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**AKODON OF PERU AND BOLIVIA—REVISION OF THE  
FUMEUS GROUP (RODENTIA: SIGMODONTINAE)**

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ABSTRACT.—Myers, P. and J. L. Patton. 1989. The Akodon of Peru and Bolivia—Revision of the fumeus group (Rodentia: Sigmodontinae). *Occ. Pap. Mus. Zool., Univ. Michigan*, 721:1-35, figs. 1-11. A new species of the genus *Akodon* is described from Puno and Cusco departments, southern Peru. It appears to be similar and perhaps closely related to *Akodon fumeus*, a species that inhabits the eastern slopes of the Andes in extreme southern Peru and Bolivia. These two species are informally united as the *Akodon fumeus* group. We further demonstrate that *Akodon mollis*, a species of wide distribution in Peru and Ecuador, shares several similarities with members of the *fumeus* group that may suggest a close relationship.

Key words: *Akodon*, *mollis*, *fumeus*, *kofordi*, *Peru*, *Bolivia*, *Rodentia*, *Sigmodontinae*, *South America*, *systematics*, *taxonomy*.

INTRODUCTION

*Akodon fumeus* Thomas is a poorly known species described from "... the high paramos north and north-west of Cochabamba [Bolivia]..." at 3500 m elevation (Thomas, 1902:126). In reviewing the "*boliviensis* group" of *Akodon* (Myers *et al.*, in press), we discovered that the type series of *Akodon subfuscus*, from Puno Department, Peru, comprises two taxa, one similar to *Akodon boliviensis*, *Akodon puer*, and

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their relatives, and one apparently close to *Akodon fumeus*. In this paper, we take advantage of collections from southeastern Peru, plus new material from Bolivia, to reexamine and rediagnose *fumeus*. We believe that the Peruvian population is sufficiently distinct from *fumeus* to be accorded formal recognition, and we provide a name and description for it.

Although an analysis of phylogenetic relationships within *Akodon* is not possible at this time, we suspect that *fumeus* and the new species will prove to be very closely related to each other and probably to *Akodon mollis*, a species of wide distribution in central and northern Peru and Ecuador. We shall refer to *fumeus* and the new species together as the “*Akodon fumeus* group,” but we stress that the relationship between these two, while striking, is so far based on overall similarity rather than on a demonstration of phylogenetic proximity.

Following a description of the methods used in this study, we present an account of general characteristics shared by *fumeus* and the new species. We then describe and diagnose each species individually and discuss their similarity with *mollis* and other *Akodon*.

## METHODS AND MATERIALS

We rely heavily on traditional measurements and observations of the crania, teeth, and pelage. The four external and 19 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.

Condylar-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 rostrum across the nasolacrimal capsule.

Mid-rostral width, RW2: breadth of the 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 of the root of M<sup>1</sup>.

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

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

Alveolar width, AW: width of the palate measured across the lateral margins of the alveoli of right and left M<sup>1</sup>'s.

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 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 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, believed to represent age classes, range from one (M<sup>3</sup> newly erupted) to five (surfaces of all molars bowl-shaped with topographical features obliterated by wear) and are described by Myers (1989). In these species

of *Akodon*, as in other sigmodontines (e.g., Myers, 1989; Myers, *et al.*, in press), growth continues beyond sexual maturity (which is probably attained during age classes two or three), and it is imperative that comparisons be made between animals of similar age categories. The measurements given below and in Table 1 are based on individuals in age classes three to five.

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

A few specimens preserved in formalin and stored in 70% ethanol were available. 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 is provided in the Appendix.

### THE *AKODON FUMEUS* GROUP

DIAGNOSIS.—The two taxa of this group can be distinguished from all other *Akodon* from southeastern Peru and Bolivia (including *aerosus*, *albiventer*, *andinus*, *boliviensis*, *budini*, *dayi*, *jelskii*, *puer*, *subfuscus*, *varius*, and the closely related *Microxus mimus*) by the following combination of characters: small to intermediate size (HF averages 21.5 mm [range 17 - 25 mm], MTRL 4.1 mm [range 3.70 - 4.44 mm], IOC 4.8 mm [range 4.50 - 5.20 mm], ZP 2.2 mm [range 1.78 - 2.70 mm]); pelage dark brown with olivaceous or rufous overtones, lacking conspicuous patches of sharply contrasting colors on the head, body, or behind the pinnae; dorsal surface of hind feet covered by agouti (not pure white) hairs; ventral pelage color not sharply distinct from dorsal; interorbital region hourglass-shaped or with weakly divergent edges, sides may be squared in old individuals but never with overhanging ledges; mesopterygoid fossa conspicuously broad (1.5 mm, range 1.20 - 1.91 mm), with approximately parallel to lyre-shaped sides and a rounded anterior margin that sometimes includes a conspicuous median spine; parapterygoid plates deeply excavated and with sharply convex lateral margins.

DESCRIPTION.—*Pelage*: The dorsal color is uniformly medium to dark brown with olivaceous or rufous tones. Abundant black guard

hairs give the dorsal pelage a streaked appearance. These hairs are long, protruding over the rump beyond the level of the body fur by about 4 mm. On the sides, the dorsal pelage grades gradually into the ventral. The cheeks resemble the top of the head in color or are slightly grayer. Hairs on the ventral surface of the body are slate gray basally with buff or orangish tips about 1/5 the length of each hair. The chin usually has a small area of entirely white hairs, but the throat is buff or gray.

As appears to be the case for most *Akodon*, the vibrissae are relatively short and sparse compared to those of many other sigmodontines. When reflected posteriorly, the mystacial vibrissae reach approximately to the base of the ears. One or two superciliary and one or two genal vibrissae may be present, but if so they are usually barely distinguishable from nearby guard hairs. Similarly, a few interramal and ulnar-carpal vibrissae are usually present but very inconspicuous.

The dorsal surfaces of the fore and hind feet are covered with agouti hairs that may be whitish or very pale buff but that have gray bases. The claws are moderately well developed and strongly curved. They are enclosed in tufts of white hairs that extend 1–1.5 mm beyond their tips.

The pinnae are small and darkly pigmented; close examination reveals a sparse covering of short and fine agouti hairs inside and out.

The tail is relatively long (45% of total length), unicolored or bicolored, and sparsely covered with agouti hairs that extend the lengths of two to three scales. There is no suggestion of a tuft or pencil at the tip.

*Cranium* (Figs. 1–3; Table 1): Viewed dorsally, the skull appears to have a narrow and pointed rostrum. The nasals project into the frontal region well beyond the ends of the premaxillae, and their posterior ends are squared or rounded. Frontal sinuses are distinctively swollen, especially in younger animals. The lacrimal is tiny or often absent (perhaps due to loss in preparation). The zygomatic notches are moderately narrow and shallow, as is typical of most *Akodon*, but some variation exists among populations in the shape of this structure. The interorbital area is neither remarkably constricted nor broad. Its sides are rounded in most individuals but become increasingly squared with age. The zygomatic arches are moderately developed and flared laterally. The frontal-parietal suture varies from V-shaped to a smooth crescent, and weakly developed temporal ridges run posteriorly from the orbits. Mastoid ridges are present but not strongly expressed. As in most other *Akodon*, the interparietal is present but small.

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. Localities of capture are given in the Appendix.

	<i>kofordi</i>	<i>subfuscus</i>	<i>fumeus</i>	<i>puer</i>	<i>aerosus</i>	<i>mollis</i>	<i>dayi</i>	<i>Microxus mimus</i>
TOTAL	173.9 (7.52) 16	160.3 (5.98) 19	171.2 (12.64) 32	142.2 (12.35) 50	190.2 (13.31) 131	169.8 (14.00) 17	196.8 (14.16) 34	194.4 (9.17) 111
TAIL	77.6 (5.14) 16	70.3 (5.67) 19	76.2 (5.67) 32	60.7 (6.91) 50	84.4 (7.05) 131	72.0 (8.54) 17	79.0 (7.71) 34	96.0 (6.62) 111
HF	22.5 (0.97) 16	20.9 (0.75) 20	21.4 (1.44) 32	18.8 (2.21) 51	24.5 (1.16) 139	20.4 (1.77) 17	26.1 (1.50) 34	24.3 (0.97) 113
EAR	15.3 (0.49) 12	14.4 (1.12) 13	15.9 (1.57) 29	12.8 (1.21) 51	16.5 (0.69) 90	11.0 (2.65) 17	18.7 (2.41) 21	17.9 (1.23) 81
CIL	23.15 (0.70) 17	22.09 (0.82) 46	23.48 (0.85) 35	20.89 (1.01) 62	25.62 (1.09) 130	23.14 (0.76) 33	27.68 (1.22) 29	24.51 (0.57) 118
ZB	12.65 (0.36) 17	12.10 (0.38) 46	12.81 (0.38) 34	11.31 (0.46) 62	14.43 (0.61) 139	12.54 (0.40) 33	15.16 (0.69) 33	13.39 (0.38) 119
IOC	4.67 (0.10) 17	4.43 (0.13) 46	4.75 (0.16) 36	4.24 (0.18) 62	5.49 (0.22) 145	5.04 (0.22) 33	5.19 (0.26) 41	5.64 (0.17) 119

RL	9.76 (0.35) 17	9.02 (0.38) 46	9.78 (0.36) 35	8.27 (0.48) 60	10.62 (0.49) 143	9.87 (0.46) 33	10.83 (0.69) 12	11.08 (0.35) 117
NL	9.80 (0.45) 17	8.89 (0.43) 46	9.76 (0.38) 35	8.29 (0.57) 60	10.55 (0.54) 143	9.72 (0.55) 33	11.23 (0.73) 40	11.14 (0.51) 117
RW	4.70 (0.12) 17	4.51 (0.22) 46	4.81 (0.24) 36	4.19 (0.29) 62	5.29 (0.31) 145	4.67 (0.31) 33	5.72 (0.32) 41	4.86 (0.26) 119
RW2	4.07 (0.17) 17	3.79 (0.17) 46	4.05 (0.18) 36	3.64 (0.24) 62	4.44 (0.23) 145	3.99 (0.20) 33		4.17 (0.22) 119
OL	8.30 (0.24) 17	7.96 (0.27) 46	8.21 (0.33) 35	7.48 (0.37) 62	8.87 (0.41) 142	7.82 (0.25) 33	9.81 (0.30) 12	8.17 (0.26) 119
DL	6.60 (0.28) 17	6.17 (0.29) 46	6.61 (0.37) 36	5.69 (0.36) 62	7.23 (0.40) 145	6.51 (0.36) 33	7.75 (0.42) 41	7.20 (0.33) 119

TABLE 1.—cont.

	<i>kofordi</i>	<i>subfuscus</i>	<i>fumeus</i>	<i>puer</i>	<i>aerosus</i>	<i>mollis</i>	<i>dayi</i>	<i>Microxus mimus</i>
MTRL	3.95 (0.12) 17	3.85 (0.15) 46	4.07 (0.17) 36	3.61 (0.16) 62	4.59 (0.20) 144	4.08 (0.12) 33	4.81 (0.20) 32	4.58 (0.17) 118
IFL	5.73 (0.28) 17	5.20 (0.38) 46	5.94 (0.33) 36	4.84 (0.47) 62	6.00 (0.44) 145	5.40 (0.31) 33	6.80 (0.34) 41	5.71 (0.30) 119
AW	5.18 (0.15) 17	4.94 (0.19) 46	5.18 (0.14) 36	4.56 (0.21) 62	5.67 (0.21) 145	5.17 (0.20) 33	5.97 (0.34) 41	5.68 (0.23) 119
OCW	5.96 (0.09) 17	6.08 (0.16) 46	6.19 (0.15) 34	5.81 (0.22) 62	6.89 (0.28) 127	6.42 (0.20) 32		6.61 (0.19) 117
MB	11.08 (0.23) 17	10.72 (0.25) 46	11.13 (0.30) 35	10.28 (0.32) 62	12.06 (0.44) 129	11.10 (0.29) 32	12.51 (0.45) 30	11.69 (0.29) 117
BOL	3.39 (0.22) 17	3.35 (0.27) 46	3.63 (0.21) 35	3.29 (0.25) 62	3.88 (0.26) 129	3.62 (0.18) 32		3.56 (0.18) 118



MFL	4.07 (0.27) 17	3.66 (0.26) 46	4.10 (0.26) 34	3.37 (0.26) 61	4.51 (0.27) 134	3.90 (0.23) 33		4.08 (0.23) 118
MFW	1.45 (0.12) 17	1.13 (0.15) 46	1.54 (0.17) 35	1.01 (0.16) 61	1.92 (0.18) 141	1.57 (0.15) 33	1.71 (0.16) 8	1.67 (0.15) 118
ZP	2.30 (0.10) 17	2.13 (0.16) 46	2.17 (0.17) 36	2.13 (0.19) 62	2.34 (0.20) 145	2.89 (0.26) 33	2.89 (0.26) 41	1.71 (0.17) 119
CD	9.47 (0.21) 17	9.34 (0.24) 46	9.41 (0.31) 34	8.78 (0.26) 62	10.31 (0.35) 134	9.38 (0.25) 33	10.83 (0.29) 3	9.96 (0.30) 118
BB	11.46 (0.21) 17	11.26 (0.27) 46	11.68 (0.21) 33	10.61 (0.29) 62	12.92 (0.35) 138	11.61 (0.26) 33	12.52 (0.25) 20	12.08 (0.32) 118

From lateral view, the dorsal profile of the cranium appears gently curved, especially in young individuals. The zygomatic plates are of medium breadth, and their ventral root is directly below their dorsal root (Fig. 2). The anterior edge of the plate is straight or barely concave. Within the orbit, a sphenopalatine foramen is sometimes present and about the length of  $M^2$ , or it may be obstructed by the molar roots. The anterior alar fissure is slightly larger than the optic foramen. An alisphenoid strut, a squamoso-alisphenoid groove, and a sphenofrontal foramen are present. The masticatory-buccinator foramen tends to be very small, and its subdivision may be complex with more than two foramina resulting. The buccinator groove is well-defined and deep. The opening of the transverse canal is about half the area of the foramen ovale accessorius. The tympanic hook is narrow and delicate.

In most respects the ventral aspect of the skull is very similar to that of members of the *boliviensis* group (Myers *et al.*, in press). The incisive foramina are broad but of average length for *Akodon*. They are widest at their midpoints. No masseteric tubercle is present on the inferior zygomatic root, but the origin of the superficial masseter tends to be conspicuously roughened. The bony palate has shallow longitudinal grooves and extends from about the proto/paracone of  $M^1$  to just beyond  $M^3$ . There is a single pair of posterior palatine foramina and usually one or two pairs of posterior palatine pits. The mesopterygoid fossa is distinctively broad (Fig. 3). The parapterygoid plates are also unusual, with deeply excavated surfaces and outer edges that flare sharply laterally. The sphenopalatine vacuities are distinctive in that they are either small and slitlike or completely obstructed by bone. The foramina ovale are large but not remarkably so. In the region of the bullae, the stapedial foramina are large, which with the presence of sphenofrontal foramina, squamoso-alisphenoid grooves, and a well developed carotid canal on the medial surface of the bullae, corresponds to the pattern of basicranial circulation referred to by Voss (1988) as "pattern 1." The bullae themselves are flask-shaped, and bullae and eustachian tubes are of average size and position for the genus.

*Teeth* (Fig. 4): The teeth of the two members of the *fumeus* group generally resemble those of other *Akodon* ("*varius* group," Myers, 1989; *boliviensis* group, Myers *et al.*, in press). The terminology used below follows Reig (1977).

The incisors appear relatively small and lightly constructed. They are approximately orthodont in orientation.

The deep anteromedian flexus of  $M^1$  defines anterolabial and an-

terolingual conules of approximately equal size and remains conspicuous in all but the most worn  $M^1$ 's ( $n = 20$ ). A well developed anteroloph is present. Protocone, paracone, metacone, and hypocone are all large and conspicuous. Mesoloph and mesostyle are present and prominent; none of the specimens examined, however, has any trace of an enterostyle. The teeth of even the youngest specimens examined (age class 2) are too worn to show a posteroflexus or posteroloph, but it is unlikely that these structures could have been large. The  $M^2$  lacks an anterolingual conule, but the anteroloph/parastyle is prominent and projects to the margin of the tooth. The four major cusps are prominent. The mesostyle of  $M^2$  is well developed, but no trace of posteroloph/posteroflexus is found. The  $M^3$  is relatively small, about half the length of  $M^2$  or slightly greater. The outline of its occlusal surface varies from a simple oval to distinctively "8-shaped," a result of having a moderately well developed mesoflexus and hypoflexus.

The configuration of the surface of the lower teeth is difficult to interpret, in large part because structures disappear quickly with wear and few young animals are available. In  $M_1$ , a deep anteromedian flexid divides the anterior face of the tooth into approximately equal anterolingual and anterolabial portions. The protostylid is large and connected to a conspicuous anterolabial cingulum. Even among the few animals available to us, however, considerable variation characterizes the size of these structures. Enterostylid and enterolophid vary from present but small to absent, as do the parastylid and anterolophid. A paralophulid is sometimes present. All  $M_1$ 's have a mesostylid, but it varies in size from large and conspicuous to very small. A metalophulid is sometimes present. The posteroflexid is deep and the posterolophid conspicuous.

The  $M_2$  has a conspicuous anterolabial lophid but no anterolingual structure. A small ectostylid is sometimes present, while metalophulid and protolophulid are lacking. Some individuals possess a small mesostylid or entolophulid. As in  $M_1$ , the posteroflexid is deep and the posterolophid well defined.

The  $M_3$  is relatively simple and about 2/3 the length of  $M_2$ . There is occasionally a trace of an anterolabial cingulum. The major cusps appear to be protoconid, metaconid, and probably a fused entoconid and hypoconid.

*Soft anatomical features:* While at least partial fluid specimens of each of the two members of the *fumeus* group were available, unfortunately only hind foot structure could be examined for both species. The skulls of all specimens of *fumeus* had been removed for cleaning prior

to our examination of them, preventing description of palatal rugae for that species. The only specimens of the new species preserved in fluid are female; details of its phallic morphology are known only from rehydrated dried glandes. We describe here the general features of the plantar surface of the hind feet for both species, since these share characters in common, and we report on palatal structure or male phallus insofar as possible in the separate accounts, below.

The plantar surface of the hind feet (Fig. 5) has the general structure typical for *Akodon* (Myers, 1989; Myers *et al.*, in press), with two metatarsal and four interdigital tubercles. The first digit is short, extending just to the base of the second interdigital tubercle; the fifth digit is long, with the fleshy tip extending well beyond the third interdigital tubercle. The lateral metatarsal tubercle (hypothenar; LMT) is large, subequal in size to the interdigital ones, and about 1/2 the size of the medial metatarsal tubercle (thenar; MMT). The distal edge of the MMT does not quite reach the proximal edge of the LMT, so that a slight gap between the two tubercles is apparent. The foot itself appears proportionately rather short and broad, so that the MMT is positioned less than 1/2 the distance between the calcaneal extension and the base of digits 2–4.

COMPARISONS.—Members of the *fumeus* group may occur sympatrically, or nearly so, with a number of other species of *Akodon* or the related genera *Microxus* and *Bolomys*. The small size of members of this group immediately distinguishes them from *Akodon varius* and its allies (*A. dayi*, *A. simulator*, and *A. toba*; see Myers, 1989), all of which have average maxillary tooththrow lengths in excess of 4.5 mm. They can be told from *Akodon aerosus* in southern Peru and Bolivia by the larger overall size and broader interorbital region (average constriction 5.5 mm) of that species. *Akodon aerosus* also has relatively short, crisp fur, a broader rostrum, and a more deeply grooved palate. Members of the *fumeus* group are slightly larger in size and have much broader, more parallel-sided or lyre-shaped mesopterygoid regions than do members of the *boliviensis* group (including *boliviensis*, *subfuscus*, *puer*; Myers *et al.*, in press). The margins of the parapterygoid plates of *fumeus*-group species are also distinctively convex, in contrast to the more nearly straight (but sometimes slightly convex) margins in members of the *boliviensis* group (Fig. 3). Skins of members of the latter group can also be recognized by the dorsal surfaces of their hind feet, which are covered with all-white hairs. Members of the *fumeus* group are easily distinguished from *Akodon andinus* by the broad cranium, dorsal surfaces of the hind feet clothed with all-white hairs, and white postauricular tufts of the lat-

ter; from *Akodon jelskii* by the propensity of that species to have brightly colored rufous and white patches of fur; from *Akodon albiventer* by *albiventer's* white venter and very large auditory bullae; and from *Akodon budini* and a new species related to *budini* (Myers and Patton, 1989) by the broad interorbit, narrow and weak zygomatic plates, and more hypsodont dentition of those two species. Members of the *fumeus* group differ strikingly from *Microxus mimus* in the shape and slope of the zygomatic plates, which are very narrow and with the ventral root of the plate placed well anterior to the dorsal root in *mimus*. Finally, *fumeus*-group members are easily distinguished from all *Bolomys* by the highly divergent, beaded interorbital region of members of that genus and numerous other cranial features.

The most difficult distinction to make is between the *fumeus* group and *Akodon mollis*, and in fact we concur with Gyldenstolpe's (1932) suggestion that these species are probably very closely related. These mice are similar in size, general conformation of the skull (Figs. 1-3), and in particular, in the broad and (in the case of one of the species) parallel-sided mesopterygoid regions. The known range of *Akodon mollis*, however, extends southward only to Huancavelica Department, Peru, leaving a gap of 450 km between it and Peruvian populations of the *fumeus* group. Further, *mollis*, itself a species with considerable geographic variation, can generally be distinguished from *fumeus* and the new species by several quantitative and qualitative characters, including in *mollis* a very small foramen ovale, especially narrow and shallow zygomatic notches, a broad interorbital region, relatively narrow zygomatic plate (Fig. 2), parapterygoid plates without sharply convex lateral borders (Fig. 3), and M<sup>1</sup>'s usually (but not always) with an anteromedian flexus that is very shallow or, often, entirely lacking (Fig. 4). Given these differences, which are consistent across the range of each species, we prefer to treat members of the *fumeus* group and *mollis* separately, but clearly their relationship is unresolved.

### SPECIES ACCOUNTS

The Limbani drainage in northern Puno department, Peru, contains a rich fauna of akodont rodents. *Akodon subfuscus* and *Akodon jelskii* inhabit grasslands at high elevations. Lower, *Microxus mimus* and *Akodon aerosus* can be found in wet forested areas. Between these zones, in altiplano moist grass and scrubland at around 2800 m elevation, a fifth species occurs. As will be shown, this species appears

closely similar to the Bolivian *Akodon fumeus* in many respects, but it is distinctive in several characteristics of external, cranial, and dental morphology. We name this form

*Akodon kofordi*, new species

HOLOTYPE.—MVZ 171666, mature female (age class 3), collected on 31 July 1985 by J. L. Patton, original number 12207, skin, skull, karyotype, tissue.

TYPE LOCALITY.—Agualani, 9 km N by road Limbani, Depto. Puno, Peru, elevation 2840 m.

DIAGNOSIS.—A medium-sized *Akodon* (Table 1; CIL 23.15 mm, range 22.20 - 25.0 mm; MTRL 3.97 mm, range 3.80 - 4.27 mm); with a broad and usually lyre-shaped mesopterygoid fossa, the anterior margin of which has a well developed median spine (MFW 1.44 mm, range 1.27 - 1.79 mm); interorbital region moderately broad (IOC 4.70 mm, range 4.5 - 5.1 mm) and hourglass-shaped; zygomatic plate and zygomatic notches relatively broad (ZP 2.28 mm, range 1.98 - 2.50 mm); relatively inconspicuous squamoso-alisphenoid groove; tendency for both the sphenopalatine vacuities and postglenoid foramina to be partially or completely obstructed by bone; presence of an island in M<sup>1</sup> (described below); dark brown-olivaceous pelage without patches of contrastingly colored fur; hind feet clothed with banded hairs; unicolored or at most faintly bicolored tail; and other characteristics listed above that place it in the *Akodon fumeus* group.

HABITAT.—This species occupies moist bunch grass and disturbed shrub habitats at the upper edge of the elfin forest at the contact between *Páramo Pluvial Subalpino Subtropical* and *Bosque Muy Húmedo Montano Subtropical* of the Holdridge system (after Tosi, 1960). *Akodon kofordi* is very common along rock walls of old terraces and buildings and in thick clumps of grass and shrubs in the relatively more open and disturbed areas; *Microxus mimus* occurs in the adjacent closed-canopy elfin forest (Fig. 6).

REFERRED SPECIMENS.—24 specimens from the following localities in Puno Dept., Peru: type locality (7 males, MVZ 171660, 171662, 171664, 171665, 171668–171670; 6 females, MVZ 171661, 171663, 171666, 171667, 173813, 173814); 3 mi N Limbani, 9500 ft. (3 males, MVZ 116105, 116106, 139541; 2 females, MVZ 116104, 139542); Limbani (3 males, FMNH 52553, 52554, 52556; 2 females, FMNH 18181, 52555). One specimen from Cusco Dept., Peru: Marcapata, Amacho, 2750 m (1 male, FMNH 75483).

GEOGRAPHIC DISTRIBUTION.—Known from the Limbani and Marcapata drainages between 2750 and 2900 m.

ETYMOLOGY.—Named in honor of Carl Koford, in recognition of his work on the ecology, natural history, and systematics of the mammals of Peru.

DESCRIPTION.—*Skin*: The dorsal color is uniformly medium brown with an olivaceous tone. The hairs are long, on average about 13 mm in length, and the pelage is thick. Pheomelanin bands on individual hairs are around 1.5 mm in length and approximately Yellow Ochre in color. No trace of an eye ring can be seen, and the head is similar to the dorsum in color. The tail appears furry to the unaided eye; it is covered with agouti hairs that extend about three scale-lengths. On the ventral surface of the body, hairs are slate gray basally with pale buff tips about 1/5 the length of each hair.

*Cranium* (Figs. 1–3): Most aspects of cranial morphology are described above under the discussion of the *fumeus* group. Important characteristics include the mesopterygoid fossa, which as noted, has slightly constricted sides that give the fossa a distinctive lyre-like shape. A well developed spine is almost always present on the posterior margin of the palate. The sphenopalatine vacuities are very narrow or, often, completely closed by bone. The opening of the postglenoid foramen is also much reduced. The zygomatic plates appear broad and the zygomatic notches are relatively deep compared to most other *Akodon*.

*Teeth*: Dentally, *kofordi* is a typical member of the *fumeus* group in most aspects. It is unique, however, in the shape of the paraflexus of the M<sup>1</sup>. This fold is remarkably deep, extending nearly to the posterior limit of the paracone. A small section of the paraflexus appears to be isolated by wear relatively early in development, forming a distinctive island. This island was seen in the youngest individuals examined (age class 2), but it was obliterated by wear in some animals of age class 3 and in most individuals of higher age classes. No animals with unworn or only lightly worn M<sup>1</sup>'s lacked the island.

*Phallus*: No fluid-preserved specimens of male *kofordi* are available. However, general features noted from dried and reconstituted phalli are similar to those described in detail below for *fumeus*. The glans is short and thick, somewhat barrel-shaped, with well developed dorsal and ventral grooves, a thick and crenulated crater lip well separated from the spinous epidermis, a dense clothing of epidermal spines, protrusion only of the medial bacular mound distal to the crater lip, urethral flaps contained wholly within the crater and not exposed

externally, and a thick dorsal papilla surrounded by lateral folds of tissue extending from the medial mound to the inner crater wall.

The baculum is typical of members of the genus *Akodon*. The proximal bony part has a straight and stout shaft and a laterally flared base, and the distal component is tri-digitate and cartilaginous, with the lateral digits about 2/3 the length of the medial one.

*Palate*: The palatal rugae of *kofordi* consist of the usual two complete diastemal and four incomplete interdental ridges typical of most *Akodon* (Fig. 7; Myers *et al.*, in press). The first diastemal ruga forms a smooth arc across the anterior palate, and the second has a deep but rounded median notch. All interdental rugae are divided at the midline; they are simple, forming a uniform set of rather parallel and straight ridges perpendicular to the long axis of the palate.

*Karyotype* (Fig. 8): Cytologically, *A. kofordi* is unremarkable, with  $2n=40$ ,  $FN=40$ , and a karyotype that is probably primitive for *Akodon sensu stricto* (following Reig, 1987; Vitullo *et al.*, 1986). The autosomal complement is composed of 18 pairs of uniarmed elements. One of these is distinctly larger than the remainder, which grade evenly in size from medium to small. There is a single pair of very small metacentric elements. The X-chromosome is a medium subtelocentric with very short second arms, and the Y is a very small acrocentric equal in size to the pair of small biarmed autosomes.

COMPARISONS.—*Akodon kofordi* can be distinguished from *A. fumeus* by *kofordi*'s distinctive mesopterygoid fossa,  $M^1$  with an island, relatively broad and deep zygomatic notches, olivaceous pelage, unicolored tail, and other characteristics discussed above and in the emended diagnosis of *fumeus*, which follows. It can easily be distinguished from other *Akodon* by a combination of its intermediate size, well developed zygomatic plates, lack of areas of contrasting color in its pelage, broad mesopterygoid fossa, and other characteristics described in the discussion of the *fumeus* group, above.

The palate of *kofordi* is distinctive relative to that of all other *Akodon* or *Akodon*-like taxa examined by us to date in the simplicity and conformation of the interdental rugae. It shares a medially notched second diastemal ruga with *A. subfuscus*, with a new species from Bolivia related to *A. budini* (Myers and Patton, 1989), and with *Microxus mimus*. It differs from *A. subfuscus* by having a smoothly arched rather than noticeably angled first diastemal ruga, and from *M. mimus* by having the more usual four as opposed to five interdental ridges. Unfortunately, however, the palates of most species of *Akodon* have not been examined.

Distinguishing *A. kofordi* from two species of *Akodon*, *A. subfuscus*



and *A. mollis*, is especially difficult or critical. *Akodon subfuscus* was described by Osgood (1944) from specimens collected near Limbani, close to the type locality of *kofordi*. Superficially, it is similar to *kofordi*, and in fact, the series of "topotypes" of *subfuscus* mentioned by Osgood (1944) in the description of that species includes both species. The two species can be distinguished easily by the relatively longer and less bicolored tail, darker hind feet, broader and more lyre-shaped mesopterygoid fossa, M<sup>1</sup> with an island, and other characteristics of *kofordi* described above and in Table 1.

*Akodon mollis* is a species known primarily from Ecuador and Peru south approximately to Junín Department. The range of *Akodon kofordi* does not overlap that of *A. mollis*; in fact, the two are not known to occur within several hundred kilometers of each other. *Akodon kofordi* is more similar morphologically to *mollis*, however, than to any other *Akodon* except *fumeus*. As currently constituted, *mollis* has a very large geographic range, extending at least from central Peru northward through Ecuador. The taxon exhibits substantial geographic variation, especially in size and color, and may eventually prove to include several species. We have examined specimens from throughout its range, but our comparisons have focused on populations in central and northern Peru, which live closest to the more southern distribution of *kofordi*.

Qualitative characteristics of *kofordi* that distinguish it from *mollis* include an island in M<sup>1</sup>, lyre-shaped mesopterygoid fossa, relatively broad zygomatic plates and zygomatic notches, and other characteristics mentioned above under the discussion of the *fumeus* group. These differences, while often subtle and only obvious when like-age animals are compared, appear to be consistent across the ranges of both species. Quantitative comparisons of *mollis*, *kofordi*, and *fumeus* will be made in the discussion of *Akodon fumeus*, below.

### *Akodon fumeus* Thomas

*Akodon fumeus* Thomas, 1902; Ann. Mag. Natur. Hist., ser. 7, 9:137-138 (type description).

*Akodon mollis fumeus*, Gyldenstolpe, 1932; Kungl. Sv. Vetensk. Handl., 11(3):106.

HOLOTYPE.—BMNH 2.1.1.80, skin and (damaged) skull of an old female collected by Perry O. Simons in 1901. Thomas also listed a second specimen from the same locality.

TYPE LOCALITY.—Choro, Cochabamba, Bolivia, at 3500 m.

EMENDED DIAGNOSIS.—*Akodon fumeus* is an *Akodon* of intermediate size (Table 1) with the following combination of characters:  $M^1$  lacking an island; relatively broad zygomatic plates (ZP 2.2 mm, range 1.78 - 2.70 mm); zygomatic notches not especially broad; interorbital area of intermediate breadth (IOC 4.8 mm, range 4.5 - 5.1 mm) and with smoothly rounded to squared (but never beaded) edges; squamoso-alisphenoid groove conspicuous; mesopterygoid fossa broad (MFW 1.5 mm, range 1.20 - 1.91 mm) and usually with a rounded anterior margin (no palatal spine); lateral margins of parapterygoid plates slightly to moderately convex; sphenopalatine vacuities and postglenoid foramina not obstructed by bone; pelage dark brown with rufous tones dorsally, without any sharp distinction between dorsal and ventral regions or any areas of contrastingly colored fur; tail weakly to strongly bicolored; and dorsal surface of feet clothed with agouti (not monochrome) hairs.

GEOGRAPHIC RANGE.—Eastern slope of the Andes in Bolivia, entering Peru in the northeastern part of Puno Department. Known from La Paz, Cochabamba, Santa Cruz, and Tarija Departments in Bolivia and Puno Department in Peru.

HABITAT.—Northern populations appear to inhabit the lower reaches of paramo grasslands (at around 3500 m) to cloud forest (down to about 2800 m). The southernmost population in Tarija was found in a wet, relictual *Podocarpus* forest at about 1000 m.

DESCRIPTION.—A general description of members of the *fumeus* group is given above. The following remarks apply to *fumeus* alone.

*Skin*: The pelage of *fumeus* from populations in La Paz, Cochabamba, and Santa Cruz departments, Bolivia, has distinctly rufous overtones. Individual hairs from the mid-rump region measure 8–11 mm in length. The pheomelanin bands on the dorsal hairs average 1 mm in length and are approximately Yellow Ochre. The tips of the ventral hairs are strongly rufous, and the dorsal and ventral color patterns are not sharply differentiated. A single specimen from Tarija Department (southern Bolivia) is darker and more olivaceous with a predominantly gray venter; however, this individual is young (the  $M^3$  is only slightly worn). Most specimens have a narrow border of pale fur around each eye, giving the appearance of a faint eyering. The tails of all specimens are sparsely furred and appear scaly, with most individual hairs extending no more than the length of two scales. The tails are usually weakly bicolored, but considerable variation can be found among individuals.

*Cranium* (Figs. 1–3): The crania have moderately developed zygo-

matic arches, which at least in old individuals (those with heavily worn teeth) run parallel to each other in their middle sections. Zygomatic notches tend to be shallow but of average breadth compared to most other *Akodon*. In lateral view, the dorsal profile of the cranium is relatively flat. The squamoso-alisphenoid grooves are conspicuous. The zygomatic plates (Fig. 2) appear relatively narrow and weakly developed. Above the bullae, the postglenoid foramina appear relatively large and unobstructed. Ventrally, the mesopterygoid fossa (Fig. 3) is typically broad, but its anterior margin lacks a median spine, or if a spine is present it is small. Sphenopalatine vacuities are small but always open.

*Teeth* (Fig. 4): The teeth are as described for the species group. In no case was the island in  $M^1$  described above for *kofordi* present in *fumeus*.

*Phallus* (Fig. 9): The phallus of male *fumeus* is short, thick, and barrel-shaped, with a convex dorsum. Well developed ventral and dorsal grooves are confluent with the crater lip. The short, thick epidermal spines are nearly uniform in size throughout, increase in density proximally, and are imbedded in individual pits. The crater rim is quite distinctive, being very thick, highly crenulated, and strongly separated from the spinous part of the shaft by a well-marked fold. Single ventral and dorsal notches as well as a lateral pair are present on the rim. The rim has a distinctive topography in lateral view, with the dorsal edge thick and elevated and the ventral edge even thicker but sloping strongly inward. The medial bacular mound is exposed above the rim; the lateral mounds are not. The tip of the medial mound is oriented slightly dorsally so that in lateral profile the mound appears concave. Urethral flaps are elongated, contained wholly within the crater, taper distally with well separated tips, and lack obvious spines near the tips. The dorsal papilla is thick, spatulate, and buried in thick tissue folds extending from the medial mound to the inner crater wall.

The baculum of *fumeus* resembles that of *kofordi*, described above.

COMPARISONS.—Characteristics of *fumeus* that distinguish it from *kofordi* include a usually straight-sided (not lyre-shaped) mesopterygoid fossa without a palatal spine on its anterior margin, absence of an island in  $M^1$ , relatively large postglenoid foramen and sphenopalatine vacuities, bicolored tail, and faintly rufous (not olivaceous) dorsal pelage. *Akodon fumeus* also has a slightly narrower zygomatic plate and zygomatic notches than *kofordi*, less convex lateral margins of the parapterygoid plates, and a less strongly curved dorsal profile

of the skull, but these characteristics are obvious only when series of animals of similar age are compared.

The phallus of *fumeus* is grossly similar in general conformation to that of *Akodon aerosus*, *boliviensis*, *mollis*, and *torques*, and *Microxus mimus*. It differs from those of *A. subfuscus* and *A. puer* in the same ways as does that of *A. boliviensis* (see Myers *et al.*, in press). Features unique to *fumeus* are the distinctive topography of the crater rim in lateral view, the very deep ventral groove, and the relatively small and evenly sized epidermal spines. We do not yet know whether these features are also shared by *kofordi*.

Like *kofordi*, *fumeus* is similar to and may be confused with *Akodon mollis* and *Akodon subfuscus*. It can be distinguished from *subfuscus* by *fumeus*'s larger size, much broader mesopterygoid region, and hind feet covered by banded (not all-white) hairs. The mesopterygoid region of *subfuscus* also differs in that its walls generally diverge slightly posteriorly rather than running in parallel.

The distinction between *mollis* and *fumeus* is more subtle, and as suggested above, these species may be related. Compared to *fumeus*, *mollis* appears to have especially narrow zygomatic plates and zygomatic notches, a very small foramen ovale, a broader interorbital region, M<sup>1</sup>'s with a shallow or no anteromedian flexus, and other characteristics mentioned above in the discussion of the *fumeus* group.

To illustrate the quantitative patterns of cranial variation among these species, we performed a principal components analysis based on 19 cranial measurements. The analysis was restricted to individuals with moderately worn teeth (age class 4 of Myers, 1989) to reduce variation attributable to age (Myers *et al.*, in press). Computations were performed on the variance-covariance matrix derived from log-transformed data. The results confirm the distinctiveness of *subfuscus* and the close similarity between *fumeus* and *kofordi*, and they suggest that *fumeus* and *kofordi* are morphometrically more like *mollis* than like *subfuscus* (Table 2, Fig. 10).

To explore further the similarity of *fumeus* and *kofordi* with respect to *mollis*, we log-transformed the measurements for each individual of these taxa, computed means of the transformed measurements, and re-expressed each mean as a percentage of the mean of that measurement in *mollis*. We then plotted the results as a profile diagram (Morrison, 1976; see also Anderson, 1972). In Fig. 11, *mollis* is represented as a straight vertical line at 100 on the horizontal axis, and most of the measurements for each of the other two species can be seen to vary in a highly consistent fashion with respect to *mollis*. A

TABLE 2.—Loadings from principal component analysis of cranial measurements of *Akodon kofordi*, *A. fumeus*, *A. mollis*, and *A. subfuscus*.

	PC1	PC2
CIL	0.145	0.097
ZB	0.156	0.146
BB	0.098	0.022
IOC	0.246	-0.114
RL	0.217	0.090
NL	0.207	0.170
RW	0.163	0.223
RW2	0.197	0.270
OL	0.052	0.195
DL	0.160	0.164
MTRL	0.129	-0.013
IFL	0.159	0.326
AW	0.169	0.116
OCW	0.099	-0.122
MB	0.089	0.058
BOL	0.152	-0.050
MFW	0.762	-0.390
ZP	0.068	0.657
CD	0.069	0.088
%Variation explained	52.7	20.4

test for parallelism of the profiles of *fumeus* and *kofordi* (Morrison, 1976; based on untransformed raw measurements rather than percentages) reveals small deviations from parallel ( $T^2 = 106.39$ ,  $F = 2.635$ ,  $df = 19, 16$ ,  $p = 0.023$ ), but much larger deviations when a three-way comparison is made between *fumeus*, *kofordi*, and *mollis* (max root = 727.8,  $df = 28, 22$ ,  $p < 0.001$ ). Figure 11 shows that differences between *kofordi* + *fumeus* versus *mollis* are most extreme in measurements of zygomatic plate, incisive foramen length, diastema length (*kofordi*), and interorbital constriction. *Akodon kofordi* differs from *A. fumeus* especially in basioccipital length and diastema length, but generally both differ from *mollis* in a like manner.

At present, the significance of these similarities in an understanding of the phylogenetic relationships of these species is uncertain. The distributions of these characters among *Akodon* and its sister taxa have not been established, and as a result we cannot yet determine which resemblances represent synapomorphy and which do not. Indeed, it is not clear whether *Akodon* itself as currently envisioned is a

monophyletic assemblage (Patton *et al.*, 1989). Further work on these diverse and interesting animals is much needed.

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## 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 presented here.

*Akodon aerosus* (171 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: PUNO: 4 km NNE Ollachea, 2380 m (24 males, MVZ 172814, 172815, 172818, 172819, 172821, 172824-172827, 172830, 172832, 172834, 172836, 172837, 172839, 172841-172843, 173173, 173177-173180, 173182; 27 females, MVZ 172816, 172817,

172820, 172822, 172823, 172828, 172829, 172831, 172833, 172835, 172838, 172840, 172844–172847, 173172, 173174–173176, 173181, 173183–173188); 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); Oconeque, 6–10 mi N Limbani (3 males, MVZ 116110, 116111, 116649; 1 female, MVZ 116648); Santo Domingo, 6000 ft (5 males, FMNH 18180, 20108, 52532, 52535, 52536; 5 females, FMNH 20107, 52530, 52533, 52534, 52537); Segrario (1 male, FMNH 52539; 1 female, FMNH 52540); San Juan del Oro, 1520 m (3 males, FMNH 78372, 78374, 78375; 4 females, FMNH 78370, 78371, 78373, 78376); Oconeque, Río Quintún (5 males, FMNH 52522–52525, 52528; 2 females, FMNH 52527, 52529); Inca mines, 6000 ft (6 males, AMNH 16532, 16539–16541, 16546, 16550; 3 females, AMNH 15812, 16533, 16538).

*Akodon boliviensis* (8 specimens). PERU: PUNO: 12 km S Santa Rosa [de Ayaviri], 3950 m (3 males, MVZ 171602, 172380, 172896; 5 females, MVZ 171603–171605, 171607, 172922).

*Akodon dayi* (63 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). 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 Asunción (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* (52 specimens). BOLIVIA: COCHABAMBA: Río Secure (1 female, BMNH 2.1.1.80); Ayopoca (6 males, FMNH 74874, 74876, 74878, 74880, 74882, 74883; 3 females, FMNH 74875, 74877, 74879); 20 mi E Totorá, 9700 ft (1 male, MVZ 119924); Incacocha (2 males, AMNH 38594, 38645; 3 females, AMNH 38592, 38612, 38613); 101 km by rd SW Epizana, Siberia cloud forest, Cordillera Oriental, 2989 m (1 male, AMNH 246712); Incachaca (1 male, AMNH 38950; 1 female, AMNH 38585; 3 males, CMNH 5080, 5247, 5249; 1 female, CMNH 5252); Palmar, Yungas de Cochabamba, 2600 ft (2 females, FMNH 46143, 46144); 28 km by rd W Comarapa, 2800 m (2 males, AMNH 260462, 260499; 2 females, AMNH 260463, 260464; 1 male, MSB 55226). LA PAZ: Río Aceramarca, 10,800 ft (1 male, AMNH 73054; 1 female, AMNH 73059); Tacacoma (1 male, AMNH 91574). SANTA CRUZ: 21 km by rd W Comarapa, 2900 m (2 males, AMNH 260455, 260580; 1 male, MSB 55225); 25 km W Comarapa, Siberia, 2800 m (1 male, UMMZ 155985; 1 female, UMMZ 155863); 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, 21°27'S, 64°19'W (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 kofordi* (24 specimens). See species description.

*Akodon mollis* (38 specimens). PERU: ANCASH: 1 km N, 12 km E, Pariacoto, 8500 ft [nr 9.5°S, 77.8°W] (2 males, MVZ 135677, 135678; 2 females, MVZ 135676, 137965). JUNÍN: 15 km by rd SW San Ramón (1 male, UMMZ 158038); 16 km NNE Palca by rd, 2540 m (8 males, MVZ 173045, 173048, 173050, 173051, 173054–173057; 6 females, MVZ 173046, 173047, 173049, 173052, 173053, 173058); 22 mi E Tarma, 7300 ft (4 males, AMNH 231481, 231482, 231489, 231932; 14 females, AMNH 231464, 231469, 231471, 231472, 231474–231478, 231480, 231483, 231485, 231487, 231490); 9.5 mi N La Oroya, 13000 ft (1 female, AMNH 231337).

*Akodon puer* (99 specimens). BOLIVIA: COCHABAMBA: Choqueamate, Río Secure (1 female, BMNH 2.1.1.78); 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). LA PAZ: 7 km E of Ulla Ulla, 4560 m, 15°03'S, 69°12'W (2 males, AMNH 247850, 247851). SANTA CRUZ: 21 km by rd W Comarapa, 2900 m (2 males, AMNH 260448, 260453; 4 females, AMNH 260449, 260450, 260452, 260454); 1 km N, 8 km W Comarapa, 2450 m (2 males, AMNH 260494, 260498; 1 female, AMNH 260497). PERU: PUNO: 12 km S Santa Rosa (14 males, MVZ 171613, 171623, 171631, 171633, 171635, 171641, 171643, 171644, 172896, 172918, 173335, 173369, 173373, 173374; 27 females, MVZ 171601, 171612, 171614, 171622, 171629, 171630, 171632, 171634, 171637, 171638, 172382, 172937, 173215, 173223, 173298, 173324, 173333, 173356, 173358, 173365–173368, 173370–173372, 173375); 5 km W Puno (2 males, MVZ 115672, 115674; 1 female, MVZ 115673); 6 km S Pucará, 3850 m (15 males, MVZ 173003, 173007, 173008, 173010, 173014, 173016, 173022, 173238, 173245, 173398, 173402, 173403, 173413, 173414, 173417; 12 females, MVZ 173015, 173017, 173018, 173240–173242, 173244, 173248, 173399, 173401, 173408, 173415); 3.6 km W Muñani, 3450 m (1 male, MVZ 173419; 3 females, MVZ 173030, 173031, 173418); 11 km W and 12 km S Ananea, 4200 m (4 males, MVZ 173034–173037); 5 mi S Asilo (2 females, MVZ 116077, 116078); 4.5 km NE San Antón, 4000 m (1 female, MVZ 173382); 5 mi NW Puno (2 males, AMNH 213574, 213578); Tirapata (1 male, AMNH 16508).

*Akodon* sp. (11 specimens). BOLIVIA: COCHABAMBA: 28 km by rd W Comarapa, 2800 m (4 males, AMNH 260426, 260430, 260434, 260594; 5 females, AMNH 260427, 260428, 260431, 260432, 260590); 31 km by rd W Comarapa, 2800 m (1 male, AMNH 260578; 1 female, AMNH 260579).

*Akodon subfuscus* (67 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: CUSCO: 5 km N Huancarani, 3870 m (1 male, MVZ 172368). 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).

*Microxus mimus* (131 specimens). BOLIVIA: COCHABAMBA: 101 km by rd SW Epizana, Siberia cloud forest, Cordillera Oriental, 2989 m (13 males, AMNH 246708,

246711, 246713, 246714, 246716, 246717, 246720, 246721, 246723, 246725, 246728, 246729, 246758); 28 km by rd W Comarapa, 2800 m (8 males, AMNH 260429, 260585, 260586, 260589, 260591, 260601, 260602; 3 females, AMNH 260582, 260587, 260600; 2 males, MSB 55302, 55306; 4 females, MSB 55210, 55301, 55303, 55305); 31 km W Comarapa (2 males, AMNH 260573, 260575). LA PAZ: 10 km NE Unduavi, 2400 m (6 males, UMMZ 155880–155882, 155958, 155959, 155961; 3 females, UMMZ 155883, 155956, 155957); 18 km N Zongo, 2967 m (5 males, UMMZ 156099, 156109, 156110, 156112, 156116); 30 km N Zongo, 2000 m (2 males, UMMZ 155949, 155954; 8 females, UMMZ 155946–155948, 155950–155953, 155955); 31 km S Coroica, 2850 m (1 male, UMMZ 126779); Río Aceramarca, 2600 m (1 female, UMMZ 155884); Cocopunco, 10000 ft (1 female, AMNH 73010); Nequejahuirra, 8000 ft (12 males, AMNH 73065–73070, 73072, 73074–73078; 9 females, AMNH 73082, 73085–73088, 73090, 73091, 73095, 73096); Pongo, 12000 ft (1 male, AMNH 73042; 1 female, AMNH 73044); Río Aceramarca, 10800 ft (3 males, AMNH 73050, 73051, 73053; 5 females, AMNH 73055, 73057, 73058, 73060, 73061). 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: Limbani (1 female, BMNH 1.1.1.48); Agualani, 9 km by rd N Limbani, 2840 m (3 males, MVZ 171745, 171748, 171749; 4 females, MVZ 171746, 171747, 171751, 173815); 14 km W Yanahuaya (2 males, MVZ 171752, 171753); 4 mi N Limbani, 2670 m (5 males, MVZ 114638, 114639, 116107–116109; 2 females, MVZ 114636, 114637).

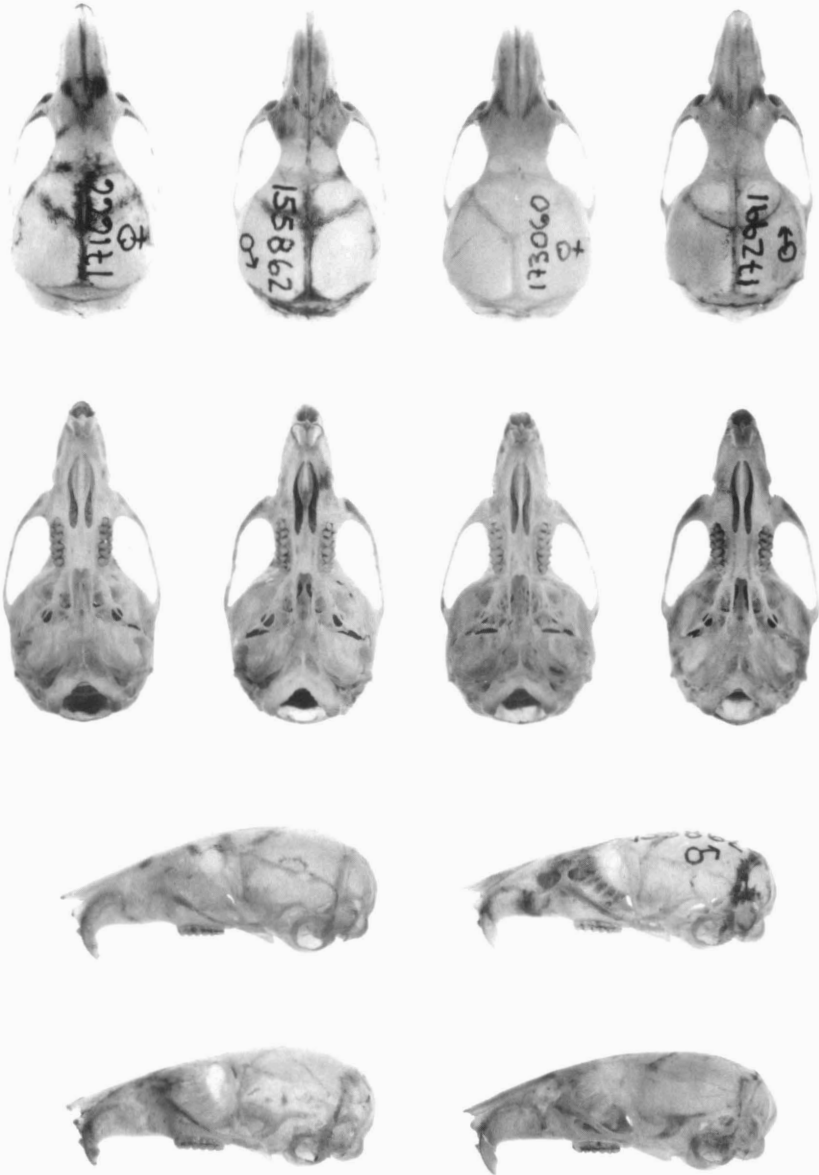


FIG. 1. Dorsal, ventral, and lateral views of selected *Akodon*. First and second rows, from left to right: *A. kofordi* (MVZ 171666, holotype); *A. fumeus* (UMMZ 155862); *A. mollis* (MVZ 173060); *A. subfuscus* (MVZ 172991). Third row: *A. kofordi* (MVZ 171666); *A. fumeus* (UMMZ 155862). Fourth row: *A. mollis* (MVZ 173060); *A. subfuscus* (MVZ 172991).

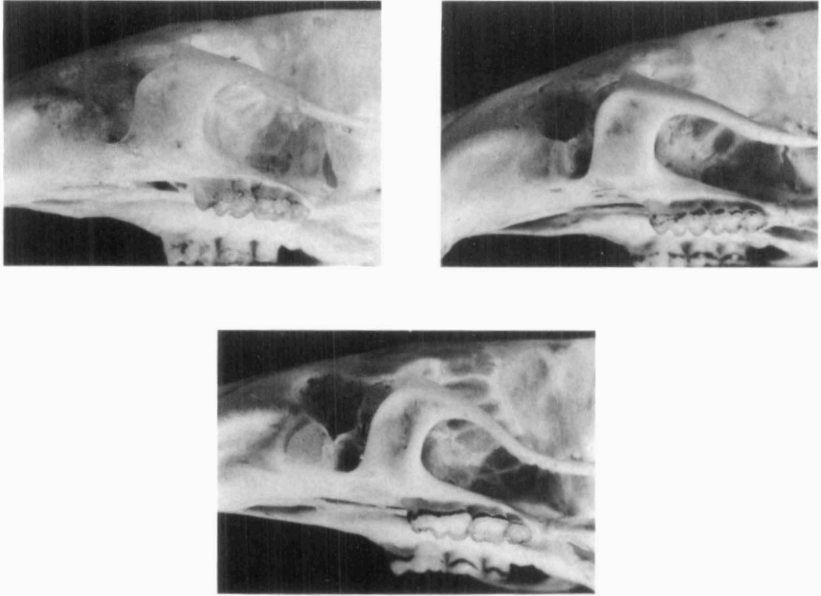


FIG. 2. Zygomatic plates of *A. kofordi* (upper left, MVZ 116105), *A. fumeus* (upper right, UMMZ 156324), *A. mollis* (bottom, UMMZ 158038).

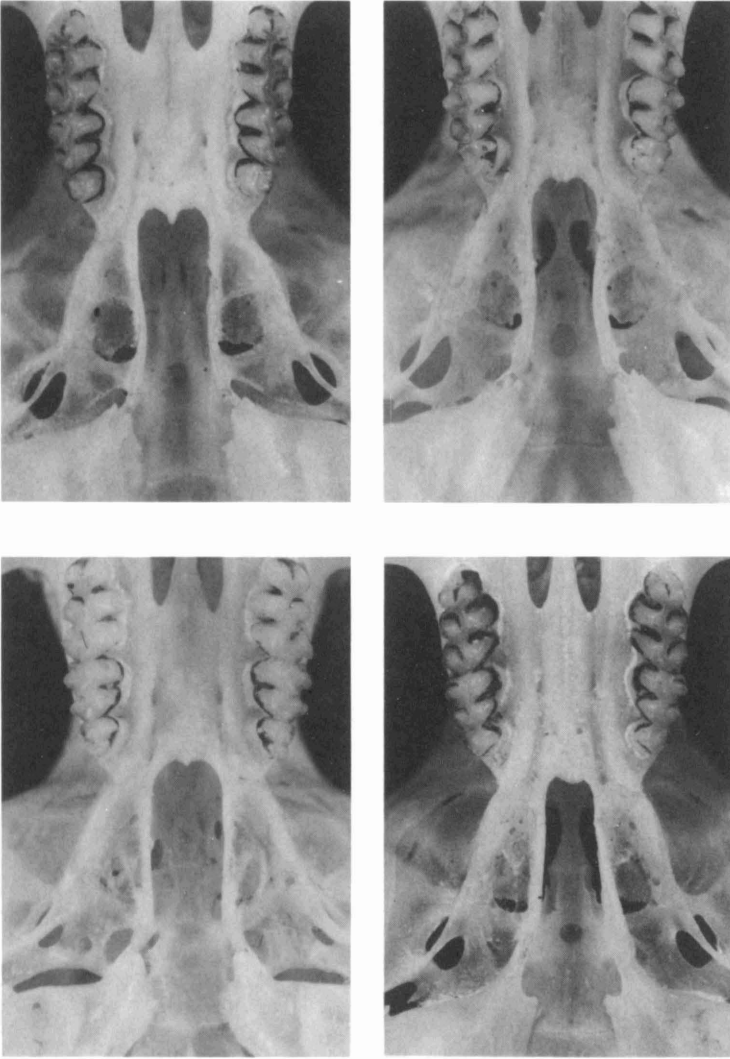


FIG. 3. Mesopterygoid regions of selected *Akodon*. Top row: *A. kofordi* (left, MVZ 171666); *A. fumeus* (right, UMMZ 155862). Bottom row: *A. mollis* (left, MVZ 173060); *A. subfuscus* (right, MVZ 172991).

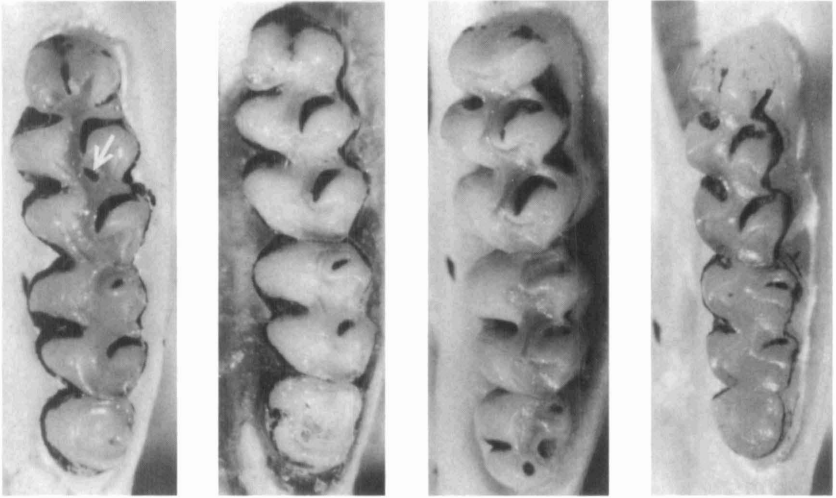


FIG. 4. Upper molar rows. From left to right: *A. kofordi* (MVZ 171666), *A. fumeus* (UMMZ 156303), *A. mollis* (MVZ 135676), *A. subfuscus* (MVZ 172991). The island in the  $M^1$  of *kofordi* is marked with an arrow.

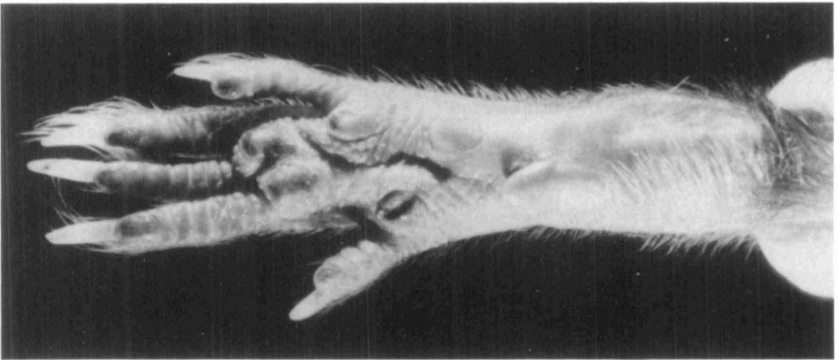


FIG. 5. Plantar surface of hind foot of *A. kofordi* (MVZ 173813).



FIG. 6. Habitat at the type locality of *Akodon kofordi*. This species is common along the rock walls of terraces forming the more open and disturbed shrub-grass habitats in the middle and left side of the photograph. The akodontine rodent *Microxus mimus* is restricted to the more undisturbed elfin forest on the right of the photograph.

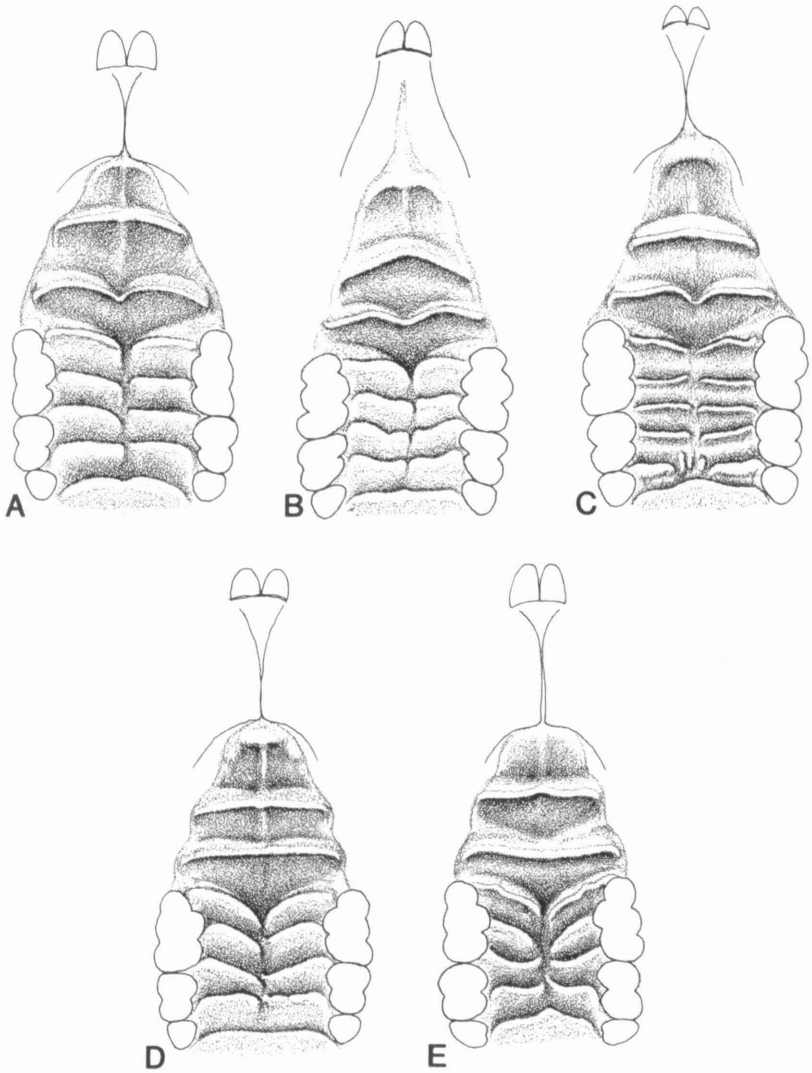


FIG. 7. Views of the soft palates of: A, *Akodon kofordi* (MVZ 173814); B, *Akodon subfuscus* (MVZ 172368); C, *Microxus mimus* (MVZ 173815); D, *Akodon puer* (MVZ 172382); and E, *Akodon boliviensis* (MVZ 172380).





FIG. 8. Karyotype of *Akodon kofordi* (MVZ 171665, male,  $2n = 40$ , FN = 40).

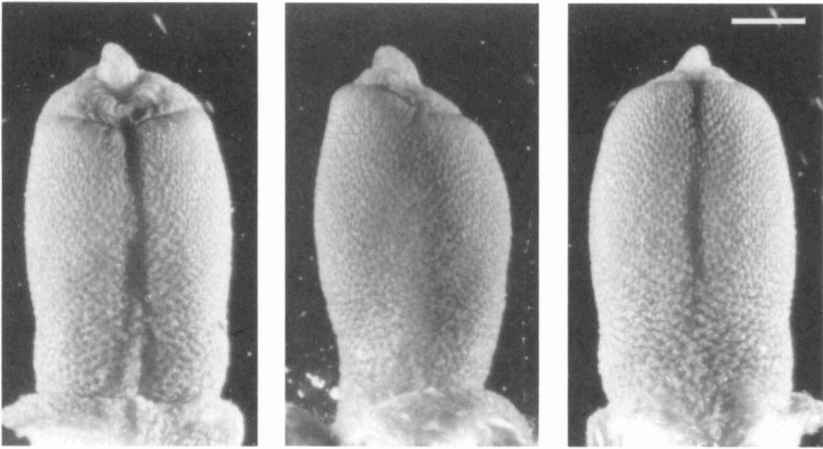


FIG. 9. Ventral, lateral, and dorsal views of the phallus of *Akodon fumeus* (UMMZ 156310). The horizontal line equals 5 mm.

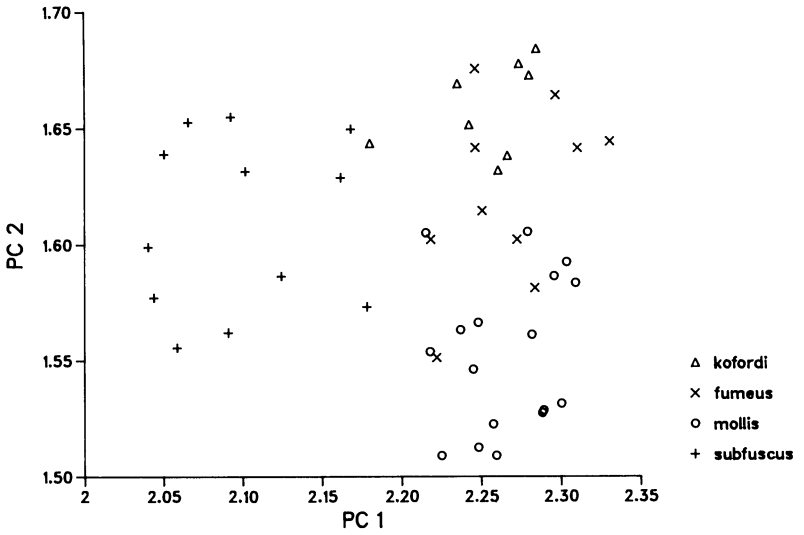


FIG. 10. Bivariate plot of the first two PC axes for representative specimens of four species of *Akodon*: *kofordi*, *fumeus*, *mollis*, and *subfuscus*. Characters used in the analysis are given in Table 2.

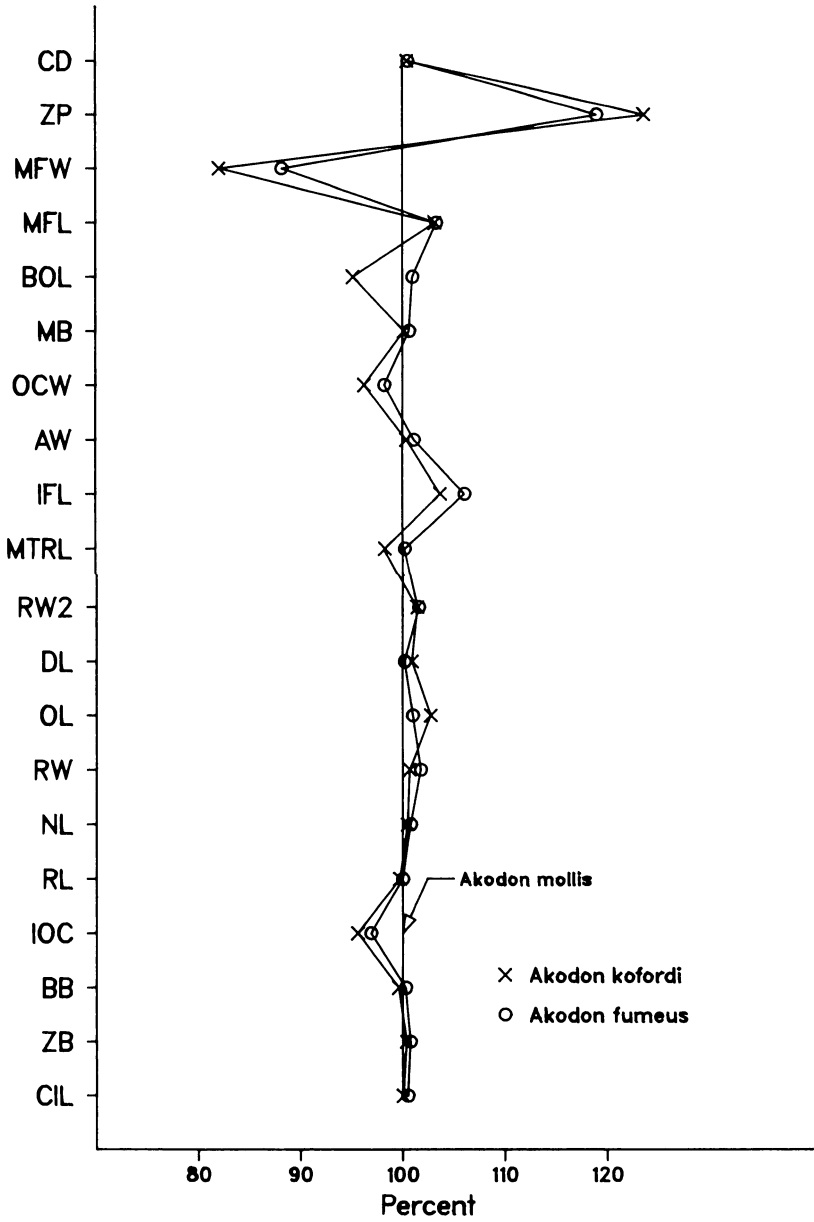


FIG. 11. Profile diagram comparing cranial dimensions for the two members of the *fumeus* group (*Akodon fumeus* and *kofordi*) relative to *A. mollis*.

