NUMBER 720 DECEMBER 11, 1989

OCCASIONAL PAPERS OF THE MUSEUM OF ZOOLOGY
THE UNIVERSITY OF MICHIGAN

ANN ARBOR, MICHIGAN

A NEW SPECIES OF *AKODON* FROM THE CLOUD FORESTS OF EASTERN COCHABAMBA DEPARTMENT, BOLIVIA (RODENTIA: SIGMODONTINAE)

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ABSTRACT.—*Myers, P. and J. L. Patton. 1989. A new species of* Akodon *from the cloud forests of eastern Cochabamba Department, Bolivia (Rodentia: Sigmodontinae). Occ. Pap. Mus. Zool., Univ. Michigan, 720:1-28, figs. 1–12.* A new species of the genus *Akodon* is described from the eastern Andes of Cochabamba Dept., Bolivia. It appears to be most closely similar to *Akodon budini*, a species in the subgenus *Hypsimys* from northwestern Argentina.

Key words: Akodon, Hypsimys, budini, siberiae, *Rodentia, Sigmodontinae, systematics, taxonomy, Bolivia, Cochabamba.*

INTRODUCTION

The genus *Akodon* includes a large number of species of small, short-tailed mice with short palates, long incisive foramina, and simple teeth. They are distributed throughout most of South America except for the lowlands of the Amazon basin. In the area around Comarapa, Bolivia, on the eastern escarpment of the Andes near the border between the departments of Santa Cruz and Cochabamba, at least five species of *Akodon* or *Akodon*-like rodents can be found. These include *Akodon puer* from high-elevation grassland, *Akodon var-*

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ius from xeric shrublands at middle and high elevations, and both *Akodon fumeus* and *Microxus mimus* from wet cloud forest or montane forest at intermediate elevations. In the latter habitat, and sympatric with both *fumeus* and *mimus*, there exists an undescribed species of *Akodon* that is the subject of this paper.

METHODS AND MATERIALS

We rely heavily on traditional measurements and observations of the crania, teeth, and pelage. The four external and 16 cranial measurements used here include the following (each measurement is given with the abbreviation used hereafter):

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.

Condylo-incisive length, CIL: distance from the anterior edge of the upper incisors to the posterior face of the occipital condyles.

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

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: a diagonal distance from the anterior margin of the orbit to the anterior tip of the nasals at the midline.

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

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

Mid-rostral width, RW2: breadth of rostrum measured at the point where the arc formed by the incisor roots reaches its apex.

Orbital length, OL: an inside dimension taken as the greatest longitudinal distance across the orbit.

Diastema length, DL: length of the diastema from the posterior margin of the upper incisors to the anterior margin (root) of M^1.

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 taken at the outside alveolus of M^1.

Occipital condyle width, OCW: width between the lateral borders of the occipital condyles.

Mastoid breadth, MB: breadth 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 anterior 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 the 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.

Cranial dimensions were measured to 0.1 mm by means of dial or digital calipers.

Specimens were placed in categories based on the condition of their molar teeth, which wear as individuals age. These categories, which are believed to represent age classes, range from one to five. They are described briefly below and in detail in Myers (1989). It is important to note that in these species, as in other sigmodontines (*e.g.*, Myers, 1989; Myers, *et al.*, in press) growth appears to continue beyond sexual maturity, and it is imperative that comparisons be made using animals of similar age categories.

The youngest animals, in age class one, have recently erupted third upper molars that show little wear. Animals in age class two show some wear on all teeth, but all major cusps are distinct. The posteroloph on M^3 (if present) is still distinguishable. Animals in age class three show increased wear on all teeth; the posteroloph on M^3 has been obliterated. By age class four, only the major cusps remain distinct. The oldest individuals, in age class five, have molars that are completely "dished out," with flat or bowl-shaped surfaces. Means of skin and cranial measurements presented below are derived from animals in age classes three to five. Individuals in these classes had adult proportions and are probably sexually mature (Myers *et al.*, in press).

Statistical calculations were performed using the Michigan Interactive Data Analysis System (MIDAS). Capitalized color terms are from Ridgway (1912). Terminology of cranial anatomy follows Brown (1971), Musser and Newcomb (1983) and Voss (1988).

We also were able to examine a few specimens preserved in formalin and stored in 70% ethanol. These enabled us to document variation in the morphology of the soft tissues of the palate, stomach, and hind foot. These structures were dissected, examined, and either drawn or photographed. The phalli of several male specimens were also examined; these were dissected, lightly counterstained with alizarin, described, and photographed as detailed by Myers *et al.* (in press).

A list of specimens examined in this study is provided in the Appendix.

Akodon ***siberiae***, new species

HOLOTYPE.—AMNH 260432, old female, collected by N. Olds on 4 September 1984, field number 388 (NK12022), skin, skull, partial skeleton, karyotype, tissue.

TYPE LOCALITY.—28 km by road W of Comarapa, Cochabamba Dept., Bolivia, elevation 2800 m, 17°51'S, 64°40'W.

DIAGNOSIS.—*Akodon siberiae* is distinguished from all other species of intermediate-to-large *Akodon* by the following combination of characters: size large (CIL > 23.5 mm, MTRL > 4.5 mm; Table 1); braincase inflated, without strongly developed crests or ridges, IOC intermediate in breadth (4.9 - 5.4 mm); mesopterygoid fossa broad with a rounded (not squared) anterior border; rostrum appearing long (RL > 10.3 mm) and narrow (RW < 5.2 mm); zygomatic plate relatively narrow and weakly developed; phallus cylindrical and very spinous; second diastemal ruga of palate with deep median notch; 2N = 38.

DISTRIBUTION.—Known only from the vicinity of the type locality.

REFERRED SPECIMENS.—18 specimens from two localities in Cochabamba Dept., Bolivia: type locality (6 males, AMNH 260423, 260426, 260430, 260434, 260456, 260594; 5 females, AMNH 260427, 260428, 260431, 260432, 260590; 3 males, MSB 55209, 55211, 55212; 2 females, MSB 55210, 55213); 31 km by rd W Comarapa, 2800 m (1 male, AMNH 260578; 1 female, AMNH 260579).

ETYMOLOGY.—This new species bears the local name given to the area it inhabits, the Siberia cloud forest.

DESCRIPTION.—*Skin*: Externally, members of this species are very dark in color. The dorsum is medium to dark brown, heavily lined with black. Two kinds of hairs are present in the middorsal region. The commonest type is characterized by a gray base extending 80% or more of the length of the hair, a subterminal pheomelanin band about 1 mm in length, and a dark tip of variable length. The pheomelanin bands are approximately Antimony Yellow to Cinnamon Buff in color. The second type of hair is gray at its base and for about 90% of its length, with the remaining 10% black. These hairs, while less abundant than the first kind, are also common. Hairs of the first type average about 12 mm long; those of the second kind are 1-2 mm longer.

The dorsal color pattern grades into the ventral one gradually; the sides are slightly paler than the dorsum but are also heavily streaked with black. On the head, the cheeks are similar in color to the sides of the body. The venter is paler than the dorsum and is clothed with hairs that are slate gray basally but distally pale buff or tan for about 20% of their length. The chin has a very small and inconspicuous area of contrasting, all-white hairs.

The ears are large, 18–20 mm, and clothed on the anterior surface with tiny hairs. These hairs are agouti near the bases of the ears but mostly or entirely black or dark brown near the edges. The fur is less dense on the posterior surface of the pinna; individual hairs are short and uniformly dark brown or black.

The vibrissae appear to be relatively short, barely reaching the base of the ears when reflected posteriorly on study skins. The skins available to us have from zero to two superciliary vibrissae on each side. Genal, interramal and ulnar carpal vibrissae are inconspicuous or absent.

The fore and hind feet are sparsely covered dorsally with a mixture of whitish and agouti hairs. Bristles at the ends of the toes are whitish and extend beyond the nails in most specimens. The nails appear rather long, slightly curved, and strongly built.

The tail is nearly as long as the head and body and unicolor or weakly bicolor. To the unaided eye it appears nearly naked. Individual hairs on the dorsal surface of the tail are dark and short, extending at most 1.5 to 2.0 scales in length. The scales themselves are of average size for the genus, with about 20 scale rows/cm near the base of the tail.

Several individuals in the type series have large areas of highly distinctive, silky black pelage. The length of individual hairs in these patches, which vary from a small area on the rump (AMNH 260432) to almost the entire dorsal surface (AMNH 260428), is 7–8 mm long and very uniform within the patch. Other individuals in the series

TABLE 1.—Skin and cranial measurements of several species of akodonts. For each measurement, the mean is given in mm, followed by the standard deviation (in parentheses) and the sample size. Specimens included are those listed in the Appendix unless noted otherwise.

	siberiae	*budini*	*puer**	*fumeus**	*varius*	*dayi*	*aerosus*†	*Microxus mimus**
TOTAL	191.1 (12.06) 7	176.9 (12.74) 7	150.7 (8.34) 13	173.0 (11.08) 10	192.6 (14.14) 26	196.8 (14.16) 34	189.3 (12.59) 15	190.9 (8.41) 28
TAIL	89.1 (8.76) 7	77.0 (8.81) 7	66.9 (6.42) 13	77.3 (5.19) 10	84.8 (7.59) 26	79.0 (7.74) 34	83.2 (5.58) 15	94.1 (4.99) 28
HF	24.1 (0.99) 8	25.6 (0.98) 7	19.8 (1.34) 13	21.4 (1.26) 10	23.3 (1.93) 29	26.1 (1.50) 34	23.8 (0.95) 17	24.0 (1.05) 28
EAR	18.5 (1.07) 8	20.2 (0.98) 6	14.1 (0.86) 13	15.2 (0.92) 10	19.0 (2.92) 28	18.7 (2.41) 21		18.3 (1.22) 28
CIL	24.88 (0.49) 10	25.09 (0.87) 7	21.41 (0.73) 17	23.79 (0.75) 13	26.76 (1.02) 26	27.68 (1.22) 29	25.87 (1.07) 17	24.51 (0.79) 28
ZB	13.76 (0.31) 11	14.01 (0.43) 7	11.79 (0.28) 17	12.92 (0.33) 12	14.66 (0.47) 25	15.16 (0.69) 33	14.64 (0.60) 17	13.33 (0.44) 28
IOC	5.15 (0.16) 11	4.96 (0.24) 7	4.46 (0.16) 17	4.75 (0.16) 13	5.08 (0.17) 30	5.19 (0.26) 41	5.32 (0.13) 17	5.55 (0.10) 28

RL	10.63 (0.31) 4	10.61 (0.56) 6	8.42 (0.37) 17	9.83 (0.48) 13	10.57 (0.54) 10	10.83 (0.69) 12	10.68 (0.58) 17	11.15 (0.32) 27
NL	10.50 (0.59) 11	10.09 (0.61) 6	8.54 (0.45) 17	9.90 (0.40) 13	10.80 (0.54) 28	11.23 (0.73) 40	10.74 (0.73) 17	11.50 (0.40) 27
RW	4.73 (0.23) 11	4.76 (0.23) 7	4.48 (0.18) 17	4.86 (0.29) 13	5.38 (0.23) 29	5.72 (0.32) 41	5.25 (0.27) 17	4.94 (0.29) 28
OL	8.43 (0.22) 11	8.78 (0.22) 7	7.64 (0.29) 17	8.28 (0.26) 13	9.72 (0.35) 10	9.81 (0.30) 12	8.89 (0.40) 17	8.19 (0.25) 28
DL	7.27 (0.26) 11	7.07 (0.41) 7	5.85 (0.28) 17	6.82 (0.34) 13	7.36 (0.42) 29	7.75 (0.42) 41	7.34 (0.36) 17	7.26 (0.35) 28
MTRL	4.81 (0.20) 11	4.98 (0.19) 7	3.78 (0.19) 17	4.13 (0.18) 13	4.72 (0.20) 30	4.81 (0.20) 32	4.55 (0.19) 17	4.50 (0.11) 28
IFL	6.37 (0.23) 11	6.17 (0.40) 7	5.40 (0.23) 17	6.06 (0.33) 13	6.50 (0.26) 30	6.80 (0.34) 41	6.14 (0.30) 17	5.78 (0.23) 28

TABLE 1, cont.

	siberiae	*budini*	*puer**	*fumeus**	*varius*	*dayi*	*aerosus*†	*Microxus mimus**
AW	5.68 (0.11) 11	5.68 (0.17) 7	4.75 (0.12) 17	5.17 (0.20) 13	5.97 (0.27) 30	5.97 (0.34) 41	5.56 (0.15) 17	5.50 (0.20) 28
MB	11.95 (0.32) 10	12.07 (0.32) 6	10.55 (0.32) 17	11.09 (0.35) 13	12.26 (0.27) 25	12.51 (0.45) 30	12.08 (0.40) 17	11.55 (0.27) 28
MFW	1.66 (0.15) 11	1.61 (0.19) 7	1.06 (0.15) 17	1.61 (0.16) 13	1.45 (0.10) 6	1.71 (0.16) 8	1.82 (0.17) 17	1.64 (0.11) 28
ZP	2.12 (0.13) 11	2.36 (0.23) 7	2.19 (0.19) 17	2.13 (0.17) 13	2.78 (0.24) 30	2.89 (0.26) 41	2.36 (0.21) 17	1.86 (0.13) 28
CD	9.57 (0.26) 11	10.07 (0.35) 7	8.91 (0.23) 17	9.49 (0.30) 13	10.56 (0.51) 7	10.83 (0.29) 3	10.44 (0.30) 17	9.92 (0.24) 28
BB	12.35 (0.35) 11	12.70 (0.17) 7	11.03 (0.21) 17	11.67 (0.23) 13	12.81 (0.37) 14	12.52 (0.25) 20	12.87 (0.33) 17	11.85 (0.22) 28

*Specimens from the vicinity of Comarapa, Cochabamba and Santa Cruz Departments, Bolivia.
†Specimens from La Paz Department, Bolivia.

lack these patches entirely. Under close examination, the skin underlying the areas of peculiar fur appears to be covered with tiny scabs or scars, and we suggest that this pelage is abnormal and may have been the result of a severe infestation of ectoparasites. Similarly, the vibrissae, which appear both small in size and few in number, may have been damaged by parasites.

Cranium (Figs. 1–5): From dorsal perspective, the cranium has a long and narrow rostrum; narrow and shallow zygomatic notches; moderately strong zygomatic arches that flare broadly posteriorly but with midsections that appear to converge anteriorly; nasals with rounded or pointed projections that extend posteriorly slightly beyond the posterior borders of the premaxillae; a broad interorbital region, with the sides of the orbit rounded anteriorly and squared (but never beaded) posteriorly; frontal sinuses that are noticeably swollen in the vicinity of the slightly depressed posterior ends of the nasals; a braincase that appears exceptionally broad and globose; temporal and mastoid ridges that are present but weakly developed; and a small interparietal.

From the side, the profile of the top of the skull is flatter than that of most *Akodon* and rather similar to *Akodon (Hypsimys) budini*, *Microxus mimus*, and *Akodon (Abrothrix) longipilis*. The dorsal curvature of the skull decreases with age in most *Akodon* (Myers, 1989), however, and the flatness of skulls in the type series of *siberiae* may be due to their relatively advanced age. The zygomatic plate is narrow, and its dorsal root is slightly posterior to its ventral root (Fig. 4). The optic foramen is approximately the same diameter as or slightly smaller than the long axis of the crown of M^3 and slightly less than or equal to the diameter of the anterior alar fissure. The sphenopalatine foramen is completely obscured by swellings around the molar roots. Squamoso-alisphenoid and buccinator grooves are present, as is a sphenofrontal foramen. An alisphenoid strut may or may not divide the foramen ovale. The masticatory-buccinator foramen is small and unusually narrow. The postglenoid and squamosomastoid foramina both appear smaller than is usual for the genus; the postglenoid is approximately the size of the crown of M^2, while the squamosomastoid is about the size of the crown of M^3. The mastoid region bulges posteriorly and appears swollen, as do the occipitals; these add to the globose appearance of the braincase. Paroccipital processes are present, relatively long, and hook-shaped.

Ventrally, the incisive foramina are similar to those of other *Akodon*. They end at the level of the paracone of M^1. Masseteric tubercles at the base of the zygomatic plates are small but unusually

FIG. 1. Dorsal, ventral, and lateral views of the crania of species of *Akodon* known to occur in the vicinity of Comarapa, Cochabamba and Santa Cruz departments, Bolivia. First and second rows, from left to right: *Akodon siberiae* (AMNH 260432), *A. fumeus* (AMNH 260464), *A. puer* (AMNH 260452), *A. varius* (UMMZ 155941). Third row: *A. siberiae* (AMNH 260432), *A. fumeus* (AMNH 260464). Fourth row: *A. puer* (AMNH 260452), *A. varius* (UMMZ 155941).

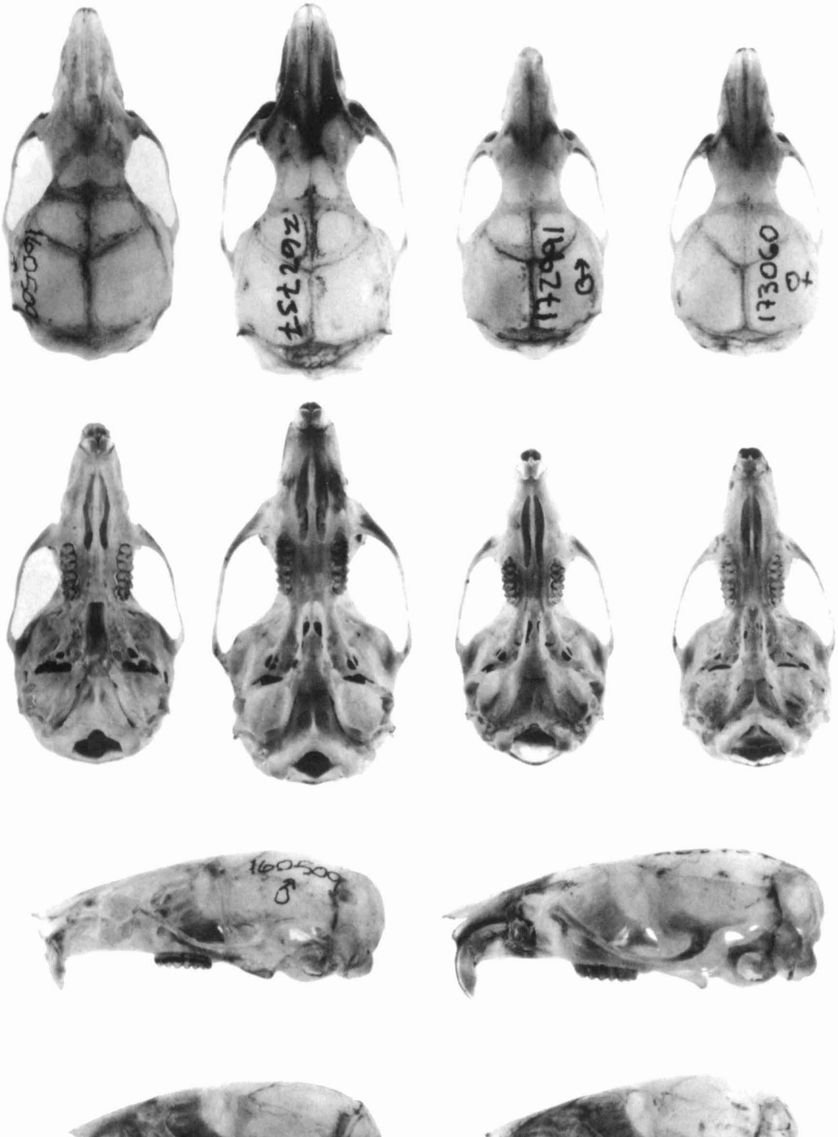

FIG. 2. Dorsal, ventral, and lateral views of the crania of selected species of *Akodon* from Bolivia and Peru. First and second rows, from left to right: *Akodon aerosus* (UMMZ 160509), *A. dayi* (AMNH 262737), *A. subfuscus* (MVZ 172991), *A. mollis* (MVZ 173060). Third row: *A. aerosus* (UMMZ 160509), *A. dayi* (AMNH 262737). Fourth row: *A. subfuscus* (MVZ 172991), *A. mollis* (MVZ 173060).

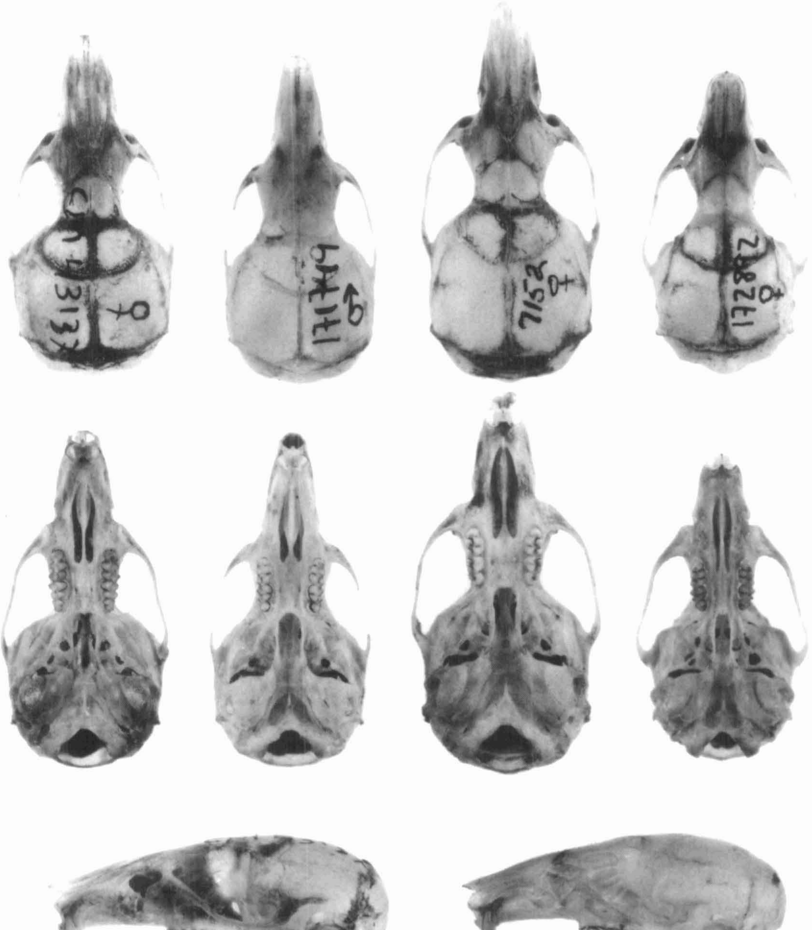

FIG. 3. Dorsal, ventral, and lateral views of the crania of several akodont rodents. First and second rows, from left to right: *Akodon* (*Hypsimys*) *budini* (CMNH 43137), *Microxus mimus* (MVZ 171749), *Akodon* (*Abrothrix*) *longipilis* (MSU 7152), *Bolomys amoenus* (MVZ 172892). Third row: *A. budini* (CMNH 43137), *M. mimus* (MVZ 171749). Fourth row: *A. longipilis* (MSU 7152), *Bolomys amoenus* (MVZ 172892).

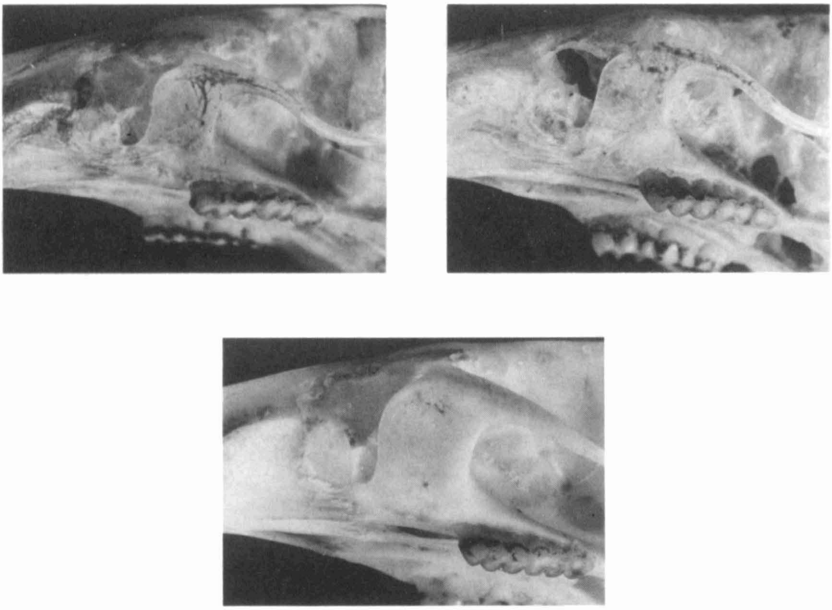

FIG. 4. Zygomatic plate of *A. siberiae* (upper left, AMNH 260432), *A. budini* (upper right, CMNH 43137), and *A. dayi* (bottom, AMNH 262729).

prominent for *Akodon*. The palate is broad and long, ending at the level of the posterior border of M^3, and shallowly grooved. There is a single anterior pair of anterior palatine foramina at about the level of the protocone of M^2, and usually a much smaller pair of palatine pits at the level of the middle of M^3. The mesopterygoid fossa is broad and approximately parallel sided (Fig. 5). Its anterior margin is usually rounded but may be interrupted by a small median spine projecting posteriorly from the palate. Sphenopalatine vacuities are small but present in most individuals examined. The parapterygoid plates are relatively broad and moderately deeply incised; their lateral margins are slightly convex. The foramen ovale appears very large, substantially greater in diameter than the crown of M^3, and the transverse canal has an opening approximately the diameter of M^3. The middle lacerate canal is of average size among *Akodon*. The bullae are flask-shaped; they and the eustachian tubes are unremarkable in shape, size, or orientation.

Characteristic measurements are given for *siberiae* and several other species of *Akodon* in Table 1.

Teeth (Fig. 6, terminology follows Reig, 1977): The teeth of all

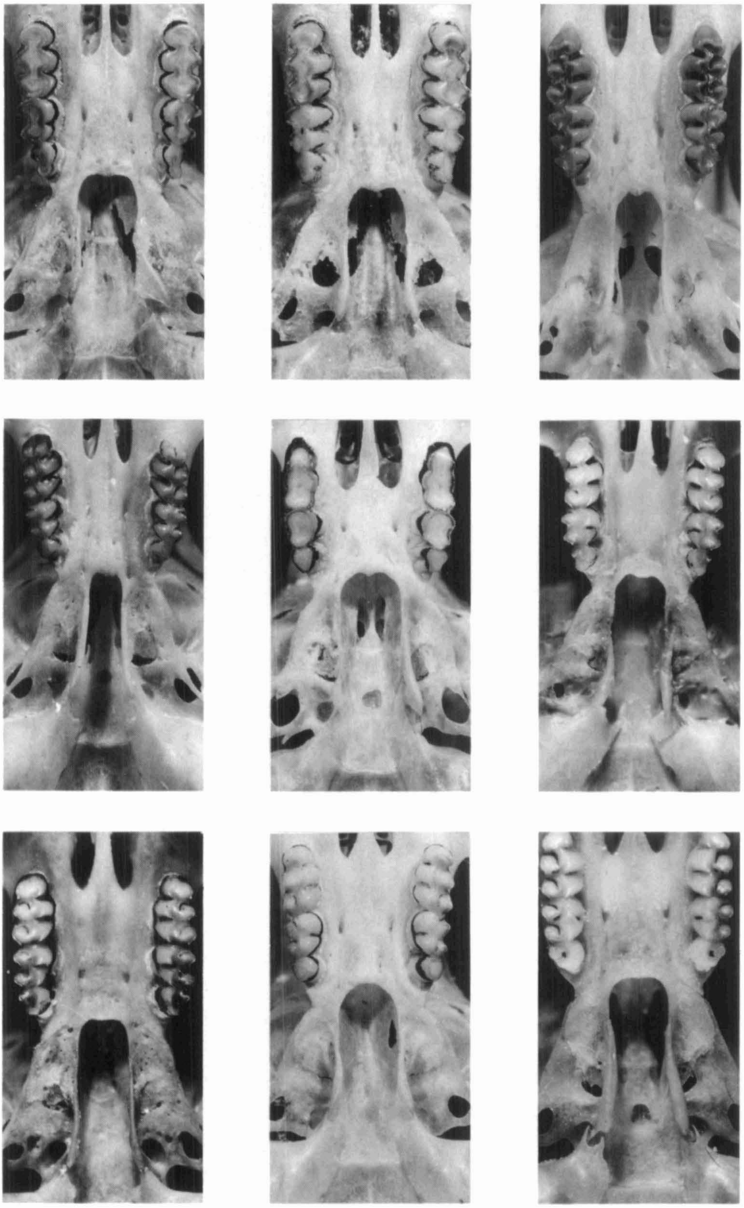

FIG. 5. Postpalatal region of the crania of several species of akodonts. Top row, from left to right: *Akodon siberiae* (AMNH 260432), *A. budini* (CMNH 43137), *A. dayi* (AMNH 262737). Middle row: *A. subfuscus* (MVZ 172991), *A. fumeus* (AMNH 260464), *A. mollis* (MVZ 173046). Bottom row: *A. aerosus* (UMMZ 160509), *Microxus mimus* (MVZ 171749), *A. longipilis* (MSU 7152).

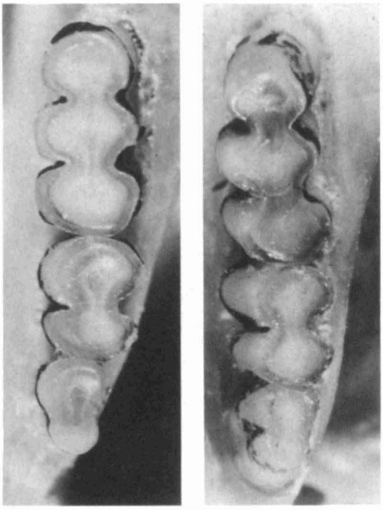

FIG. 6. Teeth of the holotype of *Akodon siberiae* (left, AMNH 260432) and *Akodon budini* (right, CMNH 43137).

specimens available to us are heavily worn, and most characters are obliterated. The incisors are relatively delicate, show no trace of a groove on their anterior surface, and are nearly orthodont in relation to the molar toothrow. The molars are not especially high-crowned but nevertheless appear at least moderately hypsodont; this appearance is due partly to the labial flexi, dorso-ventral indentations along the sides of the teeth which in this species and some others (*e.g.*, *A. budini*) are unusually deep and straight-sided, and extend from the surface of the tooth at least to the alveolus. The regularity and depth of these flexi give each tooth the appearance of being made up of a set of columns. The roots of M^1 (the swellings for which can be seen at the base of the orbit, as is true of most other sigmodontines) appear unusually deep. An anteromedian flexus is probably absent, or if present, small. M^3 is unusually elongate relative to M^1 and M^2 in this species, and it appears constricted in the middle by a pronounced mesoflexus and hypoflexus, giving it a distinctive "figure-8" shape.

Male phallus (Fig. 7): Fluid-preserved material from three male specimens (AMNH 260423, 260426, and 260434) was available for examination. In each, the glans is large, but only slightly more so than those of other species of *Akodon* that we have examined (Myers and Patton, 1989; Myers *et al.*, in press). Externally, it is tubular in shape and stocky, with the mid-shaft diameter only slightly less than

FIG. 7. From left to right, ventral, lateral, and dorsal views of the phallus of *Akodon siberiae* (AMNH 260434). Note in particular the long, thick epidermal spines at the middle and proximal portions of the glans. The line equals 5 mm.

one-half the overall length, and with the sides in all views nearly straight. Both ventral and dorsal grooves are present and confluent with the crater lip; an excrescence of tissue is present in the proximal one-half of the ventral groove. The epidermal spines are the largest known in any *Akodon* species. They are rather densely packed, so that adjacent spines overlap, particularly on the dorsal surface from mid-shaft proximally. Each spine is buried in an individual pit. The long spines give the glans a decidedly "shaggy" appearance. The crater lip is particularly thick, circumscribing the entire crater opening, but thicker on the ventral side than dorsally. It is highly crenulated and separated from the spinous epithelium by an obvious fold. Both a ventral and a dorsal notch are present in the crater lip; neither is confluent with the longitudinal groove on its respective side. A pair of lateral notches is present on either side. The medial bacular mound extrudes from the crater lip and is thus visible externally; the lateral mounds do not reach the crater lip. The tip of the medial mound is oriented vertically. Urethral flaps are well developed but relatively short, so that they are deeply buried within the crater; their tips are well separated, and spines or other ornamentation are not visible. The dorsal papilla is well developed, approximately triangular to spatulate in shape, with obvious spines on all sides near the tip. It is totally surrounded by tissue folds connecting the bacular mound with the inner surface of the crater.

Among the glandes of members of the genus *Akodon* with generally similar phallic structure (*aerosus*, *boliviensis*, *fumeus*, *mollis*, and *torques*, as well as *Microxus mimus* [Myers and Patton, 1989; Myers *et al.*, in press]), the glans of *siberiae* is readily distinguished by the combination of large size, cylindrical shape, and very dense and large epidermal spines.

Palatal rugae (Fig. 8): There are two diastemal and four inter-dental palatal rugae. The second diastemal ruga is deeply notched at its midpoint, with the ridges forming a broad and smooth arc. All four inter-dental rugae are incomplete; the ridges of the first slope sharply caudally toward the mid-line, but the remaining ridges are relatively perpendicular to the sagittal axis and thus parallel to one another. This conformation of the second diastemal ruga is unique among the species of *Akodon* that we have examined (including *aerosus*, *boliviensis*, *fumeus*, *mollis*, *puer*, *subfuscus*, and *torques*).

Stomach: Stomachs of *siberiae* are hemiglandular and unilocular; they show no obvious differences compared to those of other *Akodon* (see Carleton, 1973).

Plantar surface of hind feet (Fig. 9): The hind feet of *siberiae* are longer in absolute size than those of most other *Akodon* but are proportional to the somewhat larger size of *siberiae*. Among species of *Akodon* or *Akodon*-like inhabitants of the eastern Andean slopes, *siberiae* has hind feet that are of dimensions similar to those of *A. aerosus*, *A. torques*, and *Microxus mimus*. The plantar tubercles of *siberiae* are typical in number and position of those found in other *Akodon*, with two metatarsal and four interdigital pads (terminology follows Brown and Yalden, 1973). The position of the medial metatarsal tubercle (thenar; MMT) relative to the length of the sole (from the calcaneal extension to the base of the digits) differs, however, among these similar-sized *Akodon*, as does the spatial relationship between the MMT and the lateral metatarsal tubercle (hypothenar; LMT). The MMT is positioned closer to the digits in *siberiae* than in any of the other three taxa examined (the distance from the heel to the anterior margin of the MMT is about 61% of the distance from the heel to the base of digits 2–4, compared to 51–54% in the other taxa). The MMT is thus placed further distally in *siberiae* than in any other *Akodon* that we have examined, including the above species and taxa of both the "*boliviensis*" and "*fumeus*" groups (Myers and Patton, 1989; Myers *et al.*, in press). It also differs from *aerosus* in the placement of the metatarsal pads, which in *aerosus* are clearly distinguishable by the large gap between the distal border of the MMT and the proximal

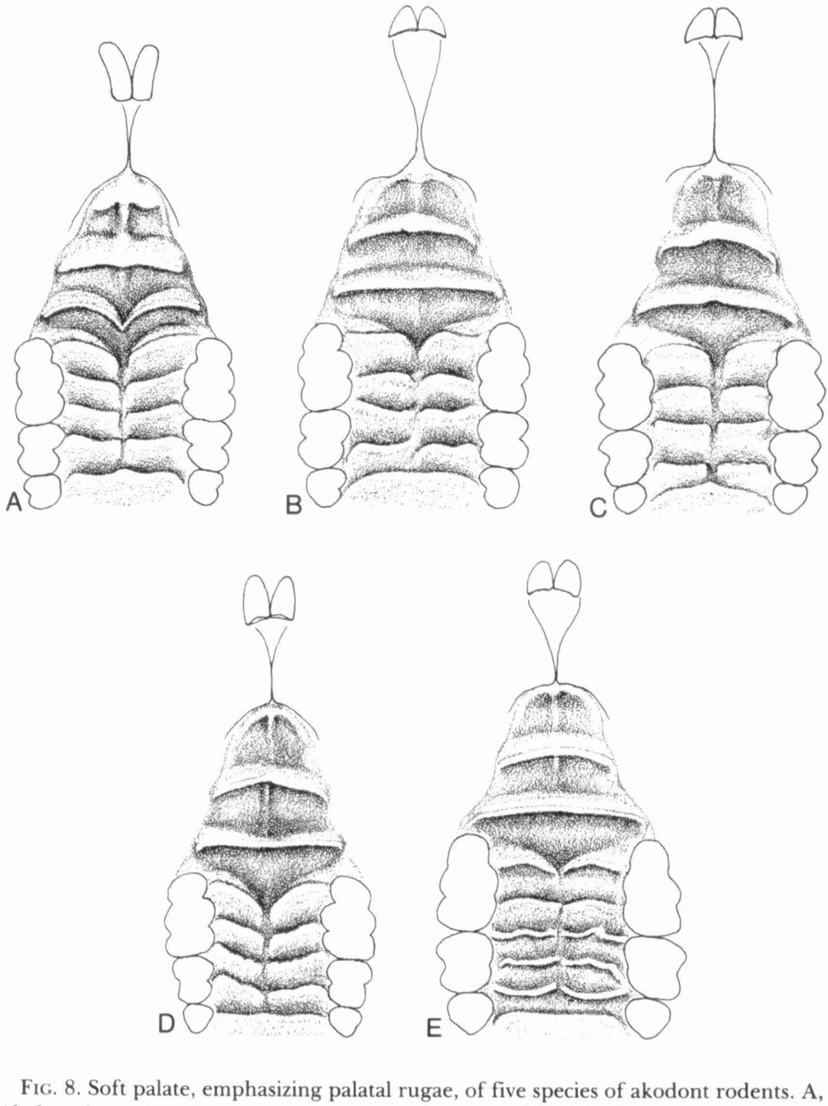

FIG. 8. Soft palate, emphasizing palatal rugae, of five species of akodont rodents. A, *Akodon siberiae* (AMNH 260456); B, *Akodon aerosus* (MVZ 172335); C, *Akodon torques* (MVZ 173812); D, *Akodon puer* (AMNH 260447); and E, *Microxus mimus* (UMMZ 156133).

border of the LMT. These two metatarsal pads overlap slightly in *torques*, and are just barely separated in both *siberiae* and *Microxus mimus*.

Karyotype (Fig. 10): The chromosome complement consists of 16 pairs of uniarmed elements grading evenly in size from medium to

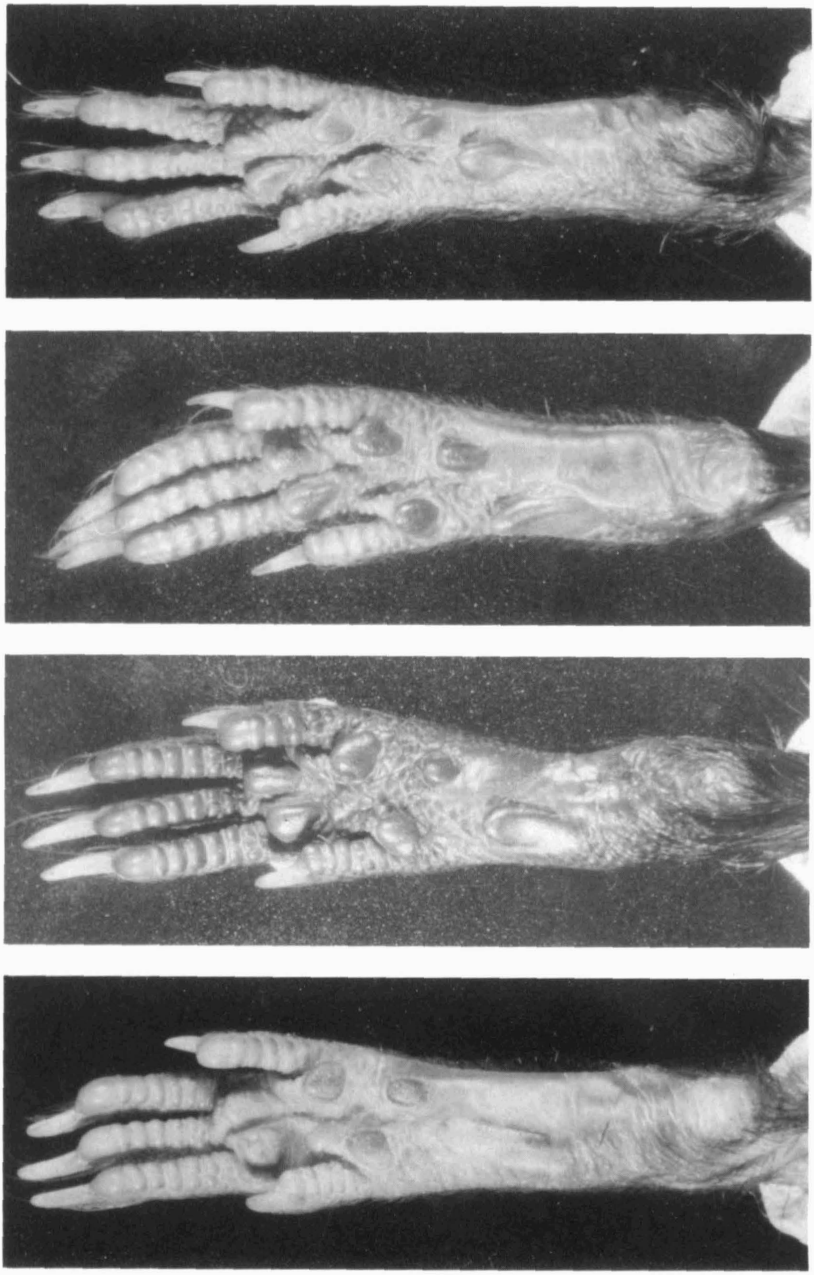

FIG. 9. Plantar surface of the left hind feet of, from left to right, *Akodon siberiae* (AMNH 260434), *Akodon aerosus* (MVZ 172336), *Akodon torques* (MVZ 170067), and *Microxus mimus* (MVZ 173815).

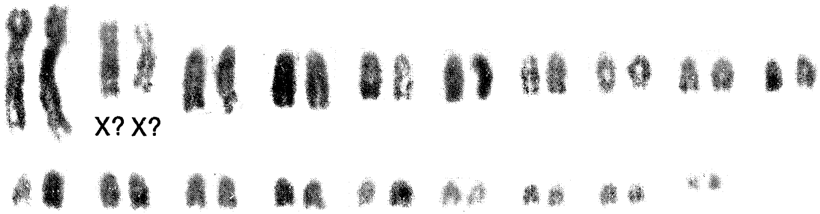

Fig. 10. Karyotype of a female *Akodon siberiae* (AMNH 260428). The presumptive X-chromosomes are indicated.

small, one pair of very large subtelocentric elements, one pair of medium-large submetacentrics, and one pair of very small metacentrics. The morphology of the sex chromosomes is unknown, as only female specimens have been examined. Comparison to other *Akodon* suggests that the X-chromosomes are probably the medium-sized submetacentrics.

This karyotype is virtually identical to that of *A.* (*Hypsimys*) *budini*, also 2n = 38, FN = 40, particularly with regard to the subtelocentric nature of the largest autosome and the morphology of the presumptive X (Vitullo *et al.*, 1986).

Morphological Comparisons.—*Akodon siberiae* is a highly distinctive species. It is substantially larger than any member of the "*bolivien csis* group" of *Akodon* (Myers *et al.*, in press), including a population of *A. puer* that occurs on the same slopes of the Andes of eastern Bolivia as *siberiae* but in grasslands and usually at higher elevations. It is further distinguished from members of the "*boliviensis* group" by its swollen braincase, flat profile of the cranium, broad mesopterygoid fossa, lateral flarings of the parapterygoid plates, and karyotype. It differs from *Akodon fumeus* (another inhabitant of the Siberia cloud forests) and the similar *A. mollis* (of central and northern Peru) in its larger size, more swollen braincase, and long and narrow rostrum. From *Akodon varius* and *Akodon dayi*, two other species of the genus occurring in eastern Cochabamba and western Santa Cruz departments, *siberiae* is distinguished by its swollen braincase, narrow zygomatic plates, relatively shallow and narrow zygomatic notches, and laterally flared parapterygoid plates. Finally, *siberiae* can be distinguished from *Akodon aerosus*, another large, dark *Akodon* inhabiting Andean forests in Peru and adjacent parts of Bolivia, by *siberiae*'s slightly smaller size, much narrower interorbital region, narrower and more delicate rostrum, and by the relative positions of the medial and lateral metatarsal tubercles of the plantar surface of the hind foot.

Microxus mimus, another akodont that inhabits the Siberia cloud forest, resembles *siberiae* in its unusually swollen braincase and in the general configuration of its mesopterygoid fossa and parapterygoid plates. *M. mimus* is easily distinguished, however, by its much broader interorbital region; even more delicate, narrower, and longer rostrum; and smaller teeth. It also has an even narrower zygomatic plate than does *siberiae*, with the dorsal root well posterior to the ventral root so that the leading edge slopes posteriorly from bottom to top.

Akodon siberiae shares its generally large size, swollen braincase, distinctive mesopterygoid region, and relatively narrow zygomatic plate with two other species, *Akodon* (*Hypsimys*) *budini* and *Akodon* (*Abrothrix*) *longipilis*. *Akodon longipilis*, a species of broad distribution in Argentina and Chile, differs in its unusually broad zygomatic notches, flared zygomatic arches, straight-sided parapterygoid region, large interparietal, and numerous other details of cranial form. It also has a radically distinct male phallus with elongated proximal baculum and no distal baculum (Spotorno, 1986).

Akodon budini was described by Thomas (1918) as the type species of a new genus, *Hypsimys*, distinguished from *Akodon* primarily by its hypsodont molars. It is known from the type series and a small number of additional collections, all from Jujuy Province, Argentina. Thomas (1921) later described *Hypsimys deceptor*, also from Jujuy Province, and differing from *budini* by its larger size and longer toothrow. Subsequent authors have considered *Hypsimys* to be a subgenus of *Akodon* and *deceptor* to be a synonym of *budini* (*e.g.*, Cabrera, 1961). We have examined specimens from near the type localities of both *budini* and *deceptor*. Based on those specimens (but pending examination of the holotypes and paratypes), we agree that there appears to be little difference between the two taxa. We also note that the length of the molar toothrow of *budini* (4.3 mm) reported by Thomas (1918) may be erroneous. It is strikingly different from the alveolar length (4.9 mm) given in the same account, which seems unusual given that the holotype is a "young male." The dimension is also contradicted by Gyldenstolpe (1932), who reports the length of the upper molars of the type of *budini* as 5.0 mm.

The resemblance between *Akodon budini* (including *deceptor*) and *siberiae* is striking. It embraces a number of aspects, including most details of the osseous palate; mesopterygoid fossa; parapterygoid region; zygomatic notches; cranial profile; dark color of skin with weakly differentiated dorsal and ventral patterns; white hairs on the chin; nearly naked and unicolor or weakly bicolor tail; and, as noted above, karyotype. The resemblance can also be seen in cranial proportions. In Fig. 11, a profile diagram (Anderson, 1972), we plot the means of a series of log-transformed cranial measurements for each of these species expressed as a percentage of the log-transformed mean value of each measurement in a member of the subgenus *Akodon*, *A. fumeus*. The similarity of *budini* and *siberiae* is obvious.

Does the resemblance extend to the structure of molars, on which the definition of *Hypsimys* is based? Unfortunately, all specimens of *siberiae* are old and have worn teeth. The degree of hypsodonty of these individuals is comparable to that of most other *Akodon*, including *budini*, of similar age. *Akodon siberiae* does resemble *budini* and differ from most (but not all) other *Akodon* in the morphology of its upper M^3's, which are elongate and distinctively "8-shaped."

Because no fluid specimens of *budini* were available to us, details of the structure of the palate, hind feet and phallus are unknown.

Akodon siberiae differs from *A. budini* in that *budini* is somewhat larger in cranial dimensions than *siberiae* and has a shorter tail, longer ears, narrower mesopterygoid fossae, and a broader zygomatic plate (Table 1; Fig. 11).

Electromorphic Comparisons.—We have examined electrophoretic variation at 26 presumptive genetic loci for the single known population of *Akodon siberiae* and comparative populations of other *Akodon* from southern Peru and Bolivia, including *aerosus* (4 samples), *boliviensis* (7 samples), *fumeus* (1 sample, sympatric with *siberiae*), *A.* sp. from Puno Dept., Peru (1 sample; Myers and Patton, 1989), *mollis* (1 sample), *puer* (7 samples, one nearly sympatric with *siberiae*), *subfuscus* (14 samples), and *torques* (3 samples), as well as *Microxus mimus* (2 samples, one sympatric with *siberiae*) and *Bolomys amoenus*. Unfortunately, specimens of *A. budini* were not available for comparison. The loci and gel running conditions are given in Patton *et al.* (1989).

Akodon siberiae is electromorphically a highly distinctive species of *Akodon*. Of the 32 alleles recorded for this species, six are unique (18.75%), and three of these are fixed. As a consequence, the genetic distance (D_R, Rogers [1972]) of *siberiae* relative to the other *Akodon* examined is high, averaging 0.2538 ± 0.0378 (standard deviation; range 0.176–0.375). In fact, *siberiae* differs more from typical *Akodon* than does *Microxus mimus*, but not so much as *Bolomys amoenus* (Fig. 12). This level of differentiation is about 75% higher on average than that among species of the "*boliviensis*" group, or between any of these and *Akodon aerosus*, *fumeus*, *mollis*, or *torques*.

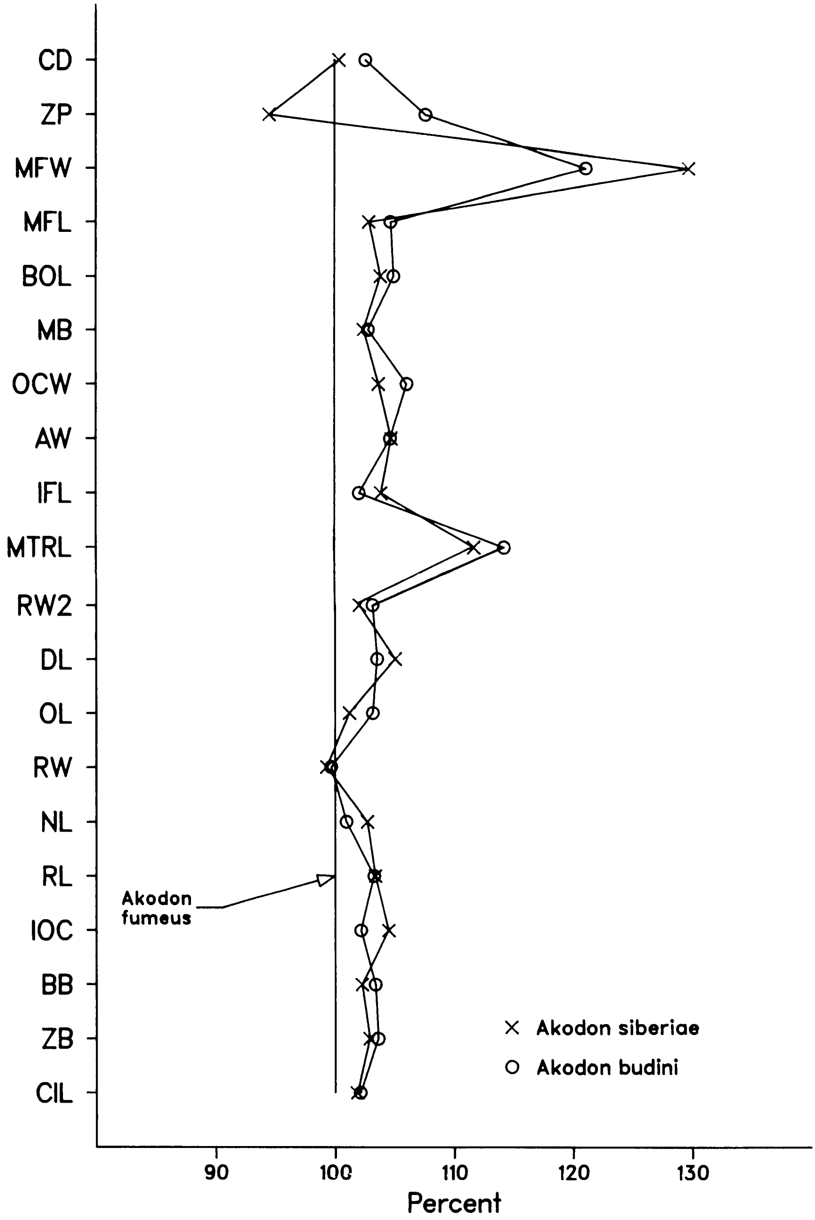

FIG. 11. Profile diagram comparing *Akodon siberiae*, *Akodon budini*, and *Akodon fumeus*.

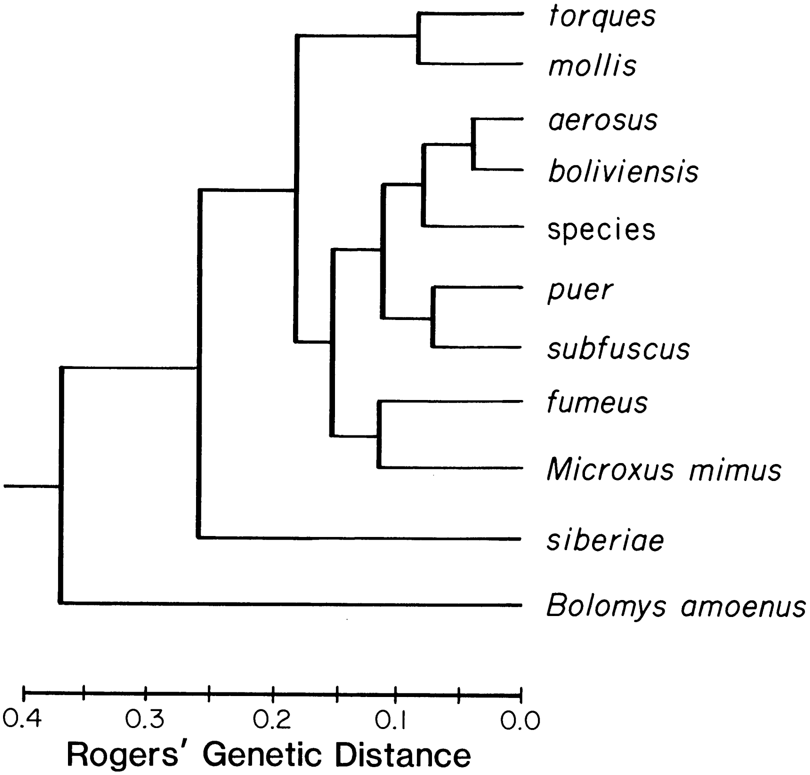

FIG. 12. UPGMA phenogram of Rogers' genetic distance based on 26 electromorphic loci for nine species of *Akodon*, *Microxus mimus*, and *Bolomys amoenus*.

RELATIONSHIPS.—While the differences between *siberiae* and *budini* are sufficient to make it unlikely that they are conspecific, these taxa are impressively similar in cranial morphology and in karyotype. We suspect that evidence that *siberiae* and *budini* form a sister group relative to other species of *Akodon* will emerge when further comparisons using both soft anatomical characteristics and molecular data are made. If this proves to be the case, then placement of both species in the subgenus *Hypsimys* (as opposed to *Akodon* [*s.s.*]) might be warranted. The phylogenetic relationships of all species of *Akodon* are highly uncertain at present (Patton *et al.*, 1989), however, and additional attention to this large and complex group of mice is much needed.

ACKNOWLEDGMENTS

We thank Dr. Sydney Anderson for his generosity in making available the *Akodon* that he and his colleagues have collected in the Siberia cloud forest, and for encouraging us to proceed with the analyses of these materials. Dr. Terry Yates provided the microscope slides from which the karyotype was prepared as well as tissue samples for the comparative electrophoretic analyses. The electrophoretic analyses were organized and performed by Dr. Margaret Smith and Ms. Monica Frelow. We thank the curators of those museums listed in the Appendix for allowing us to examine specimens in their care. R. S. Voss provided critical measurements for series of *Akodon dayi* and *varius* at the American Museum of Natural History. We are grateful to S. Anderson, S. Fink, D. Klingener, and B. Patterson for their thoughtful criticisms of the manuscript. Financial assistance was made available by the Rackham Foundation, University of Michigan, and the Museum of Vertebrate Zoology, University of California.

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Accepted for publication February 23, 1989

APPENDIX

List of Specimens Examined

Specimens from the following museums were examined: American Museum of Natural History (AMNH), British Museum (Natural History) (BMNH); Carnegie Museum of Natural History (CMNH); Field Museum of Natural History (FMNH); Museum of Southwestern Biology, University of New Mexico (MSB); Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); The Museum, Michigan State University (MSU); University of Michigan Museum of Zoology (UMMZ); and U.S. National Museum of Natural History (USNM). The specimens listed immediately below represent only those for which morphological data are actually reported in this paper; many additional specimens of each taxon were examined during the course of the study but not included in either the mensural tabulations or anatomical descriptions. Specific samples used in the electrophoretic analysis are available from J. L. Patton upon request.

Akodon aerosus (111 specimens). BOLIVIA: La Paz: Nequejahuira, 8000 ft (2 males, AMNH 72784, 73073; 2 females, AMNH 73093, 73094); Okara, 7500 ft (2 males, AMNH 73024, 73025; 3 females, AMNH 72893, 73030, 73032); Pitiguaya, 5800 ft (6 males, AMNH 72899, 72900, 72904, 72907–72909; 2 females, AMNH 72913, 73037). PERU: Cusco: 72 km NE by road Paucartambo, 1460 m (10 males, MVZ 166763–166765, 166768, 166782, 166783, 166787, 166788, 172335, 172336; 5 females, MVZ

166767, 166770, 166771, 166773, 166775; 10 males, UMMZ 160509, 160511, 160513, 160517, 160522, 160523, 160525–160528; 5 females, UMMZ 160510, 160514–160516, 160524). PUNO: 11 km NE by road Ollachea, 1875 m (18 males, MVZ 172775, 172777, 172780–172783, 172786, 172787, 172789, 172791, 172793, 172794, 172797–172799, 172810–172812; 19 females, MVZ 172776, 172778, 172779, 172784, 172785, 172788, 172792, 172795, 172800–172809, 172813); 14 km W Yanahuaya, 2210 m (11 males, MVZ 171708, 171711, 171712, 172848, 172850, 172853, 172856, 172861, 172866, 172867, 172869; 16 females, MVZ 171707, 171709, 172849, 172851, 172852, 172854, 172855, 172857–172860, 172862–172865,172868).

Akodon boliviensis (9 specimens). BOLIVIA: ORURO: 10 km by rd SW Pazña, Finca Santa Helena, 3750 m (1 male, UMMZ 156285). PERU: PUNO: 12 km S Santa Rosa [de Ayaviri], 3960 m (3 males, MVZ 171602, 172380, 172896; 5 females, MVZ 171603–171605, 171607, 172922).

Akodon budini (7 specimens). ARGENTINA: JUJUY: mtns west of Yala (1 male, CMNH 12177); Abra de las Cañas, approx. 30 km NW of Calilegua on Valle Grande Rd (3 males, CMNH 43138, 43141, 43148; 3 females, CMNH 43135, 43137, 43143).

Akodon dayi (65 specimens). BOLIVIA: BENI: Rurrenabaque (4 males, AMNH 247789, 247793, 247795, 247796; 5 females, AMNH 247790–247792, 247794, 247797). COCHABAMBA: Todos Santos, 350 m (12 males, AMNH 38582, 38655, 40808, 40812, 40814, 40815, 40819, 40821–40825; 6 females, AMNH 38579, 40806, 40811, 40813, 40817, 40818; 8 males, FMNH 21329, 21578, 21579, 21581, 21582, 21584, 21589, 21591; 7 females, FMNH 21574–21576, 21586–21588, 21590). LA PAZ: 1 mi W Puerto Linares (4 males, MSU 33024–33026, 33030; 1 female, MSU 33023). PANDO: Las Piedras, 170 m, 11°02'S, 66°07'W (1 male, AMNH 262737); Agua Dulce, 160 m, 11°01'S, 66°12'W (1 female, AMNH 262729). SANTA CRUZ: Warnes, 350 m (2 males, USNM 390140, 390141); 3.5 km W Estación Pailón, 300 m (3 males, AMNH 260467, 260503, 260506; 1 female, AMNH 260501); 10 km N San Ramón, 250 m (2 males, AMNH 261945, 261946); 6 km by rd W Asención (2 males, AMNH 260950, 260951; 1 female, AMNH 260952); 6 km N Buen Retiro, 300 m (1 male, AMNH 260544; 1 female, AMNH 260543); 25 km by rd W Buena Vista, W bank Río Yapacani, 400 m (1 male, UMMZ 156306; 1 female, UMMZ 156245); Santa Cruz (1 female, USNM 360699).

Akodon fumeus (26 specimens). BOLIVIA: COCHABAMBA: 20 mi E Totora, 9700 ft (1 male, MVZ 119924); Incacocha (2 males, AMNH 38594, 38645; 3 females, AMNH 38592, 38612, 38613); 28 km by rd W Comarapa, 2800 m (1 male, AMNH 260462; 2 females, AMNH 260463, 260464; 1 male, MSB 55226). LA PAZ: ca. 10 km by rd N Sorata, Moyabaya, Río Challapampa, 2650 m (1 female, UMMZ 156304). SANTA CRUZ: 21 km by rd W Comarapa, 2900 m (1 male, MSB 55225); 1 km N, 8 km W Comarapa, 2450 m (1 male, AMNH 260495). TARIJA: 4 km N Cuyambuyo on Río Sidras, 980 m (2 males, UMMZ 155862, 156310); 8 km N Cuyambuyo (1 male, UMMZ 156324); Rancho Tambo, 61 km E of Tarija by rd, 2100 m (1 male, AMNH 262765; 1 female, AMNH 262766; 4 males, MSB 57094, 57095, 57097, 57098; 1 female, MSB 57096). PERU: PUNO: Sandia, 7600 ft (2 males, FMNH 79892, 79893; 1 female, FMNH 79891).

Akodon longipilis (3 specimens). CHILE: Arauco: 11 km N V. Ranquil (40 km via rd N of Lebu), 820 ft (1 female, MSU 7152). MALLECO: Parque Nacional, 27 km WNW Angol, 3650 ft (2 males, MSU 7154, 7155).

Akodon mollis (21 specimens). PERU: JUNÍN: Utcuyacu, 15 km by rd SW San Ramón, 1400 m (1 male, UMMZ 158038); 16 km NNE Palca by rd, 2540 m (8 males, MVZ 173045, 173048, 173050, 173051, 173054–173057; 5 females, MVZ 173046, 173049, 173052, 173053, 173060). PIURA: 6.4 mi E Canchaque, 5500 ft (2 males, MVZ 141842, 141844; 5 females, MVZ 141840, 141841, 141843, 141845, 141846).

Akodon puer (12 specimens). BOLIVIA: COCHABAMBA: 101 km by rd SW Epizana, Siberia cloud forest, Cordillera Oriental, 2989 m (1 male, AMNH 246687); 28 km by rd W Comarapa, 2800 m (1 female, AMNH 260500). SANTA CRUZ: 21 km by rd W Comarapa, 2900 m (1 male, AMNH 260448; 6 females, AMNH 260447, 260449, 260450, 260452–260454); 1 km N, 8 km W, Comarapa, 2450 m (2 males, AMNH 260494, 260498; 1 female, AMNH 260497).

Akodon siberiae (18 specimens). See species description.

Akodon subfuscus (66 specimens). BOLIVIA: LA PAZ: Sorata (4 males, AMNH 91564, 91565, 91567, 91572; 3 females, AMNH 91561, 91563, 91569); Tacacoma (1 male, AMNH 91575; 1 female, AMNH 91576); Tacacoma-Sorata (1 male, AMNH 91577; 1 female, AMNH 91578); Alaska Mine (2 males, AMNH 72691, 72692; 1 female, AMNH 73012). PERU: PUNO: Limbani (3 males, FMNH 52558, 52563, 53137; 5 females, FMNH 52557, 52561, 52562, 53134, 53135); 3 mi N Limbani, 9500 ft (2 males, MVZ 116081, 116086; 3 females, MVZ 116082–116084); 6.5 km SW Ollachea, 3350 m (23 males, MVZ 172964, 172967–172969, 172972, 172975, 172976, 172978, 172981–172985, 172989–172994, 173230, 173233, 173234, 173237; 16 females, MVZ 172965, 172966, 172970, 172971, 172973, 172974, 172977, 172979, 172980, 172986, 172995, 173229, 173231, 173232, 173235, 173236).

Akodon torques (71 specimens). PERU: CUSCO: 3 km NE Amaybamba, 2200 m (9 males, MVZ 174045, 174047, 174048, 174050–174053, 174055, 174056; 2 females, MVZ 174049, 174054); below Abra Málaga, 90 km SE by road Quillabamba, 3540 m (12 males, MVZ 166723, 166725, 166728–166731, 166733, 166735, 166739, 166742, 166743, 170067; 14 females, MVZ 166724, 166726, 166727, 166732, 166734, 166736–166738, 166740, 166741, 166752–166755; 7 males, UMMZ 160482, 160488, 160489, 160492, 160500, 160503, 160507; 18 females, UMMZ 160481, 160483–160487, 160490, 160491, 160493–160496, 160498, 160499, 160501, 160502, 160504, 160506); 54 km NE by road Paucartambo, 2190 m (5 males, MVZ 171736, 171738, 171740, 171741, 171743; 4 females, MVZ 171737, 171739, 171742, 173812).

Akodon varius (31 specimens). BOLIVIA: CHUQUISACA: Pulce, 9400 ft (1 male, AMNH 38979). COCHABAMBA: Aquile, 2225 m (1 male, FMNH 50978; 1 female, FMNH 51929); Cochabamba, 2700–2750 m (3 males, FMNH 50160, 50980, 50983; 3 females, FMNH 50979, 50981, 50982; 1 female, BMNH 2.1.1.67); Parotani, 2500 m (1 male, FMNH 21560; 2 males, AMNH 38670, 38671; 6 females, AMNH 38665, 38667, 38668, 38673–38675); Chapare, 2600 m (1 male, BMNH 34.9.2.154); Tapacari, 3000 m (3 males, BMNH 2.1.1.68, 2.1.1.69, 2.1.1.71, 1 female, BMNH 2.1.1.70). POTOSÍ: Río Cachimayo, 8700 ft (1 male, AMNH 39000; 3 females, AMNH 38998, 38999, 39002). SANTA CRUZ: 1 km N and 8 km W Comarapa, 2450 m (2 males, AMNH 260465, 260466). TARIJA: Carlazo, 2300–2400 m (1 male, UMMZ 155941).

Bolomys amoenus (3 specimens). PERU: PUNO: 6 km S Pucará, 3850 m (2 males, MVZ 172890, 172891; 1 female, MVZ 172892).

Microxus mimus (43 specimens). BOLIVIA: COCHABAMBA: 28 km by rd W Comarapa, 2800 m (8 males, AMNH 260429, 260581, 260585, 260586, 260589, 260591, 260601, 260602; 3 females, AMNH 260582, 260587, 260600; 2 males, MSB 55302, 55306; 4 females, MSB 55210, 55301, 55303, 55305). LA PAZ: 30 km (by rd) N Zongo, Cement Mine, 2000 m (1 female, UMMZ 156133). SANTA CRUZ: 25 km by rd W Comarapa, Siberia, 2800 m (15 males, UMMZ 155962, 155964–155966, 155968, 155971, 155972, 155974, 155976, 155978, 155980–155983, 156242; 9 females, UMMZ 155963, 155967, 155969, 155973, 155975, 155977, 155979, 155984, 155985). PERU: PUNO: Agualani, 9 km N Limbani (1 male, MVZ 171749).