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Una nueva especie de ratón campestre, género *Akodon* Meyen, 1833 (Rodentia, Sigmodontinae), de las Yungas centrales del Perú

A new species of grass mouse, genus *Akodon* Meyen, 1833 (Rodentia, Sigmodontinae), from the central Peruvian Yungas

Carlos F. Jiménez[1*] and Víctor Pacheco[1, 2]

[1] Departamento de Mastozoología, Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Av. Arenales 1256, Jesús María, Lima, Perú. Apartado 140434, Lima 14, Perú. E-mail: cfja_80@yahoo.com (CJA)
[2] Instituto de Ciencias Biológicas "Antonio Raimondi", Facultad de Ciencias Biológicas, Universidad Nacional Mayor de San Marcos, Av. Venezuela s/n, cuadra 34, Cercado, Lima 11, Perú. Apartado 110058. Lima, Perú.
* Corresponding author

The genus *Akodon* is one of the most abundant and species-rich genus of Neotropical mammals. Its species-level taxonomy has been changing actively since its establishment. Currently, the genus is divided into five groups of species: *aerosus*, *boliviensis*, *cursor*, *dolores*, and *varius.* Most taxonomic studies of the genus *Akodon* have focused on *boliviensis*, *varius*, and *cursor*. Taxa from the *aerosus* group, including *A. orophilus*, remain largely unknown and poorly studied, even when several authors indicate that most species could constitute species complexes. Here we review populations currently assigned to *A. orophilus*; our results allowed the description of a new species of *Akodon*. We carried out a complete and thorough revision of species of the *Akodon aerosus* group from the central Peruvian montane forests. We included external and craniodental characters and morphometric data for our analyses. Multivariate statistics and morphological characterizations were performed in order to find differences between species. A new species of *Akodon* from Peru is described based on combined analyses of cranial morphology and morphometric data. This new species was compared with other taxa from the *aerosus* species group, it is easily distinguishable from congeners by a unique combination of pelage coloration, body size, and cranial morphology. This new species is most likely endemic to montane forests from Huánuco, and its discovery contributes to uncover the real diversity of Peruvian rodents, adding up to nine species of *Akodon* from montane cloud forests. Moreover, it supports the previous hypothesis that montane rodent species are complex species; therefore, further research is necessary.

Keywords: *Akodon aerosus* group; *Akodon orophilus*; Huánuco; montane cloud forest; Peru; taxonomy.

El género *Akodon* es uno de los roedores sigmodontinos más abundantes y diversos del neotrópico. Su taxonomía y sistemática ha ido cambiando desde su conformación. Actualmente, el género está divido en cinco grupos de especies: *aerosus*, *boliviensis*, *cursor*, *dolores* y *varius*. La mayoría de los estudios realizados se han centrado en especies del grupo *boliviensis*, *varius* y *cursor* mientras taxa del grupo *aerosus*, incluyendo a *A. orophilus*, permanecen pobremente estudiados; a pesar que varios autores indicaron que la mayoría de ellos podrían representar complejo de especies. En el presente estudio, nosotros revisamos poblaciones asignadas a *A. orophilus* del departamento de Huánuco, cuyos resultados nos permite describir una nueva especie. Se realizó una revisión completa y exhaustiva de las especies del grupo *Akodon aerosus* que ocurren en los bosques montanos del centro del Perú, así como comparaciones con otras especies que habitan estos bosques. Se incluyeron los caracteres externos y craneales y datos morfométricos en nuestros análisis. Estadísticas multivariantes y caracterizaciones morfológicas se realizaron con el fin de encontrar las diferencias entre las especies. Una nueva especie de *Akodon* de Perú se describe basándonos en un análisis combinado de datos morfológicos y morfométricos externos y craneodentales. Esta nueva especie es fácilmente distinguible de las otras especies del grupo *aerosus* por una combinación única de coloración del pelaje, tamaño corporal, morfología craneal y caracteres externos. La nueva especie es probablemente endémica a los bosques montanos de Huánuco y su descubrimiento ayuda a revelar la verdadera diversidad de los roedores peruanos en este tipo de región y eleva a nueve las especies de *Akodon* presentes en bosques montanos. Además, se apoya la hipótesis previa que indica que las especies montanas representan complejos de especies; por lo que son necesarias más investigaciones sobre ellas.

Introduction

The genus *Akodon* Meyen, 1833, contains *ca.* 39 extant species and is one of the most diverse South American genus of rodents. The taxonomy of *Akodon* has been actively changing since it was first established. For instance, the species *A. philipmyersi*, *A. polopi*, and *A. josemariarguedasi* have been recently described (Pardiñas *et al.* 2005; Jayat *et al.* 2010; Jiménez *et al.* 2013); *A. aliquantulus*, *A. oenos*, and *A. viridescens* were recently synonymized (Jayat *et al.* 2010; Pardiñas *et al.* 2011; D'Elía *et al.* 2011); finally, other forms like *A. caenosus* were elevated to full species (Jayat *et al.* 2010). In addition, two species: *A. latebricola* and *A. bogotensis*, were removed from *Akodon* and allocated to the new genus *Neomicroxus* (Alvarado-Serrano and D'Elía 2013). Still, other species, like *A. azarae*, *A. budini*, *A. pervalens*, *A. siberiae*, and *A. mimus*, have unclear phylogenetic relationships, suggesting that the radiation of *Akodon* is currently neither fully resolved nor understood.

Previous studies have suggested a monophyletic *Akodon* divided into five main groups of species: *aerosus*, *boliviensis*, *cursor*, *varius*, and *dolores* (Smith and Patton 2007; Jayat *et al.* 2010; Coyner *et al.* 2013), the first two of which occur in Peru. The *Akodon aerosus* clade was first recovered by Patton and Smith (1992) and includes the species *A. aerosus*, *A. mimus*, *A. mollis*, *A. orophilus*, and *A. torques*, all of which are distributed in Peru. Later, this species group was expanded by Smith and Patton (2007) with four additional species (*A.* cf. *budini*, *A. affinis*, *A. albiventer*, and *A. siberiae*). Both studies supported the monophyly of the group; however, a recent study by Coyner *et al.* (2013) suggested that this group is paraphyletic and includes members of the *cursor* group. This group is minimally composed of *A. aerosus*, *A. albiventer*, *A. affinis*, *A. mollis*, *A. orophilus*, *A. surdus*, and *A. torques* (Pardiñas *et al.* 2015). Meanwhile, studies of the *aerosus* group at the species level are scarce, and issues such as variable chromosome numbers (see Patton and Smith 1992; Smith and Patton 2007), the taxonomic complexity of some species (*e. g., A. aerosus* Patton and Smith 1992), and the highly divergent mitochondrial DNA between species (see Patton and Smith 1992; Smith and Patton 1991; 1993; 2007) add uncertainty to the taxonomy of the group.

Patton and Smith (1992) and Smith and Patton (1993, 2007), based on a phylogenetic analysis of cytochrome *b* sequences, suggested that *A. orophilus* encompasses more than one species. They reported sequence divergence values between 5 and 10 % between samples from Unchog (Huánuco), Puerta del Monte (San Martín), Leymebamba (Amazonas), and Palca (Junín). Later, Pacheco *et al.* (2012) described the karyotype of *A. orophilus* based on specimens from Huánuco (2n = 22). Later, Jiménez *et al.* (2013) assigned that karyomorph to a new entity, *A. josemariarguedasi*, assigning the diploid complement 2n = 26 to *A. orophilus s. s.* from Amazonas. As such, Jiménez *et al.* (2013) corroborated that *A. orophilus s. l.* is a species group. These authors restricted the distribution of *A. orophilus* to the eastern Andean slopes in Amazonas and northern San Martín departments, while *A. josemariarguedasi* was restricted to the south of the Río Huallaga in Huánuco and Junín departments. More recently, Coyner *et al.* (2013) proposed the recognition of *A. orientalis* as a distinct species from *A. orophilus* based on some morphological differences and molecular data; however, Pardiñas *et al.* (2015) retained it as subspecies following previous authors.

In 2001 and 2002, the junior author (VP) led two expeditions to the montane forests of Cordillera de Carpish (Huánuco), and collected *A. orophilus* among other species. We review these specimens and found them different from *A. orophilus s. s.,* and other species of *Akodon*. Herein, we describe these species as belonging to a new species of *Akodon* based on an assessment of craniodental and external morphological traits and analysis of morphometric data. We compare this new species with other members of the *A. aerosus* species group based on their close phylogenetic relationships established in previous molecular studies (Smith and Patton 2007; Jayat *et al.* 2010; Coyner *et al.* 2013) and summarized by Pardiñas *et al.* (2015). Finally, we also highlight the need to protect the Cordillera de Carpish given its high species diversity and endemism (Parker and O'Neil 1976; Young and Leon 1999; Beltrán and Salinas 2010).

Material and Methods

A total of 44 specimens allocated to *Akodon orophilus* and collected in Huánuco department were examined in this study (Appendix). These specimens are housed in the collection of the Departamento de Mastozoología del Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru (MUSM). Morphological descriptions and comparisons were based on qualitative external and cranial characters using the terminology of Voss (1988), Myers *et al.* (1990), Pacheco (2003), and Jiménez *et al.* (2013); molar cusps and enamel fold terminology follows Reig (1977); capitalized color nomenclature follows Smithe (1975). Age classes were estimated following the criteria of Myers (1989). Comparative measurements were taken from Jiménez *et al.* (2013) and Myers and Patton (1989).

In addition, we examined specimens of *A. aerosus*, *A. josemariarguedasi*, *A. orophilus s. l.*, *A. torques*, and *A. surdus* (Appendix) for morphological comparisons; these species were chosen for their geographic distribution in eastern montane cloud forest and close phylogenetic relationships (see Smith and Patton 2007; Jayat *et al.* 2010; Coyner *et al*. 2013, Pardiñas *et al*. 2015). Also included in the comparisons were other species that inhabit cloud forests, such as *A. kofordi, A. fumeus, A. budini*, and *A. siberiae*; comparisons with these species were based on the descriptions provided by Myers and Patton (1989) and Pardiñas *et al*. (2015).

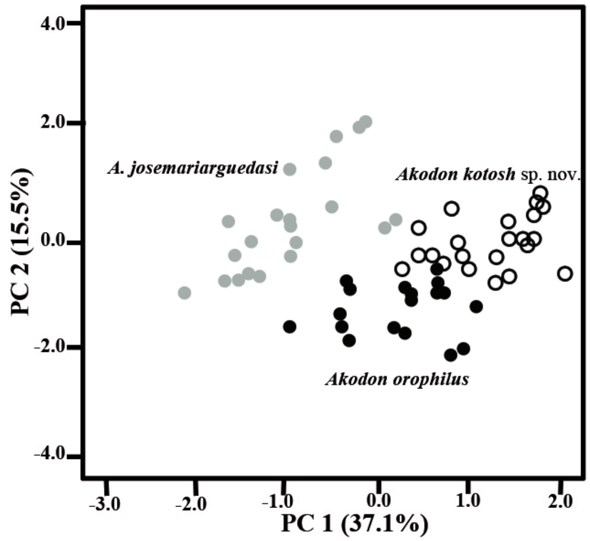
For the morphometric characterization, 19 cranial dimensions for 61 specimens of *Akodon* were recorded to the nearest millimeter using digital calipers, following Luna and Pacheco (2002) and Jiménez *et al.* (2013). These 19 measurements and their abbreviations include: greatest skull length (GSL), condyloincisive length (CIL), condylomolar length (CML), length of orbital fossa (LOF), length of nasals (LN), diastema length (DL), length of incisive foramina (LIF), length of maxillary toothrow (LM), breadth of incisive foramina (BIF), breadth of rostrum (BR), breadth of palatal bridge (BPB), breadth of first upper molar (BM1), breadth of nasals (BN), least interorbital breadth (LIB), zygomatic breadth (ZB), braincase breadth (BB), breadth of zygomatic plate (BZP), depth of incisor (DI), and height of braincase (HBC). For the multivariate analyses, we used only adult specimens of age classes 4 and 5 and after rejecting the hypothesis of sexual dimorphism by a *t*-test analysis, pooled specimens of both sexes. All 19 measurements were transformed to their natural logarithm to perform a Principal Component Analysis (PCA) on a correlation matrix, in order to assess morphometric variation. A discriminant function analysis (DA) was also carried out to examine the level of discrimination between samples. These analyses and the univariate descriptive analysis for all measurements were conducted with the program SPSS 13.0 for Windows.

Results

Morphometric analyses. The first three principal components of the PCA explained 60.85% of the total variation in the PCA. Loadings of the variables analyzed along components 1, 2, and 3 are shown in Table 1. All variables showed a positive loading on the first axis (except DI), thus indicating a general variation in size where CML, ZB, GSL, CIL, and BR had relatively large loadings. Meanwhile, LIF, DI, and DL (positives) on the second axis, and BZP (negative) on the third, had relatively large loadings. Individual scores for the components (PC1 and PC2) are plotted in Figure 1. Three main groups of specimens can be identified in the scatterplot of PC1 and PC2, one formed by *A. orophilus s. s.* from Amazonas and San Martín departments, *A. josemariarguedasi* and specimens collected in the Cordillera de Carpish (Huánuco department). Specimens of *A. orophilus s. s.* overlap marginally with specimens from the Cordillera de Carpish currently assigned to *A. orophilus*; meanwhile *A. josemariarguedasi* separates completely from *A. orophilus s. s.* and specimens collected at the Cordillera de Carpish currently assigned to *A. orophilus*, confirming the difference in size among these populations (Figure 1). A discriminant function analysis revealed a significant variation among these three groups (Wilk´s lambda = 0.027; p < 0.000) and showed a clear separation among them (Figure 1). The first discriminant function accounted for 68.4% of the variance. The most influential variables for the first and second function were BR and BN, respectively. Percentages of misidentifications were low, only one individual from the Cordillera de Carpish (Huánuco department) and *A. orophilus s. s.* were mistakenly identified, while 100% were correctly classified as *A. josemariarguedasi*. These results indicate that the specimens collected in the Cordillera de Carpish, currently assigned to *A. orophilus*, are morphometrically distinct from typical *A. orophilus* and *A. josemariarguedasi*. The mean standard deviation and range of external and cranial measurements of the specimens examined are shown in Table 2. In addition, specimens from Carpish have some morphological peculiarities, such as dark dorsal coloration, narrow parapterygoid fossa, with straight outward edges, long incisive foramina that nonetheless only reaches the protoflexus of M1, and smaller entoconid-hypoconid cusp pair of m1, which differentiates them from *A. orophilus s. s.* and *A. josemariarguedasi*.

Table 1. Loadings of the first three components of a Principal Component Analysis of 19 measurements of *Akodon orophilus s. s.* (*n* = 18), *Akodon josemariarguedasi* (*n* = 21), and *Akodon kotosh* sp. nov. (*n* = 22) of tooth-wear classes 4 and 5. Measurements are defined in Material and Methods.

Character	Principal Component		
	1	2	3
CML	0.87	0.08	-0.01
ZB	0.81	-0.08	-0.02
GSL	0.80	0.31	-0.19
CIL	0.76	0.48	-0.03
BR	0.73	-0.34	0.00
LIB	0.70	-0.18	0.34
LM	0.68	-0.23	0.23
BIF	0.66	-0.13	0.15
BN	0.65	0.17	0.30
BB	0.63	-0.45	-0.17
LOF	0.58	0.37	0.25
HBC	0.52	-0.52	-0.07
LN	0.52	0.39	0.09
BM1	0.44	-0.41	0.15
LIF	0.15	0.77	0.02
DI	-0.14	0.70	0.48
DL	0.40	0.57	-0.44
BZP	0.26	0.08	-0.73
BPB	0.60	-0.11	-0.12
Eigenvalues	7.05	2.93	1.43
% of Variance	37.11	15.45	7.51
Cumulative %	37.83	52.56	60.08



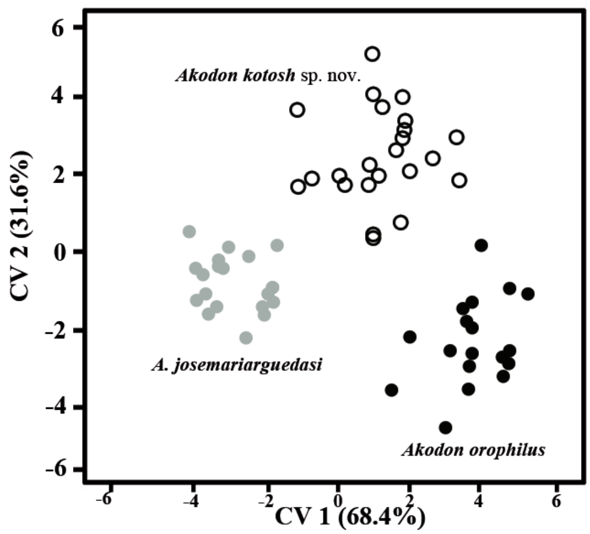


Figure 1. Specimen scores of adult individuals (age classes 4 and 5) of *Akodon kotosh* sp. nov. (white circle, *n* = 22), *Akodon josemariarguedasi* (gray circle, *n* = 21) and *Akodon orophilus s. s.* (black circle, *n* = 18) for principal components 1 and 2 generated from the correlation matrix (top) and for canonical variants extracted from a discriminant function analysis (bottom) of 19 craniodental measurements. The percent of the total variation explained by each axis is indicated.

Discussion

Based on the high level of sequence divergence for the cytochrome *b* gene, Patton and Smith (1992), suggested that *Akodon orophilus* is a complex of species. Subsequent studies (Smith and Patton 1993; 2007) that included a larger geographic range, analyzing samples from the Peruvian departments of Amazonas, San Martín, Huánuco, and Junín, supported their hypothesis. During our research we have examined specimens assigned to *A. orophilus* from Amazonas, Huánuco, and San Martín, and found morphological (see below) and morphometric differences among them that support the initial hypothesis of Patton and Smith (1992). Taking this information into consideration, and based on our combined analyses of morphology and morphometric data, we propose the recognition of populations from the Cordillera de Carpish (Huánuco department) as a new species, which is described as follows.

Akodon kotosh sp. nov.

Holotype. Adult female (age class 4) deposited at the Museo de Historia Natural of the Universidad Mayor de San Marcos (MUSM 18950), skull removed and cleaned, with tissue sample preserved in alcohol, collected on 15 August 2002 by Marina Villalobos, original field number MVC 115.

Type locality. Peru, Huánuco department, Huánuco province, Chinchao district, Caserío de San Pedro de Carpish, -9º 41.70' S, -76º 05.28''W, elevation 2,400 m.a.s.l. (Figure 2).

Paratypes. Four specimens, two males (MUSM 19006, 18998) and two females MUSM (19036, 19023), collected at the type locality in August 2002 and preserved as skulls and skins.

Nomenclature statement. A life science identifier (LSID) number was obtained for the new species *Akodon kotosh*: urn:lsid:zoobank.org:pub:DE7571D4-5F5A-4D4A-87DD-9E8CC2183FB5

Diagnosis. *Akodon kotosh* sp. nov. is distinguished from other species of the *Akodon aerosus* species group by the following combination of characters: large size (TL = 170 to 222 mm; LT = 71.5 to 100 mm), uniform dark olive brown coloration, with dorsal and ventral pelage not countershading, ventral hairs with dark bases; unicolored tail; large and broad skull (GSL= 26.06 to 28.95 mm, ZB = 12.65 to 14.40 mm); broad nasals (BD = 2.95 to 3.72 mm); large incisive foramen (LIF = 5.68 to 6.71 mm); large lacrimals; broad antorbital bridge; wide zygomatic notch being somewhat shallow in depth; conspicuous gnathic process; incisive foramen that extends backward to the protoflexus of the first upper molar M1; broad interorbital region (LIB = 5.13 to 5.68 mm); narrow parapterygoid fossa; small foramen ovale; robust jaw without a prominent capsular process; low-crowned molars; and anterior edge of the masseteric crest placed posterior to procingulum of m1; bilobed m3 with small entoconid/hypoconid cusp pair.

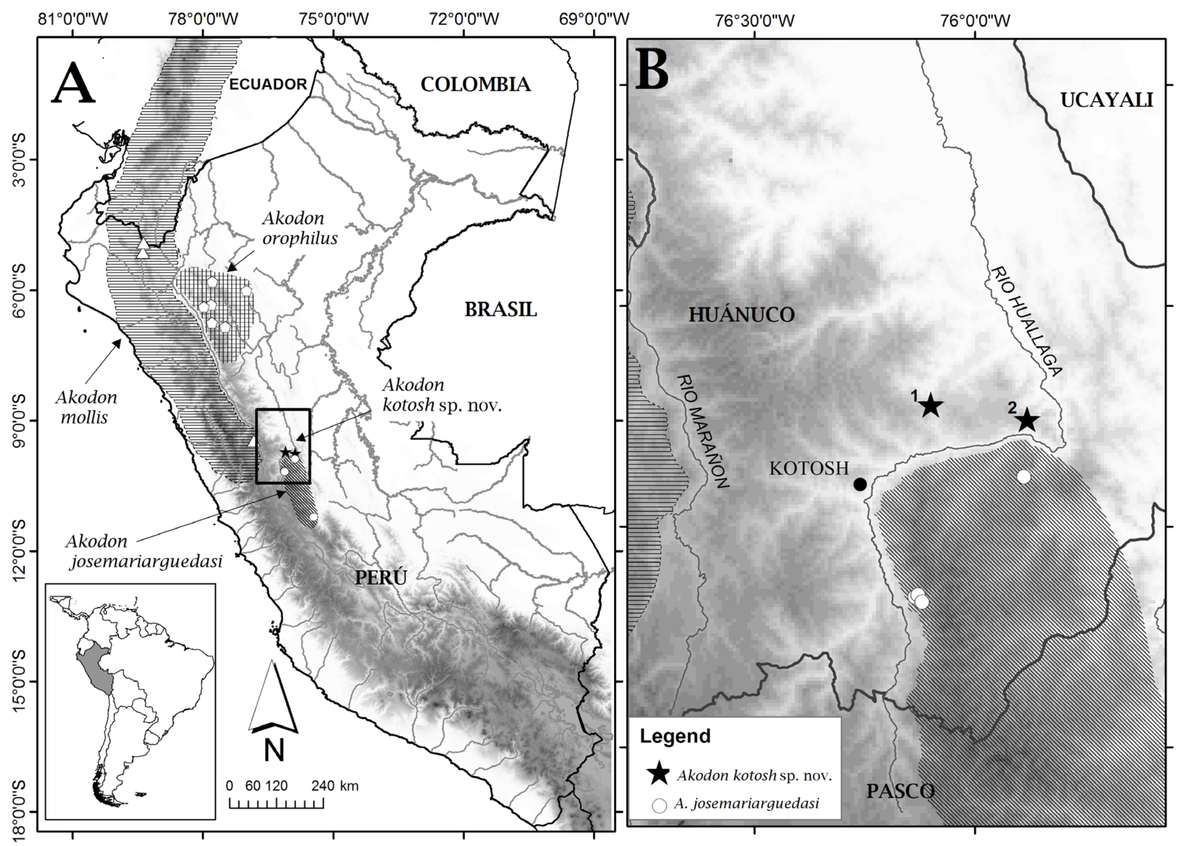


Figure 2. A: Map of Peru showing the distribution of *Akodon orophilus s. s.*, *A. josemariarguedasi*, *Akodon mollis,* and *A. kotosh* sp. nov. B: Map of central Peruvian Andes displaying a fraction of the distribution of *A. josemariarguedasi* and the collecting localities of *A. kotosh* sp. nov., 1) Carpish (Type locality), 2) Huanacaure (based on Jiménez *et al*. 2013 and Pardiñas *et al*. 2015).

Description. A large member of the genus *Akodon* (Table 2), the overall color of the dorsum is dark olive brown, fur hairs average about 10.0 mm in length, the base of which is dark gray, the subterminal band is pale brown, and the tip is dark brown. Guard hairs are gray at the base and black at the tip, extending up to 2 mm beyond fur hairs. The venter is olive gray and slightly paler than the dorsum. The chin has a small patch of white hairs (Figure 3). Eyerings are inconspicuous. Forefeet are slightly paler and covered with black or brown-based hairs. The ungual tufts on the manus are white. The hindfeet are covered by dark brown hairs. The ungual tufts of pes are brown or bicolored with white tips. Ears are covered by delicate, short hairs. Mystacial vibrissae are moderately long and reach the ears when bent, some are white and others are black; the submental and interramal vibrissae are white. One to three superciliary vibrissae are present, one of them more conspicuous, and genal-1 is present; both types of vibrissae are black. The tail is short, about 85% of the head-body length, and slightly contrasting in color; the hairs on the dorsal

Table 2. Summary statistics ($\overline{X}$, standard deviation, range) for 23 external and cranial measurements (in mm) of adult specimens (age classes 4 and 5) of *Akodon orophilus s. s.*, *Akodon kotosh* sp. nov., and *Akodon josemariarguedasi*. Variables are described in Material and Methods.

Character	*Akodon orophilus s.s.*			*Akodon kotosh sp. nov.*			*Akodon josemariarguedasi*		
	N	$\overline{X}$ ± SD	Range	N	$\overline{X}$ ± SD	Range	N	X ± SD	Range
TL	21	187.33 ± 8.88	171.00-201.00	25	198.08 ± 11.68	170.00-222.00	19	192.32 ± 11.91	176.00-221.00
LT	21	85.19 ± 7.14	74.00-100.00	25	91.10 ± 6.69	71.50-100.00	19	89.08 ± 7.94	75.00-106.00
EAR	21	16.55 ± 1.24	14.00-19.00	24	15.69 ± 1.34	14.00-19.00	19	15.61 ± 1.36	12.00-17.00
HF	21	22.76 ± 1.22	21.00-25.00	23	23.96 ± 1.30	20.00-25.50	19	22.84 ± 1.65	21.00-27.00
GSL	22	27.04 ± 0.30	26.23-27.45	33	27.48 ± 0.64	26.06-28.95	23	26.81 ± 0.38	26.06-27.49
CIL	22	24.55 ± 0.37	23.77-25.25	33	25.05 ± 0.61	23.63-26.39	23	24.47 ± 0.44	23.54-25.25
CML	22	16.59 ± 0.31	16.05-17.15	33	16.78 ± 0.38	15.95-17.46	23	16.23 ± 0.24	15.72-16.68
LOF	22	8.34 ± 0.18	8.06-8.67	33	8.61 ± 0.28	8.22-9.20	23	8.31 ± 0.17	7.97-8.67
LN	22	10.43 ± 0.36	9.79-11.22	33	10.87 ± 0.41	10.08-11.92	23	10.47 ± 0.27	9.90-10.85
DL	22	6.83 ± 0.21	6.50-7.27	32	6.98 ± 0.28	6.43-7.70	23	6.87 ± 0.22	6.51-7.16
LM	22	4.39 ± 0.17	3.97-4.82	33	4.47 ± 0.14	4.10-4.70	23	4.22 ± 0.11	3.93-4.43
LIF	22	5.82 ± 0.28	5.28-6.35	33	6.14 ± 0.25	5.68-6.71	23	6.09 ± 0.25	5.61-6.55
BIF	22	2.14 ± 0.12	1.98-2.40	33	2.21 ± 0.15	1.89-2.69	23	1.99 ± 0.11	1.72-2.25
BPB	22	2.98 ± 0.14	2.78-3.20	32	2.96 ± 0.19	2.65-3.51	23	2.71 ± 0.21	2.38-3.15
BM1	22	1.26 ± 0.06	1.17-1.40	32	1.29 ± 0.06	1.13-1.43	23	1.22 ± 0.06	1.12-1.34
BR	22	4.76 ± 0.21	4.25-5.09	33	4.70 ± 0.29	4.20-5.60	23	4.39 ± 0.16	4.07-4.67
BN	22	3.09 ± 0.14	2.89-3.32	33	3.31 ± 0.17	2.95-3.72	23	3.10 ± 0.11	2.82-3.30
LIB	22	5.27 ± 0.16	5.05-5.63	33	5.44 ± 0.15	5.13-5.68	23	5.15 ± 0.18	4.87-5.48
ZB	22	13.37 ± 0.34	12.78-14.07	33	13.51 ± 0.40	12.65-14.40	23	12.92 ± 0.31	12.24-13.40
BB	22	12.28 ± 0.31	11.95-13.02	33	12.23 ± 0.30	11.7-13.05	23	11.90 ± 0.29	11.28-12.51
BZP	22	2.08 ± 0.14	1.83-2.31	32	2.04 ± 0.19	1.56-2.60	23	2.03 ± 0.10	1.78-2.19
DI	22	1.25 ± 0.05	1.14-1.33	32	1.32 ± 0.04	1.23-1.41	23	1.33 ± 0.05	1.27-1.43
HBC	22	8.45 ± 0.27	7.80-8.85	33	8.46 ± 0.24	8.01-8.95	23	8.21 ± 0.12	8.04-8.54

Figure 3. Dorsal and ventral views of museum study-skin of *Akodon kotosh* sp. nov. (MUSM 18947; left), *A. orophilus s. s.* (MUSM 36984; center), and *A. josemariarguedasi* (MUSM 22759; right). Scale bar = 10 mm.

surface are black, while those on the ventral side are white; scales on both sides of the tail are small and black. Dorsal and ventral hairs are over 2 scales in length.

The skull is slightly elongated, with a rounded braincase (Figure 4). The profile of the skull is flat. The rostrum is arched, long, and somewhat broad. The gnathic process is conspicuous. The nasals are long and wide, extending anteriorly beyond the premaxillae, but not expanding beyond the lacrimals posteriorly. The anterior edges of nasals are pointed with posterior margins slightly blunt or somewhat pointed. The premaxilla extends posteriorly slightly behind the nasals. The fronto-parietal suture is somewhat rounded or little rounded in Huanacaure specimens.

Zygomatic notches are wide and moderately deep with rounded borders. Zygomatic arches are robust and anteriorly convergent, and the malar process is thick. Lacrimals are large. Lambdoid ridges are well developed, and the interparietal bone is reduced. The interorbital region is hourglass-shaped without ridges and broad. Incisive foramina extend only to the protoflexus of M1, not reaching the protocone and diverging on the posterior border. The maxillary septum occupies less than half of incisive foramina length. Anterior palatal pits are conspicuous and located at the level of the second upper molar (M2) hypoflexus. Posterior palatal pits are located slightly behind the anterior margin on both sides of the mesopterygoid fossa and are absent in some cases. The mesopterygoid fossa is broader than the parapterygoid fossa at midpoint and has parallel margins, extending anteriorly to the posterior border of the third upper molar (M3) or slightly anterior to it, producing a short palate; its anterior margin is slightly biconcave. The parapterygoid plate is narrow, fenestrated, and divergent with straight external margins. Sphenopalatine vacuities are usually present and slightly developed. Auditory bullae are flask-shaped and intermediate in size, with short and broad Eustachian tubes.

Laterally, the zygomatic plate is moderately broad. The anterior border is generally convex. A distinct masseteric tubercle is present in front of the root of the zygomatic plate. The posterior ascending process of the alisphenoid is always ventral to the squamoso-alisphenoid groove. The tegmen tympani slightly overlaps the posterior process of the squamosal. The dorsal aperture of the ectotympanic ring is either opened or closed. The nasolacrimal foramen is present, its diameter being smaller than or equal in size to M2. The oval foramen and foramen ovale accessorius are usually smaller than M3. The optic foramen is larger than M3. The ethmoid foramen is dorsal to M3. The carotid circulation corresponds to pattern 1 with the sphenofrontal foramen, stapedial foramen, and squamoso-alisphenoid groove present. The postglenoid foramen is large, almost twice the size of the subsquamosal fenestra, and both are rounded. The hamular process is usually thick and curved but thicker and shorter in specimens from Huanacaure. The sphenopalatine foramen is shorter than M2 and mostly closed.

The upper molars are crested, and the main cusps show an alternate arrangement. The anterolabial and anterolingual conules of M1 are approximately equal in size and are divided by a somewhat developed anteromedian flexus. The paraflexus and metaflexus are conspicuous but the anteroflexus and posteroflexus are shallow. The anteroloph, mesoloph, posteroloph, paralophule, parastyle, and mesostyle are present, while the metalophule and mesoflexus are absent. On the lingual side, the protoflexus and hypoflexus are present while the enterostyle is absent. In M2, the protocone, paracone, hypocone, and metacone show a diagonal arrangement; the paraflexus, metaflexus, protoflexus, and hypoflexus are present but the anteroloph, mesoloph, and metalophule are absent; the mesostyle, paralophule, and posteroflexus are present. The posteroloph is poorly defined. M3 has a deep metaflexus, posteroflexus, posteroloph, and hypoflexus. The paracone and protocone are larger than the metacone and hypocone. In some individuals, molars show fossettes that could represent vestigial mesoflexi. In the lower toothrow, the conids of the first lower molar (m1) and second lower molar (m2) are arranged diagonally with the metaconid and entoconid anterior to the protoconid and hypoconid, respectively. In m1, the anteromedian flexid is inconspicuous; the anterolingual conulid is smaller than the anterolabial conulid; the protostylid is well developed and the ectostylid is minute; the posterolophid and posteroflexid are well defined. The second lower molar presents a tiny mesostylid. The third lower molar is eight-shaped and small, with a small posterior lobe corresponding to the entoconid-hypoconid cusp pair (Fig. 5).

The lower jaw is similar to the one observed in other species of *Akodon,* with the mandibular rami somewhat robust. The coronoid process is delicate and falciform, and its dorsal margin lies above the condylar process. The lunar notch is deep and wide and the angular process is robust. The condylar process is moderately long, usually placed at the same level as the angular process.

Figure 4. Holotype (MUSM 18950) of *Akodon kotosh* sp. nov. Scale bar = 10 mm.

The lower incisor alveolus lacks a distinct capsular process; mandibular and mental foramina are present, although reduced. The masseteric tubercle and the lower masseteric crest are highly noticeable. The anterior edge of the masseteric crest is posterior to the procingulum of m1.

Akodon kotosh sp. nov. has 12 thoracic ribs; the vertebral column includes 7 cervical, 12 thoracic, 6 lumbar, 4 sacral, and 28 caudal vertebrae.

Etymology. The term *kotosh* derives from a noun in apposition referring to an archaeological site where a pre-Columbian temple called "*manos cruzadas*" is located. This site is about 5 km from the town of Huánuco. This pre-Columbian culture emerged about 1,800 BC. Kotosh is one of the most important archaeological sites in Huánuco department and is located 30 km southwest of the type locality.

Distribution. *Akodon kotosh* sp. nov. is currently known from two localities only: Caserío San Pedro de Carpish and Huanacaure forest, Cordillera de Carpish, Huánuco department (Figure 2).

Comparisons. *Akodon kotosh* sp. nov. can be differentiated from *A. orophilus* by its darker coloration; longer tail (91.10 mm versus 85.19 mm on average); shorter ears (15.69 mm versus 16.55 mm on

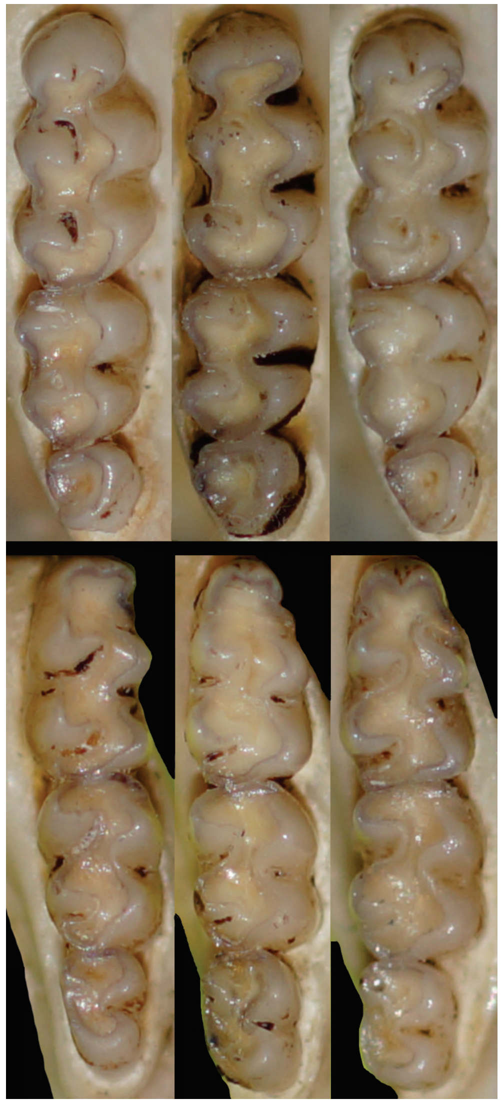


Figure 5. Detailed occlusal views of upper (top) and lower (bottom) right molar series of *Akodon kotosh* sp. nov. (MUSM 18598; left), *A. orophilus s. s.* (MUSM 36583; center), and *A. josemariarguedasi* (MUSM 22750; right).

average); longer (27.48 mm versus 27.04 mm on average) and broader skull (13.51 mm versus 13.37 mm on average); broader nasals (3.31 mm versus 3.09 mm on average) that are more projected anteriorly; longer incisive foramina (6.14 mm versus 5.82 mm on average) reaching the protoflexus of M1; smaller entoconid-hypoconid cusp pair; a conspicuous masseteric tubercle; and a narrower parapterygoid fossa with parallel sides (Figures 5, 6).

Akodon kotosh sp. nov. is distinguishable from *A. josemariarguedasi* by its darker and uniform body pelage; larger hindfoot (23.96 mm versus 22.84 mm on average); longer (27.48 mm versus 26.81 mm on average) and broader skull (13.51 mm versus 12.92 mm on average); nasal projecting little beyond the premaxilla; incisive foramina reaching only to the protoflexus of M1; broader palate (2.96 mm versus 2.71 mm on average); larger molars (4.47 mm versus 4.22 mm on average); broader mesopterygoid fossa with parallel margins; narrower parapterygoid fossa with straight outward edges; and smaller entoconid-hypoconid cusp pair; inconspicuous anteromedian flexus and flexid (Figure 5).

Akodon kotosh sp. nov. differs from *A. torques* by its slightly darker coloration. Nasals are longer (10.87 mm versus 10.65 mm on average) and broader than in *A. torques* (3.31 mm versus 3.07 mm on average); the posterior margin of nasals is less tapered and it does not extend beyond the lacrimals; the incisive foramen extends backward to the protoflexus of M1. *Akodon kotosh* sp. nov. exhibits a rounded fronto-parietal suture; narrower and longer parapterygoid fossa with straight external borders; and a larger oval foramen and broader zygomatic plate (2.04 mm versus 1.85 mm on average).

Akodon kotosh sp. nov. is distinguishable from *A. aerosus* by its darker coloration; longer tail (91.10 mm versus 87.37 mm on average); deeper zygomatic notch and narrower antorbital bridge; narrower and rectangular zygomatic plate with a convex anterior border (2.04 mm versus 2.22 mm on average); the incisive foramen extends backward only to the protoflexus of M1; smaller oval foramen and indistinct capsular process.

Akodon kotosh sp. nov. is distinguished from *A. surdus* by its more olivaceous tinge, paler toe and longer tail (91.10 mm versus 70.00 mm on average); smaller skull (27.48 mm versus 28.93 mm on average) with shorter (10.87 mm versus 11.43 mm on average) and narrower nasals (3.31 mm versus 3.60 mm on average). It has a more pointed anterior border and a less tapered posterior border; incisive foramina extend backward to the protoflexus of M1; narrower interorbital region (5.44 mm versus 5.52 mm on average); narrower antorbital bridge; narrower and slating zygomatic plate (2.04 mm versus 2.31 mm on average); narrower mesopterygoid; and parapterygoid fossa with straight external borders.

Akodon kotosh sp. nov. markedly differs from *A. budini* by its shorter ears (15.69 mm versus 20.2 mm on average); unicolored tail; less hypsodont molars; shallower zygomatic notch; incisive

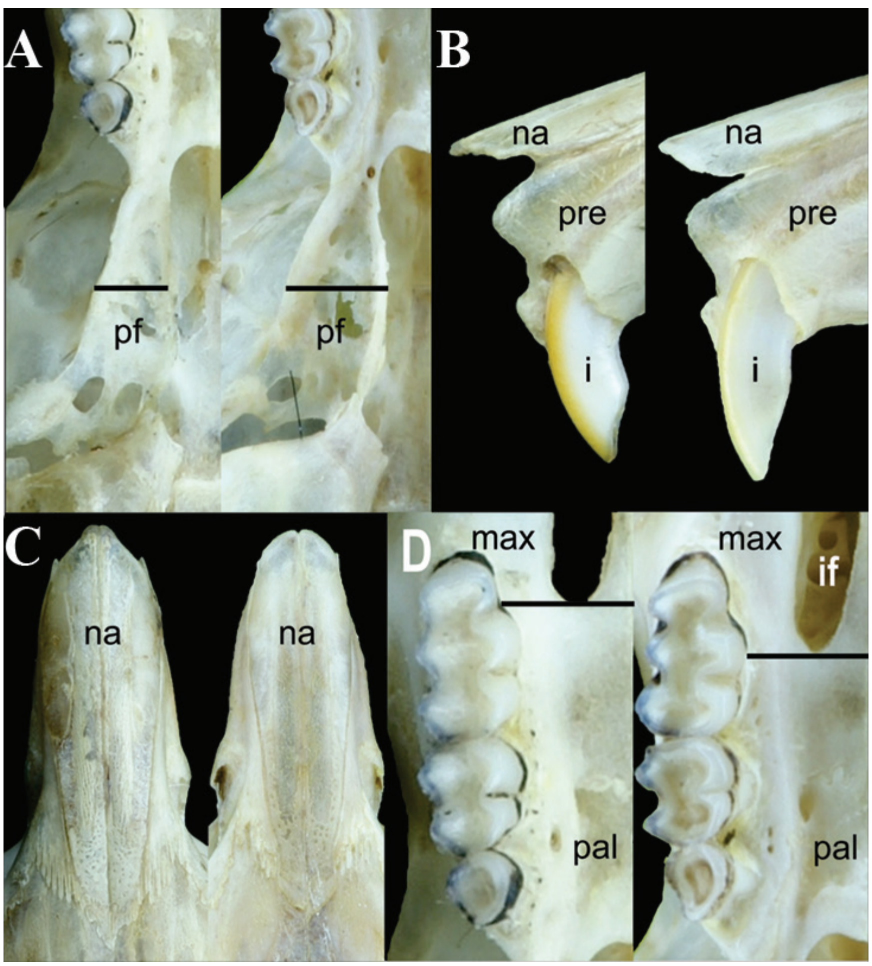


Figure 6. Cranial differences between *Akodon kotosh* sp. nov. (left) and *A. orophilus s. s.* (right). A) Narrower parapterygoid fossa in *Akodon kotosh* sp. nov. B) The nasal bone is projected more anteriorly in *Akodon kotosh* sp. nov. C) Broader nasal bone in *Akodon kotosh* sp. nov. D) Shorter incisive foramen in *Akodon kotosh* sp. nov. if = incisive foramen; max = maxillary; na = nasal; pal = palatine; pf = parapterygoid fossa; pre = premaxillary.

foramen extending backward to the protoflexus of M1; narrower mesopterygoid fossa; broader interorbital region (5.44 mm versus 4.96 mm on average); longer nasal (10.87 mm versus 10.09 mm on average); shorter molars (4.47 mm versus 4.98 mm on average); narrower zygomatic plate (2.04 mm versus 2.36 mm on average); and inconspicuous anteromedian flexid.

Akodon kotosh sp. nov. can be easily distinguished from *A. siberiae* by its shorter ears (15.69 mm versus 18.5 mm on average); shorter dorsal hairs (10 mm versus 12 mm on average); broader interorbital region (5.44 mm versus 5.15 mm on average); shorter molars (4.47 mm versus 4.81 mm on average); shorter incisive foramen (6.14 mm versus 6.37 mm on average) that extends backward to the protoflexus of M1; and narrower mesopterygoid fossa with straight lateral margins.

Two other species occur in montane forests: *Akodon fumeus* and *A. kofordi*. Both belong to the *Akodon boliviensis* species group (*sensu* Pardiñas *et al.* 2015). In general, they have a different color pattern with a dark brown dorsum with an olivaceous tone and a buff ventral side; they are smaller in most external and cranial dimensions. Both have a narrower mesopterygoid fossa and interorbital region than *Akodon kotosh* sp. nov.

Natural History. *Akodon kotosh* sp. nov. is sympatric with *Microryzomys minutus*, *Thomasomys notatus*, *T. ischyrus,* and *T. kalinowskii*. No pregnant individuals were found during fieldwork in February, May, or November.

Akodon kotosh sp. nov. inhabits mountain forests above 2,400 m.a.s.l. Carpish is a dense montane forest with trees not exceeding 20 m. Trees are conspicuously covered by epiphytes, mosses, lichens, and bromeliads. The most abundant plant families at Carpish are Orchidaceae, Asteraceae, Melastomataceae, and Rubiaceae (Beltrán and Salinas 2010).

Remarks. Molecular data for the new species is not available, although sequences are available for specimens previously assigned to *A. orophilus* by Smith and Patton (1993; 2007) that were collected in the nearby areas of Palca (Junín) and Unchog (Huánuco). The first one corresponds to *Akodon josemariarguedasi* and the second could belong to an undescribed species. Based on molecular data and some morphological features, Coyner *et al.* (2013) indicated that the specimen from Unchog (Huánuco department) belongs to *Akodon orientalis*, a form previously considered a synonym of *A. orophilus*. However, Jiménez *et al.* (2013) pointed out that there is no morphological difference between *A. orophilus orientalis* and *A. o. orophilus* except that specimens of *orientalis* from Amazonas and northeastern San Martín department are darker; meanwhile, Pardiñas *et al.* (2015) considered *orientalis* as a subspecies of *orophilus*. For us, this specimen may represent an unnamed species. This specimen exhibits some differences with *A. orophilus*, including a ventral side with whitish hair tips, larger lacrimals, serrated contour of the posterior end of nasal, and a more delicate mandible. Compared to *A. kotosh* sp. nov., the specimen from Unchog has a longer incisive foramen that extends to the protocone of M1, rounded anterior border of the nasal, and a more delicate mandible. In addition, this specimen has a more conspicuous gnathic process, a pointed posterior margin of nasal, shallow zygomatic notches, a long incisive foramen, and inconspicuous antero-palate pits, relative to *A. josemariarguedasi*.

Similarly, populations from five localities in northern Huánuco department (Kenwarajra, Pampa Hermosa, Iscarag, Campamento Provias, and Campamento regional) and two localities in central San Martín (La playa and Los Chochos) were originally allocated to *Akodon orophilus*; however, our more detailed analysis points to an inconclusive status for them due to their high morphological variability. These specimens do not fully agree with the descriptions of *A. josemariarguedasi*, *A. orophilus s. s.*, nor *A. kotosh* sp. nov. For instance, populations from northern Huánuco department have a more yellowish body coloration, square posterior border of the nasal, conspicuous posterior palatal pits, and a larger lacrimal; individuals from San Martín are slightly smaller, with larger lacrimals, a more yellowish rostrum, more conspicuous eyerings, and bicolored hairs on the ventral side of the tail, compared to *A. kotosh* sp. nov., *A. orophilus s. s.*, and *A. josemariarguedasi*. We suggest that molecular analyses could contribute to clarify this complex taxonomic scenario.

After the description of *Akodon kotosh* sp. nov., nine species of *Akodon* are known from the Peruvian montane cloud forests. In addition, our results show that further studies are still needed to clarify the true diversity of *Akodon* inhabiting the Peruvian cloud forest, particularly when other member of the *aerosus* group such as *A. mollis* and *A. aerosus* could encompass more than one species. This is also true for other rodent species that inhabit this kind of forest, which is home to a number of endemic mammal species. For that reason, the establishment of more protected areas is necessary because the montane cloud forests suffer one of the highest rates of species loss (Gentry 1992) owing to the conversion of forested land and logging.

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Appendix

Vouchers of the specimens examined are deposited in Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima (MUSM) and The Field Museum, Chicago (FMNH).

Akodon aerosus (*n* = 38) CUSCO; Carretera Paucartambo-Pillcopata, km 150 -13° 13' 38.3'' S, -71° 37' 10.6'' W (MUSM 8960-997).

Akodon kotosh sp. nov. (*n* = 44) HUÁNUCO; Chinchao, Carpish -9° 43' 27" S, -76° 6' 02" W (MUSM 18438-439, 18449, 18588, 18598-599, 18604, 18620, 18622, 18625, 18648-650, 18656, 18663, 18665, 18667-678, 18680, 18726, 18945, 18950, 18953, 18986, 18998, 19023, 19044, 19053). Huanacaure -9° 45' 26" S, -75° 52' 53" W (MUSM 36817-832).

Akodon josemariarguedasi (*n* = 70) HUÁNUCO; Ambo, Chaglla -9° 53' 12" S, -75° 53' 22" W (MUSM 17763, 17764, 17769, 17773, 17774, 17776-782, 17784-785, 17787, 17792-793, 17798). Galloganan -10º 09' 32" S, -76º 08' 10" W (MUSM 22747-763). Hatuncucho -10º 9' 16" S, -76º 7' 45" W (MUSM 22764-779). Ichocán -10° 10' 15" S, -76° 07' 12''W (MUSM 36747-765).

Akodon orophilus s. s. (*n* = 83). AMAZONAS: Bongará: Hierba Buena -5° 47' 45" S, -77° 47' 17" W (MUSM 36901-36909, 36965-36969). Chachapoyas: Leymebamba -6° 44' 37" S, -77° 47' 51" W (FMNH 19725, 19727, 19729, MUSM 36983, 36984). San Antonio -6° 19' 48" S, -77° 48' 36" W (MUSM 37005-37034). Luya: Huiquilla -6° 22' 43" S, -77° 58' 45" W (MUSM 25732-25744, 36970-36982). SAN MARTÍN: Mariscal Cáceres: Añazco Pueblo -6º 50' 24" S, -77º 29' 24" W (MUSM 24387-24389). Estación biológica Laurel -6º 41' 24" S, -77º 42' 0" W (MUSM 24390-24392). Moyobamba: Puca Tambo -6º 0' 0" S, -77º 0' 0" W (FMNH 19856).

Akodon surdus (*n* = 5) CUSCO: La Convención: Paltaybamba -13º 1' 9" S, -72º 43' 29" W (USNM 194642) + Idma -12º 52' 60" S, -72º 49 '0" W (USNM 194657). Huadquina -13º 8' 3" S, -72º 36' 25" W (USNM 194663, 194694). Monte Carmelo-Koshipiari -12º 25' 41" S, -72º 2' 36" W (MUSM 36600).

Akodon torques (*n* = 22) CUSCO: Paucartambo: P. V. Acjanaco -13° 11' 47" S, -71° 37' 11" W (MUSM 9042-9048, 9080, 9099, 9112-9114, 9167-9176).

Akodon sp. (*n* = 80) HUÁNUCO: Huacaybamba: Kenwarajra -9° 5' 19" S, -76° 47' 41" W (MUSM 22978-22983). Pampa Hermosa -8° 53' 35" S, -76° 58' 20" W (MUSM 22984-22998). Huamalies. Iscarag -9º 18' 17" S, -76º 35' 35" W (MUSM 22832, 22871). Marañón: Campamento Provias -8º 40' 5.8" S, -76º 58' 9.2" W (MUSM 22920-921). Campamento Regional; -8º 39' 54.7" S, -77º 0' 8.3" W (MUSM 22922-934). SAN MARTÍN; Mariscal Cáceres, La Playa; -7° 38' 41" S, -77° 28' 53" W (MUSM 7541-561). Los Chochos; -7° 33' 50" S, -77° 25' 30" W (MUSM 7622-642).