequipae*: 8 males, FMNH 107671, 107687, 107693, 107704, 107717, 107718, 107721, 107727; 5 females, FMNH 107667, 107681, 107698, 107705, 107710).

84. 15 km S Callalli, 4150 m (*subfuscus arequipae*: 49 males, MVZ 174107[E], 174108[E], 174114–174116 [all E], 174119[E], 174121[E], 174122[E], 174124[E], 174125[E], 174129–174131 [all E], 174135–174142 [all E], 174146[E], 174147[E], 174151[E], 174153[E], 174155[E], 174160[E], 174162[E], 174163[E], 174166[E], 174168[E], 174169[E], 174171[E], 174174–174178 [all E], 174181[E], 174183[E], 174184[E], 174187[E], 174189[E], 174193[E], 174366–174369, 174371; 51 females, MVZ 174109–174113 [all E], 174117[E], 174118[E], 174120[E], 174123[E], 174126–174128 [all E], 174132[E], 174143–174145 [all E], 174148–174150 [all E], 174152[E], 174154[E], 174156–174159 [all E], 174161[E], 174164[E], 174165[E], 174167[E], 174170[E], 174173[E], 174179[E], 174180[E], 174182[E], 174185[E], 174186[E], 174190[E]–174192[E], 174194–174196 [all E], 174198[E], 174361–174365, 174370, 174372, 174373).

85. Sumbay, 4090 m (*subfuscus arequipae*: 1 female, FMNH 49679).

86. 2 km W Sumbay, 4200 m (*subfuscus arequipae*: 11 males [all E], MVZ 174069, 174070, 174075, 174077, 174090–174094, 174098, 174101; 12 females [all E], MVZ 174071–174074, 174076, 174078, 174079, 174096, 174102, 174103, 174105, 174106).

87. Granja Chachani (*subfuscus arequipae*: 2 males, USNM 324907, 324908).

88. 2 km E Chiguata, 3180 m (*subfuscus arequipae*: 1 male, FMNH 107787). 4 km E Chiguata,

3425 m (*subfuscus arequipae*: 1 male, FMNH 107783). 8 km E Chiguata, 4090 m (*subfuscus arequipae*: 1 male, FMNH 107793; 1 female, FMNH 107794).

89. 12 km E Arequipa, 3210 m (*subfuscus arequipae*: 1 female, MVZ 136253).

MOQUEGUA:

90. 19 km NE Torata, 3610 m (*boliviensis*: 2 males, FMNH 107546, 107549; 2 females, FMNH 107530, 107544).

TACNA:

91. Tarata, 3060 m (*boliviensis*: 2 males, MVZ 141313, 141315; 2 females, MVZ 141312, 141314). 1.5 mi N Tarata, 3515 m (*boliviensis*: 8 males [all K], MVZ 139228, 139231–139234, 139241–139243; 10 females [all K], MVZ 139229, 139230, 139235–139240, 139244, 139245). 2 mi NE Tarata, 3695 m (*boliviensis*: 2 males, MVZ 141318, 141320; 3 females, MVZ 141316, 141317, 141319).

BOLIVIA

LA PAZ:

92. 7 km E Ulla Ulla, 4560 m (*puer lutescens*: 2 males, AMNH 247850, 247851).

93. Tacacoma, 3150 m (*subfuscus subfuscus*: 1 male, AMNH 91575; 1 female, AMNH 91576).

94. Sorata, 2500 m (*subfuscus subfuscus*: 4 males, AMNH 91564, 91565, 91567, 91572; 3 females, AMNH 91561, 91563, 91569). Pass between Tacacoma and Sorata, 3640 m (*subfuscus subfuscus*: 1 male, AMNH 91577; 1 female, AMNH 91578). Mt. Illampu, Sorata, 2647 m (*subfuscus subfuscus*: 3 males, RNHMS 240, 247, 248). Mt. Illampu, Chilcani, 3700 m (*subfuscus subfuscus*: 2 females, RNHMS 245, 246). Huancuni, 3050 m (*subfuscus subfuscus*: 3 males, RNHMS 217, 221, 222; 3 females, RNHMS 218, 220, 224).

95. Alaska Mine, 4150 m (*subfuscus subfuscus*: 2 males, AMNH 72691, 72692; 1 female, AMNH 73012).

96. La Paz (*boliviensis*: 1 male, BMNH [holotype of *pacificus*] 2.1.1.75).

97. 12 km by rd SW Jesús de Machaca, Río Desaguadero, 3850 m (*boliviensis*: 1 male, AMNH 262724).

98. Caracato, 2900 m (*boliviensis*: 1 female, AMNH 248998).

COCHABAMBA:

99. Ayopaca (*puer puer*: 6 males, FMNH 74884, 74885, 74887, 74888, 74890, 74891; 1 female, FMNH 74886).

100. Choquecomate, Río Secure, 4000 m (*puer puer*: 1 female, BMNH [holotype] 2.1.1.78).

100a. Liriani, 3000 m, 17°19'S, 66°20'W (*puer puer*: 1 sex unknown, RNHMS 359). Toncoma, 3200 m, 17°15'S, 66°20'W (*puer puer*: 2 sex unknown, RNHMS 367, 374). Ucho Ucho, 3526 m, 17°10'S, 66°20'W (*puer puer*: 1 sex unknown, RNHMS 391).

101. Parotani (*puer puer*: 1 male, AMNH 38661; 1 female, FMNH 21559).

102. Colomi, 3075 m (*puer puer*: 2 males, FMNH 50974, 50976; 1 female, FMNH 50975).

103. 9.5 km by rd SE Rodeo, then 2.5 km W on rd to ENTEL antenna, 3895 m (*puer puer*: 5 males, AMNH 260891, 260897–260900; 1 female, AMNH 260894).

104. 15 mi ESE Tiraque [= Tiraque Chico], 3180 m (*puer puer*: 1 male, MVZ 119923).

105. 101 km by rd SW Epizana, Siberia cloud forest, Cordillera Central, 2989 m (*puer puer*: 1 male, AMNH 246687). 28 km by rd W Comarapa, 2800 m (*puer puer*: 1 female, AMNH 260500).

SANTA CRUZ:

106. 21 km W Comarapa, 2900 m (*puer puer*: 2 males, AMNH [both E] 260448, 260453; 1 male [E], MSB 55223; 5 females [all E], AMNH 260449, 260450, 260452, 260453[K], 260454; 4 females [all E], MSB 55220, 55221, 55224, 55225). 1 km N and 8 km W Comarapa, 2450 m (*puer puer*: 2 males, AMNH 260494, 260498; 1 female, AMNH 260497; 1 female, MSB 55230).

ORURO:

107. Huancaroma, 3720 m (*boliviensis*: 1 male, AMNH 262683). 3.5 km E Huancaroma, 3720 m (*boliviensis*: 1 male, AMNH 260457; 1 female, AMNH 91555). 1 km W Huancaroma, 3730 m (*boliviensis*: 1 female, MSB 55219).

108. Pazña, Finca Santa Elena, 3750 m (*boliviensis*: 1 male, UMMZ 156285; 1 female, UMMZ 155858).

POTOSI:

109. 20 km S Potosi, 3785 m (*boliviensis*: 1 female, MVZ 119925).

TARIJA:

110. 1 km E Iscayachi, Río Tomayapo, 3450 m (*boliviensis*: 6 males, AMNH 262685, 262687, 262694, 262695, 262697, 262718; 3 males, MSB 57087, 57091, 57093; 4 females, AMNH 262684, 262686, 262699, 262719; 2 females, MSB 57088, 57090; 3 sex missing, AMNH 262704, 262712, 262720; 1 sex missing, MSB 57089).

111. 10 mi NW Tarija, 2485 m (*puer caenosus*: 1 female, MVZ 119926).

112. Rancho Tambo, 61 km by rd E Tarija, 2100 m (*puer caenosus*: 1 male, AMNH 262762).

ARGENTINA

JUJUY:

113. Santa Bárbara, 1800 m (*spgazzinii tucumanensis*: 1 male, AMNH 179977).

114. Mts west of Yala (*puer caenosus*: 3 males, FMNH 23384, 23388, 23390; 1 male, USNM 259623; 6 females, FMNH 23379, 23381, 23383, 23385, 23389, 23392; 1 female, USNM 259622). Along Yala Laguna rd, W of Hwy 9 (*puer caenosus*: 3 males, CM 43050, 43052, 43054; 3 females, CM 43053, 43056, 43406).

115. León, 1500 m (*puer caenosus*: 1 male, BMNH [holotype] 18.1.1.38).

SALTA:

116. Lower Cachi (*spgazzinii spgazzinii*: 1 female, BMNH [holotype] 97.5.5.14).

117. 30 km S Cachi along Hwy 40, 2400 m (*spgazzinii spgazzinii*: 3 males, CM 43435, 43438, 43439; 1 female, CM 43437).

118. Metán, La Represa (*spgazzinii tucumanensis*: 1 male, FMNH 46147).

119. Arroyo Los Noques, Parque Nacional El Rey (*puer caenosus*: 1 male, CM 72366).

TUCUMAN:

120. S of San Pedro de Colalao, San Pedro rd, 1000 m (*spgazzinii tucumanensis*: 2 females, CM 86399, 86400).

121. Vipos, 786 m (*spgazzinii tucumanensis*: 2 males, FMNH 29122, 29123).

122. 15 km N San Miguel de Tucumán (*spgazzinii tucumanensis*: 1 male, CM 43071). 25 km N San Miguel de Tucumán, El Cadillal Dike (*spgazzinii tucumanensis*: 5 males, CM 43076, 43077, 43087, 43088, 43090; 7 females, CM 43072, 43073, 43075, 43083, 43086, 43093, 43094. *puer caenosus*: 3 males, CM 43074, 43081, 43262; 3 females, CM 43080, 43085, 86421).

123. Sierras de Medina (*spgazzinii tucumanensis*: 2 females, CM 43380, 43382). Sierras de Medina, 25 km NE Tucumán, 800 m (*puer caenosus*: 1 male, CM 43381).

124. El Infiernillo, 19 km NW Tafi del Valle, 3000 m (*spgazzinii spgazzinii*: 6 males, CM 43014–43016, 43450, 43454, 43463; 6 females, CM 43451, 43455, 43459, 43460, 43462, 43465). Tafi del Valle, 2100 m (*spgazzinii spgazzinii*: 1 male, AMNH 41701; 1 female, AMNH 41700. *spgazzinii tucumanensis*: 3 males, AMNH 41696, 41698, 41699; 2 females, AMNH 41697, 41700). Above Tafi, 2900 m (*spgazzinii spgazzinii*: 2 males, AMNH 41826, 41828; 2 females, AMNH 41827, 41829).

126. Horco Molle, 15 km W Tucumán (*puer caenosus*: 1 female, CM 43117). Horco Molle, 25 km W Tucumán (*puer caenosus*: 3 males, CM 43328, 43484, 43489; 1 female, CM 43329. *spgazzinii tucumanensis*: 6 males, CM 43102, 43107, 43116, 43120, 43330, 43350; 2 females, CM 43103, 43104).

127. 3 km W Lules, 300 m (*spgazzinii tucumanensis*: 2 females, CM 86397, 86398).

128. Concepción, 400 m (*puer caenosus*: 1 female, FMNH 30194. *spgazzinii tucumanensis*: 4 males, FMNH 30184, 30189, 30191, 34997; 1 female, AMNH 79028; 4 females, FMNH 30181, 30182, 30185, 30196).

129. Sarmiento, 500 m (*spgazzinii*: 2 females, AMNH 41803, 41819).

Not mapped. Sierra de Tucumán (*spgazzinii tucumanensis*: 1 male, AMNH 41692; 1 female, AMNH 41682).

CATAMARCA:

130. Immediately north of Andalgalá (*spgazzinii* ssp.: 1 female, CM 43176). El Potrero Dike, 13 km N Andalgalá (*spgazzinii* ssp.: 1 female, CM 43154).

APPENDIX II
OTHER SPECIMENS EXAMINED

Specimens of the *boliviensis* group are listed above. We present here a summary list of those specimens of other species of akodonts on which our general comparisons and Table 7 are based.

Akodon aerosus.—BOLIVIA: LA PAZ: Nequejahuira, 2425 m (AMNH, 2 males, 2 females); Okara, 2275 m (AMNH: 2 males, 3 females); Pitiguaya, 1760 m (AMNH, 6 males, 2 females). PERU: AYACUCHO: Luisiana, Río Apurímac, 575 m (AMNH, 3 males); San José, Río Santa Rosa, 1000 m (LSU, 1 sex unknown); Huanhuachayo, 1660 m (LSU, 1 sex unknown); Hda. Luisiana, Río Apurímac (LSU, 1 sex unknown). CUSCO: 72 km NE Paucartambo, 1460 m (MVZ, 8 males, 5 females; UMMZ, 9 males, 5 females); Marcapata, Hda. Cadena (FMNH, 4 males, 3 females); Camante (FMNH, 1 female); Marcapata, Limacpunco, 2400 m (FMNH, 6 males, 7 females). HUANUCO: Hda. San Antonio, Río Chinchao, 900 m (FMNH, 4 males, 5 females); Hda. Buena Vista, Río Chinchao, 900 m (FMNH, 3 males, 4 females); Tingo María (FMNH, 2 females); Hda. Exito, Río Cayumba, 900 m (FMNH, 3 males); Tingahuayín, 5 km NE Acomayo, 2550 m (MSB, 1 male, 1 female). JUNIN: 3 mi SW San Ramón, Chanchamayo Valley, 840 m (AMNH, 6 males, 1 female); 2 km NE San Ramón, Chanchamayo Valley, 880 m (AMNH, 3 males, 3 females); 6 mi SW San Ramón, Chanchamayo Valley, 840 m (AMNH, 3 males, 1 female); 2 mi NW San Ramón, Chanchamayo Valley, 880 m (AMNH, 1 male, 1 female); 3.2 mi N Vitoc, Río Tulumayo, 700 m (USNM, 3 males, 3 females); Río Palca, ca. 15 km W San Ramón (USNM, 2 males); 10 km WSW San Ramón, 1275 m (MVZ, 2 males, 3 females). PASCO: Pozuzo (FMNH, 1 male). SAN MARTIN: Moyabamba (FMNH, 4 males, 2 females).

Akodon albiventer.—BOLIVIA: ORURO: Pazña, Finca Sta. Helena, 3750 m (UMMZ, 3 males, 2 females); Huancaroma, near Eucaliptus (UMMZ, 1 male).

Akodon andinus.—PERU: AREQUIPA: 2 km W Sumbay (MVZ, 2 females, 1 male); 43 rd km E Arequipa, ca. 3850 m (LSU, 5 males, 1 female); 48 rd km E Arequipa, ca. 4060 m (LSU, 1 male, 1 female).

Akodon dayi.—see Myers (1989).

Akodon fumeus.—see Myers and Patton (1989a).

Akodon kofordi.—see Myers and Patton (1989a).

Akodon mollis.—PERU: AMAZONAS: 5 km N and 5 km E Pomacochas, 1820 m (MVZ, 4 males). ANCASH: Macate (FMNH, 5 males, 3 females, 1 sex unknown); 6 mi WSW Cahuel Tunnel, 3940 m (MVZ, 2 females); Trinco, 2 km S and 15 km W Huaras, 3640 m (MVZ, 1 male); 4 mi S and 8 mi E Recuay, 3790 m (MVZ, 2 males, 2 females); Huaraz, Tullparaju, 4300 m (FMNH, 3 males, 2 females); Huaraz, Quilcayhuanca, 4000 m (FMNH, 1 female); Recuay, Ticapampa, Hda. Catac, 3500 m (FMNH, 1 male). CAJAMARCA: Cajamarca (FMNH, 3 males, 3 females); Hda. Limón, 10 mi W Balsas (FMNH, 1 male, 2 females); 35 mi WNW Cajamarca, Hda. Taulis, 1820 m (MVZ, 3 males, 1 female); Taulis, 2680 m (AMNH, 1 male, 2 females); Seques, 1515 m (AMNH, 1 male, 2 females). HUANCVELICA: Río Mantaro, 2575 m (MVZ, 1 sex unknown); 3 mi SE Izcuchaca, Río Mantaro, 2725 m (MVZ, 1 sex unknown). HUANUCO: mts., 3180 m (FMNH, 4 males, 7 females); Cullcui, Marañón River, 3150 m (FMNH, 4 males, 1 female); Panao, mts, 3120 m (FMNH, 1 female); mts, 3120 m (FMNH, 1 male); mts, 3695 m (FMNH, 4 males, 1 female); Ambo, 2030 m (FMNH, 1 male, 3 females). JUNIN: 22 mi E Tarma, 2210 m (AMNH, 4 males, 14 females); 15 km by rd SW San Ramón (UMMZ, 1 male); 9.5 mi N La Oroya, 3940 m (AMNH, 1 female); 16 km NE Palca, 2540 m (MVZ, 8 males, 5 females). LIBERTAD: Menucucho (FMNH, 5 males, 5 females); Pacasmayo (FMNH, 5 males, 3 females); Trujillo (FMNH, 4 males, 3 females); mts. near Otuzco (FMNH, 2 males, 1 female); Hda. Llegueda, NE Otuzco (FMNH, 4 males, 2 females); 7 km NE Pacasmayo, 60 m (MVZ, 1 female); 3 km SW Otuzco, 2425 m (MVZ, 1 male, 1 female). PASCO: 10 km NE Cerro de Pasco, 3940 m (MVZ, 1 sex unknown); La Quinua, 3515 m (FMNH, 3 males, 1 female); Chiquirín, 3395 m (FMNH, 3 males, 2 females). PIURA: Canchaque Tambo (FMNH, 1 male); Huancabamba (FMNH, 2 males); 6.4 mi by rd E Canchaque, 1665 m (MVZ, 2 males, 5 females); 2 km W Porculla Pass, 1970 m (MVZ, 1 female); Huancabamba (AMNH, 1 female); Huancabamba, 1960 m (FMNH, 2 females); Huancabamba, 3000 m (FMNH, 2 females). TUMBES: Tumbes (BMNH, 1 male).

Akodon siberiae.—see Myers and Patton (1989b).

Akodon simulator.—see Myers (1989).

Akodon sylvanus.—ARGENTINA: JUJUY: El Simbolar, 25 km SW Palma Sola (CM, 2 males, 1 female).

Akodon torques.—PERU: CUSCO: 32 km NE Paucartambo, 3140 m (MVZ, 13 males, 7 females; UMMZ, 1 male, 2 females); 90 km SE Quillabamba, 3540 m (MVZ, 10 males, 14 females; UMMZ, 7 males, 18 females); Valle de La Convención, 1000 m (FMNH, 3 males); Ccachubamba (FMNH, 1 male); Amacho (FMNH, 1 male); 10 km N Paucartambo, 3150 m (MVZ, 1 female); Tres Cruces, 18 km N Paucartambo, 3605 m (MVZ, 4 males); Machu Picchu, 3635 m (AMNH, 1 male, 1 female; UMZ, 4 males, 5 females; USNM, 5 males, 4 females); 39 km NE Paucartambo (MVZ, 3 males, 2 females); 54 km NE Paucartambo (MVZ, 5 males, 3 females); Lucma-Casireni Pass (USNM, 2 males, 2 females); Machu Picchu, 2425 m (USNM, 2 females); Torontoy (USNM, 6 males, 4 females); Ocabamba Valley (USNM, 7 males, 1 female); 2 km NE Amaybamba, 2000 m (MVZ, 1 female); 3 km N Amaybamba, 2200 m (MVZ, 7 males, 2 females).

Akodon varius.—see Myers (1989).

Bolomys amoenus.—PERU: PUNO: 6 km S Pucará, 3850 m (MVZ, 2 males, 1 female).

Chroemys jelskii.—PERU: AREQUIPA: 15 km S Callalli, 4150 m (MVZ, 2 females). JUNIN: 22 km N La Oroya, 4040 m (MVZ, 2 females).

Microxus mimus.—BOLIVIA: COCHABAMBA: 101 km by rd SW Epizana, Siberia Cloud Forest, Cordillera Oriental, 2989 m (AMNH, 12 males); 28 km by rd W Comarapa, 2800 m (AMNH, 8 males, 3 females; MSB, 2 males, 4 females); 31 km W Comarapa, 2800 m (AMNH, 2 males); Incachaca, 2425 m (ANSP, 1 sex unknown). LA PAZ: 18 km N Zongo, 2967 m (UMMZ, 5 males); Río Aceramarca, 2600 m (UMMZ, 1 female); 31 km S Coroica, 2850 m (UMMZ, 1 male); 10 km NE Unduavi, 2400 m (UMMZ, 6 males, 3 females); 30 km N Zongo, 2000 m (UMMZ, 1 male, 8 females); Nequejahuira, 2425 m (AMNH, 12 males, 9 females); Pongo, 3635 m (AMNH, 1 male, 1 female); Río Aceramarca, 3270 m (AMNH, 3 males, 5 females, 4 sex unknown). SANTA CRUZ: 25 km W Comarapa, Siberia, 2800 m (UMMZ, 4 males, 6 females). PERU: PUNO: 4 mi N Limbani, 2670 m (MVZ, 2 males); Agualani, 9 km N Limbani (MVZ, 3 males, 3 females); Limbani (BMNH, 1 female).

